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Author(s): Benjamin R. Smith , David R. Edds , and Jason M. Goeckler
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DISTRIBUTION AND DENSITY OF ZEBRA MUSSELS IN FOUR KANSAS RESERVOIRS

Benjamin R. Smith,* David R. Edds, and Jason M. Goeckler

Emporia State University, Department of Biological Sciences, Emporia, KS 66801-5415 (BRS, DRE)
Kansas Department of Wildlife, Parks and Tourism, Research and Survey Office, P.O. Box 1525, Emporia, KS 66801-1525 (JMG)
Present address of BRS: Lake Mead National Recreation Area, 601 Nevada Highway, Boulder City, NV 89005
**Correspondent: ben_smith@nps.gov*

Abstract—We assessed zebra mussel (*Dreissena polymorpha*) distribution and density in four newly infested manmade reservoirs in the upper Neosho River Basin, Kansas, from March–November 2011. Density was estimated via monthly plankton samples to monitor veligers, visual searches to detect recruited zebra mussels, and colonization substrates to monitor settling zebra mussels. Infested impoundments upstream were likely the source of zebra mussels dispersing into downstream impoundments in the basin. Marion Reservoir had greater veliger densities downlake than in its upper region while veliger densities in the other three reservoirs were not significantly different among lake regions. Veliger and adult densities were less in the outlet downstream from Marion Reservoir than in the downlake portion of the reservoir. Differences among reservoirs could reflect differences in time since infestation as well as variability in temperature and local physicochemical factors.

Resumen—Evaluamos la distribución y densidad del mejillón cebra (*Dreissena polymorpha*) en cuatro embalses artificiales recién infestados en la cuenca alta del río Neosho, Kansas, de marzo a noviembre de 2011. La densidad se calculó a través de muestras mensuales de plancton para monitorear las velígeras, búsquedas visuales para detectar reclutas del mejillón cebra, y los sustratos de colonización para monitorear el asentamiento de los mejillones cebra. Los embalses infestados río arriba probablemente fueron la fuente de dispersión para los mejillones cebra hacia los embalses río abajo en la cuenca. El embalse Marion tuvo densidades de velígeras más altas en su parte arriba que en su parte abajo, mientras que las densidades de velígeras en diferentes regiones de los otros tres embalses no fueron significativamente diferentes . Las densidades de velígeras y de adultos eran menos en la salida abajo del embalse Marion que en la parte baja del embalse. Las diferencias entre los embalses podrían reflejar diferencias en el tiempo desde la infestación, así como la variabilidad en la temperatura y los factores físico-químicos locales.

The highly invasive zebra mussel (*Dreissena polymorpha*) was introduced to North America in 1987 in Lake St. Clair, in the Great Lakes system (Mackie et al., 1989), and has spread quickly, primarily moved overland by recreational boat traffic that carries adults and microscopic veligers (Padilla et al., 1996; Bossenbroek et al., 2007; Strayer, 2009). The current contiguous range of zebra mussels encompasses a large portion of the eastern and central United States. These bivalves have spread from their initial point of introduction as far south as Louisiana and reach the most westward point of their established contiguous North American range in Kansas (United States Geological Survey, http://nas2.er.usgs.gov/viewer/omap.aspx?SpeciesID=5). First documented in Kansas in 2003, zebra mussels have been detected in many reservoirs and rivers in the state, including in the Neosho Basin (Smith et al., 2015).

Planktonic veligers, which are moved by currents and wave action, are the natural means of dispersal for zebra mussels (Stoeckel et al., 1997; Fahnenstiel et al., 1999; Rehmann et al., 2003). Veligers remain suspended in the water column until they mature (8–35 d), after which they settle out and attach to a suitably stable substrate (Horvath et al., 1996; Horvath et al., 1999; Horvath and Lamberti, 1999*a*). As the range of zebra mussels has spread, their biological and economic burden has increased; this will continue as they are introduced farther into western North America (Pimentel et al., 2005). Zebra mussels decrease phytoplankton populations and thus actively compete with native mussels and game fishes (MacIssac, 1996; Schloesser et al., 1996). They also commonly occlude intake pipes of water treatment and electrical generation facilities, thereby increasing expenses (Pimentel et al., 2005). These effects have been estimated to cost more than $100 million annually in North America (Strayer, 2009).

As zebra mussels expand their range, studying their distribution and density within and among reservoirs, as well as in rivers upstream and downstream, will increase our understanding of their ecology. Reservoirs can act as stepping-stones that facilitate the spread of zebra mussels across the landscape (Schneider et al., 1998; MacIsaac et al., 2004; Havel et al., 2005). No one has yet to conduct a systematic comparison of longitudinal reaches in the newly invaded, calcium-rich manmade reservoirs of the Midwest, even though reservoirs are quite susceptible to invasive species (Havel et al., 2005). We studied the density and distribution of adult and juvenile zebra mussels in four reservoirs in the upper Neosho Basin in eastern Kansas. Given the potential for accumulation of larval zebra mussels behind the dam due to downlake flow and wind-generated currents (George and Edwards, 1976), we predicted that the greatest density of veligers would occur in the downlake portion of these reservoirs. The downlake accumulation of larvae and the abundance of large, stable substrate conducive to zebra mussel colonization and growth (Marsden and Lansky, 2000) led us to predict that recruited individuals also would be more abundant in this region. Furthermore, we predicted that no zebra mussels would occur upstream from headwater reservoirs in the basin and that densities of both life stages would decrease in the outlet channel downstream from all reservoir dams due to the physical trauma inflicted by traveling through the dam structure (Horvath and Lamberti, 1999*a*).

Study Area—The upper Neosho River Basin includes four reservoirs infested with zebra mussels (Marion Reservoir, Council Grove City Lake, Council Grove Reservoir, and John Redmond Reservoir) and two infested rivers (the Cottonwood and Neosho) (Smith et al., 2015) (Fig. 1). In 2008, they confirmed the initial introduction of zebra mussels in the Neosho Basin occurred in Marion (Smith et al., 2015). Marion Reservoir is a 25-km^2 impoundment constructed on the headwaters of the Cottonwood River in 1968 (United States Army Corps of Engineers, http://corpslakes.usace.army.mil/visitors/states.cfm?state=KS). Zebra mussels were detected in Council Grove City Lake in 2010 (Smith et al., 2015); this lake is a 1.75-km^2 water source for the city of Council Grove constructed on a tributary (Canning Creek) of the Neosho River in 1942. Council Grove Reservoir is a 13.4-km^2 impoundment of the Neosho River constructed in 1964; it was declared infested with zebra mussels in 2011 (Smith et al., 2015). The Neosho River continues downstream from Council Grove Reservoir, is joined by the Cottonwood, and is impounded in John Redmond Reservoir, a 38-km^2 flood control lake constructed in 1964. They confirmed the presence of zebra mussels in John Redmond Reservoir in 2010 (Smith et al., 2015).

Materials and Methods—We sampled each of these reservoirs (Marion Reservoir, Council Grove City Lake, Council Grove Reservoir, and John Redmond Reservoir) monthly during the typical zebra mussel reproductive season (March–November) in 2011. We sampled each reservoir in three sections: upper, middle, and lower; the upper section was located closest to the inlet and the lower section was located closest to the outlet. Upper sites were typically shallow (less than 2 m deep) and generally lacked substrate larger than silt or sand. Middle sites were generally slightly deeper than upper sites, with a substrate ranging from sand to cobble. Lower sites were typically deepest (2+ m), with cobble and boulder commonly available. Additionally, for each reservoir a site in the river upstream (inlet) and a site in the outlet channel were sampled to search for zebra mussels, providing 20 sites examined monthly.

We sampled zebra mussel veligers (in all stages of development) plus juveniles and adults (in all stages of development, collectively termed "recruited individuals" given that we did not determine their sexual maturity). Sampling began when water temperatures reached 10°C, the approximate water temperature believed to trigger zebra mussel reproduction (Stanczykowska, 1977; Fong et al., 1995). Monitoring of water temperatures was via United States Geological Survey (USGS) water monitoring station 07182280 on the Neosho River at Neosho Rapids, Kansas, and USGS station 07182390 on the Cottonwood River at Neosho Rapids, Kansas; they both reached 10°C on 24 March 2011. Sampling concluded when water temperatures returned to less than 10°C; this occurred at both sites on 22 November 2011. We conducted all sampling on the 24th of each month $\pm$5 days, and the order of sites sampled each month was haphazard. We recorded local surface water temperature with an alcohol thermometer at the time of sampling. We obtained reservoir discharge and elevation from the USGS (2013) National Water Information System (http://www.usgs.gov/water/).

Veliger Sampling—We used a student plankton net with 63-µm mesh and a 127-mm mouth (Wildco®, Yulee, Florida) to sample veligers. We employed shoreline oblique tows to collect samples (Marsden, 1992); tows began at the substrate and ended at the water's surface. Post hoc analysis showed no difference between densities calculated from shoreline oblique tows and vertical tows taken by Kansas Department of Wildlife, Parks and Tourism personnel from a boat in the offshore pelagic zone during corresponding sampling periods (Holoubek et al., 2014). Each tow was approximately 6 m long; distance for volume calculation was measured by a mechanical flow meter (model 2030R, General Oceanics, Inc., Miami, Florida) affixed into the mouth of the net. We collected three samples monthly at each site. Following each tow, we washed the inside of the net with veliger-free tap water and preserved the entire sample in 70% isopropyl alcohol. After all three samples had been collected at a site, we washed the inside of the net with tap water and preserved the water in a sample jar to allow assessment of whether or not the washing process had removed all veligers. If large numbers of veligers had been found in this rinse sample (i.e., greater than 10% of the mean number of veligers found in the three samples), then calculated veliger densities could have been adjusted to account for veligers not completely removed in the washing process. However, this was not necessary because subsequent examination of these samples detected only a small number of veligers (maximum of 7% of the mean).

After sampling each site, we soaked the net in 99% isopropyl alcohol for at least 10 min to prevent contamination of viable veligers between sites. We transported the samples to the laboratory for examination under a Zeiss cross-polarized light microscope (25×, 100×, and 400× magnification). We identi-

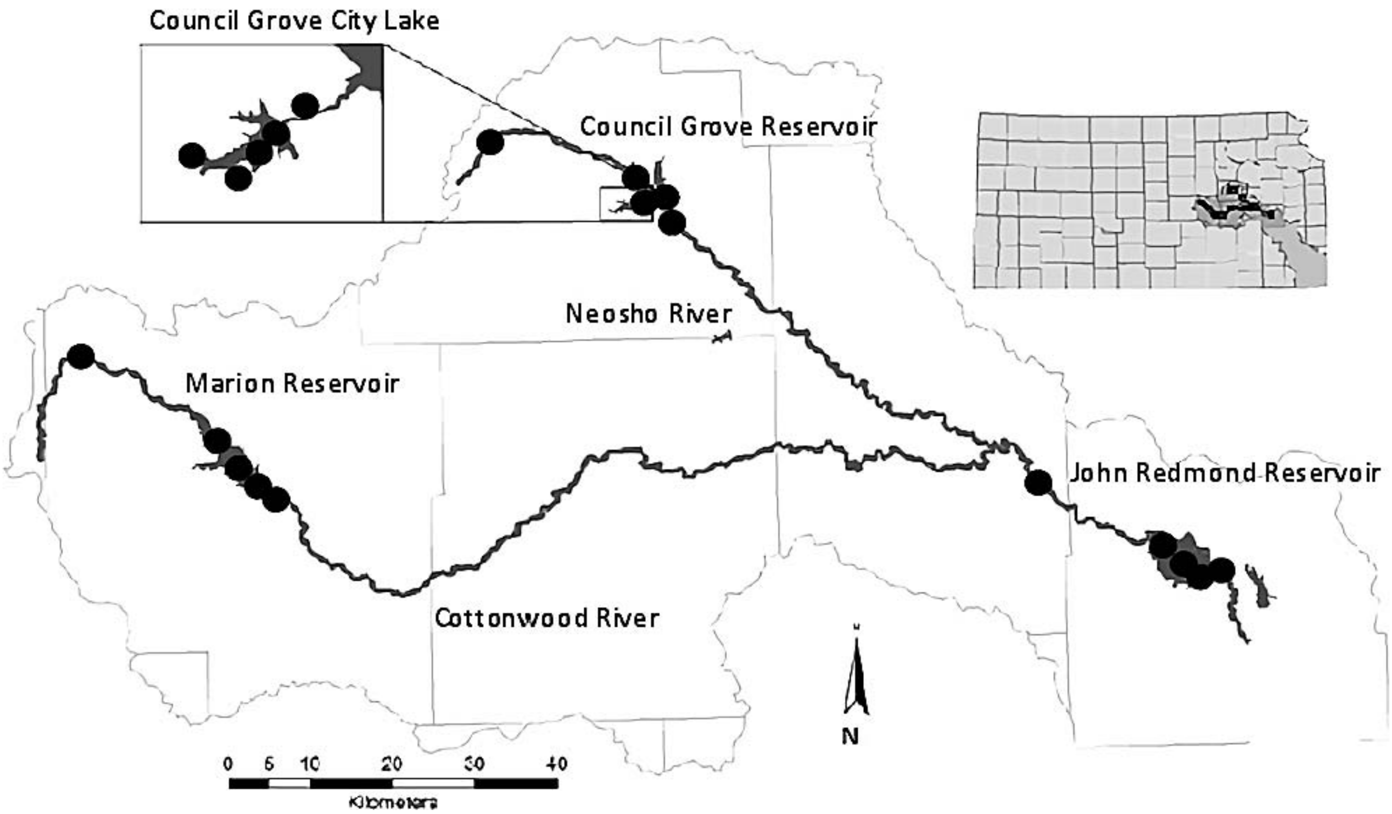

FIG. 1—Twenty sample sites for a zebra mussel survey in the upper Neosho River basin, Kansas, March–November 2011. Location of the basin in Kansas shown in inset.

fied veligers with guides from Nichols and Black (1994), Johnson (1995), and the United States Army Corps of Engineers Environmental Laboratory (http://el.erdc.usace.army.mil/zebra/zmis/zmishelp/veliger_analysis_techniques.htm) and then quantified all samples without subsampling. We calculated density (concentration) as the number of veligers per liter of water sampled.

Recruited Individuals Sampling—We sampled juveniles and adults via visual and tactile inspection at each site and within colonization units. Visual and tactile inspection consisted of 30 min of examining available substrate in accessible depths (<approximately 2.5 m) without the aid of snorkel or scuba equipment. We collected all zebra mussels encountered during the timed search, preserved them in 70% isopropyl alcohol, and transported them to the lab for counting.

Colonization units consisted of a two-holed concrete block, 40 × 20 × 20 cm, with 0.5-cm holes drilled through its wall to attach a 10 × 10 × 0.16-cm grey polyvinyl chloride (PVC) plate oriented out of direct sunlight and secured by white plastic zip ties to the inside. We placed two colonization units at each site in April, submerged to approximately 1 m depth and tethered with a galvanized steel cable to a point onshore. To evaluate colonization, we examined one unit at each site in July and the other in November by removing the PVC plate and counting visible zebra mussels attached to the exposed face.

Statistical Analysis—We conducted statistical analyses with the Statistical Analysis System (version 18.2, SAS Institute Inc., Cary, North Carolina) and considered results significant at $\alpha \leq 0.10$ (Dayton, 1998). We assessed normality and homogeneity of variance with the SAS Graphical Plotting and Univariate procedures and judged all data to be normal and homogeneous. We tested hypotheses regarding variation in zebra mussel densities at site types (upper, middle, and lower) with repeated measures analysis of variance (ANOVAR), followed by Tukey's multiple comparisons test where appropriate, for both veligers and recruited individuals.

RESULTS—We found no veligers, recruited individuals, or artificial substrate colonizers upstream from Marion Reservoir (Cottonwood River). Veligers were detected at the inlet site of Council Grove City Lake (Neosho River), approximately 500 m upstream from the lake, in July (mean = 0.47, veligers L^{-1}, *SE* = 0.06) and August (mean = 0.25 veligers L^{-1}, *SE* = 0.10). We did not detect zebra mussels at any other time, with any method, at any site upstream from a reservoir that did not have a known infested reservoir upstream from it.

At all sites and reservoirs, densities of zebra mussel veligers increased throughout the reproductive season (Fig. 2). Mean veliger densities in reservoirs ranged from 0.17 L^{-1} (*SE* = 0.11) in the upper section of Council Grove Reservoir to 3.95 L^{-1} (*SE* = 1.56) in the lower section of Marion Reservoir (Table 1). Mean number of recruited individuals per 30-min search ranged from 0.10 (*SE* = 0.11) in the upper section of Council Grove Reservoir and John Redmond Reservoir to 652.70 (*SE* = 113.25) in the lower section of Marion Reservoir (Table

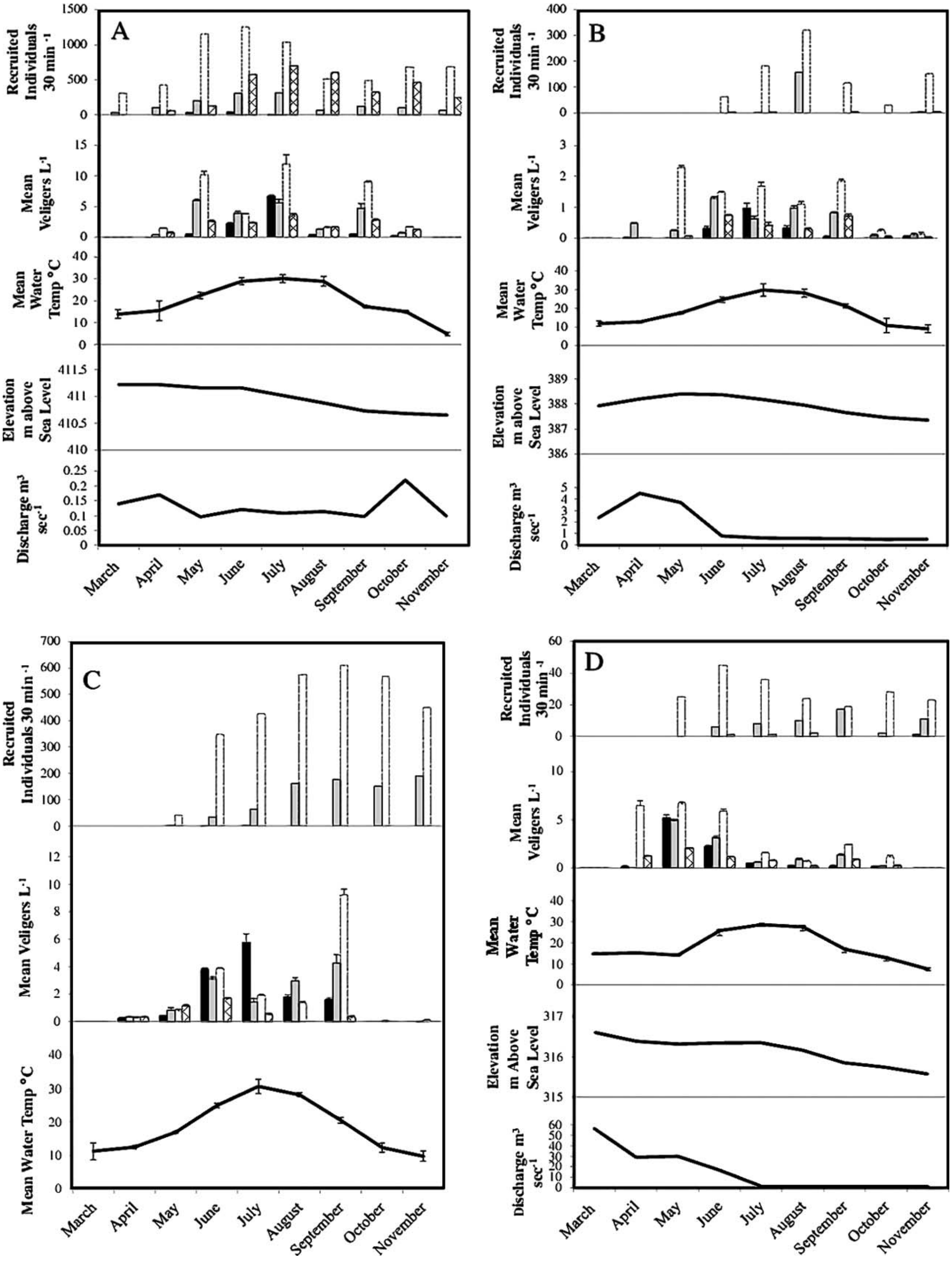

FIG. 2—Zebra mussel recruited individuals 30 min^{-1}, mean number of veligers L^{-1}, mean water temperature, reservoir elevation, and reservoir discharge for (A) Marion Reservoir, (B) Council Grove Reservoir, (C) Council Grove City Lake (discharge and elevation data unavailable), and (D) John Redmond Reservoir in the upper Neosho River basin, Kansas, March–November 2011. Reservoir sections: black bars = upper, gray bars = middle, white bars = lower, crosshatched bars = outlet. Error bars = 1 SE.

Table 1—Zebra mussel mean (*SE*) number of veligers L^{-1}, number of recruited individuals 30-min search^{-1}, and number of colonizers per m^2 on PVC substrate in inlet, upper, middle, lower, and outlet sections of four reservoirs in the upper Neosho River Basin, Kansas, March–November 2011.

Reservoir	Zebra mussel	Inlet	Upper	Middle	Lower	Outlet
Marion Reservoir						
	Veligers	0 (0.0)	1.03 (0.73)	2.24 (0.84)	3.95 (1.56)	1.45 (0.42)
	30-min search	0 (0.0)	8.89 (5.52)	130.60 (34.55)	652.70 (113.25)	308.90 (84.50)
	colonization units	0 (0.0)	0 (0.0)	1,600 (711.8)	3,700 (1613.0)	0.50 (0.50)
Council Grove City Lake						
	Veligers	0.07 (0.06)	1.33 (0.68)	1.29 (0.54)	1.76 (1.00)	0.39 (0.20)
	30-min search	0 (0.0)	0.40 (0.34)	77.70 (27.30)	301.40 (84.92)	0 (0.0)
	colonization units	0 (0.0)	0 (0.0)	6,150 (3091.1)	37,500 (16201.9)	0 (0.0)
Council Grove Reservoir						
	Veligers	0 (0.0)	0.17 (0.11)	0.46 (0.15)	0.87 (0.30)	0.23 (0.10)
	30-min search	0 (0.0)	0.10 (0.11)	16.10 (17.27)	86.20 (36.16)	1.10 (0.52)
	colonization units	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
John Redmond Reservoir						
	Veligers	0 (0.0)	0.86 (0.58)	1.10 (0.57)	2.48 (0.93)	0.44 (0.13)
	30-min search	0 (0.0)	0.10 (0.11)	5.40 (2.01)	20.00 (4.93)	0.40 (0.24)
	colonization units	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

1). Mean density of recruited individuals on colonization units ranged from 0.0 per m^2 (*SE* = 0.0) at all sites in John Redmond Reservoir, Council Grove Reservoir, and the upper sites at Marion Reservoir and Council Grove City Lake to 37,500 per m^2 (*SE* = 16,201.9) in the lower section of Council Grove City Lake (Table 1).

Only Marion Reservoir exhibited statistically different veliger densities among upper, middle, and lower sections (ANOVAR $F_{2,6} = 6.01$, $P = 0.07$; Fig. 2A). Council Grove City Lake (ANOVAR $F_{2,6} = 6.89$, $P = 0.14$; Fig. 2C), Council Grove Reservoir (ANOVAR $F_{2,6} = 6.24$, $P = 0.11$; Fig. 2B), and John Redmond Reservoir (ANOVAR $F_{2,6} = 6.35$, $P = 0.22$; Fig. 2D) did not. Tukey's test differentiated Marion Reservoir upper vs. lower sections but grouped the middle section with the other two.

None of the reservoirs showed statistically different numbers of recruited individuals found during the 30-min search among upper, middle, and lower sections (Marion Reservoir ANOVAR $F_{2,6} = 3.66$, $P = 0.13$, Fig. 2A; Council Grove City Lake ANOVAR $F_{2,6} = 3.42$, $P = 0.33$, Fig. 2C; Council Grove Reservoir ANOVAR $F_{2,6} = 4.02$, $P = 0.12$, Fig. 2B; John Redmond Reservoir ANOVAR $F_{2,6} = 4.53$, $P = 0.16$, Fig. 2D).

No reservoirs exhibited statistically different densities of zebra mussels recruited on artificial substrates among upper, middle, and lower sections (Marion Reservoir ANOVAR $F_{2,6} = 1.24$, $P = 0.11$, Fig. 2A; Council Grove City Lake ANOVAR $F_{2,6} = 0.94$, $P = 0.43$, Fig. 2C). Council Grove Reservoir and John Redmond Reservoir exhibited no colonization (Fig. 2B and D).

Significantly fewer veligers were detected in the Marion Reservoir outlet channel than in the reservoir's lower region (ANOVAR $F_{1,3} = 16.05$, $P = 0.098$; Fig. 2A), but this was not the case at Council Grove City Lake (ANOVAR $F_{1,3} = 11.47$, $P = 0.12$; Fig. 2C), Council Grove Reservoir (ANOVAR $F_{1,3} = 14.02$, $P = 0.34$; Fig. 2B), or John Redmond Reservoir (ANOVAR $F_{1,3} = 12.43$, $P = 0.18$; Fig. 2D). The number of recruited individuals per 30-min search was also less in the outlet channel than in the lower section of Marion Reservoir (ANOVAR $F_{1,3} = 7.01$, $P = 0.09$; Fig. 2A) but not in the other three reservoirs (Council Grove City Lake ANOVAR $F_{1,3} = 6.66$, $P = 0.14$, Fig. 2C; Council Grove Reservoir ANOVAR $F_{1,3} = 4.89$, $P = 0.12$, Fig. 2B; John Redmond Reservoir ANOVAR $F_{1,3} = 5.43$, $P = 0.19$, Fig. 2D). Colonization of PVC substrates at reservoir outlet sites was not significantly different from that in the lower section of any reservoir (Marion Reservoir ANOVAR $F_{2,6} = 2.01$, $P = 0.11$, Fig. 2A; Council Grove City Lake ANOVAR $F_{2,6} = 1.20$, $P = 0.22$, Fig. 2C). Council Grove Reservoir (Fig. 2B) and John Redmond Reservoir (Fig. 2D) exhibited no colonization at either site.

Discussion—Although a small number of veligers were detected in Council Grove City Lake's inlet creek, those were likely spread the short distance upstream from the infested lake by wind and waves that are known to transport plankton (George and Edwards, 1976; Verhagen, 1994; Rehmann et al., 2003). We did not detect any other zebra mussels upstream from Council Grove City Lake or Marion Reservoir. Although low water levels reduced connectivity to a short time period between the upper portion of the reservoirs and their contributing upriver site, the upriver sites and lake sites did remain connected throughout the study. We conclude that those lakes held the upstream source populations for the Neosho basin.

We detected fewer zebra mussels of both life stages in the outlet channel than in the lower reach of Marion Reservoir, but not for the other three reservoirs. It is likely that zebra mussel populations have yet to establish fully in the lower reaches of these other reservoirs, at least to an extent sufficient to demonstrate a statistical difference between these two site types (Table 1). This decrease in the outlet channel was likely due to the trauma experienced while passing through the outlet, which can damage veligers (Horvath and Lamberti, 1999*a*). Additionally, the more lotic environment might sweep dispersing veligers downstream before they have a chance to settle on the ample structure of riprap and concrete at the outlet sites (Smith et al., 2015). Orlova (2010) showed that velocities greater than 1 m sec^{-1} limit zebra mussel settlement.

Maximum veliger densities in these four reservoirs were less than those found in other studies (Horvath and Lamberti, 1999*b*; Severson, 2007), possibly indicating that the four reservoirs we studied had not reached peak veliger densities or that other factors such as temperature regime, food supply quantity or quality, or other conditions were in some way suboptimal for zebra mussels. Horvath and Lamberti (1999*b*) found that densities of zebra mussel veligers in Christiana Lake, Michigan, averaged 41 L^{-1}, ranging from 0 L^{-1} to 100 L^{-1}. Severson (2007) found maximum veliger densities of 118 L^{-1} in El Dorado Reservoir, a shallow manmade reservoir in south-central Kansas. We demonstrate the precision of our monthly estimates of veliger density by concurrence with samples taken in Marion Reservoir by Kansas Department of Wildlife, Parks and Tourism personnel (Holoubek et al., 2014). Veliger densities appeared to be more congruent with temperature than with discharge or elevation (Fig. 2). Within each reservoir, zebra mussel veligers showed pulses in density: Marion in May, July, and September; Council Grove City Lake in June, July, and September; Council Grove Reservoir in May, June, July, and September; and John Redmond Reservoir in April, May, and June. These pulses could be the result of site-specific variation in temperature or other local physicochemical properties of the water, which vary widely among populations and are known to affect the zebra mussel reproductive cycle (Nichols, 1996).

In addition to the potential for accumulation of zebra mussel veligers as a result of downlake flow of water, greater densities in lower reservoir reaches could be because zebra mussel introductions likely often occur near boat ramps and marinas (Padilla et al., 1996), which were more abundant in the lower section of the reservoirs in this study. If these areas were indeed the point of introduction, they would have had the longest time for population growth. Greater zebra mussel abundance in the downlake portion of reservoirs could also be due to the abundance of suitable substrate near the dam. Substrate in upstream portions of these reservoirs was composed mainly of silt and clay, which suffocates settling larvae (Hunter and Bailey, 1992), whereas lower portions had larger substrate, including cobble and boulder, plus riprap on the dam, which provides excellent habitat for settling zebra mussels (Hunter and Bailey, 1992). However, as our results did not show significantly greater numbers of recruited individuals in downlake portions of all reservoirs, it is difficult to determine the role of suitable substrate availability in densities of zebra mussel populations. The greater local abundance could have been due to variation in food availability, local temperature regimes, localized hydrological conditions, or a combination of various physiochemical properties of the water that were not assessed in this study.

Differences among reservoirs could be due to differences in time since infestation. Marion has been infested longer than the other reservoirs (3 y), and perhaps population variation along the length of the reservoirs is most fully expressed in older, more established populations. It is also possible that the relatively short time available for colonization of the substrates explains the lack of statistical significance in recruited individuals and colonizers. For a pattern of longitudinal variation to be exhibited, it could be that zebra mussel populations must be fully established, which could take several years following infestation (Strayer, 2009). Additionally, population densities are likely to vary throughout the year, largely dependent upon local water temperatures known to trigger reproductive processes (Fong et al., 1995). However, this variation should occur within the framework of longitudinal increase, with the highest densities found in the lower reaches of reservoirs. Knowledge of areas of lesser or greater densities is important to informing monitoring efforts directed at detecting new infestations of zebra mussels. Chances of detecting zebra mussels at initial low densities would be increased if samples were taken in areas of likely introduction—and thus greater density—such as near marinas and boat ramps and in the lower portion of reservoirs.

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