Using distance sampling to estimate densities of Zebra Mussels (*Dreissena polymorpha*) in early-stage invasions

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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 population densities are low. Statistically-valid sampling designs that account for imperfect detection of individuals are needed to estimate densities across time and space. Survey methods that yield reliable estimates allow managers to determine how invader biomass affects ecosystem services and evaluate population trends and effectiveness of control measures. We investigated the use of distance sampling via self-contained underwater breathing apparatus divers to determine densities of invasive Zebra Mussels (*Dreissena polymorpha*) in 2 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. Presence of vegetation had a greater influence on detection probability than diver identity. We also found our sampling design did not meet a key assumption of conventional distance sampling: that detection along the transect line is perfect. 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. However, further evaluation is needed to determine if changes in field sampling techniques can meet the assumptions behind conventional distance sampling for freshwater mussels. We also suggest that the efficiency of distance sampling should be compared to alternatives such as quadrat sampling across a range of mussel densities.
Key words: freshwater mussels, sampling methods, double-observer, low-density

Zebra Mussels (*Dreissena polymorpha*; Pallas 1771) and closely-related Quagga Mussels (*Dreissena rostriformis bugensis*; Andrusov 1897) are native to a small region of southern Russia and the Ukraine (Stepian et al. 2013), but have spread throughout Europe (Karatayev et al.1997; Karatayev et al. 2003) and North America (Benson 2013). These species have become one of the most widespread and damaging aquatic invasive species in the world (Karatayev et al. 2007). The economic costs of these 2 dreissenids in the United States has been estimated to be in the hundreds of millions of US dollars/y. Dreissenid impacts include fouling of hydropower facilities as well as water treatment and power plant intake pipes (O'Neill 2008, Bossenbroek et al. 2009). These mussels can also negatively influence recreation and tourism by increasing the costs of maintaining lake resources through mitigation and by impacting recreational fishers (McNickle et al. 2006, Limburg et al. 2010). Further, Zebra Mussels reach high population densities, smothering and outcompeting native mussel species. High densities of these suspension feeders lead to the removal of high volumes of planktonic organisms from lakes and rivers. These changes result in population declines and local extinctions of native mussels and other invertebrates (Karatayev et al. 1997, Ward and Ricciardi 2013), damage to fish populations

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(Strayer et al. 2004, McNickle et al. 2006, Lucy et al. 2013, Strayer and Malcom 2018), and the restructuring of aquatic food webs (Higgins and Vander Zanden 2010, Bootsma and Liao 2013, Mayer et al. 2013).

Ecological impacts scale with dreissenid density and biomass, but quantitative data on population densities are only available for a few water bodies (Higgins and Vander Zanden 2010). Control efforts, either by chemical treatments or 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. Mussels in these water bodies are difficult to locate, and even intensive underwater surveys can fail to detect mussels that remain after treatment (Lund et al. 2018). Efficient and reproducible survey designs are needed to make comparisons across space and time (Dorazio 1999) and to allow managers to determine how well treatments reduce mussel densities and how environmental conditions influence the efficacy of control efforts.

In the North American Great Lakes, ship-based surveys with Ponar grabs and sled dredges have typically been used to survey dreissenid populations (Marsden 1992, Nalepa et al. 2010, Strayer and Malcom 2018). Surveys of inland lakes occur over much smaller areas and often use a self-contained underwater breathing apparatus (SCUBA; e.g., Kumar et al. 2016), which may offer more reliable assessments of mussel distribution and density. SCUBA-based methods often use quadrats as sample units (Strayer and Smith 2003). However, quadrats may be suboptimal when attempting to survey large portions of a water body because of the time and effort required to move between distant sites (e.g., Giudice et al. 2010). Surveys that use line transects sample along a continuous path. These surveys are an attractive alternative to quadrat surveys because they allow sampling units to cover a larger area and, therefore, reduce time spent moving between sampling locations. In practice, however, this increase in survey area often comes at the price of imperfect detection.

To estimate changes in relative densities of populations separated in time or space, we need to account for changes in the detectability of individuals (Mackenzie and Kendall 2002). Techniques such as capture-recapture (Huggins 1991), removal estimators (Nichols et al. 2000), or distance sampling (Buckland et al. 2001) can account for changes in detectability that result from changing environmental conditions or a different surveyor. A common problem with line transects, however, is that the probability of detecting individuals can decline with their 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 and uses these distances to model a detection function that can then be used to correct the observed counts (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 relying on the detections of targets by 2 observers. These surveys allow the number of mussels that are detected by either or both observers to be used to estimate the detection probability of individuals on or near the transect line (Laake 1999).

Here, we use single- and double-observer distance sampling to estimate population densities of Zebra Mussels in 2 recently-invaded lakes in central Minnesota. We tested whether the underlying assumptions of conventional distance sampling were met and illustrate how to analyze these data with 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 Zebra Mussels in Lake Sylvia in Stearns County, Minnesota on August 8th and 11th of 2017 and Lake Burgan in Douglas County, Minnesota on September 11th and 12th of 2017 (Fig. 1A–B). Lake Sylvia covers an area of 34 ha and has a maximum depth of 15 m, whereas Lake Burgan covers an area of 74 ha and has a maximum depth of 13 m. Zebra Mussels were first verified in Lake Sylvia in 2015 (C. Jurek and C. Silgjord, Minnesota Department of Natural Resources, personal communication) and in Lake Burgan in 2017 (L. Raitz and M. Bolinksi, Minnesota Department of Natural Resources, personal communication).

Survey design

Lake Sylvia   We allocated survey effort with a stratified systematic sampling design (Pooler and Smith 2005). First, we surveyed a high-effort stratum that consisted of 8 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. When possible, transects in the infestation zone were each $l = 30$ m long and 3 m apart. However, we did not place transects through the thermocline because of low visibility, so transects were sometimes <30 m. We also surveyed 2 peripheral clusters of 3 transects, each 3 m apart and located 150 m to either side of the infestation zone, in a moderate-effort stratum. Finally, we surveyed the normal-effort strata of 10 single, outlying transects dispersed evenly along the remaining shoreline (Fig. 1A).

Each transect began at a depth of 3 to 8 m and was oriented perpendicular to the shoreline to cover a range of depths. Survey points were determined with a bathymetry shapefile in ArcMap (version 10.6; ESRI, Redlands, California) provided by the Minnesota Department of Natural Resources. We located the starting point of the transect with a
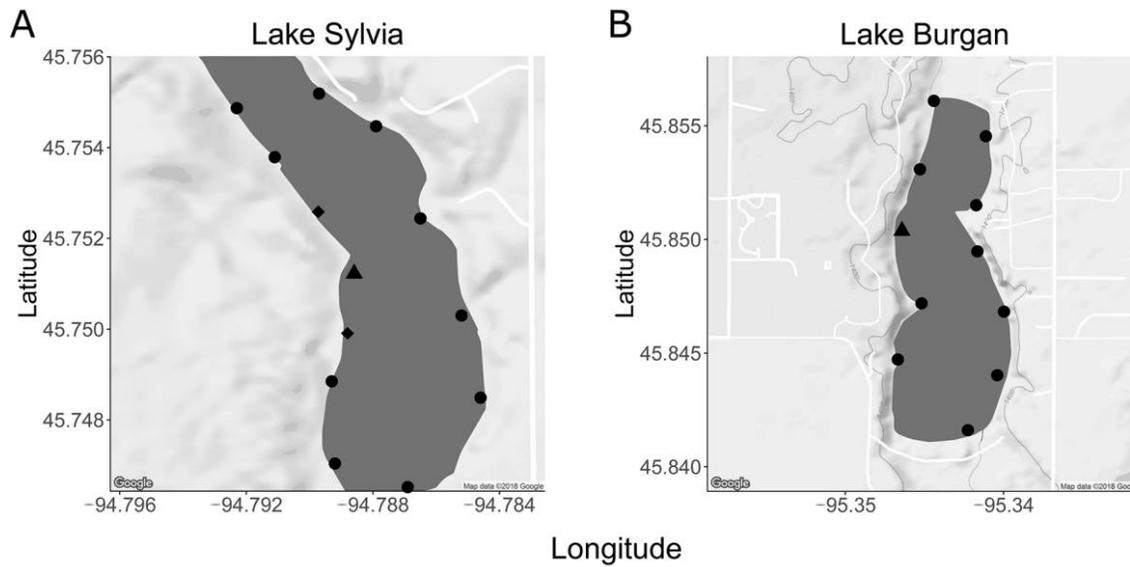
Figure 1. Transects for Zebra Mussel surveys conducted in Lake Sylvia (A) and Lake Burgan (B) in the summer of 2017. Transects in normal-effort strata are given as black dots. Triangles indicate transects in the high-effort strata, where we sampled 8 transects at each location, and diamonds represent the medium-effort strata, where we sampled 3 transects at each location.

GPS unit (Garmin GPSMAP 64s, Olathe, Kansas). Divers surveyed 1 m to either side of each transect line for a transect half-width of $w = 1$ m and total area surveyed of $2\,w\,l$ m².

Lake Burgan   The location of the Zebra Mussel infestation zone was unknown in Lake Burgan, so we modified the survey design used in Lake Sylvia. We initially surveyed 11 transects, evenly spaced along the perimeter of the lake, with the 1st transect chosen near the boat launch (Fig. 1B). After sampling these initial 11 transects, we returned to the transect with the highest observed density and sampled an additional 7 transects in this area, each spaced 3 m apart. We treated the 8 transects taken in this region as the high-effort stratum. The remaining 10 transects became the normal-effort stratum.

Data collection
Lake Sylvia   We surveyed Lake Sylvia with a single dive team of 2 people. The primary diver was responsible for detecting Zebra Mussels. Whenever the primary diver detected any Zebra Mussel individuals or clusters, she recorded the number of mussels and the distance from the transect start to the point where she made the detection (transect distance), to the nearest ~0.25 m. The diver also measured the perpendicular distance, to the nearest ¼ cm, from the closest point of the individual or cluster to the transect line (detection distance) with a meter tape. The primary diver also classified and recorded the substrate to which the Zebra Mussel was attached (fine-scale substrate). Fine-scale substrate could be 1 or more of the following categories: mud,

sand, gravel, pebble, rock, vegetation, wood, native mussel, metal, or other substrate.

In addition to the fine-scale substrate described above, the secondary diver characterized the coarse-scale substrate and the presence or absence of plant cover along the transect. We defined coarse-scale substrate as the dominant substrate type, which was classified qualitatively as mud, silt, sand, gravel, pebble, rock, or other. Whenever there was a change in the dominant substrate type or plant presence, the diver recorded the new substrate, plant presence, depth, and the transect distance where the change occurred such that each change in substrate or plant cover ended one segment and started another. Thus, each of these segments had homogeneous substrate and plant cover. The diver recorded multiple coarse-scale substrate types when there was no clear dominant substrate type.

Lake Burgan   We collected data in Lake Burgan with the same methods as described for Lake Sylvia, except that each transect was surveyed independently by 2 dive teams of 2 members each. We did not mark individuals detected by the 1st dive team because marks could have affected their detectability by the 2nd team. We alternated which team surveyed 1st on each transect. The 2nd dive team began their survey immediately after the 1st team finished so that each team collected data independently. It typically took 10 to 20 min for a team to complete a transect. We used the segments formed by substrate and plant cover changes as the sampling unit to model spatial variability in Zebra Mussel densities and detection probabilities.

All data   Study data were entered into a Research Electronic Data Capture (REDCap) 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 both quality control of data entry and auditing trails for data manipulation and export.

Statistical analyses

We present data on our survey design and data collection for both Lake Sylvia and Lake Burgan. However, we did not estimate detection probabilities or densities in Lake Sylvia because our collection methods did not meet the critical assumption of conventional distance sampling that detection was perfect near the transect line (Buckland et al. 2001; Fig. 2A–B). This assumption can be relaxed with the double-observer design we used in Lake Burgan. Therefore, the statistical methods described in the following sections apply only to the data collected in Lake Burgan.

We estimated Zebra Mussel density with a 2-stage approach, also called density surface modeling (following Miller et al. 2013 as illustrated in Fig. 3). In the 1st stage, we fit a detection function to the detection distances in each segment. In the 2nd stage, we estimated density by fitting a model to the segment-level counts, corrected for the surveyed area, and estimated detectability in each segment determined in the 1st stage (Hedley and Buckland 2004). A crit-
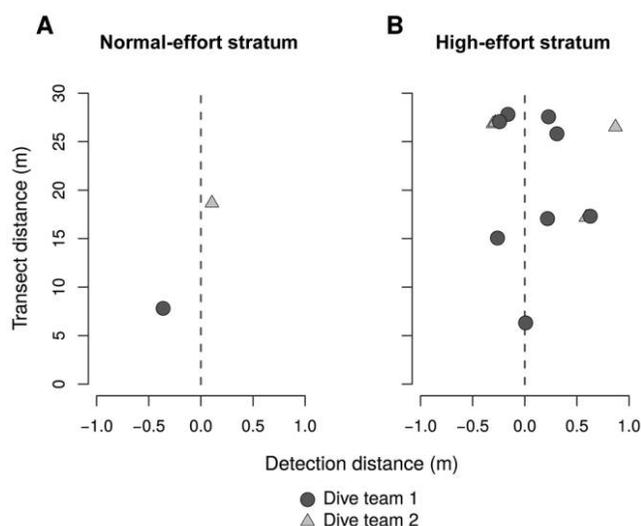

Figure 2. Detections of mussels along 2 transects in Lake Burgan by 2 dive teams. The dotted gray line denotes the transect line, and each point denotes the recorded position of a detected Zebra Mussel. Panel A illustrates a transect in the normal-effort stratum (transect 2 in Table S2), and panel B illustrates a transect in the high-effort stratum (transect 16 in Table S2). Transects were chosen because they illustrate detections made by both dive teams, as well as detections made by a single dive team. All distances are in meters.

ical assumption of this analysis and other distance sampling methods is that the true animal density does not vary with distance from the transect line. We considered this assumption to hold in our study because 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 also present 2 parallel analyses of the Lake Burgan mussel density data based on the 2-stage approach. The 1st analysis, which we refer to as the 'simple density estimator,' uses existing statistical tools to estimate density assuming a single distance detection function applies to both observers and all transects. The 2nd analysis, which we refer to as the 'covariate-modified density estimator,' also estimates the overall mussel density based on distance detection functions. However, this 2nd analysis also includes strata (high/low sampling efforts), unimodal detection functions, and environmental covariates that could affect both Zebra Mussel detection and density. This approach requires a more customized analysis than the simple density estimator. Both approaches yield reliable estimates of the overall mussel density, but the covariate-modified density estimator can be used to investigate the effects of the lake environment on both mussel detection and density. In the following sections, we describe the steps of these analyses in more detail.

Detection estimation   The 1st stage of our 2-stage modeling approach required that we estimate the detection probabilities and the associated uncertainties for each diver. We applied double-observer distance sampling in Lake Burgan to determine whether the assumption of perfect detection near the transect line was met, as required by conventional distance sampling. When this assumption is met, conventional distance sampling with a single observer can proceed. If the assumption is not met, then a double-observer approach is necessary. To test the assumption of perfect detection near the transect line, we first needed to decide which mussels were seen by both dive teams and which were seen by only 1 team. Therefore, we used the proximity of the detections by each team to classify whether a pair of Zebra Mussel detections was a resight (Fig 2A–B).

We classified 2 detection events as the same Zebra Mussel when the difference in detection distance for a pair detected by different observers was <0.2 m and the difference in transect distance for the pair was ≤0.25 m. We determined these thresholds based on input from the divers and from visualizing the distances between neighboring mussels (e.g., Fig. 2A–B), but note our analyses were extremely robust to changes in these classification distances (Appendix 2). These thresholds are relatively large but worked for our data because mussels were at low densities.

Histograms of detection distances (Fig. 4A–B) showed that most individuals were detected around 0.2 m from the transect line, so the maximum detection probability might
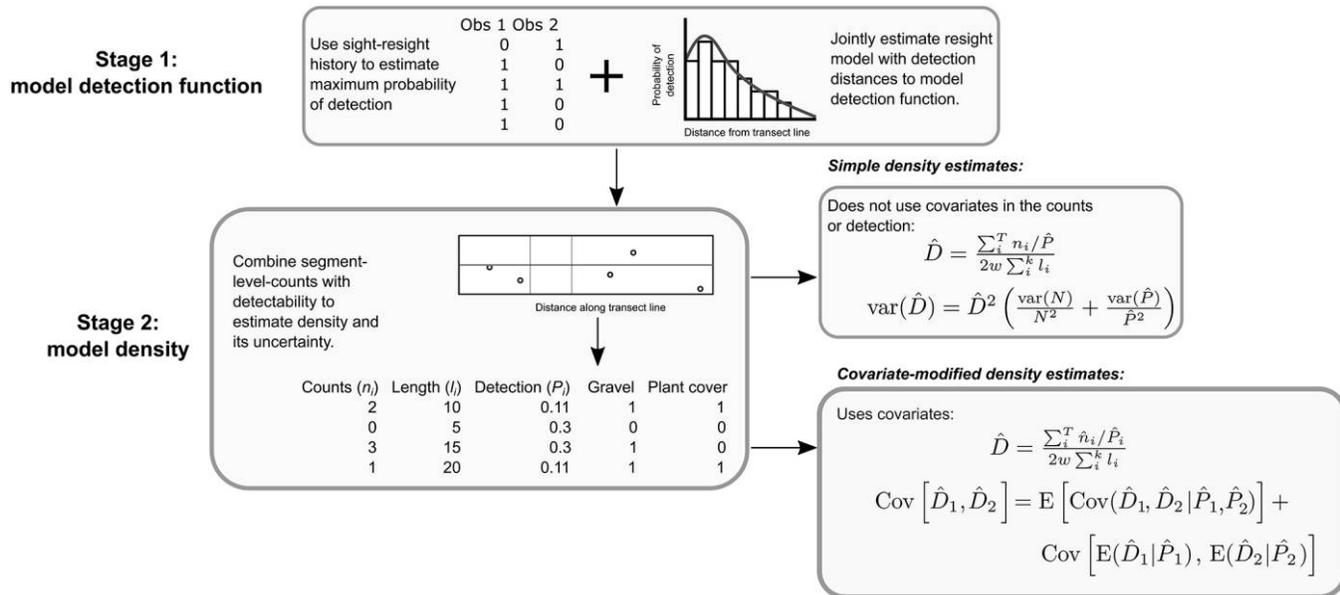
Figure 3. Workflow of the 2-stage modeling approach. Estimation of animal density requires a count of observed individuals in each transect (n_i) where the total counts over T transects is N, the length (l_i) and half-width (w) of the transect, and the detectability of animals along the transect (P_i). The density of the sample is denoted as D.

have occurred off the transect line. To ensure that we could use monotonic distance functions, we left-truncated the detection distance at 0.2 m. Truncation removed the potential effects of the peak in detection distances and allowed us to use the standard distance functions without any modifications.

We modeled detection probabilities with 2 model subcomponents. The 1st subcomponent, $g(y)$, describes how the detection distance (y) changes the probability of detection and is determined by modeling the distribution of detection distances. We used the half-normal distance function, $g(y) = e^{-(y-0.2)^2/2\sigma^2}$, where y is the detection distance, 0.2 is the truncation distance (m), and σ controls the scale of the detection function (Buckland et al. 2015). We used a 2nd subcomponent of the detection function to account for imperfect detection at the truncation distance. 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 kth dive team detects a mussel at the detection distance of 0.2 m. All estimates of both detection function subcomponents were made with the *mrds* (mark-recapture distance sampling) package in R (R Project for Statistical Computing, Vienna, Austria; Laake et al. 2018).

For the simple density estimator, we assumed the dive teams had the same detection function and estimated $\pi(0.2)$ with the *mrds* package. We then combined the 2 model components to determine the probability of detecting a Zebra Mussel cluster within our transects by integrating the distance function over the transect half-width to give the

probability of detecting a mussel along the transect, $P = \pi(0.2)\int_{0.2}^{1} g(y)dy$.

The double-observer model used the point independence assumption (Borchers et al. 2006), which accounts for the effects of unmodeled covariates that can induce unexpected correlations between observers. These correlations can occur if particular conditions affect the ability of
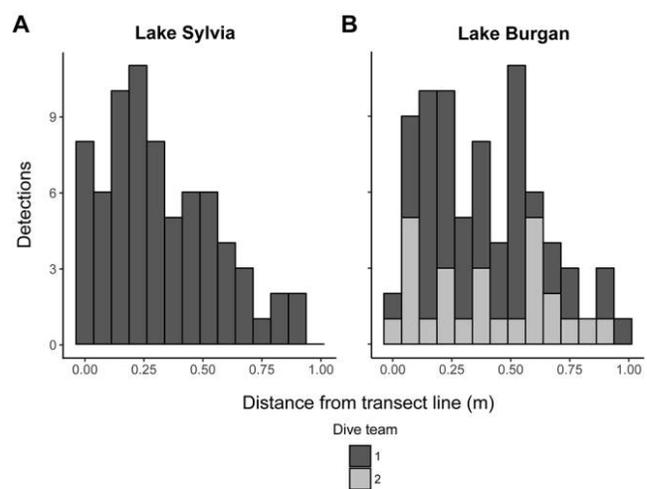

Figure 4. Stacked histogram showing the total number Zebra Mussel detections made by dive team 1 and dive team 2 in the summer of 2017. Panel A gives the total counts in Lake Sylvia from 24 transects, and panel B gives the total counts in Lake Burgan from 18 transects. Distance bin widths are 0.075 m.

both dive teams to locate a mussel. For example, a correlation would occur if both dive teams were more likely to detect larger mussels but mussel size was not included in the model. Point independence addresses correlation issues by modeling the detection probability at a single detection distance, usually specified to be where detection is maximized (here, at 0.2 m). However, left-truncating the data does not preclude including environmental covariate data in the analysis with existing tools in the *mrds* package.

Next, in the covariate-modified detection estimates 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 we thought could influence detection probabilities.

Our detection distances (Fig. 4A–B) indicated that the detection function may be unimodal, with the maximum detection probability occurring off the transect line. We tested 2 competing hypotheses that describe how detection changed with distance from the transect line. The 1st hypothesis assumed that detection was maximized on the transect line. Thus, we fit the half-normal detection function that assumes detection along the transect line is maximized. This detection function was defined as $g(y) = e^{-y^2/2\sigma^2}$ over the transect half-width ($0 \leq y \leq 1$). To test the 2nd hypothesis, we allowed for the possibility that detection was maximized off the transect line. Here, we fit the unimodal function (Becker and Christ 2015), which uses 2 truncated half-normal distributions that share a common mode, μ_k (where k designates an observer and can be 1 or 2). 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 was the scale parameter for distances less than the mode, and σ_g was 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 $g(y)$ with the *nloptr* package in R (Ypma 2015). We identified the best detection model for the Lake Burgan data based on the Akaike Information Criterion (AIC), an estimate of the Kullback–Liebler divergence that measured the relative discrepancy between each model and reality (Burnham and Anderson 2004). The AIC is a popular approach for measuring model parsimony and represents a tradeoff between model fit and complexity that achieves optimal predictive ability but avoids overfitting (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 (0 = absent, 1 = present), and Observer was an indica-

tor variable (0 = dive team 1 [$k = 1$], 1 = dive team 2 [$k = 2$]). All estimates of $\pi(\mu)$ were made with the *mrds* package.

Density estimation   For the 2nd stage of our 2-stage modeling approach, we incorporated the detection estimates from stage 1 into an analysis of mussel density. As in the detection models described above, we present 2 parallel analyses of the Lake Burgan data. The 1st analysis applied existing statistical tools to the left-truncated data (simple density estimator). We then show how to extend this analysis to account for strata and covariates that affect Zebra Mussel density (covariate-modified density estimator).

For the simple density estimator, we denote the counts for the ith transect as n_i, the total counts in T total transects as $N = \Sigma_i^T n_i$, the length of each transect as l_i, the total length of all transects as $L = \Sigma_i^T l_i$, the half-width of transects as w, and the estimated detection probability as $\hat{P}$. The estimated density is given by $\hat{D} = \frac{\Sigma_i^T n_i / \hat{P}}{2w\Sigma_i^T l_i}$ (Buckland et al. 2001) and the variance in the estimated density is

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

The 1st term in Eq. 1, $\text{var}(N)$, quantifies the variance in the total counts over all segments ($N = \Sigma_i n_i$), whereas the 2nd term quantifies the variance in the detectability, $\text{var}(\hat{P})$, estimated from stage 1. We used the design-based estimator for the variance in the total counts, $\text{var}(N) = (L\Sigma_i^T l_i (n_i / l_i - N/L)^2)/(T - 1)$, where the contribution of each segment to the total variance was weighted by the segment length. The R package *mrds* estimates $\hat{P}$ with maximum likelihood and computes the variance in detectability from the Hessian matrix (Laake et al. 2018).

In the covariate-modified density estimator model, we used the total Zebra Mussel counts at the segment-level with 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 that mussel 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 determined in stage 1 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. We recorded multiple substrate types, but gravel was the only type that had enough variation to be considered as a predictor variable because other substrates were constant or nearly constant throughout the lake. We used AIC to test whether a smoothing spline of segment location was needed to account for

spatial variation in density that was not explained by the environmental covariates. We fit density models with maximum likelihood estimation implemented in the R package *mgcv* (Wood 2006).

We estimated the density in the jth stratum with the estimator, $\hat{D}_j = \Sigma_{i=1}^{T_j}(\hat{n}_i/\hat{P}_i)/2w\Sigma_{i=1}^{T_j}l_i$, where the summation runs over all T_j segments in the stratum. The terms in the sum are: $\hat{n}_i$, the estimated number of mussels in the ith segment in stratum j; $\hat{P}_i$, the estimated detection probability in the ith segment of stratum j; and l_i, the length of segment i in stratum j. We estimated the detection probabilities with the methods described in the detection estimation section above and the counts, $\hat{n}_i$, that were modeled in the 2nd stage of the density surface model. The overall population size was determined by weighting the estimates from each stratum by the amount of area they represented in the lake, $\hat{D} = \omega_{\text{high}}\hat{D}_{\text{high}} + \omega\hat{D}$. Thus, the stratification weight for high-effort strata was $\omega_{\text{high}} = 1/11$ and for normal-effort strata was $\omega = 10/11$.

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). We calculated the total variation in density by summing the variances and covariances across all segments and used the covariance terms to account for correlation resulting from using a common detection model to adjust counts in all segments (Fieberg and Giudice 2007). The resulting covariance between the density estimates has 2 terms, analogous to the covariate independent case in Eq. 1. The covariance for segment 1 in stratum j and segment 2 in stratum j' (D_1 and D_2) is given by

$$\text{Cov}\big[\hat{D}_1, \hat{D}_2\big] = \text{E}\big[\text{Cov}(\hat{D}_1, \hat{D}_2|\hat{P}_1, \hat{P}_2)\big] + \text{Cov}\big[\text{E}(\hat{D}_1|\hat{P}_1), \text{E}(\hat{D}_2|\hat{P}_2)\big]. \quad \text{(Eq. 2)}$$

The 1st term in Eq. 2 accounts for uncertainty in the density, given the estimated detection model parameters, and the 2nd term accounts for uncertainty in the detection parameters, estimated in stage 1.

We used a parametric bootstrapping method to estimate the covariance terms in Eq. 2 following Hedley and Buckland (2004). First, we simulated 10,000 sets of parameters from the segment-level count model assuming a multivariate normal distribution. We calculated the mean of these parameters from the maximum likelihood estimates of the density model and the covariance matrix was approximated by the inverse of the estimated Hessian matrix (Bain and Engelhardt 2000). We used these simulated parameters to predict the counts for each segment, scaled these counts by the estimated segment-level detection probabilities ($\hat{P}_i$) and the amount of area surveyed in each segment. We used the covariance of these counts as the 1st term in Eq. 2.

We estimated the 2nd term in Eq. 2, the covariance matrix of the detectability correction estimates, by simulating 10,000 sets of detectability parameters from a multivariate normal distribution. We used the 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 calculate the segment-level detection probabilities, $\hat{P}_i$. We then calculated the covariance between the segment-level detectability corrections, scaled by the estimated segment-level count densities, and used the result as the 2nd term in Eq. 2.

Finally, we calculated the total variance in the density estimate with stratification weights to account for the proportion of lake area surveyed in each stratum. We scaled the full density covariance matrix, $\mathbf{V}_{\hat{D}}$, by the vector of weights (Ω) where the ith entry of the vector was ω_{high} or ω depending on whether segment i was in the high- or normal-effort stratum. The total variance in density was $\Omega^{\text{T}}\mathbf{V}_{\hat{D}}\Omega$.

RESULTS

In total, the dive team made 71 detections in Lake Sylvia (Table S1). Of these detections, 49 were of single Zebra Mussels and the average (median) cluster size was 2.02 (1) with a standard deviation of 3.18. Divers found 1 cluster of 26 mussels, and the next largest cluster was 7 mussels.

The coarse-scale substrate in the Lake Sylvia segments was predominately sand and silt (Table 1). A few segments had a combination of gravel, pebbles, and rocks. All segments with Zebra Mussels had silt and also often had sand. In general, the proportion of Zebra Mussels found in each substrate type was consistent with the available substrate frequencies. Zebra Mussels were most often attached to the fine-scale substrates gravel (attached 46% of the time) and rocks (40%).

The coarse-scale substrate in the Lake Burgan segments was predominately silt and sand (Table 1), followed by gravel and then rocks. The proportion of Zebra Mussels found in each habitat type was similar to the proportion of each habitat available, so mussels primarily occurred in sand and silt, followed by gravel and rocks. Zebra Mussels in Lake Burgan were attached to gravel, rocks, and wood. We also detected 1 mussel attached to a native mussel, 1 mussel attached to scrap metal, and 2 mussels on other materials (fabric and unidentified mollusks).

The left-truncated detection data set from Lake Burgan included 48 unique Zebra Mussel detections. The 1st dive team made 35 detections, the 2nd dive team made 19 detections, and the teams shared 6 detections. Of these unique detections, 1 was a cluster of 2 individuals, and the remaining 47 detections were of single Zebra Mussels. The full detection data set included 66 unique mussel detections. The 1st dive team made 49 detections, whereas the 2nd dive team made 26 detections, and the teams shared 9 detections (Table S2). Of these 66 unique detections, 64 were of single Zebra Mussels, and 2 were clusters of 2 individuals.

Table 1. The frequency of available substrate types in segments where Zebra Mussel detections occurred (coarse-scale substrate; potentially classified with multiple types so proportions do not sum to 1), and the type of substrate Zebra Mussels were attached to (fine-scale substrate; proportions sum to 1).

	Sand	Silt	Gravel	Pebble	Rock	Wood	Native mussel	Other
Lake Sylvia								
Available coarse spatial scale substrate	0.73	0.70	0.05	0.02	0.02	0	0	0
Coarse spatial scale substrate with mussel detections	0.53	1	0	0	0	0	0	0
Fine-scale substrate with mussel attachment	0	0	0.18	0	0.35	0.41	0.05	0.01
Lake Burgan								
Available coarse spatial scale substrate	0.88	0.90	0.55	0	0.04	0	0	0
Coarse spatial scale substrate with mussel detections	0.91	0.87	0.65	0	0.04	0	0	0
Fine-scale substrate with mussel attachment	0	0	0.46	0	0.40	0.06	0.02	0.06

Detection estimation

The 1st stage of the 2-stage density estimation required estimating a detection probability. Using the left-truncated detection data set with the simple density estimator, 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).

In our analysis of the full detection data set with the covariate-modified density estimator, the unimodal detection function was slightly more parsimonious than the half-normal model (ΔAIC = 0.23), though this small difference means these 2 models are effectively equivalent given the available data. We will, therefore, only use results from the unimodal model in the rest of the manuscript because it was found to be slightly more parsimonious, though we note that the estimates of density made in the 2nd stage of the 2-stage analysis using either the half-normal detection model used in the simple-density estimator or this unimodal model were basically identical.

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 Fig. 5.

The double-observer model coefficients suggested that the 2nd dive team had lower detection probabilities than the 1st team and that plant presence decreased the probability of detecting Zebra Mussels (Table 2). The positive clarity coefficient suggested that, as expected, detectability increased with water clarity. However, the estimated confidence intervals of the clarity effect were very wide and overlapped 0, and the confidence interval of the odds ratio also overlapped 1 (i.e., the null value for odds ratio; Table 2). Therefore, we also ran a reduced model without the clarity covariate. This model had a lower AIC (Table 3) and reduced the standard error in density because of detectability (the 2nd term in Eq. 1) from 0.05 to 0.008. Removing clarity

from the model had minimal impact on the other regression parameter estimates. Thus, we only present results based on 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 0.05 (dive team 2 with plant cover present) to 0.41 (dive team 1 with no plant cover present; Table 4). These detection probabilities are calculated by integrating the detection function, given in Fig. 5, over transect half-width. We calculated the mean and standard error of the detection probability in segments with and without plants using the bootstrap procedure described in the methods.
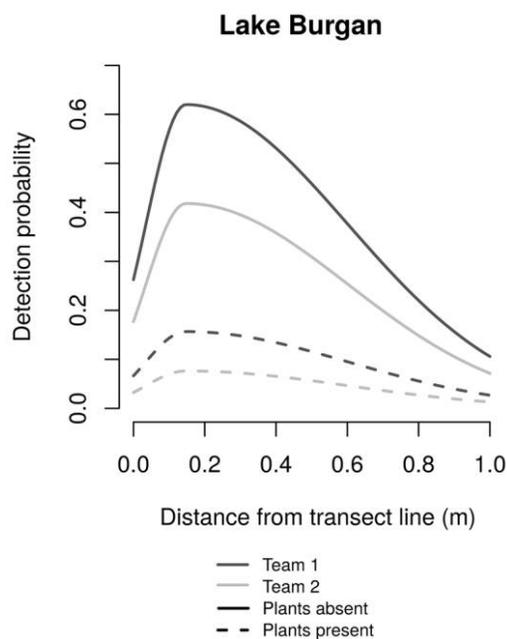

Figure 5. Estimated detection functions in Lake Burgan from the unimodal detection model. We used a double-observer survey to estimate the detection probabilities for each team in the presence or absence of plants.

Table 2. Parameter estimates in the Lake Burgan detectability model.

	Mean	Standard error	Odds ratio	95% confidence interval of odds
Intercept	−3.53	3.62		
Observer 2	−0.86	0.29	0.42	(0.24, 0.75)
Plant presence	−2.18	0.87	0.11	(0.02, 0.62)
Clarity	2.96	2.59	19.24	(0.12, 3094.12)

Density estimation

In the 2nd stage of our 2-stage analysis, we used the detection probabilities estimated above to correct for imperfect detection in the Zebra Mussel counts. We constructed 49 different survey segments from the 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 imperfect detection, was 0.08 mussels/m^2.

The 2 methods we used to estimate mussel density that corrected for detection probability gave similar results. Our estimate of the overall mussel density in Lake Burgan, based on the simple density estimator used with the left-truncated data set, was 0.24 (SE = 0.1). Sixty-seven % of the error in this estimate arose from uncertainty in the detection parameters. Our estimate of the overall mussel density in Lake Burgan, based on the unimodal detection function and covariate-modified density estimator, environmental covariates, and strata and corrected for detection, was 0.25 (SE = 0.09) mussels/m^2. Three % of this error arose from uncertainty in the detection parameters. Thus, both estimators led to a 3× increase in the estimated density relative to the observed density.

In the normal-effort stratum, our covariate-modified density estimate was 0.28 (SE = 0.11) mussels/m^2, and in the high-effort stratum our covariate-modified density estimate was 0.25 (SE = 0.09) mussels/m^2. These results may be nearly identical because we defined strata based on observed densities in the field and did not test for statistical differences among transects. The transect used to define the high-effort strata had the highest observed density of mussels, but subsequent transects in the high-effort strata had densities that were consistent with the normal-effort strata.

Our estimate of the scale parameter in the negative binomial distribution was 1.477, indicating over-dispersion of mussel densities among segments. The model that did not include spatial structure was more parsimonious than the model with the spatial smoothing term (Table 3). Parameter estimates from the generalized linear model indicated that Zebra Mussel densities tended to be lower in shallower areas and areas with plant cover, whereas gravel had a small positive effect on density (Table 5). However, all of these covariate estimates had high uncertainty with confidence intervals that included 0.

DISCUSSION

We demonstrated that line transects with double-observer surveys can allow the estimation of the density of invasive Zebra Mussels in newly-infested lakes. This method allows researchers to cover more area compared to quadrat surveys but at the cost of imperfect detection. Importantly, we found that accounting for the low detectability of Zebra Mussels led to density estimates >3× higher than the observed densities. Thus, for every Zebra Mussel our divers detected, they missed ~2.

Low-detection probabilities, such as those in our study, are common in wildlife surveys and can have a substantial impact on estimated densities (Kellner and Swihart 2014). Previous work applying distance surveys to the endangered marine bivalve, *Pinna nobilis*, found that detection in a 2-m-wide transect depended on mussel size, with detection being perfect for individuals with shell lengths >18 cm and ~50% for smaller individuals between 2 to 18 cm long (Katsanevakis 2005). By comparison, the length of an adult Zebra Mussel is around 4 to 5 cm, suggesting that we wouldn't expect to detect them perfectly (Mackie 1993). Inoue et al. (2014) used double-observer distance sampling on the freshwater mussel (*Popenaias popeii*) and found that the detection distances were uniformly distributed, indicating distance did not affect detection. This result differs from our results, which could be because of differences in the behavior of searchers or in the visibility conditions between midwestern lakes and desert streams. For example, it was not clear whether divers in Inoue et al. (2014) searched for mussels from the transect line, as our divers did, or whether they were actively searching the transect belt. The detection probability of the distance survey was not reported, but Inoue et al. (2014) also conducted a mark-recapture survey that

Table 3. Covariate selection tables for the Lake Burgan analysis. The spatial regression spline is written as (Easting, Northing).

	Log likelihood	Number of parameters	AIC	ΔAIC
Detection model				
Observer + Plants + Clarity	−50.25	5	110.50	0.55
Observer + Plants	−50.98	4	109.96	0
Density model				
Observer + Plants + Gravel + ss(Easting, Northing)	−45.50	6	143.91	2.85
Observer + Plants + Gravel	−46.65	4	141.06	0.

Table 4. Estimated probability of detecting a Zebra Mussel in Lake Burgan under different conditions with 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	0.10	0.07	0.05	0.04

estimated transect-level detection probabilities varied between 70 and 80%. This survey also found evidence of imperfect detection on the transect line, consistent with our results. We conclude that single-observer distance survey methods, which assume perfect detection on the transect line, are generally not appropriate for estimating freshwater mussel densities, but appropriateness may depend on the size of the organism and on survey conditions.

Detections in both Lake Sylvia and Lake Burgan exhibited a peak near 0.2 m from the transect line, suggesting that detection probabilities were highest just off the transect line (Fig. 4A–B). We were surprised to find this peak in our dive surveys, though similar patterns occur in many aerial surveys (Quang and Lanctot 1991). We used 2 methods that are appropriate for these data: truncation and a unimodal detection function. However, the statistical evidence supporting unimodal detection is still equivocal. More samples could help determine whether this effect is a real pattern or an artifact of sampling variation.

If the causes of unimodal detection in dive surveys are known, it may be possible to eliminate it by improving the study design. In aerial trials that display unimodal detection, low detection near the transect line arises because animals close to the transect appear to pass by more quickly than animals further away (Becker and Quang 2009). To address this effect, observers can spend more time with their eyes focused 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 practice on how to most effectively move their eyes across the width of the transect would have been helpful. We also know of at least 1 case when our lead diver missed a Zebra Mussel near the transect line 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 that could cover nearby mussels. The effect of unimodal detection can be eliminated by applying the left-truncation of detection distances, as we illustrated with the simple density estimator.

A complication in our preparation of the field data for analysis was determining whether detections made by the 1st observer were also made by the 2nd observer. We found that our analysis of density was very robust to how we clas-

sified redetections (Appendix 2). However, at higher densities of Zebra Mussels there would have been greater uncertainty, so it would have been better 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). Error in the distance measurements made classifying redetections difficult. Alternative methods exist, such as the removal design (Moran 1951, Otis et al. 1978) that calls for removal of individuals from the population once they are detected. This approach ensures that the 2nd observer always detects new individuals and may provide a robust alternative to the double-observer design tested here.

We found evidence that the ability of our divers to detect Zebra Mussels was linked to habitat, with detection being significantly lower in segments with plant cover. Design factors such as observer identity are often included as covariates in distance models, but these models rarely include habitat covariates. However, 1 study found that polar bear (*Ursus maritimus*) detectability in aerial surveys decreased with increases in habitat structure, a measure of surface flatness (Aars et al. 2009). Another study found that increases in shrub density lowered the detectability of Australian rainforest birds (Anderson et al. 2015). Here, we found some evidence that water clarity influenced detection, but this effect had very broad confidence intervals, perhaps because visibility conditions did not vary much within the lake. We found that removing the clarity covariate from our detection model lowered the contribution of uncertainty in our density estimate from detection error from 18 to ~3% of the total standard error. The remaining uncertainty in the density estimate was primarily from sampling variation in the number of detections. We suggest that including habitat covariates will be critical when applying detection models outside the sites where the model was developed. However, initial surveys that will be used to develop detection models for new sites should be designed to cover the full range of the covariates that may occur in new sites.

Several options exist for obtaining more precise distance survey estimates when faced with limited time to perform

Table 5. Estimates of covariate effects in the density and detection models of Lake Burgan.

Variable	Estimate	Standard error	95% confidence interval
Detection model			
Observer	−0.86	0.38	(−1.61, −0.10)
Plants	−2.37	0.41	(−3.18, −1.57)
Density model			
Plants	−0.43	0.54	(−1.50, 0.63)
Depth	−0.05	0.06	(−0.16, 0.06)
Gravel	0.12	0.38	(−0.62, 0.86)

surveys. It may be possible to combine transect surveys with remote-sensing technologies (e.g., acoustic surveys). For example, SCUBA-surveys could be used to calibrate more extensive, but less accurate counts made by acoustic surveys. Alternatively, remote sensing data that can link habitat covariates to Zebra Mussel density could be used for effort stratification, allowing for divers to increase their survey effort in areas where mussels are most likely to be detected. Finally, increasing the survey speed could increase the number of transects surveyed and reduce the variation in the counts but at the cost of lower detectability. This tradeoff between survey speed and detectability has not been well studied, but the optimal solution probably depends on the underlying mussel density and the spatial variation in density. Thus, there may be cases where it is advantageous to survey with lower detection probabilities if this allows divers to incorporate additional transects.

Freshwater mussels are useful for studying the constraints of time-limitation on study designs because divers have a limited time in the water and must consider how to sample most effectively. However, many other types of surveys also have implicit time-limitations based on budget considerations (e.g., Ferguson et al. 2014) or the time needed to move between sites (e.g., Giudice et al. 2010). Past work on freshwater mussels has primarily focused on the efficient discovery of rare species. For example, Green and Young (1993) explored how much effort is required to detect, with a specified degree of confidence, the presence of a rare species using quadrat surveys. Other work that has compared how timed-searches perform against slower quadrat surveys for the detection of rare species (Vaughn et al. 1997, Metcalfe-Smith et al. 2000) has found that timed searches tend to perform better. However, density estimation requires more formal designs than timed searches because of the need to measure the area surveyed. Thus, there is still a critical need to understand how the precision of density estimates from quadrat and distance sampling is influenced by the tradeoff between survey coverage and imperfect detection.

We are aware of 1 previous study that compared the efficiency of distance and quadrat sampling to estimate the density of freshwater mussels (briefly described in 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 2 survey methods decreased as mussel 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. It is necessary to control survey time (or cost), rather than the survey area, to compare survey efficiency directly. Future data collection efforts should attempt to capture information on survey effort across a range of densities, which would allow us to determine whether the optimal survey strategy changes with density. Comparisons of survey efficiencies are especially relevant for monitoring recently-invaded lakes, where densities need to be estimated over large areas of lake bottom to determine the extent of the invasion.

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