Forecasting the Expansion of Zebra Mussels in the United States

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Abstract: *Because zebra mussels spread rapidly throughout the eastern United States in the late 1980s and early 1990s, their spread to the western United States has been expected. Overland dispersal into inland lakes and reservoirs, however, has occurred at a much slower rate than earlier spread via connected, navigable waterways. We forecasted the potential western spread of zebra mussels by predicting the overland movement of recreational boaters with a production-constrained gravity model. We also predicted the potential abundance of zebra mussels in two western reservoirs by comparing their water chemistry characteristics with those of water bodies with known abundances of zebra mussels. Most boats coming from waters infested with zebra mussels were taken to areas that already had zebra mussels, but a small proportion of such boats did travel west of the 100th meridian. If zebra mussels do establish in western U.S. water bodies, we predict that population densities could achieve similar levels to those in the Midwestern United States, where zebra mussels have caused considerable economic and ecological impacts. Our analyses suggest that the dispersal of zebra mussels to the western United States is an event of low probability but potentially high impact on native biodiversity and human infrastructure. Combining these results with economic analyses could help determine appropriate investment levels in prevention and control strategies.*

Pronóstico de la Expansión de Mejillones Cebra en los Estados Unidos

Resumen: *Debido a que los mejillones cebra se expandieron rápidamente en el este de Estados Unidos a fines de la década de 1980 y comienzos de la de 1990, se ha esperado su expansión hacia el oeste de Estados Unidos. Sin embargo, la dispersión por tierra hacia lagos y represas interiores ha ocurrido a una tasa mucho más lenta que la dispersión anterior mediante vías fluviales navegables y conectadas. Pronosticamos la potencial expansión hacia el oeste de los mejillones cebra mediante el pronóstico del desplazamiento terrestre de lancheros recreativos con la producción de un modelo de gravedad limitado por la producción. También pronosticamos la abundancia potencial de mejillones cebra en dos represas occidentales mediante la comparación de las características químicas del agua con las de cuerpos de agua con abundancias de mejillones cebra conocidas. La mayoría de las lanchas provenientes de aguas infestadas con mejillones cebra fueron llevadas a zonas que ya tenían mejillones cebra, pero una pequeña proporción de esas lanchas fueron llevadas al oeste del meridiano 100°. Si los mejillones llegan a establecerse en cuerpos de agua del oeste de* E.U.A.*, pronosticamos que las densidades de población podrían llegar a niveles similares a los del medio oeste de* E.U.A.*, donde los mejillones cebra han producido impactos económicos y ecológicos considerables. Nuestros análisis sugieren que la dispersión de mejillones cebra hacia el oeste de* E.U.A. *es un evento de baja probabilidad pero de potencialmente alto impacto sobre la biodiversidad y la infraestructura humana. La combinación de estos resultados con análisis económicos podría ayudar a determinar niveles adecuados de inversión en estrategias de prevención y control.*

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Introduction

After their establishment in North America in the late 1980s, zebra mussels (*Dreissena polymorpha*) spread rapidly across the eastern half of North America and have been collected or observed in 23 U.S. states and 2 Canadian provinces (http://nas.er.usgs.gov) (O'Neill & Dextrase 1994). The rapidity of its initial expansion, mostly via connected, navigable waterways (Allen & Ramcharan 2001), slowed dramatically in less than a decade. Since 1993 the range expansion of zebra mussels has been primarily mediated by rare overland dispersal events into inland lakes and reservoirs (Johnson et al. 2006). For example, out of several thousand lakes in the upper Great Lakes region, only about 420 have been invaded by zebra mussels, mostly in Michigan and Indiana (Kraft & Johnson 2000; Johnson et al. 2006). Of these, approximately 30% were invaded via downstream dispersal from initial invasions of upstream lakes (Bobeldyk et al. 2005; Johnson et al. 2006), with overland transport accounting for the balance. The overland transport of zebra mussels has primarily been the result of recreational boating (Johnson & Carlton 1996; Johnson et al. 2001), although other mechanisms such as aquarium releases or bait buckets exist (Carlton 1993).

The decline in the rate of range expansion of zebra mussels is apparently the result of constraints on overland dispersal. Large regions of suitable habitat still have yet to be invaded in North America, including those in the southeastern and western United States (Strayer 1991; Neary & Leach 1992; Drake & Bossenbroek 2004). Given the rapid rate of the early spread of zebra mussels and the economic and ecological impacts where it has established (Nalepa & Schloesser 1993; Pimentel et al. 2000), substantial concern exists about the possibility of spread to the western waterways of the United States and Canada. The goal of the 100th Meridian Initiative (100thmeridian.org), a cooperative effort of state, federal, and provincial agencies, is to prevent the spread of zebra mussels and other aquatic nuisance species into western North America.

The range expansion of zebra mussels in North America has been the result of a combination of processes involving the dispersal of propagules within and between water bodies, the demographic conditions necessary for the establishment of new populations, and the interaction of these factors with the suitability of water bodies for zebra mussel survival, growth, and reproduction (Carlton 1993; Johnson & Carlton 1996; Johnson & Padilla 1996; Bobeldyk et al. 2005). Shipping routes in the United States enabled rapid human-mediated transport of water containing larvae (e.g., ballast water) and submerged objects fouled by adult zebra mussels (e.g., barge and ship hulls) that accelerated the downstream spread and carried zebra mussels upstream (Keevin et al. 1992). Once established in an aquatic system, natural downstream dispersal of the planktotrophic larval stage or of rafting adults on moveable substrata (e.g., aquatic vegetation; Horvath & Lamberti 1997) produces downstream spread (Horvath et al. 1996; Bobeldyk et al. 2005). All these mechanisms probably contributed to the early, rapid range expansion of the zebra mussels in the Great Lakes region and eastern United States.

Longer-distance overland dispersal will be required for additional westward expansion because no commercially navigable waterways connect the eastern and western (i.e., west of the 100th Meridian) parts of the continent. Thus, the invasion of the western United States is likely to occur in overland "jumps" by human-mediated mechanisms, especially recreational boating (Buchan & Padilla 1999; Johnson et al. 2001). Since the mid-1990s several boats carrying zebra mussels have been intercepted in California, Washington, Colorado, and elsewhere (http://cars.er.usgs.gov/Nonindigenous_Species/ZM_Progression/zm_progression.html), although it remains unknown whether the zebra mussels found on boats in the West survived the trip. Currently, no zebra mussel populations are known to exist west of the 100th Meridian in North America.

We used a gravity model of boater movements to forecast the westward spread of zebra mussels. Gravity models are used to describe how the influences of distances and the attraction of origins and/or destinations affect the flow of people (Thomas & Hugget 1980). The attractiveness of a location can also be thought of as the property that creates an incentive for trips to be made to that location. Both distance and lake size are important factors in determining the destination of recreational boaters (Buchan & Padilla 1999; Reed-Andersen et al. 2000). In Michigan and Indiana lake size is positively related to the probability of invasion (Kraft & Johnson 2000). Models of recreational boater movement patterns have thus been used to forecast the distribution of zebra mussels (Schneider et al. 1998; Bossenbroek et al. 2001; Leung et al. 2006) and other aquatic invasive species (MacIsaac et al. 2004; Muirhead & MacIsaac 2005) in the Great Lakes region. We extended these earlier forecasting efforts to a national scale and have represented the dispersal of zebra mussels as a function of boater movement. We relied on the previously demonstrated positive relationship between the number of boat trips to a waterway and the probability that zebra mussels will become established for our predictions (Bossenbroek et al. 2001; Leung et al. 2004; Leung et al. 2006).

Ours is the first quantitative estimate of the probability of range expansion by zebra mussels to western North America. To assess the potential damage of such an expansion, we used a previously published model (Ramcharan et al. 1992) to predict the potential densities of zebra mussels in two large western waterways. We focused on Lake Mead and Roosevelt Lake because they are of specific management concern and are popular destinations for boaters from across the country (Caswell 2000). The impacts of zebra mussels in the eastern United States have varied depending on location. At one extreme, zebra mussel populations in Lake Erie, which have attained population densities as high as 300,000 mussels/m^2 (Leach 1993), have caused substantial economic and environmental impacts. At the other extreme, zebra mussels in the Tennessee River exist at considerably lower densities and have caused no substantial economic impacts (Phillips et al. 2005). Thus, to assess the potential impacts of zebra mussels in new regions it is important to predict both the probability of range expansion and potential population densities.

Methods

National Gravity Model

To quantify the potential spread of zebra mussels to the western United States, we developed a production-constrained gravity model (Bossenbroek et al. 2001) to predict the movement of recreational boaters across the country. Using a gravity model, we represented the number of boaters that travel from location i to destination j with

$$T_{ij} = A_i O_i W_j c_{ij}^{-\alpha}, \tag{1}$$

where A_i is a balancing factor (see below), O_i is the number of boats at location i, W_j is the attractiveness of location j, c_{ij} is the distance from location i to location j, and α is a distance-decay coefficient defining the deterrent effect of distance (Fotheringham 1981). The A_i is defined implicitly through the relationship

$$A_i = 1 \Big/ \sum_{j=1}^{N} W_j c_{ij}^{-\alpha}, \tag{2}$$

where N is the total number of destinations and j is each destination in the study region (see Table 1 for a list of parameters). This ensures that the number of boaters leaving a location arrive somewhere else. Whereas in previous gravity models (Bossenbroek et al. 2001; Leung et al. 2004), spatial resolution was at the county level (i.e., counties were considered "locations"), our spatial resolution was at the watershed level, based on U.S. Geological Survey Hydrologic Unit Maps (adapted from Seaber et al. 1987), which are designated by an eight-digit unit code (i.e., HUC code). For this project we used the 210 watersheds in the continental United States defined by the first four digits of the HUC codes, which have an average area of 37,460 km^2.

To fit a gravity model, we required information on the location and number of recreational boaters, the location and attractiveness of potential destinations, the distribution of zebra mussels (i.e., source locations), and the distance between watersheds. To estimate the number of boaters (O_i) in each watershed, we determined the number of registered boats in each state (National Marine Manufacturers Association 2003). We then assumed that boaters in each state are allocated proportionally to each county based on the population of each county. Finally, using a geographic information system (Environmental Systems Research Institute 2002), we assigned the number of boaters in each county to each watershed based on the proportion of county area that was in the watershed.

The attractiveness (W_j) of each watershed was based on the surface area of lakes, reservoirs, and rivers (I_j) and the length of oceanic or Great Lakes coastline (S_j), such that

$$W_j = I_j + xS_j, \tag{3}$$

where x is a scalar that converts a length of shoreline to an equivalent amount of surface area in terms of attraction. For lakes, reservoirs, and rivers, the total surface area of all lakes and reservoirs >25 ha and all rivers large enough to

Table 1. Parameters of the model of movement of recreational boaters including a description and how the parameter value was determined.

Parameter	*Description*	*How value was determined*
T_{ij}	number of boaters that travel from watershed i to watershed j	Equation 5
A_i	balancing factor that ensures all boaters leaving i reach a destination j	Equation 2
O_i	number of boats traveling from watershed i	estimated from empirical data
W_j	attractiveness of watershed j	estimated from empirical data
c_{ij}	distance from watershed i to watershed j	estimated from empirical data
α	distance coefficient	fit parameter
I	area of surface water of inland lakes, reservoirs, and rivers	estimated from empirical data
S	length of oceanic or Great Lakes shoreline	estimated from empirical data
x	scalar to estimate the "attractiveness" of shorelines in terms of the "attractiveness" of inland lakes	Equation 4
Bs	number of boats traveling to a shoreline	data from surveys
Bi	number of boats traveling to an inland lake	data from surveys
δ	parameter to estimate the distance traveled within a watershed	tit parameter
T_{kj}	number of boaters that travel from state k to watershed j	Equation 6
Z_i	number of boats carrying zebra mussels traveling from watershed i	estimated from empirical data
R_{ij}	number of boats carrying zebra mussels that travel from watershed i to watershed j	Equation 8
P_j	percentage of R_{ij} that travel to each watershed j	Equation 9
Q	proportion of R_{ij} that travel to watersheds that already contain zebra mussels	Equation 10

be polygons in the National Hydrography Dataset (USGS 2000) were totaled within each watershed. We recognize that factors other than surface area of water within a watershed, such as quality of fishing, proximity to state or national parks, and water quality may also influence attractiveness, but data are not readily available to include these factors on a national scale.

The attractiveness of oceanic shorelines (including Great Lakes) was based on two surveys of recreational boaters in Wisconsin (Penaloza 1991) and Oregon (Oregon State Marine Board 2002). These two surveys were the only ones we found that contained information appropriate for comparing the attractiveness of inland waters versus shoreline by recreational boaters. For each county in these states that bordered a Great Lake or ocean, we tabulated the number of boats traveling to inland waters and oceanic shoreline and calculated length of shoreline (S) and surface area of water of inland lakes (I). By comparing the ratio of boaters going to shoreline (Bs) versus inland waters (Bi) to the ratio of S to I, we were able to estimate the relative attraction of a length of shoreline compared with an area of inland waters, such that

$$\frac{\mathrm{Bs}}{\mathrm{Bi}} = x\frac{S}{I}. \tag{4}$$

A value for the scalar x was calculated for each county in Oregon and Wisconsin that bordered an ocean or Great Lake. These values were averaged to generate an average scalar, $\bar{x}$, which was used in Eq. 3 to calculate parameter W_j.

The distance between watersheds (c_{ij}) was calculated as the Euclidean distances between watershed centroids. For the major "peninsulas" of the United States, including the lower and upper peninsulas of Michigan, Florida, and the northeast, that prevent straight-line ground travel between watersheds, distances measured included an obligatory midpoint, located at the base of each peninsula. For example, the distance from a watershed in the lower peninsula of Michigan to a Wisconsin watershed was calculated via a midpoint in southern Michigan equidistant from Lake Michigan and Lake Erie.

An estimation of the distances recreational boaters travel within a watershed (i.e., c_{ij}, where $i = j$) was also needed for those boaters that remained within a watershed. If a boater that stayed within a watershed traveled a distance of 0, the gravity model would calculate that all boaters would remain within their watershed of origin. So, we adopted the geographers' convention to estimate the distance traveled within a watershed as a proportion, δ, of the distance to the next nearest possible destination (Thomas & Hugget 1980). Thus,

$$T_{ij} = \begin{pmatrix} A_i O_i W_j c_{ij}^{-\alpha}, & i \neq j \\ A_i O_i W_j (\delta \min(c_{ij}))^{-\alpha}, & i = j \end{pmatrix}, \tag{5}$$

which results in additional parameter (δ) to be estimated.

Beyond the empirical inputs described above, two parameters were estimated by comparing model outputs to empirical metrics: α (the distance coefficient) and δ (the distance multiplier for c_{ij}, where $i = j$; see above). To estimate the α and δ parameters, we compared our gravity model with survey data collected via the 100th Meridian Initiative (D. Britton, unpublished data; 100thmeridian.org). At each of 20 reservoirs in the Great Plains, volunteers asked recreational boaters for their home state, the recent past use of their boat, and planned destinations. From these surveys we identified 13 reservoirs that were planned destinations in 50 or more surveys. Based on this subset of surveys we estimated the number of boaters leaving different states arriving at each reservoir and assumed that the number of boaters from different states that were traveling to the surveyed reservoirs was proportional to the number of boats arriving in the entire watershed. Because our gravity model was designed to predict the movement of boaters between watersheds, the model had to be modified to parallel the observed data, which recorded the movement of boats from different states to reservoirs. Thus, each watershed was assigned to a state based on the location of the centroid of the watershed. The aggregation resulted in the predicted number of boaters leaving state k traveling to watershed j, T_{kj} such that

$$T_{kj} = \sum_{i=1}^{n} T_{ij}, \tag{6}$$

where n is the number of watersheds in state k.

We used sum of squares (Hilborn & Mangel 1997) to measure goodness of fit between model predictions and the observed survey data. To identify the best-fit model, values for α and δ were systematically assessed over a range of values. Values of α ranged from 1 to 10, and values of δ ranged from 0 to 1. Parameter estimates were calculated by minimizing the following equation:

$$\min\left(\sum \left|\log(\tilde{T}_{kj} + 1) - \log(T_{kj} + 1)\right|^2\right), \tag{7}$$

where $\tilde{T}_{kj}$ is the observed number of boaters traveling from different states to specific reservoirs from the 100th Meridian boater surveys.

Once the entire gravity model was parameterized, we determined the risk of zebra mussel dispersal from a watershed with zebra mussels to another watershed. We assumed that the number of boaters carrying zebra mussels (Z_i) from a watershed was proportional to the amount of water within that watershed that is known to contain zebra mussels. Based on this assumption, we estimated the number of boats leaving water bodies with zebra mussels traveling to different watersheds, R_{ij}, as

$$R_{ij} = \begin{pmatrix} A_i Z_i W_j c_{ij}^{-\alpha}, & i \neq j \\ A_i Z_i W_j (\delta \min(c_{ij}))^{-\alpha}, & i = j \end{pmatrix}. \tag{8}$$

Although we believe only a small fraction of boats leaving a lake invaded by zebra mussels is likely to actually transport zebra mussels (Johnson et al. 2001), we did not incorporate this explicitly into the model. To simplify our discussion of model results, we report our results as the percentage of all boats traveling from waters with zebra mussels to each watershed j, P_j such that

$$P_j = \frac{\sum_{i=1}^{m} R_{ij}}{\sum R_{ij}}, \tag{9}$$

where m is the number of watersheds. Furthermore, our model was based on a single boating trip for each boat in the data set. This simplifying assumption means the results of the gravity model equation will quantify a relative rather than an absolute number of boaters traveling between different watersheds.

To assess the sensitivity of our results to our parameter estimates, we changed the value of the best-fit parameters α and δ and the estimated scalar x by adding or subtracting 25% of their value. We assessed the proportion (Q) of boaters traveling from zebra-mussel-infested waters (R_{ij}) that travel to watersheds that already contain zebra mussels across these ranges of parameters,

$$Q = \frac{\sum R_{il}}{\sum R_{ij}}, \tag{10}$$

where l is the subset of watersheds that already contain zebra mussels.

We also conducted a more detailed analysis on a subset of watersheds to examine the number of boats from invaded water bodies traveling to specific lakes currently not invaded by zebra mussels as follows. First, we assumed that the proportion of boaters traveling to a particular water body within a watershed was proportional to the attractiveness of that water body relative to the attractiveness of the entire watershed. Based on this assumption we examined the largest uninvaded lake or reservoir in each watershed to assess the relative likelihood that zebra mussels will be transported to particular water bodies. For this analysis we chose two western watersheds that were of specific management interest (the lower Colorado–Lake Mead and the Upper Columbia–Roosevelt Lake watersheds) and a third watershed as a contrast (southeastern Lake Michigan watershed) because it is one of the most highly invaded watersheds in the country. Ten other watersheds were randomly selected. This more detailed analysis of these 13 reservoirs allowed us to explore the influence of different landscape characteristics on likely dispersal. At one extreme were watersheds dominated by a single reservoir, such as the lower Colorado–Lake Mead watershed in which 86% of the surface area of water in the entire watershed belongs to Lake Mead. On the other extreme was the southeastern Lake Michigan watershed in Michigan, where one of the largest lakes in the watershed, Gun Lake, accounts for only 2% of the total surface area of water in the watershed.

Abundance Estimates

We predicted the potential population densities of zebra mussels in two specific reservoirs: Lake Mead on the Colorado River and Roosevelt Lake on the Columbia River. We used the model by Ramcharan et al. (1992), which is based on pH and phosphate concentration, to predict the density of zebra mussels (number per square meter) in these two reservoirs and in a number of other water bodies that have already been invaded by zebra mussels and for which actual densities estimates are available. Data on water chemistry for these water bodies were retrieved from the Washington Department of Ecology database (http://www.ecy.wa.gov/database.html) for Lake Roosevelt and the Environmental Protection Agency (EPA) STORET database (http://www.epa.gov/STORET) for the other water bodies. Where EPA STORET had time-series data from several sampling sites within a water body, we averaged all data retrieved for a particular water body to estimate pH and phosphate values. When possible, we used only data from the past 15 years, although for some water bodies it was necessary to use data from as far back as the 1960s. Simple linear regression was used to compare the maximum observed versus predicted densities. To estimate the potential densities of zebra mussels in Lake Mead and Roosevelt Lake, we first modeled the densities based on the Ramcharan model. The model results were then incorporated into the equation developed from the linear regression.

Results

National Gravity Model

The best-fit parameters for our gravity model from our least-squares analysis were α (distance coefficient) of 2.57 and δ (distance multiplier) of 0.73 (Fig. 1). The range of parameters that were within 10% of the minimum least squares value included a range from 1.66 to 3.62 for α and from 0.27 to 0.99 for δ (Fig. 1.) The scalar x was calculated as 0.0333 ha/km. (For Wisconsin and Oregon the mean scalar values were 0.0112 ha/km and 0.0422 ha/km, respectively.) The sensitivity analysis revealed that the model was more sensitive to changes in α than to changes in δ or x (Table 2) but was not strongly sensitive to either parameter. A 25% decrease in α resulted in a decline of 13% in Q, or the estimated number of boaters traveling from infested to watersheds that are already infested, whereas a 25% increase in α resulted in a 9% increase

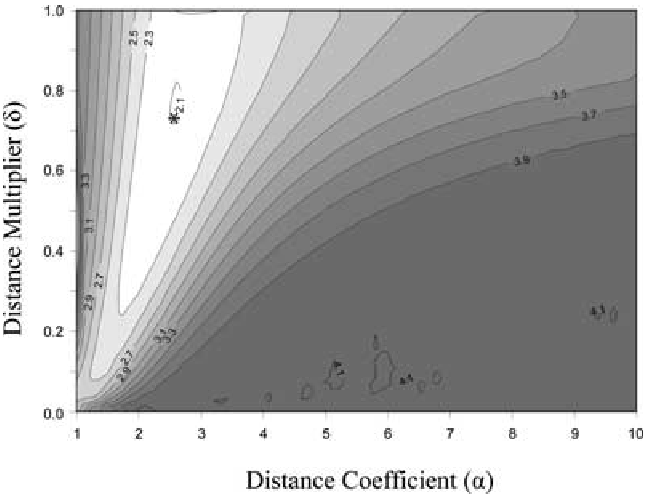

Figure 1. Results of the parameterization routine that determined the best-fit parameters of α (distance coefficient) and δ (distance multiplier) by comparing model predictions with survey data of the movement of recreational boats in the United States. Values ranging from 1 to 10 for α (distance coefficient) and from 0 to 1 for δ (distance multiplier) were considered in our parameterization routine. The ∗ indicates the minimum sums-of-squares difference between model predictions and observed values.

in Q (Table 2). In other words the uncertainty analysis provided brackets of 71–89% around the best-fit estimate that 82% of boaters traveling from zebra-mussel-invaded waters were traveling to watersheds that already have zebra mussels (Table 2). The relative pattern forecasted based on the best-fit parameters was unchanged when we used the values of our sensitivity analysis. Given this small sensitivity to large changes in parameters, we focused on model results derived from best-fit parameters.

Using the best-fit parameters, we estimated the relative number of boaters traveling from an invaded watershed to each watershed (P_j) in the continental United States (Fig. 2). Our model estimated that substantially fewer boaters from areas invaded by zebra mussels were traveling to the western United States than to many closer watersheds. For example, our model predicted that the percentage of all boaters from invaded water bodies arriving in the southeastern Lake Michigan watershed was 5.52%, whereas <0.05% of boaters from invaded water bodies were traveling to the Lake Mead (Colorado River) and Roosevelt Lake (upper Columbia River) watersheds (Table 3).

Differences in landscapes translated into different risk levels for specific lakes to the future of invasion of zebra mussels. Because of its large size, Lake Mead attracted more boaters from invaded watersheds than smaller reservoirs in Kansas, such as Lake Perry (Table 3), even though Lake Mead is three times as far from the Great Lakes as Lake Perry. Lake Mead was also more than twice as likely to attract boaters carrying zebra mussels than Roosevelt Lake (Table 3).

Abundance Estimates

Reported densities of zebra mussels in the United States ranged from 55/m^2 in the Tennessee River to over 250,000/m^2 in southern Lake Michigan (Fig. 3). These densities do not closely match the abundances we predicted based on water-quality parameters from Ramcharan's model, which ranged from 273/m^2 to 2941/m^2, but the model was positively related to the observed values ($r^2 = 0.43$, $p = 0.078$) (Fig. 3). Based on density predictions, if zebra mussels were established in Lake Mead and Roosevelt Lake, Lake Mead would have considerably higher densities of zebra mussels than Roosevelt Lake (Fig. 3). Lake Mead's potential maximum population density was in the 100,000s/m^2, whereas Lake Roosevelt's potential was more moderate populations in the 1,000s/m^2 (Fig. 3).

Discussion

The rapid spread of zebra mussels in the eastern and central regions of North America in the late 1980s and early

Table 2. Results of the sensitivity analysis of the model of movement of recreational boaters.*

α *(distance coefficient)*	δ *(distance multiplier)*	x *(scalar)*	Q *(proportion of boats)*
2.57 (best fit)	0.73 (best fit)	0.0333 (estimated)	0.82
1.93 (–25%)	0.73 (best fit)	0.0333 (estimated)	0.71
3.21 (+25%)	0.73 (best fit)	0.0333 (estimated)	0.89
2.57 (best fit)	0.55 (–25%)	0.0333 (estimated)	0.86
2.57 (best fit)	0.91 (+25%)	0.0333 (estimated)	0.80
2.57 (best fit)	0.73 (best fit)	0.0250 (–25%)	0.82
2.57 (best fit)	0.73 (best fit)	0.0416 (+25%)	0.83

**Changes in the predictions of the proportion of boaters traveling from zebra-mussel-invaded waters to watersheds that already have zebra mussels (i.e., Q) were assessed by changing the values of three parameters by increasing or decreasing their values by 25%. The three parameters were the estimated scalar* x *and the best-fit parameters α (distance coefficient) and δ (distance multiplier).*

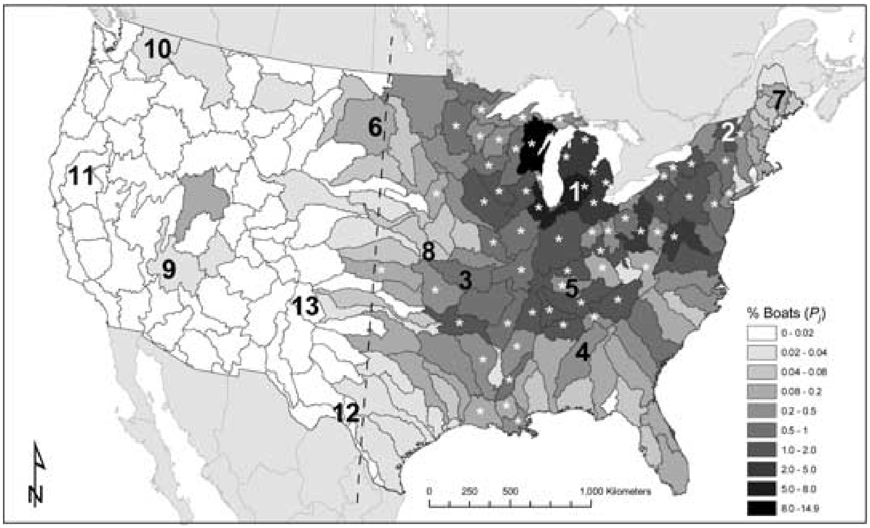

Figure 2. Percentage of boats from water bodies invaded by zebra mussels traveling to each watershed (P_j) within the United States as calculated with a gravity model. The numbers identify specific watersheds described in Table 3, which details more specific predictions of the risk of zebra mussel introductions to particular water bodies. An asterisk indicates that zebra mussels have been observed in the watershed on at least one occasion. The dashed line specifies the 100th meridian.

1990s led to an expectation of rapid range expansion of zebra mussels across the entire continent (Griffiths et al. 1991; Ludyanskiy et al. 1993; Johnson & Carlton 1996). Our model results, however, are consistent with the observed slower range expansion of zebra mussels in recent years (Johnson et al. 2006) and suggest that its range expansion to western North American waterways via transient recreational boating activity is likely to be slow. Watersheds that have been heavily invaded for years have boater visitation rates from invaded watersheds that are at least two orders of magnitude higher than those estimated here for western watersheds. Moreover, there are still many uninvaded eastern watersheds that have appropriate conditions for zebra mussels and higher boater visitation rates than western watersheds (Fig. 2).

Several considerations dictate cautious interpretation of our results, however. By not explicitly including a parameter for the per boat probability of invasion, we assumed that such a probability is independent of travel distance. This is certainly incorrect, but no data exist that could be incorporated into the model. The survival of zebra mussels of any life stage is likely to be a negative function of travel distance. Although zebra mussels can survive for weeks out of water in benign laboratory conditions

Table 3. Estimated percentage of boats traveling from water bodies invaded by zebra mussels to different watersheds (P_j) and specific water bodies within those watersheds in the United States (see Fig. 2 for locations of watersheds). [a]

Watershed	*Boats from invaded waters traveling to watershed* (P_j)	*Total surface area* (km^2) *of water in watershed* (W_j)	*Largest noninvaded water body*[b]	*Boats from invaded waters traveling to water body*[c]	*Area of water body* (km^2)
1. Southeastern Lake Michigan	5.52	460	Gun Lake, MI	0.13	11
2. Richelieu	1.60	1425	Upper Saranac Lake, NY & VT	0.02	22
3. Gasconade-Osage	0.92	714	H.S. Truman Reservoir, MO	0.25	194
4. Alabama	0.29	857	Martin Lake, AL	0.05	161
5. Green	0.28	155	Barren River Lake, VA	0.07	38
6. Missouri-Oahe	0.11	2004	Lake Oahe, SD & ND	0.07	1299
7. Penobscot	0.08	986	Chesuncook Lake, ME	0.01	113
8. Kansas	0.04	189	Perry lake, KS	0.01	47
9. Lake Mead	0.03	681	Lake Mead, AZ & NV	0.03	587
10. Upper Columbia	0.03	1071	Roosevelt Lake, WA	0.01	290
11. Sacramento	0.01	1379	Goose Lake, CA & OR	0.003	376
12. Rio Grand-Amistad	0.004	157	Amistad Reservoir, TX	0.003	134
13. Upper Canadian	0.004	94	Conchas Lake, NM	0.001	35

[a] *These estimates were made with the best-fit parameter values from Table 1.*
[b] *State abbreviations: MI, Michigan; NY, New York; VT, Vermont; MO, Missouri; AL, Alabama; VA, Virginia; SD, South Dakota; ND, North Dakota; ME, Maine; KS, Kansas; AZ, Arizona; NV, Nevada; WA, Washington, CA, California; OR, Oregon; TX, Texas; NM, New Mexico.*
[c] *The percentage of boaters that travel to these individual water bodies was calculated based on the assumption that the distribution of where boaters travel to within a watershed is directly proportional to the area of that individual water body compared with the area of all water bodies in the watershed.*

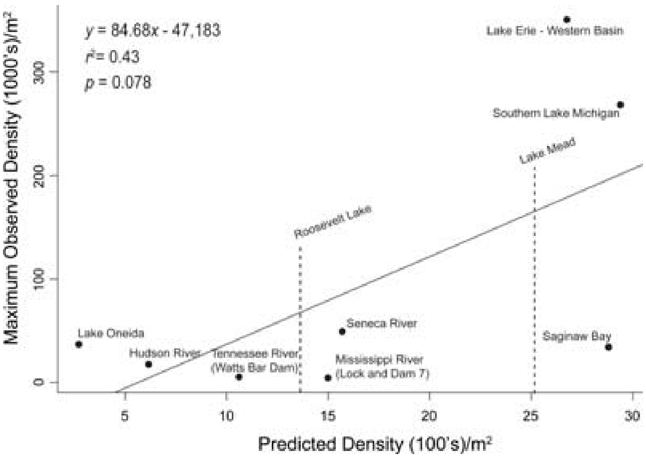

Figure 3. Maximum reported densities of zebra mussels compared with predictions calculated with the model in Ramcharan (1992). Dashed lines indicate the predicted densities of Lake Mead and Roosevelt Lake, which do not have zebra mussels. The observed values were obtained from the following sources: Nalepa et al. (2003), Saginaw Bay; Mellina et al. (1995), Lake Oneida; Caraco et al. (1997) Hudson River; Waterways Experiment Station (1995), Mississippi River (Lock and Dam 7); Leach (1993), Lake Erie—western basin; Marsden et al. (1993), southern Lake Michigan; Effler and Siegfried (1994), Seneca River; and Tennessee Valley Authority (2002), Tennessee River—Watts Bar Dam.

(McMahon & Payne 1992), survival under more realistic travel conditions suggests that mussels could not usually survive more than several days at the most (Ricciardi et al. 1995). Given the typically long travel times for boaters from eastern to western North America and the high heat and low humidity typical of western conditions in the summer when boaters are most likely to be moving, the per boat probability of invasion for east to west range expansion is likely to be much lower than for dispersal within the Great Lakes region. This suggests that our forecast for westward expansion was too high.

On the other hand, we did not distinguish different classes of boaters, some which may constitute a higher risk of invasion. We focused on transient boats (e.g., used for <1 day and stored on a trailer when not in use), which are far less likely to transport large numbers of adult zebra mussels than a boat that has been moored in invaded waters for 1 or 2 months (i.e., a resident boat). The movement patterns of these two types of boats are also likely to be quite different. Transient boats will be moved between different water bodies frequently, whereas resident boats may be moved rarely (e.g., after the purchase of waterfront property elsewhere). Because we did not model movements of resident boats, which will be rarer but possibly entail a much higher per boat probability of invasion, we may have underestimated the probability of westward range expansion.

We may also have underestimated the potential for westward range expansion by ignoring other vectors, which are less abundant than recreational boaters (Carlton 1993) but that could be important in transporting zebra mussels westward. For example, a contractor that transports dredging or waterway maintenance equipment from invaded waters of the Midwest to western waterways would have the potential to transport large numbers of zebra mussels. Alternatively, an aquarium enthusiast might collect zebra mussels while on vacation to use as a "biological filter" (as encouraged by hobbyist magazines; Tippit 2004) and later dump them in a nearby lake. Indeed, even scuba divers are suspected of transporting zebra mussels long distances and introducing them into quarries to improve water clarity, including the Millbrook Quarry in Virginia (J. Odenkirk, personal communication).

Our forecasts of potential zebra mussel abundance in Lake Mead and Roosevelt Lake are within the predicted ranges for lakes known to contain zebra mussels. Our assessment of potential impacts was based on a model that estimated densities from environmental parameters, but estimated densities were orders of magnitude lower than those observed in the field. Despite these differences, a positive trend was evident ($p = 0.078$). Even though the relationship was not very strong, we suggest that our predictions can be used on a qualitative basis to predict which water bodies will have moderate abundances, such as in the Tennessee or Mississippi rivers, or high abundances, such as Lake Erie or Lake Michigan. Our results suggest Lake Mead is at considerably higher risk than Roosevelt Lake, both in terms of the probability of establishment and the densities that zebra mussels would likely achieve if they became established.

The discrepancy between modeled and observed abundance values may have several causes. First, the original model (Ramcharan et al. 1992) was based on European populations from water bodies that had been invaded by zebra mussels for decades to centuries, in contrast to the recently invaded water bodies of North America. Second, many North American estimates were based on settling plates, which standardize sampling effort but probably overestimate abundances by offering a substratum for colonization that may be more attractive than natural surfaces. Finally, the use of densities to estimate abundance may be confounded by differences in size distribution (i.e., 1000s of recent recruits may be functionally equivalent to a single adult). Moreover, in terms of estimating impact (e.g., filtration rates), densities are usually much less useful than biomass as a measure of abundance. Despite these discrepancies, our best forecasts suggested that although colonization of western waterways by zebra mussels is likely to be slow, the impact of zebra mussels when they do establish is likely to be high because populations are likely to be moderate to high. Thus the impetus for the 100th Meridian Initiative and similar efforts to protect western waterways from zebra mussels is well founded.

Many examples exist of environmental impacts from zebra mussels in eastern North America. Even where zebra mussel densities are modest compared with Lake Erie or Lake Michigan, the ecology of the system is significantly altered (e.g., Strayer & Smith 1996; Caraco et al. 2000). Zebra mussels have had one of their largest impacts on the freshwater mussel fauna, causing recruitment declines and local extirpations (Strayer & Smith 1996; Ricciardi et al. 1998). Our model predicted that areas of high freshwater mussel endemism, primarily Tennessee and Alabama, are at risk to further introductions of zebra mussels (Fig. 2). Despite this risk of spread, most of the freshwater mussels in Tennessee that are listed as threatened or endangered have different habitat affinities than zebra mussels (J.M.B. & J. Drake, unpublished data). The western United States has relatively few freshwater mussel species, most of which are considered stable (NatureServe 2006). The potential environmental impacts of zebra mussels on western rivers will thus be different than the impacts they are having in their current range.

The western United States is home to many fish species that are of special concern, however. Several counties along the lower Colorado River have between four to seven fish species that are listed as endangered (Dobson et al. 1997). These species are already threatened by the prevalence of several nonindigenous fish species (Stohlgren et al. 2006) and could be further imperiled by the introduction of zebra mussels. In the northwestern United States there is a concern that the introduction of zebra mussels would further damage the viability of several salmonid species. Strayer et al. (2004) have shown that zebra mussels are associated with changes in the distribution of fish communities in river systems, including declines in open-water species and increases in littoral species. There is also concern that zebra mussels would attach themselves to fish ladders and cause damage to salmonids during passage (Northwest Natural Resource Group 2003).

In addition to the conservation concerns surrounding western waterways, a great deal of economically valuable human infrastructure exists that is at risk from zebra mussel invasions. Water is central to many of the regional economies of the west. In particular, water from the Colorado and Columbia rivers powers massive hydropower dams, provides habitat, sustains miles of fish ladders, provides water for thousands of miles of irrigation canals, and provides substantial amounts of municipal water. The impact that zebra mussels would have on these facilities has been estimated only crudely. Nevertheless, the economic problems created by zebra mussels in the hydropower industry on the Euphrates River in Turkey are documented (Bobat et al. 2004). Also, Phillips (2005) concluded that in the Columbia River basin "the one-time cost for installing zebra mussel control systems at hydroelectric projects could range from the hundreds of thousands of dollars to over a million dollars per facility." Because this estimate is only for hydroelectric dams and does not include irrigation or municipal water supplies, the total annual impact of zebra mussels on these major river basins could be much larger.

We believe it is important to continue to support and improve policy and management interventions to increase the effectiveness of prevention and rapid response efforts in western North America. Among the strategies that should be included are the adoption of best management practices for public agencies, which is already mandated for many federal agencies (National Invasive Species Council 2001) and private contractors. The U.S. Fish and Wildlife Service has begun HACCP (Hazard Analysis & Critical Control Points) workshops, primarily for hatchery personnel, to develop biosecurity barriers for pathways of aquatic invasive species (B. Pitman, personal communication). Commercial truckers specializing in hauling boats long distance should be prime educational targets as should the marinas to which they deliver their cargo. Public education targeted at aquarium hobbyists and water gardeners could reduce the importance of those vectors (e.g., Habitattitude campaign; http://www.habitattitude.net) (McNulty et al. 2004). Our analysis is consistent, however, with the understanding that recreational boaters are likely to be the major vector for westward expansion, perhaps in a stepping-stone manner as seen in other invasions (MacIsaac et al. 2004). Inspection and education efforts directed at recreational boaters by the 100th Meridian Initiative and other organizations should therefore be strongly supported as an important mechanism to prevent or at least slow the westward spread of zebra mussels and other aquatic invasive species by the most frequent movers of zebra mussels.

In addition, contingency plans should be established for how state, provincial, and federal agencies will respond to an initial invasion. Otherwise, valuable time for the quarantine or eradication of an initial invasion will be lost. Although such efforts may have been impossible in the Midwest where lake densities are high, the relative isolation of western lakes and reservoirs and the high frequency of public ownership will provide more amenable conditions for the containment of initial invasions.

Given the potential for large impacts on the ecosystems and human infrastructure of western waterways, a more complete and integrated bioeconomic assessment of management efforts is needed. Our analysis of the probabilities of invasion and impact in the western United States is a first step toward efficient administration of resources for managers to prevent such an introduction from occurring or respond appropriately if it does. Our analysis only examines the spread and potential abundance of zebra mussels, yet many other aquatic invasive species are transported by recreational boating, such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) (Johnstone et al. 1985) and the water fleas *Daphnia lumholtzi* (Havel & Hebert 1993) and *Bythotrephes cederstroemi* (Muirhead & MacIsaac 2005), and could cause additional economic and ecological damage in the western United States. Determining more specifically how much money should be invested and where those resources should be allocated are questions that require the integration of our results with economic models (Leung et al. 2002) of regions most at risk to the introduction of zebra mussels and other aquatic invasive species.

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