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Research Article

Spatial variation in propagule pressure and establishment of zebra mussels (*Dreissena polymorpha*) within a subtropical reservoir

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Abstract

Zebra mussels (*Dreissena polymorpha*) are one of the most economically and ecologically disruptive aquatic invasive species in North America, where they damage infrastructure and alter ecological processes. Understanding zebra mussel propagule pressure and establishment is essential for predicting expansion into subtropical lakes and reservoirs. Key water quality parameters, such as temperature, water clarity, dissolved oxygen, and primary productivity have been found to play major roles in these processes. To test if environmental variation affected zebra mussel propagule pressure and establishment within a large, subtropical lake, we measured zebra mussel larval (veliger) abundances in the water column and post-veliger abundances on hard surfaces and quantified water quality during 2011–2015 at six sites spanning 32.8 km in Lake Texoma, OK-TX which differed markedly in salinity, water clarity, and algal abundances. We found that densities of both life stages were lower at western sites with lower water clarity, higher salinity, and higher productivity. Additionally, higher numbers of zebra mussel post-veligers accrued on the undersides of deeper surfaces, suggesting preference for lower temperatures and refuge from predators. Our results suggest that in habitats that are particularly stressful for zebra mussels, water quality predicts propagule pressure and establishment of zebra mussels across a lake, emphasizing the need to consider environmental heterogeneity within large lakes when predicting the potential range and impact of this cosmopolitan invader.

Key words: Zebra mussel, subtropical lakes, Lake Texoma, invasive species, aquatic nuisance species, water quality, environmental heterogeneity

Introduction

The zebra mussel (*Dreissena polymorpha* Pallas, 1771) is a well-known aquatic invasive species with a reputation for invading and disrupting ecosystems. Originating in the Ponto-Caspian region, zebra mussels have spread across Europe (Karatayev et al. 1997) and into North America. They were first recorded in the Laurentian Great Lakes in 1986 and have since made their way into lakes and rivers across much of the eastern half of the United States (Roberts 1990). As the range of zebra mussels continues to expand (see Figure 1A), they inevitably invade water bodies on the edge of their environmental tolerances, such as subtropical rivers, lakes, and reservoirs

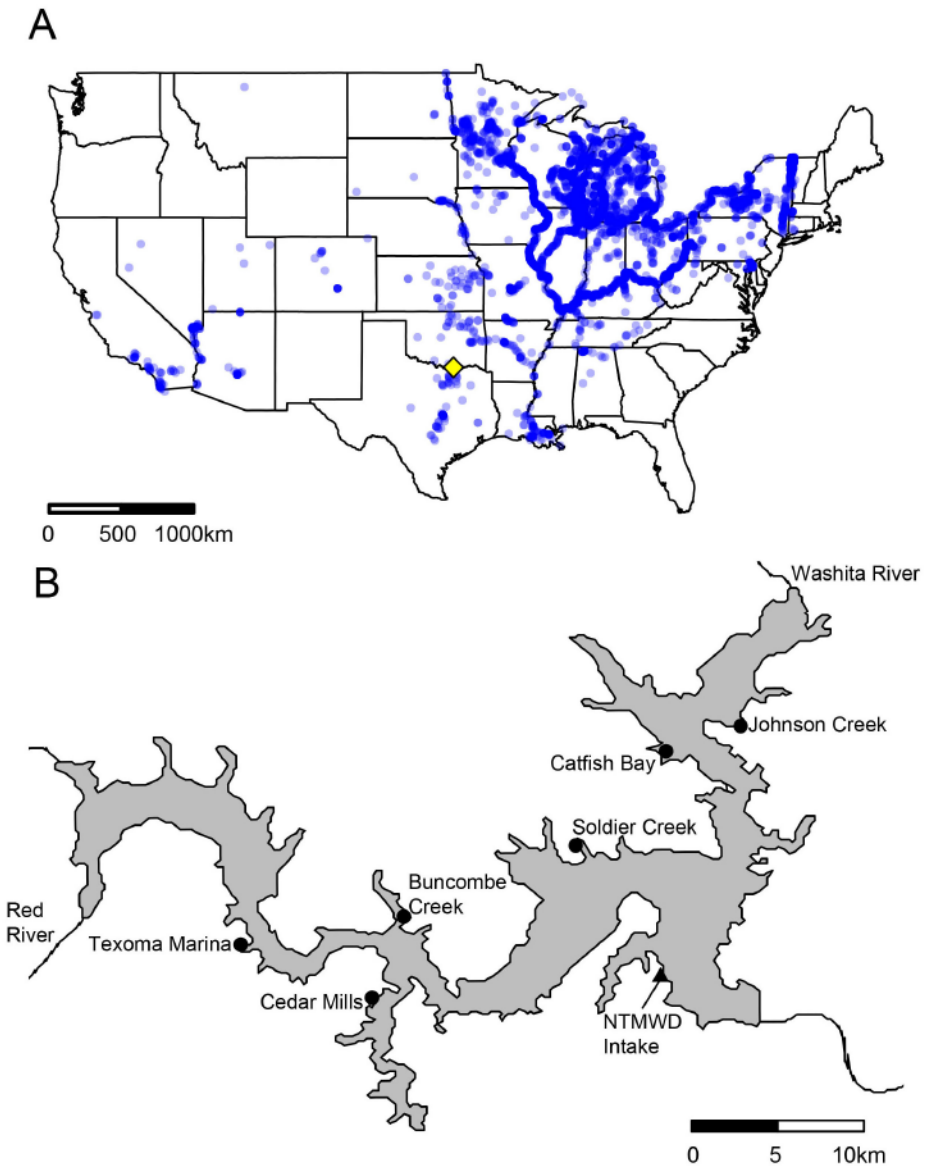

Figure 1. Panel A shows map of United States, with yellow diamond indicating location of Lake Texoma and blue circles indicating the points where zebra mussels have been collected (US Geological Survey Nonindigenous Aquatic Species Database, 2019). Panel B shows site locations (circles) and the location of the North Texas Municipal Water District Intake (triangle) on Lake Texoma.

(Allen et al. 1999; Mihuc et al. 1999; Churchill 2013; Smith et al. 2016; Churchill et al. 2017).

Environmental factors limiting zebra mussel invasion can be broadly divided by whether they limit the ability for larval zebra mussels to reach a potential settling site or whether they limit the success of adult zebra mussels (Jones and Ricciardi 2014). Zebra mussels are broadcast spawners with a planktonic larval stage, so the number of larval zebra mussels that can reach a particular site will be determined by water flow (Mackie 1991), boat traffic (Padilla et al. 1996) and hydrologic connection to reproductively active zebra mussel beds (Griffiths et al. 1991). Spawning typically occurs at temperatures greater than 12 °C (Nichols 1996). After reaching a potential settling site, zebra mussels tend to settle and attach on the edges of surfaces

in areas with moderate flow and no direct sunlight (Kobak 2005). The type of substrate also influences settling preferences, with hard textured substrates such as rocks, concrete, and wood preferred over smoother or soft substrates (Marsden and Lansky 2000).

Several key environmental factors limit habitat suitability for zebra mussels after settling, including water temperature, salinity, primary productivity, and dissolved oxygen concentration. Zebra mussels have a thermal maximum of 32 °C (Beyer et al. 2011). Warm summer water temperatures also cause low dissolved oxygen levels, particularly in eutrophic lakes. Zebra mussels are intolerant of prolonged exposure to dissolved oxygen concentrations below 6 mg L^{-1}, and are unlikely to survive in waters in which dissolved oxygen concentrations regularly drop below 3 mg L^{-1} (Matthews and McMahon 1995). Short term salinity tolerance of zebra mussels is quite high (Ellis and MacIsaac 2008), and zebra mussel populations can persist in estuaries with salinities of 8–12 ppt (Karatayev et al. 1998). However, salinity is still likely to act as a stressor, particularly when interacting with other stressors (Lemm and Feld 2017). Zebra mussel growth rates are lower at low food concentrations, but extremely high concentrations also negatively affect growth rate, due to increased clogging of the gills (Lei et al. 1996), reduced food quality (Vanderploeg et al. 2009), and stoichiometric imbalances (Morehouse et al. 2013).

With respect to dissolved oxygen, salinity, and algal abundances, Lake Texoma, a subtropical reservoir located on the Texas-Oklahoma border, USA (Figure 1A) represents a challenge for zebra mussels. Lake Texoma is a large, hypereutrophic reservoir, with pronounced variation in salinity and productivity due to the inputs of the Red and Washita rivers, two rivers with substantially different physiochemical properties (Hambright et al. 2010). Many parts of Lake Texoma routinely reach temperatures approaching the thermal maximum for zebra mussels, as well as temperatures below which spawning ceases (Hambright et al. 2015). Zebra mussels were first detected in Lake Texoma in 2008 (US Geological Survey 2019). Previous work on zebra mussel populations in Lake Texoma has found that they generally have high growth rates in the lake but are also prone to temperature stress and high summer mortality (Churchill et al. 2017). Salinity in Lake Texoma regularly exceeds 1 ppt in the region where flow is dominated by the Red River but not elsewhere in the lake (Hambright et al. 2015).

We hypothesized that local-scale variation in zebra mussel veliger abundances in Lake Texoma could be predicted using the same factors used to predict zebra mussel invasion success on a larger scale. We predicted zebra mussel veliger densities would be negatively associated with increases in summer water temperatures, increased chlorophyll, decreased water clarity, and increased salinity. Additionally, post-veliger densities should be associated with veliger densities, as well as environmental variables including turbidity and temperature. Based on

previous studies of zebra mussel settling patterns and research on the increasing predation pressures on zebra mussels in subtropical systems, we expected higher settling success in dark areas representing deeper and cooler waters, as well as restricted areas more protected from molluscivorous fish (e.g., catfish and freshwater drum).

To test these predictions, we carried out monthly monitoring of planktonic zebra mussel veliger densities, Secchi depth, water temperature, algal pigment concentrations, salinity, and dissolved oxygen concentration at six sites over four years (2011–2015) to assess how variation in environmental parameters affected zebra mussel abundances. We monitored post-veliger settling densities over the course of one year and assessed the degree to which the reproductive output of local zebra mussels corresponded to the predictions of habitat suitability.

Materials and methods

We selected six sites on Lake Texoma for monitoring, ranging from the western to eastern reaches of the lake (Figure 1B). To select sites, we first identified all public marinas on Lake Texoma. Then we used Google Maps satellite view to locate marinas that had visible docks extending into the channel. Several of the eastern sites had previously been used for routine monitoring of golden algae by Hambright et al. (2010). We contacted marina owners and managers to request access and consent for installation of samplers on pre-existing floating docks. Of those who agreed to take part in the study, we selected six sites that spanned the western to eastern reaches of the lake. All sites were located at active marinas or boat ramps that served as put-in points for small to medium sized boats. Each site was located at a dock with access to water 2–5 m deep. From August 2011 to October 2015, we carried out a monthly sampling protocol, visiting each of the six sites and measuring water quality and collecting zooplankton samples. Because atypical seasonal water level fluctuations (≥ 3 m) rendered the Johnson Creek site inaccessible over 50% of the time, we removed it from further analysis. At each site, water temperature, conductivity, pH, dissolved oxygen, and chlorophyll-*a* and phycocyanin concentrations were measured using a Hydrolab DS5 multiprobe (Hach). Conductivity was converted to salinity (PSU) using a site-specific equation. We also measured Secchi depth. Methods for water quality assessment followed Hambright et al. (2015).

We collected zooplankton samples using two vertical, depth-integrated tows across the entire water column with a Wisconsin-type zooplankton net (63-µm mesh, aperture diameter 10.5 cm). Zooplankton were filtered down in the field and immediately preserved in unbuffered 80% ethanol. Veligers were enumerated from these zooplankton samples to estimate propagule pressure and as a proxy for reproductive adult zebra mussel population sizes (Burla and Ribi 1998). We counted veligers from the entire

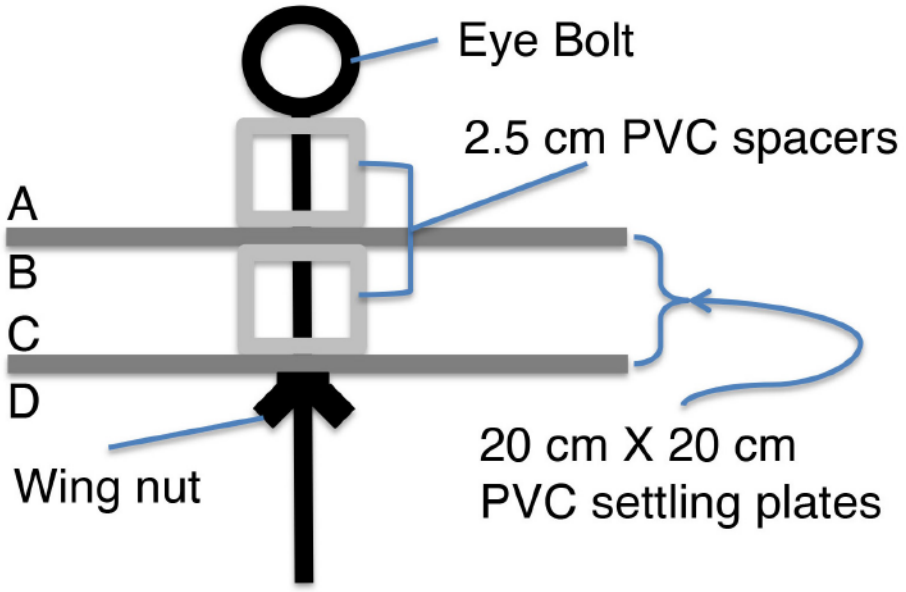

Figure 2. Schematic of zebra mussel settling sampler design. Two horizontal PVC 20 cm × 20 cm squares with a thickness of 3.2 mm were mounted on an eye bolt with a 2.5-cm segment of PVC tubing used as a spacer between them. A PVC cap with a hole drilled through the middle held the top plate in place below the eye of the eye bolt, while a wing nut below kept the plates in place. When sampling, the wing nut was loosened to grant access to all four sampling areas (the top and underside of each plate), marked A, B, C, and D. Note that this diagram is not to scale.

zooplankton sample in a gridded petri dish under a dissecting microscope at 70× magnification within two years of collection.

For measuring the settling rates of post-veliger zebra mussels, sites were sampled monthly from July 2011 through June 2012. The sampler design, inspired by a modified version of a Hester-Dendy sampler (Figure 2), consisted of two horizontal PVC plates (3.2 mm thick) mounted on an eye bolt suspended from a rope into the water. Each PVC plate was roughened with coarse sandpaper to increase its suitability as a settling surface. The plates provided available area for attachment on both top and bottom. The sampler provided the options of attaching in light (Figure 2; area A) or in darkness (areas B, C, D), settling in an area sheltered from molluscivorous fish (areas B and C), areas of higher flow (areas A and D), or areas free of sediment (areas B and D). At each sampling site, six samplers were deployed, three each at 1 and 3 m.

All samplers were secured to an existing floating dock to provide a fixed structure to keep the samplers suspended at their deployed depth regardless of fluctuation in water levels typical of reservoirs. Sampling consisted of scraping the same 5-cm × 5-cm square on PVC plates each month with a razor blade. After collecting the subsample, the area of the plate surrounding the sampling location was also scraped clean to ensure that each sample represented newly settled larvae rather than translocated zebra mussels from previous time periods. Collected samples were preserved in unbuffered 80% ethanol in scintillation vials for later enumeration. Samples were counted within an average of one year of collection on a dissecting microscope under 26× magnification in a gridded petri dish.

To evaluate differences in sediment and organic matter accumulation rates between different plate locations, we measured the total sample mass (sediment + zebra mussels) of a subset of 100 previously enumerated samples. The aim of this measure was to estimate relative accumulation among our dock sites, but not to extrapolate to other lake locations. 25 samples from each plate area (A, B, C, and D) were dried in aluminum weigh boats at 100 °C and weighed every 24 hours until there was less than a 4% change between mass for any of the samples (a total of 5 days).

All statistical analyses were carried out in R (version 4.0.0 R Development Core Team 2020). To test for differences in environmental parameters between the five sites, we used PERMANOVA, using the adonis function in the vegan package (version 2.5-6, Oksanen et al. 2020). We used site as the predictor variable and tested for differences in response variables of water temperature, salinity, concentrations of chlorophyll, phycocyanin, and dissolved oxygen, and Secchi depth (n = 134). Response variables were first centered and scaled using the scale function in R, and Euclidean distances were used as the basis for PERMANOVA. We visualized differences in environmental parameters between the five sites using nonmetric multidimensional scaling (NMDS) based on Euclidean distances using the metaMDS function in the vegan package.

To test for a significant effect of sampler area on sample dry weight, we compared sample mass using a Kruskal-Wallis test (due to uneven variance between samples) for omnibus significance, followed by a Wilcoxon rank-sum test to evaluate differences between pairs of sampler areas, with a simple Bonferroni correction applied adjust for multiple comparisons. The same approach was used to test the effect of site location on sample dry weight.

A t-test was used to test for a difference between water temperatures found at 1 m compared to 3 m for the entire year and also for just the summer months of June, July, and August, when water temperatures reach their peak. We analyzed months with the highest water temperatures separately because we hypothesized that this would be the time of year when temperature differences between depths would be most important in determining zebra mussel survival, in terms of acute thermal mortality. The Johnson Creek site was not included in any analyses due to low water levels and exposure and drying of the samplers.

To assess the impacts of environmental variables on zebra mussel propagule pressure and establishment, we modeled veliger and post-veliger abundance using random forest models. We selected this approach because random forest models can effectively model nonlinear relationships between predictor and response variables, as well as complex interactions between variables, both of which are common in ecology (De'ath and Fabricius 2000). We constructed random forest models for zebra mussel veligers and post-veligers separately. Abundance data were first $\log_{10}(x+1)$ transformed to reduce the impact of outliers, as abundances varied over four

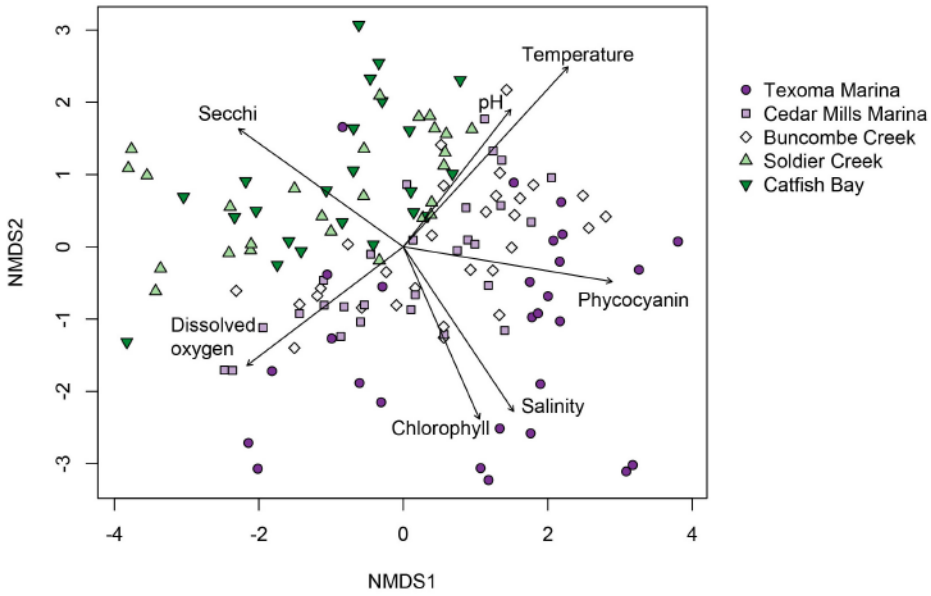

Figure 3. Results of nonmetric multidimensional scaling (NMDS) of environmental variables in Lake Texoma measured monthly at five sites from August 2011 through October 2015 (stress = 0.1546). Arrows represent the direction in which variables change most rapidly. Points indicate samples of environmental variables, with point color and shape indicating site location.

orders of magnitude. Predictor variables included Secchi depth, temperature, chlorophyll, phycocyanin, salinity, and pH. For the post-veliger stage, plate location (A, B, C, D, see Figure 2) and depth were also included as predictors. Random forest models were fit using the randomForest function in the randomForest package (version 4.6-14, Liaw and Wiener 2002). Model fit and significance were quantified using the rf.regression.fit and rf.significance functions from the rfUtilities package (version 2.1-5, Evans and Murphy 2018). Variable importance was assessed using the mean decrease in node impurity, measured by the residual sum of squares using the importance function in the randomForest package.

Results

Environmental variables were significantly different between sites (PERMANOVA, pseudo-F = 9.15, $p < 0.001$). Visualizing the environmental data with NMDS (Figure 3) showed that Secchi depth, salinity, chlorophyll, and phycocyanin drove separation of the five sites. Temperature, dissolved oxygen, and pH explained very little of the variation between sites, but were likely correlated with season (Figure 4). The five sites differed greatly both in the frequency of veliger and post-veliger occurrence (Figure 5) and their abundances (Figure 6). In general, veliger and post-veliger incidence rates and abundance increased from the westernmost site (Texoma Marina) to the easternmost site (Catfish Bay).

Physiochemical parameters varied seasonally (Figure 4). Water temperature peaked in August, with lowest dissolved oxygen concentrations recorded at the same time (Figure 4). Phycocyanin also varied seasonally, with highest concentrations recorded in August, September, and October. Secchi depth,

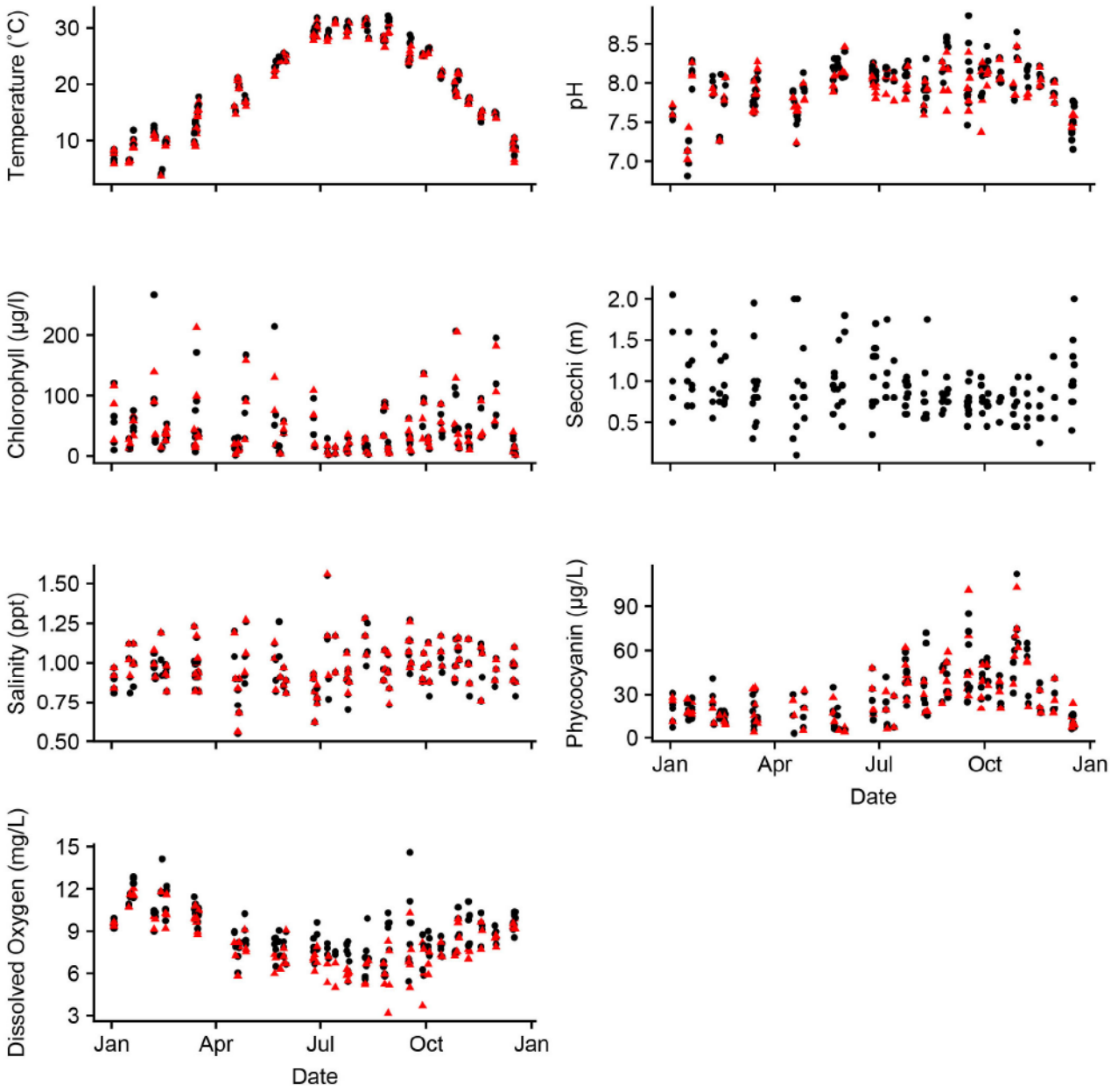

Figure 4. Plot of seasonal variation in physiochemical factors, August 2011 through October 2015. Each circle represents an observation from one site. Measurements taken at 1 m are represented by black circles, and measurements at 3 m are represented by red triangles, except in the case of Secchi depth, which is not depth-specific.

chlorophyll, pH, and salinity varied spatially but did not show clear trends over time.

Within a site, zebra mussel post-veligers were unevenly distributed across samplers at different depths, as well as across areas on a given sampler (Figure 7). Mussels were most abundant on area D, the underside of the second sampling plate, and least abundant on area C, the top of the second sampling plate. There were no differences in mussel abundances on areas A, the top of the first plate, or B, the underside of the first plate (Figure 7). Zebra mussels were significantly less abundant on 1-m samplers than on 3-m samplers (Figure 7). A paired t-test comparing water temperatures at 1 and 3 m revealed that water temperatures were significantly cooler at 3 m than

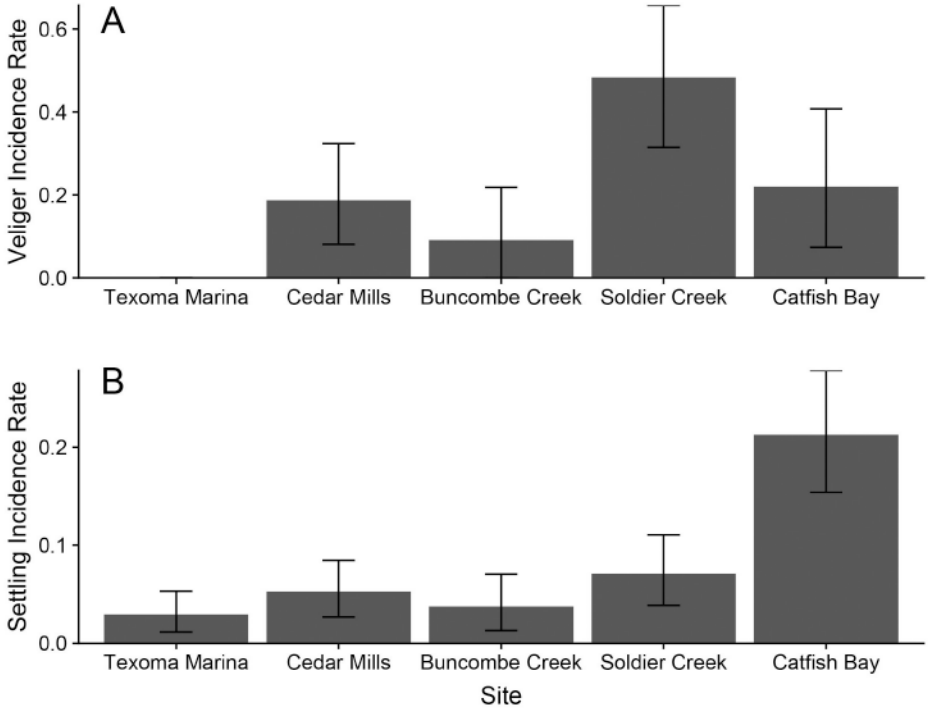

Figure 5. Incidence rates of A) planktonic and B) newly settled zebra mussels for each site, as the proportion of total samples which contained at least one individual. Bootstrapped confidence intervals for veliger and post-veliger incidence were created by resampling 1000 times, with replacement, then calculating the mean and 95% confidence interval of the 1000 samples. Settling incidence rate is calculated from plates positioned at depth of 1 m. From left to right, sites are ordered from westermost site to easternmost site. Please note difference in y-axis scales between panels A and B.

at 1 m ($t = 8.27$, $df = 110$, $p < 0.0001$), with a mean difference of 0.48 °C (Supplementary material Figure S1). The magnitude of difference was greater when only summer months (June–August) were considered in the comparison, with a significant difference in temperature between two depths ($t = 4.73$, $df = 31$, $p = 4.70 \times 10^{-05}$) and a mean difference of 0.67 °C. No other environmental parameters varied significantly with depth either in summer or during the entire year.

As a proxy for organic matter and sediment settling out of the water column, total dry mass varied by plate location (Kruskal-Wallis chi-squared = 19.246, $df = 3$, $p < 0.001$). Sample mass was significantly higher in areas B and C than A and D (Wilcoxon test with Bonferroni correction adjusted $\alpha = 0.008$, Figure S2). Sites varied significantly in dry mass (Kruskal-Wallis chi-squared = 25.813, $df = 4$, $p < 0.001$). Cedar Mills Marina had significantly lower total sample mass than the other sites (Wilcoxon tests with independent contrasts; adjusted $\alpha = 0.05/7 = 0.0071$). The other sites did not differ significantly in sample mass from one another (Figure S3).

Random forest models showed that zebra mussel veliger and post-veliger abundances could be predicted by environmental variables, but the most important variables were different in the two models (Figure 8). The random forest model for log-transformed veliger abundance was significantly better

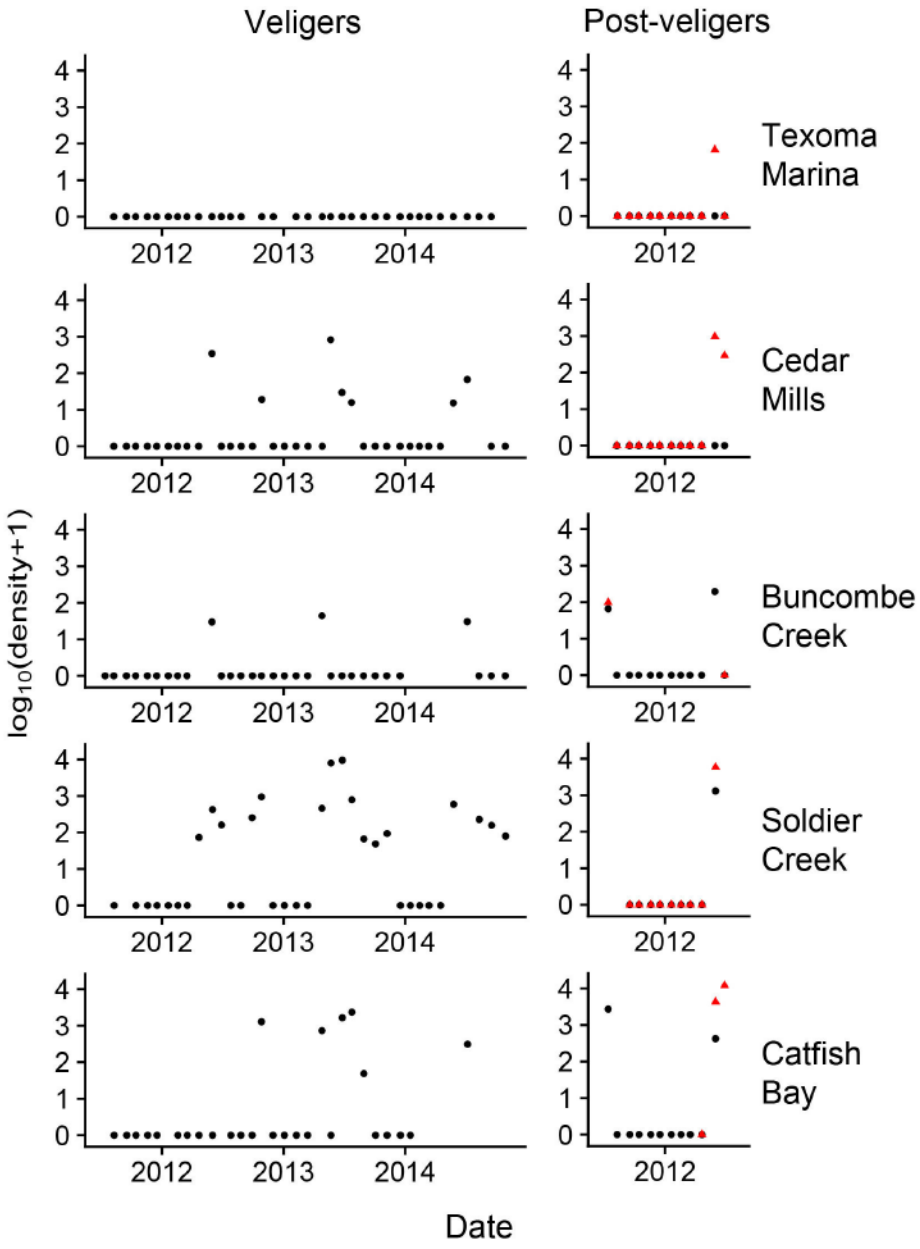

Figure 6. Density of zebra mussel planktonic veligers (left) and post-veligers (right) over time by site. Veliger density is individuals m^{-3} and post-veliger density is individuals m^{-2}. For postveligers, density on samplers at 1 m is represented by black circles, and density at 3 m is represented by red triangles. Densities are $log_{10}(x+1)$ transformed for clarity. Note: Settling samplers were only deployed July 2011–June 2012.

than the null model ($p < 0.001$) and explained approximately 38.5% of the variation in veliger abundance. The variable importance plot showed that temperature, salinity, and Secchi depth were the three most important predictors of veliger abundance (Figure 8, Figure S4). For zebra mussel post-veligers settling on plates, the random forest model was significantly better than the null model ($p < 0.001$) and explained approximately 79.5% of the variation in post-veliger abundance. Chlorophyll was by far the most important predictor of post-veliger abundance, with temperature and phycocyanin coming second and third (Figure 8). Thus, veligers and post-

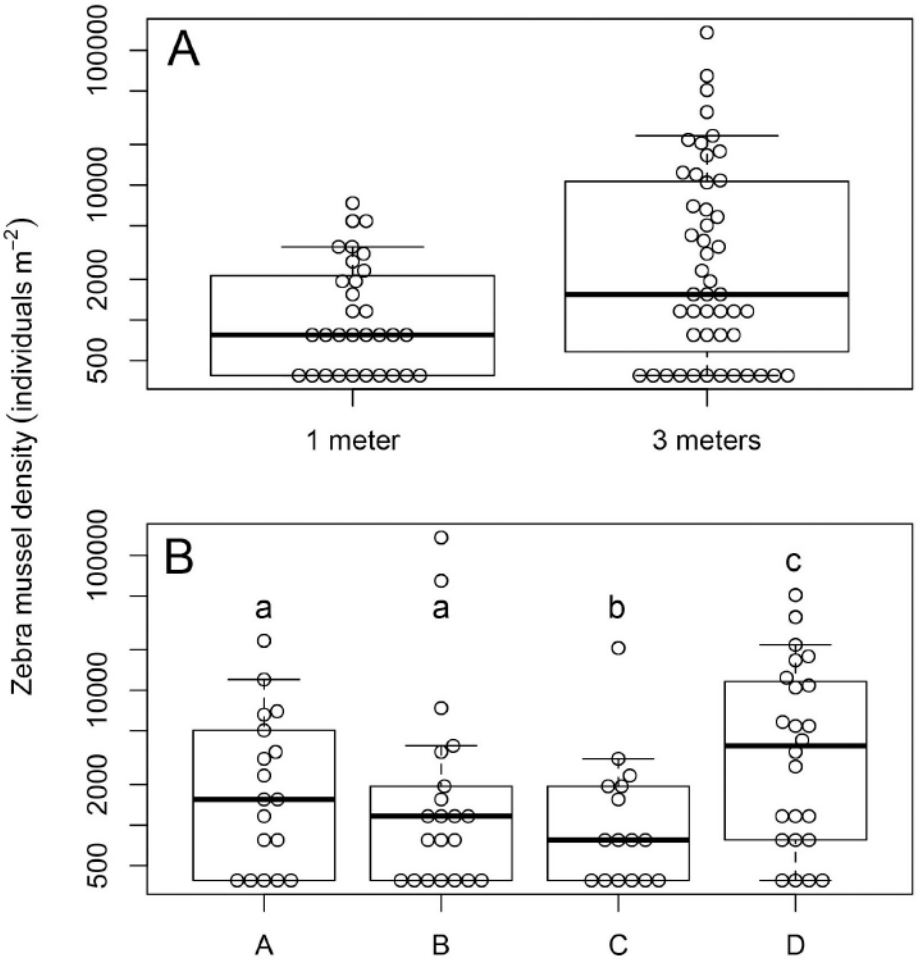

Figure 7. Density of zebra mussel post-veligers by A) depth and B) plate. Box and whisker plots indicating the median (center thick line), first and third quartiles (top and bottom of box), and range (bracketed end of lines, excluding outliers). Circles indicate densities of zebra mussel post-veligers counted on subsampled region of all sample plates and sites from July 2011 through June 2012. Samples where no zebra mussel veligers were recorded have been removed before plotting for clarity but are included in statistical analyses. Uppercase letters in lower panel refer to plates as labeled in Figure 2. Lowercase letters above boxes in (B) indicate regions of the sampler that differed significantly in post-veliger abundance according to post-hoc test results.

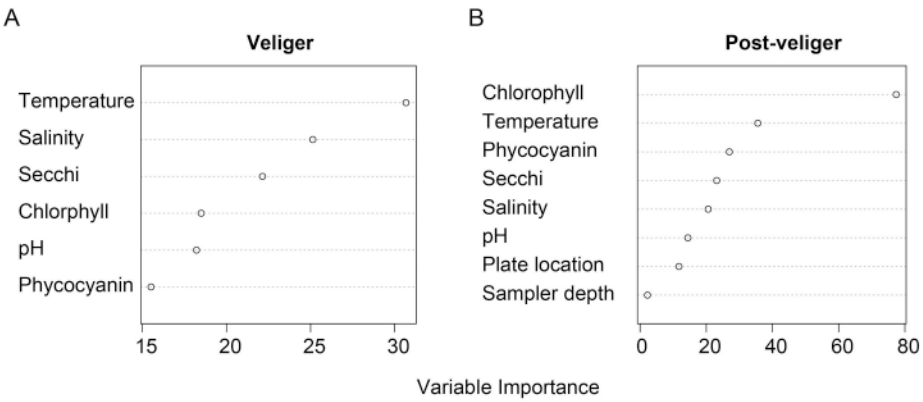

Figure 8. Variable importance for predictor variables included in random forest models for predicting log(x+1) transformed abundance of A) zebra mussel veligers and B) post-veligers. Variable importance is based on the mean decrease in node impurity, measured by the residual sum of squares.

veligers are associated with different environmental variables, and post-veligers are better predicted by these variables.

Discussion

We had hypothesized that zebra mussel veliger densities would be best predicted by water quality parameters including summer water temperatures, algal biomass (measured by chlorophyll), water clarity, and salinity. Our results supported some of these predictions; densities of both life stages were lower at western sites with lower water clarity, higher salinity, and higher algal biomass. We observed veligers from late April through early November (Figure 6). These results line up well with earlier work in Lake Texoma showing that veligers appear seasonally, with earliest veligers appearing near the dam on April 12 and last observed veligers appearing before mid-October (Churchill 2013). These dates are substantially further apart than in temperate systems such as the Laurentian Great Lakes. In Western Lake Erie, for example, veligers were first observed in June and last observed in September over a five-year period (Nichols 1996). However, zebra mussels have been detected in plankton samples as late as December in Lake Michigan (Pothoven and Elgin 2019), suggesting that there is substantial variation even within temperate lakes.

We had initially expected that summer water temperatures close to the upper lethal limit of zebra mussels would inhibit mid-summer reproduction. If zebra mussels experienced an upper thermal limit mid-summer in Lake Texoma, we would observe two discrete pulses of zebra mussel veligers in early summer and fall, as has been previously observed in Lake Texoma (Churchill 2013). However, at our littoral sites, we did not observe clear evidence of two discrete pulses of veligers (Figure 6). The highest temperature we recorded was 31.7 °C, which is just below the upper thermal limit of zebra mussels (32 °C, Beyer et al. 2011), although this temperature may be deleterious if experienced for a longer period of time (Spidle et al. 1995). It is more likely that temperature contributed to the random forest models in the form of low temperatures reducing reproduction. The hypothesized lower limit for zebra mussel spawning is 12 °C (Nichols 1996). In total, 39 of our veliger samples were collected when the water temperature was less than 12 °C, and no zebra mussel veligers were observed in these 39 samples. The lowest temperature at which we observed zebra mussel veligers present in our plankton samples was 16.8 °C.

Our highest recorded veliger density was lower than what was recorded in Lake Texoma in 2010, with peak densities reaching 9.4 veligers L^{-1} compared to 42 veligers L^{-1} recorded by Churchill and colleagues (2017). One possible explanation for this discrepancy is a difference in sampling location; the site used by Churchill was downstream of ours and positioned more on the main channel of the Red River. However, this difference in density is likely a consequence of a drought and heat wave in 2011 that caused a zebra mussel die-off (T.C. Hallidayschult *personal observation*) and likely had a persistent impact on recruitment.

Additionally, on our post-veliger samplers, we found higher abundances on deeper samplers and on the underside of the sampler, compared with the inside and upper surface. These differences are likely driven by temperature, juvenile settling choices, and post-settling mortality due to predation by Harris mud crabs (*Rhithropanopeus harrisii* Gould, 1841), another invasive species in Lake Texoma that feeds on mussels in its native range (Boyle et al. 2010). Zebra mussels up to 10 mm are highly motile after settlement. They use a suite of cues, including light, conspecific chemicals, and gravity to select a location for attaching byssal threads (Kobak 2001). Differences in abundances at 1 and 3 meters, as well as between different plates (A, B, C, and D) are likely caused, in part, by differences in light intensity. Light intensity is known to affect settling preferences of post-veligers, with individuals preferring darker areas (Kobak 2001). We found greater numbers of post-veligers on deeper samplers (Figure 7A), supporting a preference for settlement in areas of lower light intensity. However, plate A was settled as often as plate B, which suggests that light intensity may not be the main factor driving settling patterns.

Post-settling mortality also plays a large role in determining zebra mussel densities. For example, Jones and Ricciardi (2014) found that in Lake Michigan, densities of larval and juvenile zebra mussels did not predict the densities of adult zebra mussels, implying that post-settling differences in mortality drive adult zebra mussel densities more than larval settling rates. In subtropical lakes, post-settling mortality may play an even larger role, as zebra mussels experience greater levels of thermal stress (Spidle et al. 1995; Karatayev et al. 1998) and higher predation pressures from molluscivorous fish (Eggleton et al. 2004; Bartsch et al. 2005; Watzin et al. 2008).

We observed differences in variable importance and predictive ability of our random forest models for veligers and post-veligers. One explanation for this difference is that veligers are a product of both upstream reproducing populations of zebra mussels as well as the environmental variables of where they are collected. Their presence and abundance are affected by environmental variables both distant and proximate to where they are collected. Post-veligers, on the other hand, are more likely to be affected by proximate environmental variables, since they have settled in one location. This difference may be playing out in our random forest models, and may account for the observed differences in variable importance and predictive ability of the models for veligers and post-veligers.

While environmental variability is known to be an important predictor of zebra mussel abundances on a large scale, we argue that these factors play an important role within watersheds as well. Reservoirs created by damming the confluence of two rivers can vary greatly in water quality parameters from one arm of the lake to the other, creating an environmentally

heterogeneous habitat for colonizing zebra mussels. Densities of zebra mussel veligers and post-veliger juveniles were higher in areas with more favorable environmental conditions, suggesting that even within a watershed, basic physiochemical parameters may be useful for predicting the spread and ultimately the impact of zebra mussels. These implications should also be considered in the context of global climate change, where inland water temperatures are predicted to rise, meaning that, among other things, the frequency with which zebra mussels encounter habitats on the edge of their thermal tolerance is likely to increase in the coming years (Griebeler and Seitz 2007). Climate change is also causing salinization of freshwaters (Kaushal et al. 2018). These considerations will be applicable in the future in areas which currently have healthy zebra mussel populations living in a relatively low-stress environment.

Algal community differences may also play a role in controlling the abundance of zebra mussel veligers in Lake Texoma, particularly as veligers are more sensitive to unpalatable foods (Vanderploeg et al. 1996). While we did not measure phytoplankton composition, there likely is significant variation in food quality between arms of the lake. Toxigenic golden algae (*Prymnesium parvum* Carter, 1937) abundances are much higher in the western, Red River arm (Hambright et al. 2010, 2015). In pilot studies, we found no zebra mussel mortality due to exposure to golden algae. However, zebra mussels consistently ceased feeding when exposed to high concentrations of golden algae, suggesting that perhaps the toxins produced by these protists discourage feeding by zebra mussels. The presence of golden algae in the Red River arm could challenge zebra mussel population establishment. Additionally, the Red River arm tends to experience summer blooms of cyanobacteria, including members of the genera *Microcystis*, *Raphidiopsis* (formerly *Cylindrospermopsis*), *Planktothrix*, and others (Hambright *unpublished data*). Several studies have reported that *Microcystis* is a poor food source for both adult zebra mussels (Naddafi et al. 2007; Vanderploeg et al. 2009) and veligers (Vanderploeg et al. 1996), due to their large colony size and lack of essential fatty acids, as well as the presence of toxins (Juhel et al. 2006) (but see (Pires et al. 2004a, b, 2005).

We did not quantify the availability of hard substrate in Lake Texoma, which is a key component required for zebra mussels to reach high population densities (Naddafi et al. 2010). Indeed, substrate availability can explain the majority of variation in zebra mussel densities under otherwise suitable environmental conditions (Mellina and Rasmussen 1994), but is also one of the most difficult parameters to quantify, as it generally requires extensive SCUBA surveys (Adams 2010). Nonetheless, substrate availability is an important consideration and certainly plays a role in explaining the density differences between the two arms of Lake Texoma. As a further complication, even if hard substrates are predominant in an area, eutrophic lakes produce large amounts of particulate organic matter,

which can settle out on hard substrate and prevent zebra mussels from using that habitat. In Lake Texoma, we hypothesize that the high amount of sediment observed on our samplers (Figure S2) may reduce recruitment and survival of post-veligers, leading to the surfeit of zeroes in our post-veliger counts. Our samplers were adjacent to docks, and so sediment accumulation may have been affected by boating and angling activities at the docks, however all samplers were located within no-wake zones. If a large amount of the lake bottom is composed of a soft organic substrate, zebra mussel densities will be much lower due to a shortage of hard substrate (Mellina and Rasmussen 1994). As a result of this relationship between trophic status and substrate availability, low water clarity is associated (indirectly) with lower zebra mussel densities (Madon et al. 1998). Thus, in a eutrophic lake with poor water clarity, increases in Secchi depth should be positively associated with zebra mussel densities, as we observed in Lake Texoma (Figures 7, S1, and S5).

Availability of calcium and water pH are unlikely to be affecting zebra mussel differences around Lake Texoma. While calcium concentrations and pH are important in predicting zebra mussel success in many lakes (Karatayev et al. 2015), the ranges recorded for Lake Texoma exceed any documented threshold values measured for sustaining zebra mussel populations. Lake Texoma calcium levels range from 59–141 mg L^{-1} (An and Kampbell 2003), compared with the minimum level of 32 mg L^{-1} for optimal growth of zebra mussels (Hincks and Mackie 1997). The threshold pH value of 7.5 reported by (Karatayev et al. 2015) suggests that pH could offer some impediment to zebra mussels in Lake Texoma as values measured at our sites ranged from 6.9 to 8.6. Churchill (2013) found that models including pH along with temperature and chlorophyll were the best predictors of zebra mussel veliger densities at the Lake Texoma pumping site for the North Texas Municipal Water District (see Figure 1B). However, Churchill's study focused more on seasonal rather than spatial patterns. Although average calcium concentrations ranged narrowly between 79 and 87 mg/l, Churchill et al. (2017) did document a calcium gradient in Lake Texoma, decreasing from 86.9 in the west to 79.0 mg L^{-1} in the east. They also found a positive relationship between zebra mussel growth rates in Lake Texoma enclosures and calcium concentrations, so it is conceivable that, much like high salinity, borderline low calcium concentrations could potentially act as a sublethal stressor interacting with the other factors in the lake to ultimately determine zebra mussel population densities and reproductive success.

Flow is known to play a key role in governing all life stages of zebra mussels, including dispersal and settling rate, often in complex and contradictory ways (reviewed in Hasler et al. 2019). For example, higher flow and turbulence increase veliger mortality, yet zebra mussels rely on

downstream movement of water for dispersal (Horvath and Lamberti 1999). Higher flow is associated with lower settling rates of veligers (Chen et al. 2011). However, these studies are carried out primarily in riverine systems (Sanz-Ronda et al. 2014), in the main channel of large reservoirs (Chen et al. 2011), or downstream of reservoir outlets (Churchill and Quigley 2018). It is not clear if or how variation in flow affects veliger production and site selection of post-veligers in sites such as ours, located upstream in protected embayments of large, lentic reservoirs. We did not directly measure flow at our sites, and flow gauge data are not available near our sites. However, a study by Iturbe (2005) estimated flow velocity at 39 regions within Lake Texoma. The estimated flow near our sites ranged from 0.0 to 0.9 cm s^{-1}. These values are extremely low compared with flow measured in the studies listed above and are likely overestimates, as our sites were located at marinas located within sheltered embayments on tributaries feeding Lake Texoma. The flow estimates at Cedar Mills and Soldier Creek were identical (Iturbe 2005), but these sites exhibit marked differences in veliger incidence rates, suggesting that flow is not sufficient to explain propagule pressure differences across Lake Texoma. It is possible, however, that the high post-veliger abundances recorded at Catfish Bay are due to its very low flow velocity (0–0.1 cm s^{-1}). Further studies are needed within Lake Texoma to directly measure flow and its effects on zebra mussel propagule pressure and establishment.

Baseline environmental data collected from a variety of locations within a water body may represent a useful predictive tool for assessing the extent and severity of zebra mussel invasions in suboptimal habitats and allow a finer-scale understanding of how zebra mussels may be affecting the lakes that they invade. Even the moderate differences in environmental parameters seen between the two arms of Lake Texoma appear to produce a large difference in zebra mussel distribution patterns. As zebra mussels continue to invade and expand across the United States, it is essential that we collect information on their spread in conjunction with documenting key water quality parameters. By doing so, we can better quantify the fundamental niche of this problematic invader, as well as better understand how and why their actualized niches maintain such a high level of plasticity across the various locations they have invaded worldwide.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Water temperatures at 1 and 3 meters throughout the annual cycle (August 2011–October 2015).
Figure S2. Results of the sediment mass analysis by plate, showing the the dry mass for each of the 100 samples, grouped by plate area.
Figure S3. Results of the sediment mass analysis by sampling site, showing the the dry mass for each of the 100 samples.
Figure S4. Plot of density of veligers per cubic meter against environmental predictors included in model.
Figure S5. Box and whisker plots of Secchi depth by site.

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