Response of benthic macroinvertebrates to carp (*Cyprinus carpio*) biomanipulation in three tributaries of a eutrophic, Great Plains reservoir, USA

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The effects of biomanipulation through eradication of benthic omnivorous fish species on benthic macroinvertebrate fauna were investigated in three tributaries of Bowman-Haley Reservoir, North Dakota, USA. Fish were eradicated with rotenone from the lower sections of each tributary. Adult common carp (*Cyprinus carpio* L) constituted over 95% of the fish killed by weight. Barrier fences were installed to prevent adult fish from repopulating the fish-free stream sections during summer. Benthic macroinvertebrates were monitored from one month before to three months after each rotenone application both upstream and downstream of the fish barriers. Also, in the second year of the study, three 8 m x 8 m fish exclosures were constructed, one near the mouth of each stream. Benthic invertebrate samples were collected inside and outside of exclosures for approximately two months after their installation. After fish eradications in two successive years, chironomid densities increased up to 50-fold in the fish-free areas but remained low elsewhere. Chironomid length and taxa richness increased upstream of the fish barriers. In areas where submerged vegetation became established after carp removal, benthic community richness increased compared to non-vegetated, fish-free areas. Chironomid densities also increased within the exclosures but remained lower than upstream of barriers.

Key words: Cyprinus carpio, *fish eradication, Chironomidae, predation, trophic cascade*

INTRODUCTION

Fish have been shown to play an important role in the structuring of freshwater benthic communities (Healey 1984; Hixon 1986; Thorp 1986; Miller and Crowl 2006). Although many studies have found fish to significantly alter freshwater benthic macroinvertebrate densities or size distributions (Andersson et al. 1978; Post and Cucin 1984; Mittlebach 1988; Richardson et al 1990; Hayes et al. 1992), and benthic community structure (Crowder and Cooper 1982; Gilinsky 1984; Wilcox and Hornbach 1991; Diehl 1992), others have found fish to have relatively insignificant effects on freshwater benthic communities (Thorp and Bergey 1981a,b; Allan 1982; Reice 1983; Flecker and Allan 1984).

The importance of fish in structuring benthic communities and the mechanisms involved vary with the fish species, size and density, and habitat conditions. In some cases, predation by fish allowed for increased abundance of some species of benthic macroinvertebrates by suppressing benthic competitors or predators (Hall et al. 1970; Crowder and Cooper 1982; Gilinsky 1984; Morin 1984). Other studies, however, have found that increased predation by fish resulted in decreased total densities, species richness, and diversity of benthic macroinvertebrates (Wilcox and Hornbach 1991; Diehl 1992). Some studies have reported that predator-mediated habitat modification was the main cause of changes in benthic community structure (Wilcox and Hornbach 1991) whereas others found direct predation

rather than habitat change was the main influence on the benthic community (Crowder and Cooper 1982; Gilinsky 1984; Post and Cucin 1984; Hershey 1985).

Several studies in freshwater lentic environments have investigated the effects of sight feeding fishes such as bluegill (*Lepomis macrochirus*) on the benthic community using predator exclosures or enclosures (Crowder and Cooper 1982; Bohanan and Johnson 1983; Gilinsky 1984; Morin 1984; Mittlebach 1988; Butler 1989). Exclosure studies can complement more natural but less controlled field investigations. Although enclosure studies offer valuable insights into fish and benthic macroinvertebrate interactions, results may be difficult to apply to larger scales due to the effects of unnatural confinement of predator and prey (Virnstein 1978) and altered water movements (Butler 1989). Field studies often lack sufficient controls (Likens 1985), but the results they yield may be more applicable to wild populations. Comparing results from replicated small-scale exclosure experiments to those collected during larger-scale field studies, it is possible to gain a better understanding of relationships between fish and benthic macroinvertebrates.

Previous studies have been focused on the effects of benthic omnivores such as the common carp (*Cyprinus carpio*), on benthic community structure using enclosures or small ponds (Andersson et al. 1978; Wilcox and Hornbach 1991; Batzer et al. 2000), while other studies have examined these effects on a larger scale (Ball and Hayne 1952; Hayes et al. 1992). Cahn (1929) hypothesized that carp have the capacity to affect the entire food web in ecosystems in a dominant manner. Subsequent studies identified both bottom-up and top-down impacts of carp and the role of carp biomanipulations in altering the ecology of habitats (Weber and Brown 2009) through wide-ranging effects on water quality (Parkos et al. 2003), phytoplankton, macrophytes

(Batzer et al. 2000), zooplankton, benthic macroinvertebrates, forage fish, predaceous fish, and waterfowl (Miller and Crowl 2006, Bajer et al. 2009). Most of these previous studies were conducted in small ponds, exclosures and mesocosms. This study examines the response of the benthic macroinvertebrate community to fish eradication in three tributaries of a large (712-ha) eutrophic, Great Plains reservoir containing a large population of benthic omnivorous fish dominated by common carp. Natural field investigations were complemented by the use of small exclosures.

Study Area

Bowman-Haley Reservoir, located in southwestern North Dakota, U.S.A. (Fig. 1), was built in 1966 by the U. S. Army Corps of Engineers as a multi-purpose reservoir. Three tributaries, Spring Creek, Alkali Creek, and the North Fork of the Grand River (hereafter Grand River), drain 1,155 km^2 of agricultural land. Maximum depth of the reservoir is approximately 9 m with an average depth of less than 3 m. The fish community at the start of this project in 1993 was dominated by adult common carp. Carp populations were estimated at over 4,360 kg ha^{-1} (800 lbs acre^{-1}; Bonneau 1999). Other species present included walleye (*Sander vitreus*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), bluegill, white sucker (*Catostomus commersoni*), northern redhorse (*Moxostoma macrolepidotum*), and river carpsucker (*Carpiodes carpio*).

Methods

Sampling. As part of a two-year field investigation (1994 and 1995) in an attempt to reduce the carp population in the reservoir, North Dakota Game and Fish Department personnel treated, Alkali Creek, Spring Creek, and the Grand River, with rotenone during the peak of the carp spawning migration in Year 1 (June 6-24). After the application of rotenone and before its detoxification, barrier fences (4.5 cm x 9
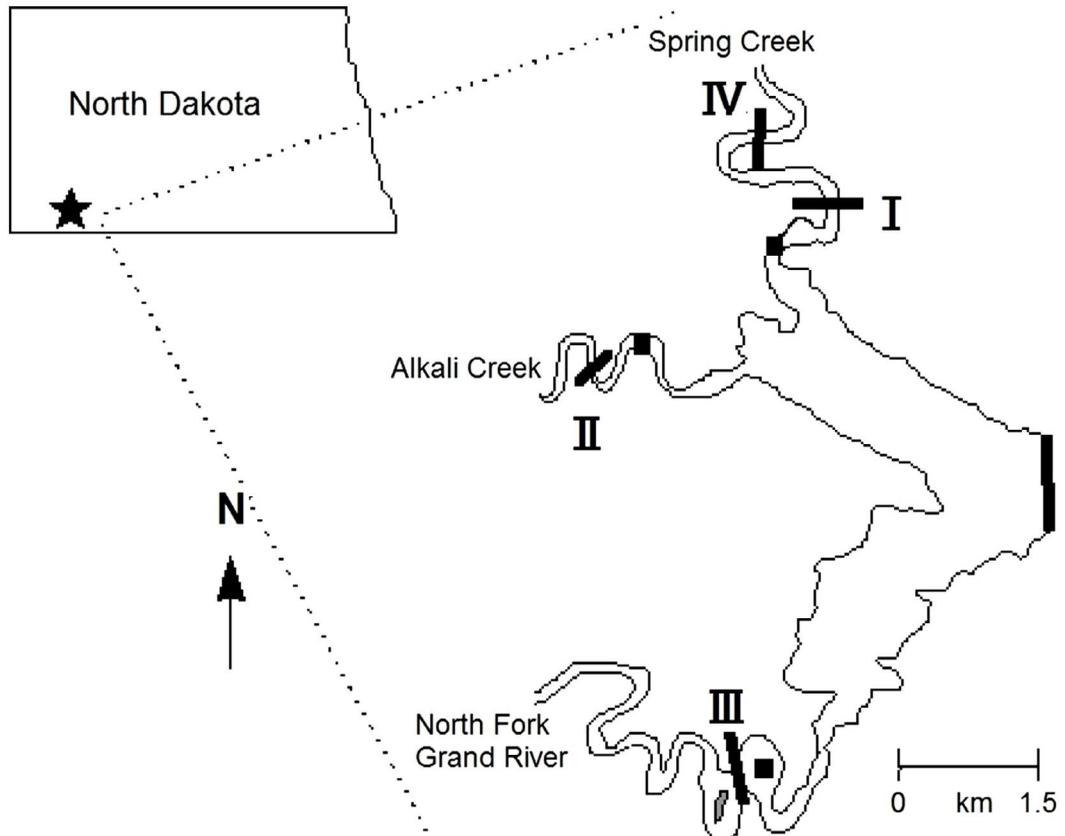
Fig. 1. Map of study area. Roman numerals I and II mark barriers used in Year 1 (1994); III and IV mark barriers used in Year 2 (1995). Squares indicate locations of fish exclosures.

cm mesh) were placed near the mouths of two of the tributaries, Spring Creek and Alkali Creek, to prevent adult carp from re-entering the streams from the reservoir. Other barrier fences in Alkali Creek and at a low-head dam in Spring Creek, both located at the upper ends of the treated stream sections, prevented adult fish from re-entering the treated sections from untreated areas upstream. The barrier fences were washed out during late winter of Year 2, allowing fish to migrate back into the tributaries from the reservoir. Rotenone was re-applied to two of the tributaries, Spring Creek and the Grand River, in early June of Year 2. A barrier fence was installed in Spring Creek and a nylon net was used to block fish passage in the Grand River. All dead fish were counted and a subset of fish were measured and weighed.

Fish barriers: upstream and downstream.
In Year 1, the benthic macroinvertebrate community in Spring Creek and Alkali Creek was sampled before carp eradications (May 25-30) and afterward (June 25 - July 10). Samples were collected with a 232.3 cm^2 Ekman grab sampler, sieved through a 1mm sieve, and preserved in 90% ethanol. The Ekman sampler was effective in collecting uniform samples in the soft, silt substrates present in the study area. Thirty samples were randomly collected upstream (10 samples before eradication and 20 samples afterward) and downstream (10 samples before eradication and 20 samples afterward) of the barrier fences. All upstream and downstream samples were collected within 0.5 km of the fish barriers to insure sampling of similar habitats on each side of the barriers. The

area sampled was within the slack water created by the reservoir. Maximum depth in this area was less than 2 m and substrates consisted mainly of silt. All samples were collected in areas devoid of submerged vegetation to avoid fouling of the sampling device.

Similarly, in Year 2, we sampled benthic invertebrates in Spring Creek and the Grand River before eradications (May 25-29) and afterward (June 27- July 2). Fifteen samples were collected upstream (5 samples before eradication and 10 samples afterward) and downstream (5 samples before eradication and 10 samples afterward) of the fish barriers. Although Alkali Creek was not treated with rotenone in Year 2, and thus contained fish, samples of benthic macroinvertebrates were collected in the same area and manner as in Year 1 (Fig. 1).

Fish exclosures. In late June of Year 1, i.e., 2 to 3 wk after carp eradications, three 8 m x 8 m fish exclosures (4.5 cm x 9 cm mesh) were installed, one near the mouth of each tributary below the fish barriers. Water depth within each exclosure ranged from 0.5 m to 1.5 m. Twelve samples of benthic macroinvertebrates were collected for each exclosure (six inside and six outside) during each of three periods: June 25-30 (referred to hereafter as June), July 15-20 (hereafter July), and August 5-10 (hereafter August; Fig. 1).

Vegetated versus non-vegetated areas. In both study years, benthic macroinvertebrates were sampled in vegetated areas as well as non-vegetated areas upstream of the fish barrier in Spring Creek. Samples collected in vegetated areas were collected with identical procedures to samples collected in non-vegetated areas. Benthic invertebrate samples were also collected from the main body of the reservoir in non-vegetated areas. Ten samples were collected in deep water (> 2 m) and 10 samples were collected in shallow water (< 2 m) in both years.

Benthic macroinvertebrates were classified into the following groups: Chironomidae, other Diptera (non-chironomid), Ephemeroptera, Odonata, Coleoptera, Oligochaeta, Amphipoda, Gastropoda, and "other" (those rarely encountered). For samples collected in Year 1, we measured total body length (mm) of a random subsample of 30 chironomids collected downstream of each barrier, 30 chironomids collected upstream of each barrier, and 50 chironomids collected from the main reservoir. For samples collected in Year 2, total body length (mm) was measured from a random subsample of 25 chironomids collected downstream of each barrier, 25 chironomids collected upstream of each barrier, and 50 chironomids collected from the main reservoir. For the August sampling period only, total body lengths were measured from a random subsample of 20 chironomids collected inside and outside of each exclosure. Although head capsule length is often chosen as a length measurement for organisms such as Chironimids that can compress their bodies (Richardi et al. 2014), body length is typically closely correlated with head capsule length (e.g. De Cássia et al. 2011), For each location and year, 50 randomly selected chironomids were identified to genus (Pennak 1978).

ANALYSIS

Homogeneity of variance was evaluated for benthic invertebrate densities and chironomid lengths using F_{max} tests (Sokal and Rolph 1969). Based on the evaluation, data were transformed with a log (x+1) transformation to obtain homogeneity of variances. All benthic invertebrate densities and chironomid lengths were compared upstream and downstream of fish barriers and inside and outside of each exclosure using Student's t- tests (two-tailed) on transformed data (Steele and Torrie 1980). Alpha for all tests was 0.05. As an indicator of heterogeneity of chironomid density distributions, variance to mean ratios were calculated for samples collected upstream and

Table 1. Total weight (kg) of fish killed following application of rotenone to tributaries of Bowman-Haley Reservoir, North Dakota, Year 1 (1994) and Year 2 (1995).

	Year 1		Year 2	
Species	Spring Creek	Alkali Creek	Spring Creek	N.F. Grand River
Adult carp	104000	20313	44147	89107
River carpsucker	261	0	1558	4451
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

downstream of fish barriers. Relatively high ratios indicate heterogeneous chironomid density distributions whereas lower ratios indicate more uniform density distributions.

RESULTS

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.

Chironomids were the dominant benthic macroinvertebrate sampled in all areas of the tributaries and in the reservoir, representing up to 100% of the organisms in a sample. In most of the samples in non-vegetated areas, chironomids and oligochaetes were the only benthic macroinvertebrates present.

Fish barriers: upstream and downstream. In Year 1, immediately prior to fish eradications, chironomid densities averaged less than 160 organisms-m^{-2} in both Spring Creek and Alkali Creek. Within 4 wk following fish eradications, chironomid densities upstream of barriers increased 50-fold in Spring Creek (mean = 8,116 organisms-m^{-2}) and 15-fold in Alkali Creek (mean = 2,476 organisms-m^{-2}). Downstream of barriers, where fish could re-inhabit, chironomid densities remained below 175 organisms-m^{-2} in both streams and were significantly lower than densities upstream of the fish barriers (P < 0.001).

Prior to fish eradications in Year 2, chironomid densities averaged less than 350 organisms-m^{-2} in both Spring Creek and the Grand River. Within 4 wk following the eradications, chironomid densities upstream of the fish barriers increased over 12-fold in Spring Creek (mean = 4,185 m^{-2}) and over 20-fold in the Grand River (mean = 7,268 m^{-2}). Downstream of the barriers chironomid densities were significantly lower than densities upstream of the barriers (P < 0.001; Fig. 2). Chironomid densities within the reservoir averaged less than 183 organisms-m^{-2} in both years.

Chironomid length also differed significantly above and below barriers. In the first year, chironomids were significantly longer above the barriers (mean = 11.8mm; n = 60) than below the barriers (mean = 5.7mm; n = 60) in Spring Creek and Alkali Creek (P < 0.001). In Year 2, chironomids sampled upstream of the barrier in Spring Creek were significantly longer (mean = 10.2mm; n = 26) than those sampled downstream of the barrier (mean = 5.8mm; n = 26; P < 0.001) but no difference in chironomid length was found upstream (mean = 5.8mm; n = 25) and downstream (mean = 5.6mm; n = 25) of the barrier in the Grand River (P > 0.1). Lengths of chironomids collected in the main reservoir were not significantly different between Year 1 (mean = 5.5mm; n = 51) and Year 2 (mean = 5.6mm; n = 51; P > 0.1) nor were they significantly different from chironomid lengths downstream of the barriers (P > 0.1; Fig. 3).
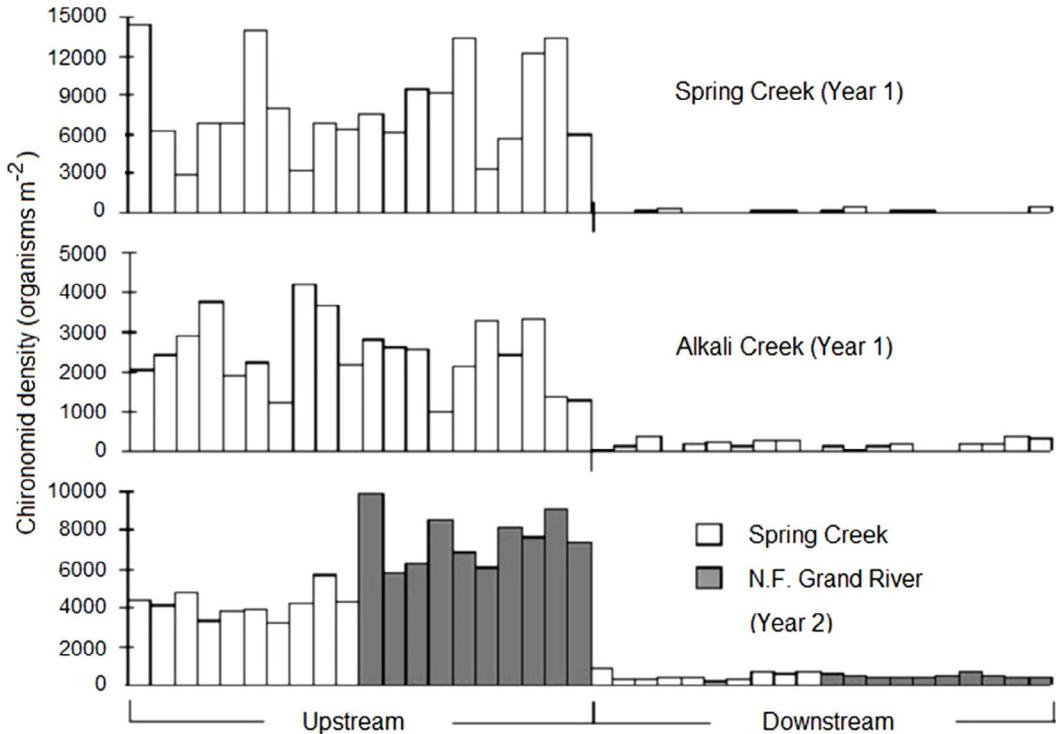
Fig. 2. Density of chironomids upstream (exclosure) and downstream of fish barriers within 4 wk following fish eradications in Spring Creek (Year 1), Alkali Creek (Year 1), and Spring Creek and N.F. Grand River (Year 2).

No change in the composition of chironomids at the genus level was detected. Over 90% of the chironomids in all locations and times were of the genus *Einfeldia*.

Although fish barriers were not maintained through the winter, repeated fish exclusion in Spring Creek from June through late winter of Year 1 and from June through August of Year 2 was associated with changes in benthic community structure. Densities of Amphipoda (P < 0.001), Ephemeroptera (P < 0.001), and Coleoptera (P < 0.05) were significantly higher during Year 2 than during Year 1 (Fig. 4). Chironomid densities, however, were lower following exclusion in Year 2 than in Year 1 (P < 0.001).

The variance to mean ratios of chironomid densities upstream of the barriers were higher than those downstream of the barriers in four of five comparisons indicating their distributions were heterogeneous. The most homogeneous chironomid distributions were in the main reservoir (Fig. 5).

Fish exclosures. Significant increases (P < 0.05) in chironomid densities occurred in all three exclosures within the first 4 wk of their installation (Table 2). Significantly higher (P < 0.05) chironomid densities were maintained inside two of the three exclosures (Spring Creek and Alkali Creek) through the two-month sampling period. Chironomid length was not significantly different inside versus outside of any exclosure in August (P > 0.05).

Vegetated versus non-vegetated areas. Although chironomids were the most abundant macroinvertebrate, their densities in the benthos were significantly lower in vegetated areas than in non-vegetated areas in both Year 1 (P < 0.001) and Year 2 (P < 0.01).
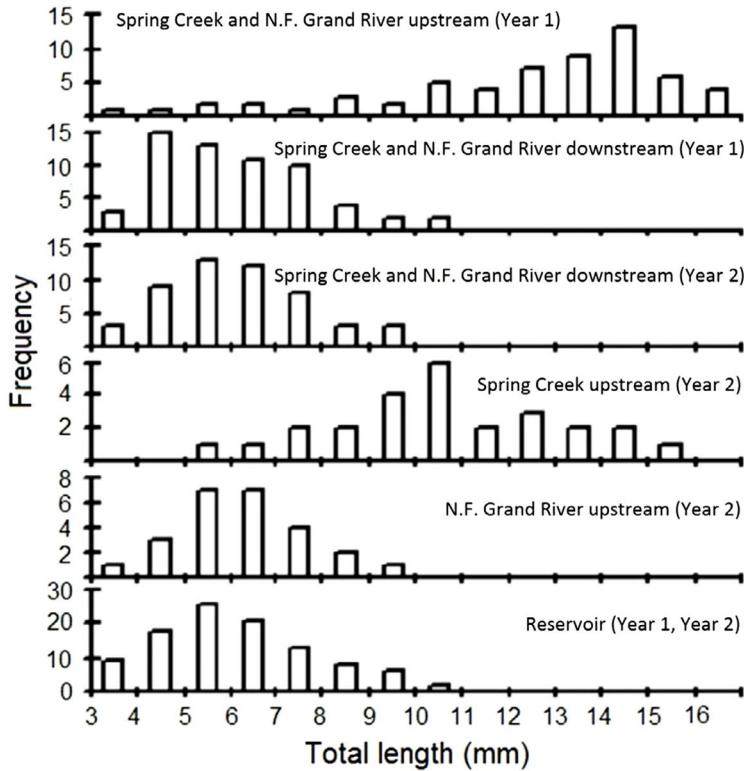
Fig. 3. Length-frequency distributions of chironomids collected upstream (exclosure) and downstream of fish barriers and in the main reservoir. Chironomid lengths were combined for the Spring Creek and N.F. Grand River (downstream) samples and for the main reservoir (Year 1 and Year 2).

Densities of other taxa also differed between vegetated and non-vegetated areas (Fig. 6). Benthic macroinvertebrate richness was higher in vegetated areas than in non-vegetated areas (Fig. 7); in the latter, chironomids and oligochaetes were often the only macroinvertebrate organisms present.

Discussion

In this study, the removal of large numbers of carp, a benthic omnivore, resulted in major changes in the benthic macroinvertebrate community. Chironomid densities, in particular, increased above all fish barriers within four weeks following carp removal. Chironomid lengths increased above both barriers in Year 1 and above one barrier in Year 2. Carp are known to actively forage on chironomids (Summerfelt et al. 1970; Eder

and Carlson 1977). The observed increases in chironomid densities and sizes after carp eradication strongly suggests that direct predation of chironomids by carp was the main cause of low chironomid densities before carp eradications and below exclusion barriers after eradications. Also, the smaller chironomid size in the presence of carp appeared to be due to high predation by carp and not to a shift in species composition.

A second result of carp eradication was the establishment of submerged macrophytes above the barriers. The ability of carp to suppress submerged macrophytes is well documented (Cahn 1929; Sigler 1955; Crivelli 1983; Bajer et al. 2009; Weber and Brown 2009). Above fish barriers in Bowman-Haley Reservoir submerged macrophyte coverage increased 10 - 100% following carp removal (Bonneau
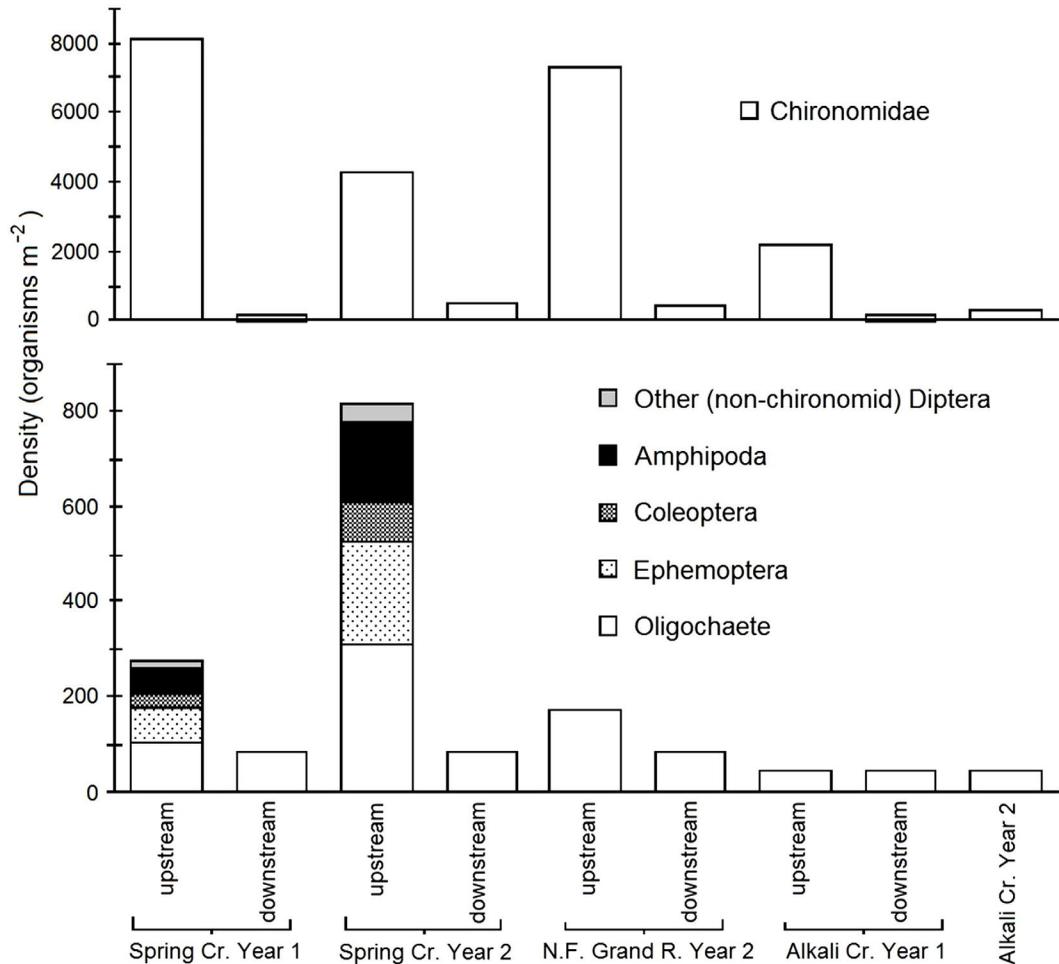
Fig. 4. Average density of organisms upstream (exclosure) and downstream of fish barriers in Year 1 and Year 2.

1999). In our study, increases in submerged macrophyte abundance were associated with increased benthic macroinvertebrate richness. Whereas chironomids and oligochaetes were often the only organisms collected in areas without submerged macrophytes; many taxa, including Amphipoda, Ephemeroptera, and Gastropoda were collected in vegetated areas. Most taxa (but not Oligocheata and Chironomidae) were more abundant in vegetated than in non-vegetated areas. Higher benthic macroinvertebrate richness in vegetated than non-vegetated areas has been widely reported (Gerking 1962; Dvorac and Best 1982; Rabe and Gibson 1984) and

is consistent with the idea that increased habitat complexity provides more niches and refuges from predators (Smith 1972; Murdoch and Oaten 1975). The importance of habitat complexity in Bowman-Haley Reservoir was underscored by our observations that fish trapnets set continuously during summer in the main reservoir were colonized by high densities of benthic macroinvertebrates even though chironomids and other taxa were rare or absent in the substrate.

Although studies of the effects of carp in particular on benthic macroinvertebrates are not common (Weber and Brown 2009, their
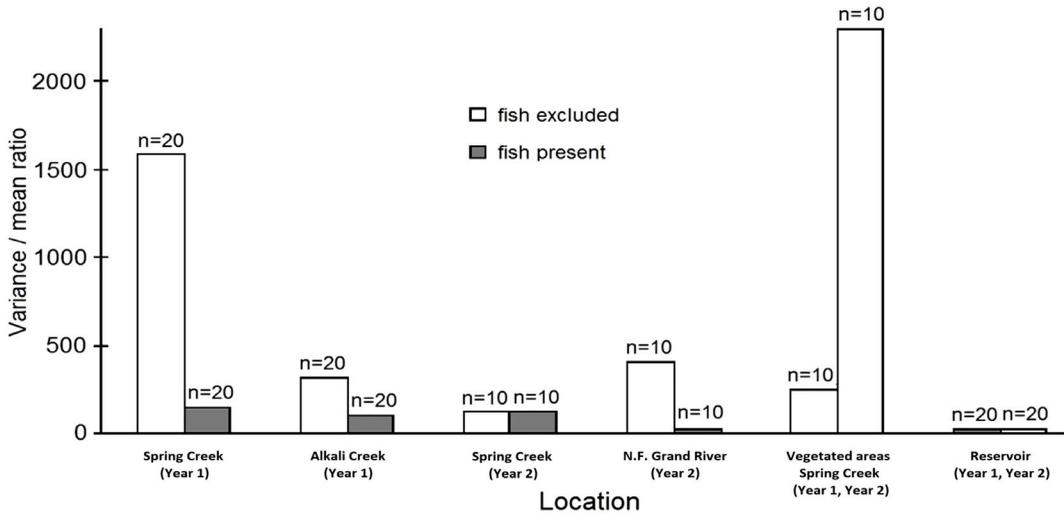
Fig. 5. Variance to mean ratios of chironomid densities upstream (exclosure) and downstream of barriers, in vegetated areas above the barrier in Spring Creek, and in the main reservoir.

Table 2), some studies support our findings. Parkos et al. (2003) found that in mesocosms, high carp biomass was negatively related to macroinvertebrate abundance. Schrage and Downing (2004) found that following fish removal (including carp) from Ventura Marsh in Clear Lake, Iowa, density of benthic invertebrates increased; they attributed the increase in size of chironomids to less predation from benthivorous fishes. Miller and Crowl (2006) found that the presence of carp was associated with a decrease in abundance and diversity of macroinvertebrates in small cages (2.5 x 2.5 x 2.0 m high), but that in large exclosures, the relation between carp and macroinvertebrates varied with the side of the lake the exclosure was on, suggesting to them that wind and wave action were important factors in the relationship as they affected the growth and persistence of macrophytes.

Although our study reported substantial changes in benthic macroinvertebrate abundance, size, and richness in the presence of various fish, similar to some other studies (e.g., Hayes et al. (1992) for white suckers in Douglas Lake, Michigan), other studies have reported no such effects (Thorp and Bergey 1981a,b; Allan 1982; Flecker and Allan 1984). Several

factors may account for this difference. First, the habitat in Bowman-Haley Reservoir and its tributaries had little diversity, consisting almost entirely of silt substrate with no submerged vegetation. Effects of benthivorous fish are often more pronounced in more uniform habitats as a result of increased foraging efficiencies (Crowder and Cooper 1982; Savino and Stein 1982; Anderson 1984; Cook and Streams 1984; Diehl 1988). Second, pre-eradication densities of carp within the tributaries were high (nearly 10,000 kg ha^{-1} in Year 1) resulting in high potential predation and perpetuation of a homogenous, vegetation-free habitat. Third, the main benthic predators in our study were large, adult carp; in studies showing no effect of predation on the benthic community the main predators were trout (Allan 1982; Flecker and Allan 1984) or were not identified (Thorp and Bergey 1981a,b). Large carp, at high densities, are exceptional in their ability to alter their habitat (Cahn 1929) as well as the benthic macroinvertebrate community. Although our study was not a small exclosure study, the strong relationship shown is probably the result of the very high densities of carp in the reservoir and the extreme change brought about by the blocking the tributaries that would otherwise have been inundated with carp.

Table 2. Density of chironomids (organisms m^{-2}) inside and outside of exclosures during summer, Year 2. Asterisks indicate significant differences between inside and outside exclosures (p < 0.05). Chironomid lengths were measured in August only.

Sampling period	Spring Creek		Alkali Creek		North Fork Grand River	
(weeks after treatment)	inside	outside	inside	outside	inside	outside
June (0 wk)	394.7±149.6	351.6±155.0	229.6±46.7	222.5±52.8	423.4±72.4	387.5±176.2
July (4 wk)	1750.9±211.3	516.7±215.8*	1047.7±395.6	401.9±141.9*	3229.2±356.9	1040.5±183.9*
August (8 wk)	889.8±155.7	279.9±79.6*	1090.8±184.5	287.0±61.7*	387.5±94.8	315.7±141.9
Lengths (mm)	(6.4±0.68)	(5.5±0.68)	(6.1±0.63)	(5.5±0.57)	(5.4±0.74)	(5.8±0.57)

Although carp in Bowman-Haley Reservoir fed primarily on zooplankton rather than benthic macroinvertebrates (Bonneau 1999), these food habits may have resulted from a depletion of benthic macroinvertebrates and the subsequent need to utilize alternative food sources. Other studies have found that carp will cease feeding on preferred foods such as chironomids and oligochaetes when they become scarce and switch to more abundant foods (Stein et al. 1975; Sibbing et al. 1986). An ability of the carp to switch to zooplankton when benthic food sources become scarce would allow densities of carp to remain high and result in the severe, sustained depletion of the benthic fauna.

Further evidence of the carp's predation on chironomids was provided by the exclosure experiments. Chironomid densities within

fish exclosures were higher than those outside exclosures during June through August in Spring Creek and Alkali Creek and June through July in the Grand River. Chironomid lengths in August were not, however, significantly different inside and outside of any exclosure. This lack of difference in lengths may have resulted from predation inside the exclosures by age-0 carp, which were abundant in August and able to swim through the mesh of the exclosures. Chironomid densities were lower within exclosures compared to those above barriers, which may have indicated that higher predation was occurring within the exclosures. Although age-0 carp could also swim through the barriers, the areas excluded by the barriers were much larger and would require many more carp to have a similar effect. Further evidence of predation by age-0 carp
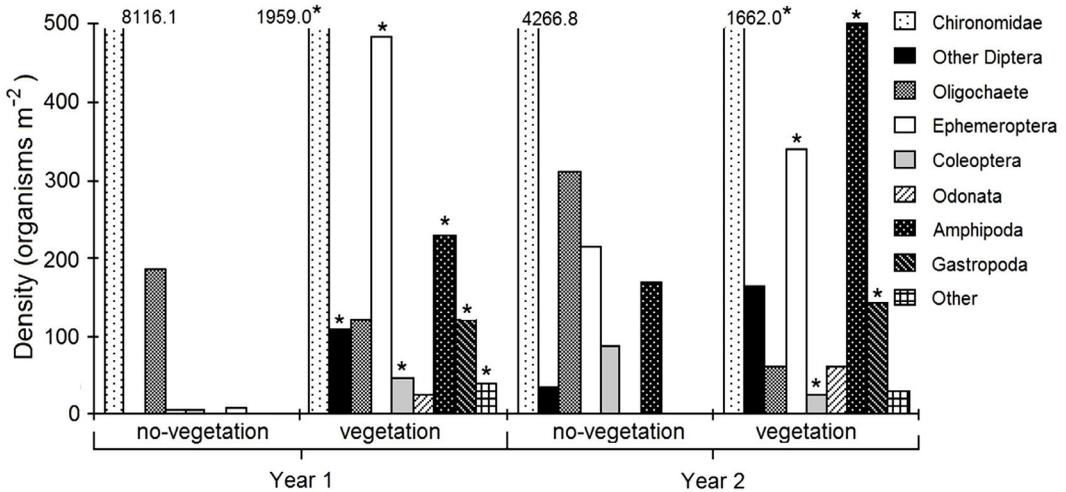

Fig. 6. Average number of benthic invertebrates m^{-2} in vegetated and non-vegetated areas upstream of the fish barrier (the exclosure) in Spring Creek in Year 1 and Year 2. Asterisks indicate a significant difference (P < 0.05) in abundance between vegetated and non-vegetated areas for that year.
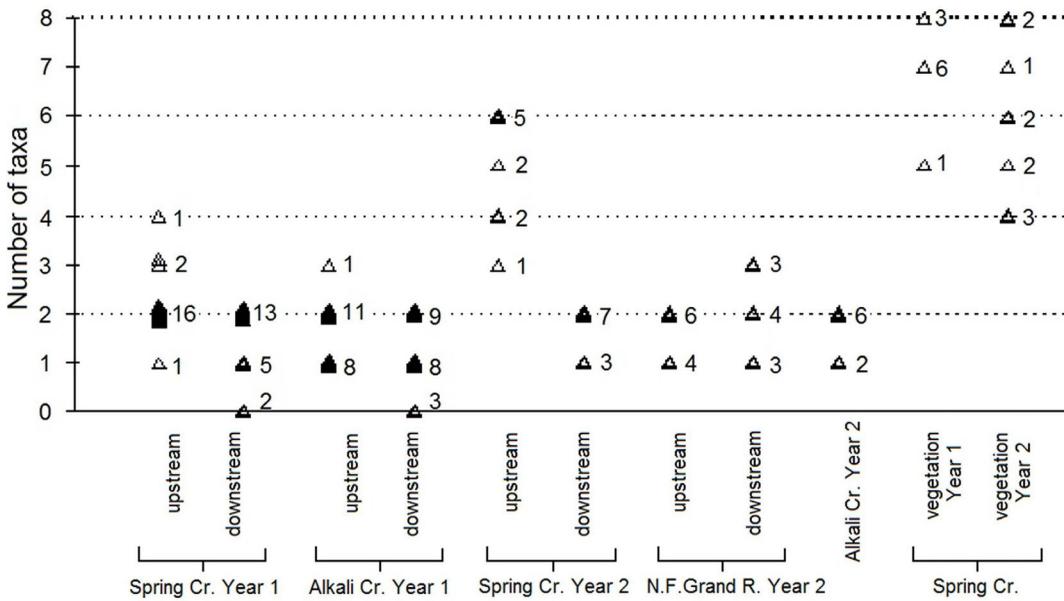
Fig. 7. Benthic macroinvertebrate richness per sample upstream (exclosure) and downstream of fish barriers (non-vegetated), Alkali Creek (Year 2), and vegetated areas in Spring Creek (Year 1 and Year 2). Numbers refer to the number of samples having a particular species richness.

was seen in the Grand River in Year 2 when chironomid lengths above the fish barrier were not significantly different than those below the fish barrier. In Year 2, age-0 carp were much more abundant in the Grand River than in the other two tributaries in either of the two years (Bonneau 1999) and could account for the smaller sizes of chironomids above the barrier.

The eradication of carp was also associated with altered spatial distributions of chironomids. Chironomids were distributed more uniformly in areas with carp than in areas without carp. This result contradicts the findings of others that predation increased the spatial heterogeneity of prey (Henrickson and Oscarson 1978; Butler 1989; Wilcox and Hornbach 1991). Wilcox and Hornbach (1991) was the only study where carp were the main benthic predator, and carp densities within their exclosures (approximately 150 - 1,100 kg ha^{-1}) were much lower than carp densities observed in Bowman-Haley Reservoir (up to 10,000 kg ha^{-1}). In our study, the greater uniformity in chironomid distribution in the presence of so many carp may have resulted

from the constant, intense predation by carp, the lack of habitat heterogeneity, and the absence of prey refuges.

Another result of carp eradication was the increase in nutrient inputs as carp decomposed. Increased nutrient supply has been known to result in a higher standing crop of benthic macroinvertebrates (Hall et al. 1970). In our study, differences in the benthic macroinvertebrate communities between areas with and without carp were not attributable to nutrient inputs; numbers of decaying fish were similar upstream and downstream of the barriers.

FUTURE STUDIES

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 Figure 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 of specific pathways by which carp may affect aquatic habitats and other aspects of the aquatic community.

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