Using constrained gravity models at large spatial scales to simulate invasive species colonization

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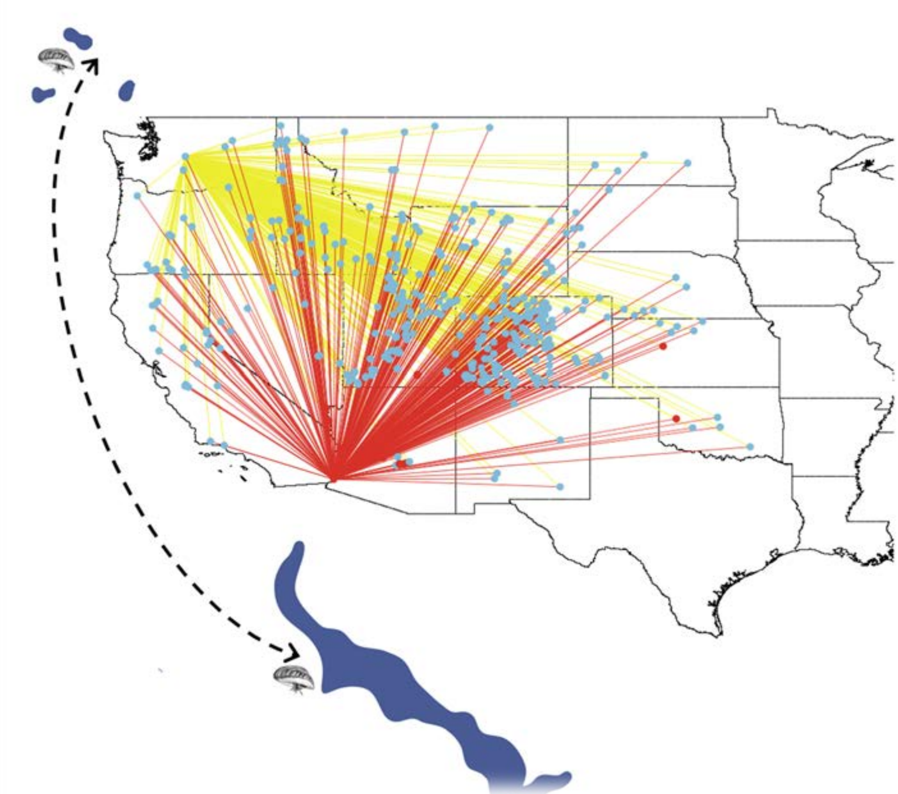

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14. ABSTRACT
Invasive dreissenid mussels pose a threat to both Reclamation facilities and the environment. Predicting the future dispersal patterns of the dreissenid mussels is important because it can help predict waterbodies at greatest risk of colonization. The dreissenid mussel model described here uses a combination of constrained gravity model equations, habitat suitability equations, and a user defined variable for mussel transport survival. Calcium and pH data from 402 waterbodies in the Western US were incorporated into the model. The model indicates that implementing a buffer zone greatly decreases the probability of waterbodies becoming infested. This model can be used to determine which waterbodies are at highest risk for dreissenid mussel invasion, given the assumptions within the model. Agencies can use the results from the model to determine what steps need to be taken to either ensure that a particular waterbody does not become infested, such as increased boat inspections and monitoring of the waterbody.

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Executive Summary

Aquatic invasive species are a worldwide problem that can have detrimental impacts on natural resources, human health, recreational opportunities, and other ecosystem services (Gurevitch & Padilla, 2004). Predicting areas at the highest risk of invasion will help natural resource managers plan and budget for invasive species management efforts. In North America, invasive dreissenid mussels (quagga mussels (*Dreissena rostriformis bugensis)* and zebra mussels (*Dreissena polymorpha*)) have cause hundreds of millions of dollars in damage to water resource and power facilities by fouling infrastructure and clogging pipes (Higgins & Vander Zanden, 2010). In addition to the economic impacts, dreissenid mussels can cause extensive ecological changes by altering the trophic dynamics of lentic systems. Since their arrival to North America, these species have spread throughout the United States, likely as a result of overland dispersal by recreational boaters (Collas, Karatayev, Burlakova, & Leuven, 2018). Predicting future dispersal patterns is difficult since regionally varying transportation patterns and water quality must be coupled with the complex, biphasic mussel life cycle.

Ecological modeling is a tool that can be used to represent this complexity in a quantitative simulation framework that can forecast different invasion patterns to determine areas at the highest risk for future colonization. Constrained gravity models are a good approach and have been used for predicting dreissenid dispersal, but they are lacking in the ability to consider alternative variables that impact dispersal (Bossenbroek, Johnson, Peters, & Lodge, 2007). Constrained gravity models are based upon the attractiveness of a waterbody (size) and distance between two waterbodies. Without additional modification, these models do not include important parameters such as habitat suitability. The Integrated Ecological Modeling Team at the U.S Army Engineer Research and Development Center collaborated with the Bureau of Reclamation (Reclamation) Ecological Research Laboratory (Eco Lab) to develop an integrated dreissenid mussel dispersal model that coupled boater behavior and habitat quality models to forecast the likelihood of dreissenid mussel spread across 402 lakes in the Western United States.

We focused this initial habitat suitability model on pH and calcium as they are known to be key limiting parameters, critical for dreissenid mussel survival. Mean calcium and pH values were obtained from various data repositories throughout the Western United States. The model simulates boater movement between lakes, the likelihood of each boat carrying dreissenid mussels, and the likelihood of those mussels surviving transport and surviving within the new lake itself. The model is formulated as a spatially explicit, grid-based model with a 1-year time step. It is composed of two submodels that represent different components of successful overland transport and survival leading to dreissenid mussel colonization: (1) A constrained gravity model that simulates boater movement among 402 lakes in the Western United States and (2) a habitat suitability model that quantifies the relationship between water quality (specifically, pH and calcium) and dreissenid mussel viability. Model equations were modified from those in Robertson et al. 2020. The model is programmed in Netlogo v6.1.1, an open source, spatially explicit multi-agent programmable platform (Wilensky & Rand, 2015). The scenarios modeled in this study explore how the survival rate of mussels being transported, the habitat suitability of destination waterbodies, and the distance boaters can travel

affect the spread of invasive mussels. Understanding the importance of each of these parameters and how they affect the spread of mussels to other waterbodies can inform more effective, targeted management.

Scenarios were developed using a null model. We developed three overarching scenarios, each of which represents a physical, spatial, or ecological process that constrains the spread of dreissenid mussels. Twenty-four different sub-scenarios were developed to explore the parameter space of the constraints and were ran for six-time steps and the resulting number of infested lakes is recorded. The percent change of total number of lakes infested between null model runs and each scenario was compared. Habitat suitability scores ranged from completely unsuitable (scores approximating zero) to optimally suitable (scores of 1) across all waterbodies. Dreissenid mussel survival probability was high (≥ 0.80 HSI) in 250 lakes and low (≤ 0.40 HSI) in 99 lakes. The implementation of buffer zones resulted in the smallest number of lakes being infested. As expected, the null model results, which were based on the size of and distances between waterbodies, resulted in the highest percentages of waterbodies that become infested. This is expected given that the null model has no constraints on boater movement or dreissenid survival.

The transport survival rate played a critical role in mussel spread. Each transport survival sub-scenario contributed to further spread of the invasive mussels. However, the magnitude of the transport survival reductions did not contribute to a corresponding reduction in the proportion of infested waterbodies over time. Decreasing veliger survival by 25% to 75% still led to infestations of 36% to 60% of all waterbodies within a consistent and short time frame. Although the resulting infestation rates are not impacted by veliger transport survival alone, the combined effect of lower survival and limited boat movement do provide a noticeable decrease in infestation rate (e.g., scenarios with a buffer and transport survival). Limiting recreational boat movement had the effect of decreasing the potential connectivity between the network of waterbodies and this effect is amplified as the spatial area of interest increases.

Habitat suitability, in general, is an important aspect of determining or modeling whether an invasive species will infest a new area. Our results show that the habitat suitability index is an important driver in determining the infestation rate. Our model indicates that movement patterns of recreational vessels have the greatest impact on dreissenid mussel infestation rates, when compared to other model parameters. Patterns of movement in which recreational boaters do not travel more than 100 miles are critically important within the modeled domain because they not only limit the distribution of spread (that is, infestation does not move beyond the buffer), but also slow the rate of transfer within and between buffered zones throughout the model domain. As the buffer is implemented into model runs, the percentage of infested lakes decreases. Shorter distance boater movements within the model reduced the infestation of waterbodies up to an additional 25% depending on the model output scenario. When boater movement is not restricted, most waterbodies in the model domain became infested over time.

Further exploration using minimum and maximum values of calcium and pH would give us a greater understanding of the sensitivity of our model with respect to habitat suitability. Other habitat factors, such dissolved oxygen and temperature are known to impact dreissenid mussel survival, and incorporation of additional parameters will be explored for future versions of the model. Similarly, management actions that impact habitat, such as seasonal draw-down should be included in the future.

1. Introduction

Aquatic invasive species are a worldwide problem that can have detrimental impacts on natural resources, human health, recreational opportunities, and other ecosystem services (Gurevitch & Padilla, 2004). These species can spread rapidly when human activities destroy the barriers that historically isolated the species to one geographic area (Vander Zanden & Olden, 2008). Predicting areas at the highest risk of invasion will help natural resource managers plan and budget for invasive species management efforts.

In North America, invasive dreissenid mussels (quagga mussels (*Dreissena rostriformis bugensis)* and zebra mussels (*Dreissena polymorpha*)) have cause hundreds of millions of dollars in damage to water resource and power facilities by fouling infrastructure and clogging pipes (Higgins & Vander Zanden, 2010). In addition to the economic impacts, dreissenid mussels can cause extensive ecological changes by altering the trophic dynamics of lentic systems. These mussels were introduced into the Great Lakes through the ballast water of transoceanic ships originating from Europe. Since their arrival to North America, these species have spread throughout the United States, likely as a result of overland dispersal by recreational boaters (Collas, Karatayev, Burlakova, & Leuven, 2018). Overland dispersal can be facilitated by veligers surviving in standing water on boats or when adults attach to hard surfaces and survive the transport to other water bodies (Johnson, Ricciardi, & Carlton, 2001). Adult mussels can survive out of water for up to 30 days depending on temperatures and humidity.

Predicting future dispersal patterns is difficult since regionally varying transportation patterns and water quality must be coupled with the complex, biphasic mussel life cycle. Ecological modeling is a tool that can be used to represent this complexity in a quantitative simulation framework that can forecast different invasion patterns to determine areas at the highest risk for future colonization. Constrained gravity models are a good approach and have been used for predicting dreissenid dispersal, but they are lacking in the ability to consider alternative variables that impact dispersal (Bossenbroek, Johnson, Peters, & Lodge, 2007). Constrained gravity models are based upon the attractiveness of a waterbody (size) and distance between two waterbodies. Without additional modification, these models do not include important parameters such as habitat suitability. Limiting dispersal to gravity model assumptions alone can lead to incorrect dispersal estimations. Using unrealistic dispersal estimations could potentially lead to implementation of misguided management actions (e.g., management actions on a waterbody that might not ever become infested (Rothlisberger & Lodge, 2010)).

The Integrated Ecological Modeling Team at the U.S Army Engineer Research and Development Center collaborated with the Bureau of Reclamation (Reclamation) Ecological Research Laboratory (Eco Lab) to develop an integrated dreissenid mussel dispersal model that coupled boater behavior and habitat quality models to forecast the likelihood of dreissenid mussel spread across 402 lakes in the Western United States. Results from this model can be used to determine not only which lakes could be most vulnerable to invasion, but also to inform management practices to assist in decreasing the invasion probability.

2. Methods

Communicating the development and application of ecological simulation models requires a deviation from the traditional methods and results format, since the model is both a method and a result. As such, the methods section is divided into two main sections: Section 2 describes the study system and how data inputs were collected from the field and Section 3 describes the model. Section 3 is organized following the format of Grant and Swannack (2008) and is composed of (a) model overview, which provides a brief, generalized summary of the model; and (b) model description, which describes quantitative formulation of the model processes. Section 4 discusses model constraints and model application, with descriptions of the scenarios we tested.

2.1 Study system

The predictive model incorporates data from 402 waterbodies in the Western United States (Figure 1). The waterbodies selected for this analysis are sites from which the Eco Lab has received plankton tow samples for dreissenid mussel early detection or population monitoring. The mussel monitoring samples are collected by a variety of collaborators from Reclamation regions and each agency prioritizes which waterbodies are sampled based on mussel habitat suitability and the presence of critical infrastructure, habitat, or recreation areas. Due to the large number of waterbodies in the Western United States, not every waterbody is sampled every year. Between 2011 and 2019, the Eco Lab received samples from an average of 194 waterbodies per year. Presence of dreissenid veligers is determined using cross polarized light microscopy and confirmed using polymerase chain reaction (PCR) and gene sequencing (Standard Operating Procedure: Field Sampling Methods for Invasive Mussel Early Detection, 2020) (Reclamation, 2020). The results of the Eco Lab's analyses were compiled and used to assign mussel presence to waterbodies within the model domain. Invasive mussels were considered established in 11 of the 402 waterbodies included in the model. For model simulations, only the 11 waterbodies with established dreissenid mussel populations served as the source populations.

Habitat suitability for dreissenid mussels was quantified using an index-based approach modified from Bartell et al. (2007). A number of water quality parameters have been correlated with dreissenid mussel habitat suitability including calcium, pH, dissolved oxygen, chlorophyll a, and dissolved nitrogen and phosphorus, among others (Mackie and Claudi 2010). Due to its role in shell formation, and veliger and adult development, calcium is considered to be critically important for dreissenid mussel survival (Claudi and Prescott 2011, Pucherelli et al 2016). Integrally linked to calcium uptake and retention, pH impacts the solubility of calcium carbonate in dreissenid mussel shells, and pH values outside of ideal ranges can severely weaken shells or inhibit development (Pucherelli et al. 2016 and references therein). We focused this initial habitat suitability model on pH and calcium as they are known to be key limiting parameters, critical for dreissenid mussel survival. A long-term goal will be to incorporate additional habitat suitability parameters into the model. Mean calcium and pH values were obtained from various data repositories throughout the Western United States. Habitat suitability equations were developed as a collaboration between the ERDC and Reclamation and is described in section 3.3.

Figure 1. Map of the 402 waterbodies included in the simulation model.

3. Model description

3.1 Model Overview

The model simulates boater movement between lakes, the likelihood of each boat carrying dreissenid mussels, and the likelihood of those mussels surviving transport and surviving within the new lake itself. The model is formulated as a spatially explicit, grid-based model with a 1-year time step. It is composed of two submodels that represent different components of successful overland transport and survival leading to dreissenid mussel colonization: (1) A constrained gravity model that simulates boater movement among 402 lakes in the Western United States and (2) a habitat suitability model that quantifies the relationship between water quality (specifically, pH and calcium) and dreissenid mussel viability. Model equations were modified from those in Robertson et al. 2020. The model is programmed in Netlogo v6.1.1, an open source, spatially explicit multi-agent programmable platform (Wilensky & Rand, 2015).

3.1.1 Data input

A georeferenced shapefile of the study area was created that included all 402 water bodies with the following information assigned to each: waterbody name, dreissenid mussel presence, mean pH, mean Ca, the number of boaters associated with each waterbody (as defined in Section 3.2.3), surface area (m^2) and XY coordinates of centroid. The GIS extension of Netlogo was used to import the shapefile.

3.2 Model Equations

The dreissenid mussel model incorporates a combination of constrained gravity model equations, habitat suitability equations, and a user defined variable for mussel transport survival to generate dispersal across the waterbodies. The following sections will further describe the constrained gravity equation, habitat suitability equations, and transport survival of veligers.

3.2.1 Constrained gravity equation

This model modifies the constrained gravity model approach used by Bossenbroek et al. (2007). The model simulates the number of boaters moving from lake i to j and is calculated as:

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

where T_{ij} represents the number of boaters that travel from watershed i to watershed j, O_i represents the number of boats traveling from watershed i, W_j represents the attractiveness of watershed j, c_{ij} represents the distance from watershed i to watershed j, *a* represents the distance coefficient, and A_i represents a balancing factor that ensures all boats leaving watershed i arrive at some watershed j.

3.2.2 Lake attractiveness (W)

This model is similar to previous gravity models in that it uses the surface area of the waterbody to determine how attractive the waterbody is to a boater (Bossenbroek et al 2007) (Rothlisberger & Lodge, 2010) (Reed-Anderson et al 2000). Larger waterbodies are generally deemed more attractive than smaller waterbodies because of their overall size and the tendency to have more recreational opportunities (Reed-Anderson et al 2000).

3.2.3 Boater numbers (O)

The number of boaters associated with each lake was estimated as follows:

$O_i = pN$	Equation 2
p = number of registered boat owners in US / population in US	Equation 3

where *p* is a constant (0.0362) that represents the per capita rate of boat ownership for the United States calculated per equation 3 and *N* is the population of adults over the age of 18 in each county within the model domain. Data for the number of boats registered in the U.S. in 2019 was retrieved from Statista (https://www.statista.com/statistics/240634/registered-recreational-boating-vessels-in-the-us/). Population data for the US were generated from ESRI-generated shapefiles of US Census data (ArcGIS 2020) (USA Counties, 2020) and the population of the U.S. in 2019 was found using Census data (United States Census Bureau, 2019).

3.2.4 Distance between lakes (C)

The pairwise distance between every lake was calculated as the Euclidean distance between the centroids of waterbodies (Equation 4).

$C_{ij} = \sqrt{(X_j - X_i)^2 + (Y_j - Y_i)^2}$, given C_{Buffer}	Equation 4
C_{Buffer} = 35, 50, 100, unlimited miles	Equation 5

Spatial Buffer

Previous studies indicate a majority of boaters (~ 90%) travel less than 50 km (35 miles) from their home to a lake (Schneider et al. 1998). To capture this phenomenon, we created a user-defined buffer zone around each lake that constrained boater movement. For scenarios where the buffer was implemented, boaters could not leave their respective zone. In the Western United States, it is common to travel more than 35 miles to reach a lake, so we explored buffer zone values of 35, 50, and 100 miles (Equation 5). For reference, Figure 2 depicts a 35-mile buffer around each waterbody. If a given waterbody did not have any other waterbodies within its buffer, it was removed from the analysis. Note that distances in Netlogo are relative to the GIS source and the number of cells in the Netlogo domain. For our model, a distance of 0.01 units translated to approximately 1 mile in the real world. This does not impact model formulation or results, rather it is a simple algebraic conversion required to maintain the same geo-referenced relationships.

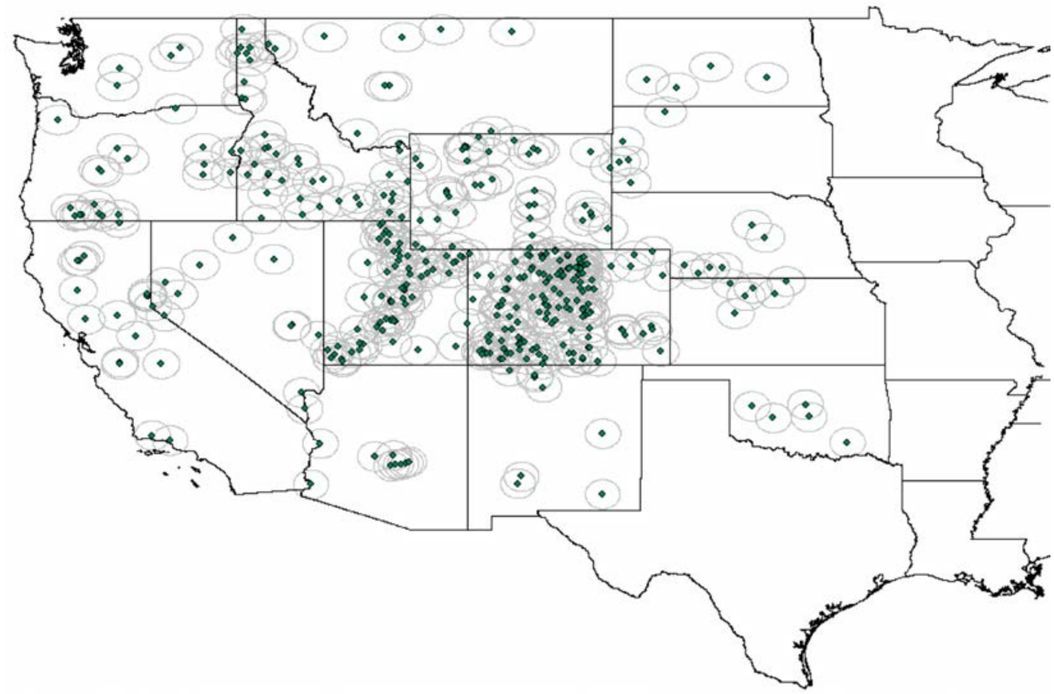


Figure 2: Buffer zones associated with each waterbody. Buffer zones are depicted at 35 miles around the centroid of each waterbody.

3.2.5 alpha (α)

The distance-decay coefficient, α, represents the relationship between interaction patterns and distance when all other interaction variables are held constant (Fotheringham 1981). In terms of a constrained gravity model, a smaller alpha value is perceived to be a strong deterrent to interaction, while a larger alpha value is perceived to be a weak deterrent to interaction. After running least squares analysis, Robertson et al. (2020) determined that an alpha value of 2.2 was the best-fit parameter, which is what is applied in this model as well.

3.2.6 Balancing Factor (A)

A_i is calculated based on the relationship:

$$A_i = 1/\sum_{j=1}^{N} W_j c_{ij}^{-\alpha} \qquad \text{Equation 6}$$

Where N is the total number of destinations and j is each destination within the model domain. This balancing factor is included to ensure that all boats reached a destination of another waterbody in the study area within an annual time step. This does not account for travel time between sites (e.g., if a boat leaves a waterbody then relaunches after x amount of time.

3.3 Habitat Suitability

Previous studies have indicated that pH and calcium are the critical parameters for dreissenid survival (Hincks and Mackie, 1997). Following this, we developed a habitat suitability model composed of 10 equations approximating the relationship between pH and veliger survival (Figure 3, Table 1) and five equations approximating the relationship between survival and calcium (Figure 4, Table 2). Each suite of equations formulated a step function with linear approximations between each step. For this model, we focus on habitat suitability of veligers only because we assumed that if a waterbody was not suitable for veligers, then introduced veligers would not survive to maturity and a population would not establish.

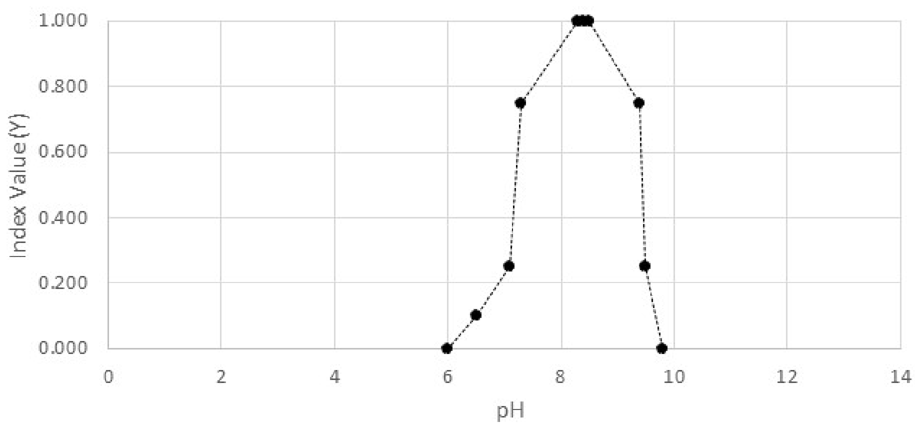


Figure 3: Linear step function describing the relationship between pH and dreissenid veliger survival.

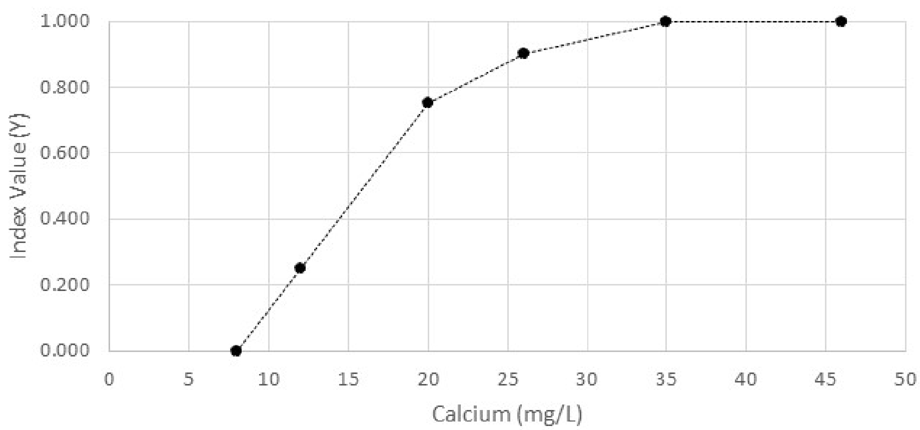


Figure 4: Linear step function describing the relationship between calcium and dreissenid veliger survival.

Table 1 : Habitat Suitability step function equations for veliger pH thresholds

pH	Equation	Equation Number
pH ≤6	HSI_{pH}=-1.2+(0.2*pH)	7
6< pH ≤6.5	HSI_{pH} =-1.53+(0.25*pH)	8
6.5< pH ≤7.1	HSI_{pH} =-17.5+(2.5*pH)	9
7.1< pH ≤7.3	HSI_{pH} =-1.08+(0.25*pH)	10
7.3< pH ≤8.3	HSI_{pH} =1	11
8.3< pH ≤8.4	HSI_{pH} =1	12
8.4< pH ≤8.5	HSI_{pH} =3.36+(-0.2778*pH)	13
8.5< pH ≤9.4	HSI_{pH} =47.75+(-5*pH)	14
9.4< pH ≤9.5	HSI_{pH} =8.17+(-0.8333*pH)	15
9.5< pH ≤9.8	HSI_{pH} =0	16

Table 2: Habitat suitability step function equations for veliger calcium thresholds

Calcium	Equation	Equation Number
Ca ≤8	HSI_{Ca} =-0.17+(0.0208*Calcium)	17
8< Ca ≤12	HSI_{Ca} =-1.42+(0.0833*Calcium)	18
12< Ca ≤20	HSI_{Ca} =0.32+(0.0167*Calcium)	19
20< Ca ≤26	HSI_{Ca} =0.58+(0.0091*Calcium)	20
26 ≤ Ca	HSI_{Ca} =1	21

Habitat suitability index models result in a numerical value that is based on the average value of all individual habitat variables (United States Environmental Protection Agency, 2016). These individual habitat variables can include any aspect of the organism's life requisites, such as the organism's structure, composition, and habitat spatial components (Roloff & Kernohan, 1999). The habitat suitability index calculation is expressed as a geometric mean as follows:

$$HSI = \prod_{i=\mathrm{I}}^{n} x_i^{I/N} \quad \text{Equation 7}$$

where n represents the total number of variables, x_i represents the individual habitat suitability score for variable i, and I/N represents the average habitat score divided by the optimum score. If a habitat suitability score was assigned a value of 0, it was recoded to have a value of 0.000001 to prevent division by zero. Following Robertson et al. (2020), if a waterbody had an overall HSI score ≥ 0.8, it was deemed suitable for colonization; HSI scores ≤ 0.4 were deemed unsuitable and scores between those values were treated probabilistically based on a logistic function.

4. Scenarios and model constraints

Scenarios were developed using a null model. In this case, the null model represents the base gravity model (Equation 1) and subsequent scenarios were compared to the results from the null model. We developed three overarching scenarios, each of which represents a physical, spatial, or ecological process that constrains the spread of dreissenid mussels. Twenty-four different sub-scenarios were developed to explore the parameter space of the constraints (Table 3). All 24 sub-scenarios are run for six-time steps and the resulting number of infested lakes is recorded. The percent change of total number of lakes infested between null model runs and each scenario is compared.

4.1 Null

The baseline scenario (the null model) is represented as the baseline gravity model (Equation 1). Each parameter within Equation 1 is initialized at its maximum value (e.g., each waterbody is optimized for maximum values of W, given its size and distance to other lakes). Null models were run for each of four buffer zones to provide better relative comparisons among sub-scenarios that used buffers (Table 3, sub-scenarios 1, 9, 17, 21). This model is initialized with 11 lakes known to contain dreissenid mussels (see appendix for the null model visualization).

4.2 Transport survival of veligers

This scenario represents survival of veligers during transport from lake *i* to *j*. Current data indicate that veligers can survive out of water for up to 30 days, depending on factors such as temperature and humidity, among others. This parameter reduces the survival percentage of veligers being transported by a user-defined percentage. To explore the constraints of this parameter, we ran three sub-scenarios setting the parameter at 25%, 50%, and 75% of its maximum (Table 3, sub-scenarios 2-4). Transport survival is considered a major factor in successful colonization and was treated as a separate parameter to facilitate future development.

4.3 Habitat Suitability

The habitat suitability submodel (Section 3.3) is treated as a separate scenario in order to isolate the effects of water quality on colonization success. When the habitat suitability submodel is run, equations 7 through 22 are applied to each waterbody to calculate habitat suitability.

4.4 Spatial buffer

The buffer zone constraint is described in Section 3.2.4. For our scenario analysis, we ran four different buffer zones: (1) no buffer, (2) 35 miles, (3) 50 miles, and (4) 100 miles. If waterbodies did not have other waterbodies within their buffer, they were removed from the analysis (Table 3 provides initial conditions for each buffered scenario). For example, for the 35-mile buffer scenario (sub-scenarios 9 through 16), there were 4 infested lakes that did not have another lake within the buffer zone so they were removed from the analysis (i.e., the model was initialized with 7 infested lakes (Table 3)).

Table 3: Model scenario summary including parameter values and resulting lake infestation numbers after six-time steps. Null scenarios (sub-scenario numbers 1, 9, 17,21) are highlighted in gray. Sub-scenarios 1-8 did not include a buffer to limit boat movement.

Scenario Parameters						
Sub-scenario Number	**Total number of lakes**	**Number of initially infested lakes**	**Survival**	**Habitat Suitability**	**Buffer (mi)**	**Total Lakes Infested after 6 Timesteps**
1	402	11	1			275
2	402	11	0.75			243
3	402	11	0.5			203
4	402	11	0.25			147
5	402	11		x		178
6	402	11	0.75	x		155
7	402	11	0.5	x		132
8	402	11	0.25	x		88
9	368	7	1		35	10
10	368	7	0.75		35	10
11	368	7	0.5		35	10
12	368	7	0.25		35	10
13	368	7		x	35	10
14	368	7	0.75	x	35	10
15	368	7	0.5	x	35	10
16	368	7	0.25	x	35	10
17	384	9	1		50	20
18	384	9	0.75	x	50	15
19	384	9	0.5	x	50	15
20	384	9	0.25	x	50	15
21	402	11	1		100	60
22	402	11	0.75	x	100	41
23	402	11	0.5	x	100	41
24	402	11	0.25	x	100	24

5. Results and Discussion

The null model resulted in 275 out of 402 (68%) waterbodies becoming infested over the course of the simulated time period (Table 3). As more constraints were added to the formulation, the overall proportion of infested lakes decreased, but spread occurred in all of the sub-scenarios without buffer zones. The set of 24 sub-scenarios resulted in 10% to 60% reductions in total lakes infested, depending on the constraints invoked. Model output of maps representing the spread for representative sub-scenarios is presented in the Appendix.

When compared to the null, decreasing veliger transport survival by 25%, 50%, and 75% resulted in 11.64%, 26.18%, and 46.55% reductions in the total number of lakes infested, respectively (Figure 5).

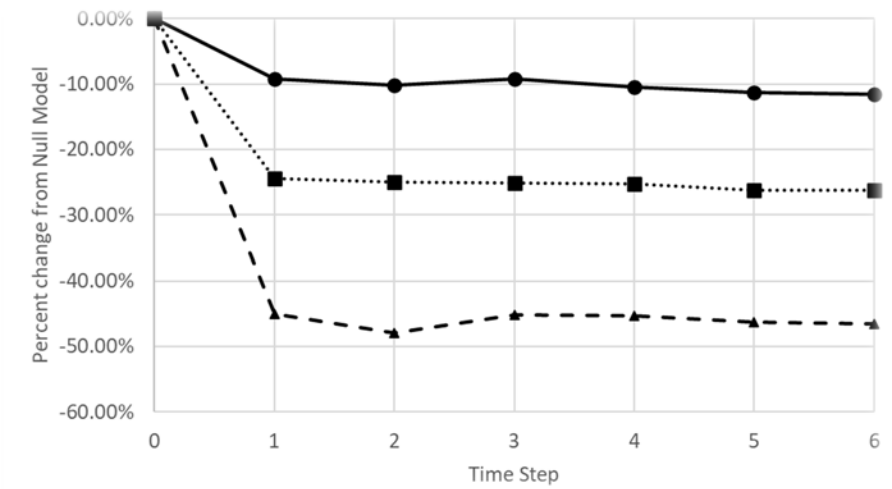


Figure 5: Percent change in total infested lakes from null model (model 1, Table 3) for scenarios with 75% veliger transport survival (solid line with closed circles), 50% (dotted line with closed squares) and 25% (dashed line with closed triangles).

Habitat suitability scores ranged from completely unsuitable (scores approximating zero) to optimally suitable (scores of 1) across all waterbodies. Dreissenid mussel survival probability was high (≥ 0.80 HSI) in 250 lakes and low (≤ 0.40 HSI) in 99 lakes (Figure 6). When the habitat quality submodel was implemented, it reduced the overall number of lakes infested by 35.61% compared to the null (Figure 7). Coupling habitat suitability with veliger transport survival percentages of 25%, 50%, and 75% resulted in a 46.91%, 53.82%, and 66.18% reduction in infested lakes compared the null (Figure 8).

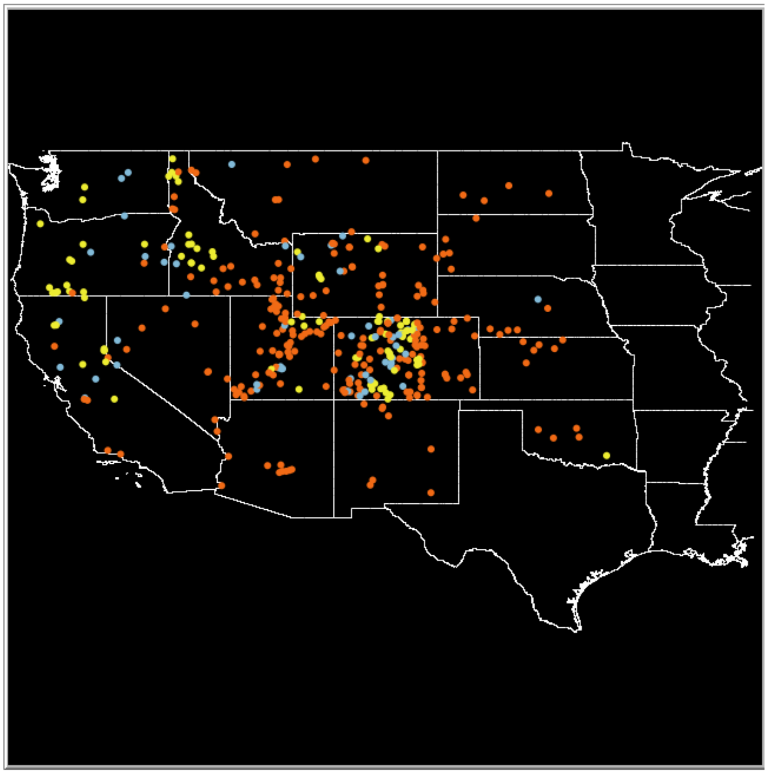


Figure 6: Representation of the habitat suitability for 402 lakes in the model domain. Low HSI scores (HSI <= 0.4) are shown in yellow. High HSI scores (HSI >= 0.8) are shown in orange. Intermediate scores are blue.

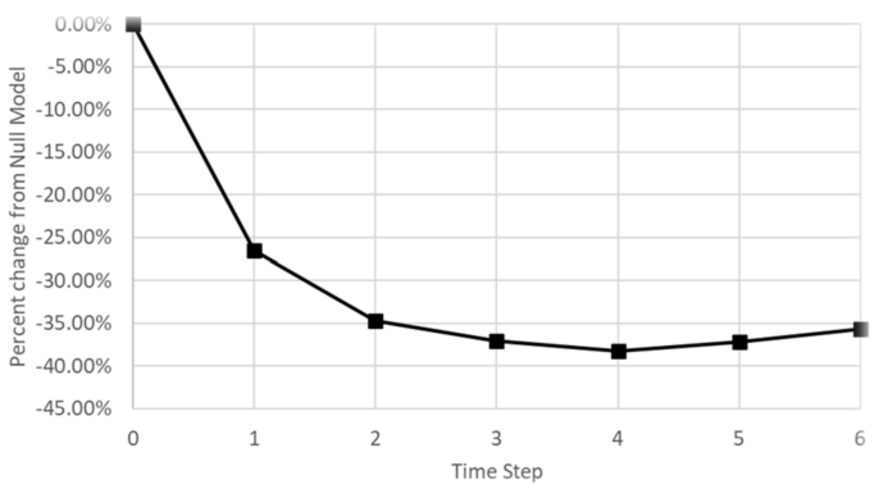


Figure 7: Percent change in total infested lakes from null model (sub-scenario 1, Table 3) for the sub-scenario that included the habitat suitability submodel (sub-scenario 5, Table 3).

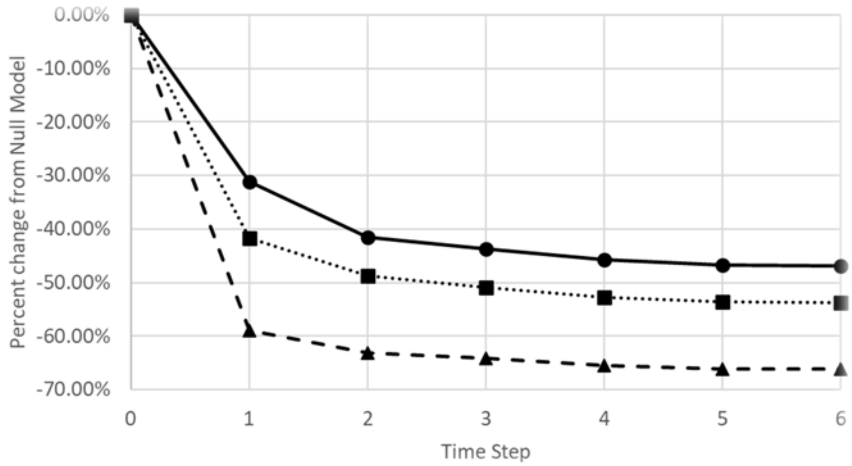


Figure 8: Percent change in total infested lakes from null model (sub-scenario 1, Table 3) for sub-scenarios that included the habitat suitability submodel coupled with 75% veliger transport survival (solid line with closed circles), 50% (dotted line with closed triangles) and 25% (dashed line with closed triangles)

The implementation of buffer zones resulted in the smallest number of lakes being infested. A comparison of null models (sub-scenarios 1, 9, 17, and 21, representing the null without a buffer and the 35, 50, and 100-mile buffers, respectively) is presented in Figure 9. Unsurprisingly, when boater movement was limited to 35 miles, there was a large (~90%) reduction in infested lakes compared to the non-buffered null. But the mussels still spread to the three additional lakes located within buffers of infested lakes. Similarly, the 50-mile buffer showed increases from nine initial lakes to 20. The 100-mile buffer incorporated the entire model domain (that is, every lake was within 100 miles of at least 1 other lake). There was a 78% decrease in infested lakes from the null sub-scenarios under the 100-mile buffer.

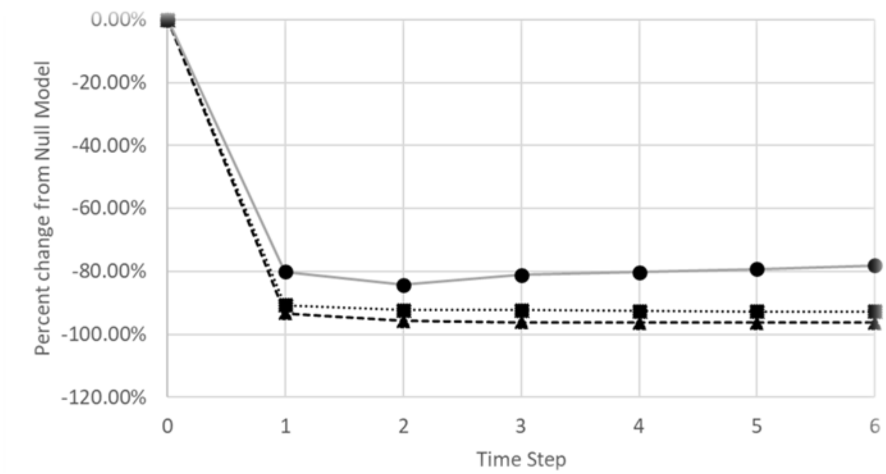


Figure 9: Percent change in total infested lakes from null model (sub-scenario 1, Table 3) and sub-scenarios with buffer zones of 35 miles (dashed line with closed triangles), 50 miles (dotted line with closed squares), and 100 miles (solid line with closed circles).

Results from sub-scenarios modifying habitat quality and veliger transport survival for both the 35- and 50-mile buffers did not differ much from their null scenario. Sub-scenarios run with for the 35-mile buffer with additional constraints were not different from its respective null (Table 3). Similarly, the 50- mile buffer only resulted in a maximum of 11 additional waterbodies being infested, regardless of the combination of constraints applied. Conversely, additional constraints coupled with the 100-mile buffer did result in fewer infested lakes, with the strongest constraints resulting in a 60% decrease in infested lakes (Figure 10).

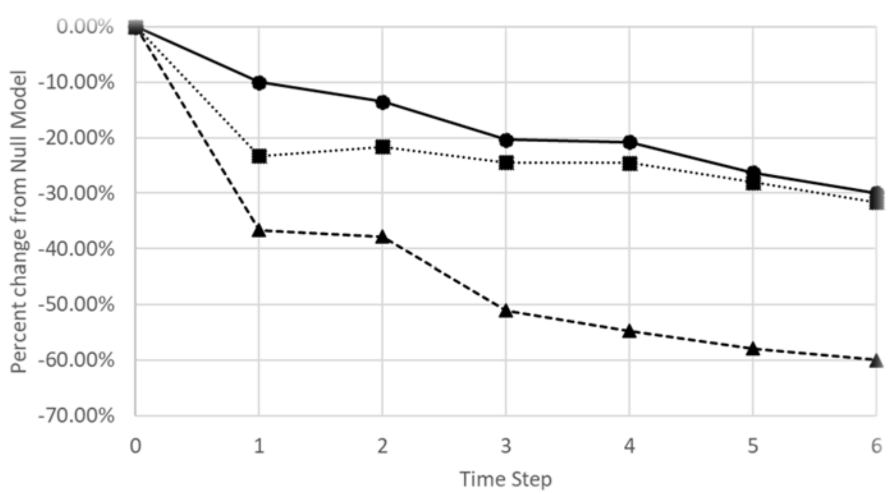


Figure 10: Percent change from 100-mile buffer null scenario for sub-scenarios that combined habitat suitability with 75% veliger transport survival (solid line with closed

circles), 50% (dotted line with closed triangles) and 25% (dashed line with closed triangles).

6. Discussion and Conclusions

This model indicates that implementing a buffer zone greatly decreases the probability of waterbodies becoming infested. This model can be used to determine which waterbodies are at highest risk for dreissenid mussel invasion (e.g., see Table 3 and the figures presented in the Appendix), given the assumptions within the model. Agencies can determine what steps need to be taken to either ensure that a particular waterbody does not become infested, or to increase the rate of testing at these at-risk waterbodies.

The scenarios modeled in this study explore how the survival rate of mussels being transported, the habitat suitability of destination waterbodies, and the distance boaters can travel affect the spread of invasive mussels. Understanding the importance of each of these parameters and how they affect the spread of mussels to other waterbodies can inform more effective, targeted management. As expected, the null model results, which were based on the size of and distances between waterbodies, resulted in the highest percentages of waterbodies that become infested. This is expected given that the null model has no constraints on boater movement or dreissenid survival. The transport survival rate played a critical role in mussel spread. Each transport survival sub-scenario contributed to further spread of the invasive mussels. However, the magnitude of the transport survival reductions did not contribute to a corresponding reduction in the proportion of infested waterbodies over time. Decreasing veliger survival by 25% to 75% still led to infestations of 36% to 60% of all waterbodies within a consistent and short time frame. Although the resulting infestation rates are not impacted by veliger transport survival alone, the combined effect of lower survival and limited boat movement do provide a noticeable decrease in infestation rate (e.g., scenarios with a buffer and transport survival). Limiting recreational boat movement had the effect of decreasing the potential connectivity between the network of waterbodies and this effect is amplified as the spatial area of interest increases.

Habitat suitability, in general, is an important aspect of determining or modeling whether an invasive species will infest a new area. Our results show that the habitat suitability index is an important driver in determining the infestation rate. In our model, isolating the impact of habitat suitability on infestation to other waterbodies revealed that activating the HSI component led to a maximum of 65% of the waterbodies becoming infested, indicating that several waterbodies were not suitable habitat for dreissenid mussels. Combining the HSI component with veliger transport survival resulted in an additional slight decrease in infestation over time. Combining the HSI component with both survival and limited boater movement reduced the maximum infestation to ~50% of the waterbodies. The interaction of habitat suitability and veliger transport survival resulted in a larger reduction than habitat suitability alone. Unlike the other scenarios, which were developed using expert opinion and general ecological theory, the constraint that invoked the habitat suitability submodel included empirically derived equations (i.e., equations 7 through 21) that represented dreissenid mussel response to water quality. These results are promising because they point to a data-driven indicator of a physical constraint controlling mussel distributions.

Our model indicates that movement patterns of recreational vessels have the greatest impact on dreissenid mussel infestation rates, when compared to other model parameters. Patterns of movement in which recreational boaters do not travel more than 100 miles are critically important within the modeled domain because they not only limit the distribution of spread (that is, infestation does not move beyond the buffer), but also slow the rate of transfer within and between buffered zones throughout the model domain. As the buffer is implemented into model runs, the percentage of infested lakes decreases. Shorter distance boater movements within the model reduced the infestation of waterbodies up to an additional 25% depending on the model output scenario. When boater movement is not restricted, most waterbodies in the model domain became infested over time.

Established populations of dreissenid populations are difficult to eradicate. Our model results indicate that reducing inter-waterbody travel of boats coupled with unsuitable habitat could potentially reduce future spread. While our model did not test management scenarios that directly reduced boater infestation, such as cleaning boats or detection/decontamination stations, our buffered scenarios can serve as a proxy for these efforts. Ultimately, what these scenarios can be used to infer is that future spread can be limited if fewer boats carrying live mussels enter a waterbody. In this model, management actions that focus on reducing the travel distance of recreational boaters from one waterbody to the next will have a greater impact on reducing the extent of infestation within a region. However, limiting movement is an unrealistic strategy within the Continental United States. Therefore, other incentives/management actions should be used that end with the same result, such as targeting these boats when conducting WID programs and targeting public outreach to boaters who travel long distances.

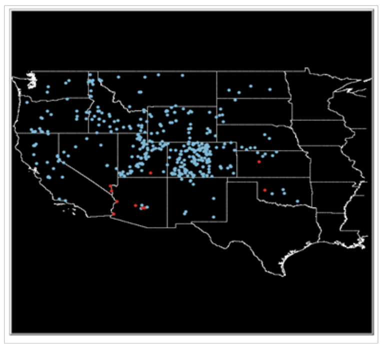
7. Recommended Next Steps

While the model provides an indication of dreissenid mussel infestation patterns over time, like all models, it also has some limitations. The model includes an extensive number of lakes, but it is also limited in that it does not include every waterbody within the Western U.S., or every waterbody within the purview of the Bureau of Reclamation. As such, the array of waterbodies included are representative of the region but are not exhaustive. Future versions of the model should incorporate a more comprehensive sample of waterbodies. and represent an extensive, but closed system. Some waterbodies were excluded from the model due to limited availability of calcium and pH data. For waterbodies that were included in the model, mean reported calcium and pH values were used to inform habitat suitability. While mean values are useful, they also have the potential to limit our habitat suitability submodel because extremes in seasonal or yearly calcium and pH variation are not well captured. Further exploration using minimum and maximum values of calcium and pH would give us a greater understanding of the sensitivity of our model with respect to habitat suitability. Other habitat factors, such dissolved oxygen and temperature are known to impact dreissenid mussel survival, and incorporation of additional parameters will be explored for future versions of the model. Similarly, management actions that impact habitat, such as seasonal draw-down should be included in the future. To estimate the number of boats, present in (and subsequent movement from) a given waterbody, we calculated a per capita estimate of number of boats based on national U.S. Census population data and national boat registration data. However, we acknowledge that boat registration is unlikely to be evenly distributed across the country. Refining this estimate by using state specific boater registration data would provide better accuracy with respect to numbers of boats expected in each lake. Some of these limitations may be addressed in future, updated model iterations.

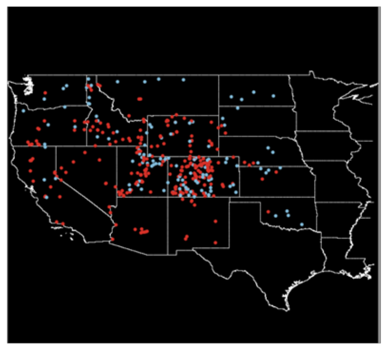
Appendix A: Mapped Output

Map of lake centroids upon model initialization and following six-time steps under various model sub scenarios. Blue points represent centroids of uninfested waterbodies, red points represent centroids of infested waterbodies. See Table 3 in text for details of each sub-scenario. * indicates a null scenario. Numbers in parentheses represent "total number of lakes"/"initial infested lakes"/"final number of infested lakes"

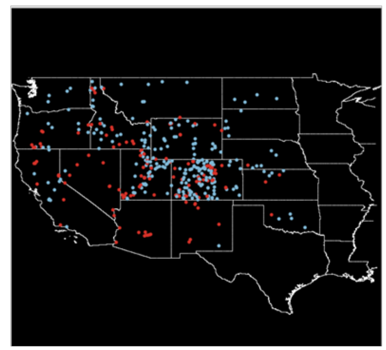
Initial Conditions* (402/11)



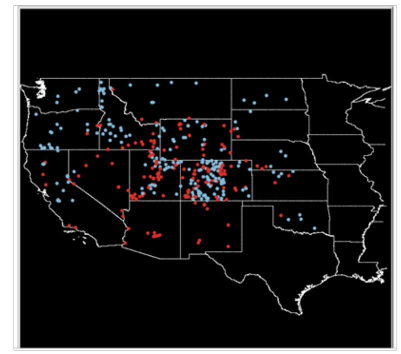
Sub-scenario 1 (402/11/275)



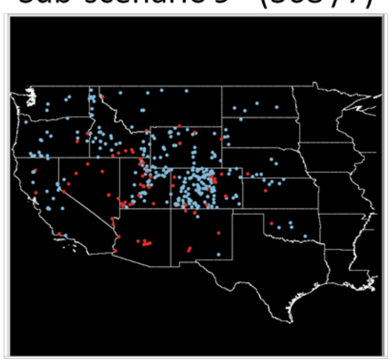
Sub-scenario 4 (402/11/147)



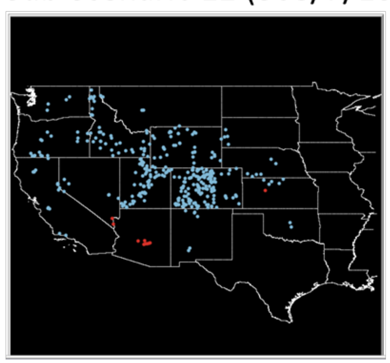
Sub-scenario 5 (402/11/178)



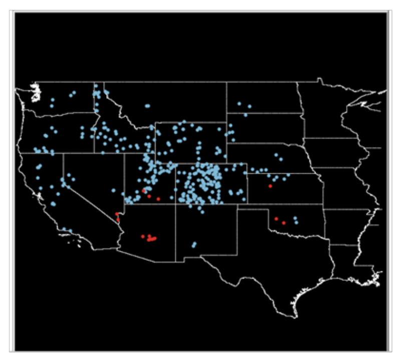
Sub-scenario 9* (368 /7)



Sub-scenario 12 (368/7/10)



Sub-scenario 20 (384/9/15)



Sub-scenario 22 (402/11/41)