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The influence of a severe reservoir drawdown on springtime zooplankton and larval fish assemblages in Red Willow Reservoir, Nebraska

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Reservoirs can be dynamic systems, often prone to unpredictable and extreme water-level fluctuations, and can be environments where survival is difficult for zooplankton and larval fish. Although numerous studies have examined the effects of extreme reservoir drawdown on water quality, few have examined extreme drawdown on both abiotic and biotic characteristics. A fissure in the dam at Red Willow Reservoir in southwest Nebraska necessitated an extreme drawdown; the water level was lowered more than 6 m during a two-month period, reducing reservoir volume by 76%. During the subsequent low-water period (i.e., post-drawdown), spring sampling (April–June) showed dissolved oxygen concentration was lower, while turbidity and chlorophyll-*a* concentration were greater, relative to pre-drawdown conditions. Additionally, there was an overall increase in zooplankton density, although there were differences among taxa, and changes in mean size among taxa, relative to pre-drawdown conditions. Zooplankton assemblage composition had an average dissimilarity of 19.3% from pre-drawdown to post-drawdown. The ratio of zero to non-zero catches was greater post-drawdown for larval common carp and for all larval fishes combined, whereas we observed no difference for larval gizzard shad. Larval fish assemblage composition had an average dissimilarity of 39.7% from pre-drawdown to post-drawdown. Given the likelihood that other dams will need repair or replacement in the near future, it is imperative for effective reservoir management that we anticipate the likely abiotic and biotic responses of reservoir ecosystems as these management actions will continue to alter environmental conditions in reservoirs.

Keywords: assemblage similarity; cladocerans; copepods; gizzard shad; Nebraska

Introduction

Most organisms must contend with living in a variable environment and environmental variability may occur on scales ranging from hours to centuries. Reservoirs can be variable and dynamic ecosystems and management of water levels in reservoirs is typically guided by hydrological and economic factors (e.g., flood control, hydropower generation, and irrigation), with little consideration given to biotic organisms (Sammons et al. 1999; Sammons and Bettoli 2000). For example, some reservoirs experience unpredictable and extreme water-level fluctuations (June 1977; Quist et al. 2003; Olds et al. 2011) that can be detrimental to the survival of zooplankton and larval fish (Carline 1986; Willis 1986; Naselli-Flores and Barone 1997).

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Variability of annual and seasonal water levels in reservoirs affects water quality (Olds et al. 2011) and zooplankton abundance (Olds et al. 2014), and leads to changes in the availability of habitat for fish at many life stages (Willis 1986). Low water levels can reduce the availability of adequate spawning (Ploskey 1986; Kallemeyn 1987) and nursery (Edwards and Twomey 1982; Werner et al. 1983; Gotceitas and Colgan 1987; Werner and Hall 1988) habitat for fish. Seasonal changes in reservoir flushing rate can cause changes in zooplankton and phytoplankton abundance; a high flushing rate can lead to low zooplankton abundance (Watson et al. 1996; Kalff 2003), which could reduce food availability for larval fish at a critical stage. Moreover, reservoirs often have high ambient levels of turbidity (Martin et al. 1981; Bremigan 1997; Naselli-Flores 1999; Gido and Matthews 2000) that can increase during periods of high inflow (Mion et al. 1998); several studies have found negative effects of high turbidity levels on zooplankton (Arruda et al. 1983; Kirk 1991) and fishes (Breitburg 1988; Miner and Stein 1993; Zingle and Paaver 2010).

Most of the dams in the USA were constructed between 1920 and 1970 (Beaumont 1978), and many of them are approaching or have exceeded their life expectancy (Poff and Hart 2002, and references therein). Therefore, extensive and prolonged drawdown for repair or replacement may soon become necessary (Juracek 2015), which could negatively affect reservoir ecosystems. Although numerous studies have examined the effects of extreme reservoir drawdown on water quality (Vernieu 1997; Furey et al. 2004; Baldwin et al. 2008; Olds et al. 2011), fewer have examined the effects of an extreme drawdown on both abiotic and biotic characteristics (see Benejam et al. 2008). A fissure in the dam at Red Willow Reservoir in southwest Nebraska necessitated an extreme drawdown to ensure the safety of the people downstream of the dam. During November and December 2009, the water level was lowered more than 6 m. The low-water period after the drawdown, which extended beyond the duration of our study, provided us with an opportunity to evaluate the effect of an extreme event on the water quality and zooplankton and larval fish assemblages at Red Willow. Our objective was to compare water-quality variables and the zooplankton and larval fish assemblages from two years pre-drawdown to two years post-drawdown at Red Willow Reservoir, thereby providing insight into the abiotic and biotic changes that can occur in a reservoir after an extreme water-level drawdown and during the subsequent prolonged low-water period.

Study site

Nebraska is typified by extreme seasonal variability in temperature and precipitation (Matthews 1988). There are several major multipurpose reservoirs located in the Republican River watershed in Nebraska; these reservoirs were originally designed for flood control but are also currently operated primarily for irrigation, recreation, and fish and wildlife (W. Peck, U.S. Bureau of Reclamation, personal communication). Water-level drawdown at these reservoirs occurs predominantly from June to September (during irrigation season), although the timing, duration, and intensity of the drawdown are predicated on regional precipitation patterns and the nuances of agricultural demands. Red Willow Reservoir (Hugh Butler Lake) is impounded by Red Willow Dam, constructed between 1960 and 1962 by the U.S. Bureau of Reclamation for flood control on Red Willow Creek, a tributary of the Republican River. Red Willow Reservoir has a watershed area of 1890 km² (Ferrari 1998), an active conservation pool elevation of 786.9 m above sea level, a maximum storage volume of approximately 10,700 ha m, and a mean depth of 16 m when filled to capacity. During recent decades, Red Willow Reservoir has

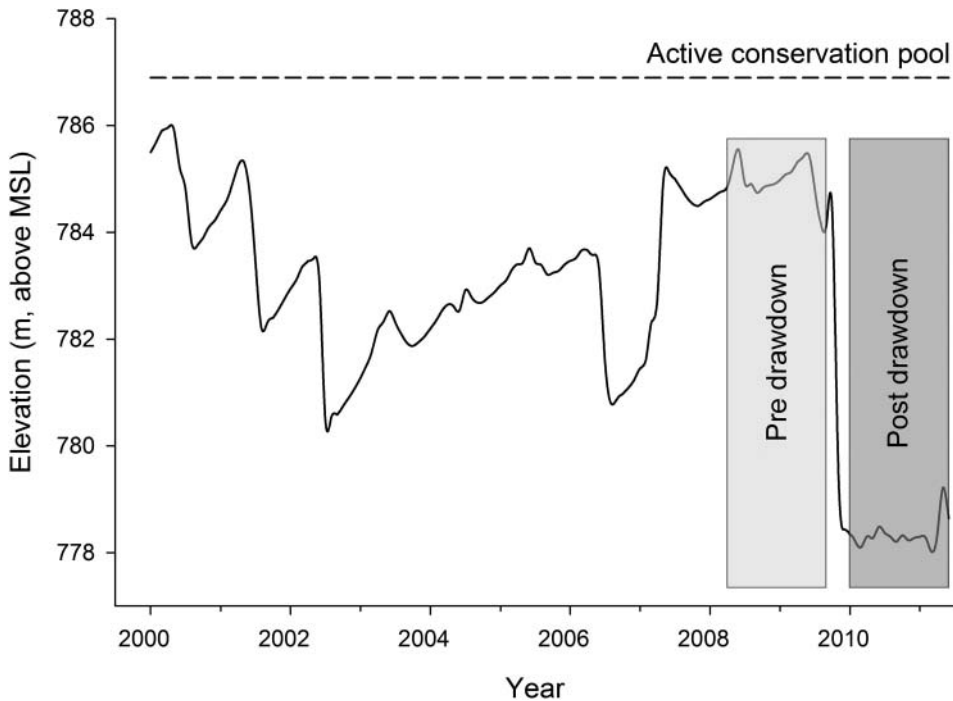


Figure 1. Water-level elevation above mean sea level (MSL) during 2000–2011 for Red Willow Reservoir (Frontier County, Nebraska, USA).

undergone episodic wet–dry cycles, including periods of long-term (2000–2003) and short-term (2006) droughts, as well as periods with ample precipitation (2003–2006, 2007–2009; Figure 1). As a consequence of a fissure in the dam, the water level in Red Willow Reservoir was lowered by more than 6 m during November and December 2009, reducing the reservoir volume by 70%. See DeBoer et al. (2013) for a more detailed description of the watershed and fish assemblage.

Methods

Data collection

We obtained reservoir data (i.e., water level, surface area, and volume) for 2008–2011 from the U. S. Bureau of Reclamation (USBR 2013). We sampled larval fishes approximately once weekly during 2008 and once weekly during 2009–2011 beginning in approximately mid-April (estimated time of larval walleye and yellow perch hatching in this system) and continuing until approximately late June. We used nine, paired nearshore and offshore transects (18 transects per week) with starting points for nearshore transects randomly selected using GIS software (ArcMap 9.3.1, ESRI, Inc., <http://www.esri.com>). Where possible, starting points for nearshore transects were located within 25 m of shore and starting points for offshore transects were located ~125 m offshore. We selected points using a stratified random sampling design (Johnson and Nielsen 1983) along the longitudinal reservoir axis, such that an equal number of sites were present in each of the three reservoir zones: upper, middle, and lower reservoir (i.e., riverine, transition,

lacustrine; Thornton 1990). Transects were parallel to shore, fixed (i.e., sampled repeatedly) within a year, and re-randomized in each subsequent year. We sampled transects after dark using two 0.5-m-diameter, 750- μm mesh, bow-mounted ichthyoplankton push nets. The nets were pushed at ~ 0.7 m/s for 5 minutes (approximately 200 m) per transect, or until nets became clogged with debris. We estimated larval fish densities by recording the volume of water filtered through each net, using a calibrated flowmeter (Model 2030 flow meter, General Oceanics, <http://generaloceanics.com>) attached to the mouth of each net.

After completing each sampling transect, we sampled the zooplankton assemblage from the top 2 m of the water column using a 2.1-m (7.5 cm diameter, 8.8 L volume) plastic tube sampler placed vertically in the water column (DeVries and Stein 1991). We filtered the sample through an 80- μm mesh net, preserved the sample with 4% sucrose–formalin solution (Haney and Hall 1973), and transported the sample back to the laboratory. We collected a 125 mL water sample from the top 1 m of the water column using the plastic tube sampler described above, filtered it through fiberglass filters with vacuum assistance, stored the sample in a dark, ice-filled cooler, and returned it to the laboratory for chlorophyll-*a* (Chl-*a*) analysis (USEPA 2002). We used Chl-*a* as a proxy for phytoplankton biomass (Gameiro et al. 2004). We measured surface turbidity (NTU) using a turbidity meter (model 2020e, LaMotte Company, <http://lamotte.com>), and surface water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L) using a multimeter (model 556, YSI Environmental, <http://www.ysi.com>).

Laboratory processing

Chl-*a*, zooplankton, and larval fish samples were processed in the Fishery Science Laboratory at the University of Nebraska-Lincoln. Chl-*a* extraction was performed using standard methods (USEPA 2002). Chl-*a* samples from 2009 and 2010 were non-viable because of storage issues. We identified, enumerated, and measured (body length, nearest 0.1 mm; up to 10 individuals per taxon) a 25% subsample of zooplankton from each sample. If < 250 total zooplankters were counted in a subsample, we processed additional 25% subsamples until ≥ 250 total zooplankters were counted. We identified calanoid and cyclopoid copepods to order, copepod nauplii to subclass, and *Bosmina* and *Daphnia* to genus. We identified all larval fishes to the lowest possible taxonomic group and enumerated all individuals in each sample.

Data analyses

We define pre-drawdown as 2008 and 2009, and post-drawdown as 2010 and 2011. We calculated weekly mean values ($n = 18$ measurements or samples per week) for each water-quality variable and for Chl-*a* concentration, and independently compared weekly means between pre-drawdown ($n = 22$ weekly means) and post-drawdown ($n = 21$ weekly means) using a repeated-measures generalized linear model (PROC GLM in SAS, Version 9.2, SAS Institute Inc., <http://www.sas.com>). We calculated mean density and body size values by taxon for each zooplankton sample ($n = 18$ samples per week), then calculated weekly mean density and body size values by taxon and independently compared density and body size between pre-drawdown ($n = 22$ weekly means) and post-drawdown ($n = 21$ weekly means) using a repeated-measures generalized linear model. We also analyzed density and body size for the five most abundant taxa (described later) pooled together. We compared zooplankton assemblage composition from

pre-drawdown to post-drawdown using percent composition, as well as one-way analysis of similarity (ANOSIM) and non-metric multidimensional scaling (Clark and Warwick 2001). We log-transformed zooplankton abundance data prior to analysis to improve normality. We used the transformed zooplankton data to calculate Bray–Curtis similarities (Bray and Curtis 1957) calculated from mean weekly densities for each taxon. We also used one-way similarity of percentages (SIMPER) to determine the percent dissimilarity between pre-drawdown and post-drawdown assemblages, and to identify the contribution of individual taxa to dissimilarity (Clark and Warwick 2001), with a cumulative dissimilarity contribution cutoff of 90%. We included taxa that comprised >1% of the assemblage in any single year in our analyses. These taxa were *Bosmina* spp., calanoid copepods, cyclopoid copepods, copepod nauplii (we did not differentiate between calanoid copepod nauplii and cyclopoid copepod nauplii), and *Daphnia* spp. We excluded rotifers from our analyses because the mesh size of our sampling gear did not collect them effectively.

The number of larval fish present in a given area can vary dramatically (Cole and MacMillan 1984; Weaver et al. 1997; Quist et al. 2003; Roseman et al. 2005). Thus, rather than compare relative abundances, we decided to use a presence–absence-based approach (*sensu* Strayer 1999; Royle and Nichols 2003), a well-documented approach in studies of terrestrial organisms. We compared the proportion of weeks with zero catch to weeks with non-zero catch from pre-drawdown to post-drawdown using independent Chi-squared tests for (1) larval gizzard shad (*Dorosoma cepedianum*); (2) larval common carp (*Cyprinus carpio*); and (3) all larval fishes combined. We focused on gizzard shad and common carp because they are the most abundant larval fish in this system. We compared larval fish assemblage composition from pre-drawdown to post-drawdown using percent composition, as well as one-way ANOSIM. We log-transformed larval fish abundance data prior to the analysis to improve normality. We used the transformed larval fish data to calculate Bray–Curtis similarities (Bray and Curtis 1957) calculated from mean annual densities for each taxon; we used annual means because mean weekly densities were highly zero-inflated, as a consequence of the patchy spatial distribution of larval fish and the phenology of larval fish assemblages (Quist et al. 2004). We also used one-way SIMPER to determine the percent dissimilarity between pre-drawdown and post-drawdown assemblages and to identify the contribution of individual taxa to dissimilarity with a cumulative dissimilarity contribution cutoff of 90%. We included taxa that comprised >1% of the catch (when gizzard shad were excluded) in any year. These taxa were common carp, freshwater drum (*Aplodinotus grunniens*), *Lepomis*, spp., *Pomoxis* spp., wall-eye (*Sander vitreus*), white bass (*Morone chrysops*), and yellow perch (*Perca flavescens*). We used SAS, R (Version 2.15.2, The R Foundation for Statistical Computing, Vienna, Austria), and PRIMER (Version 6, PRIMER-E Ltd. 2012, Plymouth, United Kingdom) for analyses with $\alpha = 0.05$.

Results

Reservoir water-level elevation decreased more than 6 m between October 2009 and December 2009 (Figure 1). Consequently, reservoir volume decreased 76%, from 2966 to 704 ha m and reservoir surface area (Figure 2) decreased 59%, from 580 to 240 ha. Water quality changed substantially from pre-drawdown to post-drawdown. Dissolved oxygen concentration decreased and turbidity and Chl-*a* concentration both increased from pre-drawdown to post-drawdown (Table 1). Although water temperature increased throughout the spring sampling season ($F = 16.47$; $df = 10, 21$; $p < 0.0001$), neither the rate of

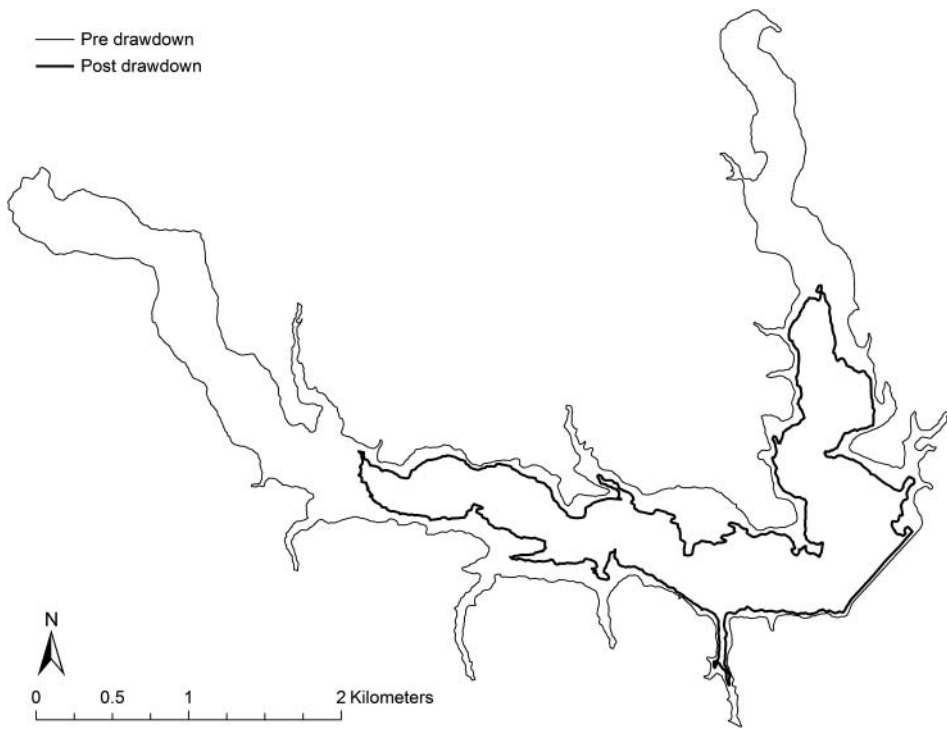


Figure 2. Red Willow Reservoir (Frontier County, Nebraska, USA) pre-drawdown and post-drawdown surface area map. Reservoir surface area decreased 59%, from 580 to 240 ha between October 2010 and December 2010.

weekly temperature increase (i.e., slope; $F = 1.12$; $df = 10, 21$; $p = 0.4$) nor the mean temperature (Table 1) differed from pre-drawdown to post-drawdown.

We observed pronounced differences in the zooplankton assemblage from pre-drawdown to post-drawdown (Figure 3). The total zooplankton density (N/L) increased from pre-drawdown to post-drawdown, as did the density of *Bosmina* spp., cyclopoid copepods, and copepod nauplii, although the density of calanoid copepods decreased from pre-drawdown to post-drawdown, and the density of *Daphnia* spp. did not change

Table 1. Mean (\pm SE) of weekly mean water-quality variable values measured pre-drawdown and post-drawdown during spring at Red Willow Reservoir, Frontier County, Nebraska, USA. Statistical significance was assumed at $\alpha = 0.05$. Percent change is only shown for significant differences.

Variable	Period		Percent change	F	df	p
	Pre-drawdown	Post-drawdown				
Temperature ($^{\circ}\text{C}$)	17.9 ± 1.1	17.5 ± 1.0		0.01	1, 31	0.9
Dissolved oxygen (mg/L)	11.2 ± 0.8	9.4 ± 0.4	-16%	5.1	1, 28	0.03
Turbidity (NTU)	9.1 ± 0.8	25.6 ± 3.1	181%	26.04	1, 31	<0.0001
Chl- <i>a</i> ($\mu\text{g/L}$)	4.2 ± 1.2	9.4 ± 1.4	124%	14.6	1, 9	0.004

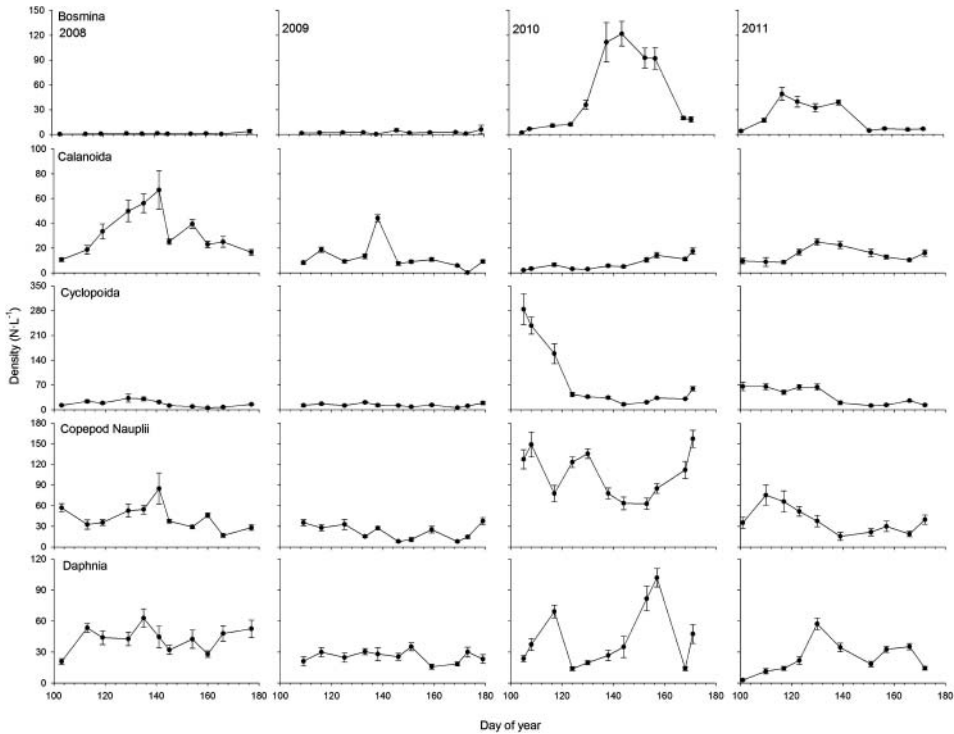


Figure 3. Density of five zooplankton taxa as a function of day of year during 2008–2011 at Red Willow Reservoir (Frontier County, Nebraska, USA). Reservoir drawdown occurred between 2009 and 2010 sampling. We only included taxa that comprised >1% of the assemblage in any single year in our analyses.

(Figure 3; Table 2). The body size of *Bosmina* spp., cyclopoid copepods, copepod nauplii, and *Daphnia* spp. all decreased from pre-drawdown to post-drawdown, whereas the size of calanoid copepods did not change (Table 2). Zooplankton assemblage structure (Figure 4) was different (SIMPER; average dissimilarity = 19.3) between pre-drawdown and post-drawdown (ANOSIM; $r = 0.625$; $p = 0.001$); the majority of the points in the NMDS plot were distinctly separated between pre-drawdown and post-drawdown (Figure 5). Most of the difference in assemblage structure was driven by a post-drawdown increase in the percent of *Bosmina* spp. (SIMPER; average dissimilarity = 7.9).

We observed differences in the larval fish assemblage from pre-drawdown to post-drawdown (Figure 6), though much of the difference seemed to be driven by gizzard shad and common carp. The ratio of zero to non-zero catches was greater post-drawdown for larval common carp and for all larval fishes combined, whereas we observed no difference for larval gizzard shad (Table 3). Although the larval fish assemblage structure (Figure 7) was dissimilar (SIMPER; average dissimilarity = 39.7) between pre-drawdown and post-drawdown, the difference was not significant (ANOSIM; $r = 0.0$; $p = 0.67$). Most of the dissimilarity in assemblage structure was driven by a post-drawdown increase in the percent of common carp (SIMPER; average dissimilarity = 14.7).

Table 2. Mean (\pm SE) of weekly mean zooplankton density (N/L) and size (μm) from samples collected pre-drawdown and post-drawdown during spring at Red Willow Reservoir, Frontier County, Nebraska, USA. Statistical significance was assumed at $\alpha = 0.05$. Percent change is only shown for significant differences.

Metric	Taxon	Period		% change	<i>F</i>	<i>df</i>	<i>P</i>
		Pre	Post				
Density	Total ^a	106.6 \pm 10.2	211.8 \pm 22.7	99%	17.3	1, 30	0.0002
	<i>Bosmina</i> spp.	1.9 \pm 0.3	33.1 \pm 8.0	1642%	14.5	1, 30	0.0006
	Calanoid copepods	21.8 \pm 3.9	11.1 \pm 1.3	-49%	6.1	1, 30	0.02
	Cyclopoid copepods	15.4 \pm 1.6	61.5 \pm 15.5	299%	9.8	1, 30	0.004
	Copepod nauplii ^b	32.9 \pm 4.1	72.7 \pm 9.3	121%	14.5	1, 30	0.001
	<i>Daphnia</i> spp.	34.5 \pm 2.8	33.4 \pm 5.3		0.1	1, 30	0.9
Body size	<i>Bosmina</i> spp.	5.9 \pm 0.4	3.6 \pm 0.1	-39%	40.2	1, 30	0.0001
	Calanoid copepods	12.1 \pm 0.4	12.9 \pm 0.8		0.3	1, 30	0.6
	Cyclopoid copepods	8.7 \pm 0.4	7.7 \pm 0.3	-11%	5.9	1, 30	0.02
	Copepod nauplii ^b	2.4 \pm 0.1	1.9 \pm 0.04	-21%	53.2	1, 30	0.0001
	<i>Daphnia</i> spp.	15.5 \pm 0.6	12.9 \pm 0.4	-17%	19.9	1, 30	0.0001

^aTotal is the sum of all five taxa listed in the table.

^bWe did not differentiate between calanoid and cyclopoid nauplii.

Discussion

Water quality

The drawdown resulted in pronounced abiotic changes in the reservoir which were associated with biotic changes. We believe that the increase in Chl-*a* concentration (used as a proxy for phytoplankton abundance) resulted from a re-suspension of benthic nutrients and suspended solids (measured as increased turbidity). Given that minimal inflow

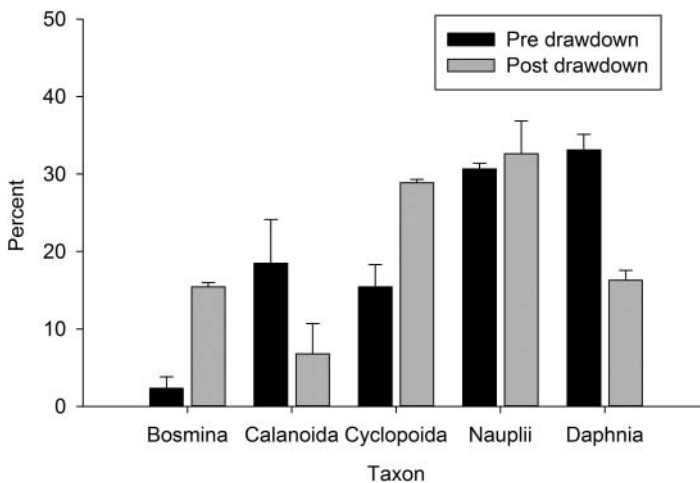


Figure 4. Zooplankton assemblage percent composition from samples collected pre-drawdown and post-drawdown during spring at Red Willow Reservoir, Frontier County, Nebraska, USA. We only included taxa that made up $>1\%$ of the assemblage in any year, and excluded rotifers.

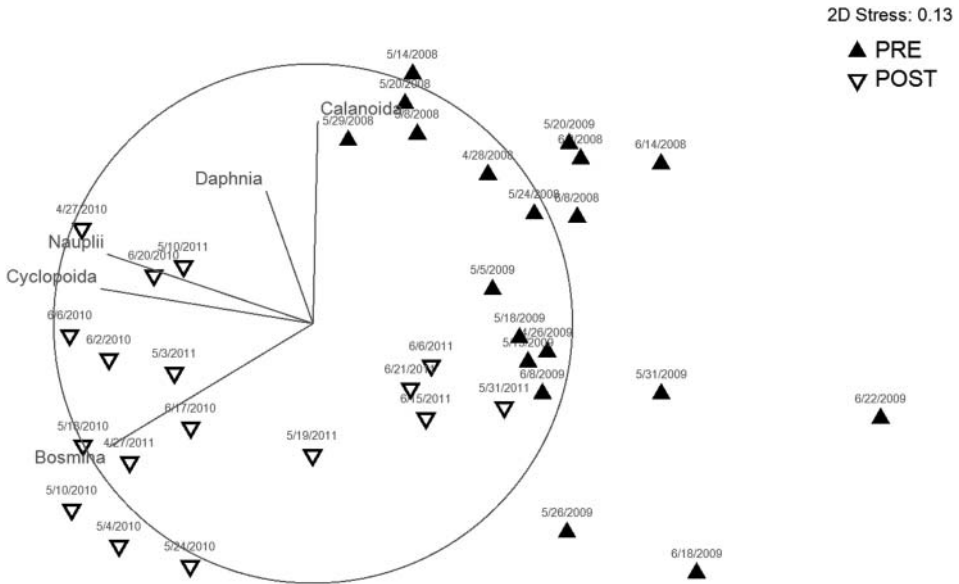


Figure 5. Non-metric multidimensional scaling plot using Bray–Curtis similarities of pre-drawdown and post-drawdown zooplankton assemblages. Taxon-specific vectors indicate Pearson correlations of abundance to period (pre-drawdown versus post-drawdown).

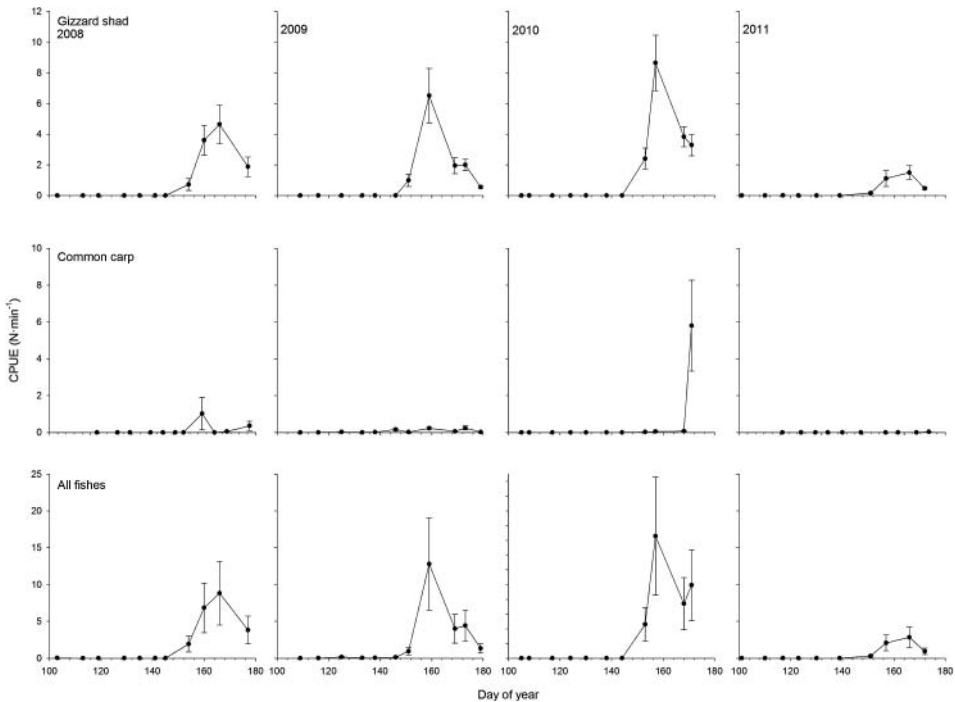


Figure 6. Catch per unit effort of larval gizzard shad (*Dorosoma cepedianum*), larval common carp (*Cyprinus carpio*), and all larval fishes combined as a function of day of year during 2008–2011 at Red Willow Reservoir (Frontier County, Nebraska, USA). Reservoir drawdown occurred between 2009 and 2010 sampling.

Table 3. Total number of weeks with zero and non-zero catches of larval fish from samples collected pre-drawdown and post-drawdown during spring at Red Willow Reservoir, Frontier County, Nebraska, USA. Statistical significance was assumed at $\alpha = 0.05$.

Taxon	Pre-drawdown		Post-drawdown		χ^2	df	p
	Zero	Non-zero	Zero	Non-zero			
Common carp	11	11	16	5	5.5	1	0.02
Gizzard shad	13	9	12	9	0.1	1	0.8
All larval fishes combined	3	19	10	11	19.7	1	<0.0001

occurred during both pre-drawdown and post-drawdown periods (USBR 2013), it is unlikely that increases in nutrient-laden runoff contributed to the increase in Chl-*a* concentration. Similar to what we observed, elevated turbidity and Chl-*a* concentrations are often recorded in conjunction with low water levels (Geraldés and Boavida 2005, 2007), particularly in nearby reservoirs (Olds et al. 2011). Despite a significant difference in dissolved oxygen concentration between pre-drawdown and post-drawdown periods, post-drawdown dissolved oxygen levels were still well above minimal requirements for all fishes in Red Willow (Davis 1975). Neither mean water temperature nor spring warming rate changed, even though the reservoir volume decreased 76%. Other studies in nearby reservoirs have also reported no change in water temperature, despite a large change in reservoir volume (Olds et al. 2011).

Zooplankton assemblage

Zooplankton abundance, population dynamics, and assemblage composition are all affected by several physical and chemical factors, which are largely influenced by water-level fluctuation (Wetzel 2001; Geraldés and Boavida 2007). We observed an increase in

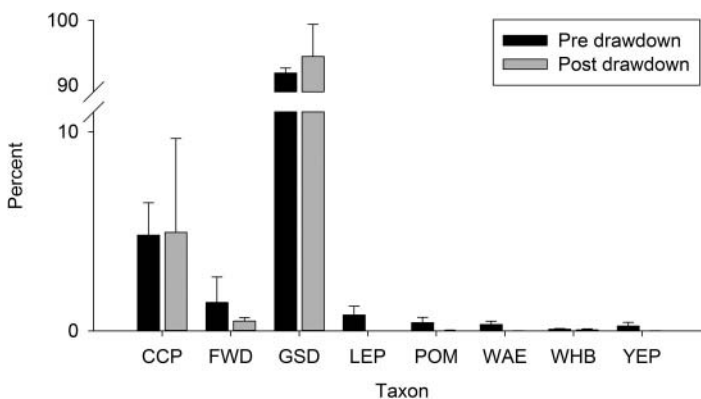


Figure 7. Larval fish assemblage percent composition (including [top panel] and excluding [bottom panel] gizzard shad) from samples collected pre-drawdown and post-drawdown during spring at Red Willow Reservoir, Frontier County, Nebraska, USA. We only included larval fish taxa that made up >1% of the assemblage in any year (when gizzard shad excluded). Taxon abbreviations are CCP, common carp; FWD, freshwater drum; GSD, gizzard shad; LEP, *Lepomis* spp.; POM, *Pomoxis* spp.; WAE, walleye; WHB, white bass; and YEP, yellow perch.

the total zooplankton density as well as the density of several individual taxa – similar to a nearby reservoir during a drought-related drawdown (Olds et al. 2014) – that could have resulted from the increase in Chl-*a* concentration (as a measure of phytoplankton biomass). The increase in Chl-*a* concentration, with a concurrent increase in cladoceran and cyclopoid copepod density and decrease in calanoid copepod density, is consistent with other studies (McNaught 1975; Allan 1976; Byron et al. 1984; Pace 1986). The change in copepod densities could be caused by differences in feeding habits between calanoid and cyclopoid copepods. Calanoid copepods create currents to obtain small food particles (1 μm to 1 mm), whereas cyclopoid copepods are grasping feeders that eat larger food items (Maly and Maly 1974; Kerfoot 1978; Wong 1984). As turbidity and Chl-*a* increased, food items for calanoids could have decreased while those for cyclopoids increased; alternatively, calanoids may have had difficulty detecting their food items as a result of the increased turbidity (Strickler 1982; Andrews 1983; Arruda et al. 1983; Price et al. 1983; DeMott 1986; Légier-Visser et al. 1986; Van Alstyne 1986). It is also possible that changes in zooplankton abundance and assemblage composition were a consequence of changes in predation by a larval fish assemblage that was dissimilar between pre-drawdown and post-drawdown (*sensu* Martin et al. 1981; Turner et al. 2005; Olds et al. 2014).

We also observed a decrease in the size of *Bosmina* spp., copepod nauplii, and *Daphnia* spp. This could have resulted from many factors, including an increase in zooplankton production (i.e., greater abundance of younger [smaller] individuals), changes in predation patterns, and lack of refugia (Turner et al. 2005). However, because we only identified *Bosmina* and *Daphnia* to genus, and copepod nauplii to subclass, it is possible that the observed changes in size were merely changes in abundances of taxa below the taxonomic level to which we identified zooplankters. Regardless, we urge caution when relating the observed changes in the zooplankton assemblage solely to a decrease in reservoir water level, because many complex abiotic and biotic interactions resulting from the drawdown likely influenced the zooplankton assemblage.

Larval fish assemblage

Although the larval fish assemblage was not significantly different between pre-drawdown and post-drawdown, the assemblages were nearly 40% dissimilar (Figures 6 and 7). We believe this lack of significance was a consequence of having to use annual mean abundances (resulting in fewer data points) rather than weekly means, which we used in the zooplankton analysis. Notwithstanding, we believe the larval fish assemblage may have been negatively affected by complex interactions of environmental factors, similar to the zooplankton assemblage.

Several studies have found negative effects (e.g., reduced consumption, decreased condition) of high turbidity levels on larvae and juveniles of several fish species, including bluegill (*Lepomis macrochirus*; Miner and Stein 1993), striped bass (*Morone saxatilis*; Breitburg 1988), and zander (*Sander lucioperca*; Zingle and Paaver 2010). These negative effects can lead to reduced growth rates and thereby impair year-class strength and recruitment. Failure to accumulate enough energy may hinder or stop fish growth during early life stages, which may prevent ontogenetic niche shifts (Werner and Gilliam 1984) that are necessary for increased growth and survival.

Decreased production of offspring could partially explain the changes we observed in the larval fish assemblage. The prolonged low-water period after the drawdown resulted in a concentration of adult sport fish, which had increased vulnerability to anglers (Chizinski et al. 2014; *sensu* Frohnauer et al. 2007) and could have resulted in decreased

adult population densities, consequently resulting in decreased production of offspring. Similarly, entrainment of adult fish through the dam during drawdown could have resulted in decreased adult population densities (*sensu* Stober et al. 1983; Post et al. 2006), thus resulting in decreased production of offspring. Loss of littoral habitat is deleterious to many fishes, particularly when the loss is a consequence of reservoir drawdown (Paller 1997; Frohnauer et al. 2007); low water levels can reduce the availability of adequate spawning habitat (Ploskey 1986; Kallemeyn 1987), which could partially explain the changes we observed in the larval fish assemblage.

Bluegill and green sunfish (*L. cyanellus*), two species present in many reservoirs in this region, are phytophillic at multiple life stages (Crowder and Cooper 1982; Werner and Hall 1977), particularly early life stages (Gotceitas and Colgan 1987; Werner and Hall 1988). Thus, they may also be negatively affected by the loss of aquatic macrophytes as a consequence of extreme reservoir drawdown (Martin et al. 1981; Bettoli et al. 1993). Juvenile walleye are also littoral (Grinstead 1971; Becker 1983) and thus may be negatively affected by the loss of littoral macrophytes as refuge from predation (Werner et al. 1983), or as a source for prey (Lyons 1987). This could explain, at least in part, why the percent composition of *Lepomis* spp. and walleye decreased post-drawdown.

It is also possible that the lack of a significant difference in the larval fish assemblage between pre-drawdown and post-drawdown is simply a function of time. Perhaps, two years were not enough time for the ecosystem to respond in an easily detectable manner given the vagaries of larval fish production, even in systems that experience much more stable conditions. Moreover, although we offer some speculation as to potential factors that may have affected the larval fish assemblage, determining the exact mechanisms involved was beyond the scope of our study.

Conclusions

Most of the dams in the USA were constructed during the 1920s to 1960s (Beaumont 1978), and many of them are approaching or have exceeded their life expectancy of approximately 50 years (Poff and Hart 2002, and references therein). Therefore, extensive and prolonged drawdown for repair or replacement may become the norm, rather than the exception, in coming years (Juracek 2015). We believe that our findings may give reservoir managers some valuable insights into the abiotic and biotic changes they might expect, given the inevitability that additional dams will need to be repaired or replaced in the near future. Our data will also be beneficial for documenting changes when the reservoir is refilled, as there are few studies that document changes in zooplankton and larval fish assemblage dynamics from pre-drawdown to post-drawdown to refill (see Paller 1997). It is important for effective reservoir management that we understand the abiotic and biotic responses of reservoir ecosystems as these imminent changes continue to alter environmental conditions in reservoirs.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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