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Zooplankton Density Increases in an Irrigation Reservoir During Drought Conditions

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Abstract
Harlan County Reservoir, located in south-central Nebraska, entered a drought in 2003, providing an opportunity to monitor the effects of drought on the zooplankton community in this irrigation reservoir. We sampled the zooplankton community at 15 standardized locations every other week from April through the third week of October from 2003-2011. Total zooplankton densities were higher (131.8 ±13.1 L^{-1}) in drought reservoir conditions (2003-2006) than under normal conditions (66.6 ± 9.0 L^{-1}) (2007-2011). The zooplankton community was dominated by copepods throughout the study, with adult and immature (nauplii) copepods contributing 86.5% of the total zooplankton, while *Daphnia* spp. made up only 9.9%. Correlational analyses showed a positive relationship between total zooplankton, copepods and copepod nauplii and chlorophyll *a* and turbidity during normal reservoir conditions. *Daphnia* species showed a negative relationship with chlorophyll *a* during normal conditions and a negative relationship with turbidity in drought conditions. Our results document the dynamics of lower trophic levels during fluctuating water availability; such information will likely improve conservation and management of aquatic ecosystems during future episodes of changing environmental conditions.

Key words: drought, zooplankton, chlorophyll a, turbidity, irrigation reservoir

Zooplankton quickly respond to environmental change, and thus are useful indicators of the trophic status and water quality of freshwater ecosystems (Gannon and Stemberger, 1978). In general, increases in temperature (Wolfinbarger, 1999); nutrients (Feuchtmayr et al., 2010); and phytoplankton (Striebel et al., 2012) increase zooplankton abundance through a bottom up mechanism as it appears some or all of these factors limit zooplankton abundance. Additionally reservoir zooplankton abundance and community composition are impacted by altitude (Illyova and Pastuchova, 2012), chemical parameters (Vincent et al., 2012), and turbidity (Arruda et al., 1983, Shuman, 1990).

Hydrological drought results in low water volume within a reservoir as well as reduced inflows and discharge rates (Lake, 2011). Previous studies on the impacts of drought on zooplankton abundance have reported conflicting results. In Lake Okeechobee, Florida, historically low water levels were associated with dramatic changes in zooplankton community composition, which persisted for five years post-drought (Havens et al., 2007). Year-long zooplankton abundance was 65% higher during a drought-caused low water period in a South American floodplain lake (Chaparro et al., 2011). Conversely, in an oligotrophic high mountain lake, monitored over 20 years, zooplankton abundance was not significantly different between a drought year and normal year, but total phosphorous concentration was higher during the drought year (Garcia-Jurado et al., 2012). Depending on the lake, its trophic status and seasonal dynamics, each body of water seems to present its own challenges to its inhabitants.

Harlan County Reservoir oscillates between lentic and lotic conditions depending on inflow. An existing long-term data set for basic water quality and gross zooplankton parameters allowed an opportunity to evaluate how the zooplankton community (density and assemblage) responded during normal and drought conditions for this region. Additionally, observed differences during this timeframe were correlated to water quality parameters that were compared with drought status previously in this reservoir (Olds et al., 2011). We hypothesized that previously documented increases in reservoir productivity as measured by chlorophyll *a* during sustained drought conditions would follow bottom-up processes and translate into higher zooplankton density compared to normal reservoir conditions.

Methods

Study Site

Located in south-central Nebraska, Harlan County Reservoir was originally built in 1952 by the U.S. Army

Corps of Engineers as a means of flood control for the Republican River basin but is now primarily used as an irrigation reservoir for south-central Nebraska and northern Kansas. The reservoir covers an area of 5,362 ha with 121 km of shoreline, a mean depth of 4 m, and a maximum depth of 18 m (USACE, 2011). Harlan County Reservoir does not thermally stratify during the year, resulting in uniform temperature and dissolved oxygen levels and is considered eutrophic to hyper-eutrophic based on total nitrogen, phosphorous and chlorophyll *a* measurements (USACE, 2007; Olds et al., 2011). Distribution and abundance of zooplankton is homogeneous throughout the reservoir and does not show differences by depth (Maline et al., 2011). As an irrigation reservoir, it exhibits a seasonal pattern of fluctuating water levels (USBR, 1996; USACE, 2011). Between 2001 and 2006, south-central Nebraska experienced a severe drought, resulting in a loss of more than 50% of the conservation pool as compared to historic levels (NOAA, 2011; Olds et al., 2011; USBR, 2011). Water volume returned to normal levels in 2007 and remained at those levels through 2011 (USBR, 2011). Average inflow during drought years was a net loss of 29,325,893 cubic meters and average discharge was 16,000,819 cubic meters, mostly released in 2003. Conversely, average inflow was 199,017,565 cubic meters and average discharge was 123,915,855 cubic meters (Table I; USBR, 2011).

Sampling and Data Collection

Sampling was conducted at 15 stations distributed across the reservoir (Peterson et al., 2005). Sampling occurred every other week except for a period in June and July when sampling was conducted on a weekly basis. Chlorophyll *a* and zooplankton samples were collected as described by Olds et al. (2011) and Peterson et al. (2005), respectively, for each sample day. Additionally water quality factors including temperature, turbidity and dissolved oxygen were recorded as described by Olds et al. (2011).

Statistical Analysis

Monthly means and standard errors were calculated for comparisons between drought and normal reservoir conditions from April to October. Because of lack of normality, chlorophyll *a* values were square root transformed, temperature values were squared and turbidity, dissolved oxygen and all zooplankton values were log transformed. We separated total zooplankton into subgroups of "copepods", "nauplii", and "*Daphnia*". "Copepods" included adult Calanoida and Cyclopoida as well as their copepodid stages. Copepod nauplius stages "nauplii" were selected, based on biological significance for some larval fish species (Dettmers and Stein, 1992; Shepherd and Mills, 1996; Nakata, 2005; Sullivan et al.; 2011) and the limits of taxonomic identification established in the database. The third taxon, "*Daphnia*", included all *Daphnia* spp., (*D. pulicaria, D. retrocurva, D. lumholtzi*) and their immature stages. Monthly means of total zooplankton, copepods, nauplii, and *Daphnia* were individually compared between drought conditions (2003-2006) and normal conditions (2007-2011) using Student t-tests in SAS (2012). Total zooplankton means were also compared by month from April through October using a one-way ANOVA using SAS (2012) with statistical significance set at $\alpha = 0.05$. In addition, a Pearson correlation matrix was calculated comparing total zooplankton, copepods, nauplii, and *Daphnia* with chlorophyll *a*, turbidity, temperature, and dissolved oxygen.

Results

Total zooplankton density was higher ($F(61)=5.68$, $p<0.0001$) during drought conditions (131.8 ±13.1 L^{-1}) than during normal conditions (66.6 ± 9.0 L^{-1}). Specifically, total zooplankton density was greater during drought conditions from June through September (Fig. 1). Similarly, *Daphnia* (drought: 13.0 ±1.7; normal: 6.7 ±0.7), nauplii, (drought: 66.6 ±9.0; normal: 32.2 ±5.2) and copepods (drought: 48.1 ±4.2; normal: 25.5 ±2.5)

Table I. Yearly means for hydrological data pertaining to Harlan County Reservoir during the study. Hydrological data is presented for irrigation purposes and thus a single year presented below (i.e. 2003) begins in October, 2002 through September, 2003. Negative inflow numbers, as reported by USBR, likely represent loss through seepage or evaporation.

Year	Condition	Volume (m^3)	Inflow (m^3)	Discharge (m^3)	Precip (cm)
2003	Drought	194,698,118	8,054,683	63,269,351	48.23
2004	Drought	141,321,349	-124,311,021	0	36.60
2005	Drought	150,172,557	18,080,482	733,926	23.62
2006	Drought	159,591,788	-19,127,714	0	49.81
2007	Normal	213,354,537	323,472,622	26,194,372	62.64
2008	Normal	352,834,081	178,012,199	58,332,928	62.64
2009	Normal	393,090,330	98,164,755	146,985,016	74.70
2010	Normal	399,072,085	258,928,811	246,660,600	87.60
2011	Normal	394,057,776	136,509,437	141,406,360	69.29

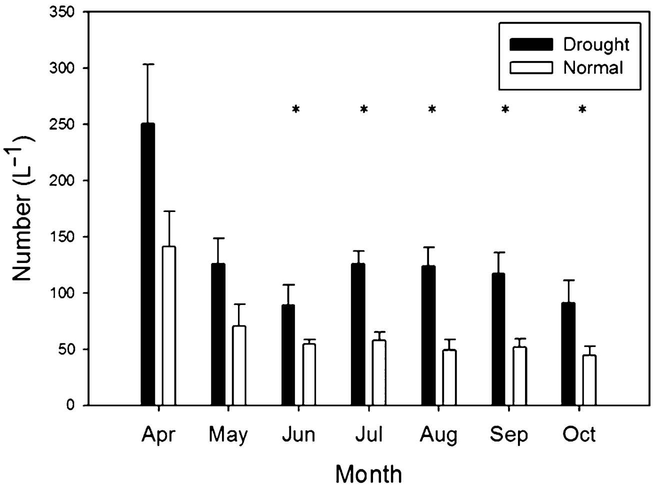

Figure 1. Monthly means of total zooplankton during drought (2003-2006) and normal (2007-2011) years for the sampling period. Asterisks denote significance between individual monthly means.

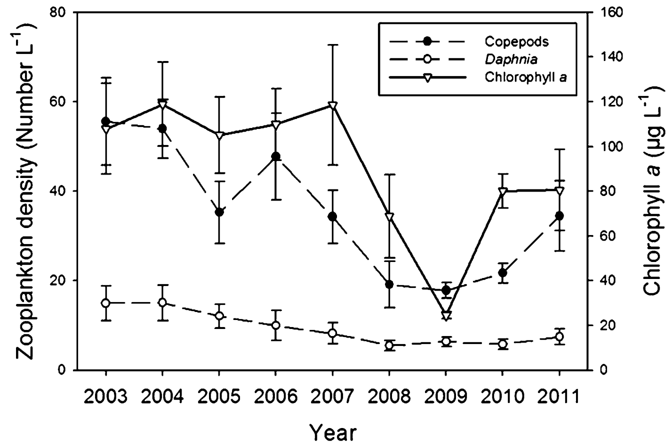

Figure 2. Yearly means of adult copepods, *Daphnia* plotted against yearly means of chlorophyll *a*. Drought conditions are 2003-2006 and normal years are 2007-2011.

were also significantly higher ($F(61)=3.21$, p=0.002, $F(61)=4.88$, p<0,0001 and $F(61)=5.52$, p<0.0001, respectively) during drought conditions. Harlan County Reservoir is dominated by copepods which constitute 86.5% of total zooplankton when adult and immature copepods are combined.

Under normal conditions, total zooplankton were positively correlated with chlorophyll *a*, but during drought conditions, there was no significant relationship. More specifically, copepods and nauplii were positively correlated with chlorophyll *a* under normal conditions, whereas *Daphnia* were negatively correlated with chlorophyll *a* under normal conditions. Similarly, total zooplankton, copepods and nauplii showed a positive correlation with turbidity during normal conditions, but no relationship under drought conditions. Conversely, *Daphnia* show no correlation with turbidity under normal conditions but a negative correlation with turbidity during the drought conditions (Table II). The yearly mean of copepods tracked with chlorophyll *a*, most years (2004-2006 and 2007-2008) (Fig. 2). In 2009, when chlorophyll *a* levels were at their lowest point, copepod density was not reduced and numbers gradually rose with increasing chlorophyll *a*.

Discussion

Our hypothesis was supported as zooplankton density, dominated by copepods, was higher during drought conditions. However, the zooplankton response to changes associated with a drought/normal cycle may be reservoir-specific as a review of literature found a wide variety of documented drought responses for zooplankton communities. No changes to

Table II. Pearson correlation matrix values for water quality parameters and zooplankton counts during drought and normal years.

		Copepods	Nauplii	*Daphnia*	Total Zooplankton
Chlorophyll *a*	Drought	0.09734	0.1676	-0.27639	0.08023
	Normal	**0.52564***	**0.51909***	**-0.3458***	**0.51609***
Turbidity	Drought	0.06437	-0.0045	**-0.5904***	-0.09153
	Normal	**0.56974****	**0.56411****	-0.18497	**0.5517****
Temperature	Drought	0.00957	-0.19565	**-0.5248***	-0.21278
	Normal	-0.31655	**-0.384***	0.17394	**-0.36838***
Dissolved Oxygen	Drought	-0.17275	0.08887	0.37287	0.04887
	Normal	0.24386	**0.3527***	-0.10077	0.31661

** $p < 0.001$
* $p < 0.05$

zooplankton communities were observed during seasonal droughts on shallow lakes (McGowan et al., 2005). Standing crop of large zooplankton was higher in a Missouri River reservoir during a low-water year (Martin et al., 1981). Alternatively, total zooplankton decreased at Lake Okeechobee during an extended drought (Havens et al., 2007); similarly, an 8 fold decrease in mesozooplankton during drought years was reported in a North Carolina estuary (Wetz et al., 2011). This disparity of results supports the need for more case study reports on zooplankton response to drought conditions as was indicated by Lake (2011).

Explanation as to why zooplankton populations increased during this drought is complicated by abiotic and biotic trophic interactions within Harlan County Reservoir. The response could be as simple as a concentration effect from reduced water quantity, as Nadai and Henry (2009) observed for a temporary drought on a marginal lake in Brazil. However, due to the length of the wet period (4 years) following the drought, we would have expected to see increasing abundances as zooplankton adjusted to the greater quantity of water.

Water residence time within the reservoir could also help explain the increased density of total zooplankton during drought conditions. Beaver et al. (2013) demonstrated increased flow rates moving water through the reservoir system can decrease zooplankton density during discharge events. Overall this pattern holds true for Harlan County Reservoir, with consistent discharge events happening only during normal years. Although 2011 suggests a more complex relationship for Harlan County Reservoir as zooplankton densities and discharge volume were high during normal years. Downstream analysis would be required to support this hypothesis.

Changes in lower (phytoplankton) or upper (zooplanktivorous fish) trophic levels could be responsible for the greater zooplankton density during drought conditions at Harlan County Reservoir. Eutrophic lakes in temperate regions showed an increase in phosphorus levels during droughts which led to an increase in phytoplankton production (Noges and Noges, 1999; Noges et al., 2003; Beklioglu and Tan, 2008). However, phytoplankton productivity and biomass have also been reported as reduced during a drought (Huang et al., 2004; Wetz et al., 2011). Increased water levels have resulted in greater macrophytic cover and stronger year-classes of larval fish which can reduce the abundance of zooplankton in reservoirs (Martin et al., 1981) and natural lakes (Havens et al., 2007). However, a top-down influence by larval fish may be absent in Harlan Reservoir, as larval gizzard shad densities were highest during drought conditions when zooplankton densities were also higher (Sullivan et al., 2011).

Response of zooplankton to drought water levels was consistent throughout the season and community assemblage remained similar. The density of total zooplankton and recorded taxa were consistently greater from April through October during drought conditions. The lack of significance for April and May is most likely a result of greater variance in abundances related to natural succession of zooplankton during these months (Hairston, Jr. et al., 2000). The stability of community assemblage observed in this study differed from most reported studies that found change in taxa during drought periods. Villar-Argaiz et al. (2002) observed an increase in rotifer abundance during drought, followed by the return of calanoid copepods when water returned to normal. The general taxonomic categories used in this study, as well as mesh size of the collection net, limit our assessment of species-specific response and possible changes in rotifer numbers, but the ratio of cladocerans to copepods was similar during drought and normal water level conditions.

Previous work on this reservoir indicated that chlorophyll *a* and turbidity were significantly lower during most months in normal conditions, while dissolved oxygen was slightly higher and temperature displayed no significant differences during normal water inflow conditions (Olds et al., 2011). The positive correlation in normal years between adult copepod, nauplii and total zooplankton densities with chlorophyll *a* and turbidity levels indicate an association between these trophic levels. In fact, these two measurements may be linked, as turbidity in Harlan County Reservoir may be driven by suspended organic material based on phytoplankton presence. The decrease in chlorophyll *a* levels and turbidity when water quantity is greater may indicate that food sources limit zooplankton abundance in these conditions. Similar relationships between drought increasing turbidity and subsequently a reduction in zooplankton abundance were described by Lake (2011) for Lake Chad. Turbulence in river systems also altered zooplankton densities (Sluss et al. 2008). Significant correlations between specific taxa and both dissolved oxygen and temperature between drought and normal conditions indicate that relationships may exist, as reported by Morales-Baquero et al. (2006).

This case study examined changes in zooplankton taxa abundance between drought and normal conditions for a northern temperate irrigation reservoir which is classified as a eutrophic system. Finding greater zooplankton densities during periods of reduced water quantity is contrary to some reported studies but similar to others and demonstrates the variable responses of different aquatic systems. Changes in water level in an irrigation reservoir assert selection pressure on organisms therein and results should apply to any body of water that has seasonal and/or annual variation in water quantity and nutrient availability. Future evaluations should consider investigating size structure and biomass changes. The authors hope that sharing of these observations will encourage others to investigate existing datasets or develop new data that will explore the trophic changes associated with drought conditions. With the stochastic nature of water availability, studies that document the dynamics of lower trophic levels across different environmental conditions will likely improve conservation and management of aquatic ecosystems.

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