LAKE TYPE AND CONNECTIVITY PREDICT ZEBRA MUSSEL (DREISSENA POLYMORPHA) PRESENCE

By

Danielle Matuszak

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ABSTRACT

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Studies that differentiate between lake type or origin, i.e., natural lakes and reservoirs, that focus solely on reservoirs, or that study invasive species in these systems are rare, especially at broad scales leading to reservoirs being less understood compared to natural lakes. Surface water connections, as well as human connections such as the trailering of recreational boats, likely also play a role in the spread of the invasive zebra mussel (*Dreissena polymorpha*) larvae. Taking a data-intensive approach at the macroscale, we ask: **Are zebra mussels more common in reservoirs than in natural lakes? How does surface water and human connectivity influence the presence of zebra mussels in reservoirs and natural lakes?** We used 907 lakes within a 17-U.S. state extent, characterized surface water connectivity using six unique lake connectivity classes based on lake and stream inflow(s)/outflow(s), and characterized human connectivity with watershed road densities (m/ha) and, for a 3-state subset, the presence of public access sites on lakes. Using logistic multiple regressions, controlling for region and lake chlorophyll *a* concentrations, we found that a higher proportion of reservoirs have zebra mussels compared to natural lakes, that more highly connected lakes were more likely to have zebra mussels present, regardless of lake type, and lakes with a public access site were more likely to have zebra mussels than those without, regardless of lake type. We conclude that not all ‘lakes’ are equally likely to have zebra mussels present and that both surface water and human connectivity are important predictors of zebra mussel presence.

This is dedicated to my family.
Thank you for supporting and believing in me from the very beginning.

ACKNOWLEDGEMENTS

I would like to acknowledge my graduate research advisor Kendra Spence Cheruvelil as well as my graduate committee, Dana Infante and Jo Latimore. Additionally, thank you to Patrick Hanley for statistical analysis and figure making guidance. Thank you to Wes Daniel for providing the boat launch/public access data. I would like to acknowledge my research lab members, Ian McCullough, Patricia Soranno, Marcella Domka, Maggie Haite, and Nicole Smith. I would like to acknowledge my undergraduate mentor Carrie Kissman for her support.

AUTHOR CONTRIBUTION STATEMENT

I use the word “we” when describing the research reported on in this thesis. This choice was a deliberate one, signifying the fact that this research was not done in isolation; rather, I conducted data-intensive research using existing datasets and with the support and help of my advisor (Kendra Spence Cheruvelil; KSC) and the research program coordinator in my lab (Patrick Hanly; PH). Therefore, these two people will be co-authors on the planned journal article based on this thesis. When I was recruited to work with Kendra, she suggested that I identify a thesis that would make use of the reservoir data product that she and others were developing. Therefore, KSC and I (Danielle Matuszak; DM) came up with the original idea that inspired this thesis. I wrote the first draft and created all tables in the thesis, with KSC providing substantive guidance and edits. All figures were created by DM with the help of PH. Data cleaning and compiling, as well as the building of statistical models was done by DM with the guidance and assistance of PH.

PREFACE

In addition to this thesis, I am co-author on a data paper, the basis of which was utilized in this thesis. The manuscript has undergone two rounds of revisions. The preliminary citation is as follows:

> Rodriguez, L, Polus, S., Matuszak, D.I., Domka, M.R., Q. Wang, P.A. Soranno, and K.S. Cheruvelil. (2022 - under review). LAGOS-US RESERVOIR: A database classifying conterminous U.S. lakes 4 hectares and larger as natural lakes or reservoirs. Limnology & Oceanography Letters.

Additionally, I am part of a large research team (Continental Limnology) that has designed, created, and utilizes the LAke multiscaled GeOSpatial and temporal databases (LAGOS; www.lagoslakes.org). As part of that team, I am a co-author on an in-progress manuscript.

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KEY TO ABBREVIATIONS

NL	Natural Lake
RSVR	Reservoir
ZM	Zebra mussel
LAGOS	LAke multiscaled GeOSpatial and temporal database

Introduction

A majority of reservoirs in the United States are less than 90 years old (Thorton 1990). In recent years, as the water control structures age, they are being removed (Habel et al. 2020). As new reservoirs are constructed and old ones altered or removed, there have been calls for this construction and removal to be based on the most up to date and reliable data available and for a balance between sustainability of fresh waters and human needs (Lehner et al. 2011).

Reservoirs have many impacts on both human society and the natural world (Lehner et al. 2011). The building of water-control structures, and thus the creation of reservoirs, has long served as a way to alter water flow for irrigation, aid navigation, create hydropower, and facilitate flood control, while also increasing tourism, fisheries, and recreation on those altered water bodies (Thornton 1990; Lehner et. al 2011; Doubek and Carey 2017; Mamun et al. 2020). Although important ecosystems, reservoirs often have high levels of human disturbance that can lead to habitat fragmentation, eutrophication, and a collapse in biodiversity (Doubek and Carey 2017; Havel et al. 2005; Lehner et al. 2011). Water control structures on reservoirs, such as dams, alter natural habitat, and lead to reservoirs generally having larger watershed sizes that are more heavily influenced by both nutrient and sediment runoff from their surrounding agricultural landscapes (Knoll et al. 2003) than their natural lake counterparts. Reservoirs also can exhibit disrupted sediment and nutrient flow (Knoll et al. 2003, Lehner et al 2011), are susceptible to accumulating contaminants, and can have different biological composition than the river systems they are associated with (Lehner et al. 2011).

The introduction of non-native species to water bodies, including reservoirs, can be detrimental to biodiversity and overall ecosystem health. Research shows that human disturbances, such as recreational boating (Johnson et al. 2001; Kelly et al. 2001), alteration of flow regimes (Bunn and Arthington 2002), and nutrient loading (Havel et al. 2005) can promote the spread of aquatic invasive species. In fact, previous research has shown that the role of humans in promoting invasions may be underestimated (Chapman et al. 2020). Therefore, building reservoirs, with the co-occurring effects of higher levels of disturbance associated with reservoirs, can create openings for introduced species to displace native biodiversity (Havel et al. 2005). For example, aquatic invasive species such as the quagga mussel (*Rostriformis bugensis*), the macrophyte Eurasian water milfoil (*Myriophyllum spicatum*), and the rusty crayfish (*Faxonius rusticus*) were introduced by boaters (Cole et al. 2019). Additionally, the invasive redclaw crayfish (*Cherax quadricarinatus*) initially invaded Australian reservoirs (Beatty et al. 2019) and the African Spiny Water-flea (*Daphnia lumholtzi*) initially invaded reservoirs in the southern United States (Havel et al. 2005). Based on the characteristics of reservoirs and invasive species examples such as these, we expect reservoirs to harbor larger numbers of invasive species compared to natural lakes.

Reservoirs Compared to Natural Lakes

Reservoirs are vastly understudied compared to natural lakes (Doubek and Carey 2017) and many studies of 'lakes' do not differentiate between natural lakes and reservoirs (Rodriquez et al. under review). Although these two types of systems are thought to be different from one another, there is conflicting evidence as to whether reservoirs or natural lakes experience greater levels of eutrophication in the U.S. (Doubek and Carey 2017). However, reservoirs tend to be warmer (Thornton 1990), have larger watersheds (Knoll et al. 2003), and have larger ratios of watershed area to waterbody surface area (Lehner and Doll 2004) compared to natural lakes. On average, reservoirs also tend to have high levels of human disturbance with associated unstable food webs (McAllister et al. 2001), contaminant accumulation (Lehner et al. 2011), and aquatic plant infestations with associated low levels of dissolved oxygen (Kennedy and Gaugush 1988). Due to these differences, studies of inland waters should account for whether water bodies are reservoirs or natural lakes.

There is also a knowledge gap regarding levels and impacts of invasive species between reservoirs and natural lakes. This fact is in part because there has not previously been a classification of lakes by type or origin (Rodriguez et al. under review). In fact, there has not even been a standard definition of 'reservoir'. Reservoirs vary in both form and function and range from run-of-the-river high-flow reservoirs to very still and less-connected water bodies. Many reservoirs have dams that regulate water levels and velocity, which alters natural habitats by disrupting sediment and nutrient flows, altering biological composition (Lehner et al. 2011). However, other reservoirs are relatively isolated with little water flow. These facts have presented barriers to a standard definition and a broad-scale lake classification by type or origin. Existing datasets with a lake-type classification typically include either only very large water bodies, water bodies with very large dams, or individual reservoirs studied for long time periods (Birkett and Mason 1995; Lehner 2011; Rodriguez et al. under review).

My thesis research takes advantage of very recent research to move beyond these knowledge gaps. First, I helped create a data product that classifies all lakes $\geq$4 ha in conterminous U.S. into either natural lakes or reservoirs (Rodriguez et al. under review). As part of this data production effort, we define "reservoir" (RSVR) and "natural lake" (NL) as follows. A "reservoir" is a lake that is likely to be either human-made or highly human-altered by the presence of a relatively large water control structure that significantly changes the flow of water. A "natural lake" is a lake that is likely to be either naturally-formed, one that does not have a relatively large, apparently flow-altering structure on or near it, or one that has a small human-made control structure on it but because the structure is small or downstream of the lake, it is assumed to mostly control water levels rather than the flow and the basin shape does not appear to be due to the structure (Figure 1, Rodriguez et al. under review). Armed with these data and definitions, my thesis research is the first of its kind – a broad-scale investigation of invasive species in natural lakes compared to reservoirs.

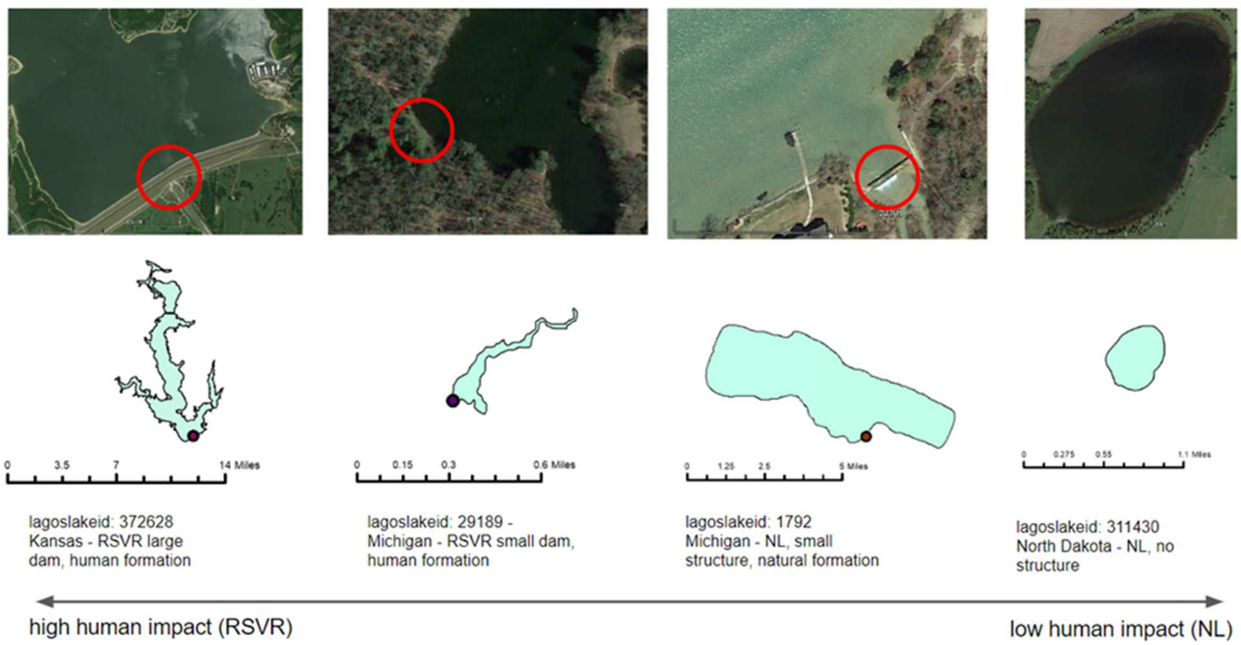


Figure 1- Examples of NLs and RSVRs showing range of human modification: Images and associated polygons depicting examples of reservoirs (left) and natural lakes (right) that show a range in the amount of human impacts caused by water control structures and the process used to visually classify all conterminous U.S. lakes $\geq$4 ha as either reservoir (RSVR) or natural lake (NL). Images left to right are a highly-modified lake with a large dam creating a characteristically dendritic reservoir on a mainstem river, a less modified lake that includes a dam on an in-coming stream that results in a reservoir, a natural lake that includes a water level control structure at one location, and a natural lake with no structure that is characteristically round. Figure credit: Rodriguez et al. under review.

Study Species: the Invasive Zebra Mussel

I use the zebra mussel (*Dreissena polymorpha*), an aquatic invasive species, as a model species to examine whether the presence of invasives differs between natural lakes and reservoirs. Zebra mussels have been documented in the Great Lakes since as early as the late 1980s (Herbert et al. 1989; Carlton 2008) and were likely introduced by the dumping of ballast water from cargo ships that contained veligers (larval stage of zebra mussels) (Herbert et al. 1989). Since that time, zebra mussels have spread widely across the U.S, particularly in the Great Lakes region, and are now dispersed throughout much of the Mississippi River basin and surrounding watersheds (Benson et al. 2021; Figure 2).

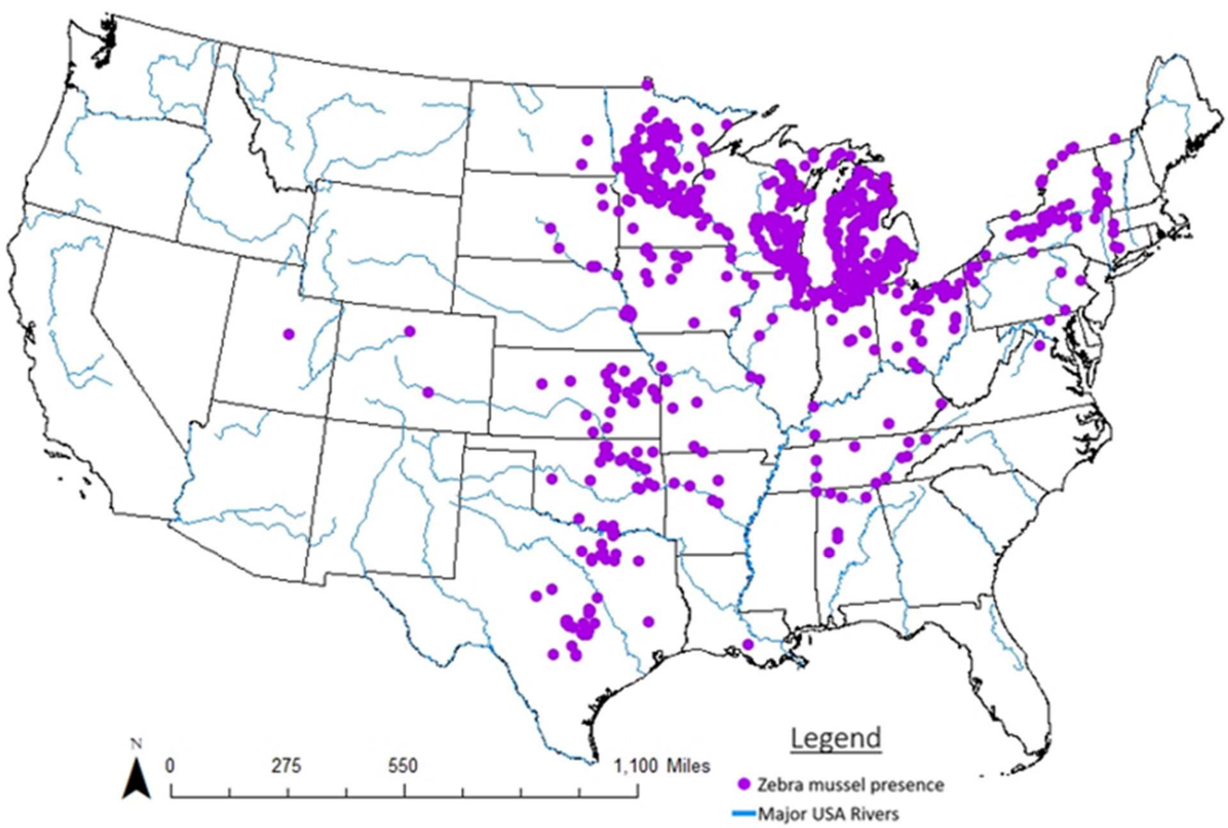


Figure 2-Invasion extent of the invasive zebra mussel in the conterminous USA: Black lines are political U.S. state boundaries, blue lines are major rivers of the U.S. Zebra mussel data from: USGS NAS Database (Benson et al. 2021).

Zebra mussels are hardy organisms with general habitat requirements that promote invasion and establishment (Ludyanskiy et al. 1993). Their larval veliger stage is ideal for dispersal through waterways and their adult stage allows them to outcompete native species (Connelly 2007; Ludyanskiy et al. 1993). After fertilization, larvae stay in this planktotrophic stage for approximately 2-4 weeks, having limited locomotion with dispersal relying heavily on water currents (Mackie 1991; Johnson and Padilla 1996). Veligers are incredibly small (70-160 um), making them hard to detect and easily spreadable via boat ballast water or uncleaned boat equipment moved between water bodies (Ackerman et al., 1994; Johnson and Carlton 1996).

As adults, zebra mussels prefer hard substrates to which they can affix themselves such as rocks, wood, or gravel (Ludyanskiy et al. 1993). Zebra mussels also often wreak havoc on pipelines and human structures. For example, the surfaces of dams or water pipes can be almost exclusively covered in adult zebra mussels (Ludyanskiy et al. 1993). These mussels will colonize water intake pipes to the extent that the pipes become clogged with them, thus impeding water flow through them (Connelly 2007). This impediment can cause a loss of revenue and slow facility productivity. In fact, a survey found that 46% of 449 U.S. and Canadian drinking water treatment and electric power generation facilities had experienced an economic impact due to zebra mussels (Connelly 2007).

In addition to economic impacts, zebra mussels have both direct and indirect negative ecological impacts. They attach to other sessile invertebrates, covering native unionids to such an extent that they are unable to fully open or close (Mackie 1991). Populations of zebra mussels also have been found to hinder the locomotion, burrowing, and feeding of native bivalves (Mackie 1991, Ricciardi et al. 1998). As a result, zebra mussels can decimate native mussel populations in a few years following their invasions (Maleski and Masteller 1994, Ricciardi et al. 1996).

Populations of zebra mussels can also have negative effects on aquatic ecosystems. They reduce available dissolved nutrients in the water column, shift nutrients to the benthos, and decrease food sources needed by native species of mussels and zooplankton (Mackie 1991). For example, zebra mussels have been shown to shunt nutrients from the water column to the benthos via filter feeding followed by excretion in the form of ammonium and phosphorus (Johengen et al 1995; Qualls et al. 2007; Vander Zanden and Olden 2008). Preferential feeding by zebra mussels can cause shifts in pelagic phytoplankton populations (Johengen et al. 1995) or extreme decreases in overall pelagic phytoplankton communities (Bastviken et al 1998). Additionally, some studies found that zebra mussels will feed on cryptophytes, chrysophytes, and dinoflagellates while rejecting cyanobacteria and chlorophytes, leading to increases in nuisance algal densities (Naddafi et al. 2007). Overall, zebra mussels can have a wide range of effects on the ecosystems they invade.

Connectivity among Natural Lakes and Reservoirs Facilitates Zebra Mussel Spread

It is well-known that aquatic invasive species introduction and dispersal is facilitated by humans (Cole et al. 2019, Kao et al. 2020, Johnson et al. 2001). It is known that the zebra mussel was first introduced to the U.S. Great Lakes through boat ballast water (Hebert et al 1989). Since that first introduction, humans are thought to serve as a primary vector in the spread of zebra mussels as well as other invasive species through recreational boating and angling (Johnson and Carlton 1996; Cole et al. 2019; Johnson et al. 2001; Kelly et al. 2013; Figure 3). In fact, zebra mussel larvae are commonly transported via the lake water that is trapped in live wells and bait buckets (Johnson et al. 2001; Kelly et al. 2013). Adult mussels are often inadvertently transported by macrophytes that have become entangled on the boat and trailers (Johnson et al. 2001). Thus, lake access through roads and public access sites are likely to be important predictors of zebra mussel presence.

In addition to human dispersal of invasive species, many invasive species can disperse through surface water connectivity (i.e., connections among lakes and streams and rivers) (Cole et al. 2019; Kao et al. 2020; Johnson et al. 2001; Figure 3). For example, many studies have shown that fish invasions are promoted by surface water connections (e.g., Hein et al. 2011; Jaeger et al. 2014; Laske et al. 2016) and that downstream connectivity promotes the invasion of crustaceans, mollusks, and macrophytes that have downstream□biased dispersal methods (Chapman et al 2020). Interestingly, since reservoirs are associated with dams, they may be less connected than natural lakes in terms of surface water connections. However, because zebra mussel dispersal during their larval (veliger) stages is facilitated by stream currents (Mackie 1991; Johnson and Padilla 1996), dams may not negatively affect zebra mussel spread. Therefore, it remains an open question as to whether reservoirs formed from the building of dams and other impoundments will be more likely to harbor zebra mussels compared to natural lakes, as well as to what extent surface water and human connections affect zebra mussel presence (Figure 3).

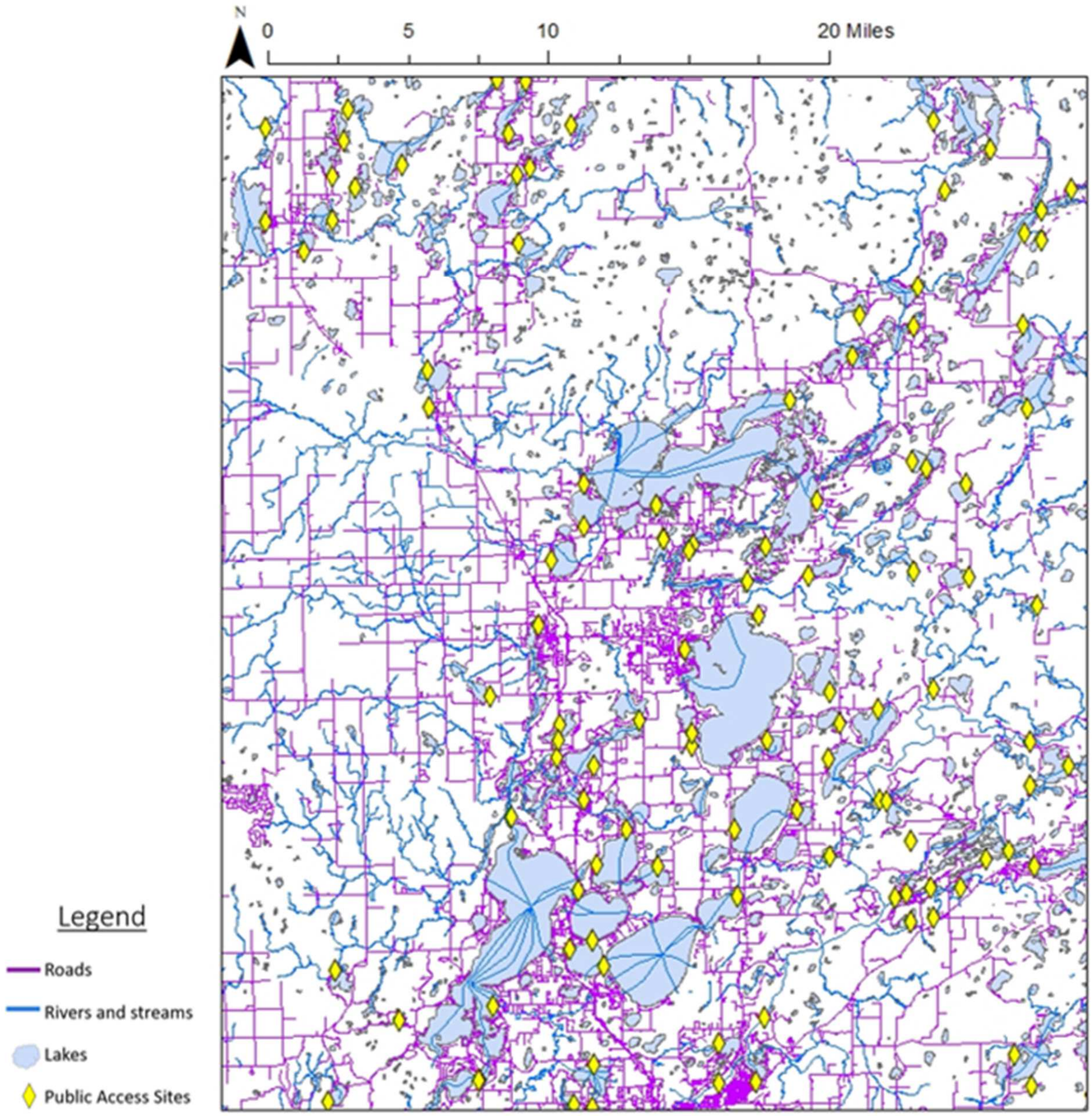


Figure 3-Lake rich area in MN showing public access sites, road, and stream connectivity: Depiction of the different types of connectivity that facilitate invasive species introduction and spread: human connections via roads (purple lines) and public lake access sites (yellow diamonds) and surface water connections via streams and rivers (blue lines) in an area with high lake (light blue polygons) density in Minnesota, USA. Image courtesy of ArcGIS (ESRI).

With this study, we aim to fill these knowledge gaps by asking: (1) are zebra mussels more commonly found in natural lakes or in reservoirs and (2) how does surface water and human connectivity influence the presence of zebra mussels in natural lakes and reservoirs? Because reservoirs have higher levels of disturbance and recreational use, we expect them to more likely have zebra mussels than natural lakes. Based on the importance of both human and surface water connectivity for zebra mussel spread, we expect that highly connected systems are more likely have zebra mussels, regardless of whether they are reservoirs or natural lakes. Our research will increase scientific understanding of reservoirs and how both human and surface connectivity influence the presence of the invasive zebra mussel. This increased understanding can be used to identify which systems are most likely to be invaded, information that will be critical for targeting lakes for management actions.

Methods

Our study extent is the 17 states in the lake-rich Northeastern region of the United States (Figure 4). We use data from LAGOS-NE (Soranno et al. 2017, 2019) and LAGOS-US (Cheruvelil et al. 2021) in this study. LAGOS is a research-ready data platform for broad-scale studies of lakes (Soranno et al. 2015, 2017, Cheruvelil et al. 2021). LAGOS-US RESERVOIR, which classifies the 137,465 lakes 4 hectares and larger in conterminous U.S. as natural lakes (NL) or reservoirs (RSVR) (Polus et al. 2021, Rodriguez et al. *under review*), forms the basis of our research (Figure 5). We also make use of limnological data in LAGOS-NE and watershed road density data in LAGOS-US GEO (Smith et al. 2022).

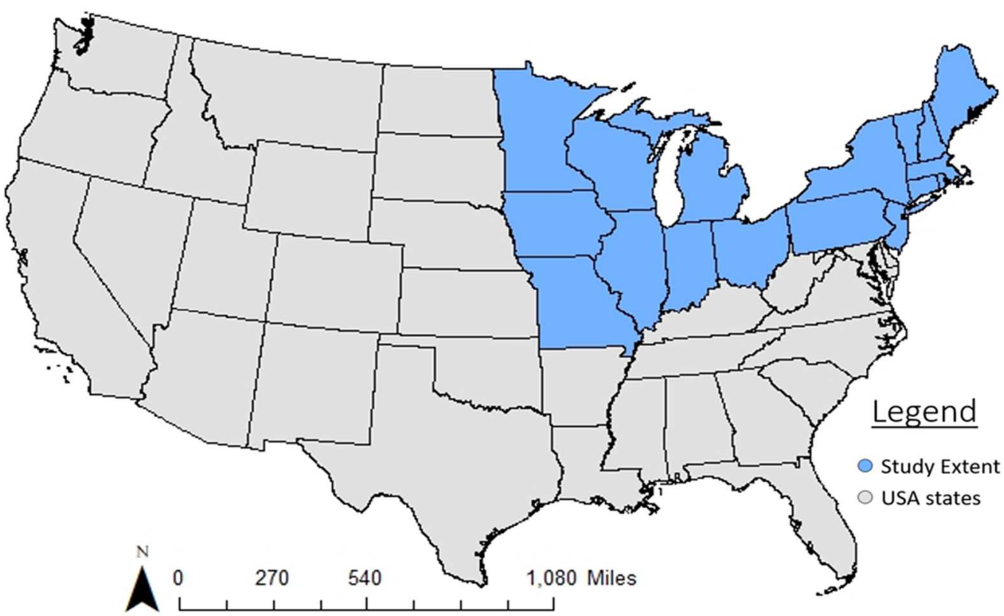


Figure 4-Study extent : Extent spanning 17 northeastern states in the U.S., highlighted in blue.

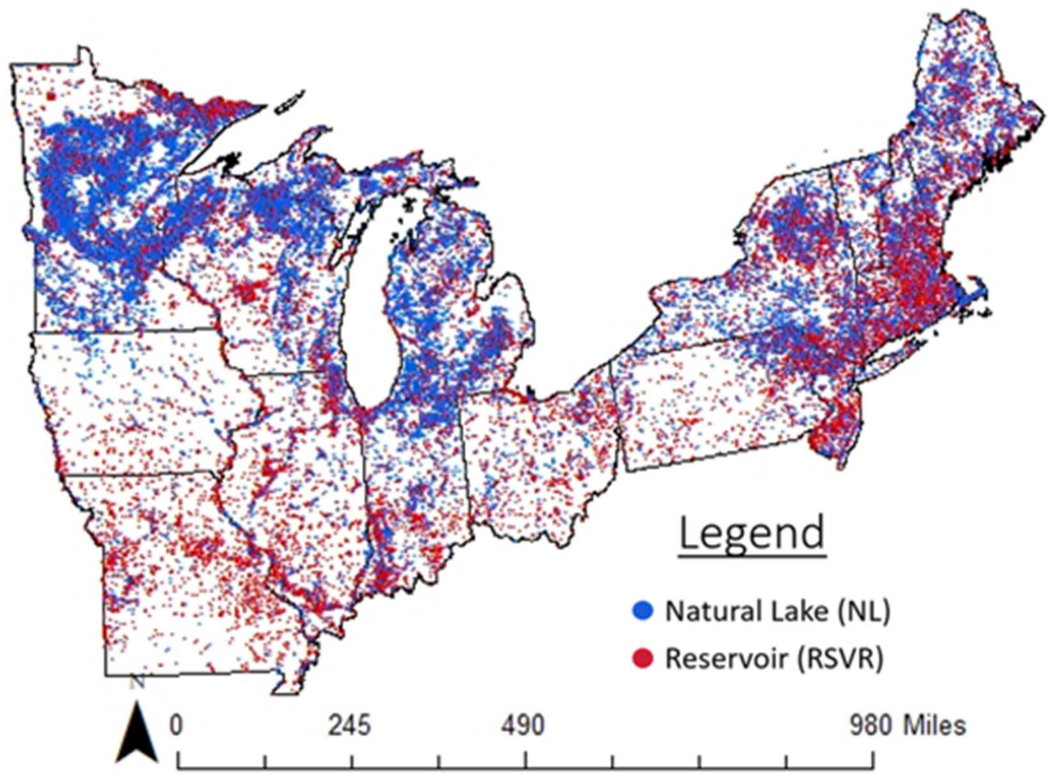


Figure 5-Water bodies by lake class (NL vs RSVR): Lakes ≥ 4 ha in 17 northeastern U.S. states classified by lake type with natural lakes in blue (n = 31330; NL - most likely naturally formed) and reservoirs in red (n = 22,149; RSVR - entirely human made or highly altered by humans). Total n = 53,356.

LAGOS-NE contains a variety of limnological water quality data including lake total phosphorus, total nitrogen, and chlorophyll *a* concentrations (Soranno et al. 2017, Table 1). We filtered these data to include those from the mid-summer productive phase of June 15th to September 15th. Additionally, we averaged multiple measurements in individual lakes within the productive phase to get one value per lake. Years of sampling ranged from 1975 to 2017; when a lake was sampled more than one year averaged across years.

Table 1-Descriptive statistics for limnological water quality variables: Descriptive statistics for limnological data for the study lakes extracted from LAGOS-NE (Soranno et al. 2017) and prior to imputations. Concentrations measured in µg/l.

Extent	Variable Name	Minimum	Maximum	Mean	Median	n
17 Northeastern States	Mean Total Nitrogen	98.0	15037.5	835.6	560	629
	Mean Total Phosphorus	1	1730	54.7	22	725
	Mean Chlorophyll *a*	0.2	789.8	22.4	5.8	630
3 State Subset	Mean Total Nitrogen	165	15038	1370	788	137
	Mean Total Phosphorus	3	1122.5	108.9	45	141
	Mean Chlorophyll *a*	1.1	789.8	41.8	14.6	139

To control for regional spatial differences in lake and landscape characteristics, we utilized the USGS's 2 digit hydrologic units (HU2) (Seaber et al. 1987). The study extent includes nine HU2s (Figure 6): New England (01, n = 6741), Mid-Atlantic (02, n = 4919), Great Lakes (04, n = 13,365), Ohio (05, n = 4100), Upper Mississippi (07, n = 17,486), Lower Mississippi (08, n = 134), Souris-Red-Rainy (09, n = 4977), Missouri (10, n = 1518), and Arkansas-White-Red (11, n = 116). We used hydrologic units as opposed to other regionalization frameworks such as ecoregions because they are based on river watersheds, which we know are important for zebra mussel dispersal and because hydrologic units have been found to characterize regional patterns in many landscape variables important for lakes (Cheruvelil 2008 & 2013).

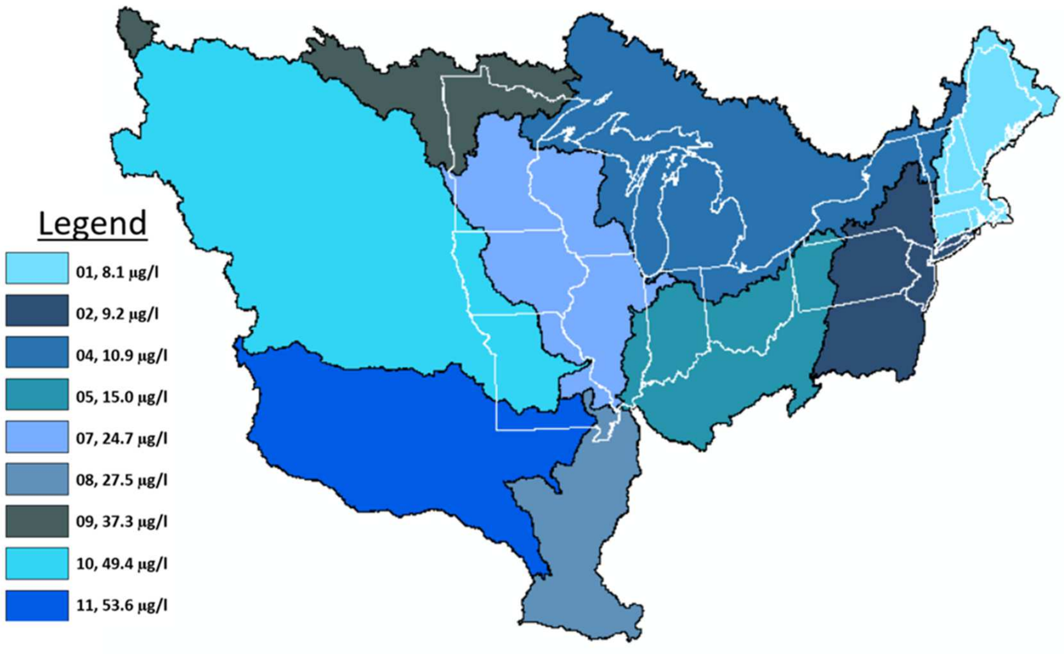


Figure 6-Chlorophyll *a* concentrations by region: Study extent with HU2s delineated with black lines and states in white lines. Numbers in legend are the 2-digit HU code followed by the mean chlorophyll *a* concentration in µg/l. See text above for HU2 names associated with each 2-digit code in the legend.

We used the United States Geological Survey's Nonindigenous Aquatic Species database to obtain presence data for zebra mussels (Benson et al. 2021). The data used in this research was download from the domain in December of 2021 and no further updates were added to the downloaded data. Zebra mussel presence was classified as either "ZM" meaning it had a documented sighting or it was classified as "unknown" when there were no data about zebra mussel presence for that lake. Zebra mussel data were overlaid on LAGOS lake polygons using ArcMap (ESRI v10.8.1 2020) with a 500 meter buffer zone around each lake to associate points with LAGOS lakes and their LAGOS unique lake identifier (lagoslakeid; Cheruvelil et al. 2021). Note that this database is updated frequently. Therefore, if a lake is not included in the dataset, that fact does not necessarily mean that the lake is zebra mussel free. Rather, that lake has an "unknown" zebra mussel status.

We characterized connectivity three ways: surface water, watershed road density, and boat launch presence. We used surface water connectivity classes from the LAGOS-US RESERVOIR data module (Polus et al. 2021). There are six surface water connectivity classes that are geographically spread across the study extent (Figure 7). These classes are based on the presence of inflow(s) and outflow(s) and upstream lakes (Cheruvelil et al. 2021). Drainage and Drainage-Lake classes have inflow(s) and may or may not have outflow(s), with the Drainage-Lake class also having one or more upstream lake(s) that are ≥10 ha (Figure 8). The Headwater class has outflow(s) only and Isolated water bodies have no outflows or inflows. The Terminal lake classes have only inflow(s), with Terminal-Lakes also including one or more upstream lake(s) that are ≥10 ha (Figure 8, Cheruvelil et al 2021).

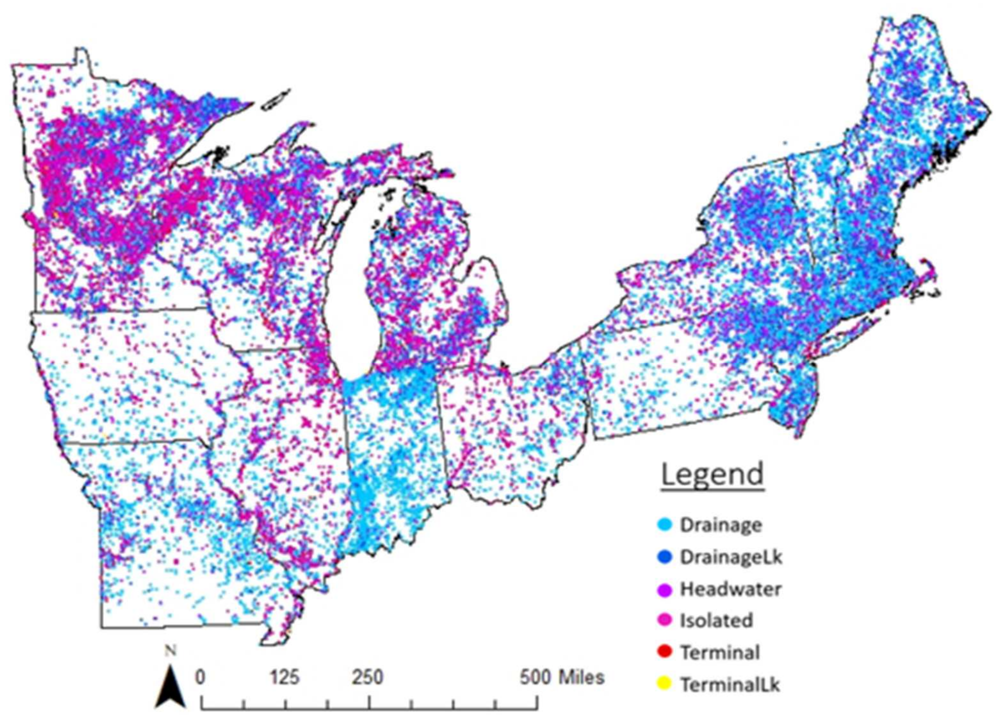


Figure 7- Distribution of lakes by connectivity class: Distribution of 53,356 lakes ≥ 4ha in 17 Northeastern U.S. states by lake connectivity class. Drainage (n = 17,456), Drainage-Lake (n = 9158), Headwater (n = 7486), Isolated (n = 18,107), Terminal (n = 1054) and Terminal-Lake (n = 203). See Figure 8 for depictions of these classes.

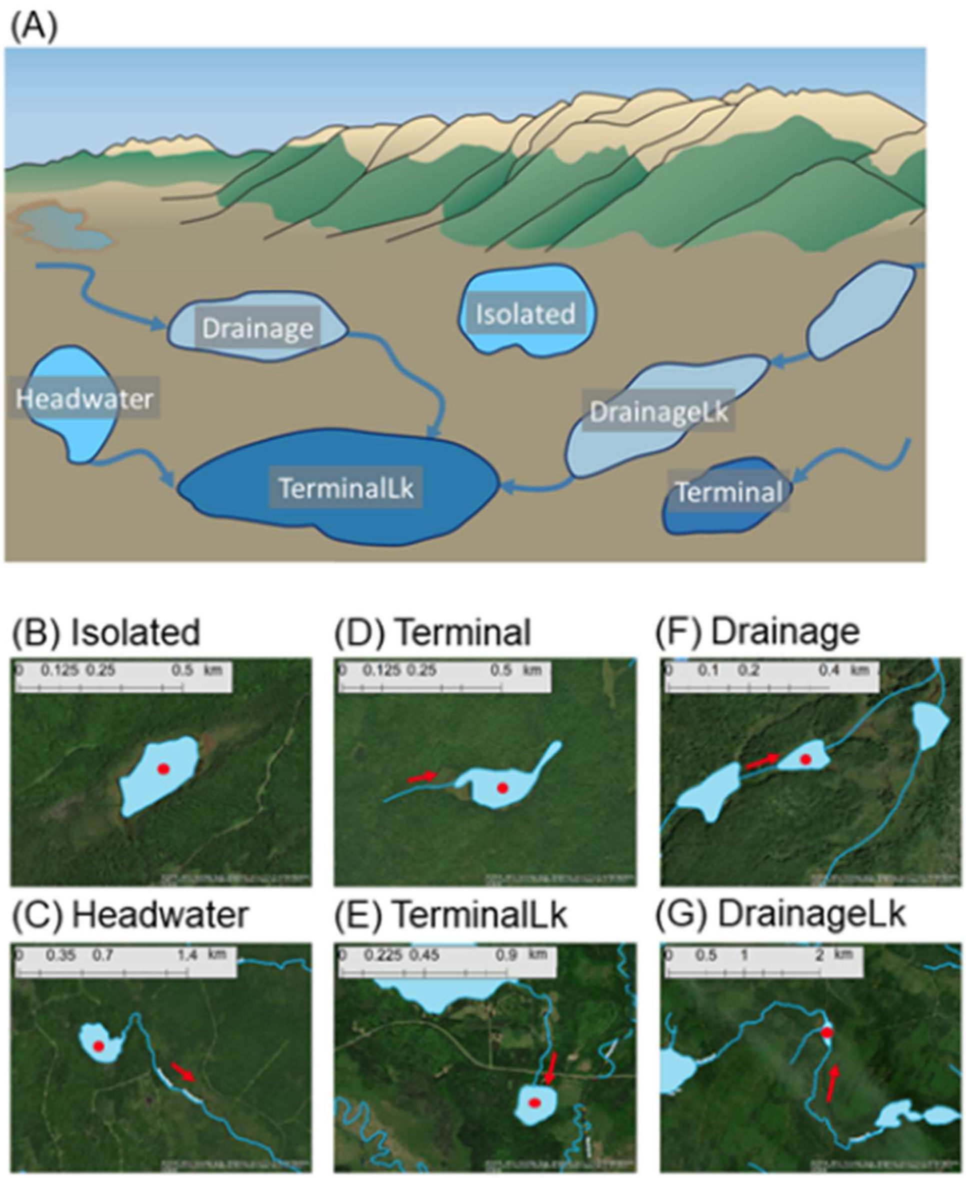


Figure 8-Visualization of different lake connectivity classes: Cartoon (top) and aerial images (bottom; B-G) depicting the six lake connectivity classes. Image attribution: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols) (Figure adapted from Cheruvelil et al. 2021) .

We characterized human connectivity in two ways. First, we used road density within each lake's watershed. This metric ranged from 0 to 977 meters per hectare across the study extent, with an average of 27 meters per hectare (Appendix Figure 1, Appendix Figure 2). Second, for the subset of the study extent with available data (3 U.S. states of Minnesota, Missouri, and Iowa), we used presence of public boat launches and boat ramps (total public access lakes n =2531) (Wesley Daniel, USGS, personal communication). All boating access sites (boat launch, boat ramp, dock, etc…) were classified as "public access sites" and each lake was assigned a Y (yes) or N (no) for the presence of any public access site(s) (Figure 9). Public access site point data were overlaid on LAGOS lake polygons using ArcMap with a 500 meter buffer zone around each lake to associate points with LAGOS lake identifiers.

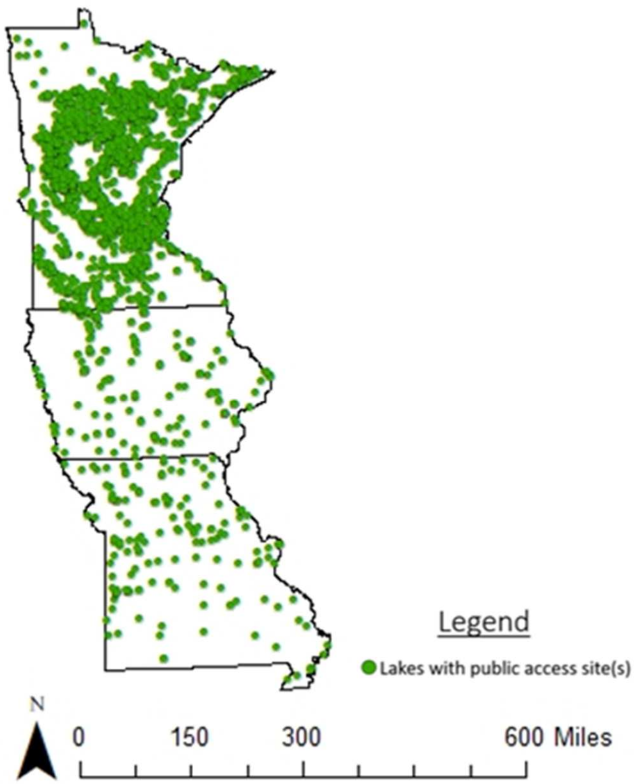


Figure 9-Lakes in MN, IA, MO with a public access site: All lakes $\geq$ 4ha with public access sites across Minnesota, Iowa, and Missouri (n = 2531; data from personal communication with Wes Daniel, USGS). See Table 1 for descriptive statistics of limnological characteristics for these lakes.

Analytical Approach

To meet assumptions for statistical tests, imputations were conducted for missing limnological water quality data and limnological water quality variables were natural-log transformed. Correlational tests were run between total phosphorus, total nitrogen, and chlorophyll *a* that demonstrated that these variables were highly correlated ($r > 0.73$). We chose to include chlorophyll *a* in our models due to the direct impact that zebra mussels have on concentrations due to filter feeding.

We built a series of three models. The first was for the entire 17-state study extent with zebra mussel presence as the response variable and lake type (NL/RSVR) as the predictor variable to answer question one, whether natural lakes or reservoirs are more likely to have zebra mussels. The second model built on the first one by adding surface water and human connectivity measured as watershed road density to answer question two, investigating what impacts connectivity and lake class have on zebra mussel presence. In these first two models, we account for the regional patterns in lake and landscape characteristics by including region membership and chlorophyll *a* concentration in our models (Appendix Figure 3). The third model was also to answer question two and is built with similar variables. However, because it was for only the 3-state region that had public boat access site data, this model does not include regions.

The first model was a binomial logistic regression model with lake chlorophyll *a* concentration, region membership (HU2), and lake type (NL/RSVR) as predictor variables. The second model was a series of generalized binomial logistic regressions using Akaike's information criterion to choose the best fit model (i.e., that with the lowest AIC). These models included lake type, surface water connectivity class, lake chlorophyll *a* concentration, region membership (HU2), and watershed road density as predictor variables. The third model was fit for the smaller study region to further investigate the impacts of human connectivity on zebra mussel presence. We fitted a series of generalized binomial logistic regressions, also using

Akaike's information criterion to choose the best fit model (i.e., that with the lowest AIC). Human connectivity measured both as watershed road densities and public access sites, as well as surface connectivity, lake type, and lake chlorophyll *a* concentration were predictor variables.

Results

Within our 17-state study extent, we found that 907 lakes ≥ 4ha that had zebra mussels present, of which 524 were natural lakes and 383 were reservoirs (Figure 10). For lakes with zebra mussels present, all lake connectivity classes were represented, although drainage lakes and terminal lakes were over- and underrepresented, respectively (Figure 11). Within our tri-state subset, we found that 224 lakes with a public access site also had zebra mussels present. Furthermore, of the 224 lakes with both a public access site and a zebra mussel presence, 67% were natural lakes (n = 150) and 33% were reservoirs (n = 74) (Figure 12).

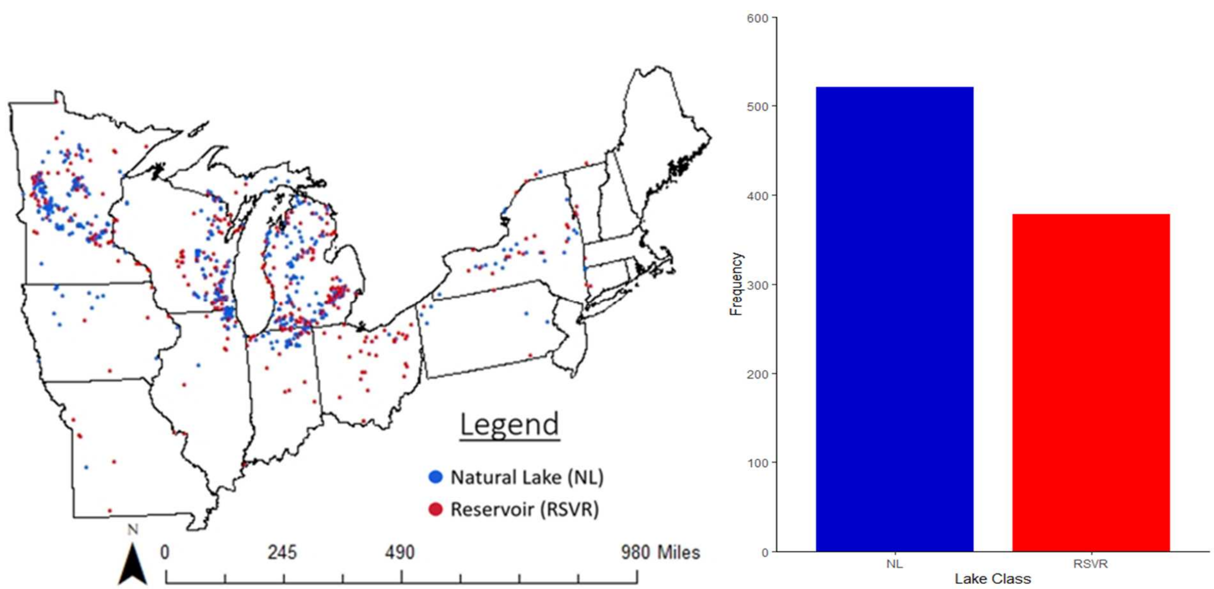
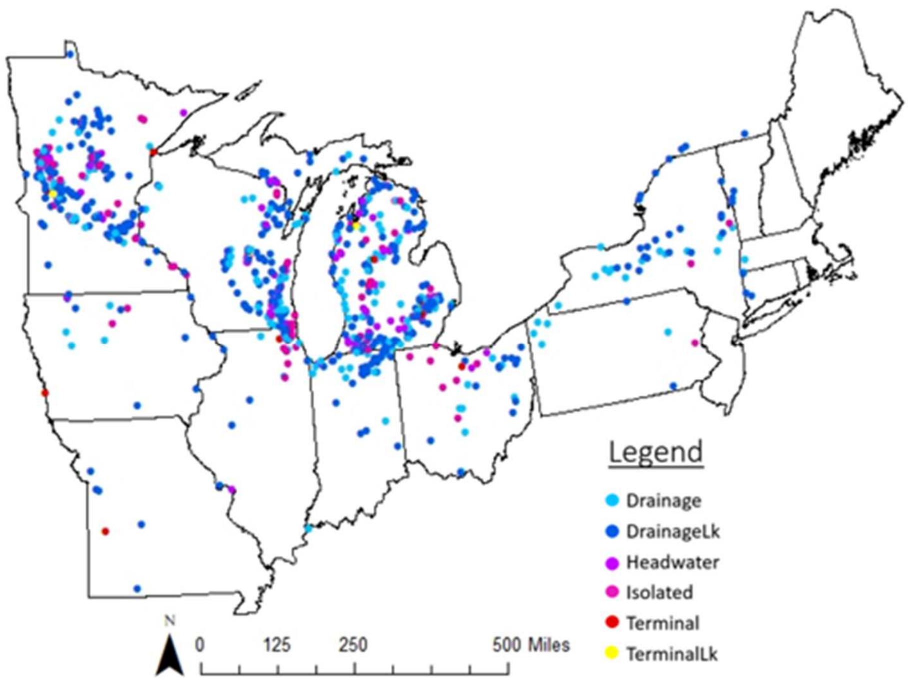


Figure 10-Lakes with a zebra mussel presence by lake class (NL vs RSVR): The 907 lakes ≥ 4 ha with a zebra mussel presence in 17 northeastern U.S. states classified by lake type (left). Frequency of zebra mussel lakes by lake type (NL vs RSVR) (right).



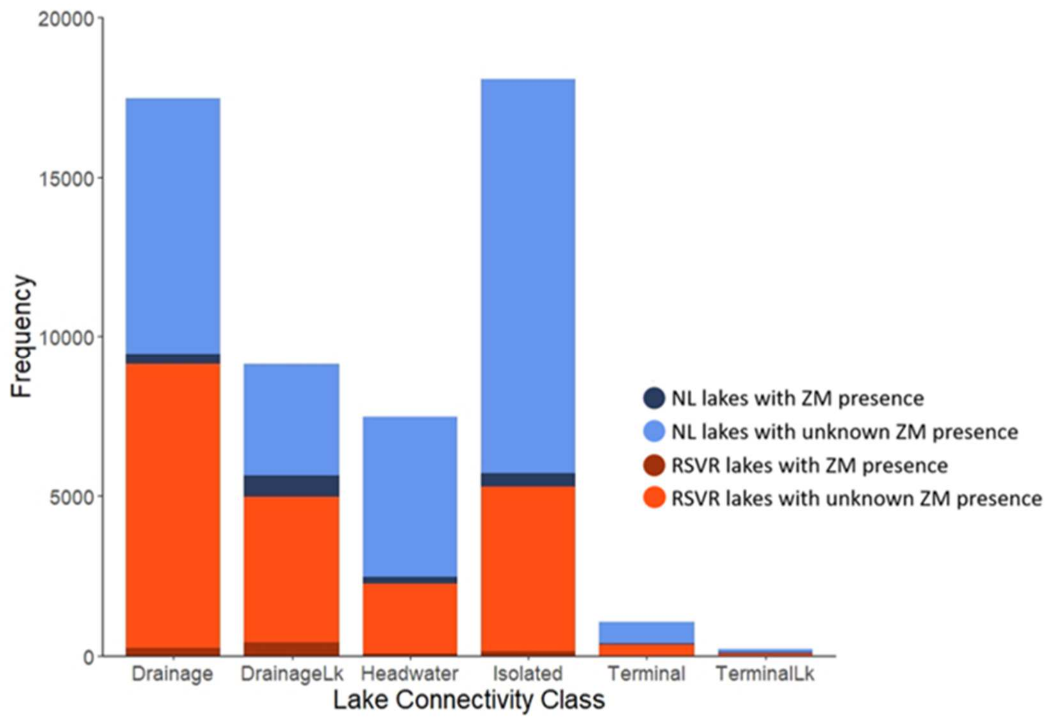


Figure 11- Lakes with a zebra mussel presence by lake connectivity class: The 53,356 lakes $\geq$ 4 ha in the study extent, of which 907 lakes have a zebra mussel presence classified by lake connectivity . Drainage (n = 198 ZM lakes), DrainageLk (n = 498 ZM lakes), Headwater (n = 73 ZM lakes), Isolated (n = 117 ZM lakes), Terminal (n = 15 ZM lakes) and TerminalLk (n = 6 ZM lakes) (top). Frequency of lakes within the six lake connectivity classes relative to lake class and zebra mussel presence (bottom).

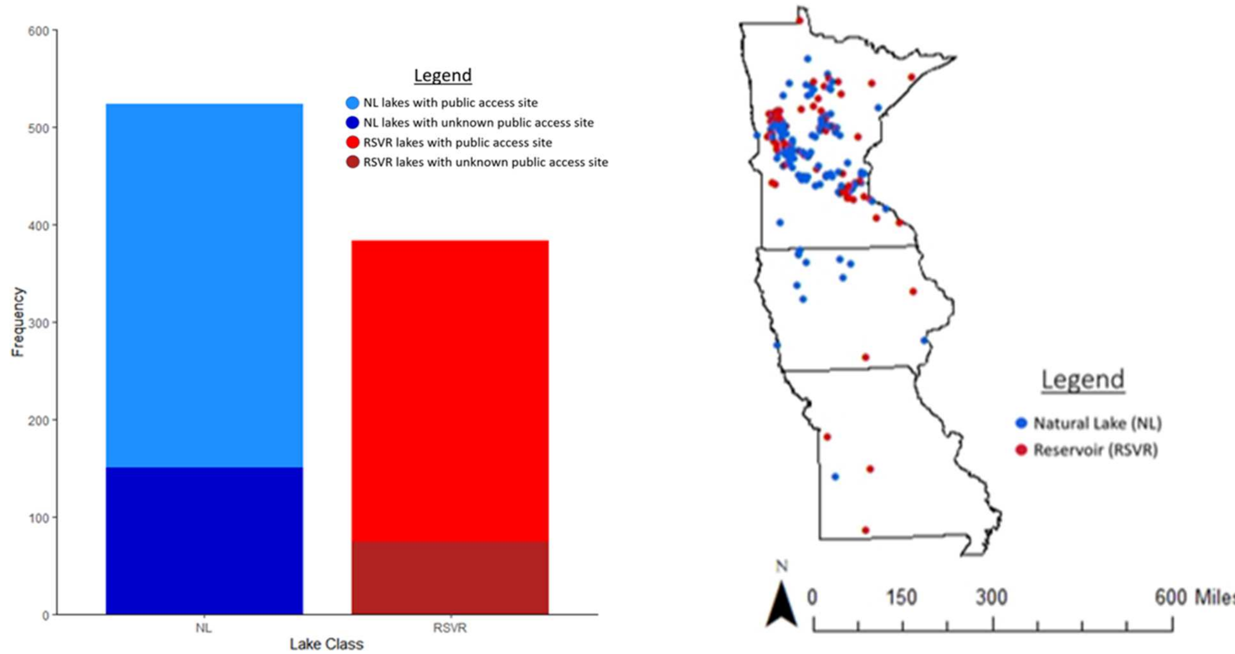


Figure 12-Frequency of lakes with a public access site by lake class (NL vs RSVR): Frequency of zebra mussel lakes by lake type within a three U.S. state extent and with and without a public access site (n = 907) (left). A map showing locations of the subsets of water bodies with a zebra mussel presence and a public access site (n =224) (right).

Inferences from these raw numbers should be interpreted with caution, however. The best model (lowest AIC) for predicting zebra mussel presence included lake type, lake chl *a*, and region (Table 2). In fact, after accounting for region membership and lake chlorophyll *a* concentration, we found that reservoirs were more likely to have zebra mussels present than natural lakes ($p \leq 0.003$; Table 3, Figure 13, Appendix Figure 4, Appendix Figure 5).

Table 2- AIC model selection for the entire 17 state study extent: Results of a model selection process using Akaike's information criterion to determine the best model for predicting ZM presence within our 17 U.S. state extent. Model_4, which included lake type, region, and lake chl *a* as predictors, had the lowest AICc. K represents the number of estimated parameters for each model, AICc represents the information criterion for each model, the Delta AICc represents the appropriate delta AIC component based on the information criterion selected, AICcWt representing the the Akaike weights, Cum.Wt represents the cumulative Akaike weights, and LL represents the log-likelihood of each model.

Model	K	AICc	Delta AICc	AICcWt	Cum.Wt	LL
Model_4	18	7673.05	0	1	1	-3818.52
Model_2	17	7686.42	13.37	0	1	-3826.2
Model_3	22	7686.42	13.88	0	1	-3821.45

Table 3-Lake class model output for binomial logistic regression for 17 state extent: Model_4 outputs for predicting ZM presence by lake type, region, and lake chl *a*. Variables that are bolded with an asterisk were statistically significant ($p < 0.004$); other variables were not statistically significant (p-values were 0.94 and 0.07 for HU 08 and HU 11, respectively).

	Estimate	Std. Error	Z Value
***Intercept**	-7.49	0.45	-16.63
***Lake Type (RSVR)**	0.21	0.07	0.07
Chlorophyll *a	0.14	0.03	4.95
***HUC 02 (Mid Atlantic Region)**	1.45	0.51	2.84
***HUC 04 (Great Lakes Region)**	3.74	0.45	8.30
***HUC 05 (Ohio Region)**	2.63	0.47	5.58
***HUC 07 (Upper Mississippi Region)**	3.01	0.45	6.63
HUC 08 (Lower Mississippi Region)	-8.71	125.46	-0.07
***HUC 09 (Souris-Red-Rainy Region)**	2.45	0.47	5.18
***HUC 10 (Missouri Region)**	1.85	0.55	3.38
HUC 11 (Arkansas-White-Red Region)	1.99	1.10	1.80

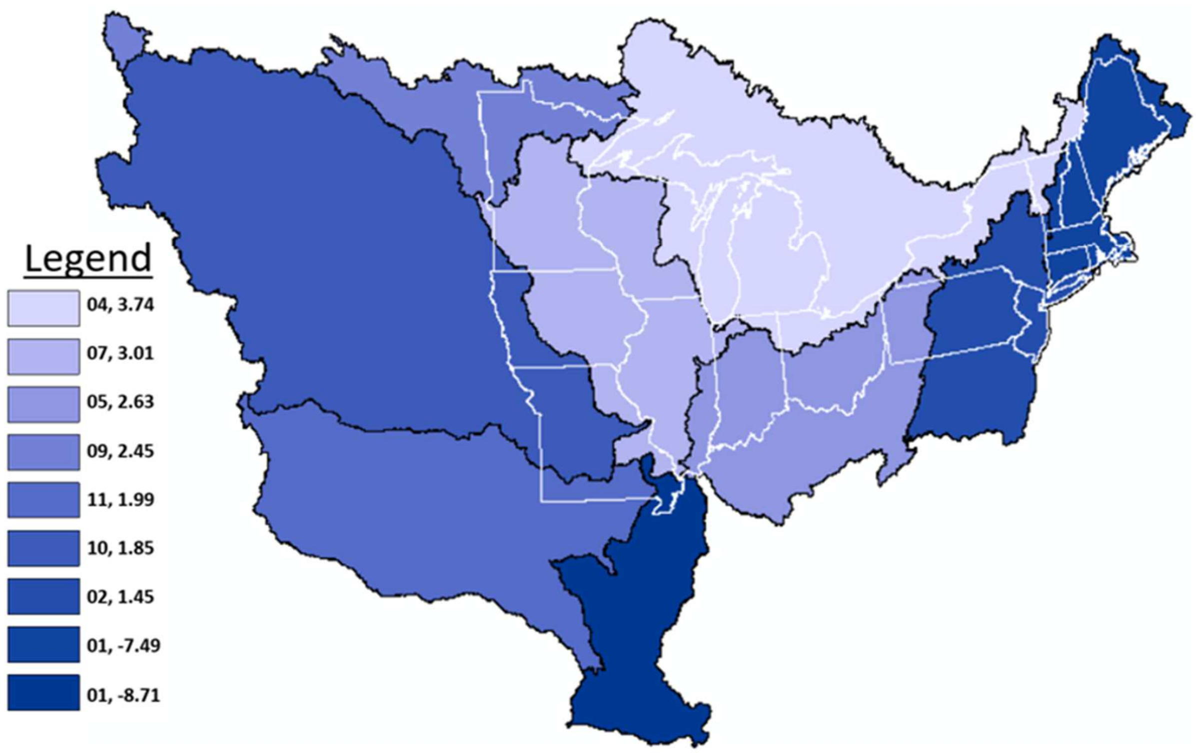


Figure 13-Regional predictiveness of zebra mussel presence: Lighter colors represent HU2s that are significantly more likely to have lakes with zebra mussels. Numbers in legend are the 2-digit HU code followed by the estimated likelihood of ZM presence.

Lakes with a higher chlorophyll *a* concentration were more likely to have zebra mussels ($p < 0.0001$, Table 3, Appendix Figure 3). We also found a regional pattern in zebra mussel presence, with seven of nine HU2 regions significant ($p < 0.005$, Table 3). We saw that regions surrounding the Great Lakes, HU 04 (Great Lakes region) and HU 07 (Upper Mississippi region), are more likely to have lakes with a zebra mussel presence (Figure 14). The two regions that were not significant were HU 08 (Lower Mississippi) and HU 11 (Arkansas-White-Red), which are located in the southwestern portion of our study extent and included very few lakes (Figure 10).

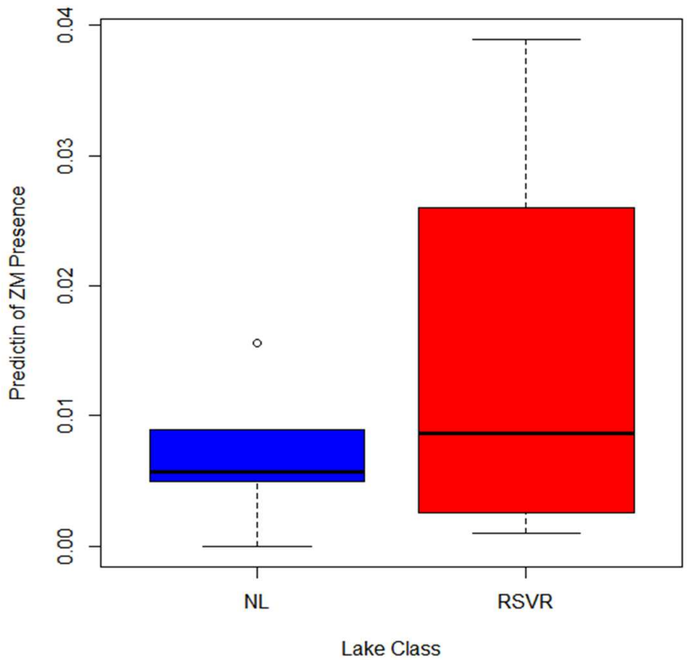


Figure 14-Zebra mussel prediction by lake class (NL vs RSVR): Boxplot showing zebra mussel prediction across lake type (NL = natural lake, RSVR = reservoir) after accounting for region (HU2) and lake chlorophyll *a* concentrations ($p < 0.004$).

We next explored the role of connectivity on zebra mussel presence. We found that the best model (lowest AIC) included region, chl *a*, lake type, lake connectivity, human connectivity, and interaction terms (Table 4). Being a highly connected water body in the Drainage-Lake connectivity class (55% of ZM lakes) significantly predicted zebra mussel presence ($p \leq 0.0001$, Table 4). Additionally, lakes from both isolated (13% ZM lakes) and headwater (8% of ZM lakes) connectivity classes were less likely to have a zebra mussel presence ($p \leq 0.0001$, Table 4). Human connectivity measured as watershed road density also predicted zebra mussel presence ($p < 0.001$, Table 4). Interestingly, lake type was not significant in this model, meaning that after accounting for the effects of surface water and human connectivity, natural lakes and reservoirs were equally likely to have zebra mussels present. There was also a significant interaction such that reservoirs with high road densities were unlikely to have a zebra mussel presence ($p < 0.0001$, Table 4).

Table 4-Connectivity model output for binomial logistic regression for 17 state extent: Model outputs for predicting ZM presence with lake type, region, lake chlorophyll *a*, and connectivity. Human connectivity was measured as watershed road density and surface water connectivity was measured using 6 unique classes. Variables that are bolded with an asterisk were statistically significant ($p < 0.01$). Insignificant p-values are as follows: Lake Type ($p = 0.18$), chlorophyll *a* ($p = 0.16$), HU 08 ($p = 0.96$), Terminal connectivity lake class ($p = 0.53$), and Terminal-Lake connectivity lake class ($p = 0.27$).

	Estimate	Std. Error	Z Value	P Value
***Intercept**	-8.30	0.46	-18.15	0.00
Lake Type (RSVR)	0.12	0.09	1.35	0.18
***Watershed Road Density**	0.02	0.00	14.25	0.00
Chlorophyll *a*	0.04	0.03	1.41	0.16
***HUC 02 (Mid Atlantic Region)**	1.63	0.51	3.17	0.00
***HUC 04 (Great Lakes Region)**	4.15	0.45	9.20	0.00
***HUC 05 (Ohio Region)**	3.13	0.47	6.63	0.00
***HUC 07 (Upper Mississippi Region)**	3.56	0.46	7.829	0.00
HUC 08 (Lower Mississippi Region)	-8.77	195.29	-0.05	0.96
***HUC 09 (Souris-Red-Rainy Region)**	3.21	0.47	6.77	0.00
***HUC 10 (Missouri Region)**	2.49	0.56	4.41	0.00
***HUC 11 (Arkansas-White-Red Region)**	2.80	1.11	2.53	0.01
***Drainage-Lake connectivity lake class**	1.46	0.09	16.46	0.00
***Headwater connectivity lake class**	-0.37	0.14	-2.59	0.01
***Isolated connectivity lake class**	-1.12	0.12	-9.06	0.00
Terminal connectivity lake class	-0.17	0.27	-0.63	0.53
Terminal-Lake connectivity lake class	0.47	0.42	1.11	0.27
***Lake Type (RSVR) X road density**	-0.01	0.00	-3.94	0.00

There was variation in the relative effect of these variables on predicting zebra mussels across this 17-U.S. state extent. Although coefficients are not directly comparable since they are not standardized, they may aid interpretation. For example, region played a larger role in predicting zebra mussels than chlorophyll *a* and lake type (estimates > 1.6, except HU 08 and HU 01, vs. < 0.14 and 0.12, respectively). Additionally, when examining the roles of connectivity, we found that surface water connectivity was a stronger predictor (orders of magnitude) of zebra mussel presence compared to human connectivity (e.g., estimates for Drainage-Lake = 1.46, Isolated lakes = -1.12 vs. watershed road density = 0.02). Although significant, the lake type by watershed road density interaction estimate was also small, indicating less importance in predictive models of zebra mussel presence (estimate = -0.01).

For the subset of three states with public lake access data, the best model (lowest AIC) included lake type, lake connectivity, human connectivity, and interaction terms (Table 5). For this smaller study extent, we did not include region in our modeling, and chl *a* concentration was not significant in the best model. Public access sites and lake type were important predictors of zebra mussel presence (estimate = 3.05 and -1.16, p-values < 0.0001 and 0.005, respectively; Table 6). We also found that highly connected lakes are more likely to have zebra mussels ($p < 0.0001$, Table 6). This was especially the case for those in the Drainage-Lake connectivity class that were also reservoirs ($p < 0.01$, Table 6). Isolated lakes were found to be less likely to have zebra mussels ($p < 0.004$, Table 4), unless they were also reservoirs ($p < 0.003$, Table 4). Although it had a very small coefficient, watershed road density also predicted ZM presence ($p < 0.0001$, Table 6).

Table 5-AIC model selection for 3-state subset: Model selection using Akaike's information criterion for predicting ZM presence with lake type, human connectivity, and surface water connectivity for a three-state extent with public lake access data. Human connectivity was measured as watershed road density and public access sites. Surface water connectivity was measured according to lake and stream connections. K represents the number of estimated parameters for each model, AICc represents the information criterion for each model, the Delta AICc represents the appropriate delta AIC component based on the information criterion selected, AICcWt representing the the Akaike weights, Cum.Wt represents the cumulative Akaike weights, and LL represents the log-likelihood of each model.

Model	K	AICc	Delta AICc	AICcWt	Cum.Wt	LL
Model_10	14	1976.61	0	0.62	0.62	-974.29
Model_9	9	1979.06	2.45	0.18	0.80	-980.52
Model_11	10	1979.87	3.26	0.12	0.92	-979.93
Model_12	10	1980.65	4.05	0.08	1.00	-980.32

Table 6- Connectivity model output for binomial logistic regression for 3 state extent: Model_10 output for understanding the role of connectivity and lake type on zebra mussel presence in a three-state extent with public lake access data. Variables that are bolded and have an asterisk were statistically significant ($p < 0.004$). Insignificant p-values are as follows: Headwater connectivity lake class ($p = 0.06$), Terminal connectivity lake class ($p = 0.57$), Terminal-Lake connectivity lake class ($p = 0.55$), Reservoir lake class X Terminal connectivity lake class ($p = 0.4$), and Reservoir lake class X Terminal-Lake connectivity lake class ($p = 0.97$).

	Estimate	**Std. Error**	**Z Value**	**P Value**
***Intercept**	-5.84	0.24	-23.84	0.00
***Lake Type (RSVR)**	-1.16	0.41	-2.87	0.00
***Drainage-Lake connectivity lake class**	0.73	0.22	3.30	0.00
Headwater connectivity lake class	-0.70	0.38	-1.87	0.06
***Isolated connectivity lake class**	-0.81	0.28	-2.88	0.00
Terminal connectivity lake class	-0.31	0.55	-0.56	0.57
Terminal-Lake connectivity lake class	0.46	0.77	0.61	0.55
***Public Access Site**	3.05	0.18	16.98	0.00
***Road Density**	0.01	0.00	6.07	0.00
***Lake Type (RSVR) X Drainage - Lake connectivity class**	1.15	0.44	2.60	0.01
Lake Type (RSVR) X Headwater connectivity class	1.19	0.78	1.52	0.13
***Lake Type (RSVR) X Isolated connectivity class**	1.64	0.54	3.06	0.00
Lake Type (RSVR) X Terminal connectivity class	1.01	1.21	0.84	0.40
Lake Type (RSVR) X Terminal-Lake connectivity class	-11.27	278.14	0.04	0.97

Discussion

Taking a macroscale approach, we found that water bodies in the Great Lakes and Upper Mississippi regions, those with higher chlorophyll *a* concentrations, and those that were reservoirs were most likely to have zebra mussels present. The regional pattern supports previous research demonstrating that regions are important to account for at macroscales (e.g., Cheruvelil et al. 2013) and makes sense in light of what is known about the introduction and spread of zebra mussels. Since zebra mussel were introduced first in the Great Lakes before spreading further (Herbert et al 1989), it may be that lakes and watersheds farther from the Great Lakes that have a lack of zebra mussels present are due to the invasion having not reached them, a lack of zebra mussel sampling in lakes farther from the source of the initial invasion, or a lack of reporting of the invasive zebra mussels. Our results also provide evidence that lakes with higher chlorophyll *a* concentrations (potentially eutrophic levels) are more likely to have zebra mussels. Zebra mussels have long been linked to algal biomass and chlorophyll *a* concentrations due to their selective filter feeding (Bastviken et al 1998). Finally, our result show that reservoirs are more likely to have zebra mussels than natural lakes, which may be because reservoir construction, changes in flow regimes, and high levels of human disturbances are all known to facilitate the spread and establishment of invasive species (Johnson et al. 2008; Vander Zanden and Olden 2008; Johnson et al. 2001; Kelly et al. 2013, Havel et al 2005). However, our study is the first to document these patterns using hundreds of natural lakes and reservoirs at the macroscale.

We also found that both surface water and human connectivity predicts the presence of zebra mussels, regardless of whether systems are reservoirs or natural lakes. For example, lakes that are highly connected to streams and lakes (i.e., drainage lakes) were most likely to have zebra mussels. This result is likely because being highly connected by surface water facilitates zebra mussel veliger dispersal (Johnson and Padilla 1996; Connelly 2007; Ludyanskiy et al. 1993). We also found that watershed road density predicts zebra mussel presence. This result fits with previous knowledge about how aquatic invasive species introduction and dispersal is facilitated by humans (Cole et al. 2019, Kao et al. 2020, Johnson et al. 2001). Since their introduction, humans are thought to serve as a primary vector in the spread of zebra mussels as well as other invasive species through trailering of recreational boats, especially those used for angling (Johnson and Carlton 1996; Cole et al. 2019; Johnson et al. 2001; Kelly et al. 2013). Lakes with higher road densities near them may have higher human recreational use. Additionally, adult mussels are often inadvertently transported by macrophytes that have become entangled on boats and trailers (Johnson et al. 2001). Thus, it makes sense that lake access facilitated by roads and public access sites are important predictors of zebra mussel presence. Because estimates of surface water connectivity were magnitudes larger than those for human connectivity, our results support an increased focus on the role of lake-stream connections for the spread of zebra mussels.

It is thought that the earliest stages of zebra mussel range expansion after introduction to the Great Lakes was through a combination of larval drift in surface waters and human mediated transportation (Johnson and Padilla 1996). Interestingly, our models with both human and surface water connectivity were sometimes complicated by interactions. For example, lakes that were reservoirs and had higher watershed road densities were less likely to have a zebra mussel presence (Table 4). This conundrum may be explained by the fact that all reservoirs are not the same. For example, it may be that reservoirs with high road densities are a specific type of reservoir (e.g., drinking water reservoirs), have a specific use that calls for high road density near them (e.g., industrial), or may have fast water residence times that make zebra mussel establishment difficult (Hasler et al. 2019). Although this study used a binary classification of lake type, natural lakes and reservoirs are actually on a gradient of human impact. Therefore, future studies could use a finer classification of reservoirs and natural lakes, further classify reservoirs according to characteristics such as type, use, dam height, or water residence time, or add variables such as those to models. Doing so, however, will require extensive data collection, because those data do not exist at the macroscale for large numbers of lakes.

For the subset of three states with public lake access data (Minnesota, Iowa, and Missouri), we were surprised to find that reservoirs were less likely to have zebra mussels than natural lakes, which contrasts with our results from the entire 17 state extent. This result may be due to natural differences in the water bodies or differences in how they are managed in these states as compared to the entire extent. For example, water bodies in these three states that have public access sites may have different management strategies applied to them, particularly if they are also reservoirs. Finally, it is important to note that this result is based mainly on water bodies in Minnesota because out of the 224 in the subset, only 15 lakes in Iowa and Missouri had zebra mussels and public access sites, with only five of them being reservoirs.

Consistent with our larger 17 state extent analyses, we found that highly connected lakes, both by human and surface water connections, in the 3-state subset were more likely to have zebra mussels. Interestingly, although Isolated lakes were less likely to have zebra mussels, when those Isolated lakes were also reservoirs, they were more likely to have zebra mussels. This result may be due to the very low number of lakes in this study extent that are both Isolated and are reservoirs (n=33). Also consistent with our larger study extent models, Drainage-Lake connectivity classes that were also reservoirs were more likely to have zebra mussels. This is unsurprising due to the large extent that Drainage-Lakes are connected with other lakes and rivers, facilitating zebra mussel dispersal in their veliger stage (Mackie 1991; Johnson and Padilla 1996).

In the 3-state subset, our result that zebra mussels are found more in water bodies with public access sites is consistent with existing knowledge about trailering and boating as vectors for invasive species spread (Johnson and Carlton 1996; Cole et al. 2019; Johnson et al. 2001; Kelly et al. 2013). Water bodies that have high levels of human connectivity (i.e., those with high watershed road density and public access sites) have a higher likelihood of having zebra mussels. This result also supports boater survey responses that showed a willingness to travel long distances between lakes (Cole et al 2019). Although not directly comparable, the fact that the coefficients for public access sites were magnitudes larger than those for watershed road density points to the likely importance of public access sites for zebra mussels. Therefore, we argue for compiling lake access data at the macroscale for use in research that informs management.

Conclusions and Future Directions

We conclude that not all ‘lakes’ are equally likely to have zebra mussels present in them, with reservoirs more likely to have zebra mussels than natural lakes, especially reservoirs that have high surface water connections and a public access site. In fact, our results support the idea that reservoirs may serve as zebra mussel invasion “hubs” (Johnson et al 2006; Muirhead and MacIsaac 2005). Because both surface water and human connectivity were important for predicting the presence of zebra mussels, we suggest that protective legislation and management focus on uninvaded systems that are highly connected reservoirs. Efforts for targeted management focused on high-risk lakes, like those at the top of a chain of lakes or that are highly connected, and lakes that are already invaded could slow the spread of the zebra mussels to other key lakes.

Management geared towards prevention of spread through overland dispersal is not only warranted but can also help to disrupt the overland movement of zebra mussels (Kao et al. 2020; Schneider et al. 1998). This disruption could lower the risk of lakes being invaded (Schneider et al. 1998). Studies have shown that while it is labor intensive, boat inspection not only helps prevent further spread of aquatic invasive species such as the zebra mussel, but it also provides opportunities to educate boaters on invasive species issues (Cole et al. 2019). Finally, further research on zebra mussels that takes into account lake type, connectivity and lake nutrient levels will be beneficial to management, particularly when applying that knowledge to the prevention of harmful algal blooms and the increased microcystin toxin levels that can be associated with zebra mussels (Bastviken et al 1998; Knoll et al. 2011).

Policy and management are hampered by a lack of knowledge about the differences between natural lakes and reservoirs. Our research makes use of a newly available lake classification that identifies reservoirs of the U.S. as well as a new dataset of public lake access sites, albeit for just a 3-state extent. Our results and the availability of data such as these, will facilitate macroscale study of reservoirs and invasive species, which will increase understanding of the effects of impoundments as they are removed and built. Because non-native species can be detrimental to biodiversity and overall lake and reservoir health, we suggest that managers consider lake type and public access when deciding what at-risk lakes to target for invasive species management and mediation tactics such as boat washing stations. In addition, we suggest that the demographics surrounding the lake be investigated and considered when determining lakes to target for sampling, funding, or management. For example, lakes in areas with higher percentages of minorities are drastically under sampled compared to lakes with less minorities in the surrounding area (Diaz Vasquez et al 2022 - under review). Therefore, prioritizing management efforts with a clear strategy for invasive species prevention and mediation and effectively communicating those strategies will help to garner much needed support for programs in areas that have been historically under sampled and under supported.

Our research on zebra mussels demonstrates that further study of the effects of connectivity and lake type on the spread of aquatic invasive species may benefit management and prevention of their spread. This research framework and methods may be applicable to other free floating invasive species such as invasive aquatic plants that reproduce by fragments, plankton, or other invasive mussels. In fact, combining information about dispersal methods of aquatic invasive species and the LAGOS databases has the potential to increase understanding of at-risk lakes for particular invasive species.

APPENDIX

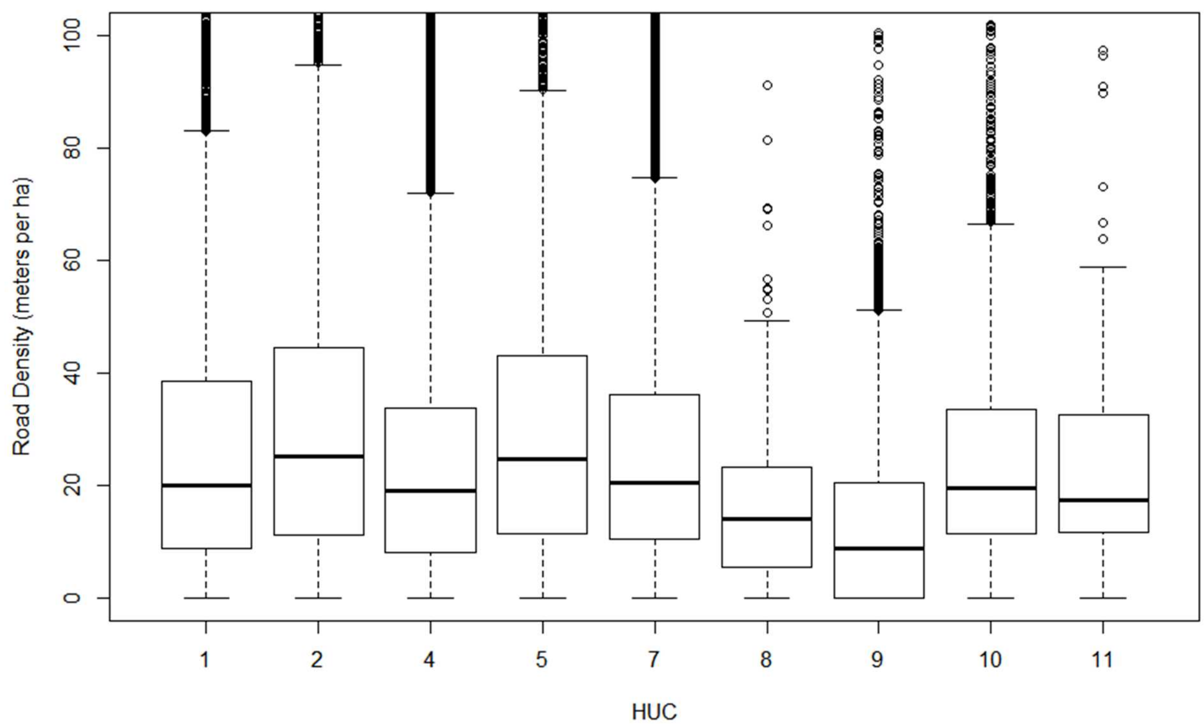


Figure A1-Watershed road density (m per ha) by HU2 regions: New England (01, n = 6741), Mid-Atlantic (02, n = 4919), Great Lakes (04, n = 13,365), Ohio (05, n = 4100), Upper Mississippi (07, n = 17,486), Lower Mississippi (08, n = 134), Souris-Red-Rainy (09, n = 4977), Missouri (10, n = 1518), and Arkansas-White-Red (11, n = 116) ($p < 0.001$).

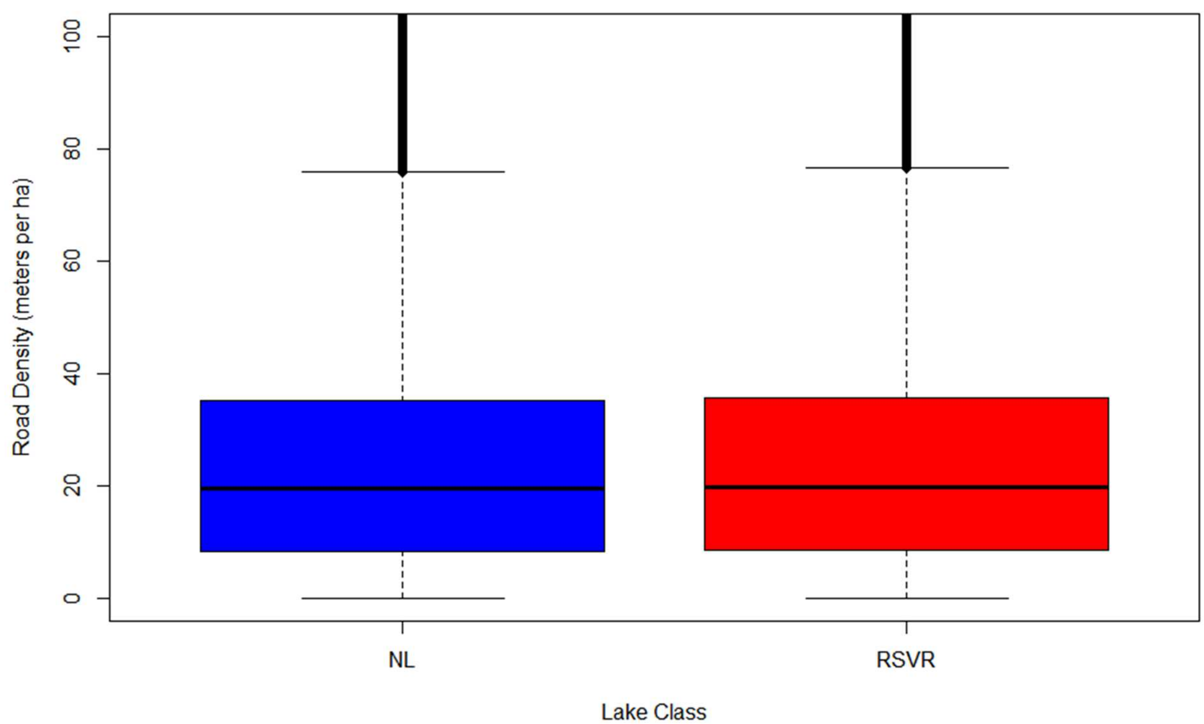


Figure A2- Watershed road density by lake class: Watershed road density (m per ha) by lake type (Natural lake vs Reservoir) in 17 northeastern states in the U.S ($p < 0.005$).

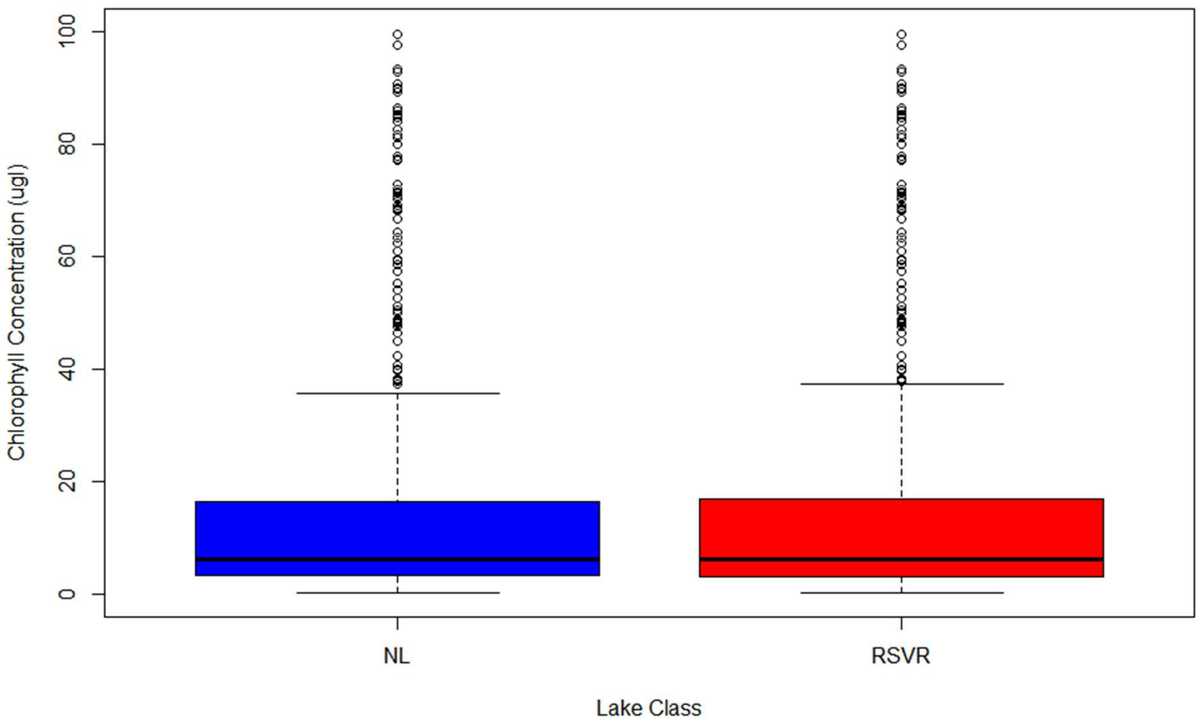


Figure A3- Chlorophyll a concentrations (µg/l) by lake class: Chlorophyll *a* concentrations (µg/l) by lake class (NL vs RSVR) for lakes > 4ha in 17 northeastern states in the U.S ($p < 0.01$).

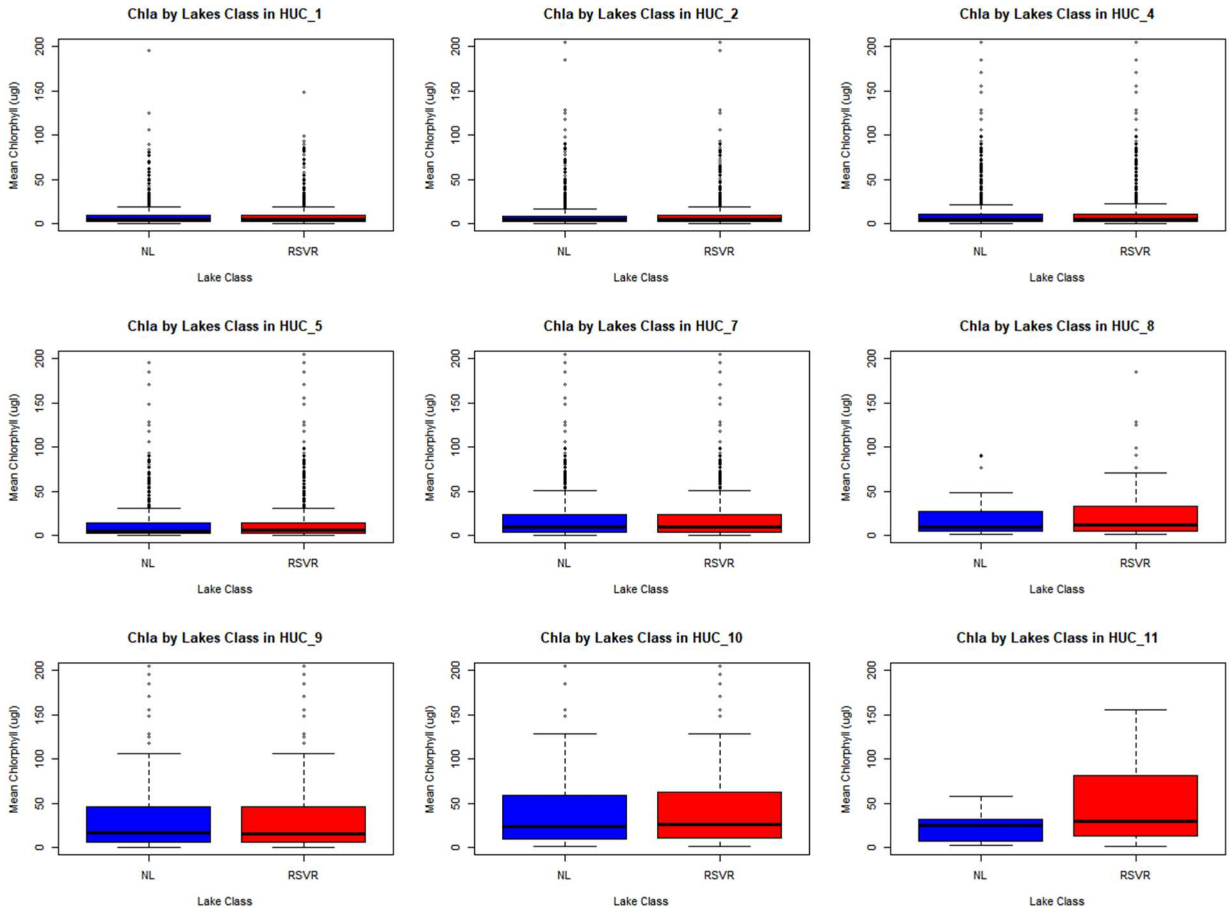


Figure A4-Regional chlorophyll a concentrations (µg/l) by lake class: Chlorophyll *a* concentrations (µg/l) for lakes > 4ha from 17 U.S. states by lake type (NL vs RSVR) across HU2 regions. See text for codes and Figure 6 for location of HU2s.

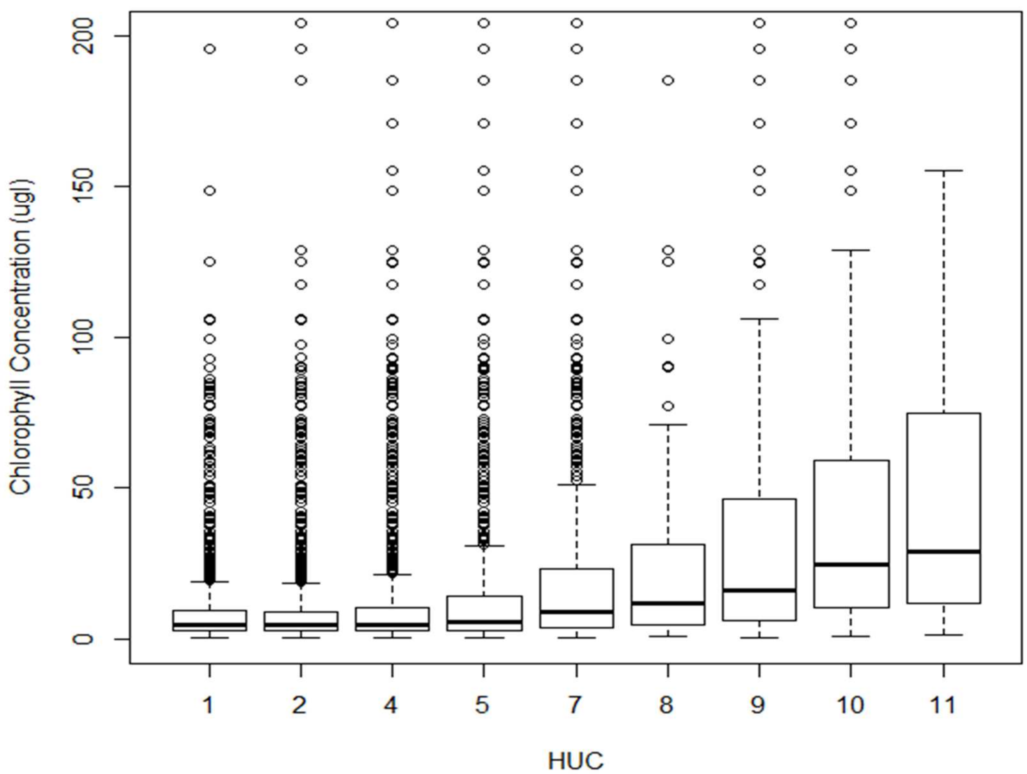


Figure A5: Chlorophyll *a* concentrations for lakes > 4ha across 9 HU2 regions:

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