Species distribution models effectively predict the detection of *Dreissena* spp. in two connecting waters of the Laurentian Great Lakes

Shay S. Keretz[a]*, David T. Zanatta[a], Todd J. Morris[b], Ashley K. Elgin[c], Edward F. Roseman[d], and Daelyn A. Woolnough[a]

[a]Department of Biology and Institute for Great Lakes Research, Central Michigan University, Mount Pleasant, Michigan, USA, 48859
[b]Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, Ontario, Canada, L7S 1A1
[c]National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 1431 Beach, St., Muskegon, Michigan, USA 49441
[d]U.S. Geological Survey Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan, USA, 48105

*Corresponding author: shaykeretz1@gmail.com

Abstract

Among the highest profile invasive species in the Laurentian Great Lakes region are *Dreissena polymorpha* and *D. rostriformis bugensis* (collectively dreissenids). Despite their abundance and ecosystem-wide effects, little is known about dreissenid distribution in large connecting channels between lakes. The objectives of this study were to estimate and document dreissenid densities and their habitat characteristics throughout the St. Clair River, to compare dreissenid species demographics, and predict spatial distributions between two connecting waters of the Great Lakes: the St. Clair and Detroit rivers. Two types of species distribution models (SDMs), MaxEnt and classification and regression tree analysis (CART), were created using dreissenid and habitat data collected in both the Detroit and St. Clair rivers. The SDMs were then used to predict presence of dreissenids in the St. Clair River. The St. Clair River had more *D. r. bugensis* (mean density = 486 ± 152 individuals/m^2) than *D. polymorpha* (mean density = 3 ± 1 individuals/m^2). The SDMs created from the Detroit River data reliably predicted presence of dreissenids in the St. Clair River. Depending on the river and species, CART models identified velocity and depth to be important predictor variables, while distance to river inlet/outlet were the most influential variables in the MaxEnt models. Most research on dreissenid distribution modeling is focused on determining areas for potential spread; however, this study presents a unique perspective by modeling dreissenid presence, both *D. polymorpha* and *D. r. bugensis* separately and together, where they have been established for more than 30 years.

Keywords: MaxEnt, Dreissenids, Species Distribution Modeling, Large Rivers, CART analysis

Introduction

The Laurentian Great Lakes (hereafter Great Lakes), which contain the planet's second largest volume of surface freshwater, have a history of many threats to ecosystem health (Hartig et al., 2020) including, but not exclusive to, water pollution, overexploitation, habitat fragmentation or degradation, habitat destruction, and invasive species (Dudgeon et al., 2006; Reid et al., 2019; Strayer and Dudgeon, 2010). With more than 180 non-native species documented, the Great Lakes have a long and well-known history of invasion (Ricciardi, 2006; Sturtevant et al., 2019). Common vectors of introduction for non-native species into the Great Lakes include both unintentional and intentional release, such as release from international shipping vessel ballast water (Havel et al., 2015; Sturtevant et al., 2019). Non-native species become invasive when they cause harm to ecosystem functioning, biodiversity, economy, and/or human health (Ricciardi, 2006). Among the highest profile invasive species in the Great Lakes region that have caused considerable ecological (both biotic and abiotic) alterations are *Dreissena polymorpha* and *D. rostriformis bugensis* (collectively dreissenids; Karatayev et al., 2015; Karatayev and Burlakova, 2022a; Madenjian et al., 2015).

Both dreissenid species were introduced to the Great Lakes via shipping vessel ballast water, with *D. polymorpha* being introduced in the mid-1980's and *D. r. bugensis* introduced in the late 1980's (Hebert et al., 1989; Sturtevant et al., 2019). Dreissenids have a high reproductive potential, with a free-swimming planktonic veliger stage (*e.g.,* larval stage) and an epifaunal benthic adult stage (Karatayev et al., 2015; Karatayev and Burlakova, 2022a). Following their introduction to the Great Lakes region, they spread rapidly throughout the Great Lakes basin, including Lake St. Clair and the connecting waterways (Schloesser et al., 2006, 1998; Schloesser and Nalepa, 1994; Sturtevant et al., 2019). Within the Great Lakes, initial dreissenid densities were high, with a max density of 30,000 individuals/m^2 in Lake Erie (Griffiths et al., 1991). Specific to the survey area in the current study, the Lake Huron – Erie corridor, mean dreissenid densities estimated in Lake St. Clair were 1,237 individuals/m^2 in 1997 (Nalepa et al., 2001) and 2,211 individuals/m^2 in 2014-2015 (Pawlowski et al., 2019). In 2014-2015, mean dreissenid densities were 981 individuals/m^2 and 1,895 individuals/m^2 in the Detroit and St. Clair rivers, respectively (Pawlowski et al., 2019). Most recently, mean dreissenid densities in the Detroit River were 308 individuals/m^2 (Keretz et al., 2021).

The effects of the dreissenid invasion on the Great Lakes have been well-documented and include altered plankton communities (Kerfoot et al., 2010; Strayer et al., 1998), impacted food web structure (Madenjian et al., 2015), increased water clarity (Kerfoot et al., 2010; Nalepa et al., 1996), and increased toxic *Microcystis* blooms through selective filtering (Vanderploeg et al., 2001). Dreissenids can negatively affect native freshwater mussels (Bivalvia: Unionidae, unionids), a highly imperiled faunal group (Haag and Williams, 2014). Great Lakes unionid populations are negatively affected by the dreissenid invasion through direct impacts like fouling (Burlakova et al., 2000; Ricciardi et al., 1995) and induced unionid shell deformities (Ricciardi et al., 1996), and the presence of dreissenids has indirect impacts on unionids through competition for food and/or habitat (Burlakova et al., 2000; Strayer and Malcom, 2007; Strayer and Smith, 1996). Additionally, dreissenids have negatively impacted both juvenile and adult fishes through their impacts on food webs (Heath et al., 1995; Madenjian et al., 2015; Strayer et al., 2014) with documented negative effects of dreissenids on recruitment for commercially and recreationally important fish like Walleye (*Sander vitreus*) and Lake Whitefish (*Coregonus clupeaformis*) (Gobin et al., 2015; Hoyle et al., 2008; McNickle et al., 2006; Rennie, 2014).

Because of the strong negative effects of dreissenids, there is an increased need for updated surveys of dreissenid distributions in large connecting channels such as the St. Clair River. Additionally, previous dreissenid models have focused on their spread, distribution, and potential impact, but few studies have focused on modeling dreissenid presence decades after their introduction and establishment. A predictive model of dreissenid occurrence in the St. Clair and Detroit rivers could assist with dreissenid management as well as the protection of impacted species. Therefore, the objectives of this study were to 1) document dreissenid densities throughout the St. Clair River and to 2) compare dreissenid species demographics and predict spatial distributions between two connecting rivers of the Great Lakes: the St. Clair River and the Detroit River. Species spatial distributions were compared by creating predictive species distribution models (SDMs) using MaxEnt and classification and regression tree analysis (CART) and the Detroit River dreissenid data from Keretz et al. (2021) to predict dreissenid locations in the St. Clair River.

Methods

Study Area

The St. Clair – Detroit River System is part of the Huron – Erie corridor in the Great Lakes and forms the international border between the United States and Canada. The St. Clair River (Port Huron, MI; 42°58′49″N 82°26′15″W) is 65 km long, has a surface area of 67 km^2, and flows from Lake Huron to Lake St. Clair, with the outflow into Lake St. Clair branching into the St. Clair Delta (St. Clair Flats). The Detroit River (Detroit, MI; 42°19′53″N, 83°2′45″W) is 44 km long, has a surface area of 96 km^2, and flows from Lake St. Clair to Lake Erie. Generally, the St. Clair River is colder, narrower, and flows faster than the Detroit River (Fischer et al., 2018). Flow through the St. Clair – Detroit River System is mainly determined by the water level differences between Lake Huron and Lake Erie (Anderson et al., 2010; Anderson and Schwab, 2011); and therefore, unlike many other large river systems, flow remains relatively constant and minimal changes in velocity are observed year-round and through time, with the exception that strong wind events have been shown to temporarily disrupt mean flow rates (Anderson and Schwab, 2011; Fischer et al., 2018, 2015). Mean yearly discharge for the St. Clair – Detroit River System is 5,300 m^3/s and the mean water retention time is 19 hours in the Detroit River and 21 hours in the St. Clair River (Burniston et al., 2018; Derecki, 1984; Fischer et al., 2018). The St. Clair – Detroit River System has been regularly dredged since the mid-1800's as a part of the International Great Lakes Shipping Channel and a 10 m minimum depth throughout the shipping channel is currently maintained (Bennion and Manny, 2011).

St. Clair River Dreissenid Surveys

The St. Clair River was surveyed for dreissenids during July – August 2021. The Detroit River was surveyed for dreissenids during July – August 2019, and results from this survey are described in Keretz et al. (2021). Sites in the Detroit and St. Clair rivers were selected using similar criteria and briefly, entailed a mixture of randomly selected, historically surveyed, and potential refuge sites for unionids that spanned the entire length of each river. Site selection was specifically designed to effectively survey the entire river for native unionid mussels; therefore, historically surveyed sites were previously surveyed for unionids in the 1980's and 1990's (W. Kovalak, Detroit Edison Company, personal communication, May 2019; Schloesser et al., 1998) and potential unionid refuge sites were chosen based on expert knowledge of unionid refuge space (Keretz et al., 2021; Zanatta et al., 2015, 2002). Further details on site selection are located in Keretz et al. (2021). For both rivers, the GPS coordinates, site depth (m), surface water temperature (°C; Garmin ECHOMAP PLUS 95 SV Canada 9" with GT52 Transducer, Garmin, Kansas, U.S. or Helix 7 CHIRP MEGA DI GPS G4, Humminbird, Wisconsin, U.S.), and Secchi tube depth (measure of water clarity; Dahlgren et al., 2004; cm; 120 cm Fieldmaster Secchi Tube, Science First, Florida, U.S.) were recorded at each site. Macrophyte coverage (%) and sediment composition (%) for the site were estimated during each SCUBA survey. Estimates of sediment composition for the site followed the Wentworth scale (Wentworth, 1922). Six sediment samples were collected per site using a petite PONAR grab (grab area = 0.0225 m^2; 6" Petite PONAR, Wildco, Michigan, U.S.), and all sediments were stored in plastic bags and returned to the laboratory for processing.

Estimation of dreissenid densities followed the protocol specified in Keretz et al. (2021). Briefly, the PONAR-collected sediments were stored in plastic bags for 1 to 4 months at room temperature and then rinsed with water through 4 mm and 1 mm sieves to separate out the dreissenid mussels. The mussels were then identified to species and categorized as either a shell or live individual. Similar to classifications used for recently dead unionid shells (Crail et al., 2011), live dreissenids were assumed to have at least two of the following characteristics: intact hinge, intact periostracum, emergent byssal threads on the ventral side, or tissue present. Individuals that did not have at least two of these characteristics were categorized as shells (i.e., dead at the time of PONAR collection). The number of live individuals and shells counted were divided by the petite PONAR area (0.023 m^2) to estimate dreissenid densities per m^2 (Caldwell et al., 2015). All live *D. polymorpha* and *D. r. bugensis* were measured to the nearest mm with calipers. Further details on dreissenid data collection (*e.g.,* half and whole shell calculation) can be found in Keretz et al. (2021). Dreissenid shell data are reported in Electronic Supplementary Materials (ESM Table S3, Fig. S3, and Fig. S4) to provide insight into changes in the ecosystem but were not used to model dreissenid presence.

MaxEnt Model Building

MaxEnt software (Phillips et al., 2006) has been used previously to model dreissenid distributions on local and global scales to attempt to predict dreissenid spread into new habitats (Barnes and Patiño, 2020; Bosso et al., 2017; Quinn et al., 2014). MaxEnt predicts the probability of a species' detection using two parameters: known locations of the target species and environmental data that is presented in equally sized spatial cells (Elith et al., 2011). Species detection is then given as a probability distribution over the predicted area (Phillips et al., 2006). MaxEnt benefits include its use of presence-only data, that it works well with small sample sizes, that it can handle correlated variables, and that its output is continuous which allows for habitat distinctions to be made on a finer scale (Bean et al., 2012; Elith et al., 2011; Phillips et al., 2006; Rhoden et al., 2017). Because of these benefits, MaxEnt was chosen as one of the species distribution modelling methods in this study.

Continuous environmental variables from the Detroit and St. Clair rivers were considered for model construction: depth (m), total water velocity (m/s), east/west velocity (m/s), north/south velocity (m/s), and river distance (m) to the respective river's inlet, outlet, and nearest tributary. Depth, total water velocity, east/west velocity, and north/south velocity were obtained from a regional hydrological model created by Thompson (2016). ArcGIS software (ArcGIS Desktop: Release 10.8.2; ESRI, 2011) was used to interpolate depth, total water velocity, east/west velocity, and north/south velocity across the Detroit River Area of Concern GIS shapefile (EPA, 2006) and the St. Clair River Area of Concern GIS shapefile (EPA, 2019). All tributaries for both rivers, regardless of size, were considered and were identified using Google Earth and the National Geographic basemap in ArcGIS (National Geographic et al., 2011, n=5 Detroit River tributaries and n=16 St. Clair River tributaries). Interpolated variable layers were created using the Inverse Distance Weighting (IDW) interpolation tool with a cell size of 650 m^2. River distances to the river's inlet, outlet, and nearest tributary were estimated using the Euclidean Distance Tool (ESRI, 2011) to determine the shortest Euclidian distance around barriers. A 400 m buffer (200 m each side) around the Great Lakes International Shipping Channel was removed from both river search areas since this area was not sampled due to safety concerns. With the 400 m buffer around the shipping channel removed, the modeled surface areas for the Detroit and St. Clair rivers were 81 km^2 (84% remaining) and 42 km^2 (63% remaining), respectively.

MaxEnt was used to create SDMs for dreissenids (both species combined) and SDMs for *D. polymorpha* and *D. r. bugensis* separately using dreissenid occurrence (detection/non-detection) data collected in the Detroit River in 2019 (Keretz et al., 2021). Within MaxEnt, each model was created from an average of 10 iterations, using a different training (80%) and validation (20%) data set for each iteration (standard proportions; Phillips et al., 2006). The following default settings were applied: remove duplicate presence records, 500 iterations, regularization multiplier fixed to 1, and a selection of 10,000 background points. Other settings used include random seed and a sub-sample replicate run-type. The selection of 10,000 background points from the environmental data represents background environmental conditions (Phillips and Dudik, 2008). The random seed and sub-sample replicate run-type were used to ensure that a different training data set was used for each replicate (Ward et al., 2009). All models were created using the previously described environmental variables in combinations designed to avoid using variables directly related to one another (*e.g.*, river distance to river's inlet and outlet). An example combination of variables is depth, total water velocity, and river distance to the river's outlet and nearest tributary. Correlation coefficients were determined for all variables using the Band Collection Statistics tool in ArcGIS (ESRI, 2011; ESM Tables S1, S2). The initial model included all the variables from each systematic set after which the variable with the least importance based on the MaxEnt jackknife output was eliminated until only two variables remained (Yiwen et al., 2016). The MaxEnt jackknife output, or the test of gain method, is a heuristic approach for assigning the contribution of each variable to the model (Yiwen et al., 2016).

Each model was visualized in the Complementary Log-Log (ClogLog) output format, which displays the model output as a range from 0 to 1 as an estimate of occurrence probability (Phillips et al., 2017, 2006). The resulting models from the Detroit River were then projected to the St. Clair River to predict dreissenid, *D. polymorpha*, or *D. r. bugensis* occurrence in the St. Clair River. Models projected to the SCR are denoted by -SCR in the model name; see Table 1 for a complete list of the models visualized and their annotation.

All models were assessed using the area under the receiving operator curve (AUC), a metric of the probability that the model is able, in predicted space, to correctly differentiate between detection locations and random locations throughout the survey area (Phillips et al., 2006). Generally, a perfect model would have an AUC of 1, an excellent predictive model would have an AUC between 0.9 and 1, a good predictive model would have an AUC between 0.7 and 0.9, and a model with an AUC of 0.5 means the model is equivalent to random prediction (Bean et al., 2012; Phillips et al., 2006; Reiss et al., 2011). In the current study, the model with the highest AUC was selected as the final model and was visualized in ArcGIS (ArcGIS Desktop: Release 10.8.2; ESRI, 2011). If two models tied for the highest AUC or had close AUC values, the model with the fewest contributing variables was selected as the final model to align with the law of parsimony. Previous studies have cautioned against heavy reliance on AUC for determining model fit, especially for presence-only modeling programs like MaxEnt (Lobo et al., 2008; Merow et al., 2013). In the current study however, the AUC was used to select the final model and the final model was further evaluated with empirical methods and additional validation in the field similar to other recent MaxEnt studies (Almarinez et al., 2021; Bossenbroek et al., 2018; Westwood et al., 2020).

Evaluation and Field Validation of the MaxEnt Models

The sites surveyed in the Detroit River during 2019 and the final $DR_{dreissenid}$ model (Table 1) were used to determine threshold occurrence probability values for dreissenid occurrence in the Detroit River. Similar to Bean et al., (2012) and Bossenbroek et al., (2018), a threshold occurrence probability value classifies the model's continuous output into discrete areas of detection and non-detection. Mean and range occurrence probabilities were calculated for Detroit River sites where dreissenids were detected and where dreissenids were not detected. The threshold occurrence probability values assessed increased in increments of 10% from the minimum to the mean occurrence probabilities (30-70%) for dreissenid detection sites. Areas with occurrence probability greater than the threshold were classified as areas with a high likelihood of dreissenid detection. Then, the different threshold occurrence probabilities were assessed by determining the number of sites that were correctly identified as either dreissenid detection or non-detection sites.

Sites where dreissenids were detected in 2021 in the St. Clair River were then used to evaluate the $DR_{dreissenid}$-SCR projection using each of the threshold occurrence probability values. The prediction success of the $DR_{dreissenid}$-SCR projection was determined based on the number of St. Clair River sites correctly identified as dreissenid detection or non-detection sites using the different occurrence probability thresholds. Additionally, estimates of dreissenid densities calculated from field data collected in the St. Clair and Detroit rivers were compared using a non-parametric Mann-Whitney test.

The St. Clair River models ($SCR_{dreissenid}$, SCR_{poly}, and SCR_{bug}; Table 1) were then created using the MaxEnt model building methods described above and the St. Clair River dreissenid data collected in 2021. The $SCR_{dreissenid}$ model was then compared to the $DR_{dreissenid}$-SCR projection and assessed for differences using the following equation:

$$(1)\ |\ DR_{dreissenid}\text{-SCR projection} - SCR_{dreissenid}\ |$$

The differences between the two models were then visualized in ArcGIS.

Additionally, the individual DR_{poly}, SCR_{poly}, DR_{bug}, and SCR_{bug} models were compared and assessed for differences in and between the Detroit and St. Clair rivers using the following equations:

$$(2)\ |\ DR_{poly}\text{-SCR projection} - SCR_{poly}\text{ model}\ |,$$

$$(3)\ |\ DR_{bug}\text{-SCR projection} - SCR_{bug}\text{ model}\ |,$$

$$(4)\ |\ DR_{poly}\text{ model} - DR_{bug}\text{ model}\ |,$$

$$(5)\ |\ SCR_{poly}\text{ model} - SCR_{bug}\text{ model}\ |$$

The differences between the models from the above equations were then visualized in ArcGIS.

Classification and Regression Tree Analysis

Local scale environmental data collected during both Detroit River and St. Clair River surveys were analyzed using a classification and regression tree (CART) analysis (*rpart*; Therneau and Atkinson, 2019). For both the Detroit and St. Clair rivers, six CART models were made encompassing detection and non-detection data for *D. polymorpha* and *D. r. bugensis* separately and combined (all dreissenids). The variables used to construct the CART models were site depth (m), water velocity (m/s), estimated submerged macrophyte coverage (%), and estimated site composition (%) of clay, silt, sand, pebbles, and cobbles. All variables used in the Detroit River models and St. Clair River models were visualized in a correlation matrix and tested for correlation using linear regressions in order to adhere to the CART model assumption that habitat variables are independent. Results are reported as R^2 values and p-values less than Bonferroni-corrected α (0.002; ESM Fig. S1 and Fig. S2). The optimal tree was found by over-building the model and then pruning the tree using 10-fold cross-validation and the resulting optimal complexity parameter (*caret*; Kuhn, 2020; Jarošík, 2011). Each pruned CART model was then tested for generality using the entire data set by assessing the accuracy of each node. An AUC value was calculated for all CART models using the *pROC* package (Robin et al., 2011).

All CART modeling and statistical analyses were done using the R Core Team (2019) statistical software using the *caret*, *rpart*, and *pROC* statistical packages cited above. Statistical tests were considered significant at α of 0.05 and all abiotic and biotic variables are reported as mean ± standard error, unless otherwise noted.

Results

St. Clair River Dreissenid Survey

Dreissenids were detected at 40 of 51 sites surveyed in the St. Clair River. Sites where dreissenids were detected had a mean depth of 4.7 ± 0.5 m, a mean water velocity of 0.49 ± 0.03 m/s, and a mean estimated macrophyte coverage of 46 ± 5% (Table 2). *Dreissena polymorpha* were detected at 10 sites and *D. r. bugensis* were detected at 40 sites. Mean total dreissenid density in the St. Clair River was 490 ± 152 individuals/m^2. The mean densities of *D. polymorpha* and *D. r. bugensis* in the St. Clair River was 3 ± 1 individuals/m^2 and 486 ± 152 individuals/m^2, respectively (Fig. 1). Densities were highly variable and ranged from 0 to 43 individuals/m^2 for *D. polymorpha* and 0 to 5,928 individuals/m^2 for *D. r. bugensis* (Fig. 1 and 2). *Dreissena polymorpha* had a mean length of 7.3 ± 0.8 mm and *D. r. bugensis* had a mean length of 7.9 ± 0.1 mm. Of the live dreissenids collected, 99.4% were *D. r. bugensis* and 0.6% were *D. polymorpha* (Fig. 2). Mean dreissenid, *D. polymorpha* and *D. r. bugensis* densities were all significantly different between the St. Clair and Detroit rivers, with the St. Clair River having significantly higher total dreissenid densities, significantly higher *D. r. bugensis* density, and significantly lower *D. polymorpha* density than the Detroit River (all p-values < 0.01). Dreissenid shell data were collected during the St. Clair River survey and is presented in the supplementary materials (ESM Table S3, Fig. S3, and Fig. S4).

Species Distribution Models – MaxEnt

The final $DR_{dreissenid}$ model used the variables river distance to the river's inlet and nearest tributary and had an AUC of 0.736 (Tables 1 and 3, Fig. 3A). The mean occurrence probability for Detroit River sites where dreissenids were detected was 67.4 ± 0.03% and ranged from 24.0% to 96.6%. Five different threshold occurrence probability values ranging from 30% to 70% were assessed and the $DR_{dreissenid}$ model's optimal probability thresholds for predicting dreissenid detection and non-detection were 30% and 70%, respectively (Table 4). The range of threshold occurrence probability values were then used to evaluate the accuracy of the $DR_{dreissenid}$-SCR projection (Fig. 4A) at predicting dreissenid detection sites in the St. Clair River. Among the 40 St. Clair River sites where dreissenids were detected, 18-38 sites were correctly categorized as dreissenid detection sites by the $DR_{dreissenid}$-SCR projection (45.0% - 95.0% accuracy; Tables 1 and 4). Among the 11 St. Clair River sites where dreissenids were not detected, 3-8 sites were correctly categorized as dreissenid non-detection sites by the $DR_{dreissenid}$-SCR projection (27.3% - 72.7% accuracy; Table 4). Among all 51 St. Clair River sites surveyed, 26-41 sites were correctly categorized as either dreissenid detection or non-detection sites by the $DR_{dreissenid}$-SCR projection (51.0% - 80.4% accuracy; Tables 1 and 4).

The final $SCR_{dreissenid}$ model used the variables depth, river distance to the river's outlet, and river distance to the nearest tributary and had an AUC of 0.782 (Tables 1 and 3, Fig. 4B). The $SCR_{dreissenid}$ model was assessed using the threshold occurrence probability values ranging from 30% to 70%. Of the 40 St. Clair River sites where dreissenids were detected, 20-37 sites were correctly categorized as dreissenid detection sites by the $SCR_{dreissenid}$ model (50.0% - 92.5% accuracy; Table 1; ESM Table S6). Among all 51 St. Clair River sites surveyed, 27-42 sites were correctly categorized as either dreissenid detection or non-detection sites by the $SCR_{dreissenid}$ model (52.9% - 82.4% accuracy; Table 1; ESM Table S6). The largest difference between the $DR_{dreissenid}$-SCR projection and the $SCR_{dreissenid}$ model was 73.1% (Fig. 4C).

The final DR_{poly} model used the variables river distance to the river's outlet and nearest tributary (Table 3). The DR_{poly} model had an AUC of 0.781 (Table 1, Fig. 3B). With the threshold occurrence probability values ranging from 30% to 70%, the DR_{poly} model was 40.0% - 93.3% accurate at categorizing the 30 *D. polymorpha* detection sites (Table 1; ESM Table S4). The DR_{poly}-SCR projection (Fig. 5A) was 70.0% - 90.0% accurate at classifying the 10 St. Clair River *D. polymorpha* detection sites (Table 1; ESM Table S4). The final SCR_{poly} model used the variables river distance to the river's inlet and river distance to the nearest tributary and had an AUC of 0.764 (Tables 1 and 3, Fig. 5B). The SCR_{poly} model was 60.0% - 100% accurate at classifying the 10 St. Clair River *D. polymorpha* detection sites (Tables 1; ESM Table S6). Comparing the DR_{poly}-SCR projection and the SCR_{poly} model, the largest difference between the two models was 39.4% (Figure 5C).

The final DR_{bug} model used the variables depth, North/South velocity, East/West velocity and river distance to the river's outlet and nearest tributary (Table 3). The DR_{bug} model had an AUC of 0.744 (Table 1, Fig. 3C). With the threshold occurrence probability values ranging from 30% to 70%, the DR_{bug} model was 54.6% - 96.4% accurate at categorizing the 28 Detroit River *D. r. bugensis* detection sites (accuracy; Table 1; ESM Table S5). The DR_{bug}–SCR projection (Fig. 6A) was 25.0% - 80.0% accurate at classifying the 40 St. Clair River *D. r. bugensis* detection sites (Table 1; ESM Table S5). The final SCR_{bug} model used the variables depth and river distance to the river's inlet and had an AUC of 0.764 (Tables 1 and 3, Fig. 6B). The SCR_{bug} model was 62.5% - 90.0% accurate at classifying the 40 St. Clair River *D. r. bugensis* detection sites (Table 1; ESM Table S6). Comparing the DR_{bug}–SCR projection and the SCR_{bug} model, the largest difference between the two models was 66.6% (Figure 6C). The largest difference between the DR_{poly} model and the DR_{bug} model was 46.5% (Figure 7A) and the largest difference between the SCR_{poly} model and the SCR_{bug} model was 70.5% (Figure 7B).

Species Distribution Models – CART

The Detroit River dreissenid CART model used the following variables to classify the training data set: estimated composition of pebbles and silt, site depth, and water velocity (Fig. 8) and had a 55% accuracy at predicting the full data set after pruning the model. An estimated sediment composition with >7% pebbles was identified for dreissenid detection sites. Water velocity, depth, and percent composition of silt were the proceeding variables for sites with <7% pebble composition. For Detroit River *D. polymorpha* detection, site depth and water velocity were the variables used to classify the training data set and the model performed with 64% accuracy at predicting the full data set after pruning (Fig. 8). For Detroit River *D. r. bugensis* detection, site depth was the only variable used to classify the training data set and the model performed with 60% accuracy at predicting the full data set after pruning (Fig. 8). *Dreissena r. bugensis* detection sites in the Detroit River were categorized by site depth >5.85 m (Fig. 8).

The St. Clair River dreissenid CART model used site depth, estimated composition of pebbles, and estimated submerged macrophyte presence to classify the training data set (Fig. 8) with a 77% accuracy at predicting the full data set after pruning. The St. Clair River *D. polymorpha* CART used water velocity, estimated submerged macrophyte presence, site depth, and estimated composition of clay to classify the training data set and performed with 78% accuracy at predicting the full data set after pruning (Fig. 8). Sites with water velocity >0.8 m/s were determined as sites with *D. polymorpha* detected. The St. Clair River *D. r. bugensis* CART used site depth, estimated composition of pebbles and silt, water velocity, and estimated submerged macrophyte presence to classify the training data set and performed with 78% accuracy at predicting the full data set after pruning (Fig. 8).

Discussion

St. Clair River Dreissenid Surveys

Dreissenids have been well-established in the St. Clair – Detroit River System for >30 years (Sturtevant et al., 2019); however, routinely monitoring dreissenid populations can give insight for their management as well as the restoration of river habitat and the conservation of native species. Soon after establishment, dreissenid densities were high, with a max density of 30,000 individuals/m^2 in Lake Erie in 1991 (Griffiths et al., 1991). Mean dreissenid densities estimated in Lake St. Clair were 1,237 individuals/m^2 in 1997 (Nalepa et al., 2001) and 2,211 individuals/m^2 in 2014-2015 (Pawlowski et al., 2019). In 2014-2015, mean dreissenid densities were 981 individuals/m^2 and 1,895 individuals/m^2 in the Detroit and St. Clair rivers, respectively (Pawlowski et al., 2019). However, recently, mean dreissenid densities in the Detroit River were estimated at 308 individuals/m^2 (Keretz et al., 2021) and mean dreissenid densities in the St. Clair River were 490 ± 152 individuals/m^2. While it is possible that the dreissenid densities in the current study are an overestimation, because the methodology for counting live dreissenids might identify recently dead individuals as live, current density estimates are still lower than the densities reported by Griffiths et al. (1991), Nalepa et al. (1997), and Pawlowski et al. (2019).

Overall, more *D. r. bugensis* and fewer *D. polymorpha* were detected in the St. Clair River than the Detroit River (Keretz et al., 2021). *Dreissena r. bugensis* made up 99% of dreissenids in the St. Clair River (Fig. 2) and 84% of dreissenids in the Detroit River. The higher composition of *D. r. bugensis* in the St. Clair River could be because the St. Clair River is deeper, cooler, and has faster flows than the Detroit River which creates more desirable habitat for *D. r. bugensis* than *D. polymorpha* (Karatayev et al., 2015; Mills et al., 1996). Niche partitioning between *D. r. bugensis* and *D. polymorpha* occurs as *D. r. bugensis* have a higher tolerance for and can spawn and grow at lower temperatures and are therefore found at deeper depths and colder temperatures than *D. polymorpha* (Karatayev et al., 1998; Stoeckmann, 2003). Additionally, dreissenid composition in Lake Huron, the upstream source for the St. Clair River, has been reported as almost entirely *D. r. bugensis* (Karatayev et al., 2020; Kirkendall et al., 2021). The change from *D. polymorpha* to *D. r. bugensis* has been documented in many lakes of the Great Lakes (French et al., 2009; Karatayev et al., 2022, 2021; Stoeckmann, 2003; Strayer et al., 2019).

Species Distribution Models – MaxEnt

Regardless of the species composition differences between the two rivers, the accuracy of the $DR_{dreissenid}$ model predicting dreissenid occurrence in the St. Clair River was decent, ranging up to 95.0% depending on the occurrence probability threshold used (Table 4). There are multiple methods for determining an occurrence probability threshold for model assessment (see Bean et al., 2012) depending on the sensitivity or specificity required. Therefore, a range of occurrence probability thresholds are presented in the current study to show the range of possible outcomes. Regardless of the chosen occurrence probability threshold, the $DR_{dreissenid}$ model performed well, and the $DR_{dreissenid}$-SCR projection was able to identify dreissenid detection sites in the St. Clair River which could aid with the prediction of these invasive bivalves. Additionally, for all MaxEnt models in the current study, the AUC (range: 0.736-0.782; Table 1) were slightly lower but comparable to other invasive species MaxEnt studies (range: 0.798-0.970; Barnes and Patiño, 2020; Bosso et al., 2017; Quinn et al., 2014; Padalia et al., 2014; West et al., 2016).

In the $DR_{dreissenid}$ model, dreissenid occurrence was negatively correlated to distance to the river's inlet while in the $SCR_{dreissenid}$ model occurrence was positively correlated with distance to the river's outlet. Additionally, both the Detroit River and St. Clair River dreissenid models relied on distance to the nearest tributary to predict dreissenid occurrence. High predictive overlap (Figure 4C) in the St. Clair River between the $SCR_{dreissenid}$ model and the $DR_{dreissenid}$-SCR projection may be due to the similarity in contributing variables. In both rivers, dreissenids were more likely to occur in the upstream sections of the river (Fig. 2, 3A and 4B) suggesting that both rivers have a source population near their inlet or in their upstream section that disperses downstream to less favorable habitat (*e.g.*, lacking suitable substrates or inadequate dissolved oxygen levels; Quinn et al., 2014; Strayer, 1999). The increased concentration of dreissenids upstream was also found during the 2014-2015 surveys of the Detroit and St. Clair rivers (Pawlowski et al., 2019) and this pattern follows a source-sink population pattern that has been previously demonstrated in dreissenid mussel populations (Bobeldyk et al., 2005; Horvath et al., 1996) implying that the potential source in the Detroit and St. Clair rivers is near the inlets and the sink is potentially near the outlets. Previous research modeling dreissenid occurrence with MaxEnt has done so at the local scale (Barnes and Patiño, 2020; Gallardo and Aldridge, 2018), the regional scale (Drake and Bossenbroek, 2004), and the global scale (Gallardo et al., 2013; Quinn et al., 2014). These studies all used EnviroClim variables (*e.g.*, mean annual water temperature, mean annual air temperature, mean annual rainfall) to create the models, which would be difficult to use within a single system (*e.g.*, the St. Clair – Detroit River System) due to lack of variation in variables and spatial resolution used across the region. Therefore, this study more closely aligns with previous studies that have modeled dreissenid distributions well after their introduction to investigate continued dispersal following establishment (Bobeldyk et al., 2005; Mehler et al., 2017; Naddafi et al., 2011; Smith et al., 2015). Although the variables used in the current study were the best available at the time, additional variables that could be included in future studies include surficial geology and ion concentrations (*e.g.*, calcium levels for predicting veliger survival and mussel shell growth) as these have been successful at predicting dreissenid occurrence in other systems (Mehler et al., 2017; Naddafi et al., 2011; Quinn et al., 2014; Ramcharan et al., 1992).

Dreissena polymorpha occurrence in the Detroit River was positively correlated to distance to the river's outlet but was negatively correlated with distance to the river's inlet in the St. Clair River. Therefore, the similar occurrence probability predictions by the DR_{poly}-SCR projection and the SCR_{poly} model is likely because the *D. polymorpha* models in both rivers had highly similar contributing variables (Fig. 5A-C). This pattern was also observed for the DR_{bug}-SCR projection and the SCR_{bug} model (Fig. 6A-C). These similarities between the DR_{poly}, SCR_{poly}, DR_{bug} and SCR_{bug} models very likely contributed to the prediction success of the $DR_{\text{dreissenid}}$-SCR projection with the St. Clair River dreissenid data, as it appears that *D. polymorpha* specimens as well as *D. r. bugensis* specimens are using similar habitat in both the Detroit and St. Clair rivers (*e.g.*, habitat close to the river's inlet; Bobeldyk et al., 2005).

However, it was unexpected that the DR_{poly} and DR_{bug} models and the SCR_{poly} and SCR_{bug} models showed similar distributions for the two species in both rivers (Fig. 7A-B). It was unexpected because a large literature base demonstrates niche partitioning between both species (Barnes and Patiño, 2020; Collas et al., 2018; Karatayev et al., 2015; Mills et al., 1996; Peyer et al., 2009; Quinn et al., 2014; Rudstam and Gandino, 2020; Stoeckmann, 2003) and *D. r. bugensis* constituted a much higher percentage of the total composition than *D. polymorpha* in both the Detroit and St. Clair rivers (84% and 99% respectively; Fig. 2; Keretz et al., 2021). This result is different from previous modelling studies which demonstrated that *D. polymorpha* and *D. r. bugensis* distributions varied from one another on a global or regional scale (Quinn et al., 2014; Barnes and Patiño, 2020). The overlap seen between the DR_{poly} and DR_{bug} models as well as the SCR_{poly} and SCR_{bug} models could be due to an insufficient sample size of *D. polymorpha* sites (particularly in the St. Clair River) for the model to properly display niche partitioning between *D. polymorpha* and *D. r. bugensis*. Additionally, in the Detroit River, only a few sites had only *D. polymorpha* present while in the St. Clair River, there were no sites with only *D.*

polymorpha present as all sites either had both species or only *D. r. bugensis* present, which could further account for the similar distributions predicted by the SDMs in the current study.

Species Distribution Models – CART

Water velocity is a defining habitat characteristic for *D. polymorpha* detection in both the Detroit and St. Clair rivers' CART models, with *D. polymorpha* occurring at sites with water velocity lower than 0.12 m/s in the Detroit River and at sites with water velocity >0.8 m/s in the St. Clair River (Fig. 8). Higher flow rates are known to have a negative impact on *D. polymorpha*, influencing veliger development and settlement, juvenile attachment, and feeding and growth rates in adults (Ackerman, 1999; Hasler et al., 2019). Negative impacts on feeding rates and byssal thread production have been documented at as low as 0.2 m/s; however, *D. polymorpha* have been documented in flows ranging up to 1.3 m/s and can maintain byssal thread adhesion in flows up to 1.8 m/s (Hasler et al., 2019; Peyer et al., 2009). Therefore, flows where dreissenids were detected in both the Detroit and St. Clair rivers are below the maximum threshold for dreissenid byssal thread adhesion. However, due to low sample sizes (n=10 sites), interpretations of the St. Clair River *D. polymorpha* CART model should be considered with caution. Alternatively, the *D. r. bugensis* CART model showed depth to be a defining habitat characteristic for *D. r. bugensis* detection, with *D. r. bugensis* occurring at sites with deeper depths in both the Detroit and St. Clair rivers (5.85 m and 1.15 m, respectively; Fig. 8). *Dreissena r. bugensis* are found at deeper depths than *D. polymorpha* in multiple Great Lakes since *D. r. bugensis* have a higher tolerance for and can spawn at lower temperatures (Karatayev et al., 1998; Mills et al., 1993; Stoeckmann, 2003).

In the Detroit River, where *D. r. bugensis* accounted for 84% of the dreissenid species composition (Keretz et al., 2021), the full dreissenid CART model is markedly different from the individual species models with percent composition of pebbles being the main defining characteristic for dreissenid detection, although water velocity and depth are also still defining habitat characteristics (Fig. 8). Research has shown *D. polymorpha* and *D. r. bugensis* individuals prefer to attach to large substrates, including boulders, cobbles, and pebbles, with fewer specimens attaching to smaller substrates like sand and silt (Bobeldyk et al., 2005; Horvath et al., 1996; Karatayev et al., 1998; Smith et al., 2015). The most common substrates in the Detroit River were silt, sand, and clay, followed by cobbles and pebbles (Keretz et al., 2021) and the substrate data collected in the current study for the St. Clair River reflects a similar pattern.

Alternatively, in the St. Clair River, where *D. r. bugensis* constituted 99% of the dreissenid species composition, the full dreissenid CART model is similar to the *D. r. bugensis* CART model (Fig. 8) with depth >1.15 m as the first defining habitat characteristic and identical defining characteristics for sites <1.15 m depth. As mentioned above, *D. r. bugensis* has been shown to succeed at lower temperatures (Karatayev et al., 1998; Mills et al., 1993; Stoeckmann, 2003) which can increase the species' success in the deeper waters of the St. Clair River (Boase et al., 2011; Fischer et al., 2018).

Implications and Further Research

The models provided by this study, especially if applied to other large river systems, could be used to determine areas to survey to find the optimal dreissenid density for unionid persistence, unionid re-introduction, and habitat rehabilitation for other at-risk species. Co-existence between invasive dreissenid and native unionid mussels is possible in large systems decades or centuries following dreissenid introduction (Keretz et al., 2021; Lucy et al., 2014; Newton et al., 2011; Sietman et al., 2004; Strayer and Malcom, 2007), but it is unknown how sustainable this co-existence is in North America, with many unionid species either extirpated or below the limits of detection. In Europe, however, research shows sustained co-existence between unionids and dreissenids can occur (Lucy et al., 2014). Therefore, when selecting locations for possible habitat restoration or unionid conservation programs (*e.g.*, translocation or reintroduction), it is necessary to consider dreissenid presence and distributions. In addition to unionid restoration, it could also be beneficial to consider dreissenid distributions when selecting future locations for artificial spawning reefs for walleye and lake whitefish. Currently, throughout the St. Clair – Detroit River System, there are ongoing fish habitat restoration projects focused on constructing artificial spawning reef habitats for Lake Sturgeon (*Acipenser fulvescens*), walleye, and lake whitefish (Fischer et al., 2018; Manny et al., 2015). Previous research has documented the negative impacts dreissenids have on reef habitats by biofouling the reef substrate which reduces space for egg incubation, depletes available oxygen, and increases waste (Baetz et al., 2020; Fitzsimons et al., 1995). Therefore, the results of this study and model application to other large river systems could benefit ongoing fish reef restoration projects.

The MaxEnt models in the current study were generally more accurate at predicting dreissenid occurrence than the CART models, especially when the two species were combined into a single model (Table 1). There are numerous benefits to MaxEnt (*e.g.*, performs well compared to other modeling systems and provides a continuous output), but there are disadvantages as well (Elith and Graham, 2009; Phillips et al., 2006). Dreissenid densities cannot be used in presence-only data modeling and therefore densities cannot be inferred from MaxEnt models (Ward et al., 2009). The lack of density can be problematic for the construction of SDMs because the environmental data surrounding a solitary dreissenid detection is given the same consideration as the environmental data surrounding a point with a large estimated dreissenid density (Elith et al., 2011; Phillips et al., 2006). Additionally, prediction of dreissenid absence or non-detection should be interpreted with caution since the models created in the current study are made to predict dreissenid occurrence. The $DR_{dreissenid}$-SCR projection did not consistently predict dreissenid non-detection sites (*e.g.*, potential absence) in the St. Clair River (27.3%-72.7% accuracy). It is important to note that MaxEnt is a presence-only modeling output (Phillips et al., 2006) which uses a generative and not a discriminative modeling approach (*e.g.*, CART modeling; Phillips and Dudik, 2008). As absence of a species is difficult to demonstrate in the environment, even with a sessile species like dreissenids, most absence data only indicates that the species was not detected at the time of collection (Graham et al., 2004; Lobo et al., 2010). In the current study, live dreissenids may have not been collected in the six PONAR samples taken or could have been mis-categorized as a shell, leading to live dreissenids not being detected at a site. It is also possible that dreissenid densities were overestimated since the categorization method for live dreissenids could count recently dead individuals as live. Finally, MaxEnt requires the environmental variables to have a continuous resolution in order to create a continuous output (Phillips et al., 2006), limiting the type of habitat data that can be used. Regardless of the limitations, MaxEnt has been rated highly among similar modeling algorithms (Elith and Graham, 2009) and continues to be used to model invasive species distributions in aquatic systems (Barnes and Patiño, 2020; Lopes et al., 2017; Mamun et al., 2018; Yiwen et al., 2016; this study).

The CART models in the current study complement the MaxEnt models by addressing the limitations described above. Dreissenid densities, non-detection sites, and local-scale habitat variables can all be taken into account by CART analyses (Jarošík, 2011). One limitation for both CART analysis and MaxEnt is small sample size. Although the sample sizes used in the current study were generally large (Detroit River: n=35 dreissenid sites, n=28 *D. r. bugensis* sites, and n=30 *D. polymorpha* sites. St. Clair River: n=40 dreissenid sites, n=40 *D. r. bugensis* sites, and n=10 *D. polymorpha* sites), caution should be used when interpreting the SCR *D. polymorpha* models (CART and MaxEnt) due to lower sample sizes. Although MaxEnt reportedly can perform well with as few as 5 detection locations (Bean et al., 2012; Rhoden et al., 2017), small sample sizes can represent bias in the data set and can lead to an overestimate of model accuracy (Bean et al., 2012).

The dreissenid MaxEnt and CART models created from the Detroit River data were able to successfully predict dreissenid presence in the St. Clair River and this study presents a unique perspective by modeling dreissenid distributions, both species together and separately, in rivers that dreissenids have been established in for more than 30 years. Additionally, previous dreissenid modeling has been largely focused solely on *D. polymorpha* (Bosso et al., 2017; Drake and Bossenbroek, 2004; Ricciardi, 2003); but recent research, including this study, have expanded to include *D. r. bugensis* (Barnes and Patiño, 2020; Collas et al., 2018; Quinn et al., 2014), as *D. r. bugensis* continues to dominate in the Great Lakes and spread to the Southwestern United States (Karatayev and Burlakova, 2022b; Nalepa, 2010; Strayer et al., 2019). In future research, these models could be applied to other river systems and used for the management of impacted species in the Detroit and St. Clair rivers such as unionids or reef-spawning fishes.

Acknowledgements

Freshwater mussel collections were conducted under Canadian SARA permit 21-PCAA-00023 (contact: T.J. Morris) and U.S. Fish and Wildlife Service Native Endangered Species Recovery permit (#TE71821A-3). Project funding was provided by the U.S. Fish and Wildlife Great Lakes Fish and Wildlife Restoration Act with in-kind support from the Central Michigan University (CMU) Institute of Great Lakes Research, and Fisheries and Oceans Canada’s Species at Risk program. Stipend support for SSK was provided by the CMU Earth and Ecosystem Sciences doctoral program and a 2021 Cooperative Institute for Great Lakes Research Graduate Fellowship. Special thanks to CMU student researchers (K. Cushway, L. Daniels, S. LaValley, M. Layer, D. Powell, N. Ring, A. Rittmaier, G. Sanfilippo, E. Smrcka, J. Sokol, H. Torolski, N. Trombley, N. VanTassel, and J. Willsie), Fisheries and Oceans Canada staff (M. Goguen, K. McNichols-O’Rourke, M. Dolan, L. Dutheil, B. Foucault, E. MacLennan-Nobrega, K. Smith, S. Turner, and K. Zammit), Michigan Department of Natural Resources staff (P. O’Neill, K. Snyder, S. Thomas, J. Francis, E. Plant, D. Tar, B. Utrup, T. Wills, and B. Yonker), Environment and Climate Change Canada staff (B. Gray, C. Duggon, A. Morden, C. Treen, C. Weavers, and C. Yonch), and U.S. Geological Survey technician K. Keretz. This is NOAA GLERL Contribution No. XXXX and contribution No. XXX of the CMU Institute for Great Lakes Research. Any trade, firm, or product names are used for descriptive purposes and do not imply endorsement by the U.S. Government.

Literature Cited

Ackerman, J.D., 1999. Effect of velocity on the filter feeding of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*): Implications for trophic dynamics. Can. J. Fish. Aquat. Sci. 56, 1551–1561. https://doi.org/10.1139/f99-079

Almarinez, B.J.M., Fadri, M.J.A., Lasina, R., Tavera, M.A.A., Carvajal, T.M., Watanabe, K., Legaspi, J.C., Amalin, D.M., 2021. A bioclimate-based maximum entropy model for *Comperiella calauanica* Barrion, Almarinez and Amalin (Hymenoptera: Encyrtidae) in the Philippines. Insects 12, 26. https://doi.org/10.3390/insects12010026

Anderson, E.J., Schwab, D.J., 2011. Relationships between wind-driven and hydraulic flow in Lake St. Clair and the St. Clair River Delta. J. Great Lakes Res. 37, 147–158. https://doi.org/10.1016/j.jglr.2010.11.007

Anderson, E.J., Schwab, D.J., Lang, G.A., 2010. Real-time hydraulic and hydrodynamic model of the St. Clair River, Lake St. Clair, Detroit River system. J. Hydraul. Eng. 136, 507–518. https://doi.org/10.1061/(asce)hy.1943-7900.0000203

Baetz, A., Tucker, T.R., DeBruyne, R.L., Gatch, A., Höök, T., Fischer, J.L., Roseman, E.F., 2020. Review of methods to repair and maintain lithophilic fish spawning habitat. Water 12, 1–37. https://doi.org/10.3390/w12092501

Barnes, M., Patiño, R., 2020. Predicting suitable habitat for dreissenid mussel invasion in Texas based on climatic and lake physical characteristics. Manag. Biol. Invasions 11, 63–79. https://doi.org/10.3391/mbi.2020.11.1.05

Bean, W.T., Stafford, R., Brashares, J.S., 2012. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography 35, 250–258. https://doi.org/10.1111/j.1600-0587.2011.06545.x

Bennion, D.H., Manny, B.A., 2011. Construction of shipping channels in the Detroit River: History and environmental consequences. U.S. Geological Survey. 14 p.

Boase, J.C., Diana, J.S., Thomas, M.V., Chiotti, J.A., 2011. Movements and distribution of adult Lake Sturgeon from their spawning site in the St. Clair River, Michigan. J Appl Ichthyol 27, 58–65. https://doi.org/10.1111/j.1439-0426.2011.01827.x

Bobeldyk, A.M., Bossenbroek, J.M., Evans-White, M.A., Lodge, D.M., Lamberti, G.A., 2005. Secondary spread of Zebra Mussels (*Dreissena polymorpha*) in coupled lake-stream systems. Ecoscience 12, 339–346. https://doi.org/10.2980/i1195-6860-12-3-339.1

Bossenbroek, J.M., Burlakova, L.E., Crail, T.C., Karatayev, A.Y., Krebs, R.A., Zanatta, D.T., 2018. Modeling habitat of freshwater mussels (Bivalvia:Unionidae) in the lower Great Lakes 25 years after the *Dreissena* invasion. Freshw. Sci. 37, 330–342. https://doi.org/10.1086/697738

Bosso, L., De Conno, C., Russo, D., 2017. Modelling the risk posed by the Zebra Mussel *Dreissena polymorpha*: Italy as a case study. Environ. Manage. 60, 304–313. https://doi.org/10.1007/s00267-017-0882-8

Burlakova, L.E., Karatayev, A.Y., Padilla, D.K., 2000. The impact of *Dreissena polymorpha* (PALLAS) invasion on unionid bivalves. Int. Rev. Hydrobiol. 85, 529–541. https://doi.org/10.1002/1522-2632(200011)85:5/6<529::AID-IROH529>3.0.CO;2-O

Burniston, D., Dove, A., Backus, S., Thompson, A., 2018. Nutrient concentrations and loadings in the St. Clair River–Detroit River Great Lakes interconnecting channel. J. Great Lakes Res. 44, 398–411. https://doi.org/10.1016/j.jglr.2018.02.005

Caldwell, T.J., Rosen, M.R., Chandra, S., Acharya, K., Caires, A.M., Davis, C.J., Thaw, M., Webster, D., 2015. Temporal and basin-specific population trends of Quagga Mussels on

soft sediment of a multibasin reservoir, in: Wong, W.H., Gerstenberger, S.L. (Eds.), Biology and Management of Invasive Quagga and Zebra Mussels in the Western United States. CRC Press, Boca Raton, Florida, USA, pp. 33–52.
Collas, F.P.L., Karatayev, A.Y., Burlakova, L.E., Leuven, R.S.E.W., 2018. Detachment rates of dreissenid mussels after boat hull-mediated overland dispersal. Hydrobiologia 810, 77–84. https://doi.org/10.1007/s10750-016-3072-4
Crail, T.D., Krebs, R.A., Zanatta, D.T., 2011. Unionid mussels from nearshore zones of Lake Erie. J. Great Lakes Res. 37, 199–202. https://doi.org/10.1016/j.jglr.2010.12.006
Dahlgren, R.A., Nieuwenhuyse, E. Van, Litton, G., 2004. Transparency tube provides reliable water-quality measurements. Calif. Agric. 58, 149–153. https://doi.org/10.3733/ca.v058n03p149
Derecki, J.A., 1984. Detroit River physical and hydraulic characteristics. National Oceanic and Atmospheric Administration. 11 p.
Drake, J.M., Bossenbroek, J.M., 2004. The potential distribution of Zebra Mussels in the United States. Bioscience 54, 931–941. https://doi.org/10.1641/0006-3568(2004)054[0931:TPDOZM]2.0.CO;2
Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. Biol. Rev. 81, 163–182. https://doi.org/10.1017/S1464793105006950
Elith, J., Graham, C.H., 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography 32, 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x
Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x
EPA. 2006. Detroit River AOC boundary map. Environmental Protection Agency. Accessed from: https://www.epa.gov/great-lakes-aocs/detroit-river-aoc-boundary-map [Oct. 22, 2019]
EPA. 2019 St. Clair River AOC boundary map. Environmental Protection Agency. Accessed from: https://www.epa.gov/great-lakes-aocs/st-clair-river-aoc-boundary-map-0 [Oct. 22, 2019]
ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute. Redlands, California.
Fischer, J.L., Bennion, D., Roseman, E.F., Manny, B.A., 2015. Validation of a spatial model used to locate fish spawning reef construction sites in the St. Clair-Detroit River system. J. Great Lakes Res. 41, 1178–1184. https://doi.org/10.1016/j.jglr.2015.09.019
Fischer, J.L., Pritt, J.J., Roseman, E.F., Prichard, C.G., 2018. Lake Sturgeon, Lake White fish, and Walleye egg deposition patterns with response to fish spawning substrate restoration in the St . Clair – Detroit River System. Trans. Am. Fish. Soc. 147, 79–93. https://doi.org/10.1002/tafs.10016
Fitzsimons, J.D., Leach, J.H., Nepszy, S.J., Cairns, V.W., 1995. Impacts of Zebra Mussel on Walleye (*Stizostedion vitreum*) reproduction in western Lake Erie. Can. J. Fish. Aquat. Sci. 52, 578–586. https://doi.org/10.1139/f95-058
French III, J.R.P., Schaeffer, J.S., Roseman, E.F., Kiley, C.S., Fouilleroux, A., 2009. Abundance and distribution of benthic macroinvertebrates in offshore soft sediments in western Lake Huron, 2001-2007. J. Great Lakes Res. 35, 120–127.

https://doi.org/10.1016/j.jglr.2008.11.006
Gallardo, B., Aldridge, D.C., 2018. Inter-basin water transfers and the expansion of aquatic invasive species. Water Res. 143, 282–291. https://doi.org/10.1016/j.watres.2018.06.056
Gallardo, B., zu Ermgassen, P.S.E., Aldridge, D.C., 2013. Invasion ratcheting in the Zebra Mussel (*Dreissena polymorpha*) and the ability of native and invaded ranges to predict its global distribution. J. Biogeogr. 40, 2274–2284. https://doi.org/10.1111/jbi.12170
Gobin, J., Lester, N.P., Cottrill, A., Fox, M.G., Dunlop, E.S., 2015. Trends in growth and recruitment of Lake Huron Lake Whitefish during a period of ecosystem change, 1985 to 2012. J. Great Lakes Res. 41, 405–414. https://doi.org/10.1016/j.jglr.2015.03.003
Graham, C.H., Ferrier, S., Huettman, F., Moritz, C., Peterson, A.T., 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol. Evol. 19, 497–503. https://doi.org/10.1016/j.tree.2004.07.006
Griffiths, R.W., Schloesser, D.W., Leach, J.H., Kovalak, W.P., 1991. Distribution and dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. Can. J. Fish. Aquat. Sci. 48, 1381–1388. https://doi.org/10.1139/F91-165
Haag, W.R., Williams, J.D., 2014. Biodiversity on the brink: An assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735, 45–60. https://doi.org/10.1007/s10750-013-1524-7
Hartig, J.H., Krantzberg, G., Alsip, P., 2020. Thirty-five years of restoring Great Lakes Areas of Concern: Gradual progress, hopeful future. J. Great Lakes Res. 46, 429–442. https://doi.org/10.1016/j.jglr.2020.04.004
Hasler, C.T., Leathers, J., Ducharme, A., Casson, N.J., 2019. Biological effects of water velocity and other hydrodynamic characteristics of flow on dreissenid mussels. Hydrobiologia 837, 1–14. https://doi.org/10.1007/S10750-019-03976-6/TABLES/1
Havel, J.E., Kovalenko, K.E., Thomaz, S.M., Amalfitano, S., Kats, L.B., 2015. Aquatic invasive species: Challenges for the future. Hydrobiologia 750, 147–170. https://doi.org/10.1007/s10750-014-2166-0
Heath, R.T., Fahnenstiel, G.L., Gardner, W.S., Cavaletto, J.F., Hwang, S.-J., 1995. Ecosystem-level effects of Zebra Mussels (*Dreissena polymorpha*): An enclosure experiment in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 501–516.
Hebert, P.D.N., Muncaster, B.W., Mackie, G.L., 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46, 1587–1591. https://doi.org/10.1139/f89-202
Horvath, T.G., Lamberti, G.A., Lodge, D.M., Perry, W.L., 1996. Zebra Mussel dispersal in lake-stream systems: Source-sink dynamics? J. North Am. Benthol. Soc. 15, 564–575. https://doi.org/10.2307/1467807
Hoyle, J.A., Bowlby, J.N., Morrison, B.J., 2008. Lake Whitefish and Walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosyst. Heal. Manag. 11, 403–411. https://doi.org/10.1080/14634980802530392
Karatayev, A.Y., Burlakova, L.E., 2022a. *Dreissena* in the Great Lakes: What have we learned in 30 years of invasion. Hydrobiologia 1–28. https://doi.org/10.1007/s10750-022-04990-x
Karatayev, A.Y., Burlakova, L.E., 2022b. What we know and don't know about the invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels. Hydrobiologia. https://doi.org/10.1007/s10750-022-04950-5
Karatayev, A.Y., Burlakova, L.E., Mehler, K., Danniel, S.F., Elgin, A.K., Nalepa, T.F., 2020. Lake Hurun benthos survey: Cooperative science and monitoring initative 2017. Buffalo,

NY. 48 p.
Karatayev, A.Y., Burlakova, L.E., Mehler, K., Elgin, A.K., Rudstam, L.G., Watkins, J.M., Wick, M., 2022. *Dreissena* in Lake Ontario 30 years post-invasion. J. Great Lakes Res. 48, 264–273. https://doi.org/10.1016/j.jglr.2020.11.010
Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2015. Zebra versus Quagga Mussels: A review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746, 97–112. https://doi.org/10.1007/s10750-014-1901-x
Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 1998. Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (PALL.). J. Shellfish Res. 17, 1219–1235.
Karatayev, A.Y., Karatayev, V.A., Burlakova, L.E., Mehler, K., Rowe, M.D., Elgin, A.K., Nalepa, T.F., 2021. Lake morphometry determines *Dreissena* invasion dynamics. Biol. Invasions 23, 2489–2514. https://doi.org/10.1007/s10530-021-02518-3
Keretz, S.S., Woolnough, D.A., Morris, T.J., Roseman, E.F., Elgin, A.K., Zanatta, D.T., 2021. Limited co-existence of native unionids and invasive dreissenid mussels more than 30 Y post dreissenid invasion in a large river system. Am. Midl. Nat. 186, 157–175.
Kerfoot, W.C., Yousef, F., Green, S.A., Budd, J.W., Schwab, D.J., Vanderploeg, H.A., 2010. Approaching storm: Disappearing winter bloom in Lake Michigan. J. Great Lakes Res. 36, 30–41. https://doi.org/10.1016/J.JGLR.2010.04.010
Kirkendall, D.S., Bunnell, D.B., Armenio, P.M., Eaton, L.A., Trebitz, A.S., Watson, N.M., 2021. Spatial and temporal distributions of *Dreissena* spp. veligers in Lake Huron: Does calcium limit settling success? J. Great Lakes Res. 47, 1040–1049. https://doi.org/10.1016/j.jglr.2021.04.001
Kuhn, M. 2020. Caret: classification and regression training. R package version 6.0-86. https://CRAN.R-project.org/package=caret
Lobo, J.M., Jiménez-Valverde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography 33, 103–114. https://doi.org/10.1111/j.1600-0587.2009.06039.x
Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: A misleading measure of the performance of predictive distribution models. Global Ecol. Biogeogr. 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x
Lopes, T.M., Bailly, D., Almeida, B.A., lia L Santos, N.C., G Gimenez, B.C., Landgraf, G.O., L Sales, P.C., Lima-Ribeiro, M.S., S Cassemiro, F.A., Rangel, T.F., Diniz-Filho, J.A.F., Agostinho, A.A., Gomes, L.C., 2017. Two sides of a coin: Effects of climate change on the native and non-native distribution of *Colossoma macropomum* in South America. PLoS One 12, e0179684. https://doi.org/10.1371/journal.pone.0179684
Lucy, F., Burlakova, L., Karatayev, A., Mastitsky, S., Zanatta, D., 2014. Zebra Mussel impacts on unionids: A synthesis of trends in North America and Europe, in: Nalepa, T., Schloesser, D. (Eds.), Quagga and Zebra Mussels: Biology, Impact, and Control. CRC Press, Boca Raton, pp. 623–646. https://doi.org/10.1201/b15437-48
Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., Clark, R.D., 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: A synthesis. J. Great Lakes Res. 41, 217–231. https://doi.org/10.1016/j.jglr.2015.08.009
Mamun, M., Kim, S., An, K.-G., 2018. Distribution pattern prediction of an invasive alien species Largemouth Bass using a maximum entropy model (MaxEnt) in the Korean peninsula. J. Asia-Pacific Biodivers. 11, 516–524.

https://doi.org/10.1016/j.japb.2018.09.007
Manny, B.A., Roseman, E.F., Kennedy, G., Boase, J.C., Craig, J.M., Bennion, D.H., Read, J., Vaccaro, L., Chiotti, J., Drouin, R., Ellison, R., 2015. A scientific basis for restoring fish spawning habitat in the St. Clair and Detroit rivers of the Laurentian Great Lakes. Res. Eco. 23, 149-156. https://doi.org/10.1111/rec.12159
McNickle, G.G., Rennie, M.D., Sprules, W.G., 2006. Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by Zebra Mussels (*Dreissena polymorpha*), and potential effects on Lake Whitefish (*Coregonus clupeaformis*) diet and growth. J. Great Lakes Res. 32, 180–193.
Mehler, K., Burlakova, L.E., Karatayev, A.Y., Biesinger, Z., Bruestle, E., Valle-Levinson, A., Castiglione, C., Gorsky, D., 2017. Integrating remote sensing and species distribution modelling to predict benthic communities in a Great Lakes connecting channel. River Res. Appl. 33, 1336–1344. https://doi.org/10.1002/rra.3169
Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography 36, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x
Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., Spidle, A.P., 1993. Colonization, ecology, and population structure of the "Quagga" Mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 50, 2305–2314.
Mills, E.L., Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., Bernie, M., 1996. A review of the biology and ecology of the Quagga Mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. Am. Zool. 36, 271–286.
Naddafi, R., Blenckner, T., Eklöv, P., Pettersson, K., 2011. Physical and chemical properties determine Zebra Mussel invasion success in lakes. Hydrobiologia 669, 227–236. https://doi.org/10.1007/s10750-011-0689-1
Nalepa, T.F., 2010. An overview of the spread, distribution, and ecological impacts of the Quagga Mussel, *Dreissena rostriformis bugensis*, with possible implications to the Colorado River System. U.S. Geological Survey. 10 p.
Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., 2001. Recent population changes in freshwater mussels (Bivalvia: Unionidae) and Zebra Mussels (*Dreissena polymorpha*) in Lake St. Clair, U.S.A. Am. Malacol. Bull. 16, 141–145.
Nalepa, T.F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L., Lang, G.A., 1996. Changes in the freshwater mussel community of Lake St. Clair: From Unionidae to *Dreissena polymorpha* in eight years. J. Great Lakes Res. 22, 354–369. https://doi.org/10.1016/S0380-1330(96)70961-9
National Geographic, ESRI, DeLorme, NAVTEQ, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC, 2011. National geographic world map, digital topographic basemap of the world. Accessed from: http://www.arcgis.com/home/item.html?id=b9b1b422198944fbbd5250b3241691b6 [April 7, 2020]
Newton, T.J., Zigler, S.J., Rogala, J.T., Gray, B.R., Davis, M., 2011. Population assessment and potential functional roles of native mussels in the Upper Mississippi River. Aquat. Conserv. Mar. Freshw. Ecosyst. 21, 122–131. https://doi.org/10.1002/aqc.1170
Padalia, H., Srivastava, V., Kushwaha, S.P.S., 2014. Modeling potential invasion range of alien invasive species, *Hyptis suaveolens* (L.) Poit. in India: Comparison of MaxEnt and GARP. Ecol. Inform. 22, 36–43. https://doi.org/10.1016/j.ecoinf.2014.04.002

Pawlowski, M., Wick, M., Bolgrien, D., Nord, M., Launspach, J., Angradi, T., 2019. Special report for the Great Lakes: 2015 national coastal condition assessment and 2014-2016 connecting river system pilot assessment. U.S. Environmental Protection Agency. Washington, D.C. Accessed from: https://www.epa.gov/national-aquatic-resource-surveys/national-coastal-condition-assessment-related-studies [Oct. 12, 2023]
Peyer, S.M., McCarthy, A.J., Lee, C.E., 2009. Zebra Mussels anchor byssal threads faster and tighter than Quagga Mussels in flow. J. Exp. Biol. 212, 2027–2036. https://doi.org/10.1242/jeb.028688
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: An open-source release of Maxent. Ecography. 40, 887–893. https://doi.org/10.1111/ecog.03049
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190, 231–259.
Phillips, S.J., Dudik, M., 2008. Modeling of species distributions with MaxEnt: New extensions and a comprehensive evaluation. Ecography 31, 161–175. https://doi.org/10.1111/j.2007.0906-7590.05203.x
Quinn, A., Gallardo, B., Aldridge, D.C., 2014. Quantifying the ecological niche overlap between two interacting invasive species: The Zebra Mussel (*Dreissena polymorpha*) and the Quagga Mussel (*Dreissena rostriformis bugensis*). Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 324–337. https://doi.org/10.1002/aqc.2414
R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/
Ramcharan, C.W., Padilla, D.K., Dodson, S.I., 1992. Models to predict potential occurrence and density of the Zebra Mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 49, 2611–2620. https://doi.org/10.1139/f92-289
Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., Maccormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94, 849–873. https://doi.org/10.1111/brv.12480
Reiss, H., Cunze, S., König, K., Neumann, H., Kröncke, I., 2011. Species distribution modelling of marine benthos: a North Sea case study. Mar. Ecol. Prog. Ser. 442, 71–86. https://doi.org/10.3354/meps09391
Rennie, M.D., 2014. Context-dependent changes in Lake Whitesh populations associated with dreissenid invasion, in: Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and Zebra Mussels: Biology, Impact, and Control. CRC Press, Boca Raton, Florida, USA, pp. 661–680. https://doi.org/10.1201/b15437-50
Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers. Distrib. 12, 425–433. https://doi.org/10.1111/j.1366-9516.2006.00262.x
Ricciardi, A., 2003. Predicting the impacts of an introduced species from its invasion history: An empirical approach applied to Zebra Mussel invasions. Freshw. Biol. 48, 972–981. https://doi.org/10.1046/j.1365-2427.2003.01071.x
Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Can. J. Fish. Aquat. Sci. 52, 1449–1461.

Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. 53, 1434–1444.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Mueller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 8, 12–77.

Rudstam, L.G., Gandino, C.J., 2020. Zebra or Quagga Mussel dominance depends on trade-offs between growth and defense- Field support from Onondaga Lake, NY. PloS ONE 15, 1–17. https://doi.org/10.1371/journal.pone.0235387

Schloesser, D.W., Kovalak, W.P., Longton, G.D., Ohnesorg, K.L., Smithee, R.D., 1998. Impact of Zebra and Quagga Mussels (*Dreissena* spp.) on freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. Am. Midl. Nat. 140, 299–313.

Schloesser, D.W., Metcalfe-smith, J.L., Kovalak, W.P., Longton, G.D., Smithee, R.D., 2006. Extirpation of freshwater mussels (Bivalvia : Unionidae) following the invasion of dreissenid mussels in an interconnecting river of the Laurentian Great Lakes. Am. Midl. Nat. 155, 307–320.

Schloesser, D.W., Nalepa, T.F., 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the Zebra Mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 51, 2234–2242. https://doi.org/10.1139/f94-226

Sietman, B.E., Anderson, E.A., Nyboer, R., Hutto, F.R., 2004. Native freshwater mussels (Bivalvia: Unionidae) and infestation by Zebra Mussels at the Lost Mound Unit of the Upper Mississippi River National Wildlife and Fish Refuge. Trans. Illinois State Acad. Sci. 97, 235–254.

Smith, B.R., Edds, D.R., Goeckler, J.M., 2015. Lowhead dams and the downstream dispersal of Zebra Mussels. Hydrobiologia 755, 1–12. https://doi.org/10.1007/s10750-015-2211-7

Stoeckmann, A., 2003. Physiological energetics of Lake Erie dreissenid mussels: A basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. Can. J. Fish. Aquat. Sci. 60, 126134. https://doi.org/10.1139/F03-005

Strayer, D.L., Adamovich, B. V., Adrian, R., Aldridge, D.C., Balogh, C., Burlakova, L.E., Fried-Petersen, H.B., G.-Tóth, L., Hetherington, A.L., Jones, T.S., Karatayev, A.Y., Madill, J.B., Makarevich, O.A., Marsden, J.E., Martel, A.L., Minchin, D., Nalepa, T.F., Noordhuis, R., Robinson, T.J., Rudstam, L.G., Schwalb, A.N., Smith, D.R., Steinman, A.D., Jeschke, J.M., 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): A cross-system analysis. Ecosphere 10, e02701. https://doi.org/10.1002/ecs2.2701

Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. J. North Am. Benthol. Soc. 29, 344–358. https://doi.org/10.1899/08-171.1

Strayer, D.L., Hattala, K.A., Kahnle, A.W., Adams, R.D., 2014. Has the Hudson River fish community recovered from the Zebra Mussel invasion along with its forage base? Can. J. Fish. Aquat. Sci. 71, 1146–1157. https://doi.org/10.1139/cjfas-2013-0549

Strayer, D.L., Malcom, H.M., 2018. Long-term responses of native bivalves (Unionidae and Sphaeriidae) to a *Dreissena* invasion. Freshw. Sci. 37, 697–711. https://doi.org/10.1086/700571

Strayer, David L, Malcom, H.M., 2007. Effects of Zebra Mussels (*Dreissena polymorpha*) on native bivalves: The beginning of the end or the end of the beginning? North Am. Benthol.

Soc. 26, 111–122.
Strayer, D.L., Smith, L.C., 1996. Relationships between Zebra Mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the Zebra Mussel invasion of the Hudson River. Freshw. Biol. 36, 771–779.
Strayer, D.L., Smith, L.C., Hunter, D.C., 1998. Effects of the Zebra Mussel (*Dreissena polymorpha*) invasion on the macrobenthos of the freshwater tidal Hudson River. Can. J. Zool. 76, 419–425. https://doi.org/10.1139/z97-212
Sturtevant, R.A., Mason, D.M., Rutherford, E.S., Elgin, A., Lower, E., Martinez, F., 2019. Recent history of nonindigenous species in the Laurentian Great Lakes; An update to Mills et al., 1993 (25 years later). J. Great Lakes Res. 45, 1011–1035. https://doi.org/10.1016/j.jglr.2019.09.002
Therneau, T. and B. Atkinson. 2019. Rpart: recursive partitioning and regression trees. R package version 4.1-15. https://CRAN.R-project.org/package=rpart
Thompson, A. 2016. Huron-Erie corridor RMA2 velocity hydrological model. “Delist Areas of Concern Metadata and Mapping System.” Accessed from: http://delistaoc.glier.uwindsor.ca/geonetwork/srv/eng/catalog.search#/metadata/c1c8e5bb-fabc-4432-ab77-c18974c02f3c [Jan. 21, 2020]
Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58, 1208–1221. https://doi.org/10.1139/cjfas-58-6-1208
Ward, G., Hastie, T., Barry, S., Elith, J., Leathwick, J.R., 2009. Presence-only data and the EM Algorithm. Biometrics 65, 554–563. https://doi.org/10.1111/j.1541-0420.2008.01116.x
Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392.
West, A.M., Kumar, S., Brown, C.S., Stohlgren, T.J., Bromberg, J., 2016. Field validation of an invasive species Maxent model. Ecol. Inform. 36, 126–134. https://doi.org/10.1016/j.ecoinf.2016.11.001
Westwood, R., Westwood, A.R., Hooshmandi, M., Pearson, K., LaFrance, K., Murray, C., 2020. A field-validated species distribution model to support management of the critically endangered Poweshiek Skipperling (*Oarisma 29oweshiek*) butterfly in Canada. Conservation Sci Pract 2. https://doi.org/10.1111/csp2.163
Yiwen, Z., Bi Wei, L., Yeo, D.C., 2016. Novel methods to select environmental variables in MaxEnt: A case study using invasive crayfish. Ecol. Modell. 341, 5–13. https://doi.org/10.1016/j.ecolmodel.2016.09.019
Zanatta, D.T., Bossenbroek, J.M., Burlakova, L.E., Crail, T.D., Szalay, F. de, Griffith, T.A., Kapusinski, D., Karatayev, A.Y., Krebs, R.A., Meyer, E.S., Paterson, W.L., Prescott, T.J., Rowe, M.T., Schloesser, D.W., Walsh, M.C., 2015. Distribution of native mussel (Unionidae) assemblages in coastal areas of Lake Erie, Lake St. Clair, and connecting channels, twenty-five years after a dreissenid invasion. Northeastern Naturalist 22, 223–235. https://doi.org/10.1656/045.022.0115
Zanatta, D.T., Mackie, G.L., Metcalfe-Smith, J.L., Woolnough, D.A., 2002. A refuge for native freshwater mussels (Bivalvia: Unionidae) from impacts of the exotic Zebra Mussel (*Dreissena polymorpha*) in Lake St. Clair. J. Great Lakes Res. 28, 479–489. https://doi.org/10.1016/s0380-1330(02)70599-6

List of figures

Fig. 1. Densities of *Dreissena polymorpha* (left) and *D. rostriformis bugensis* (right) estimated by petite PONAR samples from all sites surveyed in the 2021 St. Clair River sampling season. Dreissenid mussels were identified to species. Note: inset displays a smaller density scale to visualize all *D. polymorpha* densities.

Fig. 2. Densities of *Dreissena polymorpha* (white) and *D. rostriformis bugensis* (black) estimated by petite PONAR samples from all sites surveyed in the July – August 2021 St. Clair River sampling season.

Fig. 3 Color. The Detroit River models created using MaxEnt and presence locations for (A) dreissenids, (B) *Dreissena polymorpha*, and (C) *D. rostriformis bugensis*. In all models, the dredged shipping channel was not considered for model creation and is represented with the background blue. Major contributing variables to each model were as follows: (A and C) river distance to inlet and nearest tributary and (B) river distance to outlet and nearest tributary. Higher occurrence probability as determined by the model is represented by red shading.

Fig. 3. The Detroit River models created using MaxEnt and presence locations for (A) dreissenids, (B) *Dreissena polymorpha*, and (C) *D. rostriformis bugensis*. In all models, the dredged shipping channel was not considered for model creation and is represented with the background white. Major contributing variables to each model were as follows: (A and C) river distance to inlet and nearest tributary and (B) river distance to outlet and nearest tributary. Higher occurrence probability as determined by the model is represented by darker shading.

Fig. 4 Color. (A) The St. Clair River with the projected Detroit River model ($\text{DR}_{\text{dreissenid}}$-SCR projection) created using MaxEnt and Detroit River dreissenid presence locations. (B) The St. Clair River model ($\text{SCR}_{\text{dreissenid}}$) created using MaxEnt, St. Clair River dreissenid presence locations, and major contributing variables river distance to outlet and nearest tributary. In (A) and (B), higher occurrence probability determined by the respective model is represented by red shading. (C) The difference between the two models (Absolute value (A-B)) where dark red shading represents large discrepancies in estimated occurrence probabilities. In all models, the dredged shipping channel was not considered for model creation and is represented with the background blue.

Fig. 4. (A) The St. Clair River with the projected Detroit River model ($\text{DR}_{\text{dreissenid}}$-SCR projection) created using MaxEnt and Detroit River dreissenid presence locations. (B) The St. Clair River model ($\text{SCR}_{\text{dreissenid}}$) created using MaxEnt, St. Clair River dreissenid presence locations, and major contributing variables river distance to outlet and nearest tributary. Higher occurrence probability in A and B as determined by the respective model is represented by darker shading. (C) The difference between the two models (Absolute value (A-B)) where dark shading represents large discrepancies in estimated occurrence probabilities. In all models, the dredged shipping channel was not considered for model creation and is represented with the background white.

Fig. 5 Color. (A) The St. Clair River with the projected Detroit River model (DR_{poly}-SCR projection) created using MaxEnt and Detroit River *Dreissena polymorpha* presence locations.

(B) The St. Clair River model (SCR_{poly}) created using MaxEnt, St. Clair River *D. polymorpha* presence locations, and major contributing variable river distance to inlet. In (A) and (B), higher occurrence probability determined by the respective model is represented by red shading. (C) The difference between the two models (Absolute value (A-B)) where dark red shading represents large discrepancies in estimated occurrence probabilities. In both models, the dredged shipping channel was not considered for model creation and is represented with the background blue.

Fig. 5. (A) The St. Clair River with the projected Detroit River model (DR_{poly}-SCR projection) created using MaxEnt and Detroit River *Dreissena polymorpha* presence locations. (B) The St. Clair River model (SCR_{poly}) created using MaxEnt, St. Clair River *D. polymorpha* presence locations, and major contributing variable river distance to inlet. In (A) and (B), higher occurrence probability determined by the respective model is represented by darker shading. (C) The difference between the two models (Absolute value (A-B)) where dark shading represents large discrepancies in estimated occurrence probabilities. In all models, the dredged shipping channel was not considered for model creation and is represented with the background white.

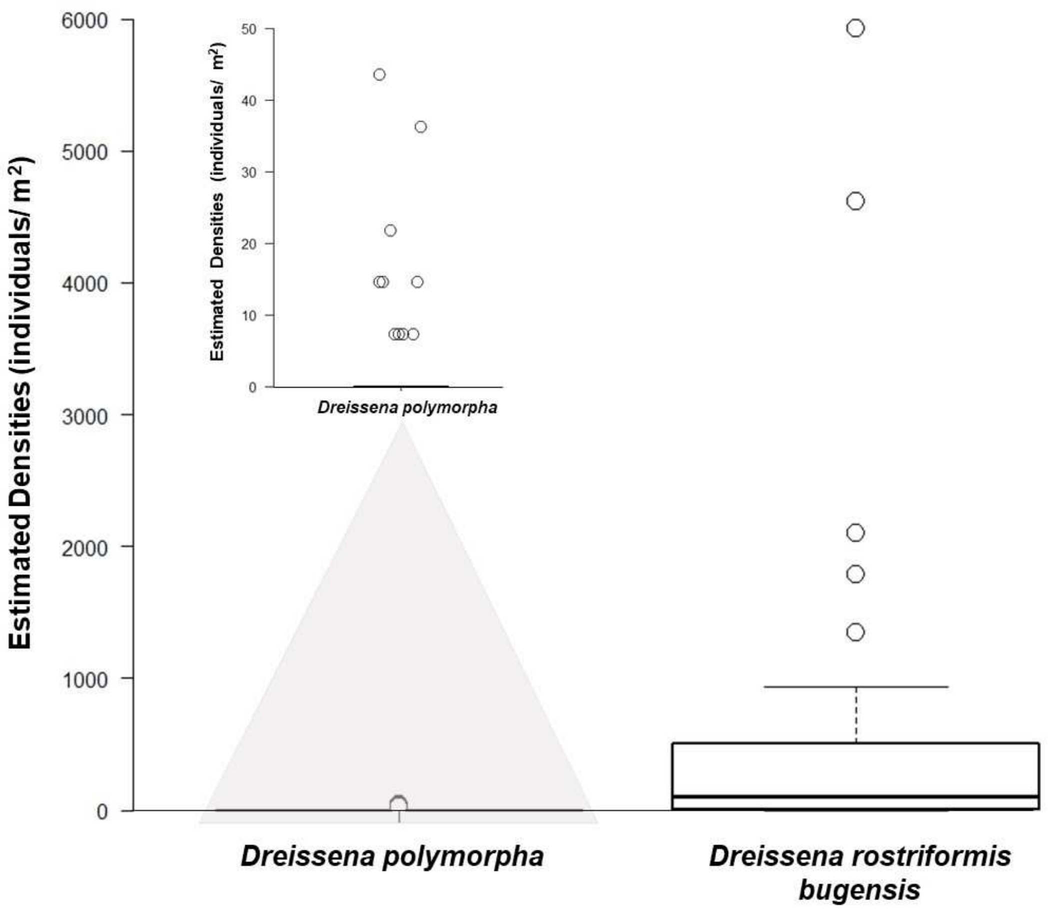
Fig. 6 Color. (A) The St. Clair River with the projected Detroit River model (DR_{bug}-SCR projection) created using MaxEnt and Detroit River *Dreissena rostriformis bugensis* presence locations. (B) The St. Clair River model (SCR_{bug}) created using MaxEnt, St. Clair River *D. r. bugensis* presence locations, and major contributing variable river distance to inlet. In (A) and (B), higher occurrence probability determined by the respective model is represented by red shading. (C) The difference between the two models (Absolute value(A-B)) where dark red shading represents large discrepancies in estimated occurrence probabilities. In all models, the dredged shipping channel was not considered for model creation and is represented with the background blue.

Fig. 6. (A) The St. Clair River with the projected Detroit River model (DR_{bug}-SCR projection) created using MaxEnt and Detroit River *Dreissena rostriformis bugensis* presence locations. (B) The St. Clair River model (SCR_{bug}) created using MaxEnt, St. Clair River *D. r. bugensis* presence locations, and major contributing variable river distance to inlet. In (A) and (B), higher occurrence probability determined by the respective model is represented by darker shading. (C) The difference between the two models (Absolute value(A-B)) where dark shading represents large discrepancies in estimated occurrence probabilities. In all models, the dredged shipping channel was not considered for model creation and is represented with the background white.

Fig. 7 Color. Differences between *Dreissena polymorpha* and *D. rostriformis bugensis* models for (A) the Detroit River (Absolute value (3B-3C)) and (B) the St. Clair River (Absolute value (5B-6B)). Dark red shading represents large discrepancies in estimated occurrence probabilities between the two models.

Fig. 7. Differences between *Dreissena polymorpha* and *D. rostriformis bugensis* models for (A) the Detroit River (Absolute value (3B-3C)) and (B) the St. Clair River (Absolute value (5B-6B)). Dark black shading represents large discrepancies in estimated occurrence probabilities between the two models.

Fig. 8. Classification and regression tree (CART) for dreissenid detection (D) and non-detection (ND) sites using environmental data collected during the 2019 Detroit River and 2021 St. Clair River sampling seasons. Environmental data used in the CART analyses were site depth, estimated macrophyte coverage, water velocity, and estimated composition of clay, silt, sand, pebbles, and cobbles. Shown are the splitting values for each environmental variable, the number of sites corresponding to each node (n), the accuracy (%) of the branch using the whole data set, and the number of sites for each detection category that correspond to that node in brackets.



Estimated Densities (individuals/ m2)
6000
5000
4000
3000
2000
1000
0
Dreissena polymorpha
Dreissena rostriformis bugensis
Estimated Densities (individuals/ m2)
50
40
30
20
10
0
Dreissena polymorpha

Fig. 1.

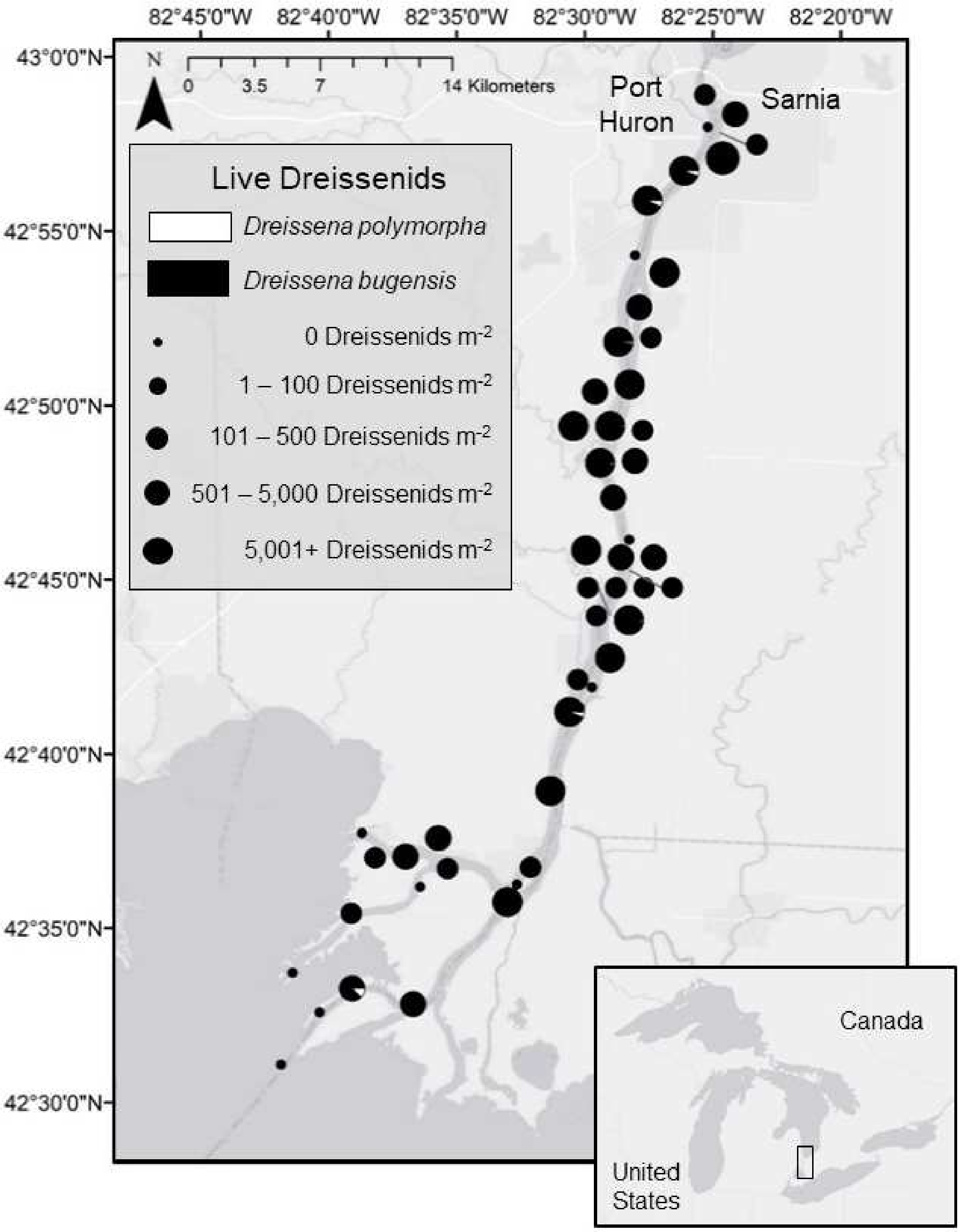

82°45'0"W
82°40'0"W
82°35'0"W
82°30'0"W
82°25'0"W
82°20'0"W
43°0'0"N
42°55'0"N
42°50'0"N
42°45'0"N
42°40'0"N
42°35'0"N
42°30'0"N
N
0
3.5
7
14 Kilometers
Port Huron
Sarnia
Live Dreissenids
Dreissena polymorpha
Dreissena bugensis
0 Dreissenids m-2
1 – 100 Dreissenids m-2
101 – 500 Dreissenids m-2
501 – 5,000 Dreissenids m-2
5,001+ Dreissenids m-2
Canada
United States

Fig. 2.

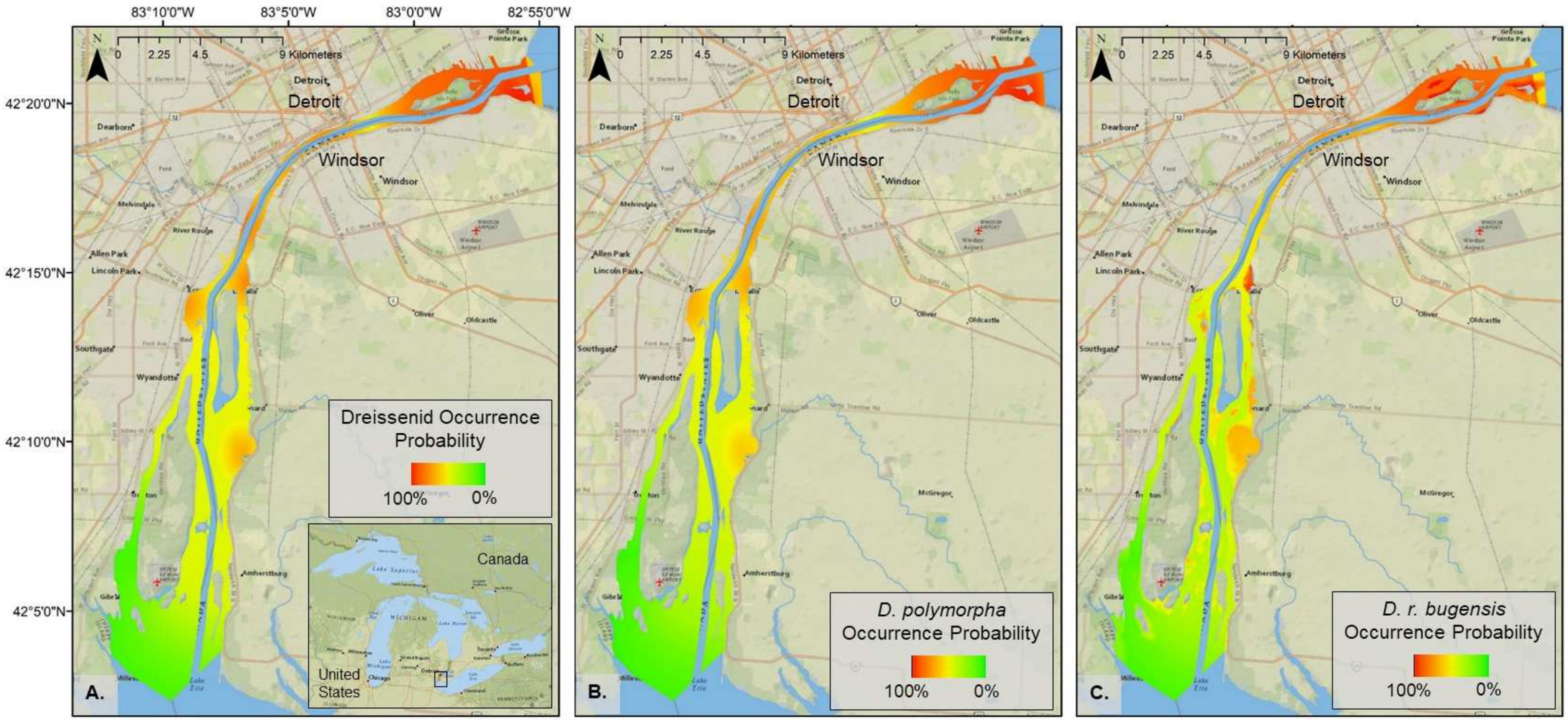

83°10'0"W
83°5'0"W
83°0'0"W
82°55'0"W
42°20'0"N
42°15'0"N
42°10'0"N
42°5'0"N
0 2.25 4.5 9 Kilometers
Detroit
Windsor
Dreissenid Occurrence Probability
100% 0%
Canada
United States
A.
B.
D. polymorpha Occurrence Probability
100% 0%
C.
D. r. bugensis Occurrence Probability
100% 0%

Fig. 3. (colour)

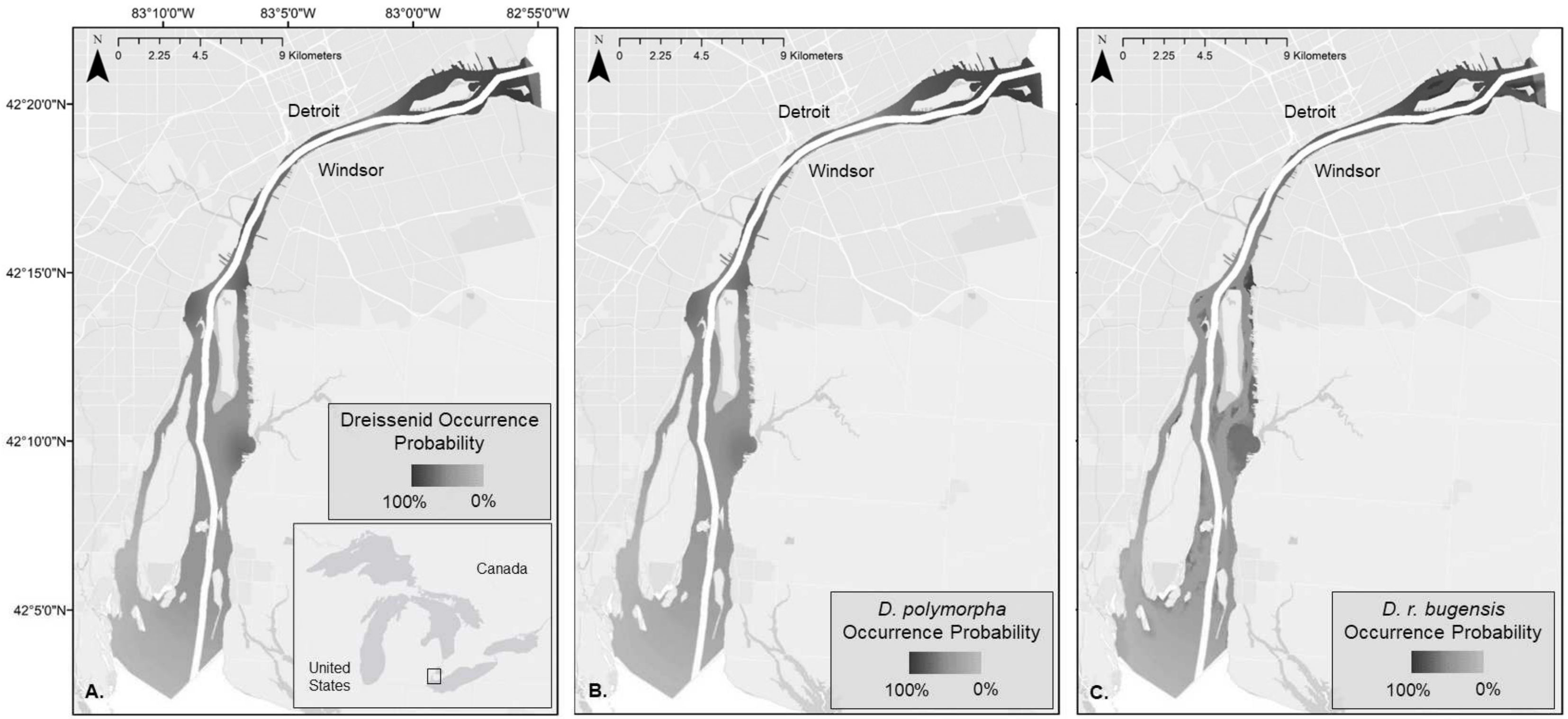


Fig. 3 (grayscale)

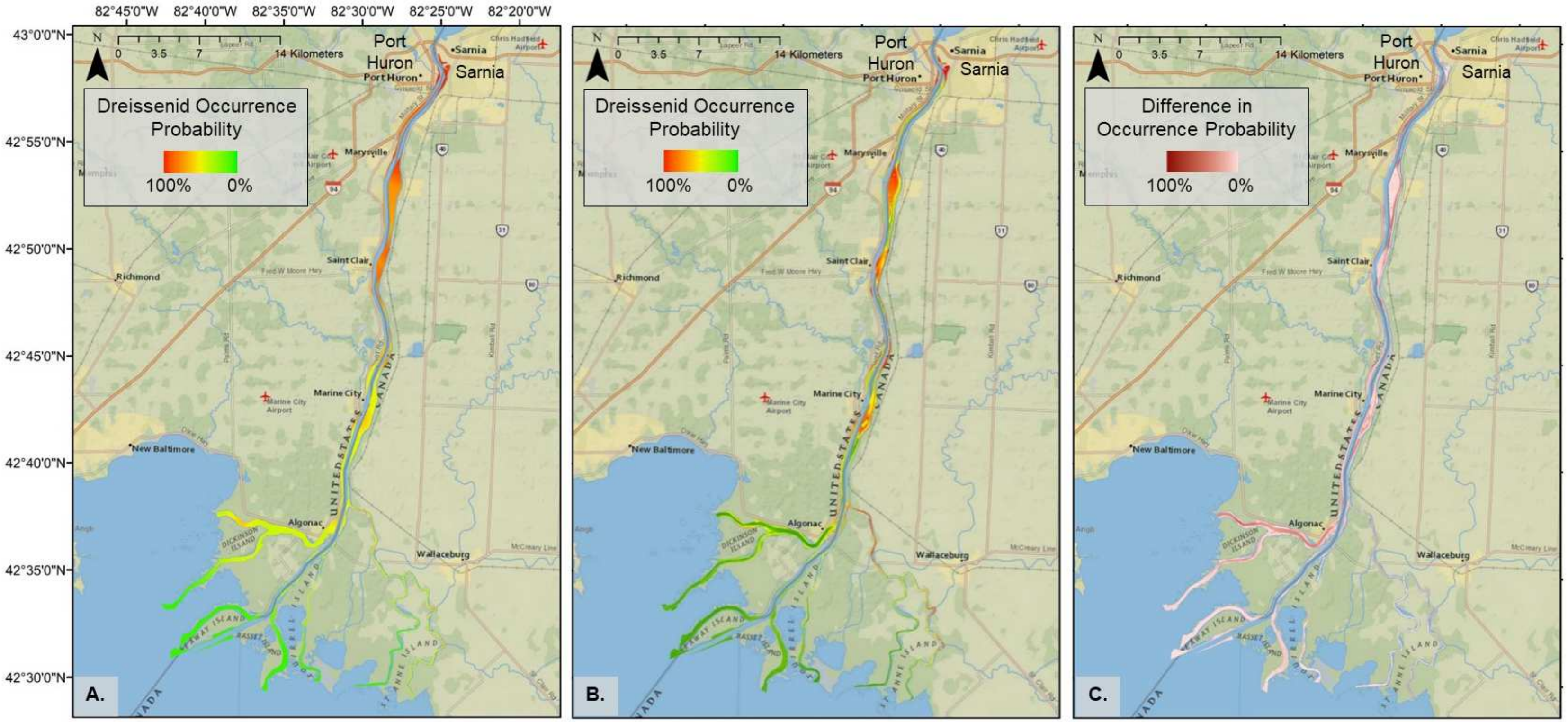

82°45'0"W
82°40'0"W
82°35'0"W
82°30'0"W
82°25'0"W
82°20'0"W
43°0'0"N
42°55'0"N
42°50'0"N
42°45'0"N
42°40'0"N
42°35'0"N
42°30'0"N
0 3.5 7 14 Kilometers
Port Huron
Sarnia
Dreissenid Occurrence Probability
100% 0%
Difference in Occurrence Probability
Marysville
Saint Clair
Richmond
Marine City
New Baltimore
Algonac
Wallaceburg
UNITED STATES
CANADA
A.
B.
C.

Fig. 4 (colour)

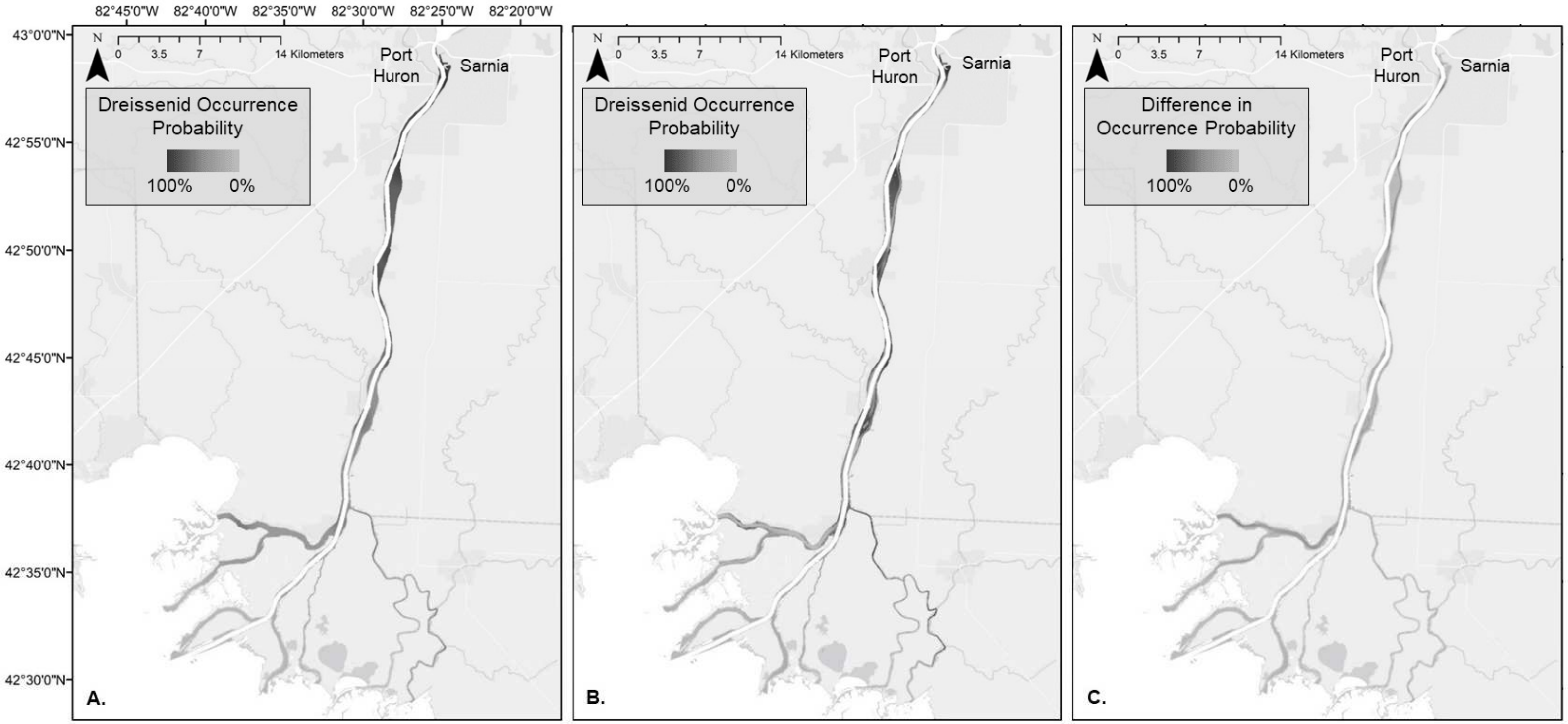


Fig. 4. (grayscale)

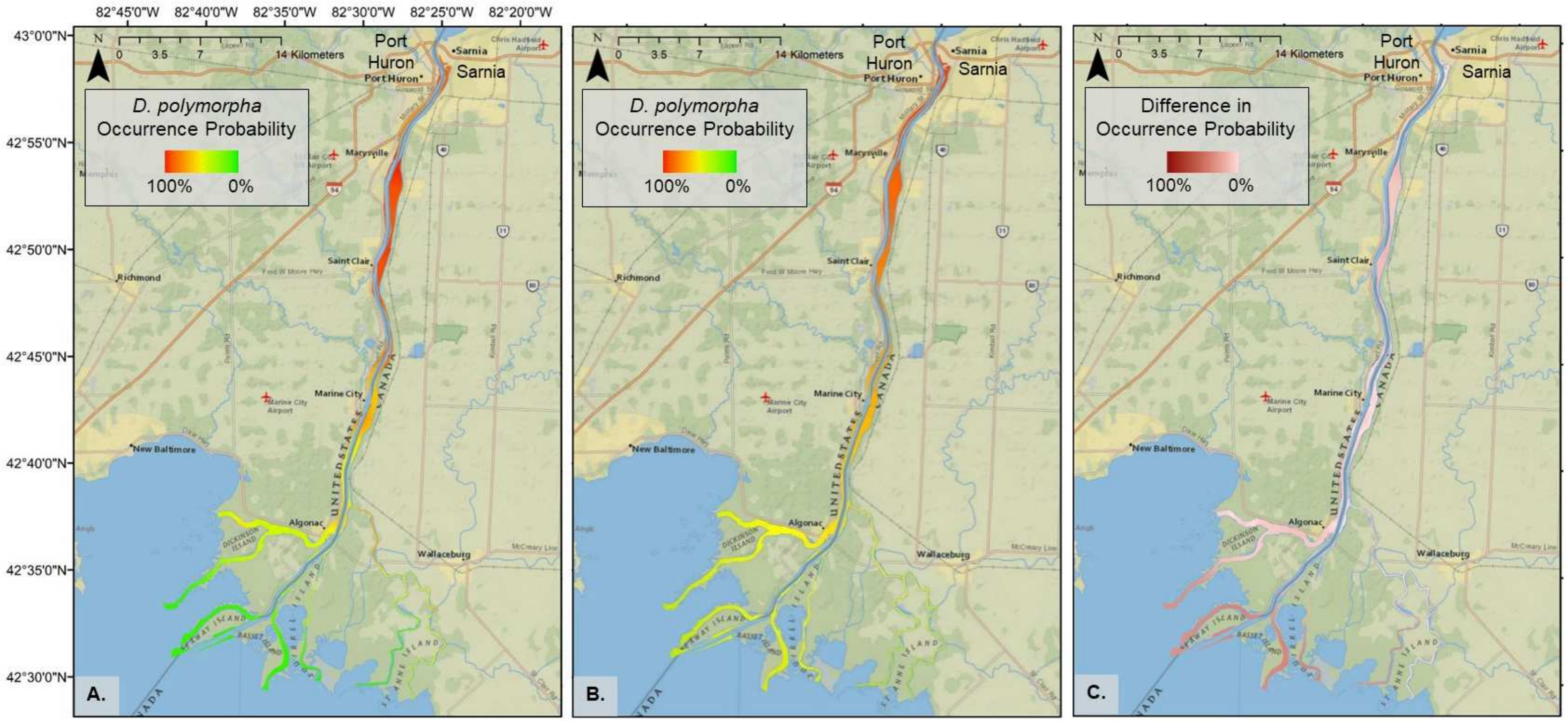

82°45'0"W
82°40'0"W
82°35'0"W
82°30'0"W
82°25'0"W
82°20'0"W
43°0'0"N
42°55'0"N
42°50'0"N
42°45'0"N
42°40'0"N
42°35'0"N
42°30'0"N
0 3.5 7 14 Kilometers
Port Huron
Sarnia
D. polymorpha
Occurrence Probability
100% 0%
Difference in
Occurrence Probability
Marysville
Saint Clair
Richmond
Marine City
New Baltimore
Algonac
Wallaceburg
A.
B.
C.

Fig. 5 (colour)

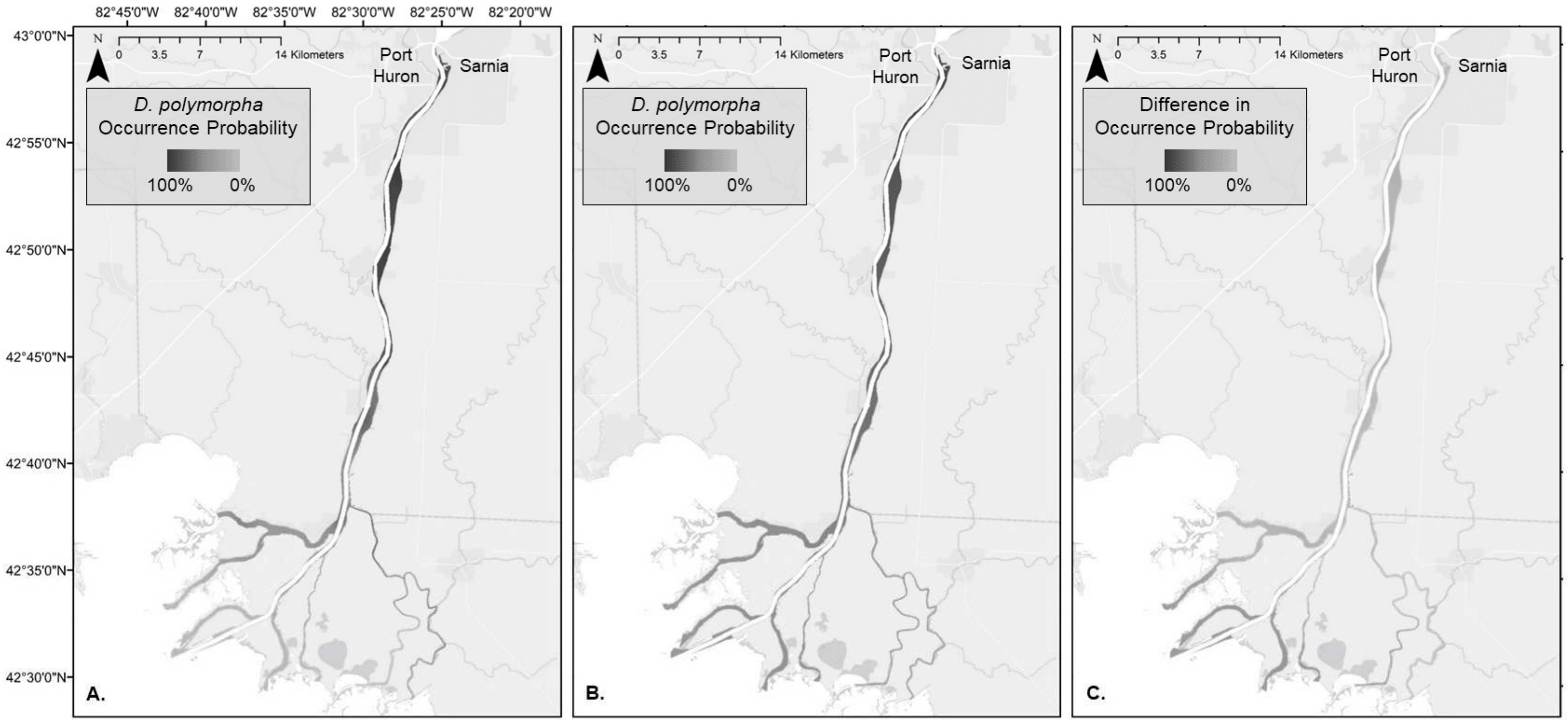
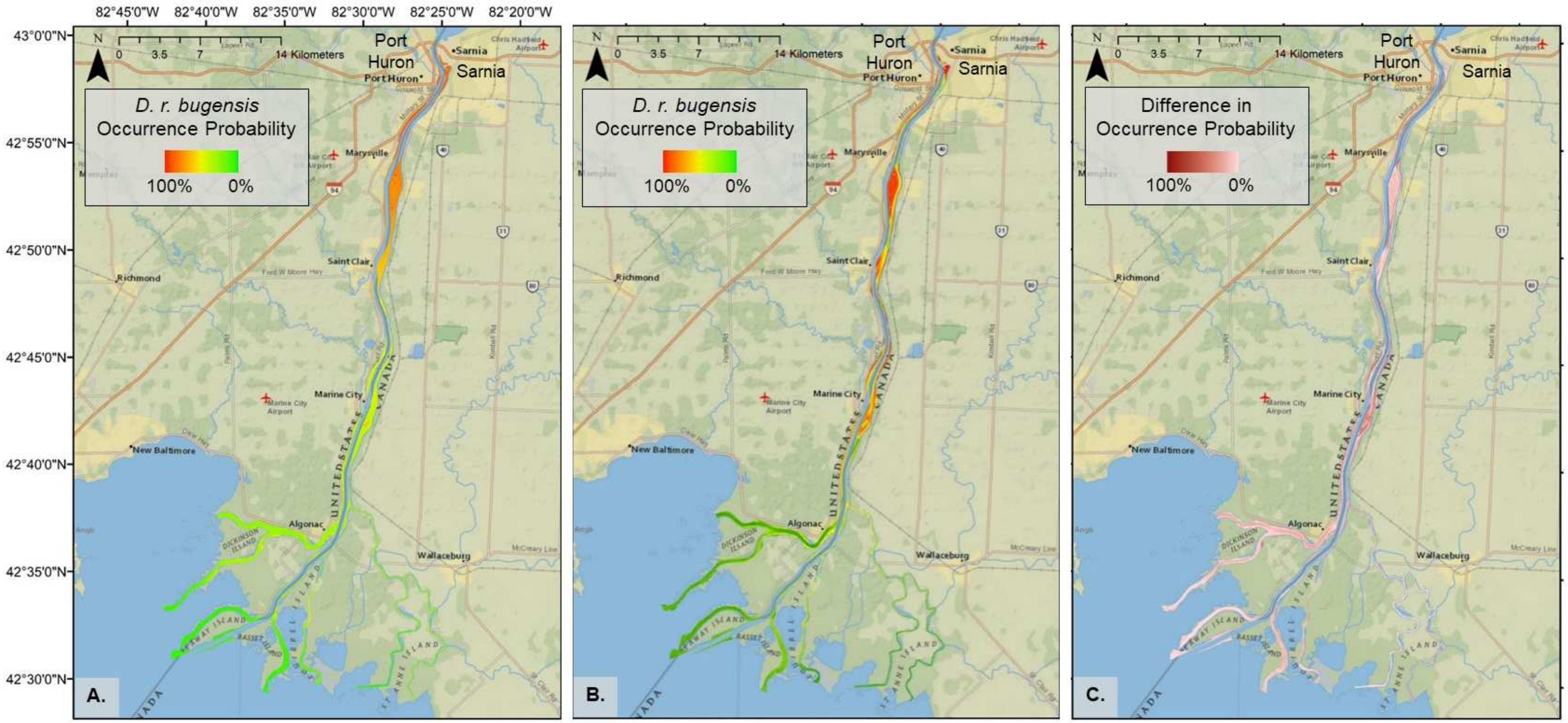


Fig. 5. (grayscale)



82°45'0"W
82°40'0"W
82°35'0"W
82°30'0"W
82°25'0"W
82°20'0"W
43°0'0"N
42°55'0"N
42°50'0"N
42°45'0"N
42°40'0"N
42°35'0"N
42°30'0"N
0 3.5 7 14 Kilometers
Port Huron
Sarnia
D. r. bugensis Occurrence Probability
100% 0%
Difference in Occurrence Probability
Marysville
Saint Clair
Richmond
Marine City
New Baltimore
Algonac
Wallaceburg
DICKINSON ISLAND
UNITED STATES
CANADA
A.
B.
C.

Fig. 6 (colour)

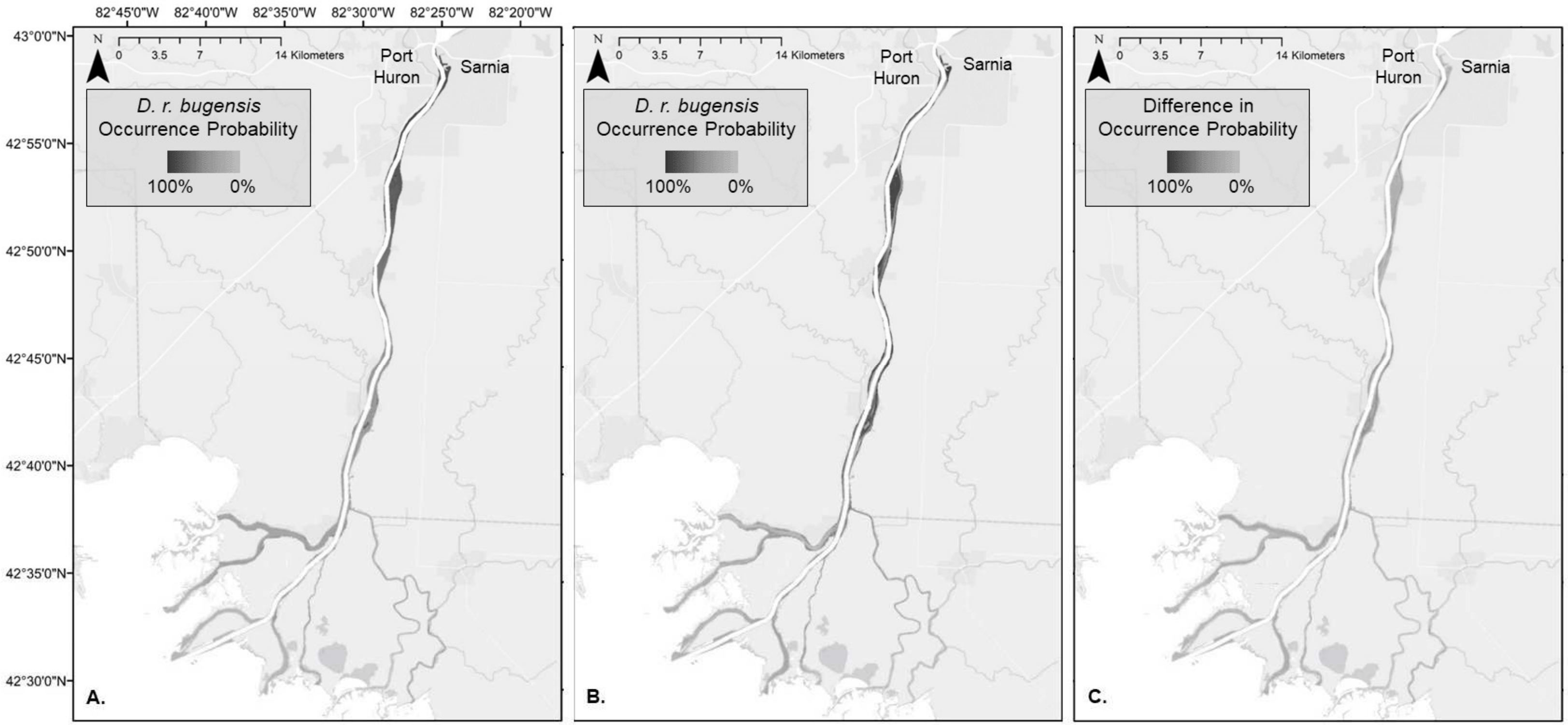


Fig. 6. (grayscale)

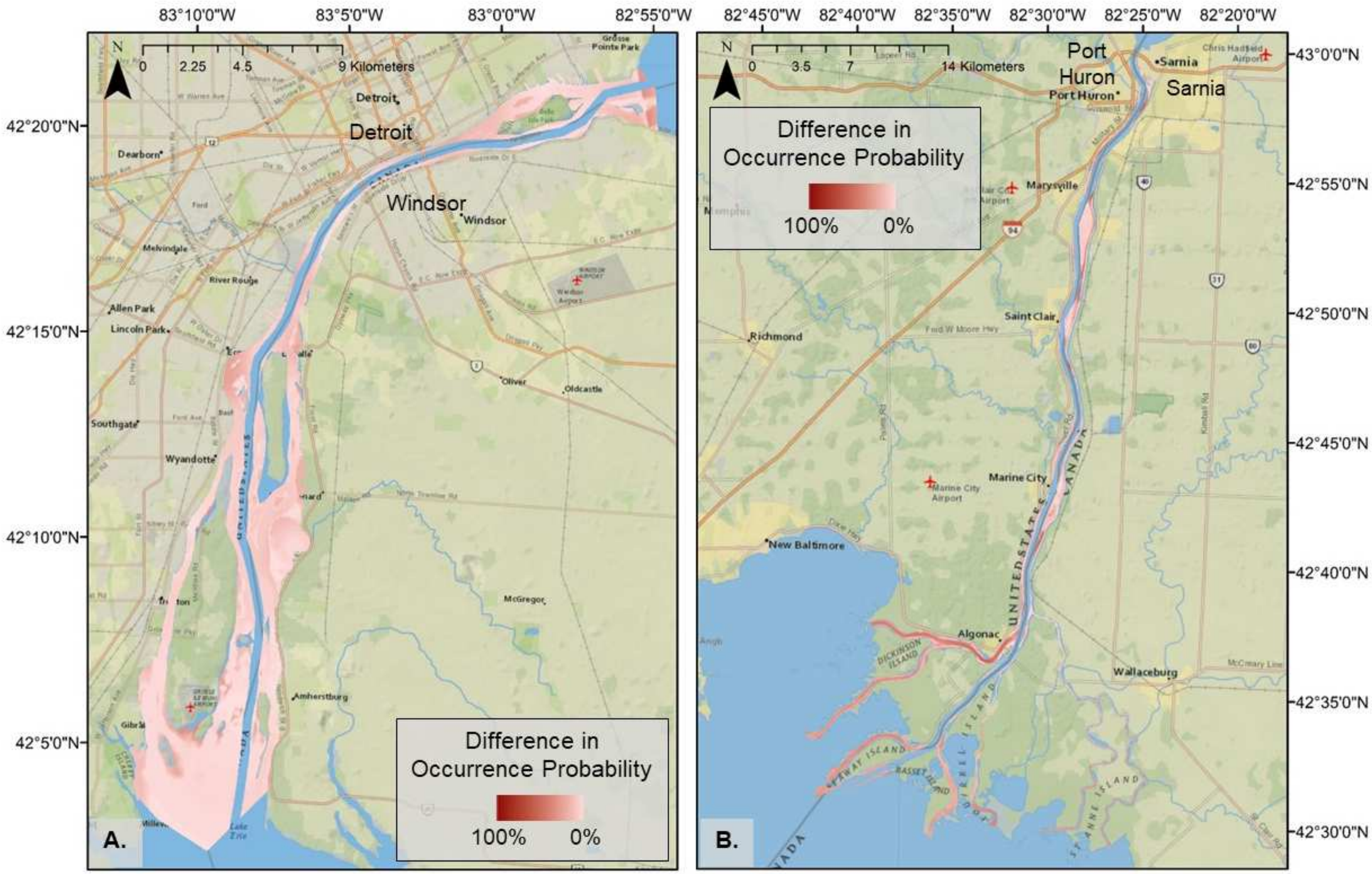

83°10'0"W
83°5'0"W
83°0'0"W
82°55'0"W
82°45'0"W
82°40'0"W
82°35'0"W
82°30'0"W
82°25'0"W
82°20'0"W
42°20'0"N
42°15'0"N
42°10'0"N
42°5'0"N
43°0'0"N
42°55'0"N
42°50'0"N
42°45'0"N
42°40'0"N
42°35'0"N
42°30'0"N
0 2.25 4.5 9 Kilometers
0 3.5 7 14 Kilometers
Detroit
Windsor
Port Huron
Sarnia
Difference in Occurrence Probability
100% 0%
Difference in Occurrence Probability
100% 0%
A.
B.

Fig. 7 (colour)

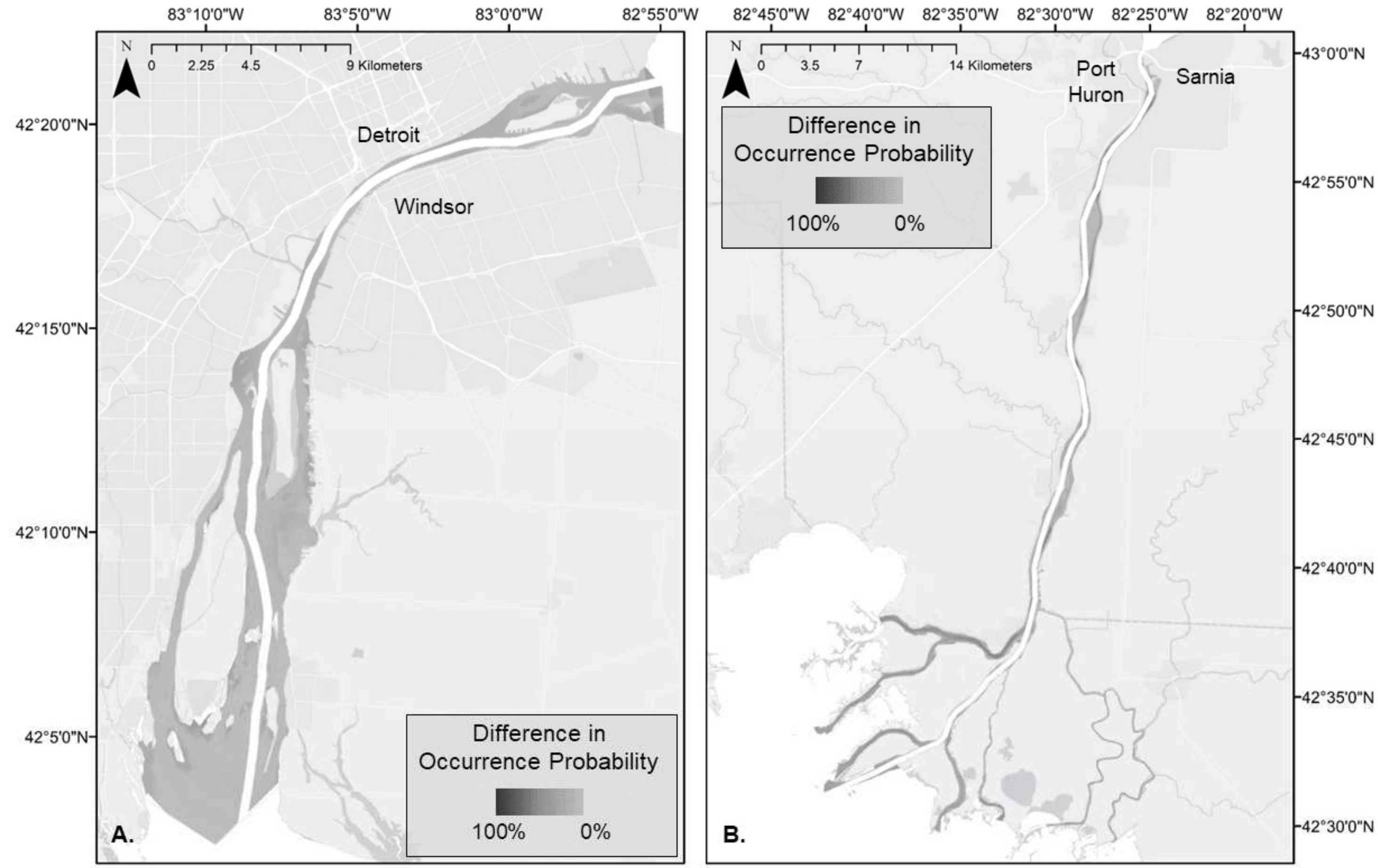
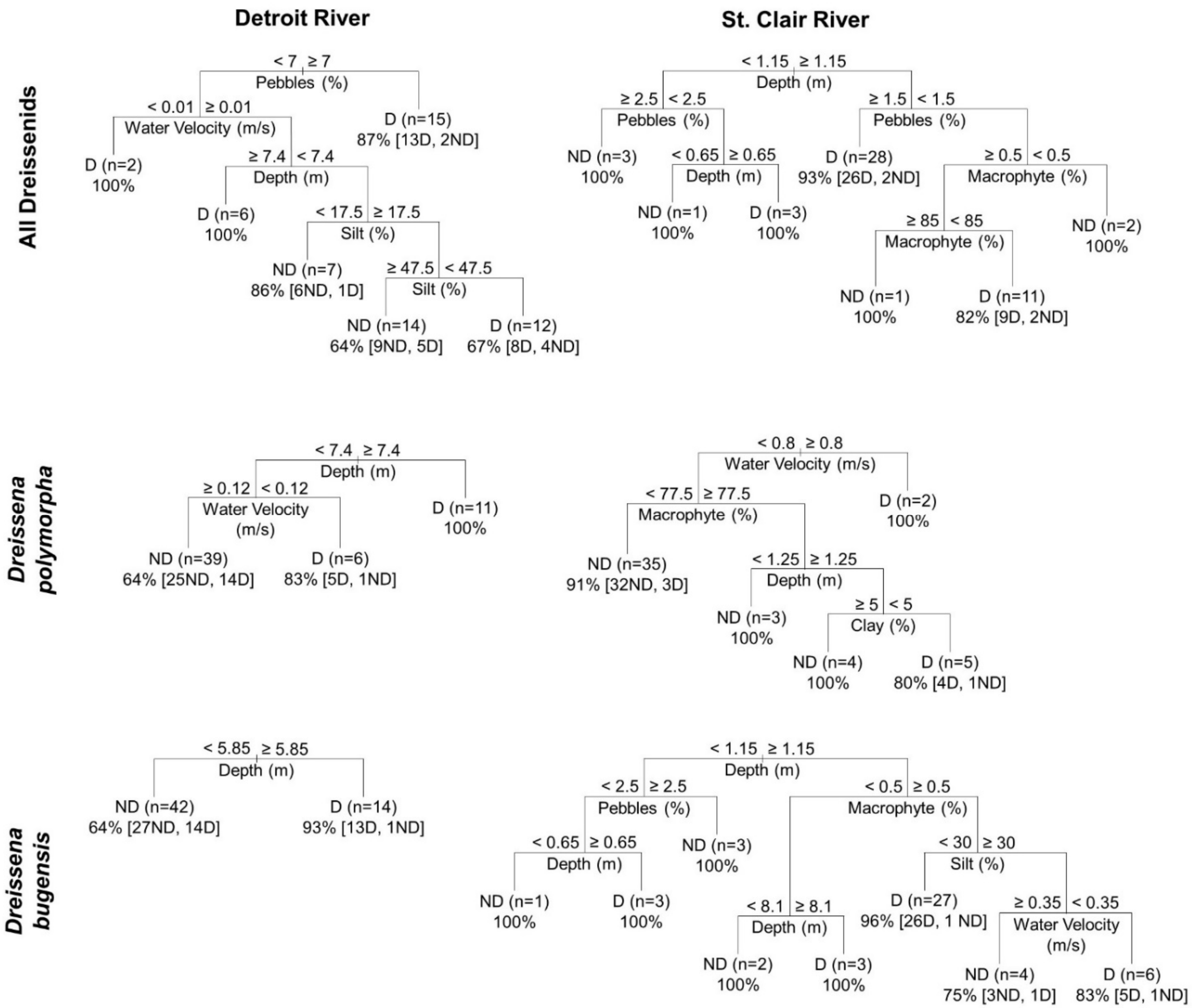


Fig. 7. (grayscale)



Detroit River
St. Clair River
All Dreissenids
Dreissena polymorpha
Dreissena bugensis
< 7 ≥ 7
Pebbles (%)
< 0.01 ≥ 0.01
Water Velocity (m/s)
D (n=15)
87% [13D, 2ND]
D (n=2)
100%
≥ 7.4 < 7.4
Depth (m)
D (n=6)
100%
< 17.5 ≥ 17.5
Silt (%)
ND (n=7)
86% [6ND, 1D]
≥ 47.5 < 47.5
Silt (%)
ND (n=14)
64% [9ND, 5D]
D (n=12)
67% [8D, 4ND]
< 1.15 ≥ 1.15
Depth (m)
≥ 2.5 < 2.5
Pebbles (%)
ND (n=3)
100%
< 0.65 ≥ 0.65
Depth (m)
ND (n=1)
100%
D (n=3)
100%
≥ 1.5 < 1.5
Pebbles (%)
D (n=28)
93% [26D, 2ND]
≥ 0.5 < 0.5
Macrophyte (%)
≥ 85 < 85
Macrophyte (%)
ND (n=1)
100%
D (n=11)
82% [9D, 2ND]
ND (n=2)
100%
< 7.4 ≥ 7.4
Depth (m)
≥ 0.12 < 0.12
Water Velocity
(m/s)
ND (n=39)
64% [25ND, 14D]
D (n=6)
83% [5D, 1ND]
D (n=11)
100%
< 0.8 ≥ 0.8
Water Velocity (m/s)
< 77.5 ≥ 77.5
Macrophyte (%)
D (n=2)
100%
ND (n=35)
91% [32ND, 3D]
< 1.25 ≥ 1.25
Depth (m)
ND (n=3)
100%
≥ 5 < 5
Clay (%)
ND (n=4)
100%
D (n=5)
80% [4D, 1ND]
< 5.85 ≥ 5.85
Depth (m)
ND (n=42)
64% [27ND, 14D]
D (n=14)
93% [13D, 1ND]
< 1.15 ≥ 1.15
Depth (m)
< 2.5 ≥ 2.5
Pebbles (%)
ND (n=3)
100%
< 0.65 ≥ 0.65
Depth (m)
ND (n=1)
100%
D (n=3)
100%
< 0.5 ≥ 0.5
Macrophyte (%)
< 8.1 ≥ 8.1
Depth (m)
ND (n=2)
100%
D (n=3)
100%
< 30 ≥ 30
Silt (%)
D (n=27)
96% [26D, 1 ND]
≥ 0.35 < 0.35
Water Velocity
(m/s)
ND (n=4)
75% [3ND, 1D]
D (n=6)
83% [5D, 1ND]

Fig. 8.

Table 1. A summary of the all the models created and visualized for dreissenids, *Dreissena polymorpha* (poly), and *D. rostriformis bugensis* (bug) in the Detroit (DR) and St. Clair Rivers (SCR). AUC represents Area Under the Curve which was used to assess and select the model. "-" indicates that the AUC does not differ between the DR model and the DR model projection. Overall accuracy represents the model's ability to predict both detection and non-detection sites while live detection accuracy represents the model's ability to predict detection sites only.

	Model Abbreviation	Created using	Visualized on	Figure	AUC	Overall Accuracy (min-max)	Live Detection Accuracy (min-max)
MaxEnt Models	**DR$_{\text{dreissenid}}$**	DR dreissenid detection sites	DR	3A	0.736	70.6 – 88.2%	45.7 – 97.1%
	DR$_{poly}$	DR *D. polymorpha* detection sites	DR	3B	0.781	62.7 – 88.4%	40.0 – 93.3%
	DR$_{bug}$	DR *D. r. bugensis* detection sites	DR	3C	0.744	74.5 – 88.2%	54.6 – 96.4%
	DR$_{\text{dreissenid}}$-SCR	DR dreissenid detection sites	SCR	4A	-	51.0 – 80.4%	45.0 – 95.0%
	DR$_{poly}$-SCR	DR *D. polymorpha* detection sites	SCR	5A	-	27.5 – 51.0%	70.0 – 90.0%
	DR$_{bug}$-SCR	DR *D. r. bugensis* detection sites	SCR	6A	-	37.3 – 72.6%	25.0 – 80.0%
	SCR$_{\text{dreissenid}}$	SCR dreissenid detection sites	SCR	4B	0.782	52.9 – 82.4%	50.0 – 92.5%
	SCR$_{poly}$	SCR *D. polymorpha* detection sites	SCR	5B	0.764	19.6 – 64.7%	60.0 – 100%
	SCR$_{bug}$	SCR *D. r. bugensis* detection sites	SCR	6B	0.764	62.8 – 80.4%	62.5 – 90.0%

CART Models	**DR Dreissenid**	DR dreissenid detection sites	-	8	0.986	55%	-
	DR *D. polymorpha*	DR *D. polymorpha* detection sites	-	8	0.858	64%	-
	DR *D. r. bugensis*	DR *D. r. bugensis* detection sites	-	8	0.928	60%	-
	SCR Dreissenid	SCR dreissenid detection sites	-	8	0.995	77%	-
	SCR *D. polymorpha*	SCR *D. polymorpha* detection sites	-	8	0.611	78%	-
	SCR *D. r. bugensis*	SCR D. *r. bugensis* detection sites	-	8	0.995	78%	-

Table 2. Mean (± standard error) measurements of abiotic and biotic variables recorded at sites surveyed in the Detroit (2019) and St. Clair (2021) rivers. Abiotic variable means for the Detroit River are taken from Keretz et al. (2021).

	Detroit River			**St. Clair River**		
	Dreissenids Detected	**Dreissenids Not Detected**	**All Sites**	**Dreissenids Detected**	**Dreissenids Not Detected**	**All Sites**
N	35	21	56	40	11	51
Surface Water Temperature (°C)	23.5 ± 0.1	23.5 ± 0.1	23.5 ± 0.1	21.4 ± 0.1	21.3 ± 0.1	21.4 ± 0.1
Site Depth (m)	5.1 ± 0.5	3.4 ± 0.3	4.4 ± 0.4	4.7 ± 0.5	3.0 ± 0.8	4.3 ± 0.5
Water Velocity (m/s)	0.35 ± 0.04	0.27 ± 0.03	0.32 ± 0.03	0.49 ± 0.03	0.38 ± 0.06	0.47 ± 0.03
Macrophyte Coverage (%)	36 ± 5	47 ± 6	40 ± 4	46 ± 5	47 ± 10	47 ± 4

Table 3. Variables used with MaxEnt to create species distribution models and the percent contribution of those variables towards the Detroit and St. Clair River dreissenid models. [1]*D. r. b.* is an abbreviation for *Dreissena rostriformis bugensis* and *D. p.* is an abbreviation for *Dreissena polymorpha*. "-" indicates the variable was not used in the final model.

			Model Contribution (%)					
			Detroit River			**St. Clair River**		
Variable	**Definition**	**Source**	**Dreissenid Model**	***D. p.*[1] Model**	***D. r. b.*[1] Model**	**Dreissenid Model**	***D. p.* Model**	***D. r. b.* Model**
Depth	A measure of the water column (m)	Thompson (2016)	-	-	12.0	21.4	-	21.4
Total Velocity	Water velocity (m s^{-1}) estimated using a hydrologic model	Thompson (2016)	-	-	-	-	-	-
East/West Velocity	Water velocity (m s^{-1}) in the East/West direction estimated using a hydrologic model	Thompson (2016)	-	-	0.3	-	-	-
North/ South Velocity	Water velocity (m s^{-1}) in the North/ South direction estimated using a hydrologic model	Thompson (2016)	-	-	0.6	-	-	-
Inlet	River distance (km) to the river's inlet source (Lake Huron for the St. Clair River and Lake St. Clair for the Detroit River	ArcGIS Euclidean Distance	61.2	-	71.4	-	100	78.6
Outlet	River distance (km) to the river's outlet source (Lake St. Clair for the St. Clair River and Lake Erie for the Detroit River)	ArcGIS Euclidean Distance	-	65.7	-	40.2	-	-
Nearest Tributary	River distance (km) to the nearest tributary within the river	ArcGIS Euclidean Distance	38.8	34.3	15.8	38.5	<0.1	-

Table 4. Assessment of potential Optimal Probability Threshold (OPT) values for evaluating the accuracy of the Detroit River dreissenid species distribution model ($DR_{dreissenid}$) in the Detroit River (DR) and the Detroit River dreissenid model - St. Clair River projection ($DR_{dreissenid}$-SCR) in the St. Clair River (SCR).

Occurrence Probability Threshold (OPT)	**30%**	**40%**	**50%**	**60%**	**70%**
# DR dreissenid detection sites ≥ OPT	34	33	26	23	16
# DR dreissenid detection sites < OPT	1	2	9	12	19
Accuracy of the $DR_{dreissenid}$ model for DR dreissenid detection sites (n=35)	97.1%	94.3%	74.3%	65.7%	45.7%
# DR dreissenid non-detection sites ≥ OPT	11	9	4	3	1
# DR dreissenid non-detection sites < OPT	10	12	17	18	20
Accuracy of the $DR_{dreissenid}$ model for DR dreissenid non-detection sites (n=21)	47.6%	57.1%	80.9%	85.7%	95.2%
Accuracy of the $DR_{dreissenid}$ model for all DR sites (n=56)	86.3%	88.2%	84.3%	80.4%	70.6%
# SCR dreissenid detection sites ≥ OPT	38	35	28	26	18
# SCR dreissenid detection sites < OPT	2	5	12	14	22
Accuracy of the $DR_{dreissenid}$–SCR projection for SCR dreissenid detection sites (n=40)	95.0%	87.5%	70.0%	65.0%	45.0%
# SCR dreissenid non-detection sites ≥ OPT	8	6	4	3	3
# SCR dreissenid non-detection sites < OPT	3	5	7	8	8
Accuracy of the $DR_{dreissenid}$–SCR projection for SCR dreissenid non-detection sites (n=11)	27.3%	45.5%	63.6%	72.7%	72.7%
Accuracy of the $DR_{dreissenid}$-SCR projection for all SCR sites (n=51)	80.4%	78.4%	68.6%	66.7%	51.0%