Cascading food-web effects of piscivore introductions in shallow lakes

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Summary

1. Anthropogenic landscape modifications have resulted in increased water depths and greater connectivity among the remaining shallow lakes throughout eastern portions of the Prairie Pothole Region of North America. This has created conditions favourable for the establishment of planktivorous fish populations, notably fathead minnows Pimephales promelas. Such fish populations may reach high densities and reduce zooplankton and macroinvertebrate abundance and diversity. Resulting reductions in algal grazing by zooplankton favour transition to a turbid-water state, characterized by increased phytoplankton, decreased water clarity, and reduced macrophytes. Ultimately, such lakes are characterized by low habitat complexity and biodiversity, and conditions less favourable for waterbirds and other wetland-dependent species.

2. We conducted a 3-year study to assess the efficacy of walleye Sander vitreus stocking as a means of initiating trophic cascades, thus testing the ecological theory that piscivore addition can promote shifts from the turbid to the clear-water state by suppressing planktivores (fathead minnows), increasing zooplankton and macroinvertebrates, and reducing phytoplankton. Treatments consisted of six sites stocked with walleye fry, six lakes stocked with walleye age-1 and older, and six control lakes containing antecedent fathead minnows only.

3. Stocking walleye fry resulted in much lower densities of fathead minnows and higher densities of cladocerans and some macroinvertebrates. Chlorophyll a also decreased in the fry treatment sites. Stocking age-1 and older walleye induced few changes at the stocking density we tested.

4. The success of walleye fry appears to be partly attributable to their rapid diet shift to fish prey and their ability to consume and suppress all life stages of planktivores (fry, juveniles, and adults). However, most responses to walleye fry additions were short-lived, indicating that achieving long-term improvements may require repeated restocking.

5. Synthesis and applications. The available evidence indicates that catchment-level restoration alone is often of limited utility in restoring clear-water conditions in shallow lakes. Our results indicated that stocking piscivorous fish has the potential to improve ecological characteristics of shallow lakes, overcoming tendencies towards phytoplankton dominance. We suggest that managers consider using piscivorous fish stocks, ideally in conjunction with catchment-level restoration measures, to stimulate improvement of ecological characteristics in shallow lakes.

Key-words: alternative stable states, biomanipulation, fathead minnow, planktivores, shallow lakes, trophic cascades, turbidity, walleye, zooplankton

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Introduction

Research on freshwater lentic ecosystems has traditionally focused on deep lakes but recent efforts have emphasized the numerous functions, values, and ecological contributions of wetlands and shallow lakes, including flood abatement, water quality improvement, and habitat contributions for aquatic and semi-aquatic species (reviewed by Zedler 2003; Hanson et al. 2005). Despite recent advances (Batzer & Wissinger 1996; Scheffer et al. 2006), our understanding of mechanisms structuring biological communities and processes in shallow aquatic habitats is still surprisingly limited.

One related information gap is the role of biotic interactions as determinants of ecosystem structure in some shallow aquatic habitats (Hanson et al. 2005). Extensive literature has documented strong food-web interactions in shallow lakes around the world (reviewed by Scheffer 1998), yet comparatively little work has been done on continuously-flooded wetlands such as those of the Prairie Pothole Region (PPR) in North America, a 715,000-km² grassland-wetland landscape ranging from Alberta (Canada) to Iowa (USA) (Euliss, Wrubleski & Mushet 1999). The consequences of changing trophic interactions may be especially difficult to predict in such wetlands, as community structure is strongly influenced by the interplay of abiotic (hydrology, inter-annual precipitation, winter severity, Euliss et al. 2004), anthropogenic (modification of hydrological patterns and land use), and biotic factors (fish) (Angeler et al. 2003; Hanson et al. 2005). However, the effects of fish and their interactions with abiotic factors may be especially important in these systems. In eastern portions of the PPR, fish distribution and abundance can be highly variable from year to year and within individual sites (Zimmer, Hanson & Butler 2002; Herwig & Zimmer 2007), reflecting annual precipitation, winter severity, and anthropogenic modification of landscape features (Hanson et al. 2005). Fathead minnows Pimephales promelas (Cope 1868) are the dominant and often the only fish in many PPR shallow lakes (Zimmer, Hanson & Butler 2000). They can have major influences on water quality, nutrient cycling, and abundances of amphibians, aquatic invertebrates, submerged plants, and phytoplankton (Zimmer, Hanson & Butler 2003a, b; Zimmer, Herwig & Laurich 2006). Large, permanently-flooded PPR shallow lakes are well described in light of their unique features (high nutrient availability and primary productivity, influences of underlying groundwater, surface isolation, and dynamics; Kantrud, Krapu & Swanson 1989; Euliss et al. 2004). These habitats have traditionally been considered wetlands (Cowardin et al. 1979) but because our particular study sites are permanently flooded, they have no functional distinction from shallow lakes (sensu Scheffer 1998).

Ecological comparisons among shallow prairie lakes with contrasting food webs have been reported (see Hanson et al. 2005), and at least one study described diverse ecosystem responses to shifts between two versus three dominant trophic levels (with and without planktivorous fish, Zimmer, Hanson & Butler 2001). However, little is known about the ecological consequences of four dominant trophic levels (primary producers, grazing invertebrates, planktivores, piscivores), or how these systems respond to shifts between three and four trophic levels due to colonization or winterkill of piscivores. These are important questions because both presence and abundance of piscivorous fishes are highly variable among shallow lakes and within individual sites over time (Duffy 1998; Ward 2003). Given contrasting predictions of odd-link vs. even-link food-web models for terrestrial and lake ecosystems (Oksanen et al. 1981; Persson et al. 1992; Mazumder 1994) and the large differences observed between lakes with two versus three dominant trophic levels (Zimmer et al. 2002; Hanson et al. 2005), the effects of piscivores may be strong and may represent a key source of temporal and spatial variation in the ecosystem structure of PPR lakes.

Understanding the effects of piscivores in shallow lakes may improve management of these habitats. Shallow prairie lakes appear to stabilize in one of two alternative states, either a clear-water, macrophyte-dominated state, or turbid-water, phytoplankton-dominated state (Zimmer et al. 2003b). Most management strategies strive for the maintenance of a clear-water state, providing higher anticipated benefits for aquatic birds, submerged aquatic macrophytes, and other species (reviewed by Scheffer 1998). Conversely, high densities of fathead minnows are thought to stabilize the turbid-water condition and prevent shifts to a clear-water state via predation effects on zooplankton (Herwig & Zimmer 2007) as well as by translocation of nutrients from ingested sediments to the water column (Zimmer et al. 2006). Food-web models predict that piscivore addition to turbid lakes with high densities of minnows should induce trophic cascades, perhaps favouring shifts to the clear-water state (Scheffer 1998).

Here we report the results of experimental introductions of piscivorous walleye Sander vitreus (Mitchell 1818) into shallow prairie lakes having high turbidity and dense populations of fathead minnows. We hypothesized that walleye would reduce minnow (planktivore) abundance, subsequently triggering changes including increased aquatic invertebrates, reduced phytoplankton biomass, and increased abundance of submerged macrophytes, ultimately favouring shifts from turbid- to clear-water states. Our design included lake-scale replication, allowing us to observe both treatment effects and among-site variability in response to piscivore introductions.

Methods

STUDY SITES AND SAMPLING DESIGN

The study lakes were distributed across approximately 6765 km² in western Minnesota, USA, in the eastern part of the Prairie Pothole Region. We selected 18 lakes based on these criteria: hydroperiod, depth, antecedent fish populations, lack of surface connectivity, size, and accessibility. Study sites ranged in size from 4.4–27.6 ha (surface area) and mean depths ranged from 1.2–1.9 m. All sites contained fathead minnows and, occasionally, low densities of other planktivorous fishes. Lakes were randomly assigned to one of three treatments, which were blocked according to initial fathead minnow densities (high, medium, or low) based on surveys conducted in April 2001, prior to the start of the study. Six sites were stocked with

Data Collection

We sampled fathead minnows monthly from May to September using six unbaited minnow traps (203 × 203 × 457 mm, 6-35 mm mesh) randomly deployed in near-shore areas in each lake. Fathead minnow abundance was recorded as the mass of all fathead minnows caught in each trap, and mean values from six traps were used as an index of abundance in each lake. During 2002, we also sampled larval fathead minnows monthly using an ichthyoplankton net (0·5 m diameter; 0·8 mm mesh). The net was pushed at approximately 5 km h⁻¹ just below the surface for 120 s at three fixed transects parallel to shore, thus providing estimates of abundance for each lake. A calibrated flow meter mounted inside the net was used to determine the volume of water sampled for larval fish density estimates. We used the mean value from all three transects to estimate larval fathead minnow abundance in each lake.

Macroinvertebrates were sampled monthly during May–September 2001–2002 using activity traps (ATs) (Murkin, Abbott & Kadlec 1983). In each lake, five ATs were placed at the margin of emergent vegetation to the lake centre, and (iii) a transitional site one-half the distance from the margin of emergent vegetation to the lake centre. ATs were established along each transect and included one location at each of: (i) the interface of emergent vegetation and open water, (ii) open water zone, one-half the distance from the margin of emergent vegetation to the lake centre, and (iii) a transitional site one-half the distance between the locations described above. One additional sample was collected at the centre of each lake. At each sampling station, four rake-throws were taken and species presence/absence was recorded as a value of 1–4, corresponding to the number of times a species was sampled at each location. Location totals were summed to provide an index of abundance for each species in each study site. An overall macrophyte abundance score for each lake consisted of the sum of location totals for all species combined.

A surface dip sample was collected monthly from the centre of each lake during April–August each year. Each water sample was analysed for total phosphorous (TP), total nitrogen (TN), and chlorophyll a, following methods described in Greenberg, Clesceri & Eaton (1992).

In 2002, we also estimated total dissolved phosphorous (TDP) and particulate phosphorous (PP) at the same time we sampled all other water chemistry variables. TDP was analysed by filtering water through acid-washed GF/F filters, freezing the filtered water, and using high temperature persulphate oxidation followed by ascorbic acid colorimetry. PP was analysed by filtering water through an 80 µm mesh to remove zooplankton, filtering water onto an acid-washed GF/F filter, freezing filters, and using high temperature persulphate oxidation followed by ascorbic acid colorimetry. The analysis of TDP and PP was restricted to 16 of the 18 lakes in 2002 only; one reference and one adult lake were not included due to logistical constraints.

Analysis

Data were analysed separately by year using monthly values for each lake. Natural-log transformations were applied to all fish, invertebrate, and water quality data to better approximate assumptions of ANOVA. We used two approaches for analysing response variables. First, we applied mixed model repeated-measures ANOVA (SAS PROC MIXED, Littell et al. 1996) to assess potential treatment effects in our response variables. Significance was inferred at P ≤ 0·05. ANOVA models contained terms for treatment, time, and treatment × time interaction. Block terms for initial minnow density were also included in 2001 models, but not in 2002 and 2003 analyses because, in later years, minnow populations were unrelated to initial densities. Lack of block effects (P > 0·05) for all response variables (except for fathead minnows in 2001) indicated that initial minnow densities did not influence our results; thus, we do not report block effects. We expected significant time and treatment × time interactions for all response variables, but because we were most interested in changes associated with walleye treatments, we reported effects associated with walleye stocking only. When treatment effects were detected, we used SAS LSMEANS (Littell et al. 1996) to identify differences. Second, we also estimated treatment effect sizes by calculating differences between least squares means associated with the fry and reference, or adult and reference treatments. Estimated differences and confidence
intervals were then back-transformed to original units. Resulting back-transformed values represent the ratio of geometric means (multiplicative differences between treatments means) and provided estimates of effect sizes.

**Results**

Introductions of walleye fry were associated with dramatic changes in the food webs of prairie shallow lakes, but observed changes associated with the adult walleye treatment were muted relative to the fry treatment.

**FATHEAD MINNOW POPULATIONS**

Repeated measures ANOVA (R-ANOVA) indicated overall walleye treatment effects for fathead minnow catch per unit effort (CPUE) in both 2001 ($P = 0.0479$) and 2002 ($P < 0.0001$), but not in 2003 ($P = 0.0946$). R-ANOVA also indicated an overall treatment effect on larval fathead minnow densities during 2002 ($P = 0.0492$). Walleye fry stocking resulted in a decline in adult fathead minnows beginning in 2001 (Figs 1a, 2, LSMEANS$^{2001}$, fry vs. reference: $P = 0.048$; Table 1, effect size = 6.6). This trend persisted throughout 2002, when walleye continued to suppress fathead minnow populations (LSMEANS$^{2002}$, fry vs. reference: $P < 0.0001$; Table 1, effect size = 316.2). By 2003, the first year after walleye stocking ceased, fathead minnow populations recovered in several lakes and were similar to reference sites (Fig. 1a, LSMEANS$^{2003}$, fry vs. reference: $P = 0.0519$).

The overall fry treatment response in 2003 was strongly influenced by a single site that was colonized by fathead minnows from an adjacent shallow lake during the spring high water period in April–May (Fig. 2). Fathead minnow populations also recovered in two other lakes by late summer 2003 (Fig. 2). Walleye fry also reduced densities of larval fathead minnows in 2002 (Fig. 1b, LSMEANS$^{2002}$, fry vs. reference: $P = 0.030$; Table 1, effect size = 2.1).

Stocking adult walleye caused some suppression of fathead minnow populations. Although fathead minnow CPUE did not differ between adult and reference lakes in 2001 (Fig. 1a, LSMEANS$^{2001}$, adults vs. reference: $P = 0.0826$), by 2002 fathead minnow abundance was 14.3 times lower in adult than reference lakes (Fig. 1a, LSMEANS$^{2002}$, adults vs. reference: $P = 0.0003$). While adult fathead minnow populations were suppressed in the adult treatment relative to reference lakes, fathead minnow CPUE was still > 130 g trap$^{-1}$ in the adult lakes on three of five sampling dates in 2002. During 2003 (1 year after walleye stocking ceased), fathead minnow CPUE did not differ between adult and reference lakes (Fig. 1a, LSMEANS$^{2003}$, adults vs. reference: $P = 0.692$). Adult walleye stocking did not, however, result in significantly reduced densities of larval fathead minnows relative to reference lakes in 2002 (Fig. 1b, LSMEANS$^{2002}$, adult vs. reference: $P = 0.940$).

![Fig. 1. Average monthly fathead minnow abundance (± 1 SE) in the three treatment groups during 2001-2003 for (a) juvenile and adult minnows (catch per unit effort (CPUE), > 35 mm total length) from minnow trap sampling, and for (b) larval minnows (densities, < 20 mm total length) from ichthyoplankton push net sampling.](https://example.com/f1.png)

MACROINVERTEBRATES

R-ANOVA indicated an overall treatment effect for macroinvertebrate CPUE in both 2001 ($P = 0.0285$) and 2002 ($P = 0.0026$). R-ANOVA also indicated an overall treatment effect for amphipod CPUE in both years (2001, $P = 0.0106$; 2002, $P < 0.0001$). Macroinvertebrates did not differ significantly between fry and reference lakes during 2001 (LSMEANS$_{2001}$, fry vs. reference: $P = 0.4032$); however, by 2002, macroinvertebrates were more abundant in the fry treatment lakes (Fig. 3a, LSMEANS$_{2002}$, fry vs. reference: $P = 0.0013$; Table 1, effect size = 4.0). Amphipod CPUE increased significantly in fry sites the first year following fry stocking (Fig. 3b, LSMEANS$_{2001}$, fry vs. reference: $P = 0.0116$; Table 1, effect size = 3.6), and this response was even more obvious during 2002 (Fig. 3b, LSMEANS$_{2002}$, fry vs. reference: $P < 0.0001$; Table 1, effect size = 16.4).

Adult walleye had considerably less influence on macroinvertebrate abundance than did walleye fry. Macroinvertebrate CPUE was marginally lower in adult than reference lakes in 2001 (Fig. 3a, LSMEANS$_{adults}$ vs. reference: $P = 0.0533$), but not significantly in 2002 (Fig. 3b, LSMEANS$_{adults}$ vs. reference: $P = 0.9221$; Table 1, effect size = 0.0).

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Table 1. Effect sizes for the walleye treatments relative to reference treatments for response variables showing significant effects. Values represent ratios of geometric means (thus multiplicative differences ± 95% CI) of the walleye treatment sites relative to the reference lakes in 2001–2003 for (a) walleye fry, and (b) adult walleye. Arrows indicate direction of responses in walleye treatments relative to reference lakes.

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<th>2001</th>
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<td>(a) Walleye fry versus reference</td>
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<tr>
<td>Fathead minnow CPUE</td>
<td>↓6.6 (1.5, 30.1)</td>
<td>↓316.2 (91.8, 1089.9)</td>
<td>NS</td>
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<tr>
<td>Larval fathead minnow density</td>
<td>↓2.1 (1.04, 4.2)</td>
<td>↑4.0 (1.9, 8.4)</td>
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<tr>
<td>Macroinvertebrate CPUE (ATs)</td>
<td>NS</td>
<td>↑2.1 (4.4, 9.1)</td>
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<tr>
<td>Amphipod CPUE (ATs)</td>
<td>↑3.6 (1.4, 9.1)</td>
<td>↑16.4 (6.4, 42.2)</td>
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<tr>
<td>Large cladoceran density</td>
<td>↑3.0 (1.1, 8.0)</td>
<td>↑154 (61.3, 391)</td>
<td>↑2.7 (1.05, 7.1)</td>
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<td>Chlorophyll $a$ concentration</td>
<td>NS</td>
<td>↓2.6 (1.1, 5.9)</td>
<td>↓2.9 (1.2, 7.1)</td>
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<td>TP concentration</td>
<td>NS</td>
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<td>TDP concentration</td>
<td>NS</td>
<td>↑1.5 (1.2, 1.9)</td>
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<td>PP concentration</td>
<td>NS</td>
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<td>Submerged macrophytes</td>
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<td>(b) Adult walleye versus reference</td>
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<tr>
<td>Fathead minnow CPUE</td>
<td>NS</td>
<td>↓14.3 (4.2, 49.4)</td>
<td>NS</td>
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<td>Larval fathead minnow density</td>
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<td>Macroinvertebrate CPUE (ATs)</td>
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<tr>
<td>Amphipod CPUE (ATs)</td>
<td>↑4.2 (1.7, 10.7)</td>
<td>↑4.7 (1.8, 12.2)</td>
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<tr>
<td>Large cladoceran density</td>
<td>NS</td>
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<td>Submerged macrophytes</td>
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CPUE, catch per unit effort; ATs, activity traps; NS, not significant; ‘.’ = no data.

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Fig. 2. Time series showing mean abundance of adult fathead minnows (catch-per-unit-effort; > 20 mm TL) in the six fry treatment sites throughout 2001–2003. Arrows depict the times at which walleye fry were stocked and the timing of the colonization event that occurred in a fry treatment site during 2003.
but indistinguishable in 2002 (LSMEANS <sub>adults vs. reference</sub>: \( P = 0.5593 \)). Amphipods, however, were more abundant in adult than reference lakes in both 2001 (Fig. 3b, LSMEANS <sub>adults vs. reference</sub>: \( P = 0.0056; \) Table 1, effect size = 4.2) and 2002 (LSMEANS <sub>adults vs. reference</sub>: \( P = 0.0031; \) Table 1, effect size = 4.7).

**PHYTOPLANKTON**

R-ANOVA indicated no overall treatment effect on phytoplankton abundance, measured as chlorophyll \( a \) concentration (Chl \( a \)) during the first year of the study (2001; \( P = 0.5473 \)). However, overall treatment effects were observed for Chl \( a \) during both 2002 (\( P = 0.0405 \)) and 2003 (\( P = 0.0197 \)). Chl \( a \) concentrations were significantly lower in the fry treatment relative to the reference treatment during 2002 (Fig. 3d, LSMEANS <sub>fry vs. reference</sub>: \( P = 0.0260; \) Table 1, effect size = 2.6) and this continued throughout 2003 (Fig. 3d, LSMEANS <sub>fry vs. reference</sub>: \( P = 0.0236; \) Table 1, effect size = 2.9).

Adult walleye stocking did not appear to influence Chl \( a \) concentrations during 2001 (Fig. 3d, LSMEANS <sub>adults vs. reference</sub>: \( P = 0.5714 \)), 2002 (LSMEANS <sub>adults vs. reference</sub>: \( P = 0.9697 \)), and 2003 (LSMEANS <sub>adults vs. reference</sub>: \( P = 0.6476 \)). Chl \( a \) concentrations generally increased in both adult and reference lakes throughout the summer months, with mean values > 50 \( \mu g \) L\(^{-1}\) during July–September.

**MACROPHYES**

Submerged aquatic plant abundance did not differ significantly among treatments in any year (ANOVA: 2001, \( P = 0.4342; \) 2002, \( P = 0.4957; \) 2003, \( P = 0.2063 \)) (Fig. 4). However, macrophyte responses in fry treatment sites were highly variable (ranging from a 490% increase to 100% decrease in comparing 2002–2003 levels to 2001 levels), with apparent improvements observed in about half of the fry treatment wetlands.
MAJOR NUTRIENTS

There were no treatment effects for TP (R-ANOVA: 2001, \( P = 0.4803 \); 2002, \( P = 0.7570 \); 2003, \( P = 0.3038 \); Fig. 5a) or TN (2001, \( P = 0.3235 \); 2002, \( P = 0.6285 \); 2003, \( P = 0.2958 \); Fig. 5b) in any year. In contrast, our detailed phosphorous analysis in 16 lakes in 2002 showed a significant treatment effect for TDP (\( P = 0.0125 \)), with higher TDP observed in fry treatment sites relative to reference sites (Fig. 6, LSMEANS-fry vs. reference: \( P = 0.0109 \); Table 1, effect size = 1.5). There was also a significant treatment effect on PP (\( P = 0.0421 \), with lower PP in fry versus adult sites (LSMEANS fry vs. reference: \( P = 0.0430 \); Fig. 6).

Discussion

This study represents a rare account of biomanipulation involving lake-scale replication. The results indicated that the addition of walleye fry quickly induced major changes in food webs and broad ecological features of the study lakes. Relative to unmanipulated reference lakes, sites receiving walleye fry experienced reductions in planktivores (adult and larval fathead minnows), abrupt increases in large-bodied cladocerans and some macroinvertebrates, and lower phytoplankton abundance together with a non-significant trend toward higher relative abundance of submerged macrophytes. Responses of large cladocerans and phytoplankton persisted for 1 year post-walleye stocking. Submerged macrophytes showed weaker trends that persisted 1–2 years post-stocking in some sites. Young walleye experience rapid ontogenetic diet shifts and became predominantly piscivorous at a length of 30–40 mm, initially feeding on larval minnows (5–6 mm), then on progressively larger minnows (Ward 2003). Fathead minnows prey heavily on zooplankton and macroinvertebrates (Price, Tonn & Paszkowski 1991; Duffy 1998; Herwig & Zimmer 2007); thus, we believe the changes we observed resulted mostly from increased piscivory (Ward 2003; Ward et al. 2008). Our results are consistent with the findings of Zimmer et al. (2001) who described similar responses of zooplankton, water transparency, macroinvertebrates, and phytoplankton biomass following removal of fathead minnows from a shallow Minnesota lake using the fish toxicant rotenone. Our findings are informative because replicated field tests of classic food-web models (Fretwell 1977; Oksanen et al. 1981), trophic cascade theory (Carpenter & Kitchell 1993), and equilibrium responses (Scheffer 1998) are very rare in the literature.
In contrast to the walleye fry treatment, we observed only limited changes in lakes stocked with adult walleye. We believe that predation by adult walleye was insufficient to induce changes because they failed to reduce densities of larval fathead minnows. Although adult minnow CPUE was reduced in the adult walleye treatment in 2002, larval minnow densities were not, and reached twofold and fivefold higher densities than in reference and fry treatment sites, respectively. Various mechanisms may explain this response. For example, larger walleye may be ineffective predators on larval fathead minnows, regardless of their density. Alternatively, stocking rates of adult walleye may have been too low (i.e. if walleye densities had been higher, they may have consumed larval minnows). Regardless of the mechanism involved, adult walleye diets did not include larval minnows. In contrast, diet data from walleye fry provided strong evidence that fry predation was responsible for reduced abundance of both larval and adult minnows in 2001 and 2002. Ward et al. (2008) showed that walleye fry in these sites consumed larval minnows by mid-June 2001, with prey size increasing to include adult minnows by August that same year. Walleye fry predation rates on adult minnows in 2001 and 2002. Ward et al. (2008) showed that walleye fry in these sites consumed larval minnows by mid-June 2001, with prey size increasing to include adult minnows by August that same year. Walleye fry predation rates on minnows were high; bioenergetics modelling indicated that consumption of fathead minnows by walleye fry from June to September of 2001 averaged 99 kg ha\(^{-1}\) (Ward et al. 2008). Thus, high predation on larval minnows in early summer, and adult minnows in later summer, coupled with high natural post-spawn mortality of adult minnows (reviewed by Duffy 1998), resulted in reduced abundance of adult and larval minnows. This supports the findings of Hansson et al. (1998), who showed that unless piscivores suppress all planktivore life stages (adult, juvenile, larvae), the likelihood of successful biomanipulation is low.

Failure of our adult walleye treatment may also have resulted from low stocking rates (5–6–7 kg walleye ha\(^{-1}\) yr\(^{-1}\) or year-two densities of 65–130 walleye ha\(^{-1}\)). Other successful North American biomanipulation studies using adult piscivorous species have stocked at much higher rates (3000 largemouth bass ha\(^{-1}\), Spencer & King 1984; 26 kg northern pike ha\(^{-1}\), Elser et al. 2000). However, our goal was to assess the utility of stocking piscivores at densities potentially available to shallow lake managers. Although stocking at higher densities may increase the probability of success, our results probably reflect what could be expected for lake managers using obtainable numbers of adult walleye. In contrast, we suggest that walleye fry are often readily available from existing hatchery programmes. Balancing observed outcomes and logistical constraints, we view walleye fry stocking as the more viable option for shallow lake restoration, particularly when goals include rehabilitating multiple basins.

In several ways, our results are consistent with observations of Hanson & Butler (1994), Chow-Fraser (1998), Zimmer et al. (2000, 2001, 2002), Hanson et al. (2005) and others who reported strong influences of food-web configuration on shallow lakes in central North America. First, in response to walleye fry stocking, we observed strong top-down influences on planktivores, zooplankton, macroinvertebrates, and phytoplankton. Secondly, although we detected no changes in TP or TN in response to additions of walleye fry or adults, we did find higher concentrations of TDP in our walleye fry treatments. The increased TDP in fry lakes probably indicates that phytoplankton shifted from nutrient to grazer limitation, owing to increased abundance of zooplankton. These results support the conclusions of Elser et al. (2000), who found that piscivore addition to eutrophic lakes increases TDP concentrations and has strong effects on nutrient dynamics and availability. Finally, our results are also consistent with Scheffer’s (1998) models, predicting increased water clarity and rapid expansion of submerged macrophytes, indicating shifts to a clear-water state following suppression of planktivorous fish stocks. We caution that it is debatable whether we actually observed transitions to a clear-water stable state because we did not document significant macrophyte increases in either walleye treatment. Macrophyte responses were highly variable in the fry treatment lakes, ranging from a 490% increase to a 100% decrease during 2002–2004 compared to 2001 levels, perhaps reflecting variable seed banks and recolonization rates. Improvements in macrophytes, defined as > 2× increase in abundance from 2001 levels, persisted for just 1 year in four of the study lakes (one lake showed improvement in 2002, three lakes showed improvement in 2003), while improvements persisted for 3 years in a fifth study lake. A sixth study lake had high macrophyte abundance throughout the study (2001–2004). Coupling these trends in plant abundance with more robust responses in large-bodied zooplankton, macroinvertebrates, and phytoplankton, characteristics typically associated with the clear-water state in shallow lakes, suggests that our walleye fry treatment brought these systems at least to the verge of a transition to clear water. Lake managers should be prepared to expect lag effects and should anticipate variable macrophyte responses when applying biomanipulation.

Responses of nektonic and benthic macroinvertebrates to changing fish stocks are complex and more difficult to predict than are responses of large-bodied zooplankton (see reviews by Strayer 1991 and Northcote 1988). However, some authors have documented abrupt, broad taxonomic shifts to fish introduction or removal from ponds and lakes in Europe and North America (Luecke 1990; Pierce & Hinrichs 1997; Svensson, Bergman & Andersson 1999; Leppä, Hämäläinen & Karjalainen 2003, and others), especially in benthic habitats with little physical complexity. Our walleye fry stocking induced changes in nektonic macroinvertebrates and amphipods, and results from additional benthic samples generally corroborated trends observed from data based on activity trap sampling, as some benthic macroinvertebrate groups responded positively (e.g. Gammarus, Hyalella, Zygoptera, Trichoptera), but others were unresponsive (e.g. chironomids) (data not shown). Increases in invertebrates can be explained by prey consumption characteristics of fathead minnows, and directly reflect decreased consumption rates by minnows (Herwig & Zimmer 2007).

Most recent lake management has focused on catchment- level maintenance or restoration of water levels and hydrologic conditions, nutrient abatement, or improving characteristics of adjacent upland areas (Aceman et al. 2007; Jeppesen et al. 2008).
2007). Less attention has been directed towards developing lake management plans integrating food-web characteristics. Hydrogeomorphic setting may ultimately establish boundaries for shallow lake characteristics throughout the PPR region of North America (Euliss et al. 2004). We suggest that where hydrology and climate favour the establishment of fish communities in shallow lakes, food-web interactions may be major determinants of ecological features; thus, biomanipulation may be a useful tool (Angeler et al. 2003).

We believe the successful results we observed can be attributed to the following. First, as suggested by Hanson et al. (2005), biotic interactions (food-web dynamics) are important determinants of community structure in prairie lakes. Secondly, the lakes that we studied fell within a range of these areas provide aesthetic and biological functions (shallow lakes, influencing biodiversity and the extent to which characteristics in shallow lakes. We recommend that shallow lake managers consider biomanipulation in conjunction with catchment-level restoration measures, especially nutrient abatement (Moss, Madgwick & Phillips 1996), should have priority for shallow lake protection and enhancement. However, our results support claims of Angeler et al. (2003) and Jeppesen et al. (2007) that within-lake processes contribute to the ecological characteristics in shallow lakes, influencing biodiversity and the extent to which these areas provide aesthetic and biological functions (sensu Moss et al. 1996; Hansson et al. 2005). Havens et al. (2001) suggested that catchment-level restoration alone has limited potential to mitigate effects of eutrophication in shallow lakes. We recommend that shallow lake managers consider biomanipulation in conjunction with catchment-level restoration measures to improve water quality and enhance ecological characteristics in shallow lakes.

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