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The zooplankton community of a turbid Great Plains (USA) reservoir in response to a biomanipulation with common carp (*Cyprinus carpio*)

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The effects of a biomanipulation with adult carp (*Cyprinus carpio*) removals on water quality and the abundance, composition, and body size of zooplankton were investigated in Bowman-Haley Reservoir, North Dakota in a two-year study. In both years, decreases in zooplankton abundance, *Daphnia* body size, and *Daphnia* clutch size in carp-uneradicated areas coincided with the appearance and subsequent domination of the blue-green algae *Aphanizomenon.* Concurrently, in areas where carp were eradicated, water clarity increased, total suspended solids decreased, and prevalence of blue-green algae blooms decreased. As a result of these improved feeding conditions, zooplankton abundance, *Daphnia* size, and *Daphnia* clutch size increased. Because adult carp, which fed to a very limited extent on zooplankton in spring, represented over 95% of the fish removed, changes in the zooplankton community were not attributable to decreased predation by fish. Furthermore, it is unlikely that predation by fish significantly affected the zooplankton community in the extremely turbid water observed prior to fish removals. In this study, depletions of the benthivorous carp in areas of a shallow, turbid reservoir resulted in changes to zooplankton communities similar to those observed with removal of planktivorous fishes in other water bodies. These results indicate that bioturbation by carp can affect zooplankton in ways similar to predation by planktivorous fishes.

Key words: carp, invasive fishes, zooplankton, biomanipulation, reservoir ecology

INTRODUCTION

Whether aquatic ecosystem productivity is controlled from the "bottom-up" by food availability and related physical-chemical factors (Lindeman 1942; Hall and Hyatt 1974; Schindler 1978) or from the "top-down" by predation or other influences from higher trophic levels (Carpenter et al. 1987; Elser and Carpenter 1988, Northcote 1988) remains a matter of much discussion and investigation. Carpenter et al. (1985) suggested that systems are regulated by both; nutrient supply establishes potential productivity, or capacity, for production; food web structure determines actual productivity.

Studies of zooplankton population dynamics and respective influences of fish (from the top-down) and phytoplankton (from the bottom-up) have added much to the debate. Predation by planktivorous fishes has been shown to affect abundance, composition, and size of zooplankton (Brooks and Dodson 1965; Galbraith 1967; Hutchinson 1971; Post and McQueen 1987; Elser and Carpenter 1988). Similarly, zooplankton community structure has been used to determine if planktivorous fishes are over-abundant (Mills et al. 1987). Both top-down and bottom-up processes affecting zooplankton may also act in a given instance or site through changes in fish species composition (Williams and Moss 2003) and confounding natural variations in environment associated with fish exclusion or introduction experiments (Lougheed et al. 2004).

Most studies investigating zooplankton control mechanisms, however, have been performed in relatively deep, clear, dimictic water bodies containing large crops of planktivorous fishes (Lammens et al. 1990). Under these conditions, high densities of sight-feeding, planktivorous fishes are capable of directly and significantly altering zooplankton communities. Only a few studies, e.g., Hanson and Butler (1990), have investigated effects of fish on zooplankton in shallow, wind-swept, turbid water bodies dominated by benthivorous fishes. Although it may seem reasonable that under these conditions direct predation by fish would have minimal effects on zooplankton communities, fish may still play an important role in indirectly determining zooplankton community structure and abundance. Bioturbation (sediment disturbance) by benthivorous fishes such as the common carp (*Cyprinus carpio*) can affect turbidity, aquatic vegetation, nutrient cycling, and phytoplankton (Robel 1962; Crivelli 1983; Meijer et al. 1990; Breukelaar et al. 1994) and can therefore affect zooplankton.

Knowledge of zooplankton community structure and factors that influence it can thus give valuable insight into lake restoration strategies. Manipulation of zooplankton populations is often used as a lake rehabilitation strategy to improve water quality (Shapiro et al. 1975; Shapiro and Wright 1984). By reducing predation pressure on zooplankton, large cladocerans can increase in abundance, along with their ability to control algae blooms. In relatively clear water bodies, reducing the abundance of planktivorous fishes by direct removal or by stocking piscivorous fishes often results in increased abundance of large cladocerans and improved water quality (Mills et al. 1987).

In shallow, turbid reservoirs dominated by benthivorous fishes, it is unclear whether such manipulations of the fish community will result in changes to zooplankton communities. In turbid water bodies with few planktivorous fishes, more information is needed on the potential to improve water quality and influence zooplankton communities through the removal of abundant benthivorous fishes.

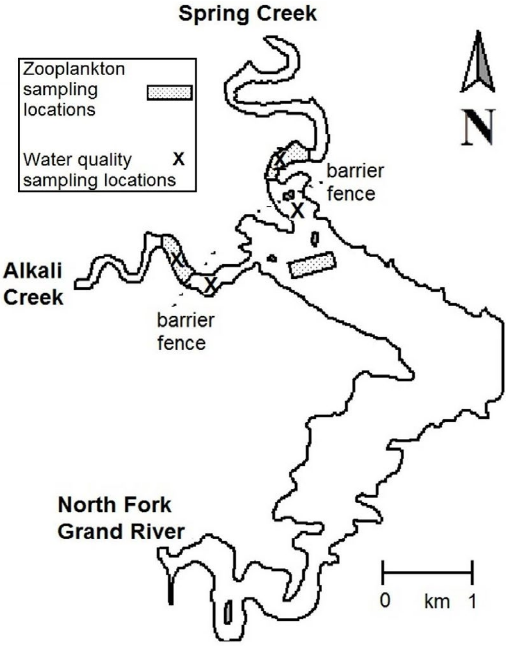

Figure 1. Map of study area including zooplankton and water quality collection locations.

The objective of this two-year study was to evaluate the potential to improve water quality and affect zooplankton communities by biomanipulation through removal of a dominant benthivorous fish, the common carp. Our hypothesis was that carp removals would result in indirect benefits to water quality through increased water clarity and decreased occurrence of blue-green algae, thus improving feeding conditions for zooplankton. With improved feeding conditions, zooplankton would increase in abundance and size and cladocerans would become more prevalent.

Study site - Bowman-Haley Reservoir, a 712 ha, eutrophic impoundment in southwestern North Dakota, USA, has a maximum depth of approximately 9 m, an average depth of less than 3 m, and does not stratify. Three tributaries, Spring Creek, Alkali Creek, and the North Fork of the Grand River, drain 896 km^2

of agricultural land. Study areas in the Spring Creek and Alkali Creek arms were within the slackwater created by the reservoir, had maximum depths of 3 m, and no measurable current during summer.

The reservoir is shallow and wind-swept. High turbidities often result from windy periods when waves stir shallow sediments. Such stirring, exacerbated by a lack of submerged vegetation, also causes a re-suspension of nutrients. When sediments settle and water begins to clear during periods of calm weather, blooms of blue-green algae occur. Data collected in 1988 (Martin 1989) indicated that phytoplankton were dominated by green algae until early June when blooms of the blue-green algae *Aphanizomenon* began to dominate. During summer, 1988, *Aphanizomenon* was from 50 to over 100 times more abundant than all other phytoplankton combined (Martin 1989).

The fish community of Bowman-Haley Reservoir had for several years prior to this study been dominated by benthivorous fishes, predominantly carp (more than 1,000 kg/ha), and densities of planktivorous fishes were low (about 1 kg/ha; Bonneau 1999).

METHODS

Carp removal - To reduce carp abundance in the reservoir, powdered rotenone was applied at 4 ppm near the mouths of Spring Creek and Alkali Creek during peak carp spawning migrations in early June, 1994 (hereafter Year 1) , and again near the mouth of Spring Creek in early June, 1995 (hereafter Year 2). After rotenone application and before detoxification, barrier fences of 4.5 x 9 cm wire mesh were placed near the mouths of Spring Creek and Alkali Creek in Year 1 and Spring Creek in Year 2 to prevent adult carp from re-entering these areas from the reservoir. A second barrier fence in Alkali Creek and a low-head dam in Spring Creek, both located at the upstream ends of rotenone-treated sections, prevented adult carp from re-entering these sections from upstream, untreated areas (Fig. 1). These fences remained in place until the ice moved them out in late fall.

Water quality - Presence or absence of blue-green algae blooms was documented visually at approximately daily intervals from May through August in treated areas and in the main reservoir near the dam. Relative frequency and severity of blue-green algae blooms were documented for treated and untreated sites for each month. Abundance of blue-green algae at each site was then classified as absent, rare, common, or abundant for each month from May through August. Water transparency was measured with a Secchi disk above and below carp barriers approximately each week for four weeks prior to carp removals and each week for four weeks following carp removals. Water samples were collected near the surface with a VanDorn water sampler at the same locations weekly from mid-May through July. Water samples were analyzed by the North Dakota State Department of Health and Consolidated Laboratories (Bismarck, ND) for total suspended solids (mg/l), total dissolved solids (mg/l), total nitrate + nitrite (mg/l) , and total phosphorous (mg/l).

Zooplankton - In Year 1, zooplankton were sampled in treated areas near the mouths of Spring Creek and Alkali Creek, and in untreated areas in the main reservoir approximately every two weeks (seven occasions) beginning the last week of April and ending in mid-July. In Year 2, zooplankton were collected in the untreated areas in the main reservoir, in treated areas of Spring Creek, and in untreated areas of Alkali Creek approximately every two weeks (seven occasions) beginning the last week of April and ending in mid-July. All samples were collected with a No. 20 plankton net towed horizontally just under the surface along transects. On each sampling date, three tows were made at each location. Samples were adjusted to an exact volume of 250 ml and two 2 ml subsamples

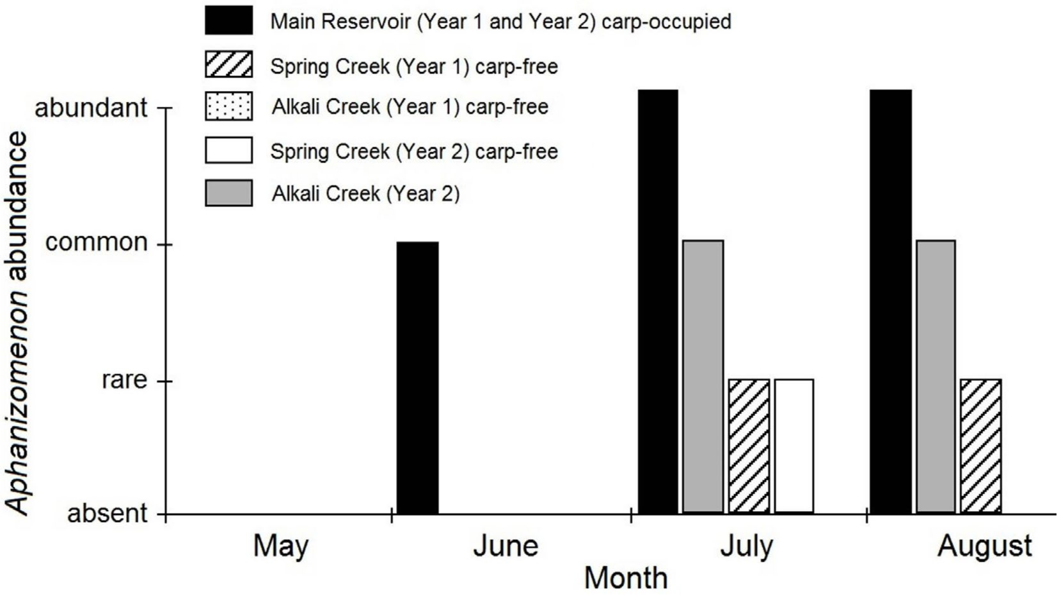

Figure 2. Relative abundance (4 possible ranks) of the blue-green algae A*phanizomenon* in carp-occupied and carp-free areas of the main reservoir, Spring Creek, and Alkali Creek.

were counted from each sample. Zooplankton were identified as *Daphnia* spp., *Bosmina* spp., other cladocerans, cyclopoid copepods, calanoid copepods, and copepod nauplii. A subsample of 50 *Daphnia* from each location and sampling date was measured and eggs per *Daphnia* enumerated (Paloheimo 1974).

Daphnia size (length) was evaluated for differences between rotenone-treated and untreated areas with a t-test. *Daphnia* clutch size through time within treated and untreated areas was evaluated with ANOVA (F-test). We hypothesized that *Daphnia* length would be greater in treated areas than untreated areas, and that clutch size would increase through summer in treated areas. In both cases, a $P<0.05$was required for significance.

RESULTS

Benthivorous fish (carp) removal - Adult carp constituted 99.5% of the fish killed by weight in Year 1 and 94.9% of the fish killed by weight in Year 2 (Table 1). Carp densities within the tributaries exceeded 9,900 kg ha^{-1} in Year 1. Fenced, treated areas remained carp-free through summer.

Table 1. Total weight (kg) of fish killed following application of rotenone to tributaries of Bowman-Haley Reservoir, North Dakota.

	1994		1995	
Species	Spring Creek	Alkali Creek	Spring Creek	NF Grand River
Adult carp	104 000	20 313	44 147	89 107
River carpsucker	261	0	1 558	4 451
White sucker	108	0	50	16
Northern redhorse	19	1	77	30
Juvenile carp	88	8	540	360
Walleye	33	3	4	12
Other	42	4	10	20

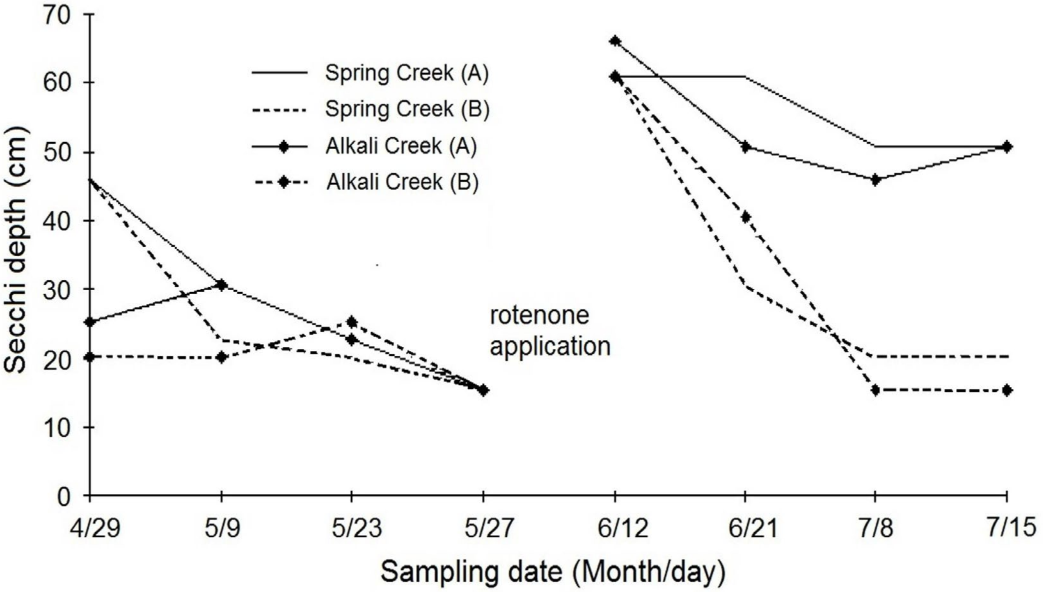

Figure 3. Secchi depths in Spring Creek and Alkali Creek before and after rotenone applications. Dashed lines represent those areas to which carp were allowed to return.

Water Quality - During summers of Years 1 and 2, severe blooms of blue-green algae characteristic of earlier years were common in the main reservoir and in untreated areas in the tributaries. In rotenone-treated areas, however, blooms of blue-green algae occurred only rarely in some locations and not at all in others (Fig. 2).

Water clarity.- Water clarity increased within 24 hours of rotenone applications. Two weeks following carp removals, Secchi depths remained at approximately 50 cm deeper than pre-removal Secchi depths. In areas where carp were allowed to return, Secchi depths decreased by 30 to 40 cm, but in nearby areas where carp were excluded, Secchi depths decreased by approximately 10 cm (Fig. 3). Plumes of clearer water often extended from the mouths of tributaries into the main body of the reservoir during the weeks following carp removals. At one point, a distinct plume of clear water extended over 400 m into the reservoir from the mouth of the Grand River before a change in wind direction mixed the water.

Nutrients and suspended and dissolved solids- No change was observed in total phosphorous concentrations or total dissolved solids following carp removals; phosphorus concentrations typically fluctuated between 0.1 and 0.4 mg/l. Total nitrate+nitrite concentrations increased briefly following removals but never exceeded 0.02 mg/l. Total suspended solids decreased in the tributaries following each rotenone application (Fig. 4). Suspended solid concentrations gradually increased in areas where carp were allowed to return but remained at lower levels in areas where carp were excluded.

Zooplankton abundance - Zooplankton were completely removed from areas treated with rotenone in both Year 1 and Year 2. Rotenone toxicity lasted for approximately one week and within two weeks zooplankton were present in low numbers. After five weeks, zooplankton were from three to five times more abundant than before carp removals at each location in both years. Zooplankton densities in untreated areas (main reservoir in Years 1 and 2 and Alkali Creek in Year 2, however, were declining from May through July (Fig. 5).

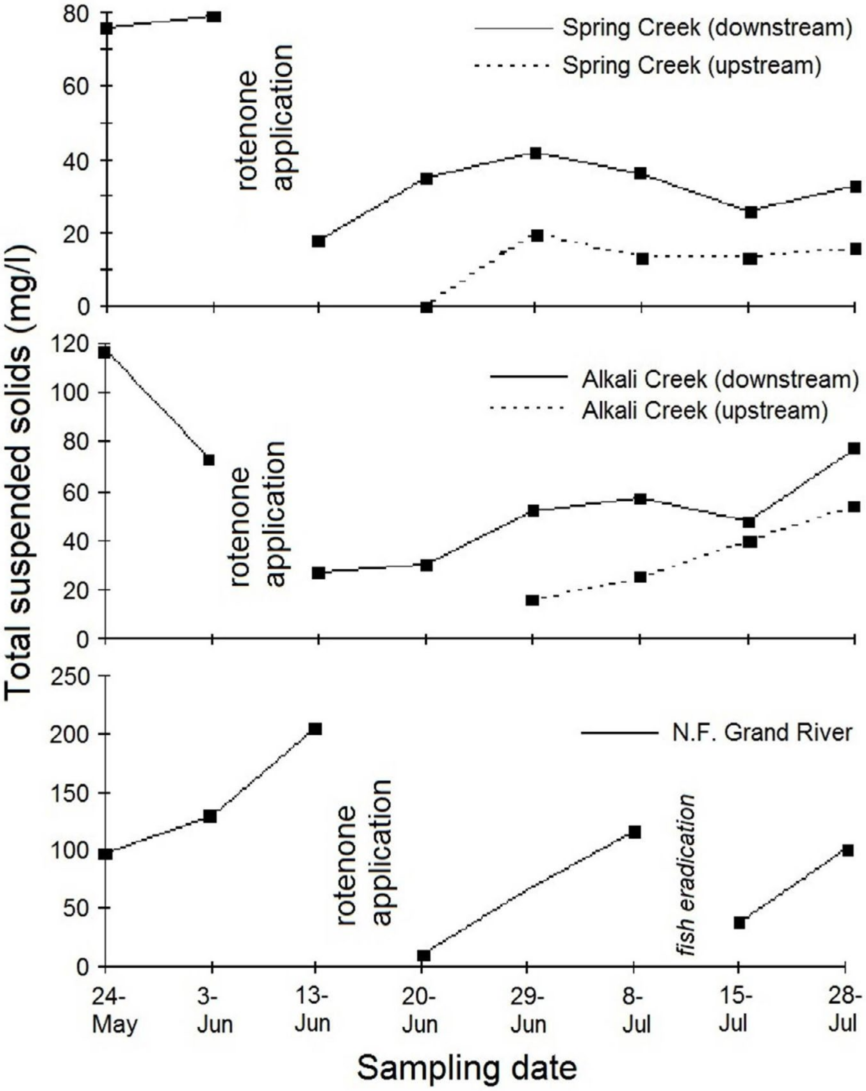

Figure 4. Concentrations of total suspended solids in Spring Creek, Alkali Creek, and the Grand River before and after rotenone applications. Dashed lines represent those areas to which carp were allowed to return.

Bosmina, cyclopoid copepods, and copepod nauplii increased most in abundance in treated areas. *Bosmina* were nearly absent at all locations prior to carp removals but increased up to 100 fold in treated areas. Copepods remained the dominant group of zooplankton throughout the study at all locations, constituting from 50 to over 90% of the zooplankton. During mid-May, *Daphnia* constituted nearly 50% of the zooplankton community but declined in abundance thereafter.

***Daphnia* size and clutch size -** *Daphnia* were the largest zooplankton collected in all samples but large *Daphnia* were absent or at least extremely rare or absent (Fig. 6). No *Daphnia* over 1.2 mm in length were sampled at any location or time. *Daphnia* size increased significantly in rotenone-treated areas (t-test; $P<0.05$) within two months of carp removals even though *Daphnia* size was decreasing in the reservoir at this time. Prior to fish removals,

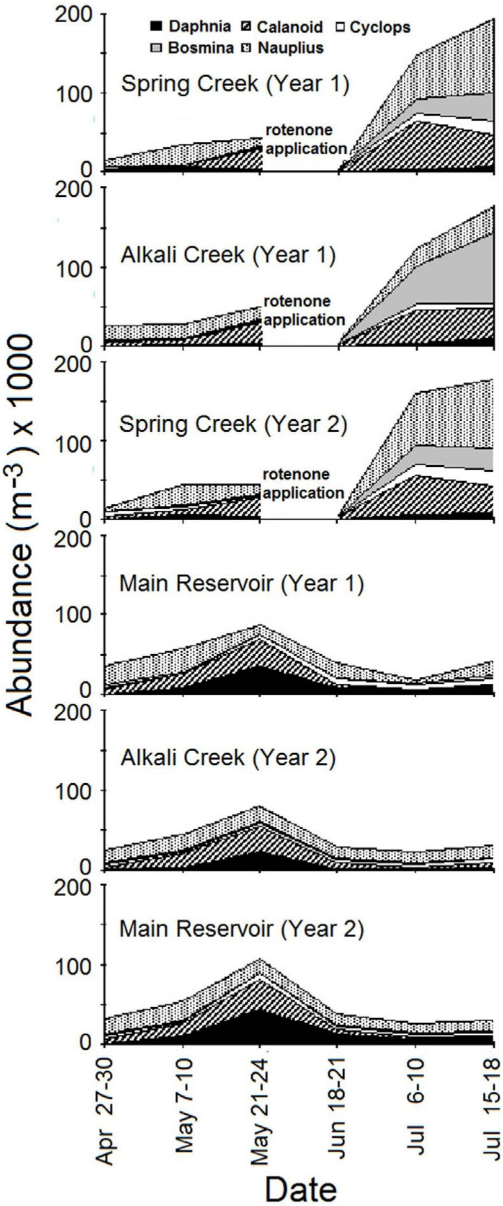

Figure 5. Zooplankton abundances before and after rotenone applications in Year 1 (Spring Creek and Alkali Creek) and Year 2 (Spring Creek) and in Alkali Creek, Year 2 (carp-occupied) and in the main reservoir (carp-occupied), years 1 and 2.

from 4 to 10% of *Daphnia* were longer than 0.9 mm. Five weeks following carp removals, 23 to 32% of *Daphnia* were longer than 0.9 mm whereas only 5% of *Daphnia* exceeded this length in untreated areas (main reservoir and Alkali Creek in Year 2).

In both years, *Daphnia* clutch size decreased steadily through spring and summer in untreated areas. In treated areas, however, *Daphnia* clutch size increased (F-test; $P<0.05$; Fig. 7).

DISCUSSION

In areas of rotenone application, where benthivorous fish (mainly carp) were removed, water clarity increased, total suspended solids decreased, and blooms of blue-green algae diminished. Coinciding with improvements to water quality were changes in zooplankton community structure such as increases in zooplankton abundance and *Daphnia* size.

Concurrently, decreases in zooplankton abundance and size in the reservoir occurred through late spring and summer as blue-green algae increased in abundance. Blue-green algae is a poor food source for zooplankton (Lampert 1987) and has been shown to decrease zooplankton size (Gliwicz and Lampert 1990), feeding rates (Gliwicz and Siedlar 1980), and clutch sizes (Matveev 1986; Luecke et al. 1990), and increase zooplankton mortality rates (Gentile and Maloney 1969). During periods when blue-green algae were not abundant, inorganic turbidity was often high. Like blue-green algae, inorganic turbidity has been shown to limit zooplankton abundance and size by interfering with feeding (McCabe and O'Brien 1983; Hart 1987, 1988; Kirk 1991).

Further evidence indicates that feeding conditions rather than predation by fish was structuring the zooplankton community. The zooplankton community of Bowman-Haley Reservoir was dominated by copepods and lacked large cladocerans. High densities of copepods relative to cladocerans is expected in the presence of blue-green algae and high turbidity (Hart 1987; Koenings et al. 1990). Copepods are better able to feed under these

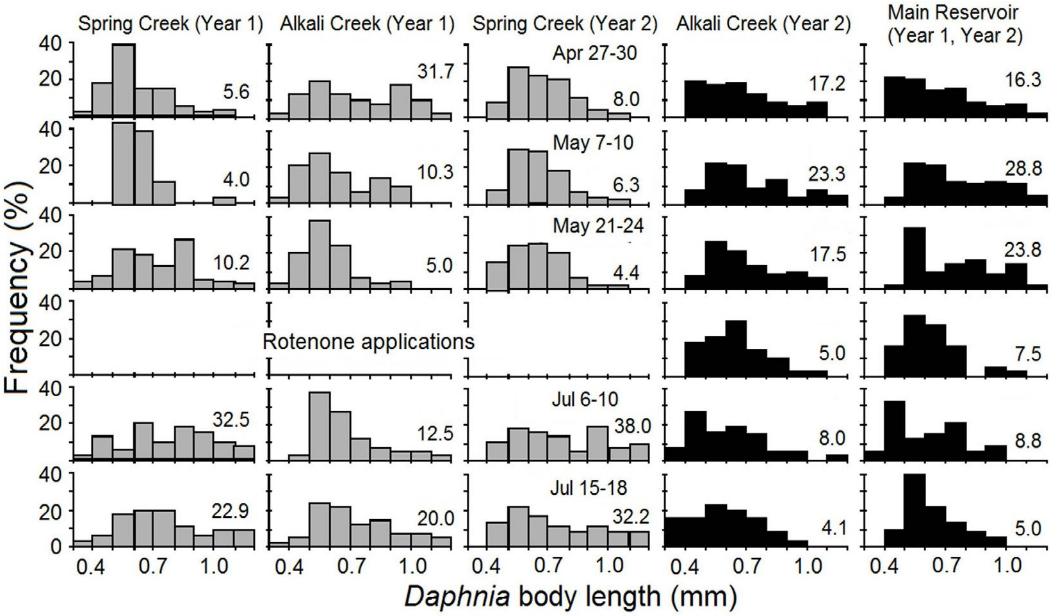

Figure 6. Length distributions of *Daphnia* before and after rotenone applications in Year 1 (Spring Creek and Alkali Creek) and Year 2 (Spring Creek) and in Alkali Creek, Year 2 (carp occupied) and in the main reservoir (carp occupied). Numbers represent the percent of *Daphnia* exceeding 0.9 mm in length.

conditions because they are selective feeders and are better able to avoid blue-green algae (Gliwicz 1977; Pace 1986). If predation by fish were determining zooplankton community structure, one would expect *Bosmina*, which were among the smallest zooplankton present, to have an advantage (Post and McQueen 1987) yet they were not abundant in the reservoir or in the tributaries prior to fish removal. As feeding conditions improved (decreased blue-green algae abundance and turbidity) following fish removals, however, *Bosmina* abundance increased up to 100 fold. Also, adult carp represented 95 to 99% of the fish removed. Although carp collected from the main reservoir fed to a limited extent on *Daphnia* and other large zooplankton in summer, carp collected in spring prior to removals fed mainly on chydorids (Bonneau 1999). This is not surprising since turbidity was extremely high prior to fish removals. Furthermore, changes in the zooplankton community were not observed in the main reservoir in either Year 1 or Year 2 even though total fish biomass was reduced by nearly 75 percent. Changes in water quality (and improved feeding conditions for zooplankton) within the main body of the reservoir, however, did not become evident during this study.

Although predation by planktivorous fish has been shown in clear waters to exert strong control over zooplankton populations (Lammens et al. 1990), in turbid waters, zooplankton communities are probably more affected by unfavorable feeding conditions rather than by predators (Lougheed et al. 1998; Lougheed and Chow-Fraser 1988). In Bowman-Haley Reservoir, carp removal resulted in improved feeding conditions for zooplankton by increasing water clarity, increasing abundance of submerged macrophytes, decreasing turbidity, and decreased occurrence of blue-green algae blooms. The resulting increases in zooplankton abundance and size is desirable for improved water quality (Shapiro et al. 1975; Shapiro and Wright 1984) and sport fish production (Mills et al. 1987).

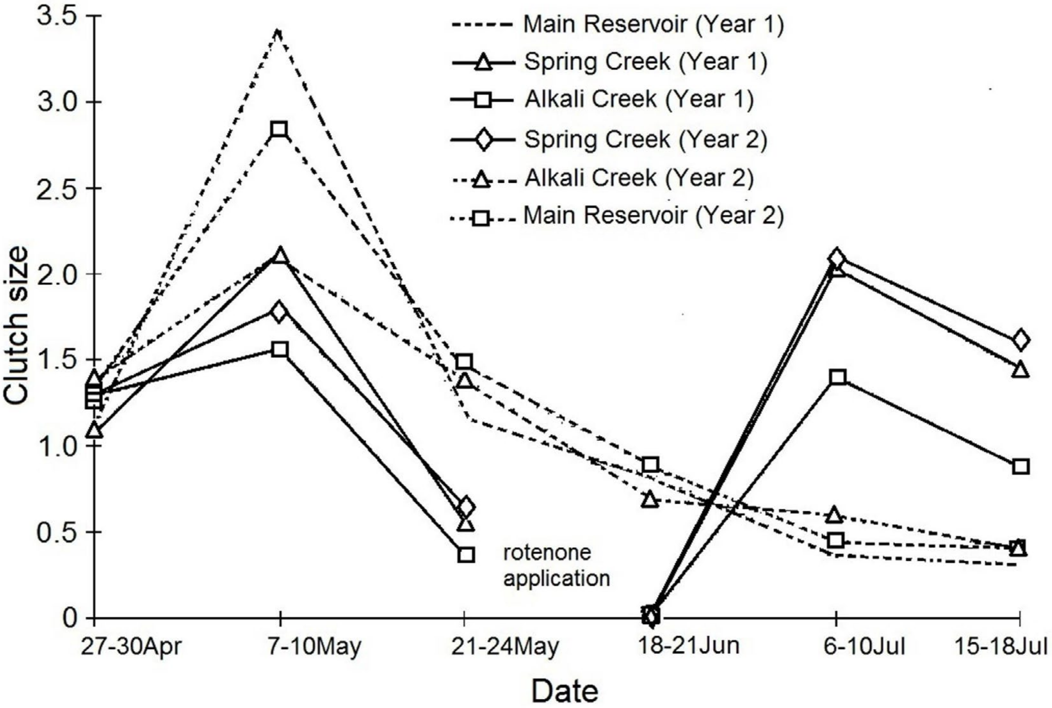

Figure 7. *Daphnia* clutch size before and after rotenone applications in Year 1 (Spring Creek and Alkali Creek) and Year 2 (Spring Creek) and in Alkali Creek, Year 2 (carp-occupied) and in the main reservoir (carp occupied).

The indirect effect of carp exclusion shown in this study has been seen elsewhere. A study in experimental enclosures found that although carp did not have a direct effect on zooplankton community structure in the enclosures, they exerted an indirect effect as more carp led to higher turbidities and nutrient load, resulting in reduced total zooplankton biomass (Loughheed et al. (1998,a,b). In contrast, Khan et al. (2003) found that carp in ponds consumed zooplankton and led to a trophic cascade, where Cladocerans were eliminated and algal blooms resulted. Whether through direct or indirect effects, a species such as carp, which has proved to be a dominant species in many waters (Cahn 1929; Weber and Brown 2009), can thus be an effective agent for initiating biomanipulation efforts of lakes, ponds, and of reservoirs (Bonneau 1999), changing the water body from a turbid system prone to algal blooms to a clearer system with more macrophytes and better habitat for sight-feeding predators, including many sport fishes. Observations suggest that shifts in zooplankton community structure have likely persisted following this study. Fisheries managers at Bowman-Haley Reservoir reported improved water clarity in the tributaries and in the main reservoir during the three years following this study (Emil Berard, North Dakota Game and Fish, unpublished data). Secchi depths, which rarely exceeded 0.6 m prior to carp removals, increased to 3 m during summer, 1998. Blooms of blue-green algae, which occurred throughout summer prior to and during this study, were much less frequent and severe. Reductions in carp abundance did not result in noticeable changes in water quality or the zooplankton community within the main body of the reservoir during this study; significant increases in water clarity and submerged macrophyte abundance and decreases in blue-green algae abundance did not become apparent until three years later. Improved feeding conditions have likely resulted in changes to the zooplankton community which will further benefit water quality and fish production. Future research should investigate shifts in zooplankton community structure that have occurred as a result of changing reservoir ecology.

In a review of the effects of carp on aquatic ecosystems, Weber and Brown (2009) depicted a schematic of how aquatic restoration might be conducted in relation to deliberate changes in carp populations (biomanipulation; their Fig. 3). That figure builds on empirical food web considerations of how carp can be used in biomanipulation efforts in waters such as Bowman-Haley Reservoir (Bonneau 1999). Additional detailed field studies are needed to further identify specific pathways by which carp biomanipulations may affect aquatic habitats and other aspects of the aquatic community in different situations. The dominance of carp in influencing habitat (Cahn 1929; Weber and Brown 2009) and their numerical dominance in Bowman-Haley Reservoir exert a strong impact on the system. Their reduction and maintenance control may result in major changes in the habitat and aquatic community. In contrast, in some other situations, biomanipulations with other fish species may yield more subtle responses and may be more difficult to maintain. In both situations, and especially the latter, bottom-up nutrient control through improved watershed practices may yield the best long-term solution (Jeppesen et al. 2007).

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