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Research Article

Assessing the influence of different inland lake management strategies on human-mediated invasive species spread

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Abstract

Species introduced to the Great Lakes region through shipping, pet and nursery trade, and as biological control have caused significant environmental damages and have increased the direct and indirect costs to boat owners and various water-dependent industries. Once established, recreational boating becomes the primary vector of spread for some of these species, such as zebra mussels (*Dreissena polymorpha* Pallas, 1771). Prevention and mitigation efforts in the past have focused on boater education, boat washing stations, and inspections; yet these management actions can be expensive with limited or largely unknown effectiveness. In this study, we used a gravity model framework to accurately simulate the spread of an aquatic invasive species. After parameterization, the constructed model effectively simulated the human-mediated movements of the historical dreissenid spread patterns, correctly predicting an average accuracy of 78.2% (standard deviation = 0.01%) lakes invaded per model run. We then used the model to determine the effectiveness of three different invasive species management scenarios in Michigan: deterring boaters from lakes with a high likelihood of invasion, targeted education at high-risk lakes, and a large-scale education effort. Results indicated that deterring boaters from high-risk lakes is effective in the first five years of an invasion, targeted education is more effective at late stages of an invasion, and large-scale education is effective at all stages of an invasion. Our results indicate that managers should be flexible in their management actions and that different strategies are likely more effective at different stages of an invasion.

Key words: gravity model, zebra mussels, spread, invasive species management, adaptive management

Introduction

The introduction of invasive species results in measurable environmental and economic impacts (Mack et al. 2000; Sakai et al. 2001; Vitousek et al. 1997) and threatens the integrity of ecosystems (Sala et al. 2000). As a major hub of international shipping, the Great Lakes have become a global epicenter of non-native species introductions and dispersal (Ricciardi 2006). Invasive species from shipping alone are likely to cause $138 million worth of economic damages each year in the Great Lakes region to commercial and sport fishing, raw water use, and wildlife watching (Rothlisberger et al. 2012). Established invasive species in the Great Lakes are further dispersed to inland lakes through recreational boating, upstream dispersal, and bait trade (Bossenbroek et al. 2001; Vander Zanden and Olden 2008; Drake et al. 2011). During this secondary spread, the Great Lakes act as a gateway for invasive species into nearby lakes and connecting waterways (Leung et al. 2006) resulting in rarely accounted for economic damages (Keller et al. 2008). The role of recreational boaters as a vector for secondary spread is well documented (Vander Zanden and Olden 2008; Rothlisberger et al. 2010; Kelly et al. 2013), thus management actions that reduce boat movement between lakes, or reduce the number of boats contaminated with invasive species, will likely be an effective approach for reducing economic and environmental damage.

The Great Lakes region presents unique challenges to invasive species management due to the large population of recreational boaters. Each boater has the potential to unintentionally contribute to the spread of invasive species into new lakes and rivers. Preventing the initial dispersal and establishment of potentially invasive species to the Great Lakes is considered an important preventative measure (Ricciardi 2006). Management efforts in the form of prevention and eradication have been implemented in the past with the goal of diminishing the harmful effects of invasive species (Simberloff 2003a). For example, state agencies use large-scale education efforts and boat washing stations to reduce the number of boats arriving with invasive species (Jensen 2010). Likewise, states have banned the transportation of firewood in an effort to prevent the spread of the emerald ash borer (*Agrilus planipennis* Fairemaire, 1888; Muirhead et al. 2006). In situations where these preventative measures fail and an invasive species becomes established, successful eradication is unlikely without early detection and a large and rapid investment of resources. If, however, an invasive species becomes established, its spread may be slowed, and thus the costs of its impacts spread out over many years by management interventions (Rejmánek and Pitcairn 2002; Simberloff 2003b; Bossenbroek et al. 2015). Identifying the lakes most at risk of invasion allows for more informed management responses and the efficient expenditure of management resources in preventing or eradicating invasions (Leung et al. 2006).

Establishment of new populations is highly dependent on propagule pressure, especially at local scales (Lockwood et al. 2009; Von Holle and Simberloff 2005). Given that the number of recreational boaters visiting a lake is proportional to propagule pressure (Leung et al. 2006), the locations most at risk for the establishment of aquatic invasive species may be predicted through the use of methods that simulate potential boater traffic. In this study, we predicted recreational boater traffic using production-constrained gravity models. These models have been used previously to estimate the spread of multiple species, including zebra mussels (*Dreissena polymorpha* Pallas, 1771; Bossenbroek et al. 2001 and 2007; Leung et al. 2006), and emerald ash borer (Muirhead et al. 2006; Prasad et al. 2010). Some of these models described the spread of their target species fairly accurately, but identified important limitations in using gravity models to guide specific decisions about invasive species intervention (Rothlisberger and Lodge 2010). These limitations primarily arise from the stochastic nature of colonization processes and a lack of correspondence in the temporal scale at which gravity models are assessed for accuracy (i.e., multiple years or decades) and the temporal scale for which they would be used to make management decisions (i.e., the next year).

In order to provide more thorough suggestions to managers, we modified a gravity model framework to allow the potential effects of management on the patterns and intensities of an invasion to be observed through time. The objective of this research is to develop a realistic model of the movement of recreational boats and thereby the spread of aquatic invasive species in order to examine the effects of different management strategies. We expect that our results will thus inform future natural resource management decisions. The management strategies that we assessed included: 1) a reduction in the use of a destination (i.e., lakes) determined to be at high risk for invasion by reducing its attractiveness, 2) a reduction in the probability that a human vector (e.g. recreational boaters) visiting a high-risk source location would further spread the invasive species, and 3) a global reduction in the probability that any human-mediated vector would spread a species after visiting infested locations. The management strategies that were assessed in the project were developed through conversations with managers of state, federal, and non-governmental agencies such as The Nature Conservancy (W. Chadderton, pers. comm.).

Methods

Spread model

Movement patterns of recreational boaters are governed by structural properties of the landscape, such as the distribution of people, distance between sources and destinations, and variables contributing to the attractiveness of a boating destination. The models used in this study followed the methods of Bossenbroek et al. (2001), which estimated zebra mussel dispersal to inland lakes in several Great Lakes states via recreational boaters based on distance and lake surface area. In these models, a boater's incentive to visit a particular lake is based on travel distance and lake area. We expanded on the methods of Bossenbroek et al. (2001) by manipulating the attractiveness of individual lakes, the probability of establishment, and the probability of infestation, to represent the effects of differing management strategies that could potentially be applied to these systems.

Study area and data acquisition

To test the management strategies proposed, we developed a recreational boater spread model based on the historical dreissenid invasion in the state of Michigan. Our approach to parameterize the spread model was not to create an exact replica of this invasion, but rather to construct an appropriately realistic interpretation of an invasion upon which management model scenarios could be applied and observed. The data needed to construct the model includes: boater registration data, road data, the location and size of inland lakes, the location of boat ramps, and the historical distribution of zebra mussels in the Great Lakes region, which was used for model training. Boater registration data that was appropriate for an invasion taking place throughout the 1990s was needed to properly estimate the boater population of the time. These data were obtained from a 1994 recreational boating survey conducted in Michigan by Stynes et al (1998). A 2012 TIGER/Line shapefile from the U.S. Census Bureau was used for the road network (US Census Bureau) and lake data was calculated from the NHDPlus Version 1 dataset (USEPA and USGS 2005). Only lakes greater than 0.25 km^2 that have a boat access ramp were included in the model. Boat ramp locations were provided by the Michigan Department of Natural Resources. Historical dreissenid invasion locations from 1986-2005 were obtained from the Great Lakes Information Network (GLIN) website (http://www.great-lakes.net) and from data provided by the Nature Conservancy (Chadderton unpubl. data). All data was managed in ArcGIS 10.0 (ESRI 2011) and models were created using the statistical software R (v. 2.15.3, R Development Core Team 2008).

Model development

The model to test the management scenarios was designed to follow a series of steps: 1) estimate the number of boaters traveling from their home to each lake, designated as ramps, in an initial trip based on the number of registered boaters and their distance to each lake, 2) calculate the proportion of boaters that travel from infested lakes to other lakes in a secondary trip, and 3) use a binomial probability to determine the infestation status of lakes based on the number of boaters traveling from infested lakes to non-infested lakes.

In the first step, the number of registered boaters traveling from their county of origin to boat ramps around the Great Lakes watershed was calculated based on road distance, where the source was the geometric centroid of each county and the destinations were the boat ramp locations on each lake. Following the work by Bossenbroek et al. (2001), the gravity model equation used was:

$$equ.1 \quad T_{ij} = \sum_{i=1}^{K} A_i O_i W_j D_{ij}^{-\alpha},$$

where T_{ij} indicates the number of boaters that travel from county centroid i to boat ramp j, K is the number of counties, O_i is the boater population in county i, W_j is the attractiveness of boat ramp j based on lake area in km^2, D_{ij} is the road distance from county centroid i to boat ramp j calculated using ArcGIS, and α is a distance coefficient describing boater travel preferences (a lower α causes boaters to prefer farther lakes than those nearer to their origin). In the previous equation, A_i is described by:

$$equ.2 \quad T_{ij} = \frac{1}{\sum_{j=1}^{L} W_j D_{ij}^{-\alpha}},$$

where L indicates the number of boat ramps in the model. The result of this formula is a distribution of boaters from each county across all boat ramps with ramps on larger, more attractive lakes that are closer to population centers receiving a larger proportion of the boater traffic. For D_{ij} we set a minimum threshold for distance traveled, as very low distances have the potential to skew the patterns of movement that could result from a county centroid being very close to a boat ramp (see Table 1). Also, W_j for Great Lakes boat ramps had to be estimated as the size of each Great Lake is on a different scale than the size of inland lakes (see Table 1).

The next step utilized a second gravity calculation and a binomial probability to determine the number and distribution of boaters that made a secondary trip from an infested lake and caused an invasion in a previously non-infested lake. While many individuals would make a secondary trip, this calculation allowed for some individuals to return home, and removed them from the model as a potential vector. The second step utilized the same formula as the first, but used the calculated boat ramp populations at invaded lakes from the first step as origin populations and every other lake in the model as potential destinations. The binomial probability was determined in the subsequent parameterization routine (Table 1). Since this model was built using the dreissenid mussel invasion, the initial source locations were the boat ramps of Lake Erie and Lake St. Clair, where dreissenid mussels were first discovered in 1988 (Hebert et al. 1989). Only boats visiting Lakes Erie and St. Clair in the first year had a chance

Table 1. Parameters used by the spread model and their best-fit values as determined by the parameterization routine.

Parameter	Purpose	Parameterization Range	Best-fit Value
Great Lakes Ramp Attractiveness	Sets attractiveness value for ramps on the Great Lakes equal to an inland lake of this size.	1 km^2 - 200 km^2	94.4
Infestation Probability	Probability that a single boat in the model will infest its destination lake after visiting an infested lake.	0% - 0.01%	0.0006
County to Ramp Alpha	Describes boater preference for shorter or longer trips between county centroids and destination boat ramps (county to ramp alpha) and in between ramps (ramp to ramp alpha).	1 - 20	10.4
Ramp to Ramp Alpha		1 - 20	5.8
County to Ramp Minimum Distance	Sets a minimum possible distance between county centroids and ramps or between ramps. All distances below this threshold are raised to this value.	1 km - 200 km	79.9
Ramp to Ramp Minimum Distance		1 km - 200 km	38.8

to infest another lake if the binomial distribution selected them for a secondary trip. The higher the number of boaters that were potential carriers of an invasive species visiting a lake increased the probability that the lake would become infested.

After the second step, boater populations were reset to their original locations and the model restarted from step one. One cycle through these steps was considered a time step in the model representing one year. Ramps that were invaded in any given year, along with all other ramps that share the same lake, were considered infested for the remainder of the model. Boat ramps on the Great Lakes were exempted from these spread mechanisms to avoid becoming infested too quickly and driving the spread, overwhelming the model. Instead, these were infested on a schedule following the dreissenid invasion (GLIN 2008). Lakes Michigan and Superior were infested in the second year of the model (1989), and Lake Huron was invaded in the third year of the model (1990). These steps incorporated a temporal component and a spread mechanism into the model, allowing the invasion to be tracked through time. Each model consisted of 20 time steps representing the years 1986–2005 of the zebra mussel invasion.

Model parameterization

A parameterization routine was required to choose appropriate values for six parameters in the model that are difficult to quantify: county-to-ramp and ramp-to-ramp α values, county-to-ramp and ramp-to-ramp minimum distance values, the attractiveness of Great Lakes ramps to inland ramps, and the probability of an invasive species infestation per individual boat (Table 1). Presence data describing the distribution of *Dreissena polymorpha* in Michigan inland lakes was used to carry out the parameterization routine. By running the model with different values for these parameters, the relationships between each parameter and both the number of infested ramps and the proportion of correctly predicted ramps could be examined. In order to be considered "correctly predicted", the invasion status of a ramp was required to match that of its real-world counterpart at the end of the 20 year model, taking into account both presences and absences.

To ensure that the predicted invasion was not over- or underestimating the number of infested lakes in the dreissenid invasion, the parameters that most affected the total number of predicted infestations were identified. In 1,000 trials of the model, values for each of the six parameters were randomly chosen from a wide uniform distribution (Table 1). An additional 1,000 trials were run, altering infestation probability and Great Lakes ramp attractiveness along a range of values and holding the four other parameters constant at arbitrary values. The relationships of these two parameters to the number of infested ramps were described using simple linear regression. The desired number of infested ramps (254) could be substituted into the equations generated from the linear regression to discern the best-fit values for both parameters.

The remaining four parameters were fit by holding infestation probability and Great Lakes ramp attractiveness constant at their best-fit values while randomly choosing values over a wide distribution for the remaining parameters in another 1,000 model runs. Since the number of infested ramps was relatively constant due to the stationary infestation probability and Great Lakes ramp attractiveness, the best-fit values for

Table 2. The three management strategies, the model parameters that they affect, and the potential actions that they may represent.

Management Strategy	Parameter Affected	Potential Actions
1. Reduce Attractiveness of Selected Lakes	*Wj* Ramp Attractiveness of 25 selected lakes	In-state boat launch fees and motor restrictions, reduce available parking
2. Reduce Infestation Probability of Boats Leaving Selected Lakes	*Infestation Probability* Boats leaving 25 selected lakes	Boat and trailer inspections, boat washing stations, signs at ramps
3. Reduce Overall Infestation Probability	*Infestation Probability* All boats, regardless of lakes visited	Television and radio commercials, billboards, ads in general audience publications

the remaining four parameters were based on model accuracy. The training dataset consisted of 889 total inland ramps, with 635 non-infested ramps and 254 infested ramps. By comparing the infestation status of the modeled ramps against the actual dreissenid distribution, the proportion of ramps that were correctly predicted by the model was calculated for each trial. Our test metric was overall accuracy, which is the proportion of true results (i.e. the sum of true positive results plus the sum of true negatives divided by the total population). A local regression model (LOESS) was applied to the resulting data, using each point's neighboring data values and a smoothing function to fit a line to the data. Though a LOESS model does not produce a global function, the maximum point of the resulting curve can be used to identify the best-fit values for each parameter when comparing parameter values against the proportion of correctly predicted ramps.

Modeling management strategies

Educational efforts, advertising campaigns and mandatory boat washes have achieved varying degrees of success when implemented by state management agencies. However, most attempts have been hampered by the high cost of implementation and staffing and the low willingness of recreational boaters to pay additional fees (Jensen 2010). Because of this, the lakes that are chosen to receive management interventions must be low in number and ideally have the greatest beneficial effect on invasive species control. To decide which lakes to manage in the model, 1,000 trials of the model were run with the best-fit parameter values. The top 25 lakes that were invaded most often were chosen to receive management interventions. Lakes that were within 10 km of any Great Lakes were excluded from consideration to avoid managing lakes that have stream connectivity directly to a Great Lake.

Using the parameterized model, three different approaches to invasive species management were investigated, each representing the potential effects of different real-world actions. Management strategy #1 decreased the attractiveness of the 25 lakes chosen to be managed. The goal of the first strategy is to divert recreational boaters away from lakes at high risk for invasion. Management actions to implement this strategy could include increased boat fees or motor restrictions at these lakes. Management strategy #2 decreased the probability of invasive species establishment via boats entering a second lake after first visiting one of the 25 chosen lakes. This is representative of a containment strategy: targeted education efforts at managed lakes such as signage, boat washing stations, and DNR-conducted inspections for invasive stowaways before leaving the lake. Management strategy #3 reduced the infestation probability for all boats in the model regardless of which lake they had previously visited. This represents state-wide education efforts in the form of television and radio commercials, billboards, and other types of large-scale public outreach.

The value of a relevant parameter in the model for each management strategy, described in Table 2, was reduced by 10%, 50%, and 90%.

The management interventions were applied before the invasion began and remained for the entirety of the model, running 1,000 times for the intervals of each management strategy for a total of 9,000 trials. The number of newly infested lakes was recorded for each year of the trials. We used fixed effects ANOVAs to compare each management strategy in Years 3, 5, 10, 15, and 20. The ANOVAs had four factors with the base invasion as the control, and the three different management intensities as treatments. Each ANOVA was followed by a Tukey's HSD test to determine significance between the different intensities.

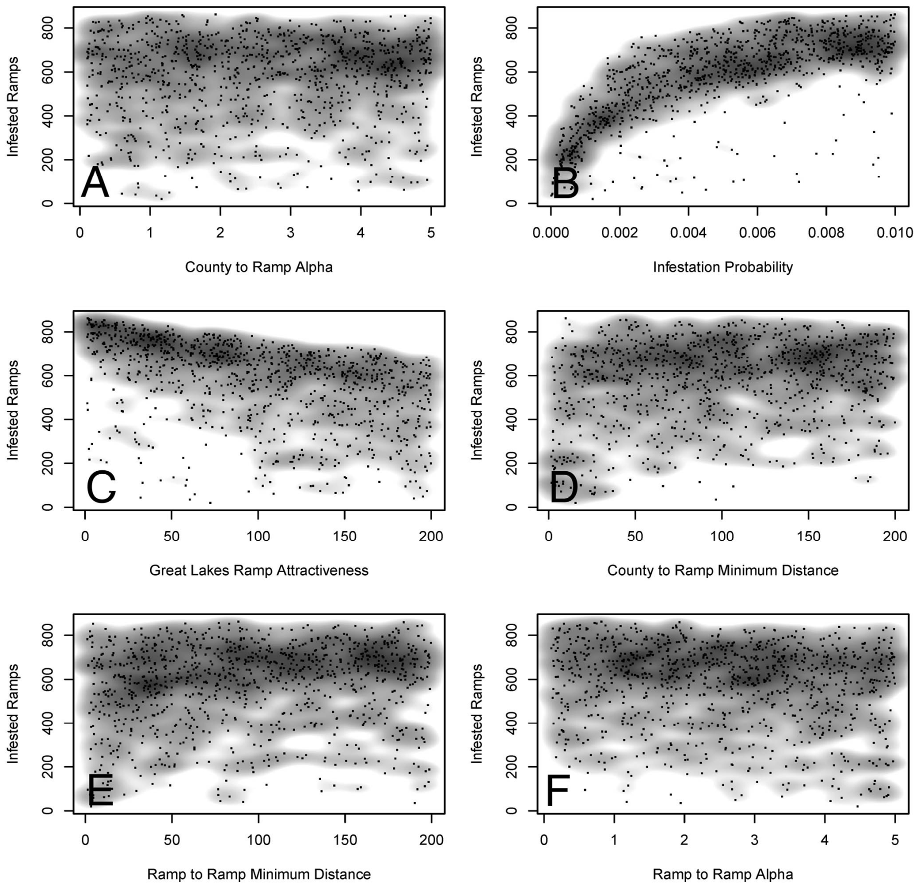

Figure 1A-F. Comparison of the number of infested boat ramps predicted by the model over a range of parameter values. Points are individual model runs and darker areas of the graphs indicate a higher density of points. Infestation probability (B) and Great Lakes ramp attractiveness (C) have a noticeable effect on the total number of ramps predicted as infested by the model, while County to Ramp Alpha (A), County to Ramp Minimum Distance (D), Ramp to Ramp Minimum Distance (E) and Ramp to Ramp Alpha (F) have little predictable influence.

Results

Great Lakes boat ramp attractiveness and infestation probability had the most apparent effect on the number of ramps predicted to be invaded by the model (Figure 1). In these trials, the range of infestation probability was between 0 and .01 (0–1% chance of a boat infesting a secondary ramp) with a best-fit value of 0.0006, and Great Lakes ramp attractiveness between 1 km^2 and 200 km^2, with a best-fit value of 94.4 km^2 (Table 1), indicating that a Great Lakes ramp would be equally attractive to an inland lake of that size. Employing these values when running the spread model results in a conservative estimate of the number of infested inland ramps when compared to the training dataset, averaging 142.0 ramps (standard deviation = 16.8) for 1,000 model runs. Best-fit values as determined by the LOESS models for the α and distance parameters are listed in Table 1 and shown in Figure 2. As shown in Figure 2, the LOESS models generally reached a plateau for these parameters indicating that increasing α and distance values beyond a certain threshold no longer improved model fit. After parameterization, subsequent model runs were able to predict an average accuracy of 78.2% (standard deviation = 0.01%) of lakes correctly in each run when compared to the actual dreissenid invasion. Model sensitivity, or rate of true positives was 55.7% (standard deviation = 0.03%) and model specificity, or rate of true negatives, was 91.4% (standard deviation = 0.02%).

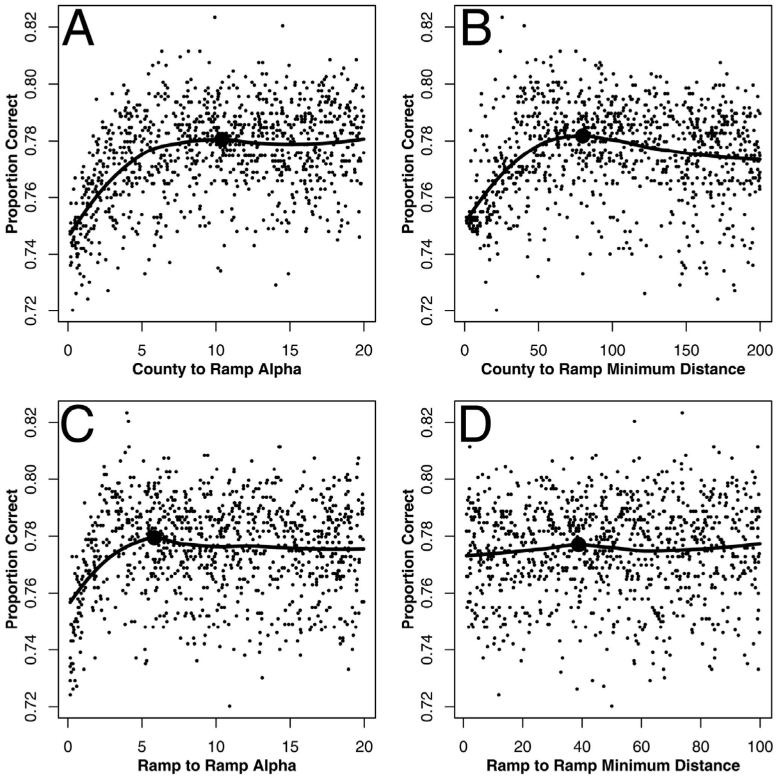

Figure 2. A-D. Range of proportion of ramps predicted correctly for County to Ramp Alpha (A), County to Ramp Minimum Distance (B), Ramp to Ramp Alpha (C), and Ramp to Ramp Minimum Distance (D). Infestation probability and Great Lakes ramp attractiveness were held constant at their best-fit values. Small points represent results of individual model runs. The superimposed line shows the curve created by the LOESS model, and the large point indicates the best-fit value as determined by the LOESS model.

Efficacy of each management strategy (described in Table 2) was determined by examining the time periods at which each level of management was significantly different from the base invasion model (a scenario with no management interventions) and from the other management strategies. Comparisons of the management strategies are described in Table 3. In management strategy #1, attractiveness management, the low and medium intensities were only significantly different from the non-management scenario in the beginning stages of the invasion, represented by years 3, 5, and 10. The highest intensity strategy (i.e. 90% reduction in attractiveness) was significantly different through the entirety of the invasion. In management strategy #2, the strategy of reducing the infestation probability of boats leaving managed lakes, all intensities were more effective in the later stages of the invasion, represented by years 10, 15, and 20. A universal reduction in infestation probability, or management strategy #3, resulted in all intensities being significantly different from the non-management scenario and other strategies at all stages of the invasion.

The number of lakes infested for each stage in the invasion differed between management strategies and intensities (Table 3). The impact of the attractiveness management strategy (#1), was also year dependent, with the greatest deviation from the non-management strategy typically occurring in the early to middle stages (years 5 and 10) of the invasion. The medium and high intensities reduced the number of lakes invaded per year by 0.538 and 1.118 on average (standard errors = 0.067 and 0.060), respectively amounting to 9.67% and 24.92% fewer lakes invaded in their peak years (Figure 3). Year 20 produced the greatest differences when reducing infestation probability of boaters leaving selected lakes (strategy #2). After 20 years of this strategy, the average number of invaded lakes was reduced by 0.197 (standard error = 0.076), 0.771 (standard error = 0.066), and 1.388 per year (standard error = 0.057) in the low, medium, and high intensity management strategies (Figure 4). With a universal reduction in infestation probability (strategy #3), the year in which the strategy was most effective was dependent on the intensity. The number of lakes

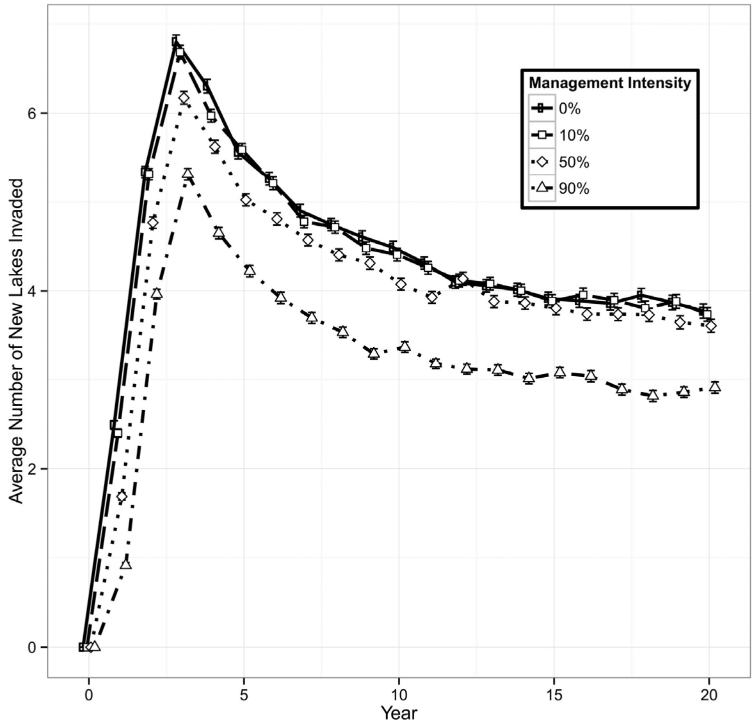

Figure 3. Number of lakes predicted to be invaded in each year with different degrees of reduction on the attractiveness value of the 25 most invaded lakes (Management Strategy #1) compared to the non-management scenario. For each management strategy 1,000 trials of the model were run. Error bars indicate standard error.

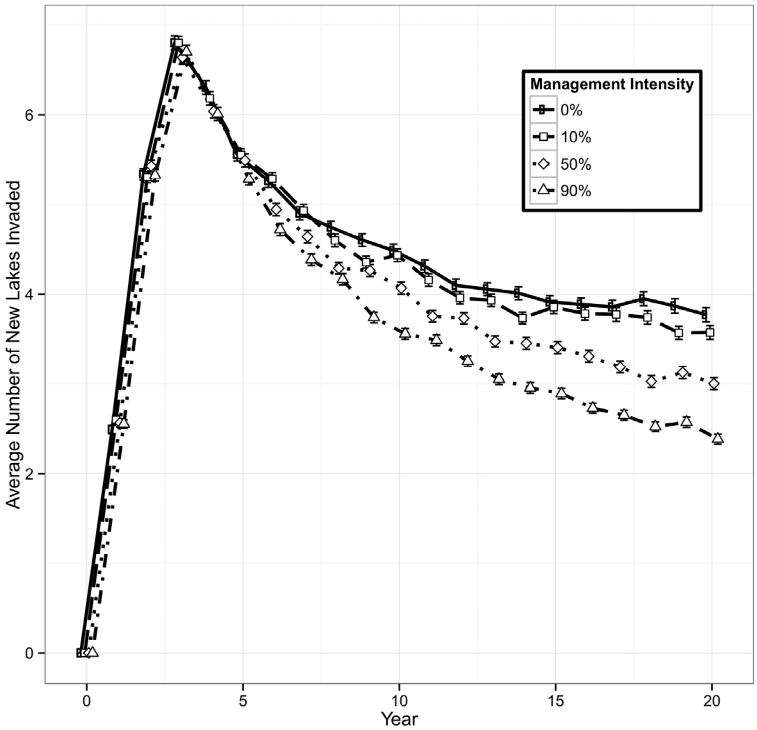

Figure 4. Number of lakes predicted to be invaded in each year with different degrees of reduction on the probability that a boater would transport an invasion from the 25 managed lakes (Management Strategy #2) compared to the non-management scenario. For each management strategy 1,000 trials of the model were run. Error bars indicate standard error.

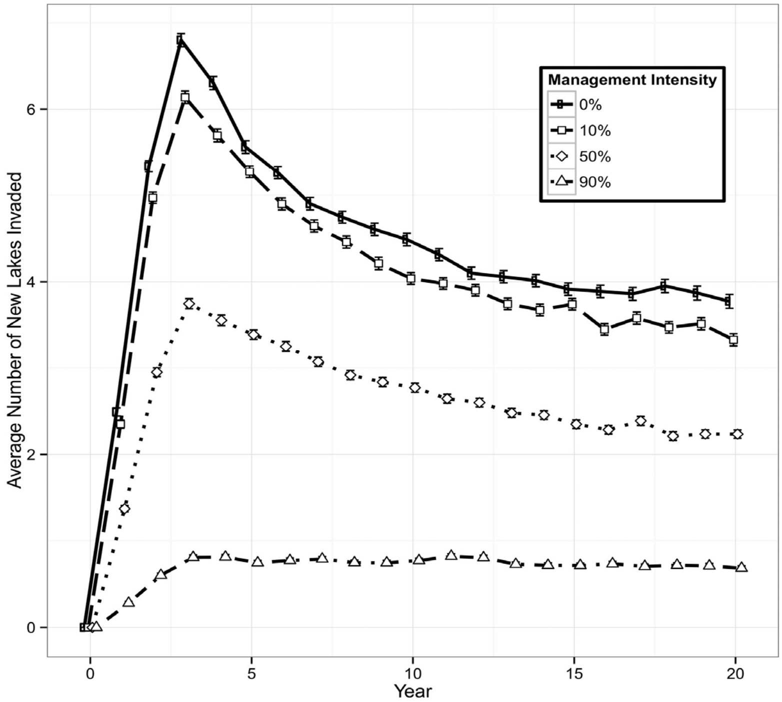

Figure 5. Number of lakes predicted to be invaded in each year with different degrees of reduction on the probability that a boater would transport an invasion from any lake in the state (Management Strategy #3) compared to the non-management scenario. For each management strategy 1,000 trials of the model were run. Error bars indicate standard error.

Table 3. ANOVA and Tukey's HSD significance results for all management strategies and intensities. The significance codes in the rows listing a management strategy indicate if there is a difference among intensity groups, while the codes in the grid indicate significance between the listed treatments as determined by Tukey's HSD. The significance codes are as follows: ** is p ≤ 0.01, * is p ≤ .05, ns is p > 0.05.

Strategies and Intensities	Year 3	Year 5	Year 10	Year 15	Year 20
Reduce Attractiveness	**	**	**	**	**
Control-10%	ns	ns	ns	ns	ns
Control-50%	**	**	*	ns	ns
Control-90%	**	**	**	**	**
10%-50%	**	**	ns	ns	ns
10%-90%	**	**	**	**	**
50%-90%	**	**	**	**	**
Reduce Infestation Probability (Selected)	ns	**	**	**	**
Control-10%	ns	ns	*	*	*
Control-50%	ns	ns	**	**	**
Control-90%	ns	*	**	**	**
10%-50%	ns	ns	ns	*	**
10%-90%	ns	ns	**	**	**
50%-90%	ns	ns	**	**	**
Reduce Infestation Probability (Overall)	**	**	**	**	**
Control-10%	**	**	**	**	**
Control-50%	**	**	**	**	**
Control-90%	**	**	**	**	**
10%-50%	**	**	**	**	**
10%-90%	**	**	**	**	**
50%-90%	**	**	**	**	**

was reduced by 0.443 (standard error = 0.026) in year 20 for the low intensity, 2.771 (standard error = 0.052) in year 10 for the medium intensity, and 5.993 (standard error = 0.072) in year 5 for the high intensity (Figure 5).

Discussion

The results of our modeling effort reinforce the ability of gravity models to accurately describe and predict the spread of aquatic invasive species, particularly dreissenid mussels. This supports previous research that suggested gravity models perform better than other commonly used model types in representing the probabilistic processes that determine which lakes boaters choose to visit (Chivers and Leung 2012). Additionally, by modifying the attractiveness of the lakes included in our model, we were able to evaluate the effectiveness of a range of management practices designed to prevent the spread of aquatic invasive species. While coupling management actions to invasive spread models has been used sparingly in the past (Sharov and Leibold 1998; Drury and Rothlisberger 2008) the results have been promising and our results suggest that gravity models can be an effective tool in the management decision making process. The scenarios modeled in this research suggest that all three types of management actions taken by an agency can have some positive effect on reducing invasion potential, or at the very least delaying an invasion. However, the effort and duration required to see long term results may vary depending on the type of action implemented.

Our first management strategy was to reduce the attractiveness to particular lakes, which has been suggested as an effective strategy to limit the impact of aquatic invasive species (Keller et al 2008; Timar and Phaneuf 2009). Our results showed a delay in the early stages of the invasion and a reduction in the number of lakes invaded. The effects of this strategy also depend on time of application and intensity of management. Low and medium intensity management actions reduce the number of lakes invaded in the first 10 years, but the effectiveness of these strategies diminishes in subsequent years. In the first 10 years, the average reduction in the number of lakes invaded in comparison to the control invasion in the low and medium intensities is 0.09 and 0.5 invasions per year, respectively. In the last 10 years, this figure is reduced to 0.01 and 0.17 invasions per year for the low and medium intensities. Reductions at low and medium levels eventually converge with the non-management scenario, making these types of management ineffective as a long-term strategy. The high intensity reduction in attractiveness offers a significant reduction throughout the 20 years modeled, but likely would incur a significant cost premium as compared to low and medium intensity strategies. Any level of reduction in the attractiveness of popular lakes may be a viable short-term management strategy if it is applied rapidly at the beginning of an invasion. However, there is little evidence to suggest that this sort of management practice has been implemented on a wide scale. Such a strategy has high level of perceived costs associated with loss of revenue, or back-lash from the boating community (Perrings et al. 2002; Timar and Phaneuf 2009). Our modeled management scenario would likely delay the invasion for a few years in a small number of popular lakes, and while this may seem to be of limited benefit, it has been shown that even short-term delays in invasions could prove to be economically beneficial to the affected region (Leung et al. 2006).

Our second management strategy, to reduce the probability that a boater leaving an infested lake will successfully transport the invasive species to a new lake, was predicted to be effective after an invasion has progressed for several years. In the first 5 years of our model, only the highest intensities of management had an effect on the number of invaded lakes, but after that, the strategy becomes increasingly effective and even low intensities can reduce the number of invaded lakes. This strategy could serve as a long-term program for reducing the effects of an invasive species as long as the ongoing costs for maintenance, such as boat washing stations, are not prohibitive. Boat washing stations require substantial effort to institute and maintain, especially for high-traffic lakes (Jensen 2010), and may inadvertently place an increased cost on visitors if they are mandatory. The effectiveness of boat washing, and the need for a high intensity management strategy in the initial stages of an invasion, is supported by research on different boat types (ski, fishing, and multi-use boats) and the effectiveness of boat washing and bilge draining in reducing the spread of zebra mussels in Lake Michigan and Lake Mead (Dalton and Cotrell 2013). However, Dalton and Cotrell (2013) demonstrated that while basic boat washing practices can reduce the veliger load, a significant number of veligers could still be transported without additional air-drying between trips. Targeted education in these areas could also be a viable management strategy. With education alone and optional boat washing, the choice of properly cleaning and inspecting boats ultimately falls on the visitor. Even if management is able to change the behavior of boaters, the benefits of this strategy are not predicted by our model to manifest until the later years in the invasion (Figure 4).

Reducing the probability that any boater in the state would spread the infestation was our third and final management strategy and was successful at reducing the predicted number of invaded lakes over the 20 years we simulated. These results suggest that even at low intensities this management strategy can help reduce the overall number of invasions. Our results are similar to those of Schneider et al. (1998), which suggest that education and inspection efforts were superior to quarantine, due to unintended consequences, such as displacement of boaters to critical habitats. While large scale education strategies have been implemented before, such as Sea Grants' Stop Aquatic Hitchhikers educational billboards and signs (Larson et al. 2011), their real-world effect on the probability of boaters transporting invasive species is difficult to discern. Minnesota Sea Grant has used wide-spread public awareness campaigns extensively in the past (Jensen 2010). In a survey conducted in 2004, they found that 70% of boaters surveyed in Minnesota took precautionary measures to reduce the risk of transporting invasive species; only 33% of Ohio boaters and 39% of Wisconsin boaters took precautions. In addition, Minnesotan boaters were more aware of the importance of deterring invasive species and methods to reduce the risk (Gunderson 2004). This survey suggests that large-scale education efforts do in fact have an effect on boater behavior, which may in turn reduce or slow the spread of aquatic invasive species.

Model performance

Our model consistently predicted lakes infested with dreissenid mussels over the 20 years of model simulation; however the model was highly stochastic between years. In the non-management scenario, the pattern of lakes invaded between individual runs was highly variable limiting the models usefulness for year to year predictions, but the overall invasion status of the lakes in the model are consistently accurate. These results suggest that when selecting lakes to focus management efforts on, a holistic, regional approach may be more efficient than selecting lakes based on their individual attributes.

Limiting our model to Michigan had several advantages and disadvantages. Excluding neighboring states inherently introduces error into the model; interstate travel has the potential to spread invasive species equally as well as intrastate travel. Despite this, including data from other states would increase uncertainty and potentially decrease the predictive capability of the model. Differing data collection protocol between states also creates inconsistencies in data compilation, availability, and reliability, which would have the potential to influence model results based on differing data quality. The state-wide scale of the model was most suitable for management recommendations and the data required were easily obtained. Additionally, boaters at Michigan lakes were more likely to be from Michigan, and tended to stay in Michigan waters more so than in comparison to neighboring states (Stynes et al. 1998). Therefore, our selection of the state of Michigan helped to minimize error in our model from out-of-state boaters, who were not included, but would still contribute to over-all boater movement.

This model was parameterized based on the dreissenid mussel invasion, and thus inherently incorporates characteristics of the species, such as desiccation rates and survivability, that influence the probability of infested boats infesting new lakes. If survivability of invasive species changes as a function of distance, the model may be adjusted to account for this with changes in the distance coefficient α. Thus, with adjustments, this model can be used to forecast the spread of other species. For example, a species spread by recreational boaters that desiccates more rapidly than dreissenid mussels (such as Eurasian water-milfoil; Barnes et al. 2013) may be less likely to establish populations at lakes far from its origin. Applying a distance decay function to the infestation probability would take the limitations of this species into consideration and potentially increase the accuracy of their modeled distribution. Similar alterations could be made to the model to account for changes in boater behavior, such as raising alpha values to simulate boater preferences for shorter trips during poor economic conditions.

Conclusion

Management actions to slow the spread of aquatic invasive species have been used widely in past decades; however, our model results suggest these strategies will only be effective if conducted at a high enough intensity. Considering cost of implementation for each strategy would be a critically important factor in order to make informed decisions for natural resource managers (Homans and Smith 2013). The scope of this study, however, was limited to the potential effects to the spread of an invasive species by applying various management strategies to an impending invasion. A cost-benefit analysis of the model results would be a valuable next step for more concrete suggestions to natural resources managers. Efficacy of the modeled management strategies also reiterates that efforts must be taken to keep invasive species out of the Great Lakes altogether. Our results highlight the importance of early detection of a potential invasion; however, the detectability of different species can vary (Mehta et al. 2007). Therefore, management priorities may need to be set based on the species-specific risk of invasion and over-all probability of detection and control (Fleischer et al. 2013; Gallardo and Aldridge 2013). Even with statistically significant reductions in the number of lakes infested per year as modeled in this study, the most intense management strategies (with the exception of the large-scale education model) reduce the number of newly invaded lakes per year by only 1–2 lakes at their peak effectiveness. Management may slightly reduce or delay the spread over the course of several years, but eradication is impossible with the strategies modeled here. Once an invasive species is introduced and established in the Great Lakes region, control and eradication is likely to be much less cost effective when compared against preventative measures (Rejmanek and Pitcairn 2002; Simberloff 2003b). Ultimately, the effectiveness of any preventative or responsive action will depend on the effort and resources that are allocated by individual management agencies. Our results show that gravity models can be a useful tool to assess the effectiveness of different management strategies and could be used with future efforts that incorporate the limitations and options available to managers and decision makers given limited resources.

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