

COMPARISON OF ZOOPLANKTON
COMMUNITIES IN OKLAHOMA: IMPLICATIONS
FOR PADDLEFISH (*POLYODON SPATHULA*)
MANAGEMENT AND RESTORATION

By

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Abstract: American paddlefish (*Polyodon spathula*) are large riverine planktivores whose populations have declined significantly over the last century. These declines are largely due to overharvest from commercial fishing and habitat alterations resulting from dam construction. Oklahoma Department of Wildlife Conservation (ODWC) and U.S. Fish & Wildlife Service have stocked paddlefish in reservoirs throughout the state with varying degrees of success. ODWC is currently evaluating Tenkiller Lake as a future paddlefish restoration site. To assess barriers to successful paddlefish recovery efforts, we evaluated prey (zooplankton) availability in seven reservoirs and their nine major river tributaries across a gradient of paddlefish population status in Oklahoma. We quantified zooplankton abundance, size (carapace length) and community structure, in addition to water quality samples for analysis of total phosphorus (nutrients) and chlorophyll *a* (primary productivity). Zooplankton were collected from rivers using a plankton pump in spring to coincide with paddlefish spawning activities and early growth of juvenile fish. We collected zooplankton from reservoirs in summer with vertical tows using a Wisconsin plankton net. Rivers flowing into Texoma (failed) and Eufaula (under evaluation) had lower water clarity and generally higher abundance of large zooplankton compared to rivers with naturally reproducing paddlefish populations (self-sustaining). However, in summer, reservoirs that have self-sustaining paddlefish populations had higher abundances of all zooplankton and large zooplankton (copepods and cladocerans) than reservoirs that have failed to establish a reproducing population. Additionally, self-sustaining paddlefish populations tended to occur in reservoirs with a higher proportion of large zooplankton. These reservoirs had higher total phosphorus compared to reservoirs without. More intensive sampling is needed in rivers to assess the effect of variable flow on zooplankton. Considering zooplankton as a lone metric for success, Tenkiller appears unlikely to succeed due to low overall abundance of zooplankton, low proportion of large taxa, and lower overall productivity. However, food availability is not the only metric of success and paddlefish establishment is influenced by spawning habitat, reproduction, and recruitment. Future studies should assess the effect of turbidity on juvenile paddlefish feeding efficiency. Additionally, a bioenergetics modeling approach could be used to understanding paddlefish carrying capacity and more complex species interactions.

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CHAPTER I

INTRODUCTION

History

American paddlefish (*Polyodon spathula*) are a large prehistoric and planktivorous riverine fish in the family Polyodontidae. Paddlefish are native to the Mississippi River drainage basin. Historically, their range within the United States extended from Montana to Ohio and Minnesota down to Louisiana (Alexander 1914, Burr 1980). Due to the rapid depletion of lake sturgeon in the late 1800s and early 1900s, demand for paddlefish skyrocketed, and an extensive paddlefish fishery appeared on the Mississippi River (Stockard 1907, Wagner 1908). Analysis of commercial harvest records shows a 50+ year decline, and currently there little to no evidence of fish in areas they historically occupied (Carlson and Bonislawsky 1981, Graham 1997). This decline, and lack of information on breeding and feeding requirements of paddlefish has generated concern that populations may be at risk of further depletion (Wagner 1908, Alexander 1914).

In addition to the increased demand for paddlefish, environmental factors have contributed to declines in their populations. Dam construction profoundly impacts habitat and is thought to be one of the driving forces behind paddlefish declines throughout the U.S. (Carlson and Bonislawsky 1981). Environmental factors that may be affected by dams include both changes to the temperature of water that is released to downstream habitats (Ward and Stanford 1979) and regulated flows, which impact cues, such as temperature and discharge, that trigger spawning migration in paddlefish (Russell 1986). Subsequent secondary effects from dam construction that may play a role in declines of paddlefish populations also include pollution, siltation, bank erosion, and changes to water quality (Pasch and Alexander 1986, Unkenholz 1986). Dams are also physical barriers, which may prevent upstream migration to spawning habitat. Additionally, dams may degrade, or in some instances destroy, spawning areas by preventing sediment transport, which is needed to maintain gravel habitat necessary for successful spawning (Carlson and Bonislawsky 1981, Sparrowe 1986, Unkenholz 1986, Schooley and Neely 2018).

Although dam construction generally has a negative impact on paddlefish populations, this is not a homogenous result. Some paddlefish populations have adapted to survive, or even thrive, in reservoirs after dam construction. The formation of reservoirs can lead to abundant zooplankton communities, and with proper management, can result in thriving paddlefish populations (Rosen 1976, Russell 1986, Paukert and Fisher 2001b). Some of these stable paddlefish populations in reservoirs include Keystone and Grand Lake, OK (Nealis 2013, Scarnecchia et al. 2011), Lake Sakakawea, ND (Fredericks and Scarnecchia 1997), and Fort Peck Lake, MT (Kozfkay and

Scarnecchia 2002). However, Unkenholz (1986) surmises that the cumulative effect of dam construction on paddlefish is negative.

Reproduction and Habitat Use

Paddlefish have long life spans and typically take many years to reach sexual maturity. The age of sexual maturity in paddlefish varies based on latitude, with populations further north maturing at a slower rate (Carlson and Bonislowsky 1981). Male paddlefish mature quicker and are typically able to reproduce every year once they reach sexual maturity, whereas female paddlefish are only likely to reproduce every 2-4 years (Russell 1986, Jennings and Zigler 2000). Additionally, some paddlefish populations exhibit inconsistent or episodic recruitment, taking advantage of years with high river discharge and elevated water levels within reservoirs (Scarnecchia et al. 2011, 2014, Schooley et al. 2014, Schooley and Neely 2018). For example, the Grand Lake paddlefish population is dominated by the 1999 year class (Schooley et al. 2014). Due to the life history and biology of paddlefish, recruitment in many environments may not keep pace with exploitation and populations may continue to be negatively affected unless properly managed (Pasch and Alexander 1986).

Once mature, paddlefish respond to environmental triggers to migrate upriver to spawn. Three primary environmental cues trigger staging in the mouth of the river and migration upriver: photoperiod, water temperature, and flows (Russell 1986). Water temperatures around 50°F trigger staging in the lower reaches of the river, while subsequent increases in water flows trigger the migration upriver to inundated spawning habitat (Purkett 1961, Pasch et al. 1980, Russell 1986). Paddlefish deposit their eggs on

gravel beds in flowing water (Purkett 1961). Once paddlefish hatch, they swim toward the surface and catch the current. The current then carries them downstream, away from seasonally inundated spawning habitat (Purkett 1961, Russell 1986).

Feeding Ecology

Feeding by juvenile paddlefish is important for both survival and subsequent recruitment, and necessary for population stability. Paddlefish are primarily planktivores (Forbes 1878, Stockard 1907, Wagner 1908, Coker 1923), but in some cases have been documented to consume aquatic insects (Wagner 1908, Hoopes 1960, Meyer 1960, Ruelle and Hudson 1977). Methods of feeding differ as paddlefish transition through early stages of growth. Literature discussing feeding ecology of juvenile paddlefish comes from hatchery and aquaria studies, with extremely limited information from studies in the wild.

Newly hatched paddlefish live off nutrients in their attached yolk sac for approximately 2-5 days before beginning exogenous feeding (Russell 1986). Juvenile paddlefish are selective feeders (Ruelle and Hudson 1977, Unkenholz 1977, Michaletz et al. 1982). These paddlefish appear to disproportionately select the largest organisms available for consumption (Ruelle and Hudson 1977, Unkenholz 1977, Michaletz et al. 1982, Kozfkay and Scarnecchia 2002), with a near complete absence of small organisms in their diets (e.g. rotifers, nauplii, small copepods, etc.) (Ruelle and Hudson 1977, Michaletz et al. 1982). Juvenile paddlefish continue selective feeding until their gill rakers and fin rays have developed enough to begin filter feeding at approximately 120-

250 mm total length (Rosen and Hales 1981, Michaletz et al. 1982, Yeager and Wallus 1982).

Developed juveniles and adult paddlefish are indiscriminate filter feeders and swim with their mouths open to filter out organisms suspended in the water column (Coker 1923, Eddy and Simer 1929, Ruelle and Hudson 1977, Rosen and Hales 1981). Spaces between gill rakers limits prey retention, typically capturing larger prey items and omitting smaller ones (e.g. rotifers and small copepod nauplii) (Eddy and Simer 1929, Rosen and Hales 1981). Paddlefish gill rakers are spaced from 0.04 – 0.09 mm (Rosen and Hales 1981, Moore and Cotner 1998) and zooplankton < 0.20 – 0.25 mm length are mostly absent from stomach samples (Rosen and Hales 1981). Adult paddlefish stomach samples from the Missouri (SD and NE), Arkansas (OK), Mississippi and Illinois (IL) Rivers found that cladocerans and crustacean zooplankton make up > 75% of their diets (Eddy and Simer 1929; Rosen and Hales 1981; A. Nealis, J. Long, and C. Park, Oklahoma State University, unpublished data). In some instances, insects may make up a majority of paddlefish stomach contents, typically coinciding with mass emergences (Wagner 1908, Meyer 1960).

Oklahoma Reservoirs

Paddlefish inhabit several rivers in the eastern half of Oklahoma, including the Arkansas, Canadian, Grand, Neosho, Red and Verdigris. Populations reside in associated reservoirs including Eufaula, Fort Gibson, Grand Lake O' the Cherokees, Hudson, Kaw, Keystone, Oologah, and Texoma (Schooley et al. 2014). Paddlefish are heavily

monitored within Oklahoma and there are laws and harvest regulations in place to protect their populations.

Although reports of commercial fishing for paddlefish in Oklahoma were limited, laws changed in 1951 allowed for more intensive harvest (Houser and Bross 1959). However, new laws in 1992 banned commercial harvest of paddlefish. Since, researchers have monitored and studied paddlefish within the state (Houser and Bross 1959, Houser 1965, Combs 1982) and recovery efforts focused on stocking reservoirs where populations became extirpated (Schooley et al. 2014). In 2006, Oklahoma classified the status of their paddlefish fishery as increasing (Bettoli et al. 2009), although this varies across individual reservoirs and rivers.

Stocking projects were started by ODWC in conjunction with U.S. Fish and Wildlife Service in the 1990s and focused on Kaw, Oologah, Texoma, and Eufaula lakes, but have had varying success. Paddlefish populations are now self-sustaining at Kaw, Keystone, Oologah, and Grand Lake. In fact, the paddlefish population within the Grand-Neosho and Arkansas River system (Kaw and Keystone) are some of the most productive and studied in the state (Combs 1982, Paukert and Fisher 2000, 2001a, 2001b, Schooley et al. 2014). However, Lake Texoma restoration has been classified as failed. The Eufaula paddlefish population is currently being evaluated and Tenkiller is being considered future recovery efforts (Table 1).

Even among reservoirs with self-sustaining paddlefish populations, environmental and food web characteristics differ. A study by Nealis (2013) found that paddlefish body condition varied greatly between Keystone and Grand Lake. Both male and female fish from Keystone had significantly greater length, weight and gonadal fat indices than those

from Grand. Although not explicitly tested, these differences are hypothesized to be due to differences in reproductive periodicity and the presence/absence of non-native bighead carp between these two systems (Nealis 2013). Understanding underlying factors that influence differences between populations of self-sustaining paddlefish will also provide insight into potential barriers to successful restoration.

Exacerbating paddlefish sustainability and potential stocking success are non-native fish species. Three species of bigheaded carps are now documented in some Oklahoma rivers and reservoirs, including grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*). In Oklahoma, bighead carp have been documented in the Neosho River and Grand Lake system (Pigg et al. 1993, 1997, Long and Nealis 2011), and both silver and bighead carp have been found in the Red River below Lake Texoma (Patton and Tackett 2012). Both silver and bighead carp are filter feeders, consuming phytoplankton, zooplankton and other organisms suspended in the water column. There is concern that further invasion into rivers and lakes will bring competition with native planktivores, such as paddlefish. Relative growth rates of juvenile paddlefish are lower when they are raised in mesocosms with bighead carp than when they are raised alone in mesocosms (Schrank et al. 2003). However, adult paddlefish showed little diet overlap with either silver or bighead carp (Sampson et al. 2009), but these differences may be due to food availability in the study mesocosms (Sampson et al. 2009). Ultimately, more information is needed to understand interspecific competition for paddlefish and interactions between bigheaded carp species and paddlefish and the areas they co-occur.

Zooplankton in Oklahoma Reservoirs

Studies on zooplankton communities in Oklahoma reservoirs are limited and even less information is available regarding spring community dynamics in rivers, coinciding with paddlefish spawning activities. More intensive studies of zooplankton communities have occurred at Keystone Lake (Kochsiek et al. 1971) and Lake Texoma (Work and Gophen 1995, 1999). However, due to the time elapsed since these studies occurred, additional information is needed on zooplankton communities in Oklahoma reservoirs to determine how they might impact paddlefish reproduction, restoration, and/or stocking success.

Zooplankton communities in Oklahoma reservoirs have been impacted with the introduction of the non-native *Daphnia lumholtzi*. This cladoceran is native to Africa, Asia and Australia, and was first discovered in the southern U.S. in 1991 (Sorensen and Sterner 1992). These zooplankters have large helmet and tail spines that may present a barrier to consumption by small fish (Swaffar and O'Brien 1996, Kolar and Wahl 1998). Their effect on juvenile paddlefish has not been studied. *Daphnia lumholtzi* is present in many waterbodies throughout Eastern Oklahoma (Havel and Shurin 2004, OWRB unpublished data). Their abundance peaks during late summer months when other zooplankters decline in abundance (Havel et al. 1995, Stoeckel et al. 1996). The high late-summer density of this species and their ability to thrive in both lotic and lentic environments could suggest they are an additional food source for paddlefish (Kolar and Wahl 1998, Lienesch and Gophen 2001, Lemke et al. 2003). Unpublished data from Keystone and Grand Lakes, OK, shows paddlefish stomachs contain 2 – 10x higher abundance of *D. lumholtzi* than found in tow samples (A. Nealis, J. Long, and C. Park,

Oklahoma State University, unpublished data). The cumulative effect of *D. lumholtzi* invasion on reservoirs and rivers inhabited by paddlefish is not apparent.

To implement effective paddlefish restoration strategies, more work needs to assess zooplankton communities and their potential impacts on paddlefish populations within Oklahoma. This study examines spring and summer zooplankton communities in rivers and reservoirs to better understand possible factors impacting paddlefish restoration efforts (i.e., prey availability to juvenile paddlefish in rivers and whole populations in lakes).

We quantified population density and length of zooplankton, as well as seasonal and spatial dynamics across seven reservoirs and nine major river tributaries in Oklahoma. We compared reservoirs with self-sustaining paddlefish populations to reservoirs that have been stocked for restoration or are a potential future restoration site to better guide management decisions. We hypothesize that the abundances of cladocerans, copepods and other larger bodied zooplankton will be higher, and body sizes larger in systems with self-sustaining populations of paddlefish (Kaw, Keystone, Oologah, and Grand Lakes) compared to systems without self-sustaining populations (Eufaula, Texoma, and Tenkiller). Additionally, we hypothesize that systems with self-sustaining populations will have higher nutrients (phosphorus) and overall primary (measured as chlorophyll *a*) and secondary productivity (measured as total zooplankton).

CHAPTER II

METHODS

Study Area and Data Collection

The study originally included six reservoirs and their nine major river tributaries in eastern Oklahoma (Figure 1). Study reservoirs included Kaw, Keystone, Oologah, Texoma, Eufaula and Tenkiller. These reservoirs each have one or two major river inflows through the system (Table 1). Grand Lake was added as a seventh reservoir before the start of the reservoir sampling. We sampled zooplankton from nine rivers in the spring and seven reservoirs in the summer to capture both the seasonal and spatial dynamics of zooplankton communities within self-sustaining, stocked, and future restoration systems (Figure 2).

Spring River Sampling

River zooplankton were collected once per month in April and May, 2020. We collected between one and four samples from each river, based on public land access to areas suitable for bank sampling. We used a submersible Danner Pondmaster Water Pump as a modified plankton pump, which produces higher yield in total taxa

collected and more accurate abundance data compared with other riverine sampling gear (Appel et al. 2019). We collected samples from the river bank by extending a 2.4 meter PVC pole into the river channel, with the plankton pump attached to the end and submerged at a depth of 1 meter. Water was pumped into 19 liter buckets through 1.3 cm diameter hosing attached to the outflow on the pump, for a total sample volume of 60 liters. We then filtered zooplankton samples through a 63 μm mesh Wisconsin Plankton Net, and preserved the samples with equal parts residual water and 95% ethanol.

We used a Secchi Disk (SD, cm) to measure water clarity at each river site. We also collected a 0.5 liter water sample in amber Nalgene bottles from a depth of 0.5 meters for later analysis of total phosphorus and chlorophyll *a* concentrations.

Summer Reservoir Sampling

Reservoir zooplankton were collected at each reservoir once per month from July – September 2020. Reservoirs with two river tributaries were treated as two separate entities that were sampled with separate transects (i.e., the Cimarron River arm and the Arkansas River arm at Keystone Lake; the Red River arm and the Washita River arm at Lake Texoma; the Canadian River arm and North Canadian River arm at Lake Eufaula). At each reservoir, zooplankton were collected from three to five sites based on accessibility. Zooplankton abundance in reservoirs are generally lower near the mouth of the river, peak in the upper third of the reservoir, and decline linearly toward the dam (Marzolf 1990). Therefore, we sampled zooplankton along a transect in the upper two-thirds of each reservoir (Figure 3). We delineated transects from the mouth of each river (nearest boat-accessible depth), to two-thirds the length toward the dam (Figure 3,

yellow). Five sample points were evenly spaced along the transect (Figure 3, black). Secondary transects were delineated perpendicular to the shoreline at each of the five points (Figure 3, red). A random number generator was used to determine a random location along these secondary transects to determine actual sample locations, omitting 100 meters closest to shore to minimize shallow locations. However, sampling along a transect was not possible at every site. Specifically, Oologah, Texoma, and Eufaula only had three sample locations within each river arm due to accessibility constraints.

We collected zooplankton samples at each reservoir site by conducting vertical tows using a 153 μm mesh Wisconsin Plankton Net for large zooplankton (cladocerans and copepods) and 63 μm mesh net for small zooplankton (rotifers and nauplii). Vertical plankton tows were collected approximately 1 meter from the lake bottom to the surface, pulling the net through the water at a rate of 1-meter per second. All reservoir zooplankton samples were preserved with equal parts residual water and 95% ethanol. Zooplankton samples from Grand Lake were collected by ODWC using the same sampling methods.

At each reservoir site we measured water clarity using a SD. Additionally, on the first and third sample data at each reservoir, we collected a 0.5 liter water sample in amber Nalgene bottles from a depth of 0.5 meters for later analysis of total phosphorus.

Zooplankton Enumeration

River zooplankton samples collected with the 63 μm mesh net and summer reservoir samples with the 153 μm net were identified and counted using subsampling based on methods adapted from Mack et al. (2012). We diluted samples to a known

volume and used a Hensen-Stemple pipette to take 1 mL sub samples. We transferred subsamples into a Bogorov counting chamber and counted zooplankton using a dissecting microscope until >250 individuals were counted. We identified cladocerans to species, or lowest taxonomic level possible, and copepods to genus using the online key *An Image-Based Key to the Zooplankton of North America* (www.cfb.unh.edu).

We used a Sedgewick-Rafter Counting Cell (with 1000 counting squares) to count rotifers and nauplii in the samples collected with the 63 μm mesh plankton net at higher magnification under a compound microscope. We diluted samples to a known volume and 1 mL subsamples were transferred into the counting slide. Using a random number generator, we selected three sets of three rows (180 squares) for enumeration of rotifers and nauplii. We counted groups of three rows until ≥ 50 rotifers were reached.

Zooplankton length measurements are not standardized across the literature and various measurements have been used for different taxa. As juvenile paddlefish select for larger zooplankton and filter feeding paddlefish typically have low abundance of small zooplankton (rotifers and nauplii) in their diet, we measured only large zooplankton (cladocerans and copepods). We measured carapace length (mm) for all large zooplankton taxa (Culver et al. 1985, Sakamoto et al. 2007, Basińska et al. 2014, Duckworth et al. 2019) (Figures 4, 5), grouping them into cladocerans and copepods. We imaged zooplankton using an Olympus SZX2 Stereomicroscope at 4x magnification. A maximum of 50 zooplankton were measured from each sample, however, all zooplankton were measured in samples, which contained fewer than 50 individuals. Length measurements were determined by uploading imagery into ImageJ and calibrating length

measurements using a scale bar on each image (Abràmoff et al. 2004, Schneider et al. 2012).

Total Phosphorus and Chlorophyll a

Surface water samples were frozen after collection and analyzed for total phosphorus at a later date. We analyzed total phosphorus on whole water samples following digestion with potassium persulfate ($K_2S_2O_8$) using a Thermo Scientific Genesys 20 spectrophotometer (APHA 2005).

We analyzed chlorophyll *a* using acidification methods (APHA 2005). We extracted chlorophyll *a* using vacuum filtration within 24-hours of collecting water samples at each site onto Whatman 47mm Glass Microfiber filters (GF/F). The filters were wrapped in aluminum foil and stored at $-20^{\circ}C$ until processing. We placed filters in 90% methanol (10% saturated $MgCO_3$) to extract the chlorophyll *a* for approximately 20 hours in the dark at $4^{\circ}C$. We then determined the concentration of chlorophyll *a* with a Turner Trilogy Fluorometer before and after acidification.

Statistical Analysis

Zooplankton and water quality variables from the river samples were pooled across sample months and analyzed using a general linear model (function “lm”) to test for differences in response variable among rivers. Zooplankton taxa abundances and water quality variables were log-transformed to meet the assumption of normality. Tukey’s post-hoc analysis was used to make pairwise comparisons among rivers.

Summer reservoir zooplankton and water quality variables were pooled across sample months and analyzed using a general linear model (“lmer” package, function “lmer”) to test for differences in response variables (zooplankton taxa abundances, taxa lengths, and water quality variables) among reservoir arms. Individual sample locations within each reservoir arm (station) were included in the model as a random factor to identify the object that was repeatedly measured. Summer reservoir zooplankton taxa abundances and water quality parameters were log-transformed to meet the assumption of normality. We used Tukey’s post-hoc analysis to make pairwise comparisons of response variables that had a significant ($p < 0.05$) effect of reservoir arm (“emmeans” package). All analyses were completed using R Studio version 3.6.2 (RStudio Team 2021).

CHAPTER III

RESULTS

Spring – River

Zooplankton abundance and size composition varied within and among rivers. River zooplankton communities were comprised mainly of small zooplankton (rotifers and nauplii) and characterized by a low overall abundance of large zooplankton taxa. Water quality parameters were variable within and among rivers sampled. Chlorophyll *a* was higher in all rivers flowing into Kaw and Keystone (self-sustaining systems) compared with other rivers. Water clarity (SDD) was higher at rivers with self-sustaining paddlefish populations, compared with rivers that have failed to establish (Red and Washita) or are under evaluation (Canadian and North Canadian).

River zooplankton communities were dominated (> 75%) by small zooplankton (rotifers and nauplii; Figure 6). The Arkansas River above Keystone Lake (self-sustaining) had the highest proportion of large zooplankton (cladocerans and copepods), accounting for over 20% of all zooplankton present (small and large). All other rivers had proportions of large zooplankton $\leq 10\%$ (Figure 6).

Large zooplankton median abundance in rivers was low, ≤ 11 per liter, and different among river sites ($F_{8,52} = 16.037$, $p < 0.001$; Figure 7). Rivers with no evidence of natural reproduction (Red, Washita, Canadian, and North Canadian) generally had higher abundance of large zooplankton than rivers with self-sustaining paddlefish populations (Arkansas, Cimarron and Verdigris). Copepods dominated the large zooplankton (copepods and cladoceran) assemblage across all rivers (56%), followed by *Bosmina longirostris* (21%) and *Daphnia* spp. (11%).

Rotifer abundance was variable within and among rivers sampled ($F_{8,52} = 14.287$, $p < 0.001$; Figure 8). Rotifer abundance was generally higher at rivers that were stocked and have failed (Red and Washita) or are under evaluation (Canadian and North Canadian). Median rotifer abundance at rivers with naturally reproducing paddlefish populations ranged from 3 – 41 per liter, rivers that were stocked but have no natural reproduction ranged from 50 to 100 per liter and 4 per liter at the Illinois River.

Zooplankton carapace length were different between taxa and among rivers. However, both median copepod ($F_{8,51} = 2.395$, $p = 0.028$; Figure 9) and cladoceran carapace lengths ($F_{8,49} = 1.585$, $p = 0.154$; Figure 10) range from 0.27 to 0.41 mm. Cladoceran carapace length was generally higher in rivers with self-sustaining paddlefish populations, while there were no trends among rivers for copepod carapace length.

Water quality parameters were also variable within and among rivers (Table 2). All rivers with self-sustaining paddlefish populations had generally higher median water clarity (SD, cm) than rivers that have failed to establish (Red and Washita) or are currently under evaluation (Canadian and North Canadian) ($F_{8,51} = 40.314$, $p < 0.001$; Figure 11). Median water clarity for self-sustaining rivers ranged from 28 to 37 cm, 10 to

17 cm at rivers that do not have self-sustaining populations, and 200 cm at the Illinois River. Rivers with self-sustaining paddlefish populations had higher chlorophyll *a*, with the exception of the Verdigris, than all rivers without self-sustaining paddlefish populations ($F_{8,53} = 32.154$, $p < 0.001$; Figure 12). Total phosphorus concentration was variable among rivers, with both the Verdigris and Illinois Rivers having median concentrations $\leq 59 \mu\text{g/L}$, and all other rivers $\geq 106 \mu\text{g/L}$ ($F_{8,53} = 19.241$, $p < 0.001$; Figure 13).

Summer – Reservoir

Summer zooplankton abundances and water quality variables generally differed among reservoirs with and without self-sustaining paddlefish populations. Reservoirs with self-sustaining paddlefish populations generally had higher abundances of all zooplankton taxa including total zooplankton, copepods, cladocerans, rotifers and/or nauplii. Furthermore, zooplankton community structure in self-sustaining systems tended to have higher proportions of cladocerans and copepods than failed (Texoma) restoration or reservoirs that are currently being evaluated (Eufaula and Tenkiller). Reservoirs with self-sustaining paddlefish populations also tended to have higher total phosphorus concentrations and lower water clarity (Table 3).

Reservoirs, similar to rivers, were dominated by small zooplankton (rotifers and nauplii), accounting for $> 80\%$ of all zooplankton among all reservoir arms (Figure 14). Reservoirs with self-sustaining paddlefish populations generally had a greater proportion of large zooplankton (cladocerans and copepods) compared with not self-sustaining populations.

Large zooplankton abundance (cladocerans and copepods) was generally higher at reservoirs with self-sustaining paddlefish populations ($F_{9,30} = 7.356$, $p < 0.001$; Figure 15). At reservoirs with self-sustaining paddlefish populations, cladocerans range from 49 to 70% of all large zooplankton, compared with 31 to 70% at reservoirs without self-sustaining populations. Kaw Lake had significantly higher large zooplankton abundance than Grand, both the Red and Washita arms of Texoma (failed), and Tenkiller Lakes.

Reservoirs with self-sustaining paddlefish populations had generally higher abundance of copepods ($F_{9,30} = 2.904$, $p = 0.014$; Figure 16). There was much greater variability in copepod abundance among self-sustaining reservoirs, which ranged from 1 to 50 individuals per liter, while sites without self-sustaining populations ranged from < 1 to 19 copepods per liter. Across all reservoir sites, copepods accounted for 29 to 70% of all large zooplankton. Cyclopid copepods were the most abundant, accounting for an average of 76% of all copepods across all reservoir arms. Calanoid copepods accounted for an average of 16% and 8% Harpacticoid copepods across all reservoir arms.

Reservoirs with self-sustaining paddlefish populations generally had higher median cladoceran abundance ($F_{9,29} = 13.284$, $p < 0.001$; Figure 17). Lakes with self-sustaining populations of paddlefish had a median cladoceran abundance of 18 individuals per liter, while those lakes without self-sustaining populations had a median abundance of 3 cladocerans per liter.

The abundance of *Daphnia* spp. was generally low with a median less than 10 per liter among all reservoir arms ($F_{9,32} = 4.802$, $p < 0.001$; Figure 18). Kaw Lake had the highest median *Daphnia* abundance, 6 per liter, while all other self-sustaining reservoirs had < 5 per liter. Among reservoirs without self-sustaining populations, *Daphnia*

abundance was ≤ 2 per liter, with the exception of Lake Eufaula, which had 7 and 3 per liter in the Canadian and N. Canadian arms respectively. The most common and abundant species of *Daphnia* found across all reservoirs included *D. parvula*, *D. retrocurva*, and *D. lumholtzi*. The *Daphnia* spp. made up an average of 12.7% of all large zooplankton within samples among all reservoirs. Additionally, *D. lumholtzi* was collected within all reservoir arms, but present at relatively low densities.

The reservoirs with the highest median *Diaphanosoma* abundances all had self-sustaining populations of paddlefish, with the exception of Grand Lake ($F_{9,29} = 12.857$, $p < 0.001$; Figure 19). Kaw, both the Arkansas and Cimarron arms of Keystone, and Oologah Lakes had median *Diaphanosoma* abundances of 24, 12.5, 6, and 10 individuals per liter respectively. Lakes without self-sustaining populations of paddlefish, as well as Grand Lake all had median *Diaphanosoma* abundances of ≤ 3 individuals per liter. Additionally, *Diaphanosoma* spp. accounted for approximately 28.7% of all large zooplankton across all reservoirs sampled.

Rotifer abundance was high and variable both within and among reservoirs ($F_{9,29} = 3.551$, $p = 0.004$; Figure 20). Reservoirs with self-sustaining paddlefish populations had higher variability than reservoirs without, ranging from 77 – 1234 and 19 – 114 per liter respectively.

Large zooplankton (copepods and cladocerans) carapace lengths were variable among reservoirs. However, all individuals across all sites were all ≥ 0.25 mm, with the exception of one outlier at Tenkiller Lake. Copepods were significantly different among reservoirs ($F_{9,33} = 8.390$, $p < 0.001$; Figure 21). Median copepod length was .48 mm at Kaw Lake, significantly greater than all sites except for Oologah and the Canadian arm of

Eufaula. Cladocerans were not significantly different among reservoirs ($F_{9,30} = 1.152$, $p = 0.359$; Figure 22).

Total phosphorus concentration was higher in both Kaw and Keystone (both Arkansas and Cimarron arms) Lakes than all other reservoirs ($F_{8,26} = 12.851$, $p < 0.001$; Figure 23). Median total phosphorus at Kaw and Keystone was $\geq 100 \mu\text{g/L}$, and $\leq 73 \mu\text{g/L}$ among all reservoirs without self-sustaining paddlefish populations and Oologah Lake.

Water clarity (Secchi Disk Depth) was lower at Kaw and Keystone (both Arkansas and Cimarron arms) Lakes than all other reservoir sites ($F_{8,26} = 3.675$, $p = 0.005$; Figure 24). Median water clarity ranged from 55 to 66 cm at Kaw and Keystone, while all other reservoirs ranged from 59 to 120 cm, with the exception of Tenkiller Lake, which had a median SD of 150 cm.

CHAPTER IV

DISCUSSION

Larval paddlefish hatch in rivers upstream of reservoirs and utilize nutrients in their yolk sac (Russell 1986). As they mature and drift down stream, their mouthparts become developed enough to begin selectively feeding on large zooplankton (Ruelle and Hudson 1977, Unkenholz 1977, Michaletz et al. 1982). Juvenile paddlefish continue moving downstream toward the impounded reservoir, and once their gill rakers sufficiently developed, they filter feed to consume zooplankton (Coker 1923, Eddy and Simer 1929, Ruelle and Hudson 1977, Rosen and Hales 1981).

We found that zooplankton abundance at river sites was generally low and dominated by small zooplankton (rotifers and nauplii). Discharge was variable between sampling dates (April and May) and among rivers. Studies have demonstrated inverse relationships between zooplankton abundance and river discharge (Pace et al. 1992, Thorp et al. 1994, Wahl et al. 2008). Water quality variables (SDD, chlorophyll *a*, and TP) differed among rivers, where rivers with self-sustaining paddlefish populations had higher water clarity (SDD) than all other rivers, except for the Illinois.

Trends in zooplankton and water quality among rivers sampled in spring were less clear than the patterns observed in reservoirs. However, our findings from water quality samples from rivers suggest that water clarity (SDD) may affect the juvenile paddlefish feeding efficiency. Juvenile paddlefish selectively feed on large zooplankton (Ruelle and Hudson 1977, Unkenholz 1977, Michaletz et al. 1982). Higher turbidity, thus lower water clarity, has been demonstrated to adversely affect visual feeding of some fish species (Vinyard and O'brien 1976, Rowe and Dean 1998, Shoup and Wahl 2009). Rivers flowing into Texoma (failed) and Eufaula (under evaluation) had lower water clarity, which may make it difficult for juveniles to find food. While zooplankton abundance in rivers was low, it was generally higher in rivers (Red and Washita of Texoma; and Canadian and North Canadian of Eufaula) flowing into reservoirs without self-sustaining paddlefish populations (Texoma and Eufaula). This may suggest that while there is higher abundance of large zooplankton, water clarity could impact juvenile paddlefish ability to find prey items. Additional studies are needed to determine how turbidity affects the feeding rate of juvenile paddlefish under variable turbid conditions.

In upriver habitat during spring sampling, we found that overall zooplankton abundance was generally low and dominated by small zooplankton. Rotifers and copepod nauplii together make up an average of 92% of all zooplankton collected across all rivers. Previous studies have also found that rivers are dominated in early spring by small zooplankton, sometimes making up > 90% of the entire community (Pillard and Anderson 1993; Thorp et al. 1994). Our study focused on sampling near the river banks. Thorp et al. (1994) found that copepod and cladoceran abundance was higher near the banks of the Ohio River. However, Pillard and Anderson (1993) found greater

abundance of these larger zooplankton in the main river channel of the Mississippi River. Therefore, our study may not have captured variability in abundance and proportion of large zooplankton that exists throughout the stream channel. This variability in riverine zooplankton communities warrants further evaluation to determine more accurate zooplankton availability for paddlefish.

While it is important to understand how zooplankton communities are distributed in the riverine systems, it is also important to consider habitat use by juvenile paddlefish. Although habitat use by larval and juvenile age-0 paddlefish in Oklahoma is limited, researchers have identified possible additional areas to evaluate in other river systems (Fredericks and Scarnecchia 1997, Hoxmeier and DeVries 1997, Roush et al. 2003, Barry et al. 2007). For example, Hoxmeier and DeVries (1997) found significantly greater zooplankton abundances in oxbow lakes than both the main channel and backwater habitats on the Alabama River in early summer, both of which are used by juvenile paddlefish. Additionally, Dzialowski et al. (2012) found zooplankton were more abundant in slower moving waters in the lower Missouri River, which may be of use to juvenile paddlefish. Our study only focused on the banks of the main channel and may not be representative of all habitat types utilized by juvenile paddlefish. Further riverine studies of zooplankton should focus on different habitat types (backwater, side channels, minor tributaries, etc.) to assess all zooplankton abundances that may be available to juvenile paddlefish.

Paddlefish may migrate 20 – 100 km upstream to spawn in other systems (Lein and Devries 1998, Paukert and Fisher 2001b, Firehammer and Scarnecchia 2007). Once they hatch, age-0 paddlefish migrate from the riverine zone, down to the reservoir areas,

which presumably have higher food concentration (Kozfkay and Scarnecchia 2002, Scarnecchia et al. 2009). Additionally, it was found that age class strength of juvenile paddlefish was positively associated with higher water levels in reservoirs and associated higher zooplankton abundances (Kozfkay and Scarnecchia 2002, Scarnecchia et al. 2009). In Oklahoma, identifying areas in which paddlefish spawn, how far upstream they may travel in various systems, and a subsequent understanding of how quickly age-0 paddlefish move from riverine habitat to reservoir habitat, may be another important factor in evaluation efficacy of restoration efforts. With how variable paddlefish populations are among different river systems, a deeper understanding of paddlefish in Oklahoma rivers is imperative. This may better align our understanding of food resources during the time in which they use specific habitat types. It may also help us better understand if the river conditions are important or if reservoir conditions are more important in outcome of paddlefish recovery efforts.

Rivers with self-sustaining paddlefish populations tended to have higher chlorophyll *a*, while water clarity was higher in these rivers except for the Illinois River. Trends in total phosphorus were variable both among months and rivers sampled and there was no clear differences in trends among rivers with self-sustaining and those without self-sustaining paddlefish populations. Spring river sampling coincided with months of higher average precipitation and increased release of water from upstream dams. Hypolimnetic and epilimnetic release of water from upstream dams can impact the dissolved oxygen, nutrient content, and primary productivity. Additionally, land use differences within each river system could also influence amounts and types of nutrient runoff and may impact seasonal fluctuations in total phosphorus. These impacts are

important to understand because zooplankton communities, and thus paddlefish, will be affected by changes in nutrients. More research needs to be done to further evaluate these differences among water quality among rivers with self-sustaining and non-self-sustaining paddlefish populations.

Summer zooplankton abundances and water quality variables generally differed among reservoirs with and without self-sustaining paddlefish populations. Our findings suggest abundance of large zooplankton (cladocerans and copepods) and community structure in reservoirs may influence paddlefish populations. Reservoirs with self-sustaining paddlefish populations generally had a greater total abundance of large zooplankton (copepods and cladocerans) compared with non-self-sustaining reservoirs. Within cladocerans, both *Daphnia* and *Diaphanosoma* spp., which were the most abundant cladoceran taxa, were generally more abundant in self-sustaining reservoirs than reservoirs without self-sustaining populations, with the exception of Grand Lake. Additionally, although we found that all reservoir zooplankton communities consisted of > 80% rotifers and nauplii, reservoirs with self-sustaining paddlefish populations generally had a greater proportion of large zooplankton (copepods and cladocerans) within the zooplankton community structure compared to non-self-sustaining reservoirs. Studies have shown that paddlefish stomach content analysis generally have low abundances or complete absence of small zooplankton (rotifers and copepod nauplii), instead consisting of larger zooplankton, cladocerans and copepods (Rosen and Hales 1981; Hoxmeier and DeVries 1997; A. Nealis, J. Long, and C. Park, unpublished data). When adults, this may be due to the size of their gill rakers and the ability of smaller zooplankton to pass through uncaptured; when juveniles, this may be due to size selective

feeding (Moore and Cotner 1998). Our results highlight the potential importance of both abundance and proportion of large zooplankton as a major food resource for paddlefish and emphasize their role in restoration efforts.

Among reservoirs, the lengths of large zooplankton (copepod and cladoceran) were similar and always larger than the size threshold of filter feeding paddlefish based on their gill raker measurements (0.04 – 0.09 mm). Rosen and Hales (1981) found that zooplankton < 0.20 - 0.25 mm were virtually absent from paddlefish stomachs. The median copepod and cladoceran lengths in our study were 0.38 and 0.43 mm respectively among all reservoir sites. A study of zooplankton availability in Livingston Reservoir, TX, where paddlefish have been stocked and currently inhabit, found median body lengths of 0.48 and 0.44 mm for copepods and cladocerans respectively (Moore and Cotner 1998). Zooplankton body size measurement in comparison to paddlefish gill rakers suggests that variation in zooplankton size structure within specific taxa (both cladoceran and copepod) is not a major factor influencing the outcome of restoration efforts. Instead, community structure and total abundance of large zooplankton may play a larger role in these outcomes.

Lake Texoma paddlefish restoration efforts have been classified as a failure and the reservoir had relatively low zooplankton abundance. Some paddlefish, which were previously stocked in Lake Texoma, have been able to survive. However, they have not been classified as a self-sustaining population because there is no documented evidence of reproduction after stocking efforts concluded in 2007 (J. Schooley, Oklahoma Department of Wildlife Conservation, personal communication). The reason for survival without successful recruitment may be due to a variety of factors, such as lack of

spawning habitat. However, it is worth noting that there was a lower abundance and relative proportion of large zooplankton (cladocerans and copepods) that may be insufficient to support a large paddlefish population. Texoma had lower zooplankton abundance than self-sustaining reservoirs and we found that the Red River arm of Texoma was dominated by rotifers. Additionally, there was a higher overall abundance of zooplankton in the Red River arm compared to the Washita arm. These findings are supported by Atkinson et al. (1999), who also found that zooplankton densities were higher in the Red River arm. This may provide evidence for why Patterson (2005) found that paddlefish favor the Red River arm of Texoma. We found > 69% of zooplankton (not including rotifers) in Lake Texoma were copepod nauplii, similar to the results of Lienesch & Matthews (2000), who found that copepod nauplii made up > 70% of the zooplankton community. This means low overall abundance of large zooplankton, coupled with lower proportion of these taxa, may have contributed to the unsuccessful paddlefish recruitment in the Lake Texoma restoration efforts.

Lake Eufaula is currently under evaluation as stocking was completed in 2017. We found higher average total zooplankton abundances (including rotifers) at Lake Eufaula with approximately 219/L, compared with Canfield & Jones (1996) who previously reported 70/L. Lake Eufaula had higher total abundance of large zooplankton (cladocerans and copepods) than Lake Texoma. Additionally, both the Canadian and North Canadian arms of Eufaula had higher total abundances of large zooplankton than the Cimarron arm of Keystone and Grand Lake, both of which are self-sustaining populations. Therefore, there may be enough large zooplankton within these reservoirs to support existing paddlefish, but other factors, such as spawning habitat or survival of

juveniles and subsequent recruitment, may limit their ability to become a self-sustaining population.

Reservoirs with self-sustaining paddlefish populations had higher total phosphorus concentration and lower overall Secchi disk depth (SDD). Reservoirs that are not phosphorus limited may have an advantage as it could allow large zooplankton to be more abundant and available to paddlefish. Phosphorus is often a limiting nutrient in aquatic systems and can be estimated from Redfield Ratios, which is a ratio of total nitrogen and total phosphorous (Dodds and Whiles 2010). If the Redfield Ratio is greater than 16:1, the aquatic system is considered to be phosphorous limited. However, if the ratio is less than 16:1, the aquatic system is considered to be nitrogen limiting. Oklahoma Water Resource Board (OWRB 2021) water quality sampling shows that reservoirs with self-sustaining paddlefish populations generally have lower Redfield Ratios (Kaw 7:1, Keystone 6:1, Oologah 8:1, Grand 13:1) than lakes that have failed (Texoma 21:1) or are being considered (Tenkiller 31:1), suggesting that the availability of phosphorus may play a role in governing zooplankton abundances. Lake Eufaula is currently being evaluated and has a Redfield ratio of 7:1, similar to reservoirs with self-sustaining populations. Pace's (1986) study of multiple lakes demonstrated a strong positive relationship between total phosphorus concentration and biomass of both large and small zooplankton. Additionally, Yurk and Ney (1989) found a strong correlation between lake total phosphorus and planktivore biomass. These studies suggest a positive correlation between phosphorus and zooplankton abundance, which parallels our findings. A more detailed analysis of lake water quality, nutrient concentrations and seasonal relationships

to overall plankton biomass should be conducted to better understand their impact on paddlefish food resources.

Future Studies

Food webs in reservoirs are complex and can vary among reservoirs. Given this complexity, it may be necessary to examine intraspecific competitive interactions and evaluate habitat and dietary overlap with paddlefish. The introduction of bigheaded carp within some of the study reservoirs, plus competition from other planktivores could further alter zooplankton community dynamics and shift the size structure of plankton to favoring small individuals that are better able to avoid predation (Brooks and Dodson 1965). Grand Lake is the only study site with Asian carp present that also has a self-sustaining paddlefish population. Of all self-sustaining reservoirs, total large zooplankton abundance is lowest at Grand Lake, which may be affected by feeding of these non-native carp planktivores. Future studies should conduct a more extensive analysis of food web dynamics, potentially utilizing a bioenergetics modeling approach to understanding inter- and intraspecific competition/predation. Similar to the bioenergetics model Moore and Cotner (1998) employed with paddlefish in Texas, this could be used to estimate the minimum, average, and maximum theoretical capacity of paddlefish in various Oklahoma reservoirs. These models could be further improved through further research on water quality and lipid content analysis of zooplankton within Oklahoma reservoirs to better understand the quality of zooplankton resources among Oklahoma reservoirs.

A better understanding of riverine zooplankton as it corresponds with early life history of juvenile paddlefish is needed. In other river systems, paddlefish may migrate

20 – 100 km, or more upstream to spawn (Lein and Devries 1998, Paukert and Fisher 2001b, Firehammer et al. 2006, Firehammer and Scarnecchia 2007). Currently, spawning areas and habitat use by age-0 paddlefish in Oklahoma is relatively unknown across all sites where natural reproduction occurs. A deeper understanding of the early growth and development of juvenile paddlefish in Oklahoma rivers could be critical in gaining a comprehensive picture of paddlefish restoration and management efforts.

We collected zooplankton from rivers once in April and May when flows are extremely variable within and among rivers. Further studies should focus on more intensive sampling within and among rivers to better understand the relationship between river flows, water quality variables and overall zooplankton abundances.

Lastly, additional studies are needed to assess the effects of turbidity, and thus water clarity, on feeding efficiency of juvenile paddlefish. It is conceivable that zooplankton abundance could be sufficient within river systems and that decreased water clarity could impact the ability of juvenile paddlefish to visually detect and capture prey.

Conclusions and Management Implications

We found that reservoirs with self-sustaining paddlefish populations generally had higher abundances of total zooplankton and large (cladoceran and copepods) zooplankton, in addition to generally higher proportions of large zooplankton within the overall zooplankton community structure. Reservoirs with self-sustaining paddlefish populations also had higher total phosphorus (nutrients) and had higher productivity. More intensive sampling and follow up research should be done in riverine systems to

better understand spatial and temporal dynamics and their impact on zooplankton abundance and community structure, as well as water quality variables.

Oklahoma Department of Wildlife Conservation (ODWC) is considering Tenkiller Lake as a site for potential future reintroduction of paddlefish. Considering zooplankton as a lone metric for success, Tenkiller Lake appears unlikely to succeed as there is a low overall abundance of all zooplankton taxa, low proportion of large zooplankton (copepods and cladocerans), and lower productivity (chlorophyll, TP, and higher water clarity). However, additional environmental characteristics that contribute to the overall success of paddlefish need to be evaluated. Modeling theoretical carrying capacities among various reservoirs could be a useful tool in predicting restoration outcome and stocking goals.

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Table 1. Study reservoirs and their major river tributaries grouped by paddlefish population status.

* = summer 2020 reservoir zooplankton collected by ODWC.

† = no data were collected from these locations.

Reservoir	Major River Tributaries	Paddlefish Status	Paddlefish Stocked	Surface Area (ha)	Mean Depth (m)	Max Depth (m)
Kaw	Arkansas	Self-sustaining	1991 - 1994	6,880	7.9	22.9
Keystone	Arkansas, Cimarron	Self-sustaining	NA	9,600	7.6	23.2
Oologah	Verdigris	Self-sustaining	1995 - 2000	11,940	5.4	26.8
Grand*	Neosho†, Spring†	Self-sustaining	NA	18,800	11.0	42.7
Texoma	Red, Washita	Failed	1997 - 2007	36,000	9.3	30.0
Eufaula	Canadian, N. Canadian	Under evaluation	2008 - 2017	102,000	6.8	26.5
Tenkiller	Illinois	Future restoration	NA	5,200	15.5	42.1

Table 2. Summary of spring 2020 river water quality parameters (mean \pm standard error) averaged from both April and May sampling.

River	Total Phosphorus ($\mu\text{g/L}$)	Chlorophyll <i>a</i> ($\mu\text{g/L}$)	Secchi Disk Depth (cm)
Arkansas (Kaw)	182.50 \pm 10.52	49.94 \pm 4.46	26.40 \pm 4.53
Arkansas (Keystone)	101.98 \pm 5.48	34.22 \pm 1.26	35.63 \pm 1.27
Cimarron	155.50 \pm 9.89	58.68 \pm 3.63	34.75 \pm 4.59
Verdigris	57.55 \pm 0.75	8.15 \pm 2.64	34.00 \pm 2.58
Red	158.58 \pm 3.04	31.11 \pm 3.28	11.80 \pm 3.28
Washita	126.21 \pm 3.28	19.27 \pm 2.00	11.38 \pm 2.06
Canadian	124.86 \pm 11.70	21.31 \pm 2.75	11.00 \pm 3.00
N. Canadian	171.98 \pm 4.64	35.90 \pm 0.51	9.25 \pm 0.49
Illinois	35.05 \pm 0.30	2.88 \pm 12.39	184.88 \pm 12.40

Table 3. Summary of summer 2020 reservoir water quality parameters (mean \pm standard error) averaged across sampling dates.

Reservoir Arm	Total Phosphorus ($\mu\text{g/L}$)	Secchi Disk Depth (cm)
Kaw	208.72 \pm 10.88	53.47 \pm 1.99
Keystone (Arkansas)	171.75 \pm 5.18	54.93 \pm 1.38
Keystone (Cimarron)	116.01 \pm 6.13	61.13 \pm 1.51
Oologah	54.87 \pm 2.01	128.22 \pm 4.40
Texoma (Red)	57.72 \pm 3.46	92.25 \pm 4.85
Texoma (Washita)	39.04 \pm 2.50	113.25 \pm 5.08
Eufaula (Canadian)	57.99 \pm 6.71	105.44 \pm 5.10
Eufaula (N. Canadian)	69.33 \pm 6.80	78.71 \pm 6.45
Tenkiller	35.45 \pm 1.66	151.07 \pm 3.60

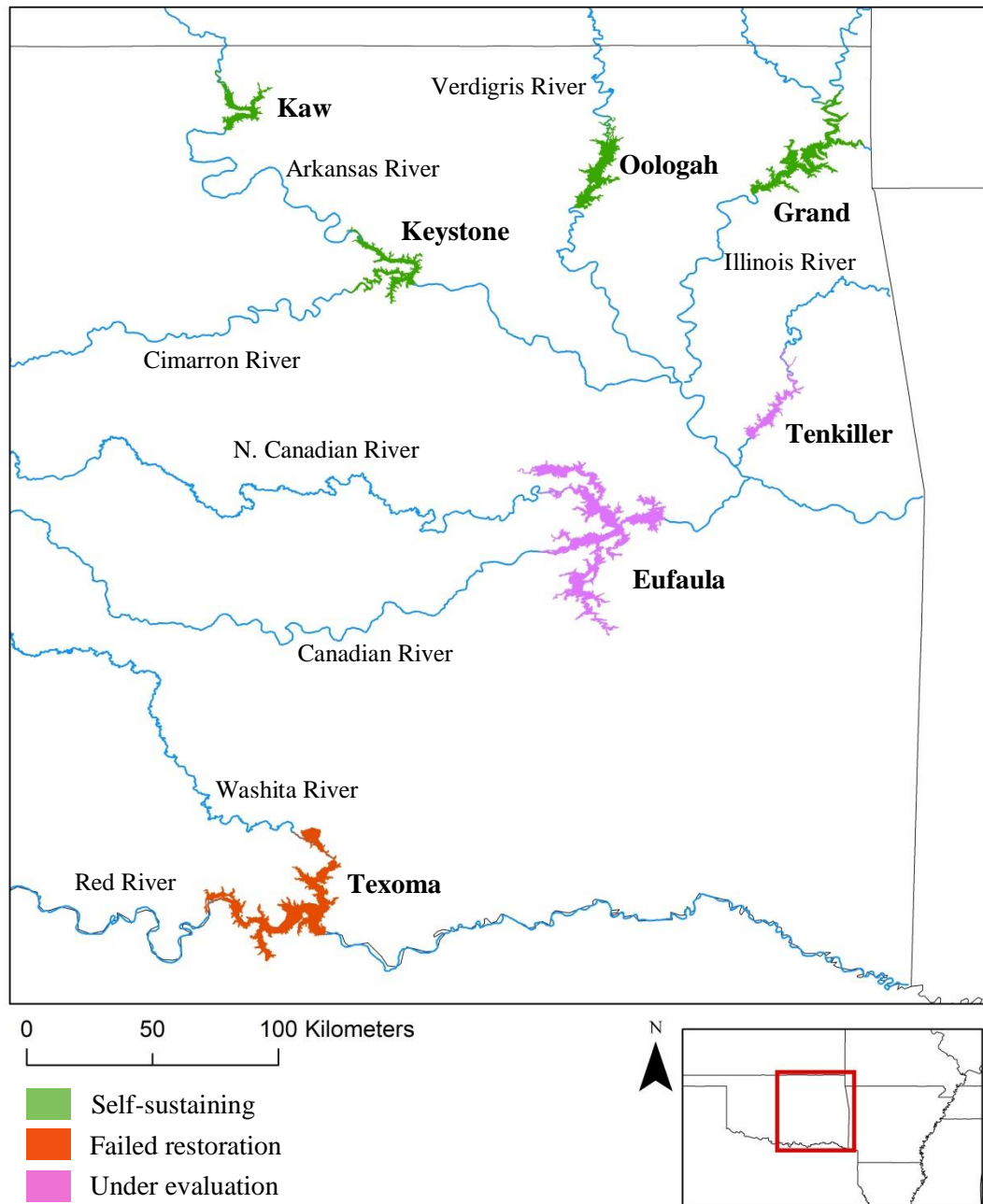


Figure 1. Study sites in Eastern Oklahoma and their corresponding paddlefish population status. Reservoirs are classified as self-sustaining, with documented reproduction (green), failed restoration (orange), and sites currently under evaluation (purple).

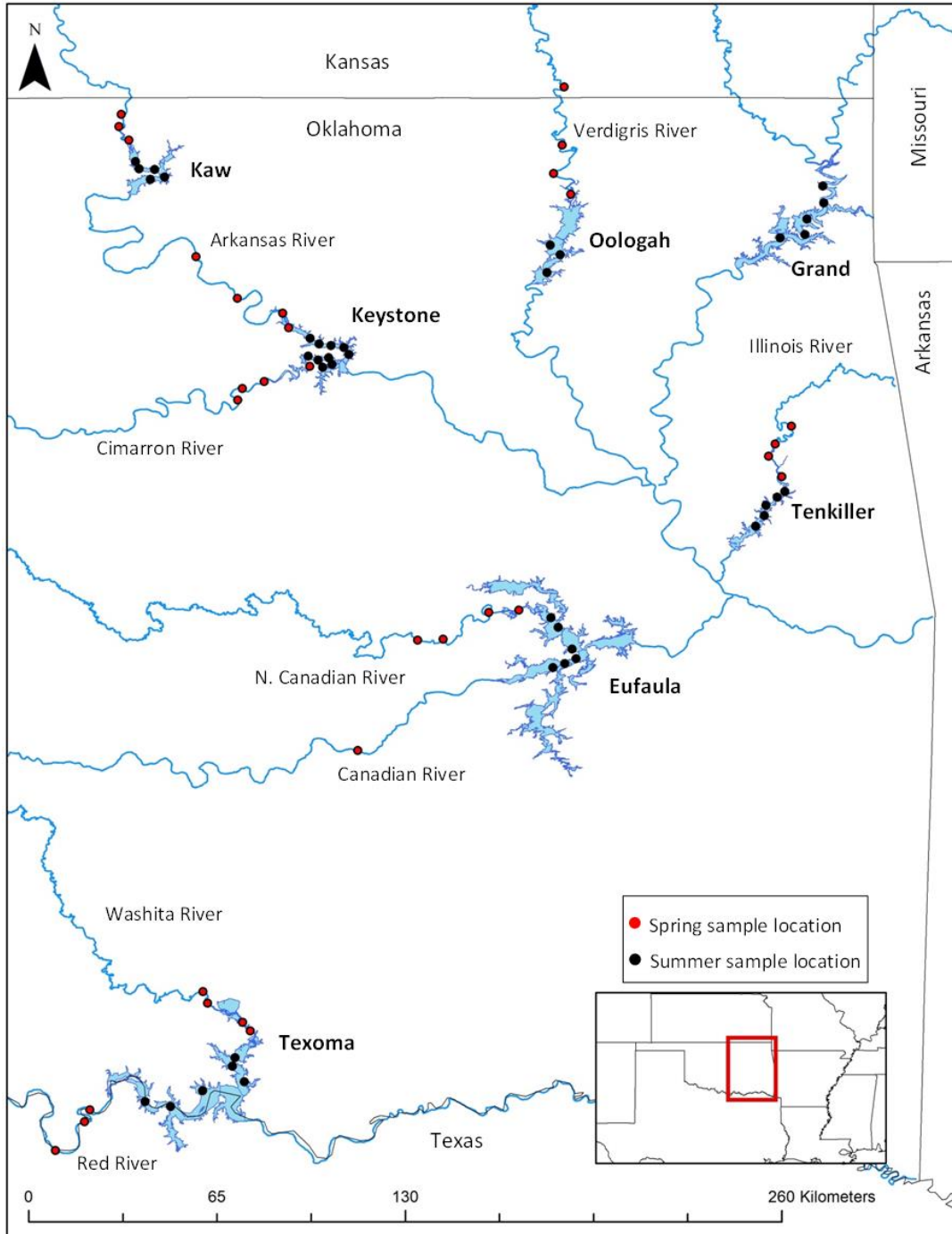


Figure 2. Location of all spring river (red) and summer reservoir (black) sample sites in 2020.

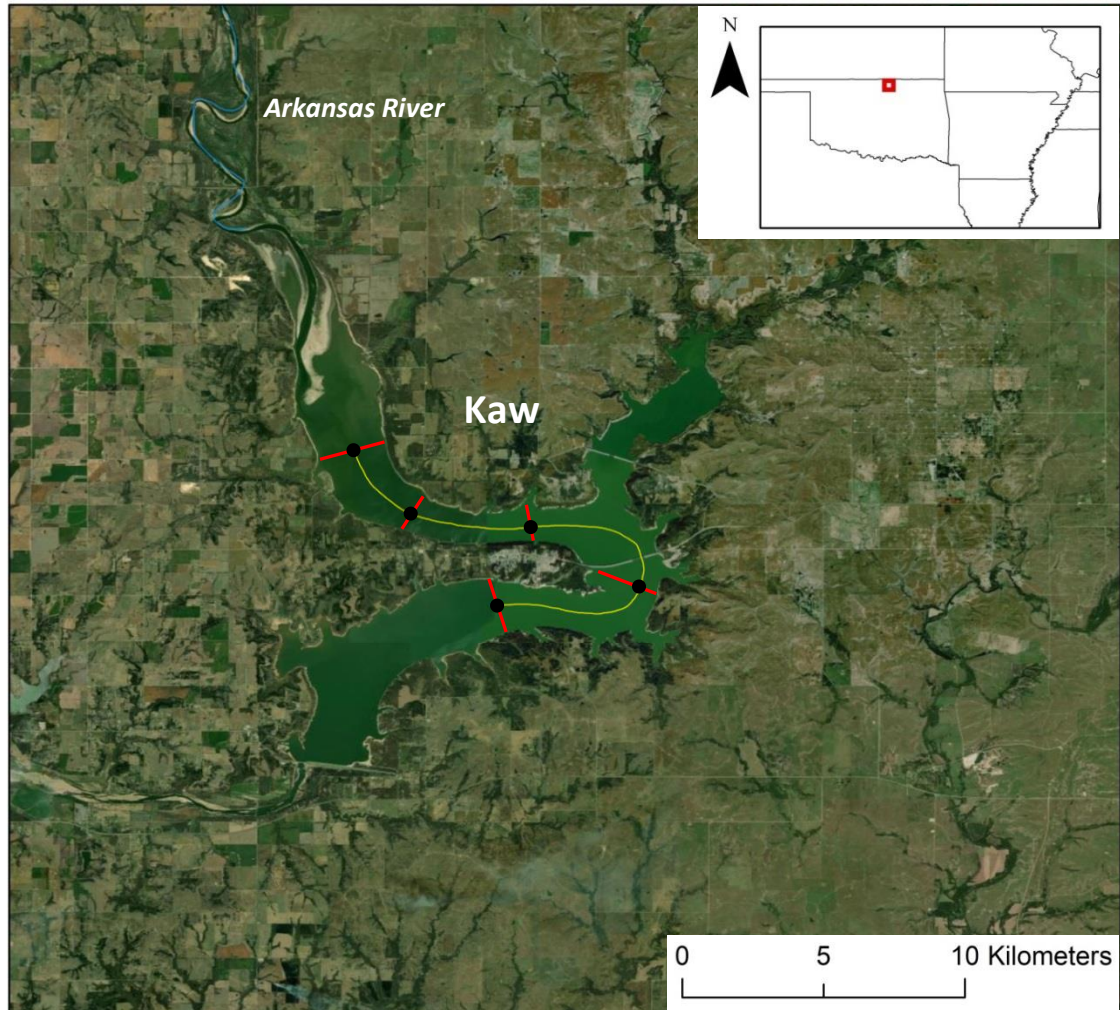


Figure 3. Example of reservoir transect delineation for selection of summer sample locations. A two-thirds transect was delineated from the river mouth or nearest depth accessible location toward the dam (yellow). Five points were evenly spaced along the transect (black) and secondary transects were delineated from bank to bank (red). Using the distance across the secondary transect, a random number was selected, which represented the actual sample location.



Figure 4. Example of carapace measurements on various Cladocera taxa, a.) *D. lumholtzi*, b.) *D. parvula*, c.) *Bosmina longirostris*, d.) Chydoridae sp. E.) *Diaphanosoma* sp., and f.) *Ceriodaphnia* sp. The yellow bar represents the plane of each taxa that was measured.

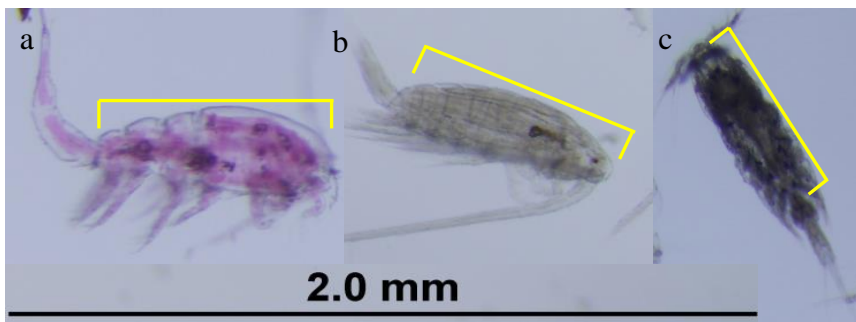


Figure 5. Example of carapace measurements on various Copepoda taxa, a) Cyclopoida, b) Calanoida, and c) Harpacticoida. The yellow bar represents the plane of each taxa that was measured.

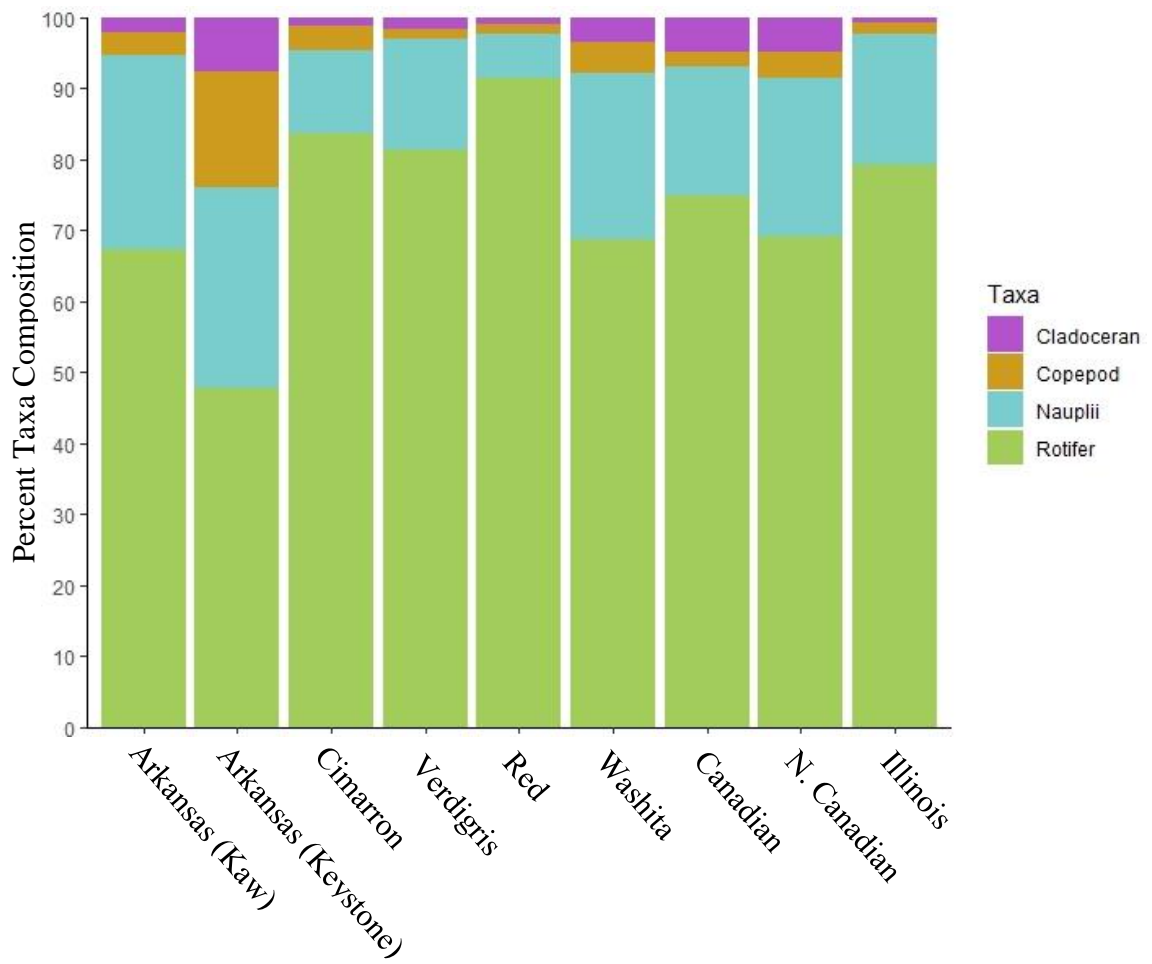


Figure 6. Total zooplankton community composition among all rivers, spring 2020.

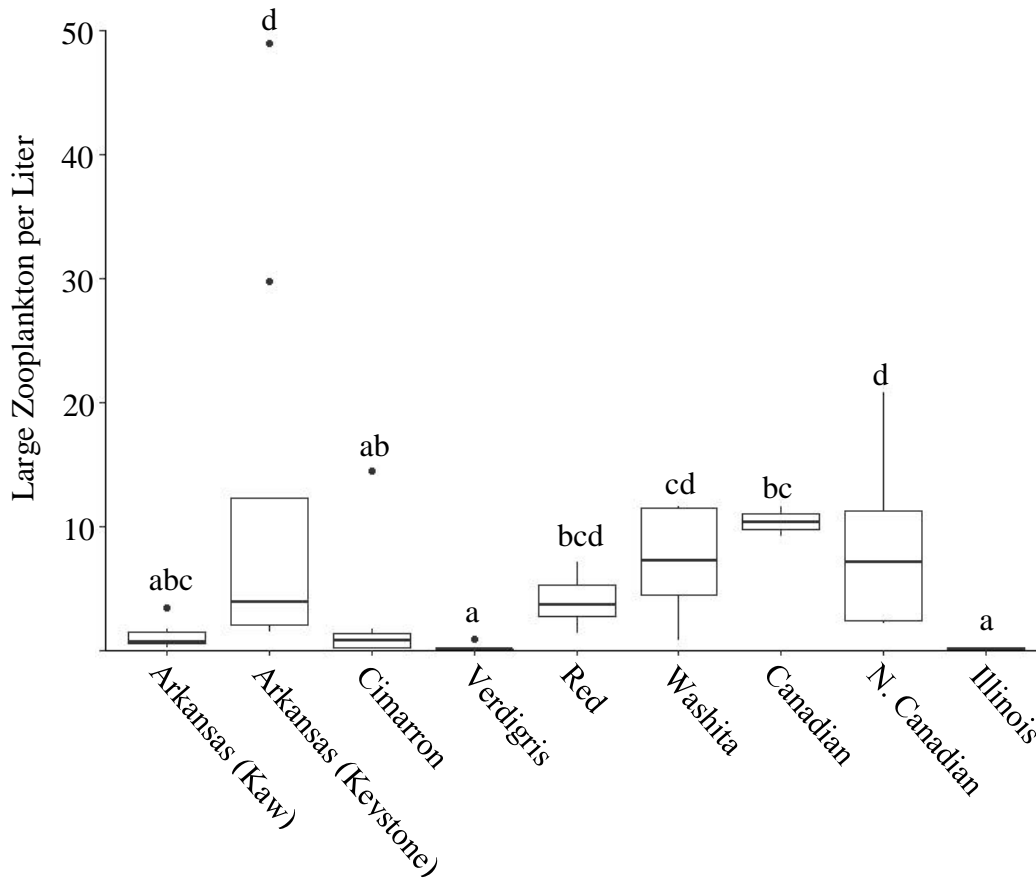


Figure 7. Boxplot of median large zooplankton (copepods and cladocerans) abundance among study rivers, spring 2020. Individual boxplots which do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

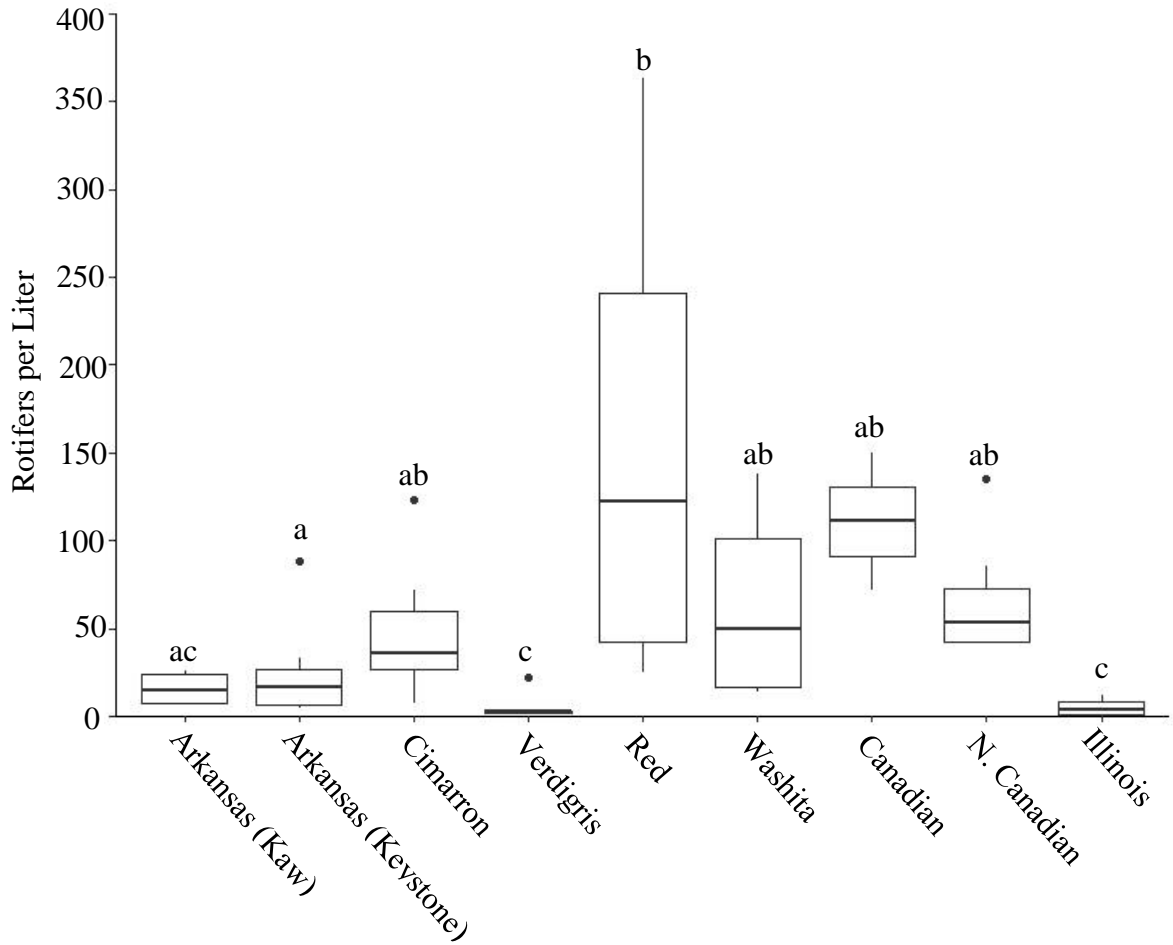


Figure 8. Boxplot of median rotifer abundance among study rivers, spring 2020. Individual boxplots which do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

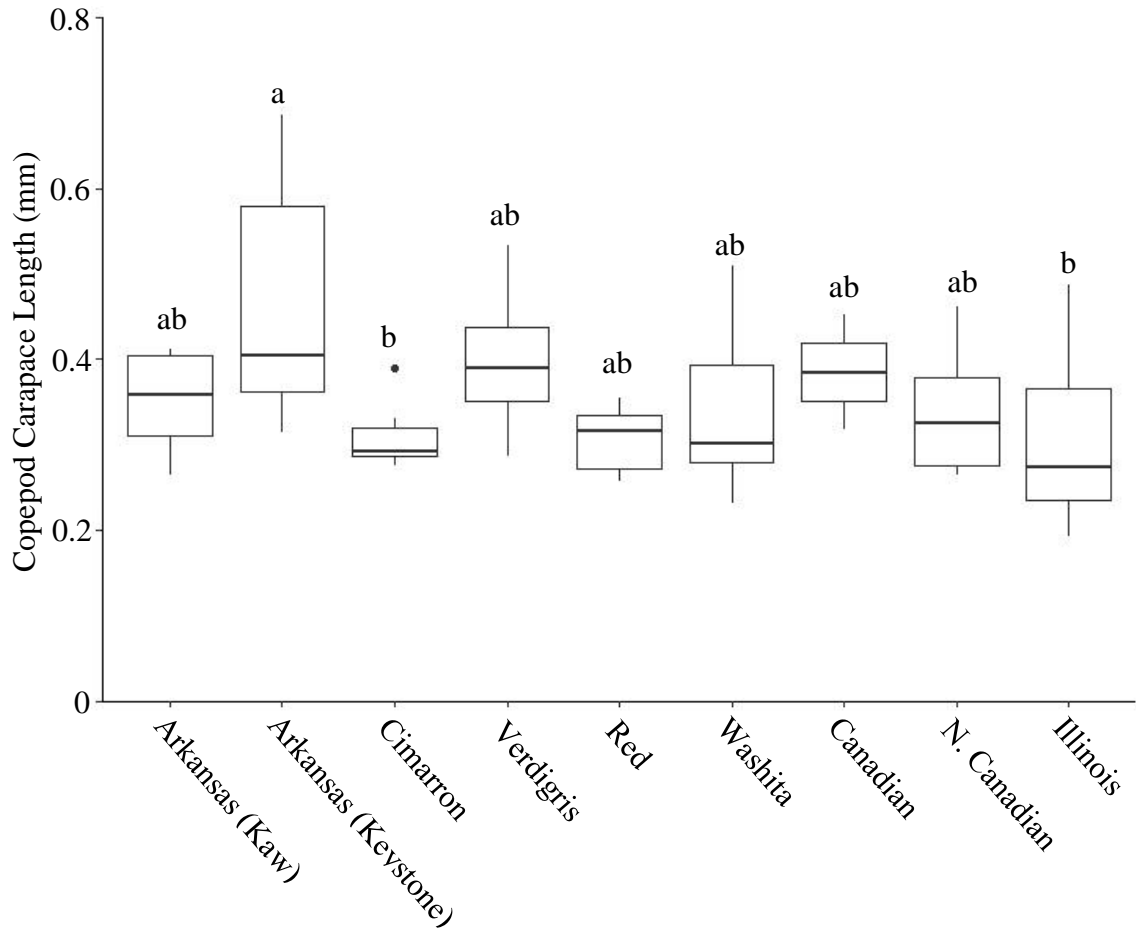


Figure 9. Boxplot of median copepod carapace lengths (mm) among study rivers, spring 2020. Individual boxplots which do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc). Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

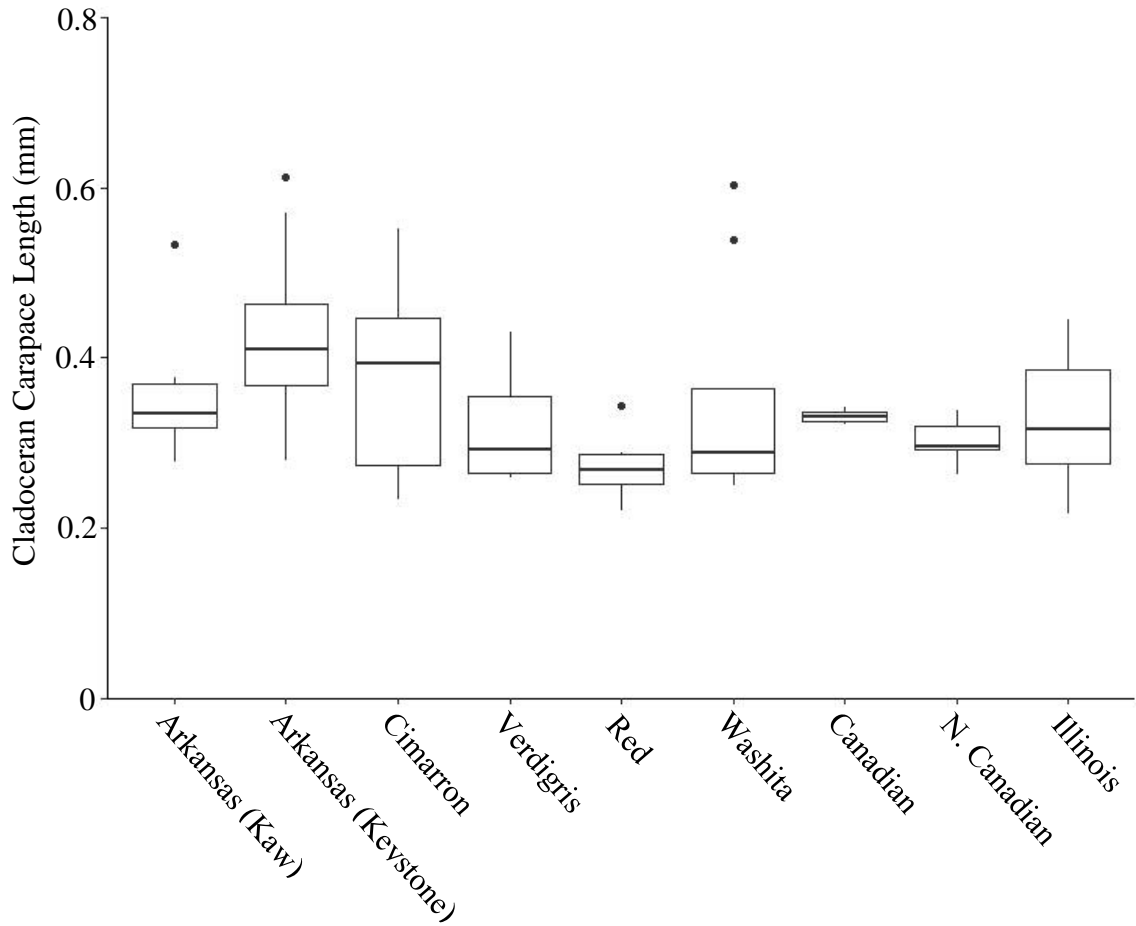


Figure 10. Boxplot of median cladoceran carapace lengths (mm) among study rivers, spring 2020. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

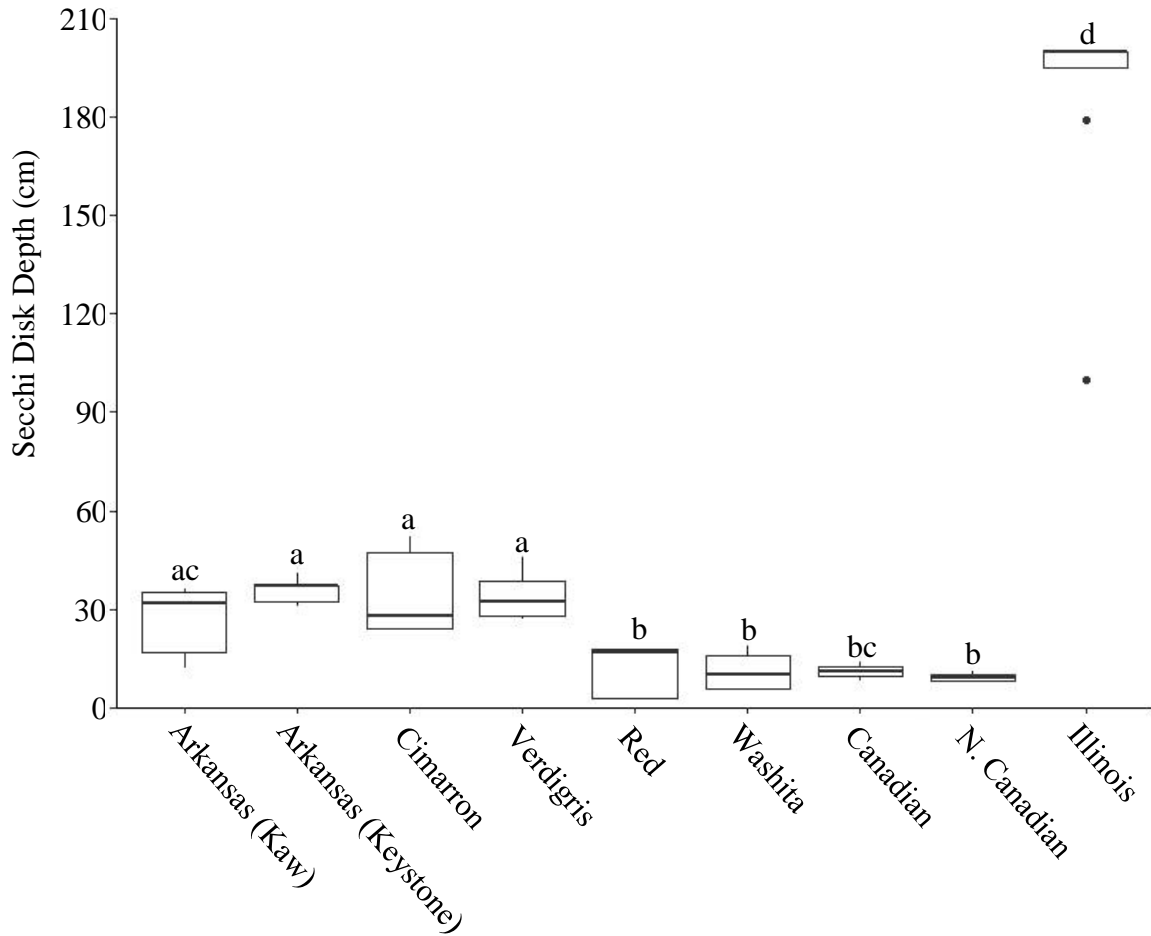


Figure 11. Boxplot of Secchi disk depth (cm) among study rivers, spring 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) using log-transformed data for analysis. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

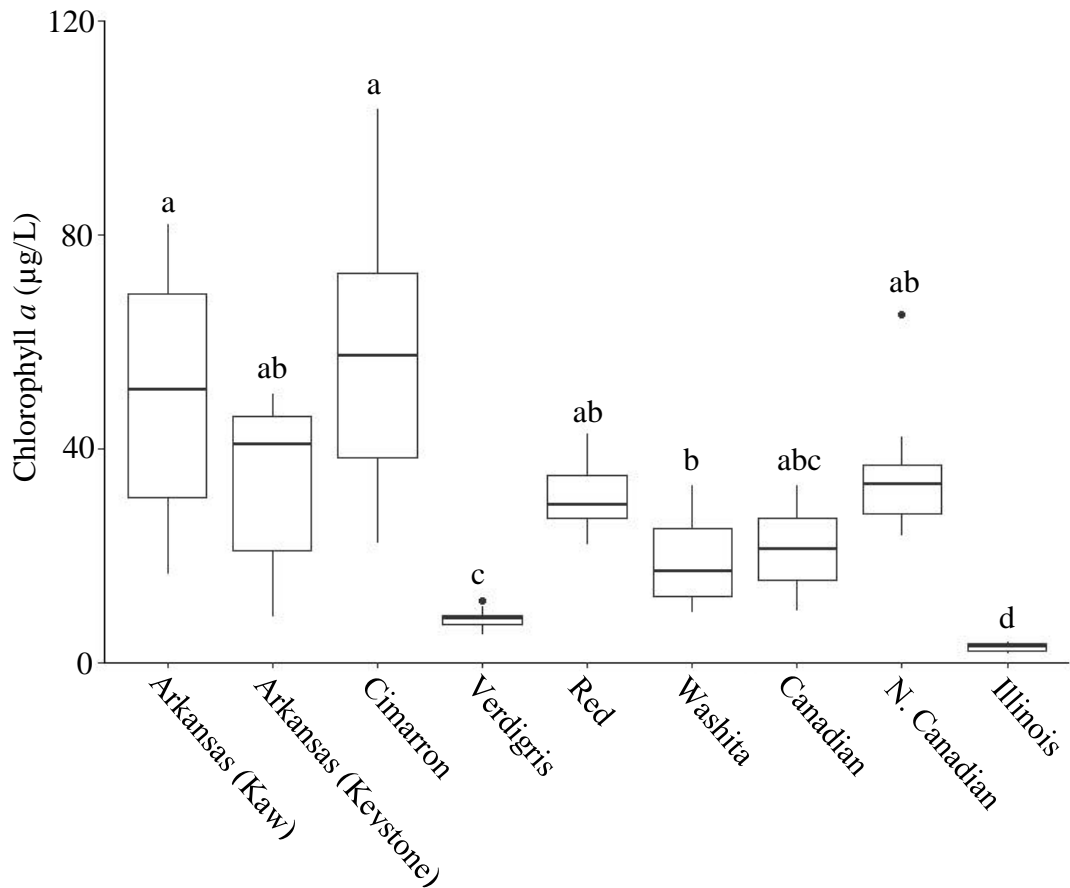


Figure 12. Boxplot of median chlorophyll *a* concentration ($\mu\text{g/L}$) among study rivers, spring 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

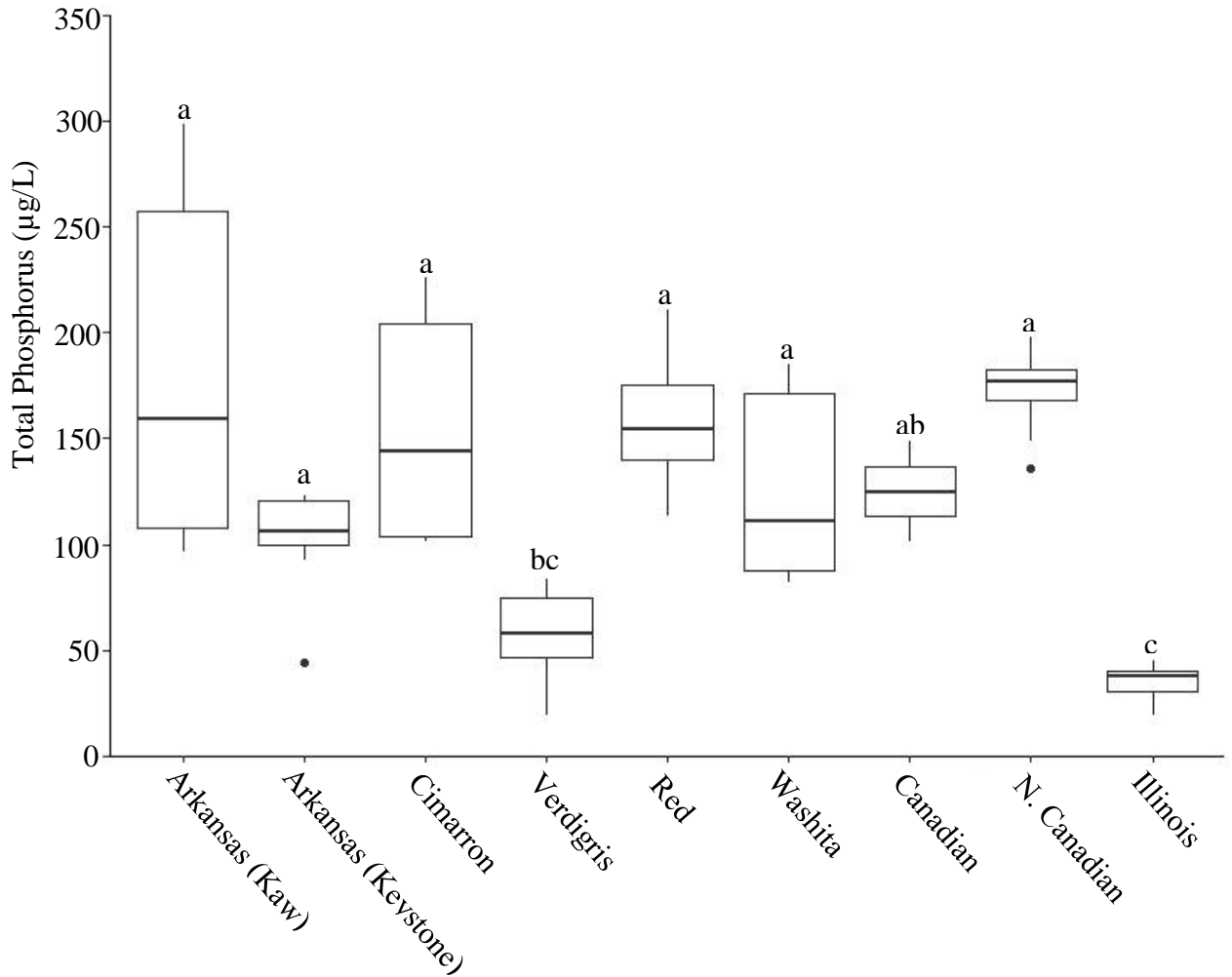


Figure 13. Boxplot of median total phosphorus ($\mu\text{g/L}$) among study rivers, spring 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Arkansas (Kaw), Arkansas (Keystone), Cimarron, and Verdigris), those where stocking has failed to restore a reproducing population (Red and Washita), and those that have not yet been assessed (Canadian, N. Canadian and Illinois).

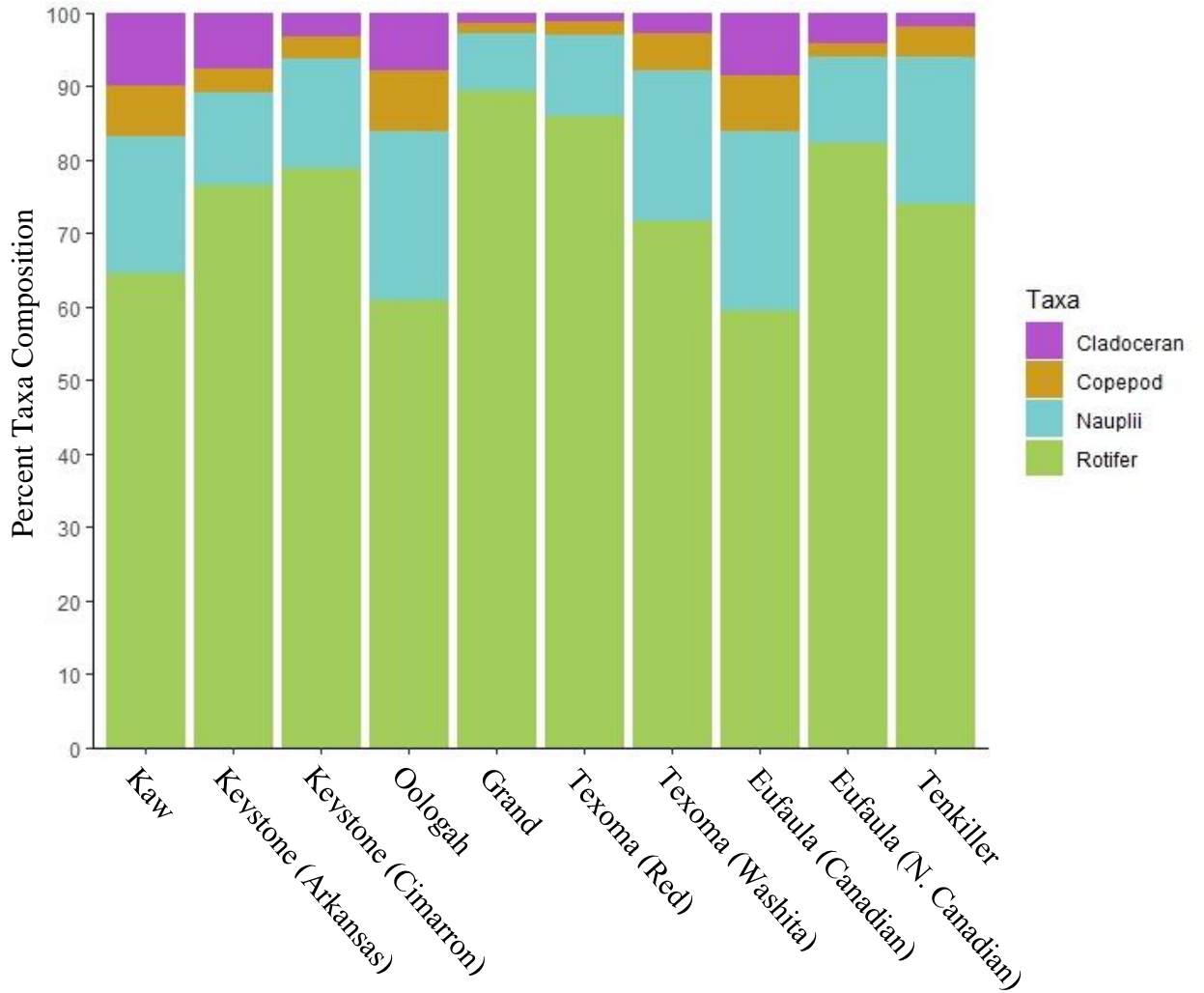


Figure 14. Total zooplankton community composition among all reservoirs, summer 2020.

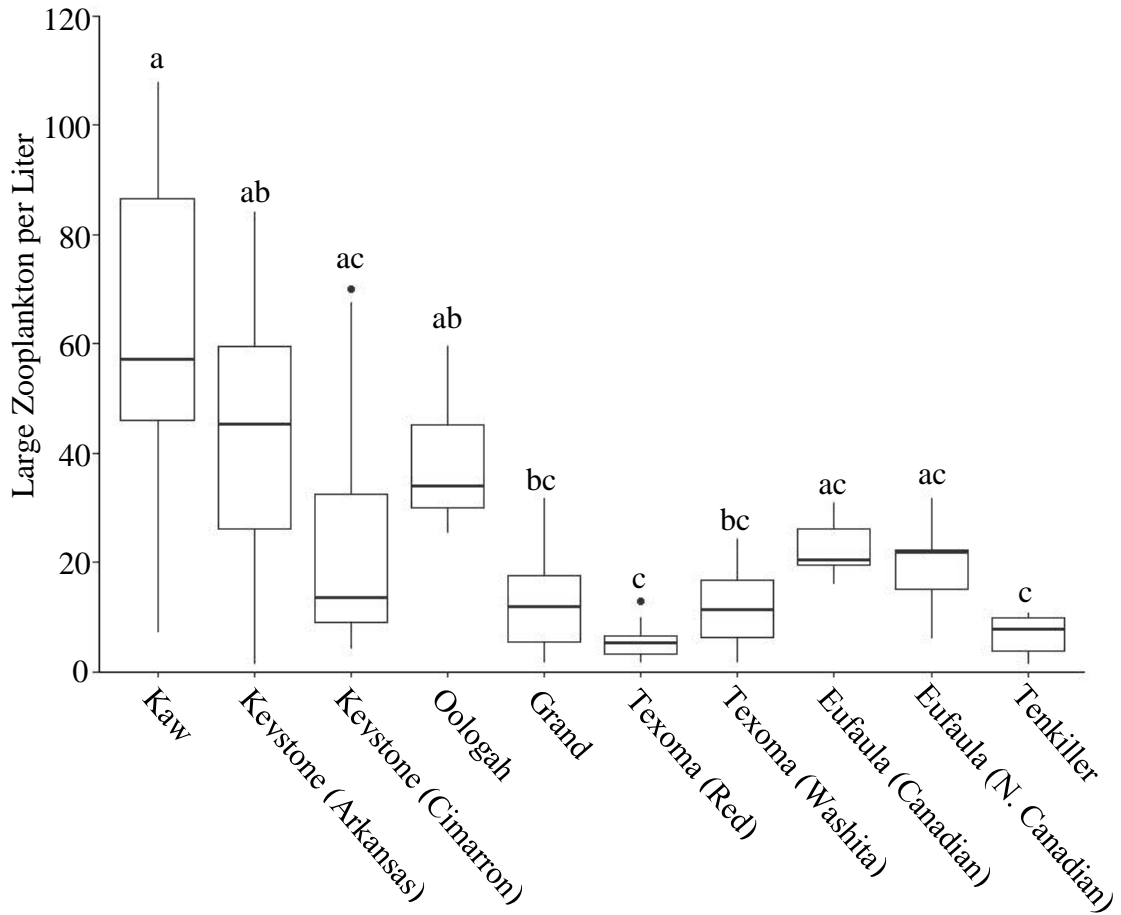


Figure 15. Boxplot of median large zooplankton (copepods and cladocerans) abundance among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

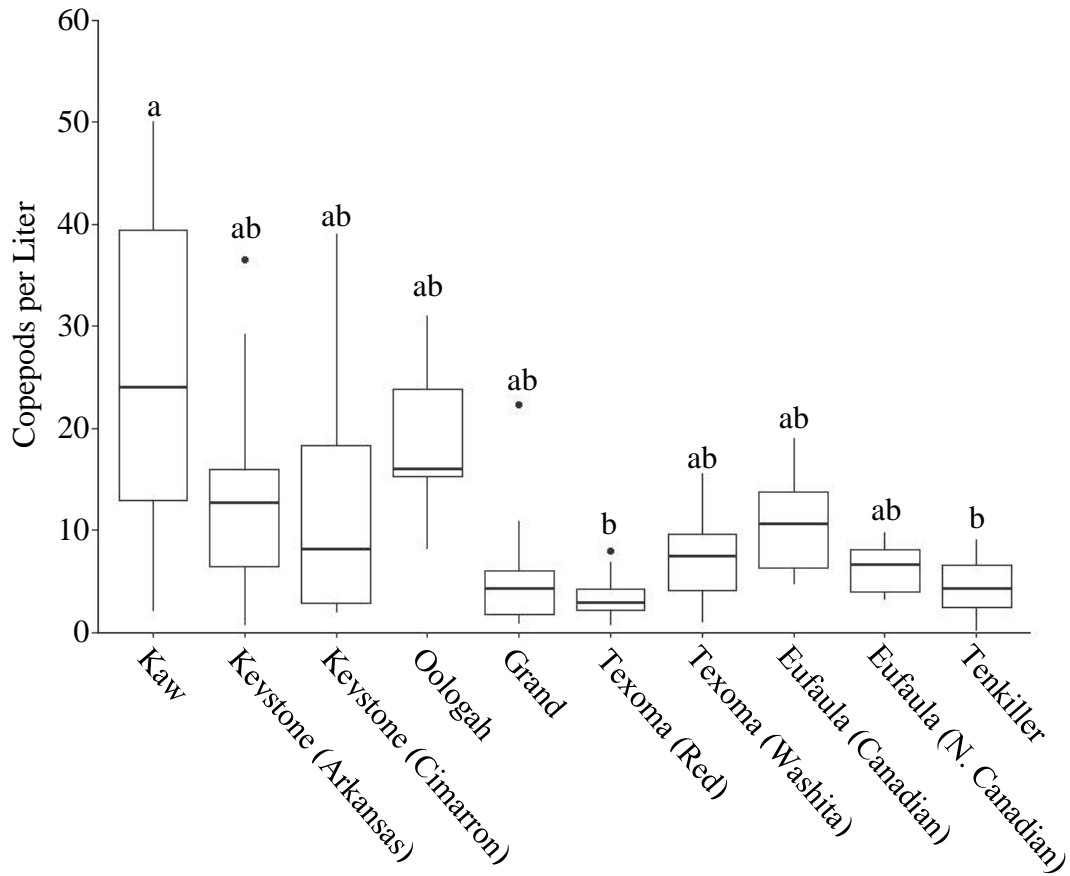


Figure 16. Boxplot of median copepod abundance among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

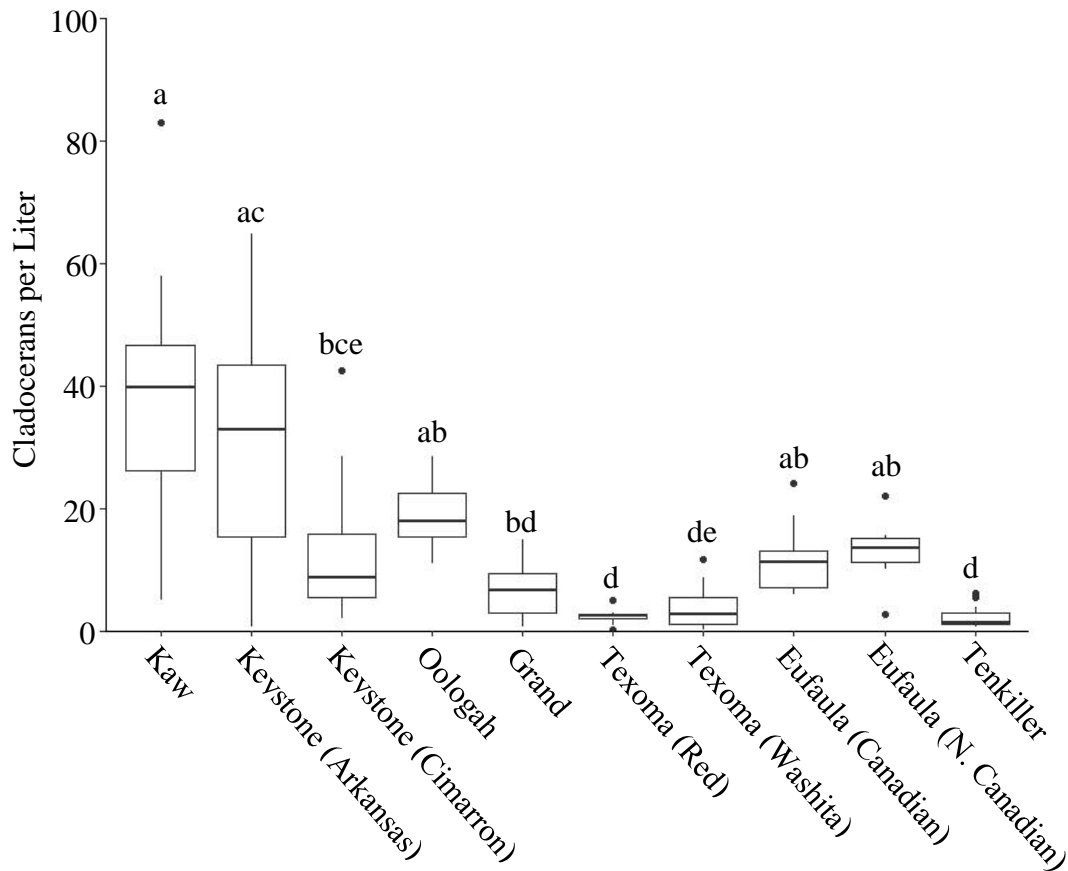


Figure 17. Boxplot of median cladoceran abundance among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

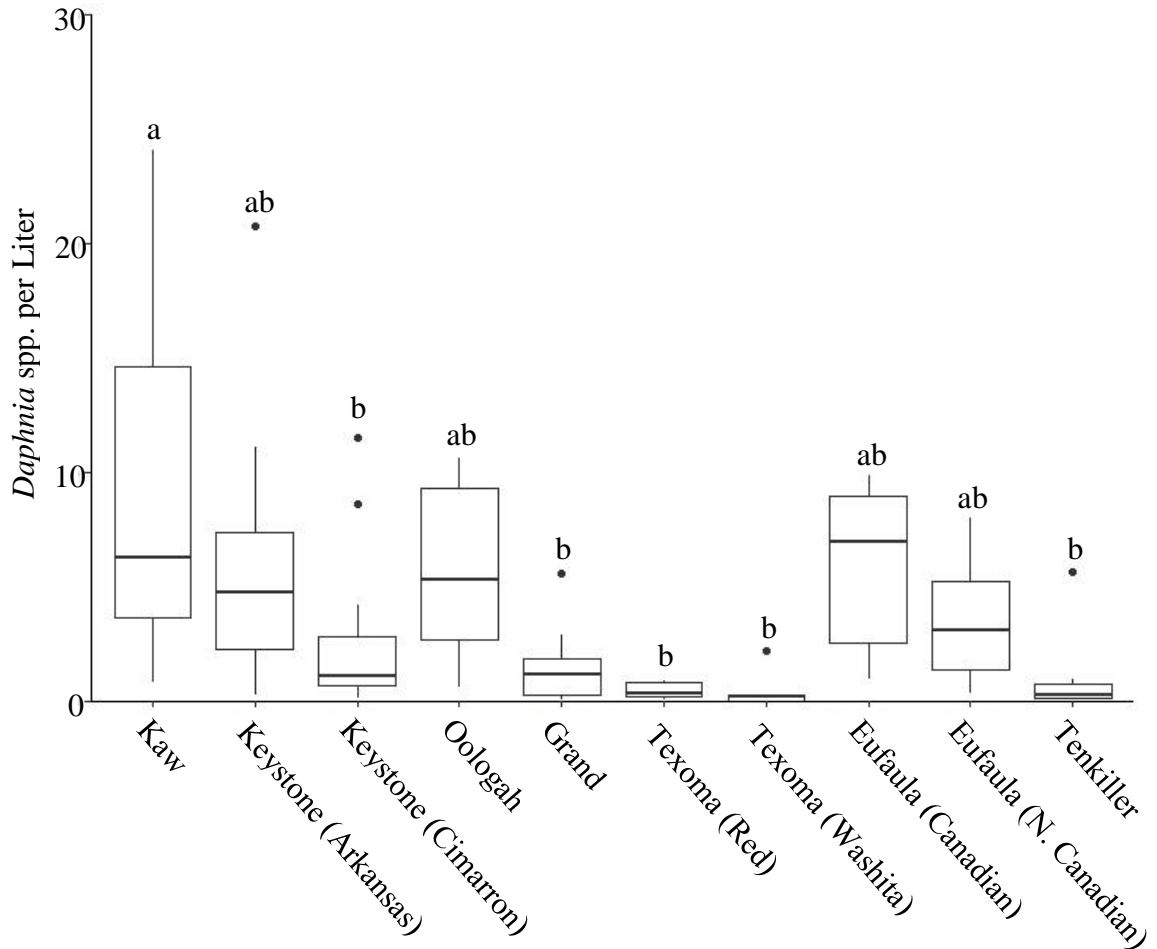


Figure 18. Boxplot of median *Daphnia* spp. abundance among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc), using log-transformed data for analysis. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

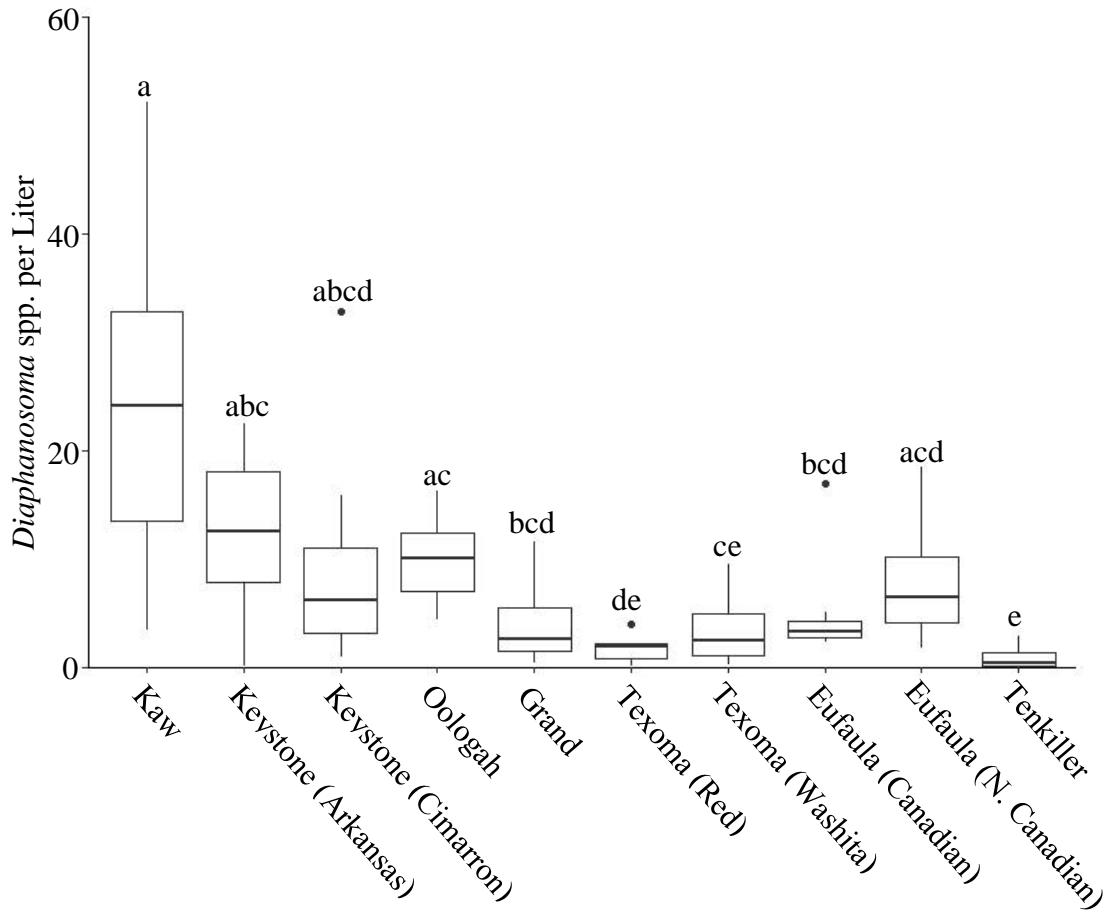


Figure 19. Boxplot of median *Diaphanosoma* abundance among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

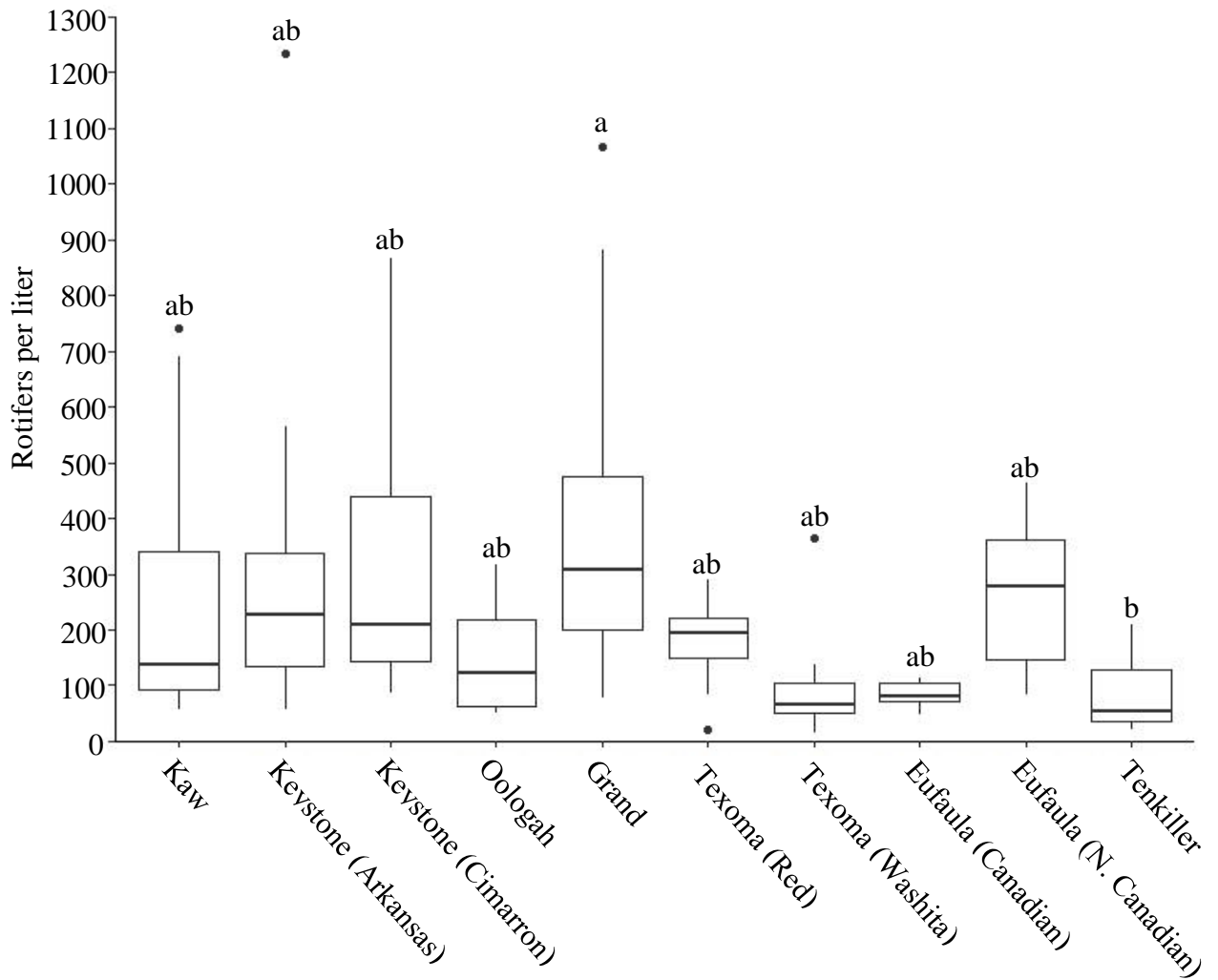


Figure 20. Boxplot of median rotifer abundance among study reservoirs, summer 2020. Individual boxplots within that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) using log-transformed data for analysis. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

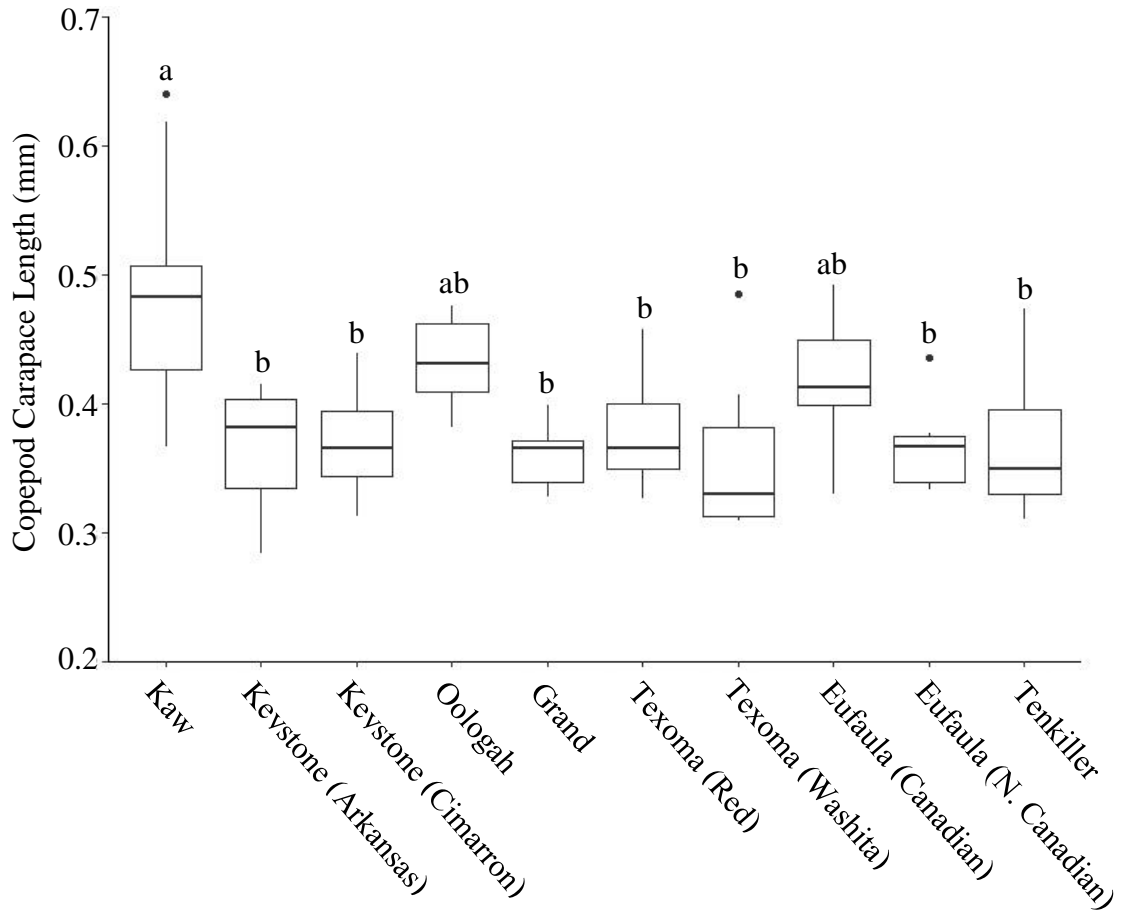


Figure 21. Boxplot of median copepod carapace length (mm) among study reservoirs, summer 2020. Individual boxplots which do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc). Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

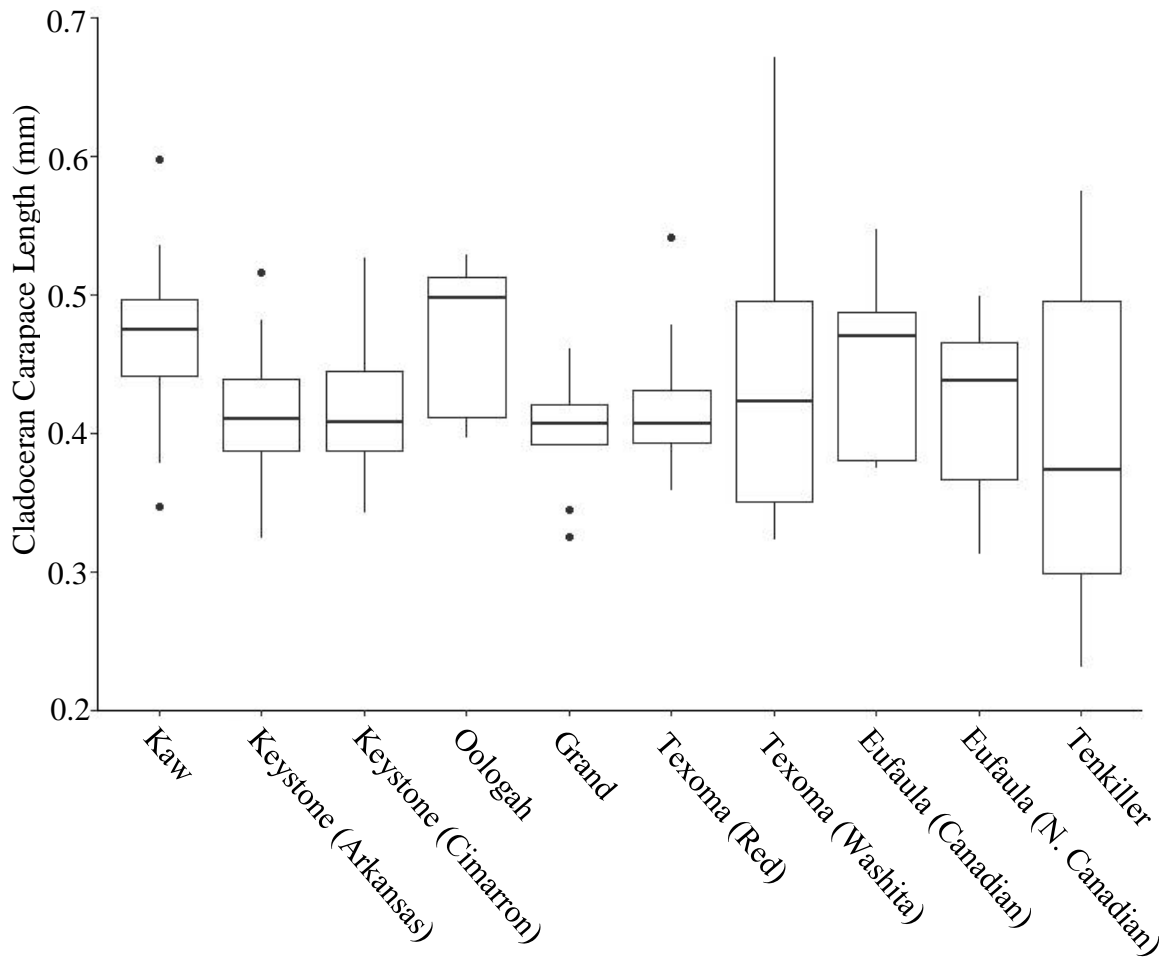


Figure 22. Boxplot of median cladoceran carapace length (mm) among study reservoirs, summer 2020. There were no significant differences among reservoir sites. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

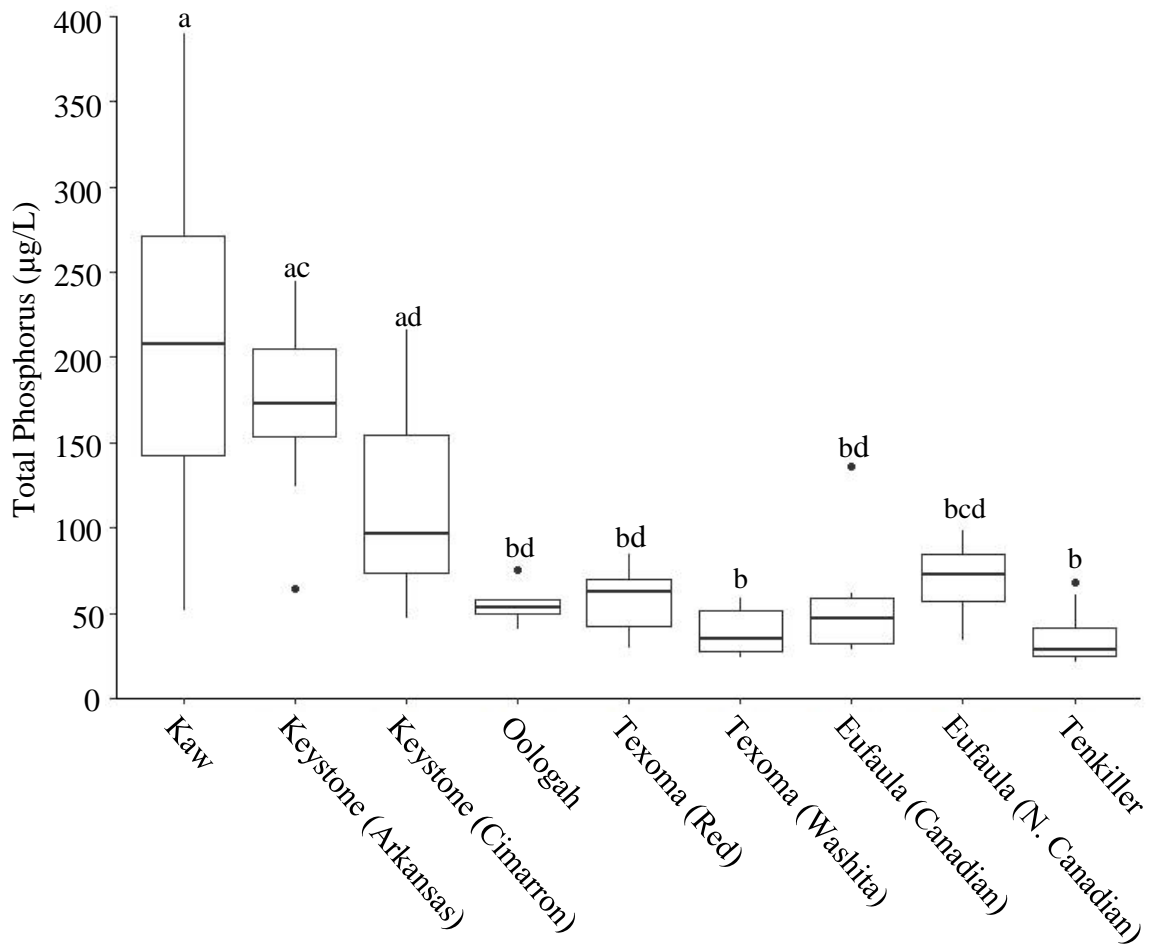


Figure 23. Boxplot of total phosphorus concentration among reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) using log-transformed data for analysis. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, and Oologah), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

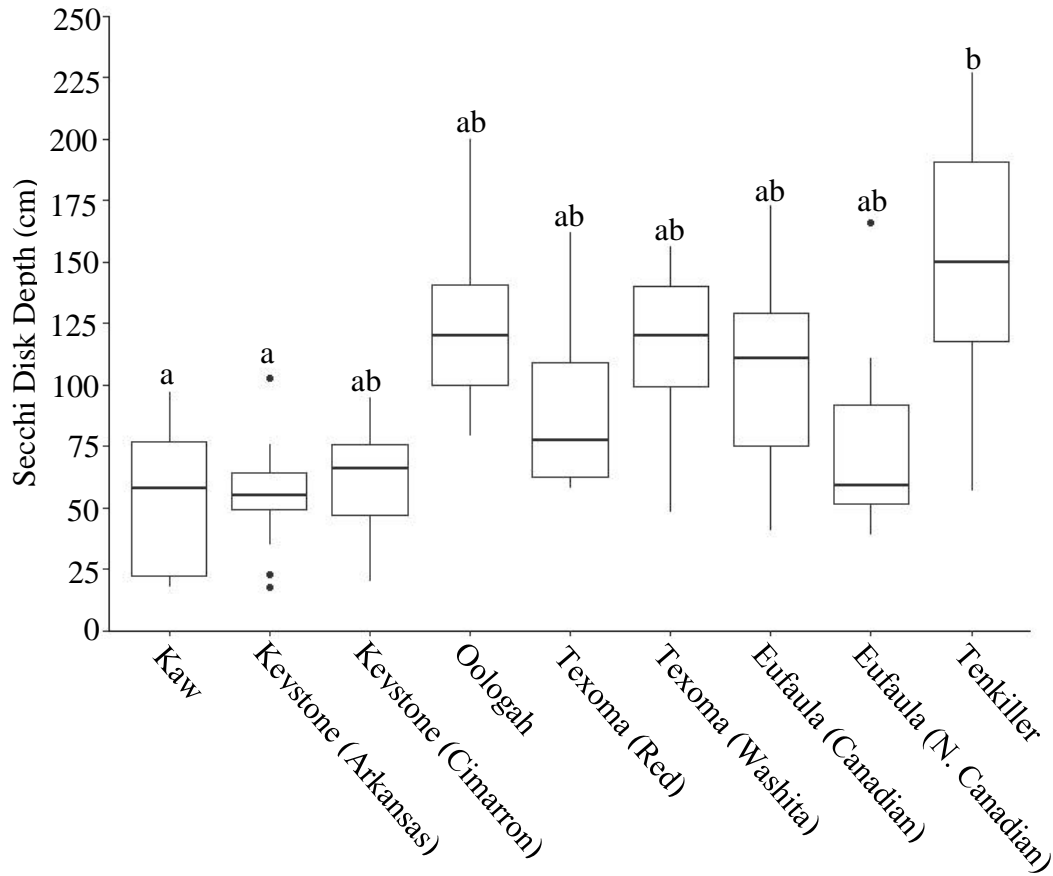


Figure 24. Boxplot of median Secchi disk depth (cm) among study reservoirs, summer 2020. Individual boxplots that do not share a common letter are significantly different ($\alpha = 0.05$, Tukey's post-hoc) based on log-transformed data. Sites are ordered from left to right from those with reproducing populations of paddlefish (Kaw, Keystone, Oologah, and Grand), those where stocking has failed to restore a reproducing population (Texoma), and those that have not yet been assessed (Eufaula and Tenkiller).

APPENDICES

Table A1. Coordinates and sample ID of spring (April and May) river sample locations, 2020.

River	Downstream Reservoir	Sample ID	Latitude	Longitude
Arkansas	Kaw	ARK(KAW)01	36.94818	-96.95456
Arkansas	Kaw	ARK(KAW)02	36.90964	-96.96215
Arkansas	Kaw	ARK(KAW)03	36.86814	-96.93106
Arkansas	Keystone	ARK(KEY)01	36.50523	-96.72217
Arkansas	Keystone	ARK(KEY)02	36.37575	-96.59389
Arkansas	Keystone	ARK(KEY)03	36.32961	-96.45392
Arkansas	Keystone	ARK(KEY)04	36.28429	-96.43469
Cimarron	Keystone	CIM01	36.06003	-96.59283
Cimarron	Keystone	CIM02	36.09542	-96.57846
Cimarron	Keystone	CIM03	36.11743	-96.51063
Cimarron	Keystone	CIM04	36.16441	-96.36912
Verdigris	Oologah	VER01	37.03369	-95.57920
Verdigris	Oologah	VER02	36.85218	-95.58540
Verdigris	Oologah	VER03	36.76402	-95.61211
Verdigris	Oologah	VER04	36.69952	-95.55908
Red	Texoma	RED01	33.72681	-97.15870
Red	Texoma	RED02	33.81585	-97.06836
Red	Texoma	RED03	33.85237	-97.05256
Washita	Texoma	WAS01	34.22046	-96.70089
Washita	Texoma	WAS02	34.18427	-96.68707
Washita	Texoma	WAS03	34.12479	-96.57797
Washita	Texoma	WAS04	34.09787	-96.55364
Canadian	Eufaula	CAN01	34.97031	-96.22038
N. Canadian	Eufaula	NCA01	35.31348	-96.03396
N. Canadian	Eufaula	NCA02	35.31626	-95.95530
N. Canadian	Eufaula	NCA03	35.39938	-95.81316
N. Canadian	Eufaula	NCA04	35.40624	-95.71992
Illinois	Tenkiller	ILL01	35.97828	-94.87404
Illinois	Tenkiller	ILL02	35.92307	-94.92403
Illinois	Tenkiller	ILL03	35.88510	-94.94483
Illinois	Tenkiller	ILL04	35.82147	-94.90320

Table 2A. Coordinates and sample ID of summer (July – September) reservoir sample locations.

Reservoir	Reservoir Arm	Sample ID	Latitude	Longitude
Kaw	Arkansas	KAWARK01	36.80098	-96.91045
Kaw	Arkansas	KAWARK02	36.77840	-96.89892
Kaw	Arkansas	KAWARK03	36.77665	-96.85091
Kaw	Arkansas	KAWARK04	36.75331	-96.82014
Kaw	Arkansas	KAWARK05	36.74565	-96.86430
Keystone	Arkansas	KEYARK01	36.25164	-96.36790
Keystone	Arkansas	KEYARK02	36.23463	-96.34004
Keystone	Arkansas	KEYARK03	36.22957	-96.30332
Keystone	Arkansas	KEYARK04	36.22354	-96.26343
Keystone	Arkansas	KEYARK05	36.20121	-96.24824
Keystone	Cimarron	KEYCIM01	36.19607	-96.37394
Keystone	Cimarron	KEYCIM02	36.18362	-96.34312
Keystone	Cimarron	KEYCIM03	36.19156	-96.31044
Keystone	Cimarron	KEYCIM04	36.17065	-96.30025
Keystone	Cimarron	KEYCIM05	36.16162	-96.32875
Oologah	Verdigris	OOLVER01	36.54096	-95.62251
Oologah	Verdigris	OOLVER02	36.51188	-95.59169
Oologah	Verdigris	OOLVER03	36.45625	-95.63260
Grand	Neosho	GL01	36.72571	-94.77632
Grand	Neosho	GL02	36.67256	-94.77356
Grand	Neosho	GL03	36.62224	-94.82558
Grand	Neosho	GL04	36.57426	-94.83210
Grand	Neosho	GL05	36.56377	-94.90857
Texoma	Red	TEXRED01	33.87794	-96.88036
Texoma	Red	TEXRED02	33.86305	-96.80126
Texoma	Red	TEXRED03	33.91239	-96.70169
Texoma	Washita	TEXWAS01	34.01531	-96.60120
Texoma	Washita	TEXWAS02	33.98772	-96.60949
Texoma	Washita	TEXWAS03	33.94002	-96.57245
Eufaula	Canadian	EUFCA01	35.22818	-95.61416
Eufaula	Canadian	EUFCA02	35.23994	-95.57791
Eufaula	Canadian	EUFCA03	35.25556	-95.54258
Eufaula	N. Canadian	EUFNCA01	35.38275	-95.62023
Eufaula	N. Canadian	EUFNCA02	35.35309	-95.59814
Eufaula	N. Canadian	EUFNCA03	35.28585	-95.55471
Tenkiller	Illinois	TENILL01	35.77558	-94.89478
Tenkiller	Illinois	TENILL02	35.75764	-94.91819
Tenkiller	Illinois	TENILL03	35.73233	-94.95294
Tenkiller	Illinois	TENILL04	35.70042	-94.95772
Tenkiller	Illinois	TENILL05	35.66771	-94.98451

VITA

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