Estimating densities of zebra mussels (*Dreissena polymorpha*) in early invasions using distance sampling

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27 May, 2019

Abstract

Estimating the density and distribution of invasive populations is critical for management and control efforts, but can be a challenge in nascent infestations when densities of populations are low. Statistically valid sampling designs that account for imperfect detection of individuals are needed to estimate densities across time and space reliably. Survey methods that yield reliable estimates allow managers to determine how invader biomass impacts ecosystem services and evaluate population trends and effectiveness of control measures. We investigated the use of distance sampling by SCUBA divers to determine densities of invasive zebra mussels (*Dreissena polymorpha*) in two recently invaded lakes in central Minnesota. This framework allows divers to cover the large areas necessary in low-density, recent infestations. We estimated that a diver could detect between 5% and 41% of the mussels present in the surveyed area, depending on the specific diver and on whether the lake bottom was vegetated. We also found that a key assumption of conventional distance sampling (e.g., perfect detection on the transect line) was not met. Therefore, accurate density estimates required a double-observer approach. These results highlight the importance of accounting for detectability when comparing estimates over time or across lakes, particularly when different observers conduct surveys. Further evaluation is needed to determine if changes in field sampling techniques can meet the assumptions behind conventional distance sampling for freshwater mussels. Furthermore, we suggest that the efficiency of distance sampling should be compared to alternatives such as quadrat sampling across a range of mussel densities.

Introduction

Native to a small region of southern Russia and the Ukraine (Stepian et al. 2013), zebra mussels (*Dreissena polymorpha* Pallas 1771) have spread throughout Europe (A. Y. Karatayev, Burlakova, and Padilla 1997; A. Y. Karatayev, Padilla, and Johnson 2003) and North America (Benson 2013) to become one of the world's most widespread and damaging aquatic invasive species (A. Y. Karatayev et al. 2007). The economic costs of these invaders in the United States is estimated to be in the hundreds of millions of US dollars per year with impacts including the fouling of water treatment and power plant intake pipes, hydropower facilities, as well as impacts to recreation, tourism, and lakefront property (O'Neill, Jr. 2008; Bossenbroek et al. 2009; Limburg et al. 2010). Ecological impacts arise from the ability of zebra mussels to reach high population densities, smothering and outcompeting native species. High densities of these suspension feeders lead to the removal of high volumes of planktonic organisms from lakes and rivers, resulting in population declines and local extinctions of native mussels and other invertebrates (A. Y. Karatayev, Burlakova, and Padilla 1997; Ward and Ricciardi 2013), damage to fish populations (D. L. Strayer, Hattala, and Kahnle 2004; McNickle, Rennie, and Sprules 2006; Lucy et al. 2013; David L. Strayer and Malcom 2018), and the restructuring of aquatic food webs (Higgins and Vander Zanden 2010; C. Mayer et al. 2013; Bootsma and Liao 2013).

Ecological impacts scale with zebra mussel density and biomass, but quantitative data on zebra mussel populations are only available for a few water bodies (Higgins and Vander Zanden 2010). Control efforts using chemical treatments and physical removal (e.g., Wimbush et al. 2009; Lund et al. 2018), have to date focused on newly invaded water bodies with low-density, localized infestations. In these water bodies, mussels are more challenging to locate, and even intensive underwater surveys can fail to detect mussels that remain after treatment (Lund et al. 2018). To determine how well treatments reduce densities and how environmental conditions influence treatment efficacy, efficient and reproducible survey designs are needed to facilitate comparisons across space and time—as is the case for surveys of native clams and other freshwater mollusks (Dorazio 1999).

In the North American Great Lakes, ship-based surveys using Ponar grabs and sled dredges have typically been used to survey zebra mussel populations (Marsden 1992; Nalepa, Fanslow, and Pothoven 2010; David L. Strayer and Malcom 2018). Surveys of inland lakes occur over a much smaller areas and are often conducted with a self-contained underwater breathing apparatus (hereafter, SCUBA) (e.g., Kumar, Varkey, and Pitcher 2016), which may offer more reliable assessments of distribution and density. SCUBA-based methods often apply quadrat surveys (D. L. Strayer and Smith 2003).

However, quadrats may be suboptimal when attempting to survey large portions of a water body due to the effort required to move between distant sites (e.g., Giudice et al. 2010; Ferguson et al. 2014). Line transects, which sample along a continuous path, are an attractive alternative to quadrat surveys because they minimize the time spent moving between sampling locations.

To estimate changes in relative densities of populations separated in time or space, we often need to account for changes in the detectability of individuals (Mackenzie and Kendall 2002). Techniques such as capture-recapture methods (Huggins 1991), removal estimators (Nichols et al. 2000), or distance sampling (Buckland et al. 2001) are commonly used to account for variation in detectability that occurs due to changing environmental conditions or due to different observers. A common issue with line transects is that the probability of detecting individuals can decline with distance from the transect line. This effect can be modeled with distance sampling, where the surveyor measures the perpendicular distance of each detected individual (or cluster of individuals) from the transect line. This additional information is then used to model how detection changes as a function of distance, and thus, to correct for imperfect detection (Buckland et al. 2015). An important assumption of conventional distance sampling is that all individuals on or near the line are detected. Double-observer designs relax this assumption by estimating the probability that both observers detect a mussel through sight-resight methods (Borchers et al. 2006).

Here, we apply single- and double-observer distance sampling to estimate population densities of zebra mussels in two recently invaded lakes in central Minnesota. We tested whether the underlying assumptions of conventional distance sampling were met and illustrate how to analyze the data using existing tools. Furthermore, we show how to extend standard approaches to account for unimodal detection functions and covariates that affect both mussel detection and density.

Methods

Study area

We surveyed for zebra mussels in Lake Sylvia in Stearns County, MN and Lake Burgan in Douglas County, MN (Figure 1). Lake Sylvia covers an area of 34 hectares and has a maximum depth of 15 meters (m) while Lake Burgan covers an area of 74 hectares and has a maximum depth of 13 m. Zebra mussels were first verified in Lake Sylvia in 2015 (personal communication Christine Jurek, Caleb Silgjord Minnesota Department of Natural Resources) and Lake Burgan in 2017 (personal communication Lucas Raitz, Michael Bolinksi Minnesota Department of Natural Resources).

Survey design

Lake Sylvia

We allocated survey effort using a stratified systematic sampling design (Pooler and Smith 2005). First, we surveyed eight transects in the area in which zebra mussels were initially discovered and reported to the Minnesota Department of Natural Resources. We concentrated effort this way because areas where mussels are first discovered—assumed "infestation zones"—are typically the sites targeted for SCUBA surveys. Transects in the infestation zone were each 30 m long and spaced 3 m apart, though transects were stopped short of 30 m if divers ran into the thermocline, where visibility was found to drop precipitously. We then surveyed two peripheral clusters of 3 transects each, located 150 m to either side of the infestation zone. The transects in these clusters were 3 m apart. Finally, we conducted ten outlying transects dispersed evenly along the remaining shoreline (Figure 1A). Survey points were determined using a bathymetry shapefile in ArcMap provided by the Minnesota Department of Natural Resources. The start of a transect was placed in a depth of 3 to 8 m and oriented perpendicular to the shoreline to cover a range of depths. We located the start point of the transect using a GPS unit (Garmin GPSMAP 64s).

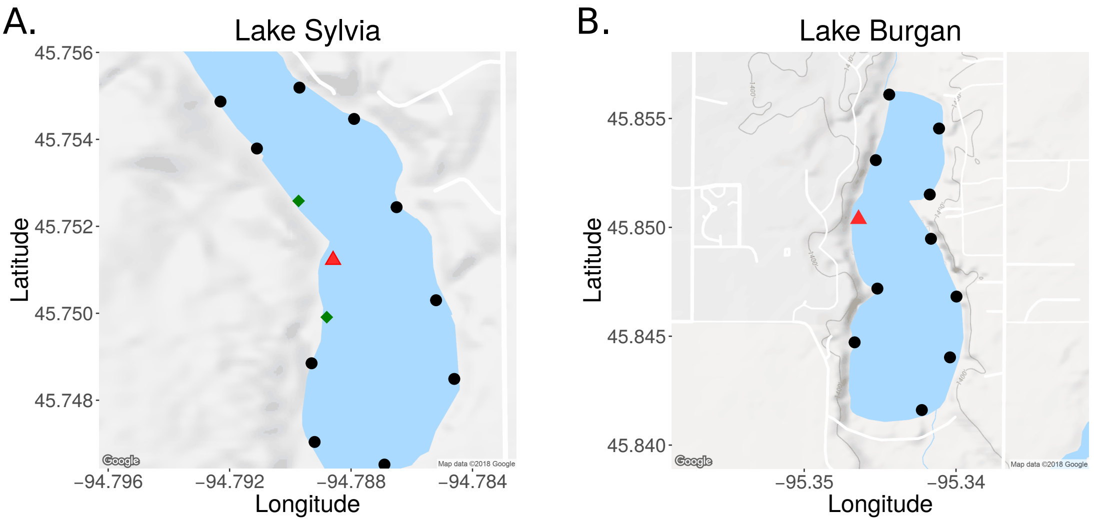


Figure 1: Transects for zebra mussel surveys conducted in Lake Sylvia (panel A) and Lake Burgan (panel B) in the summer of 2017. Transects in normal-effort strata are given as black dots. Red triangles indicate transects in the high-effort strata, where we conducted 8 transects, green diamonds represent the peripheral clusters, where we conducted 3 transects at each location.

Lake Burgan

In Lake Burgan, we did not know the initial location of the zebra mussel report so we used a modification of the above survey design. We initially surveyed eleven transects evenly spaced along the perimeter of the lake, with the first transect chosen near the boat launch (Figure 1B). After sampling these initial eleven transects, we sampled an additional seven transects, spaced 3 m apart, in the area with the highest observed density. We treated the eight transects taken in this region as a high-effort stratum. The remaining ten transects were allocated into a second, normal-effort stratum.

Data Collection

Lake Sylvia

We surveyed Lake Sylvia using a single dive team consisting of two people. The first (primary) diver was responsible for detecting zebra mussels. Whenever the primary diver detected a zebra mussel (or cluster of mussels), she recorded the number of mussels in the cluster and the distance from the transect start to the point where we made the detection (hereafter transect distance), approximated to the nearest 0.25 m. The diver also measured the perpendicular distance from the location of the detection to the transect line (hereafter detection distance) using a meter tape measured to the nearest quarter centimeter. The primary diver also classified and recorded the substrate that the zebra mussel was found on (hereafter "fine-scale substrate") using one or more of the following categories: mud, sand, gravel, pebble, rock, vegetation, wood, native mussel, metal, or other substrate. These substrate determinations were made qualitatively by the dive team.

To determine how detection and density varied due to environmental conditions, the second diver collected habitat and environmental data along each transect. The second diver classified the dominant substrate types in the current segment. Substrate classifications included mud, silt, sand, gravel, pebble, rock, and other. The diver recorded multiple substrate types when there was no clear dominant substrate type or when habitats were interspersed. In addition, the diver recorded the presence or absence of plant cover. Whenever there was a change in the substrate type or plant presence, she recorded the new substrate, plant presence, depth, and the transect distance where the change occurred. The segments formed by these changes were later used to model spatial variability in zebra mussel densities.

Lake Burgan

In Lake Burgan we collected data using the same methods as described for Lake Sylvia, except that each transect was surveyed independently by two dive teams, each team consisting of two members. We alternated which team went first on each transect, with the second dive team beginning their survey after the first team finished so that each team collected data independently.

Study data were entered into a REDCap (Research Electronic Data Capture) database hosted at the University of Minnesota (Harris et al. 2009). REDCap is a secure, web-based application designed to support reliable data capture for research studies by providing quality control of data entry, and auditing trails for data manipulation and export.

Statistical analyses

Although we present data on our survey design and data collection for both Lake Sylvia and Lake Burgan, we did not try to estimate detection probabilities or densities in Lake Sylvia because a critical assumption of conventional distance sampling, namely perfect detection near the transect line, was not met (Figure 2). This assumption can be relaxed using double-observer surveys as implemented in Lake Burgan. Therefore, the statistical methods described in the following sections only apply to the data collected in Lake Burgan.

We estimated zebra mussel density using a two-stage approach, also called density surface modeling (following D. L. Miller et al. 2013 as illustrated in Figure 3). In the first stage, we fit a detection function using the observed distances, including the use of the sight-resight data collected by our observers to estimate the maximum detection probability. This allowed us to determine whether detection is perfect near the transect line, an important assumption of conventional distance sampling (Buckland et al. 2001). In the second stage, we estimated density by fitting a model to the segment-level counts corrected for the surveyed area and estimated detectability in each segment (Hedley and Buckland 2004). A critical assumption of this analysis and other distance sampling methods is that the density of animals does not vary with distance from the transect line. We considered this assumption to hold in our study since: 1) we used a systematic-random sampling design to determine transect locations; and 2) our transects were narrow and placed in relatively homogeneous habitat.

We present two, parallel analyses of the Lake Burgan data. The first approach, which we refer to as the *simple density estimator*, uses existing statistical tools to estimate density assuming a single detection function applies to both observers and all transects. The second approach, which we refer to as the *covariate-modified density estimator*, accounts for strata, unimodal detection functions, and covariates that affect both zebra mussel detection and density. Although this approach requires a more customized analysis, it is appealing because it provides a framework for investigating the effects of covariates on detection and density. In the following sections, we describe the steps for these analyses in more detail.

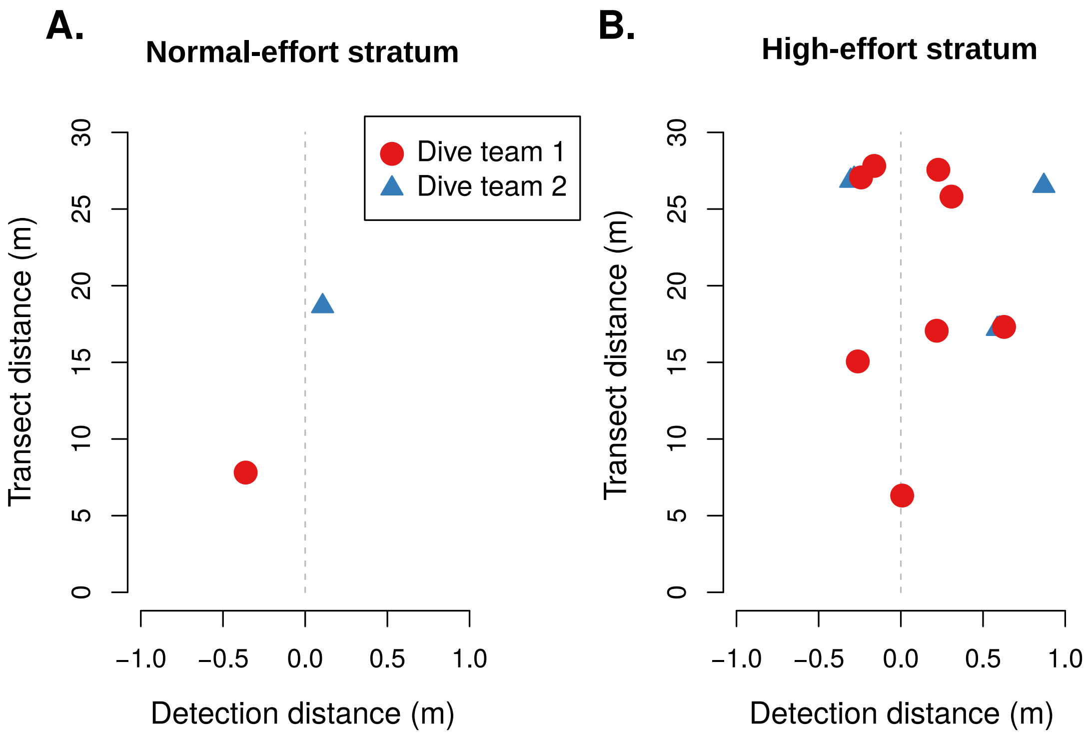
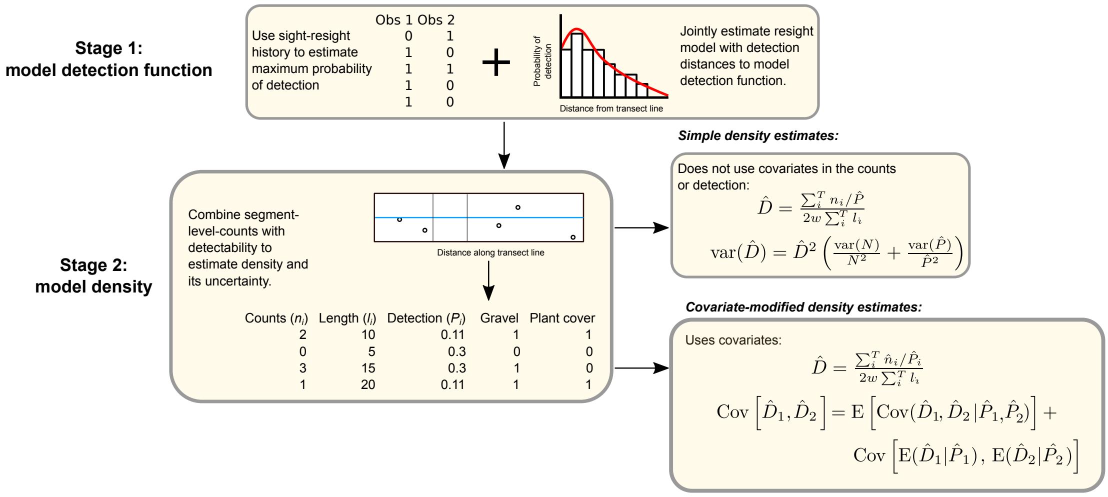


Figure 2: Detections of mussels along two transects in Lake Burgan by two dive teams. The dotted gray line denotes the transect line and each point denotes the recorded position of a detected zebra mussel. Panel A illustrates a transect in the normal-effort stratum, panel B illustrates a transect in the high-effort stratum. All distances are given in meters.



Use sight-resight history to estimate maximum probability of detection

Obs 1	Obs 2
0	1
1	0
1	1
1	0
1	0

Jointly estimate resight model with detection distances to model detection function.

Combine segment-level-counts with detectability to estimate density and its uncertainty.

Counts (n_i)	Length (l_i)	Detection (P_i)	Gravel	Plant cover
2	10	0.11	1	1
0	5	0.3	0	0
3	15	0.3	1	0
1	20	0.11	1	1

Does not use covariates in the counts or detection:

$$\hat{D} = \frac{\sum_i^T n_i/\hat{P}}{2w\sum_i^T l_i}$$

$$\mathrm{var}(\hat{D}) = \hat{D}^2\left(\frac{\mathrm{var}(N)}{N^2} + \frac{\mathrm{var}(\hat{P})}{\hat{P}^2}\right)$$

Uses covariates:

$$\hat{D} = \frac{\sum_i^T \hat{n}_i/\hat{P}_i}{2w\sum_i^T l_i}$$

$$\mathrm{Cov}\left[\hat{D}_1, \hat{D}_2\right] = \mathrm{E}\left[\mathrm{Cov}(\hat{D}_1, \hat{D}_2|\hat{P}_1, \hat{P}_2)\right] + \mathrm{Cov}\left[\mathrm{E}(\hat{D}_1|\hat{P}_1),\, \mathrm{E}(\hat{D}_2|\hat{P}_2)\right]$$

Figure 3: Work flow of the two-stage modeling approach. Estimation of animal density requires a count of observed individuals in each transect (n_i) where the total counts over T transects is N, the length (l_i) and width (w) of the transect, and the detectability of animals in the transect (P_i). The density of the sample is denoted as D.

Detection estimation

We applied sight-resight distance sampling in Lake Burgan to determine whether the assumption of perfect detection near the transect line, as required by conventional distance sampling, was met. Before we could implement this approach, we needed to decide which mussels were seen by both dive teams and which were seen by only the first or second dive team. We did not mark individuals detected by the first dive team because marks could have affected their detectability by the second team. Therefore, we used the proximity of the detections to each other to classify whether a pair of zebra mussel detections were a resight of a single zebra mussel (Figure 2).

We classified two detection events as the same zebra mussel when the difference in the detection distances for the pair was less than 0.2 m, and the difference in transect distances between the pair was less than or equal to 0.25 m. We determined these thresholds after visualizing nearest neighbor distances, but note our analyses were extremely robust to changes in these classification distances (Appendix 2). The thresholds we used here are reasonable because at these low densities it was apparent when the two dive teams detected the same mussel (e.g., Figure 2). At higher densities, there would have been much more uncertainty about whether two detections at similar locations corresponded to the same zebra mussel or not. In such cases, it would be appropriate to mark mussels and use dependent double-observer methods. Alternatively, more formal approaches to incorporating measurement error into distance sampling could be applied (Conn and Alisauskas 2018).

Simple detection estimates Histograms of the detection distances (Figure 4) suggested that the maximum detection probability might have occurred off the transect line. To ensure that standard, monotonic distance functions could be applied, we left-truncated the detection distance at 0.2 m. Truncation removed the potential effects of the hump and allowed us to use the standard distance functions without any modifications.

We modeled detection probabilities using two model subcomponents. The first subcomponent, $g(y)$, describes how distance (y) leads to changes in the probability of detection and is determined by modeling the distribution of detection distances. We applied the half-normal distance function, defined as $g(y) = e^{-(y-0.2)^2/2\sigma^2}$, where $y - 0.2$ is the

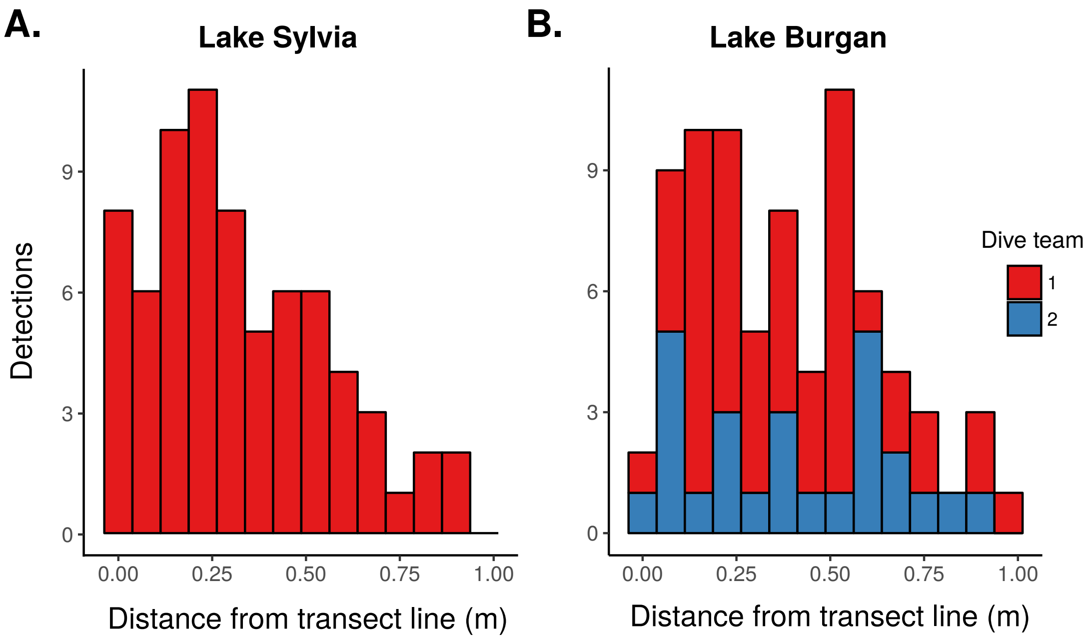


Figure 4: Stacked histogram showing the total number zebra mussel detections made by dive team 1 and dive team 2 in the summer of 2017. Panel A gives the total counts in Lake Sylvia from 24 transects and panel B gives the total counts in Lake Burgan from 18 transects. Distance bin widths are 0.075 m.

detection distance, accounting for the 0.2 m truncation distance, and σ controls the scale of the detection function (Buckland et al. 2015). All estimates for this detection model were made using the mrds (mark-recapture distance sampling) package in R (J. Laake et al. 2018).

We used a second subcomponent of the detection function to scale the distance function by the maximum probability of detection, estimated from the sight-resight data. This second piece of the detection function used a sight-resight model to estimate the detection probability at 0.2 m. The probability of detection by either observer at the truncation distance is $\pi(0.2) = \pi_1(0.2) + \pi_2(0.2) - \pi_1(0.2)\pi_2(0.2)$, where $\pi_k(0.2)$, for $k = 1, 2$, is the probability that the k^{th} dive team detects a mussel at the detection distance of 0.2 m.

For the simple density estimator, we assumed the dive teams had the same detection function and estimated $\pi(0.2)$ using the mrds (mark-recapture distance sampling) package in R (J. Laake et al. 2018). We then combined the two model components to determine the probability of detecting a zebra mussel cluster within our transect by integrating the distance function over the transect width to give the probability of detecting a mussel in the transect, $P = \pi(0.2) \int_{0.2}^{1} g(y)\, dy$.

The sight-resight model used the point independence assumption described by Borchers et al. (2006), which accounts for the effects of unmodeled covariates that can induce unexpected correlations between observers. This can occur if, for example, both dive teams find it easier to detect larger mussels and mussel size is not included in the model. Under these conditions the observers' detections may be correlated even though dive teams act independently. Point independence addresses this issue by modeling the detection probability at a single detection distance, usually specified to be where detection is maximized (here, at 0.2 m).

Covariate-modified detection estimates Next, we explored estimators of detection and density that relaxed some of the assumptions of the simple density estimator. In particular, we fit a unimodal detection function and included covariates that were thought to influence detection probabilities.

Our detection distances illustrated in Figure 4 indicated that the detection function may be unimodal, with the maximum detection probability occurring off the transect line. We tested two alternative models describing how detection changed with distance. The first model we fit was the half-normal detection function, which assumes detection is maximized on the transect line. This detection function was defined as $g(y) = e^{-y^2/2\sigma^2}$ over the width of the transect ($0 \leq y \leq 1$). Second, we fit the unimodal function of Becker, Christ, and Reed (2015), which uses two truncated half-normal distributions that share a common mode, μ_k (where $k = 1$ or 2 for each of the observers). The unimodal detection function for observer k was defined as $g(y) = e^{-(y-\mu_k)^2/2\sigma_l^2}$ for $0 \leq y \leq \mu_k$ and $g(y) = e^{-(y-\mu_k)^2/2\sigma_g^2}$ for $\mu_k < y \leq 1$. In this model, σ_l served as the scale parameter for distances less than the mode and σ_g served as the scale parameter for distances greater than the mode. We assumed that the detection peak was the same for both observers ($\mu_1 = \mu_2$) and estimated parameters by maximizing the log-likelihood of $g(y)$ using the nloptr package in R (Ypma 2015). We selected the best detection model in each lake using AIC, an estimate of the Kullback-Liebler divergence, which measured the relative discrepancy between each model and reality. The AIC is a popular approach for measuring model parsimony, representing a trade-off between model fit and complexity with the goal of achieving optimal predictive ability (Taper and Ponciano 2016).

In the unimodal model, the probability of detection by either observer at the mode, μ, was modeled as a logit-linear function of the observed covariates: plant presence, water clarity, and observer. Thus, the detection probability at the mode for observer k in segment j was modeled as $\text{logit}(\pi_{k,j}(\mu_{k,j})) = \beta_0 + \beta_1\text{Plant}_j + \beta_2\text{Clarity}_j + \beta_3\text{Observer}_k$, where Clarity was a continuous variable, Plant was an indicator variable that was 0 when plants were absent and 1 when present, and Observer was an indicator variable that was 0 for dive team 1 ($k = 1$) and 1 for dive team 2 ($k = 2$). All estimates of $\pi(\mu)$ were made using the mrds (mark-recapture distance sampling) package in R (J. Laake et al. 2018).

Density estimation

We estimated densities in Lake Burgan following the two-stage approach described in Hedley and Buckland (2004). As in the detection models described above, we present two parallel analyses of the Lake Burgan data. The first analysis applied existing statistical tools to the truncated data. We then showed how to extend this analysis to account for strata and covariates that affect zebra mussel density.

Simple density estimator Denote the counts for the i^{th} transect as n_i, the total counts in the lake over T total transects as $N = \sum_i^T n_i$, the length of each transect as l_i, the total length of all transects as $L = \sum_i^T l_i$, and the estimated detection probability as $\hat{P}$. The estimated density was then $\hat{D} = \frac{\sum_i^T n_i/\hat{P}}{2w\sum_i^T l_i}$ (Buckland et al. 2001). The variance in the estimated density was

$$\text{var}(\hat{D}) = \hat{D}^2 \left(\frac{\text{var}(N)}{N^2} + \frac{\text{var}(\hat{P})}{\hat{P}^2} \right). \tag{1}$$

The first term in equation 1, $\text{var}(N)$, was the variance in the total counts over all segments ($N = \sum_i n_i$), while the second piece was the variance in the detectability, $\text{var}(\hat{P})$. We used the design-based estimator for the variance in the total counts, $\text{var}(N) = \left(L \sum_i^T l_i(n_i/l_i - N/L)^2 \right) / (T-1)$, where the contribution of each segment to the total variance was weighted by the segment length. The R package mrds estimates $\hat{P}$ using maximum likelihood and computes the variance in detectability from the Hessian matrix (J. Laake et al. 2018).

Covariate-modified density estimates We modeled the total zebra mussel counts at the segment-level, using covariates to explain variation in density. Segments were defined based on changes in habitat characteristics along the transect as described in the data collection section. We assumed, conditional on environmental covariates, that abundance within each segment followed a Negative Binomial distribution. We used the log of the segment survey area multiplied by the estimated average probability of detection in the segment as an offset in the model to control for survey effort and detectability. This transformed the observed counts into zebra mussel densities. We used a log-link to model the effects of plant presence (classified as presence/absence), depth, and gravel substrate (classified as presence/absence) as covariates of zebra mussel density. Although we recorded multiple substrate types, gravel was the only type that had enough variation to be considered as a predictor variable. We used AIC to test whether a smoothing spline of segment location was needed to smooth the spatial variation in density that was not explained by the environmental covariates. Density models were fit using maximum likelihood estimation implemented in the R package mgcv (Wood 2006).

We estimated the density in the j^{th} stratum using the estimator, $\hat{D}_j = \sum_{i=1}^{T_j} \left(\hat{n}_i/\hat{P}_i\right) /2w \sum_{i=1}^{T_j} l_i$, where the summation runs over all T_j segments in the stratum. The terms in the sum are, $\hat{n}_i$, the estimated count in the i^{th} segment in stratum j, $\hat{P}_i$, the estimated detection probability in the i^{th} segment of stratum j, and l_i, the length of segment i in stratum j. The detection probabilities were estimated using the methods described in the previous section, and the counts, $\hat{n}_i$, were modeled in the second stage of the density surface model. The overall population size was determined by weighting the estimates from each stratum in proportion to the amount of area in the lake they represented, $\hat{D} = w_{\text{high}}\hat{D}_{\text{high}} + w_{\text{low}}\hat{D}_{\text{low}}$, where the stratification weight for high-effort strata was $w_{\text{high}} = 1/11$ and for normal-effort strata was $w_{\text{low}} = 10/11$.

We applied the conditional covariance formula (Bain and Engelhardt 2000) to derive a variance expression that propagated the uncertainty from the detection model through to the uncertainty estimate for zebra mussel density (derivation given in Appendix 1). The total variation in density was calculated by summing the variances and covariances across all segments, with the covariance terms used to account for correlation resulting from using a common detection model to adjust counts in all segments (J. Fieberg and Giudice

2007). The resulting covariance between the density estimates has two terms, analogous to the covariate independent case in equation 1. Below we indicate the covariance for segment 1 in stratum j and segment 2 in stratum j' (D_1 and D_2):

$$\mathrm{Cov}\left[\hat{D}_1, \hat{D}_2\right] = \mathrm{E}\left[\mathrm{Cov}(\hat{D}_1, \hat{D}_2 | \hat{P}_1, \hat{P}_2)\right] + \mathrm{Cov}\left[\mathrm{E}(\hat{D}_1 | \hat{P}_1),\, \mathrm{E}(\hat{D}_2 | \hat{P}_2)\right]. \tag{2}$$

The first term in equation 2 accounts for uncertainty in the counts, given the estimated detection model parameters, while the second term accounts for uncertainty in the detection parameters.

We determined the covariance estimates using a parametric bootstrap (Hedley and Buckland 2004). For the first term in equation 2, we simulated 10^4 sets of parameters obtained from segment-level count model using a multivariate normal distribution with mean given by the maximum likelihood estimates of the density model and covariance matrix approximated by the inverse of the estimated Hessian matrix (Bain and Engelhardt 2000). We used the simulated parameters to predict the counts for each segment, and then scaled these counts by the estimated segment-level detection probabilities ($\hat{P}_i$) and the amount of area surveyed in each segment. The covariance of these scaled counts was then plugged into the first term of equation 2.

We estimated the second term in equation 2, the covariance matrix of the detectability correction estimates, by simulating 10^4 sets of detectability parameters from a multivariate normal distribution with mean given by the maximum likelihood estimates of the detectability function and covariance matrix approximated by the inverse of the estimated Hessian matrix (Bain and Engelhardt 2000). We used the simulated detection parameters to estimate the segment-level detection probabilities, $\hat{P}_i$. Lastly, we calculated the covariance between the segment-level detectability corrections, scaled by the estimated segment-level count densities, and plugged the result into the second term of equation 2.

Finally, we the calculated the total variance in the density estimate by using the stratification weights to account for the proportion of lake area surveyed in each strata. We scaled the full density covariance matrix, Σ, by the vector of weights (W) where the i^{th} entry of the vector was w_{high} or w_{low}, depending whether transect i was in the high- or normal-effort stratum. The total variance in density was then given by $W^{\mathrm{T}}\Sigma W$.

Results

Substrate in the Lake Sylvia segments was predominately sand and silt (Table 1). We also had a few segments with gravel, pebbles, and rocks. We found that zebra mussels were always found in segments with silt and often in segments with sand, broadly consistent with the available substrate frequencies. The fine-scale substrates that we found zebra mussels predominately attached to in Lake Sylvia, in order of frequency, were wood, rocks, and gravel.

Substrate in the Lake Burgan segments was predominately silt and sand (Table 1), followed by gravel, and rocks. We found zebra mussels in habitats at rates similar to availability with detections occurring primarily in sand and silt, followed by gravel and rocks. Zebra mussels in Lake Burgan were found attached to gravel, rocks, and wood. We also detected one mussel attached to a native mussel, one mussel attached to scrap metal, and two detections were on other materials such as fabric and unidentified mollusks.

Table 1: The frequency of available substrate types in segments and substrate types in segments where zebra mussel detections occurred (potentially classified with multiple types so proportions do not sum to 1), and the type of substrate zebra mussels were attached to (proportions sum to 1).

	Sand	Silt	Gravel	Pebbles	Rocks	Wood	Native mussel	Other
Lake Sylvia								
Available coarse spatial scale substrate	0.73	0.70	0.05	0.02	0.02	0.00	0.00	0.00
Coarse spatial scale substrate with mussel detections	0.53	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Fine-scale substrate with mussel attachment	0.00	0.00	0.18	0.00	0.35	0.41	0.05	0.01
Lake Burgan								
Available coarse spatial scale substrate	0.88	0.90	0.55	0.00	0.04	0.00	0.00	0.00
Coarse spatial scale substrate with mussel detections	0.91	0.87	0.65	0.00	0.04	0.00	0.00	0.00
Fine-scale substrate with mussel attachment	0.00	0.00	0.46	0.00	0.40	0.06	0.02	0.06

In the left-truncated detection data set from Lake Burgan, the first dive team made 35 detections, and the second dive team made 19 detections, with 6 detections being shared by both teams for a total of 48 unique zebra mussel detections. In the full detection data set, the first dive team made 49 detections while the second dive team made 26 detections; 9 of the detections were made by both teams for a total of 66 unique zebra mussel detections. Of these 66 unique detections, 64 were of single zebra mussels and 2 were of clusters of size 2.

Detection estimation

Simple detection estimates In the left-truncated detection data, set we estimated the scale parameter, $\hat{\sigma}$, of the detection function to be 0.43 (SE = 0.07). The estimated probability of detecting a zebra mussel, $\hat{P}$, was 0.24 (SE = 0.08).

Covariate-modified detection estimates In our analysis of the full detection data set, the unimodal detection function was more parsimonious than the half-normal model (ΔAIC = 0.23). This small difference means we were unable to reliably distinguish between these two models.

We estimated the location of peak detection in the unimodal detection function, μ, at 0.15 (SE = 0.08) m. The scale coefficient for distances less than μ was estimated as $\sigma_l = 0.11$ (SE = 0.09) m and for distances greater than μ was $\sigma_g = 0.45$ (SE = 0.07) m. The detection functions for different observers and with plants present and absent are illustrated graphically in Figure 5.

The sight-resight model coefficients suggested that the second dive team had lower detection probabilities than the first team and plant presence decreased the probability of detecting zebra mussels (Table S1). The positive clarity coefficient suggested that detectability increased with water clarity as expected. However, the estimated confidence intervals of the clarity effect were very wide and overlapped 0 (Table S1). Therefore, we also ran a reduced model with the clarity covariate removed. The model without clarity had a lower AIC (Table 2), and reduced the standard error in density due to detectability (the second term in equation 1) from 0.05 to 0.008; removing clarity had minimal impact on the other regression parameter estimates. Thus, moving forward, we

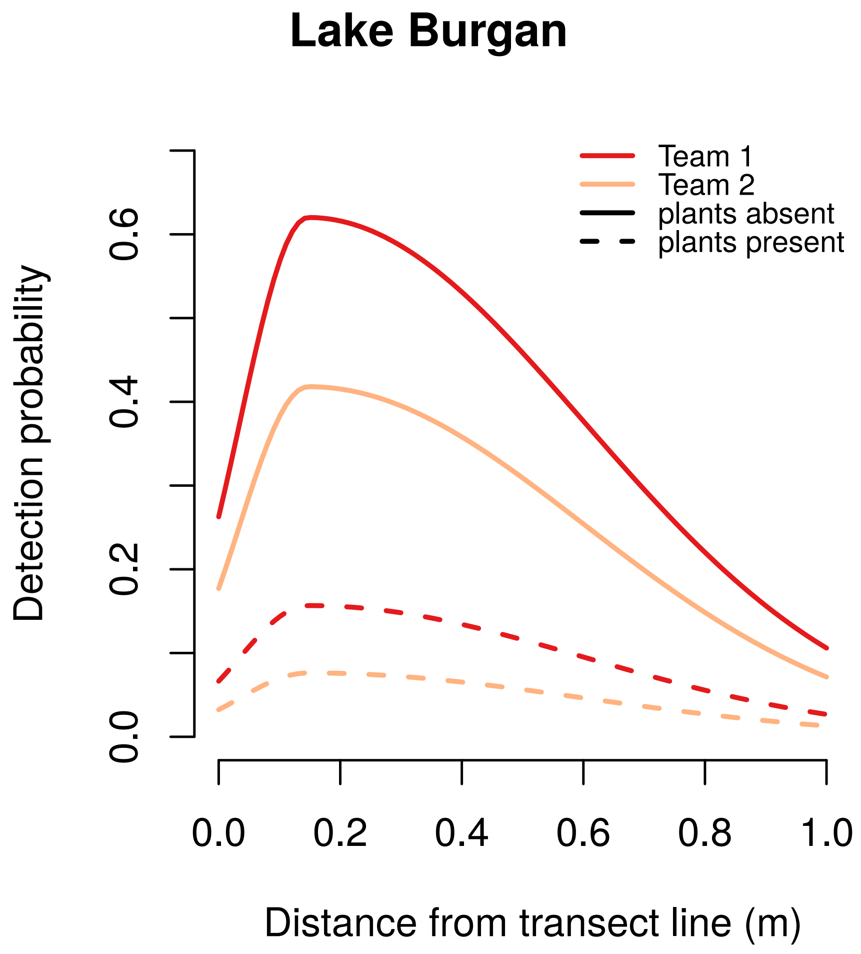


Figure 5: Estimated detection functions in Lake Burgan from the unimodal detection model. We used a double-observer survey to estimate the detection probabilities for each team in the presence or absence of plants.

Table 2: Covariate selection tables for the Lake Burgan analysis. The spatial regression spline is written as s(Easting, Northing).

	log-likelihood	k	AIC	ΔAIC
Detection model				
Observer + Plants + Clarity	-50.25	5	110.50	0.55
Observer + Plants	-50.98	4	109.96	0.00
Density model				
Depth + Plants + Gravel + s(Easting, Northing)	-45.50	6	143.91	2.85
Depth + Plants + Gravel	-46.65	4	141.06	0.00

Table 3: Estimated probability of detecting a zebra mussel in Lake Burgan under different conditions using the reduced detection model (without the water clarity covariate).

	Observer 1		Observer 2	
	Estimate	Standard error	Estimate	Standard error
No plant cover	0.41	0.08	0.28	0.08
Plant cover present	0.1	0.07	0.05	0.04

only present results using the reduced detection model. The estimated probability of detecting a zebra mussel in Lake Burgan for each of the dive teams was low, even under favorable conditions, and ranged from 0.08 (dive team 2 with plant cover present) to 0.62 (dive team 1 with no plant cover present) (Table 3).

Density estimation

We constructed 49 different survey segments from the original 18 transects in Lake Burgan. Segments were based on observed habitat transitions as described in the methods and varied in length from 1 to 30 m. The observed density of zebra mussels in Lake Burgan, uncorrected for detection, was 0.08 mussels per square-meter (m^{-2}).

Simple density estimates In the left-truncated data set, we estimated the overall density, corrected for detection, in Lake Burgan to be 0.24 (SE = 0.1) mussels m^{-2} with 67% of this error arising due to uncertainty in the detection parameters.

Covariate-modified density estimates Using the unimodal detection function, environmental covariates, and strata, we estimated the overall density, corrected for detection, in our transects to be 0.25 (SE = 0.09) mussels m^{-2} with 10% of this error arising due

Table 4: Estimates of covariate effects in the count and detection models of Lake Burgan.

Variable	Parameter estimate	Standard error	95% confidence interval
Detection model			
observer	-0.86	0.38	(-1.61, -0.1)
plants	-2.37	0.41	(-3.18, -1.57)
Density model			
plants	-0.43	0.54	(-1.5, 0.63)
depth	-0.05	0.06	(-0.16, 0.06)
gravel	0.12	0.38	(-0.62, 0.86)

to uncertainty in the detection parameters. This estimate was consistent with the simple density estimate obtained above, and both estimators led to a three-fold increase in the estimated density relative to the observed density.

In the normal-effort stratum, we estimated densities of 0.28 (SE = 0.11) mussels m^{-2}, and in the high-effort stratum we estimated density to be 0.25 (SE = 0.09) mussels m^{-2}. Interestingly, the normal- and high-effort strata had nearly the same estimated densities. We attribute this result to defining strata in the field using observed densities and not testing for statistical differences among transects.

Our estimate of the scale parameter in the negative binomial distribution was 1.477, indicating overdispersion relative to the Poisson distribution. The model without any spatial structure was more parsimonious than the model with the spatial smooth term (Table 2). Parameter estimates from the generalized linear model indicated that zebra mussel densities tended to be lower in shallower areas and in areas with plant cover, whereas gravel had a small positive effect on density (Table 4). However, all of these covariate estimates had high uncertainty with confidence intervals that included zero.

Discussion

We have demonstrated that line transects with double-observer surveys can be suitable for estimating invasive zebra mussel densities in newly infested lakes. This method allows researchers to cover more area compared to quadrat surveys, at the cost of imperfect detection. Importantly, we found that accounting for the low detectability of zebra mussels led to estimates of density over three times higher than the observed densities. Our estimates were robust, with both the simple and covariate-modified estimators giving similar answers. Nonetheless, the double-observer survey in Lake Burgan highlighted the difficulty that our dive teams had in detecting zebra mussels even near the transect line. Thus, we conclude that single-observer methods are generally not appropriate for estimating zebra mussel densities.

Detection data from both Lake Sylvia and Lake Burgan exhibited a peak near 0.2 m from the transect line, suggesting that detection probabilities may have been highest just off the transect line (Figure 4). We were surprised to find this peak in our dive surveys, though similar patterns are known to occur in many aerial surveys (Quang and Lanctot 1991). Although we demonstrated methods that provide a solution to this phenomenon, we emphasize that the statistical evidence favoring the unimodal detection function that we used is still equivocal and more samples will be needed to determine whether this effect is real or an artifact of sampling variation. Alternatively, density can be estimated after first truncating the data to remove this peak. Truncation eases the analysis by allowing the application of standard detection functions that can be implemented in existing R packages such as mrds (J. Laake et al. 2018).

It is worth considering the potential causes of a unimodal detection function in dive surveys to determine whether it can be eliminated by improvements in study design. In aerial trials that display unimodal detection, low detection near the transect line arises due to the fact that animals close to the transect appear to pass by more quickly than animals further away (Becker and Quang 2009). One suggestion to address this effect is to have observers focus their eyes more on areas near the transect line (Buckland et al. 2015). We emphasized the importance of detecting all mussels on or near the transect line to our divers, but perhaps additional training in this area would be helpful. We also know of at least one case when our lead diver missed a zebra mussel near the transect because she returned to the transect line ahead of where she left to measure the detection distance. Finally, laying down the transect line may kick up silt and cover nearby mussels. This effect could be eliminated by having divers start their search a small distance away from the transect line.

A complication in our preparation of the field data for analysis was determining whether detections made by the first observer were also made by the second observer. Error in the distance measurements made classifying redetections more difficult than anticipated.

Alternatives, such as the removal design (Moran 1951; Otis et al. 1978), remove individuals from the population once they are detected. This ensures that the second observer always detects new individuals. The cost of this design is that the second observer's detection history is conditional on the record of the first observer. Under this constraint, we have less information for estimation and must assume that the two observers have the same detection function, an assumption that could be problematic based on the differences between observers found here. This assumption can be made more tenable by rotating the role of primary and secondary observers as we did in our surveys (Cook and Jacobson 1979).

Previous studies have found that sediment grain size affects the ability of zebra mussels to attach to lake bottoms (Berkman et al. 1995). We found no evidence that the density of zebra mussels was preferentially linked to certain substrate types, though our study was not specifically designed to detect these effects as it was not balanced across substrate types. Further, our classification of substrate types was qualitative, so we were not able to distinguish fine-scale changes in the spatial distribution of sediment size. Also, the lakes we studied were at very low densities of infestation; substrate associations may emerge as populations reach higher densities. We did find evidence that the detection of zebra mussels was linked to habitat, with detection being significantly lower in segments with plant cover. This effect on detection can make defining sampling strata post-hoc problematic when not accounting for detectability.

We see several available options for obtaining more precise distance survey estimates under the constraint of limited survey effort. It may be possible to combine transect surveys with remote-sensing technologies (e.g., acoustic surveys). SCUBA-surveys could be used to calibrate more extensive, but less accurate counts via a double-sampling approach (Thompson 2004). Alternatively, remote sensing data could be used for stratification, allowing for increased survey effort in areas where mussels are most likely to be detected. Finally, an increase in the number of transects surveyed would lead to reduced variability in the counts. Thus, it may be better to survey faster at the cost of lower detection if this allows divers to incorporate additional transects.

Several studies have used surveys of freshwater mussels to examine the trade-offs between survey efficiency, coverage, and the probability of discovering low-density mussel populations (e.g., Green and Young 1993; Metcalfe-Smith et al. 2000; Smith 2006). Understanding how these trade-offs constrain our ability to estimate population density and distribution is essential for optimizing effort and may have important implications for our ability to evaluate control measures on invasive species such as zebra mussels. A major limiting factor that prevents the broad application of optimal survey theory is that the trade-off function, describing how changes in search efficiency affects coverage and detectability, is generally unknown (Giudice et al. 2010).

We are aware of one previous study that compared distance- and quadrat-based surveys of freshwater mussels (briefly described in D. L. Strayer and Smith 2003). In that study, survey methods were implemented in equal-sized areas. Quadrats generally provided more precise estimates of density though differences between the two methods decreased as densities increased. We expect that, relative to quadrat counts, distance surveys should be able to cover a larger area in an equal amount of time. To compare survey efficiencies, it would be necessary to control survey time (or cost) rather than survey area. Future data collection efforts should attempt to capture information on survey effort, which would allow for comparisons among the efficiencies of survey methods. Comparisons of survey efficiencies are especially relevant to efforts to monitor recently invaded lakes where densities need to be estimated over large areas of lake bottom to determine the extent of the invasion.

Author Contributions

JF and MM obtained funding for the study; JF and MM designed the study with input from JMF, NSB, and LS; NSB and LS collected the data; JMF analyzed the data with input from JF; JMF led the writing of the paper and all authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

This study was funded by the Minnesota Aquatic Invasive Species Research Center with funding from the Minnesota Environmental and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources. JF received partial support from the Minnesota Agricultural Experimental Station and the McKnight Foundation. We would like to thank Kylie Cattoor and Keegan Lund of the Minnesota Department of Natural Resources for assisting us with the data collection on Lake Burgan and for productive discussions, Steve McComas of Blue Water Science for his insights on surveying zebra mussels, and Rich Rezanka and Tom Jones with the Minnesota Department of Natural Resources for advice on our initial attempts to design this study. The data and code for analysis used in this study are available on the University of Minnesota's digital conservatory *url upon acceptance.*

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