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Research Article

An initial assessment of plankton tow detection probabilities for dreissenid mussels in the western United States

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Abstract

Early detection of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) is crucial to mitigating the economic and environmental impacts of an infestation. Plankton tow sampling is a common method used for early detection of dreissenid mussels, but little is known about the sampling intensity required for a high probability of early detection using the method. We used implicit dynamic occupancy models to estimate plankton tow detection probabilities of dreissenid mussels from a long-term data set containing plankton tow samples collected across central and western United States. We fit models using a) the entire data set, including water bodies with unknown occupancy status in addition to heavily infested water bodies, b) a data subset that included water bodies with paired water temperature data, and c) a data subset that included water bodies with lower dreissenid densities. For the entire data set, we found that estimated detection probabilities varied by water body size and ranged from approximately 0.10 to 0.86. For the water temperature subset, we observed the same pattern between detection probability and water body size as we did for the full data but additionally found that the estimated detection probabilities were much higher when water temperatures were above 12 °C. For the lower dreissenid density subset, we found that the estimated probability of detecting dreissenid mussels with a single aggregated plankton tow sample was near zero. Given these estimates, we conclude that the number of aggregated plankton tow samples taken per water body in the data is far fewer than the number needed to ensure a high probability of detecting dreissenid mussels, especially if they are at low densities. We summarize the analyses with a discussion of plankton tow sampling protocol changes needed to improve estimates of dreissenid detection probabilities.

Key words: occupancy modeling, dynamic occupancy, Bayesian hierarchical modeling, zebra mussels, quagga mussels

Introduction

Early detection surveillance is a pillar of invasive species management because early detection can accelerate actions that effectively contain and control the invader (Vander Zanden et al. 2010). However, the effort required to detect an invader shortly after its initial introduction is a critical knowledge gap in many invasive species monitoring programs (Trebitz et al. 2017). Introduction events are characterized by rare individuals at low densities, so sampling efforts that are too low are likely to miss these

introductions. Delayed detections could allow an incipient population to become established, prevent any practical control efforts, and increase the magnitude of ecological and socio-economic impacts (Spear et al. 2021). Since resources are typically limited, managers need guidance on cost-effective sampling effort allocation.

The sampling effort required for reliable detection of low-density populations is difficult to determine experimentally since it is intractable to introduce a novel species into most natural systems. Observational studies are also challenged by imperfect detection, where individuals are present at a site, but fail to be detected during a survey because of environmental conditions, behavior, or inadequacies in the sampling method (Bailey et al. 2004). Occupancy models provide a tool for gaining insight about the relationship between sampling effort and detection probability (p) in natural systems. These models incorporate information from independent surveys of the same site to account for imperfect detection and estimate site-level occupancy and survey-level detection probability (MacKenzie et al. 2002). Occupancy models have resulted in considerable variation in low-density detection probabilities as functions of survey methods and site-specific covariates. For example, Schmelzle and Kinziger (2015) found that detection probabilities of endangered tidewater goby (*Eucyclogobius newberryi* (Girard, 1856)) using environmental DNA (eDNA) sampling were nearly double that of non-molecular methods, whereas Tank et al. (2021) found a three-fold difference in detection probabilities of invasive New Zealand mudsnails (*Potamopyrgus antipodarum* (Gray, 1843)) across sites using visual surveys. Given this variation, using the incorrect detection probability to guide early detection sampling effort decisions could result in costly oversampling or delayed detections that enable invasive species establishment. Thus, estimates of detection probabilities should be a priority for invasive species monitoring programs.

Zebra (*Dreissena polymorpha* (Pallas, 1771)) and quagga mussels (*D. rostriformis bugensis* (Andrusov, 1897)), hereafter dreissenid mussels, are an example of invasive species that lack ample information about the sampling effort required for effective early detection monitoring. Dreissenid mussels are prolific aquatic invaders that now occur in most major water basins in eastern North America. Once established, dreissenid mussels can cause significant economic and ecological impacts that are predicted to result in annual expenditures of 100s of millions of dollars (USD) for control and mitigation efforts (Prescott et al. 2013; Nelson 2019).

Early detection of dreissenid mussels increases the likelihood that rapid response management actions can prevent population establishment and further spread to additional water bodies. Tens of millions of dollars (USD) are invested annually to prevent, contain, and control the spread of invasive dreissenid mussel in North America, yet the sampling effort required for high probability of detection has been given minimal scrutiny (Department

of the Interior 2020). Counihan and Bollens (2017) used species accumulation theory to quantify the sampling effort required for a high probability of detecting rare planktonic taxa. Using these results, they inferred that the sampling effort expended in 2012–2014 was magnitudes too low for reliable early detection of dreissenid mussels in many Columbia River and Snake River reservoirs in the Pacific Northwest. Direct assessments of dreissenid mussel early detection monitoring using occupancy models have been challenged by the absence of appropriate data; many sites lack monitoring data prior to invasion and the sites that do have those data, often lack standardized methods and spatio-temporal replication.

Here, we take advantage of a high frequency, multi-year, standardized monitoring data set from across the western United States that emerged from a multi-jurisdictional, collaborative effort following the discovery of dreissenid mussels in Lake Mead, Nevada in 2007. This collaborative group established a standard protocol for plankton tow sampling of dreissenid mussel veligers (Western Regional Panel on Aquatic Nuisance Species 2020). Veligers are the microscopic planktonic larval form of dreissenids. Unlike adult dreissenids, veligers free swim in the water, which allows for them to be sampled by towing a fine mesh plankton net (~ 64 μm) through ≥ 1000 L of the water column. Plankton tows are collected at multiple locations per water body per season, typically sampling locations where mussel introduction is likely (e.g., boat docks and moorings). At each location, the debris from all plankton tows is aggregated into a single sample and examined using cross-polarized light microscopy for dreissenid mussel veligers. Following the microscopic evaluation, species identification is confirmed using a molecular technique such as polymerase chain reaction (Western Regional Panel on Aquatic Nuisance Species 2020).

We used implicit dynamic occupancy models to evaluate these data; our objectives were to provide initial estimates of the dreissenid mussel detection probabilities of plankton tow sampling and identify environmental covariates that may influence detection probabilities. Using model results, we provide initial guidance about early detection sampling effort allocation in the western United States and identify methodological improvements that could bolster the accuracy and precision of future detection probability estimates.

Materials and methods

Data

Plankton tow data consisting of 11,442 samples from 325 water bodies across central and western United States were collected by the Bureau of Reclamation (hereafter referred to as Reclamation) and their state, federal, and tribal partners from fall 2011 to fall 2020. The plankton tow samples were analyzed for veliger presence by Reclamation's Technical Service Center in Denver, Colorado (USA). Multiple plankton tows collected at a

given location, from the same water body, on a given day were aggregated to a single sample, therefore each sample refers to the aggregate of multiple tows. Consequently, our detection probability estimates are in terms of aggregated samples and not individual tows. Most samples lacked a description of the number of tows aggregated per sample, so we were unable to account for differences in sampling effort.

We removed water bodies that did not fit our scope of interest, such as hatcheries, water storage and treatment facilities, and one water body in Canada. Additionally, we removed observations prior to October 1, 2012 and after September 30, 2020 because the seasonal data were not complete for those time periods.

To examine if water body specific factors are associated with plankton tow sample detection probabilities, we obtained potential covariate information from multiple data sources. Few covariates of interest were collected with the Reclamation data. We focused on five covariates: water temperature, dissolved calcium, pH, water body size, and water year. Rationale for each covariate is provided below. Importantly, the associations between dreissenid mussel physiology and water temperature, dissolved calcium, and pH are approximate, as the local conditions experienced by dreissenids are difficult to accurately characterize and vary across geographic regions, environmental conditions, and seasons (Claxton and Mackie 1998; Jones and Ricciardi 2005; Whittier et al. 2008; Claudi et al. 2012; White et al. 2015). Water temperature, dissolved calcium, and pH were extracted from the Water Quality Portal (WQP, https://www.waterqualitydata.us/) as described in Supplementary material Appendix 1 (National Water Quality Monitoring Council, 2012). For each covariate of interest, the WQP data was joined with the Reclamation data as detailed in the Appendix 1. The WQP data were collected for other purposes and likely do not reflect the exact values at the time of the plankton tow samples. Consequently, we split each of the covariates into distinct categories to mitigate uncertainty in the measurements.

For each of the covariates, the categories and their associated covariate values are displayed in Table 1; justification for the category choices and a brief description of the biological relevance of each of the covariates follows.

Dreissenid survival and reproduction can be limited by water temperature. Mortality increases as water temperatures exceed 28 °C (Karatayev et al. 2010) and reaches acute thermal limits between 30 and 32 °C (Garton 2013). Temperatures that are too cool (< 12 °C) can inhibit gametogenesis; primary spawning occurs when temperatures are 16–18 °C (Garton et al. 2013). We treated water temperature as a sample-specific covariate since it varies seasonally within a water body. However, on a given day, water temperatures were treated as constant across all sampling locations within a water body.

Dreissenids are also sensitive to pH, however the physiological mechanisms are unclear. Changes in acidification can lead to differing calcification rates, shell strength, and mortality rates (Claudi et al. 2012). To ensure there were

Table 1. Water body temperature, pH, dissolved Calcium, and water body size categories used for modeling. The pH and dissolved calcium category names correspond to the presumed risk for dreissenid mussel presence, whereas the category names for water temperature and water body size describe the variables themselves. To create the water body size variable, surface area measurements were divided using quantiles so that the number of samples per category was approximately the same.

	Category	Value
Water Temperature (°C)	Low	≤ 12
	Mid	> 12 to 28
	High	> 28
pH	Minimal	< 7 or > 9.6
	Moderate	7.0 to 7.3 or 9.4 to 9.6
	High	> 7.3 to < 9.4
Dissolved Calcium (mg/L)	Minimal	< 8
	Moderate	8 to 20
	High	> 20
	Unknown	Missing
Water Body Size (km²)	Stream	Stream
	Small	≤ 5.105
	Medium	> 5.105 to 12.533
	Large	> 12.533 to 40.465
	Larger	> 40.465

pH data for all water bodies, pH was treated as constant for a given water body across the entire study period. pH category breaks are based on data presented in Ramcharan et al. (1992) and Claudi et al. (2012).

In both native and invaded areas, dreissenids are sensitive to dissolved calcium values because calcium is required for shell building and for metabolic functions (Jones and Ricciardi 2005; Whittier et al. 2008). For a given water body, we considered dissolved calcium as constant across the entire study period.

Water body size is another factor that may influence plankton tow detection probabilities. If dreissenids occur at similar abundance in small and large water bodies, then all else being equal, more samples are needed to detect dreissenids in a large water body. Larger water bodies are also likely to attract a larger number of motorized watercraft recreation, and so may be at increased risk of dreissenid mussel introductions (Robertson et al. 2020). Surface area (km^2) estimates were taken from the USGS National Hydrography Dataset's (NHD) Waterbody feature class, which is comprised of polygons representing water bodies in the NHD. The surface areas are approximations since water bodies have fluctuating water levels and source data were compiled over a period of several decades, therefore we split water body size into categories to mitigate the uncertainty in the measurements. With the exception of the stream category, we divided the surface area measurements using quantiles so that the number of samples per category was approximately the same.

Finally, water year was added as a seasonal variable describing the 12-month period that spans from October 1 of a given year to September 30 of the following year. This variable was added to allow for potential changes in occupancy status of a water body over time, assuming within a season

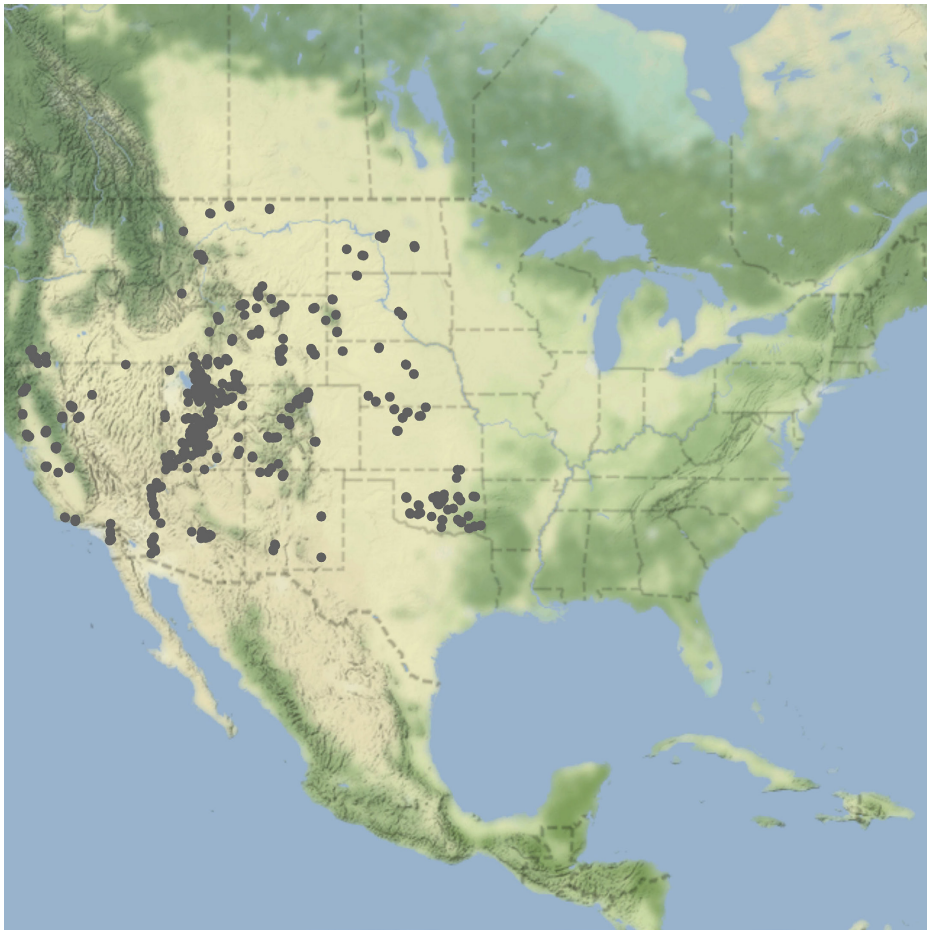

Figure 1. A map of the plankton tow Reclamation survey locations, where each point represents a plankton tow survey site within a water body (Google 2021).

Table 2. Number of samples, number of water bodies, and average number of samples per water body sampled per season.

Dates	Season	Number of Samples	Number of Water Bodies	Average Number of Samples
10/1/12–9/30/13	1	1,268	146	8.68
10/1/13–9/30/14	2	1,288	146	8.82
10/1/14–9/30/15	3	1,342	156	8.60
10/1/15–9/30/16	4	1,353	159	8.51
10/1/16–9/30/17	5	1,572	164	9.59
10/1/17–9/30/18	6	1,546	157	9.85
10/1/18–9/30/19	7	1,449	190	7.63
10/1/19–9/30/20	8	1,185	162	7.31

the occupancy status of water bodies does not change. Additionally, the use of water year allowed us to capture peak spawning periods within each season since peak spawn periods depend on water temperature, which varies geographically over the study region.

After the data were cleaned, there were 11,003 observations from 288 water bodies (Figure 1). In any given season, several water bodies were only sampled once. The maximum number of samples at a single water body taken in any single season was 104. During each season, about 50–65% of all water bodies in our data set were sampled (Table 2). Since water bodies were not consistently sampled every season, we used the implicit parameterization of the dynamic occupancy model described by MacKenzie et al. (2017).

Dynamic Occupancy Models

The implicit parameterization of the dynamic occupancy model, detailed by MacKenzie et al. (2017), was used to estimate occupancy and detection probabilities for water body/season combinations. The implicit parameterization of the dynamic occupancy model is appropriate for answering the questions of interest since the probability of detecting dreissenid mussel veligers using plankton tow surveys is of foremost interest. In this parameterization, samples taken in prior seasons do not influence the occupancy status of the site in the current season. Since colonization and local extinction were not modeled here, the model assumes that the underlying process that results in changes in occupancy is random, and that the probability a previously occupied site remains occupied is equal to the probability of colonization at a previously unoccupied site (MacKenzie et al. 2017). In the model, Z_{it} is defined as the binary presence ($Z_{it} = 1$) or absence ($Z_{it} = 0$) of the species of interest at site i during season t. The model formulation for the latent occupancy state is found in (1). Site-specific covariates can be included using the relationship described in (2).

$$Z_{it} \sim Bernoulli(\psi_{it}) \tag{1}$$

$$logit(\psi_{it}) = \mathbf{x}'_{it}\boldsymbol{\beta} \tag{2}$$

In (1) and (2), ψ_{it} denotes the probability site i is occupied by the species of interest during season t, $\mathbf{x}'_{it}$ represents the covariates for site i during season t, and $\boldsymbol{\beta}$ represents the corresponding vector of regression parameters. A relationship between the occupancy probability and season can be specified in the models by including season as a covariate in Equation 2 as done by Field et al. (2005).

At the sample level, Y_{ijt} is the binary detection of the species of interest in sample j from site i during season t. The model formulation for the binary response variable is found in (3). Sample-specific covariates can be included using the relationship described in (4).

$$\mathrm{Y_{ijt}|z_{it}} \sim \mathrm{Bernoulli}(\mathrm{z_{it}p_{ijt}}) \tag{3}$$

$$\mathrm{logit}(\mathrm{p_{ijt}}) = \mathrm{w'_{ijt}}\alpha \tag{4}$$

In (3) and (4), z_{it} is the latent occupancy state for site i during season t, p_{ijt} denotes the probability that the species of interest is detected in the jth sample from site i during season t, conditional on the species being present at site i during season t, $\mathbf{w}'_{ijt}$ are the sample specific covariates for sample j from site i during season t, and $\boldsymbol{\alpha}$ is the corresponding vector of regression parameters.

Using this model with the plankton tow data, we treated each water body as a site, which is reasonable if we assume that the entire water body was occupied with dreissenid mussels during a season if any sample from

that water body was positive. It is important to note that a sample is considered the aggregate of multiple plankton tows taken from a given sampling location within a water body on the same date. Additionally, a sample was considered positive if at least one veliger was detected using microscopy. The definition of a positive sample used here is not the same as the definition of a positive water body used by the Western Regional Panel on Aquatic Nuisance Species (WRP) since the WRP requires multiple subsequent sampling events where, for the same sample, there are two independent lab results that confirm presence (Western Regional Panel on Aquatic Nuisance Species 2020).

As previously mentioned, the implicit dynamic occupancy model assumes that the probability that an occupied site remains occupied is equal to the probability of colonization of an unoccupied site. It seems unlikely that the probability that an occupied water body remains occupied, and the probability that an unoccupied water body is colonized by dreissenids are equal; however, these model estimates are used to provide initial guidance for plankton tow monitoring of dreissenid mussels. The model also assumes that there are no false positive detections, meaning that if Reclamation detected dreissenid mussel veligers in a sample from a water body, then there were truly dreissenids in that sample and consequently in the water body. Finally, the model assumes that the occupancy status of a water body is constant within a season, but can change from season to season. We could not formally evaluate whether assumptions were satisfied; consequently, model results should be considered as a useful first step to understand detection probabilities and to inform future directions for model refinement and data collection.

Modeling Plankton Tow Detection Probabilities

To estimate the plankton tow detection probability and associated covariates, we examined three different scenarios: 1) the full data set, 2) a subset of the data where the water body temperatures retrieved from the WQP are within 14 days of the plankton tow sample, and 3) a subset of the data that contains water bodies with lower density populations. The anonymized data are available at https://github.com/meaghanwinder/Plankton_Tow_Data. All models were fit using NIMBLE, a package for fitting Bayesian models in R (de Valpine et al. 2020; R Core Team 2021). Each model was fit using four chains of 5,000 iterations, of those, half were discarded for burn-in. Resulting trace-plots were inspected to insure model convergence. For each scenario, any model comparisons to address the impact of the various covariates were done with Watanabe-Akaike information criterion (WAIC). The default WAIC values calculated by NIMBLE are the conditional WAIC values corresponding to *WAIC2* in Gelman et al. 2013; de Valpine et al. 2020. Smaller WAIC values generally indicate better fit for models fit to the same data set. Models with WAIC

values within 2 units of each other are considered similar. Additionally, for all models fit, a *Normal* (0.2^2)prior was used for each of the α and β parameters to be estimated; the prior distribution was chosen because it is a relatively uninformative prior when the logit-link function is used.

Full Data

With the full data set, we identified potential covariates associated with the effectiveness of plankton tow sampling for dreissenid mussels. In order to accurately model detection probability, we accounted for potential differences in occupancy probability due to environmental covariates. We considered a model that included an additive relationship between pH, dissolved calcium, water body size, and season to attempt to model any potential differences in occupancy probability, in addition to water body size as a covariate to describe any changes in detection probability. Since all covariates used for modeling are categorical, we examined contingency tables of the covariates to assess any potential relationships between the explanatory variables themselves. For the full data, water bodies that had a high risk of dreissenid mussels based on pH also often had a high risk of dreissenids based on dissolved calcium; there did not appear to be strong relationships between the remaining combinations of variables. As a result, we fit models that included water body size as a covariate for detection probability along with either pH or dissolved calcium as a covariate for occupancy probability. Additionally, we fit a model that described heterogeneity in detection probability by accounting for water body size and treated occupancy probability as constant. The final model treated both occupancy and detection probabilities as constant.

Temperature Subset

For the temperature data subset, we explored the relationship between water temperature and estimated detection probability. To ensure that water temperatures used for modeling reflected the actual water temperature category on the date of the observation, we only included observations where the water temperature data pulled from the WQP was within 14 days of the plankton tow sample. After filtering, we were left with 7,574 observations from 250 water bodies. For the temperature data subset, we considered a model that included an additive relationship between pH, dissolved calcium, water body size, and season to attempt to model any potential differences in occupancy probability and an additive relationship between water body temperature and water body size to describe any potential differences in detection probability. Similar to the contingency tables for the full data set, there did not appear to be a strong relationship between variables with the exception of pH and dissolved calcium. As a result, we fit a model that included both water body size and temperature as covariates for the detection probability along with either pH or dissolved

calcium as a covariate for occupancy probability. Similarly, we fit a model that included only water body size to account for potential changes in detection probability and either pH or dissolved calcium to model potential changes in occupancy probability. Additionally, we fit a model that described heterogeneity in detection probability by accounting for water body size and water temperature and treated occupancy probability as constant. Furthermore, we fit a model that described any differences in detection probability using water body size as a covariate and treated occupancy probability as constant. The final model treated both occupancy and detection probabilities as constant.

Low Population Density Subset

To provide insight on estimates of the plankton tow sampling in water bodies early in their dreissenid infestation, we explored the estimated detection and occupancy probabilities for a subset of water bodies with low population densities. Based on direction from Reclamation, we used 527 observations from three water bodies where dreissenid presence is confirmed, but veligers are only occasionally detected. For this subset of data, we fit a singular model with constant occupancy and detection probabilities.

Estimating the Required Number of Samples

Using model results, several derived quantities can be calculated. In this case, we were interested in the required number of samples to obtain a target probability of detecting dreissenid veligers at least once if present in a water body. For a constant detection probability p, the probability of detecting dreissenids, if present, in least one of n samples is specified in (5). Using (5), for a given constant detection probability, we calculated the number of samples required to obtain a target probability of detecting dreissenid mussel veligers at least once.

$$\mathrm{p}^{*} = 1 - (1 - \mathrm{p})^{\mathrm{n}} \tag{5}$$

Additionally, using the model results and (5), we calculated a set of initial guidelines for future plankton tow sampling for dreissenid veligers. Using model results, we grouped estimates of water body size and temperature categories with similar estimates of detection probability to form various sampling conditions. Under each sampling condition, we calculated the approximate number of samples for a worst-case scenario and an expected scenario. For the low abundance condition, estimates from the model fit to the low population density subset were used; the estimated lower 95% credible interval boundary was used to calculate the approximate number of samples for a worst-case scenario and the estimated mean was used to calculate the approximate number of samples for an expected scenario. For all other conditions, the number of samples required for the worst-case scenario was estimated using the minimum

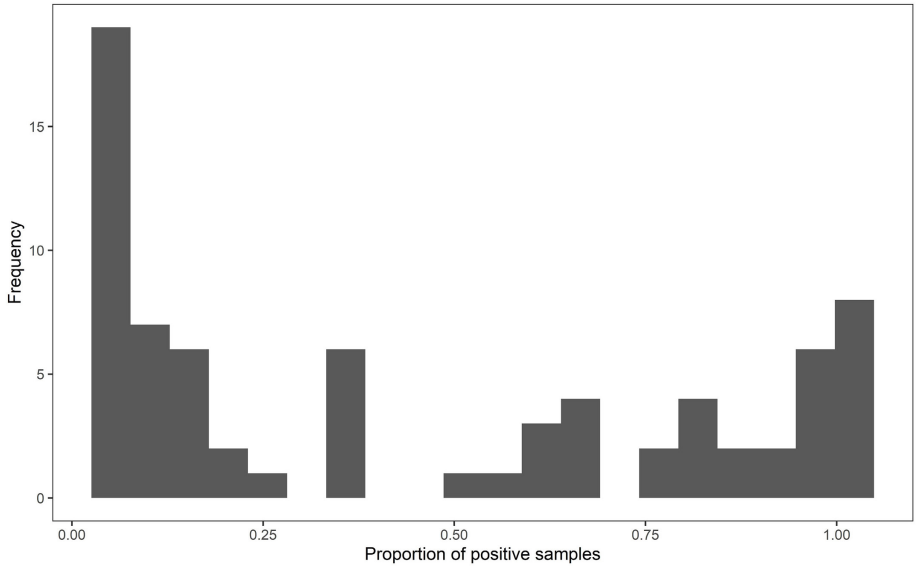

Figure 2. For water bodies with at least one positive sample in a given season, a histogram of the proportion of positive samples during that season. Of the water body/season combinations with at least one positive detection, there were 8 water body/season combinations in the data set where all samples were positive, and 10 water body/season combinations where veligers were observed in 5% or fewer samples.

lower 95% credible interval boundaries for combinations of water body size and temperature included in the condition, and the number of samples required for the expected situation was calculated using the minimum of the estimated mean detection probabilities for combinations of water body size and temperature included in each condition.

Results

A naive understanding of detection probabilities was gained by visualizing the proportion of positive samples during a given season, in water bodies with at least one positive sample that season. Of the 288 water bodies in the full data, 39 had at least one detection in one or more seasons (Figure 2). Based on the histogram, the detection probability appears non-constant across water body/season combinations. There are 8 water body/season combinations in the data set where, if dreissenids veligers were observed at least once, they were observed in all samples taken from that water body during that year. However, there are 10 water body/season combinations where veligers were observed in 5% or fewer samples, conditional on being observed at least once. Notably, the data set included both early detection data from locations with unknown mussel populations and data from long-term population monitoring projects at water bodies with mussel infestations.

Full Data

Three models were plausible, as they had similar low WAIC scores, and therefore predictive performance (Table 3). These models treated detection probability as a function of water body size and occupancy probability as either constant, a function of pH, or a function of dissolved calcium.

Table 3. WAIC for models fit to the full data set.

Occupancy	Detection	WAIC
Ca	Size	1902.28
Constant	Size	1902.44
pH	Size	1903.92
pH, Ca, Size, Season	Size	1912.58
Constant	Constant	2350.24

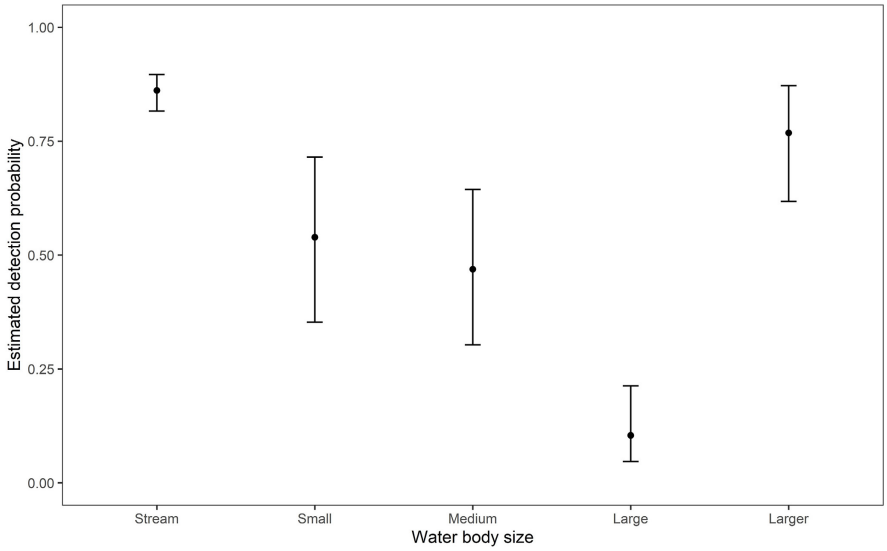

Figure 3. Estimated detection probabilities and 95% credible intervals of detection probability by water body size for the full data set.

Table 4. WAIC for models fit to the temperature subset.

Occupancy	Detection	WAIC
Constant	Size, Temp	980.65
Ca	Size, Temp	980.88
pH	Size, Temp	980.89
pH, Ca, Size, Season	Size, Temp	992.25
pH	Size	1040.65
Ca	Size	1041.01
Constant	Size	1041.09
Constant	Constant	1438.41

We report parameter estimates based on the most parsimonious of the three plausible models, where occupancy probability was treated as constant and detection probability was treated as a function of water body size. The estimated occupancy probability was 0.073 (95% credible interval: 0.058, 0.090), meaning that about 7% of the observed water body/season combinations are expected to be occupied with dreissenid mussels. The estimated detection probability was highest for streams and water bodies larger than 40.465 km^2 (larger), lowest for water bodies between 12.533 and 40.465 km^2 (large), and about the same for water bodies up to 12.533 km^2 (small and medium) (Figure 3, Table S1).

Temperature Subset

We found support for three plausible models (Table 4), which treated detection probability as a function of water body size and water temperature

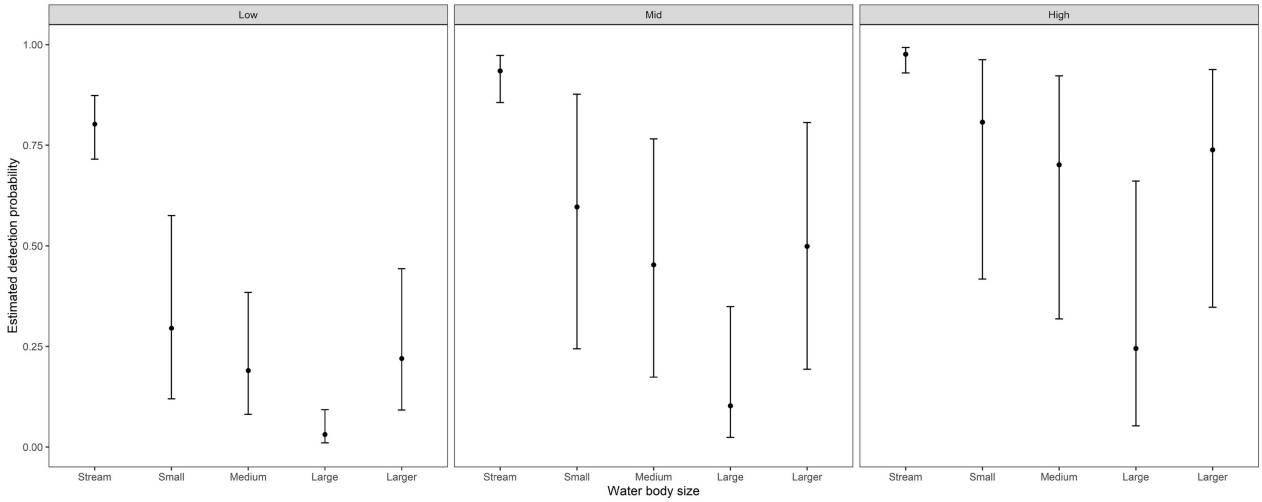

Figure 4. Estimated detection probabilities and 95% credible intervals of detection probability by water body size, faceted by water temperature for the temperature subset data.

and occupancy probability as either constant, a function of pH, or a function of dissolved calcium.

For simplicity, estimates of detection and occupancy probabilities are reported for the model that treated occupancy probability as constant and detection probability as a function of water body size and water temperature. Based on this model, the estimated occupancy probability was 0.068 (95% credible interval: 0.051, 0.088), meaning that about 7% of the observed water body/season combinations in the temperature subset are expected to be occupied with dreissenid mussels. We observed the same pattern between detection probability and water body size as we did for the full data set, where the estimated detection probability was highest for streams and water bodies larger than 40.465 km^2 (larger), lowest for water bodies between 12.533 and 40.465 km^2 (large), and about the same for water bodies up to 12.533 km^2 (small and medium), additionally, the estimated detection probability was much larger for water bodies above 12 °C (mid and high) than it is for water bodies below 12 °C (low) (Figure 4, Table S2).

Low Population Density Subset

Based on the single model fit to the low population density subset, the estimated occupancy probability was 0.611 (95% credible interval: 0.292, 0.930), meaning that between 29% and 93% of the observed water body/season combinations in the low population density subset are expected to be occupied with dreissenid mussels. The resulting occupancy estimates are not surprising because we chose water bodies that we knew had low density populations and fit a model to all seasonal data from those water bodies collected from fall 2012 to fall 2020. As expected, the estimated detection probability was smaller for the low population density subset (95% credible interval: 0.016, 0.079) than for the previous two scenarios.

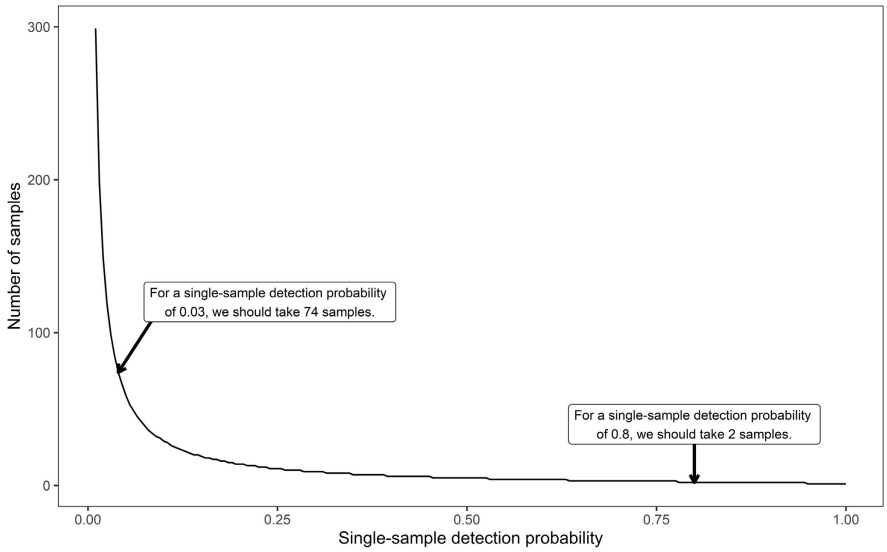

Figure 5. The required number of samples to obtain a minimum 95% probability of detecting dreissenid mussels at least once, if they are present, based on detection probabilities for a single sample.

Table 5. Number of samples needed to obtain a 95% minimum probability of detecting dreissenid mussels in at least one plankton tow sample, if they are present, for several constant single-sample detection probabilities.

Single-Sample Detection Probability	Number of Samples
0.010	299
0.030	99
0.055	53
0.130	22
0.255	11
0.380	7
0.455	5

How Many Samples?

Using (5), we calculated the number of samples required for a minimum 95% probability of dreissenid detection, if they are present, for a variety of constant single-sample detection probabilities (Figure 5 and Table 5). It is important to keep in mind when examining Figure 5 and Table 5, a sample refers to multiple aggregate tows taken on a given date at a sampling location within a water body.

Using the model results and (5), we provide a set of initial guidelines for plankton tow sampling for dreissenid veligers in the future. After grouping water body size and temperature categories with similar detection probability estimates to form sampling conditions, the approximate number of samples for a worst-case scenario and a more expected situation were calculated for each condition (Table 6). For various sampling conditions, we estimated that as few as 2 and as many as 299 samples may be required to ensure a minimum probability of dreissenid detection. Sampling effort estimates using the low population density subset model ranged from 74 to 149 samples. Whereas estimates from the model fit to the temperature subset ranged from 2 samples in streams warm enough for spawning to 299 samples in large, cooler water bodies.

Table 6. The approximate number of samples for both a worst-case scenario and an expected scenario for a variety of water conditions.

Condition	Water Body Size	Water Temperature	Worst-Case	Expected
low abundance	–	–	149	74
streams above 12° C	Stream	Mid, High	2	2
< 12.5 km² and above 12° C	Small, Medium	Mid, High	17	6
between about 12.5 and 40.5 km² and above 12° C	Large	Mid, High	149	29
> 40.5 km² and above 12° C	Larger	Mid, High	15	5
streams at or below 12° C	Stream	Low	3	2
< 12.5 km² and at or below 12° C	Small, Medium	Low	36	15
between about 12.5 and 40.5 km² and at or below 12° C	Large	Low	299	99
> 40.5 km² and at or below 12° C	Larger	Low	32	13

Discussion

Most invasive species monitoring programs have limited sampling resources compared to the area they seek to monitor. By collecting too few samples at a site, incipient populations may remain undetected until they are large and destructive; conversely, oversampling may lead to higher costs and only marginal increases in detection. Therefore, invasive programs should benefit from routine evaluation of survey effectiveness (Hoffman et al. 2016). In addition to providing a starting place for considering how to effectively allocate limited resources, these types of efforts can also identify protocol modifications needed to reduce estimated uncertainty. Here, we used available data from a multi-agency, regional, monitoring program to provide initial guidance on the plankton tow sampling intensity needed to detect invasive dreissenid mussel veligers in many western USA water bodies.

We found that a one-size-fits-all approach to sampling intensity could result in false-negatives at most sites and oversampling at a few sites. An individual sample (consisting of multiple plankton tows) had a near-zero probability of detecting mussel veligers at the water bodies where mussels occurred at lower densities; consequently, we conclude that, 74–149 samples are needed per season to ensure a 95% probability of detecting dreissenids in at least one sample if they are present (Table 6). Estimates derived from models that considered data sets with more water bodies also underscored that sampling intensities in the tens or hundreds are required for effective detection. Large water bodies require 29–299 samples per season, whereas small and medium water bodies require 6–36 samples per season (Table 6).

These estimates are in strong contrast to the sampling effort at most water bodies considered in the full data set, where 7–10 samples were collected per water body each year and at least half of the water bodies were sampled five of fewer times each season (Table 2). This low sampling effort is similar to what has occurred in water bodies in the Pacific Northwest, where 85% of water bodies had fewer than 10 plankton tows (Counihan and Bollens 2017). Only sampling intensities that occurred at streams and larger water bodies appear to be adequate for a high probability of detecting dreissenid mussel veligers when present (Table 6). Importantly, these larger water bodies included several highly infested waters such as

Lake Powell, Utah and Lake Mead, Nevada that potentially bias our understanding about the effectiveness of plankton tow sampling for low density populations.

We also found that detection probabilities were higher when water temperatures were above 12 °C, confirming that plankton tow samples should be taken when water temperatures are warm enough for dreissenids to be spawning. For a constant water body size class, if samples are taken when water temperatures exceed 12 °C, the sampling effort is about half that required for samples taken in cooler water temperatures.

Our detection probability estimates derived from the three lower density water bodies are in line with other studies that have directly or indirectly evaluated plankton tow detections of dreissenid mussel populations. Frischer et al. (2005) found that non-aggregated plankton tows had naive detection rates of zebra mussel veligers as low as 1/72 samples (0.01) and as high as 8/74 samples (0.11) at sites in Lake George, New York (USA). Lake George is thought to be representative of a low-density dreissenid mussel infestation since active control measures have kept population abundance and spread to a minimum (Wimbush et al. 2009). Counihan and Bollens (2017) used estimates of the proportion of plankton taxa detected for a given volume of water filtered with plankton tow nets to infer the effort needed to detect rare species, like low density dreissenid mussel veligers. They found that current water volumes are 1–2 orders of magnitude lower than what is needed to detect 95% of plankton taxa that occur in each of four water bodes in the Pacific Northwest. Taken together, greatly enhanced levels of plankton tow sampling intensity are needed for early detection of dreissenid mussels.

Plankton tow sampling at such high levels at multiple sites is likely to be cost prohibitive and there are few alternative detection tools that are both highly sensitive and cost effective. Environmental DNA sampling has been heralded as such a tool (Larson et al. 2020), but it still may require considerable levels of sampling to detect DNA of low-density organisms. For example, detection probabilities of invasive carp eDNA near their leading edge of spread in the Upper Mississippi River (Mize et al. 2019) and dreissenid mussel eDNA at a recently invaded reservoir in Montana (Sepulveda et al. 2019) were low, so 10s of samples are required at a site for effective surveillance. Moreover, most managers still require non-molecular confirmation of eDNA detection before initiating containment or control actions (Sepulveda et al. 2020). Thus, many monitoring programs will have to make difficult decisions about how to allocate resources for more effective early detection. Risk assessment tools can be used to identify a more tractable subset of water bodies or sites where, for example, dreissenid mussel invasions are most probable or where their invasions are likely to cause the greatest harm (Mandrak and Cudmore 2015). Higher levels of sampling efforts can be allocated to the prioritized water bodies.

Limitations and next steps

A pitfall of many monitoring programs is that methods are not explicitly designed for rigorous, statistical evaluation (Nichols and Williams 2006; Lindenmayer and Likens 2009). Consequently, assumptions must be made to conform available data to model requirements, so it is important to clarify the potential effects of these assumptions on model results. Water bodies in our data set were selected by managers due to their invasion vulnerability and socio-economic value and sampling locations within water bodies were chosen as sites where mussels were most likely to be introduced and establish (e.g., boat ramps, marinas, dams). Thus, our results only apply to the water bodies we evaluated in each of data sets and cannot be generalized. Additionally, we did not account for sample location within a water body since there were too few samples taken per year at each sample location within a water body to model any potential sampling location heterogeneity. If dreissenid veligers are most likely to occur at these vulnerable water bodies and sampling locations, then our model estimates may provide best-case estimates of detection probability and sampling intensity. Additionally, it is likely that the number of tows aggregated in each sample, or the volume of water sampled in each tow (i.e., sampling effort), varied greatly within and among water bodies. However, the majority of samples lacked a description of sampling effort so we could not account for the impact sampling effort may have had on estimated detection probabilities. Finally, when using the implicit dynamic occupancy model, we assume that the occupancy status of a water body during a given season does not depend on the occupancy status of that water body in previous seasons. Even if this assumption is violated, the results are useful for establishing initial guidance for plankton tow sampling of dreissenid mussels.

Several protocol modifications could improve the rigor of future plankton tow detection probability evaluation. Samples that are preserved as individual tows rather than aggregates of multiple tows should increase the precision of detection probability estimates and would allow for modeling potential heterogeneity in sampling locations within a water body; the trade-off is a large increase in lab time for analysis, since technicians would be performing microscopy analyses on multiple individual tows rather than one aggregate sample of the several plankton tows. Detailed recording of sampling effort (e.g., total water volume) would allow for modeling the detection probability as a function of sampling effort and allow for an understanding of the association between sampling effort and detection probability. Paired observations of tow samples with water quality covariate measurements would lead to more accurate model results, as we would not have to rely on WQP data that has unknown spatio-temporal relevance to the tow samples. If the covariate data collection was paired with tow

sampling, we could explore the impact of the quantitative covariates on occupancy and detection probabilities, rather than choosing arbitrary category bounds. The use of quantitative covariates could lend itself to a deeper understanding of how environmental factors can be used to guide early detection monitoring efforts for dreissenid mussel veligers.

Conclusion

Invasive species early detection is difficult to achieve under the best of circumstances and most invasive species programs are challenged by detection tools with low sensitivity, too many sites to monitor, and small budgets. Periodic evaluation of survey effectiveness can help guide efficient use of scarce resources, increase the probability of early detection, and reduce the likelihood of costly, delayed detections. Vast amounts of monitoring data are never analyzed, resulting in missed opportunities to improve effectiveness and the potential waste of public money (Wintle et al. 2010). In our study, we used an implicit dynamic occupancy framework to evaluate a plankton tow monitoring program for dreissenid mussels in the western USA. We found that the current sampling effort is often much lower than required for effective detection of dreissenids. Adjusting sampling effort based on water body size and increasing sampling during seasons when water temperatures are warm enough for dreissenid spawning are two initial means to more efficiently allocate sampling resources. Identification of more specific actions likely to lead to additional gains in effectiveness will require adoption of adaptive management concepts, where monitoring methods are informed by clear objectives, rigorous statistical design, routine evaluation, and iterative updating (Nichols and Williams 2006).

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Authors' contribution

MW: research conceptualization, data analysis and interpretation, writing – original draft, writing – review and editing; AJS: research conceptualization, writing – original draft, writing – review and editing; AH: research conceptualization, writing – review and editing.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Model estimates and credible intervals of detection probability for the full data set.
Table S2. Model estimates and 95% credible intervals of detection probability for the temperature subset.
Appendix 1. Data Processing.
Appendix 2. NIMBLE Model Code.

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