

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; Hansson *et al.* 2005). Despite recent advances (Batzler & 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

age-0 walleye (fry), six lakes were stocked with walleye age-1 and older (total length > 130 mm) (adult), and six control lakes were left unmanipulated (reference). Walleye fry (approximately 7 mm in total length) were added to fry treatment sites during May 2001 and 2002 at a density of 12 000 ha⁻¹ (0.0454 kg ha⁻¹), which reflects the annual stocking rate commonly used by State of Minnesota fisheries personnel in extensive rearing operations, then harvested during September each year. Fall harvesting was intended to minimize the ecological influences of older fish and to emulate operational walleye rearing by State of Minnesota fisheries personnel (Herwig *et al.* 2004). Many first-year walleye were not captured and over-wintered (Ward *et al.* 2008). 'Adult' walleye ranging in size from 110–526 mm (total length) were added at rates of 5.6–6.7 kg ha⁻¹ during May of each study year (2001 and 2002). Initial densities ranged from 21 to 48 walleye ha⁻¹ in 2001, and from 65 to 130 walleye ha⁻¹ in 2002 because the size distributions of walleye stocked into individual lakes varied and because adult walleye were allowed to remain over winter in these sites. Lakes were stocked similarly during both 2001 and 2002, thus remaining in the same treatment groups throughout 2001–2003. Response variables included concentrations of major nutrients and abundance of fathead minnows, aquatic invertebrates, phytoplankton (indexed by chlorophyll *a*), and submerged aquatic vegetation. We continued to monitor a selected set of these response variables throughout 2003 to assess additional potential changes after cessation of walleye stocking.

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 and five ATs were deployed in the open water zone. ATs were suspended approximately 30 cm below the water surface with funnels directed downwards (Muscha *et al.* 2001) for approximately 24 h. Upon retrieval, AT contents were concentrated with a 140 µm mesh, and data were pooled by lake and interpreted as relative abundance of invertebrates. Zooplankton were sampled monthly during May–September 2001–2003 using vertical column samplers (VCSs) (Swanson 1978). Two replicate samples were collected at each of five open water sampling locations in each lake, then pooled and concentrated with a 68 µm mesh to form a single sample. All invertebrate samples were preserved in 70% ethanol and organisms were identified to the lowest feasible taxonomic group using the keys of Pennak (1989) and Merritt & Cummins (1996). We calculated relative abundance of zooplankton and macroinvertebrates, and analysed three taxonomic groups. 'Large cladocerans' was defined as the sum number of *Daphnia* and *Simocephalus* in VCSs, 'amphipods' as the sum number of *Gammarus lacustris* (Sars 1864) and *Hyaella*

azteca (Saussure 1858) in ATs, and 'macroinvertebrates' as the sum number of Coleoptera, Hemiptera, Ephemeroptera, Trichoptera, Odonata, Diptera, Trombidiformes, Collembola, Nematoda, and Oligochaeta in ATs.

Relative abundance of submerged aquatic plants was assessed during late July each year using the modified techniques of Jessen & Lound (1962) and Deppe & Lathrop (1992). Plants were sampled along three random transects within each lake. Three stations 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 $P \leq 0.05$. 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 square 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, $LSMEANS_{2001, \text{fry vs. reference}}: P = 0.048$; Table 1, effect size = 6.6). This trend persisted throughout 2002, when walleye continued to suppress fathead minnow populations ($LSMEANS_{2002, \text{fry vs. reference}}: P < 0.0001$; 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, $LSMEANS_{2003, \text{fry vs. reference}}: P = 0.0519$). 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, $LSMEANS_{\text{fry vs. reference}}: P = 0.030$; 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, $LSMEANS_{2001, \text{adults vs. reference}}: P = 0.0826$), by 2002 fathead minnow abundance was 14.3 times lower in adult than reference lakes (Fig. 1a, $LSMEANS_{2002, \text{adults vs. reference}}: P = 0.0003$). While adult fathead minnow populations were suppressed in the adult treatment relative to reference lakes, fathead minnow CPUE was still $> 130 \text{ g trap}^{-1}$ 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, $LSMEANS_{2003, \text{adults vs. reference}}: P = 0.0692$). Adult walleye stocking did not, however, result in significantly reduced densities of larval fathead minnows relative to reference lakes in 2002 (Fig. 1b, $LSMEANS_{\text{adult vs. reference}}: P = 0.940$).

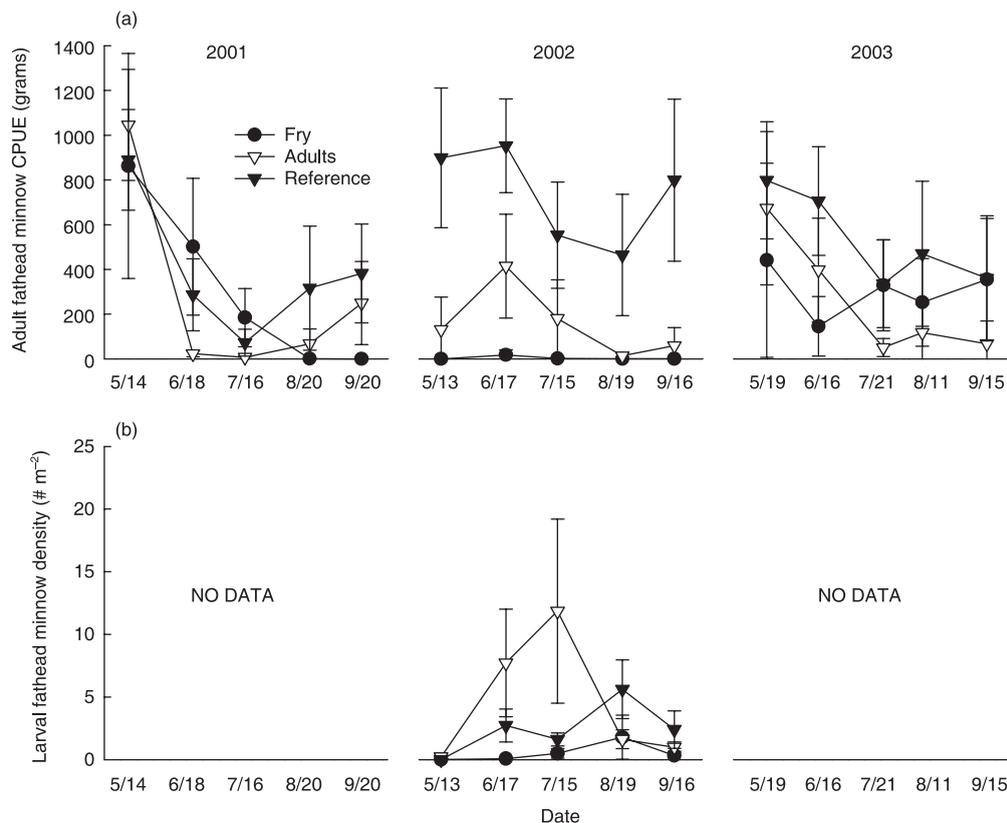


Fig. 1. Average monthly fathead minnow abundance (± 1 SE) in the three treatment groups during 2001–2003 for (a) juvenile and adult minnows [catch per unit effort (CPUE), > 35 mm total length] from minnow trap sampling, and for (b) larval minnows (densities, < 20 mm total length) from ichthyoplankton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

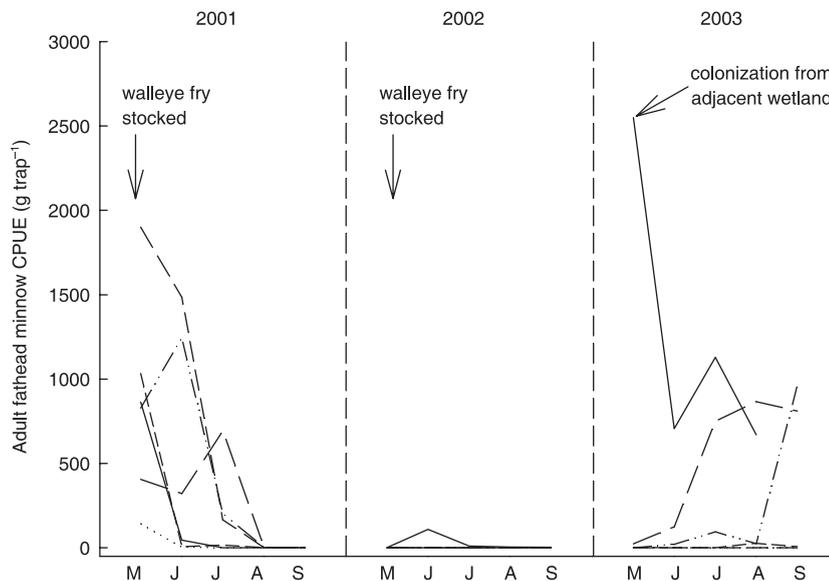


Fig. 2. Time series showing mean abundance of adult fathead minnows (catch-per-unit-effort; > 20 mm TL) in the six fry treatment sites throughout 2001–2003. Arrows depict the times at which walleye fry were stocked and the timing of the colonization event that occurred in a fry treatment site during 2003.

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 \pm 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

	2001	2002	2003
(a) Walleye fry versus reference			
Fathead minnow CPUE	↓6.6 (1.5, 30.1)	↓316.2 (91.8, 1089.9)	NS
Larval fathead minnow density	.	↓2.1 (1.04, 4.2)	.
Macroinvertebrate CPUE (ATs)	NS	↑4.0 (1.9, 8.4)	.
Amphipod CPUE (ATs)	↑3.6 (1.4, 9.1)	↑16.4 (6.4, 42.2)	.
Large cladoceran density	↑3.0 (1.1, 8.0)	↑15.4 (6.1, 39.1)	↑2.7 (1.05, 7.1)
Chlorophyll <i>a</i> concentration	NS	↓2.6 (1.1, 5.9)	↓2.9 (1.2, 7.1)
TP concentration	NS	NS	NS
TDP concentration	.	↑1.5 (1.2, 1.9)	.
PP concentration	.	NS	.
Submerged macrophytes	NS	NS	NS
(b) Adult walleye versus reference			
Fathead minnow CPUE	NS	↓14.3 (4.2, 49.4)	NS
Larval fathead minnow density	.	NS	.
Macroinvertebrate CPUE (ATs)	NS	NS	.
Amphipod CPUE (ATs)	↑4.2 (1.7, 10.7)	↑4.7 (1.8, 12.2)	.
Large cladoceran density	NS	NS	NS
Chlorophyll <i>a</i> concentration	NS	NS	NS
TP concentration	NS	NS	NS
TDP concentration	.	NS	.
PP concentration	.	NS	.
Submerged macrophytes	NS	NS	NS

CPUE, catch per unit effort; ATs, activity traps; NS, not significant; '.' = no data.

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}: $P = 0.0533$),

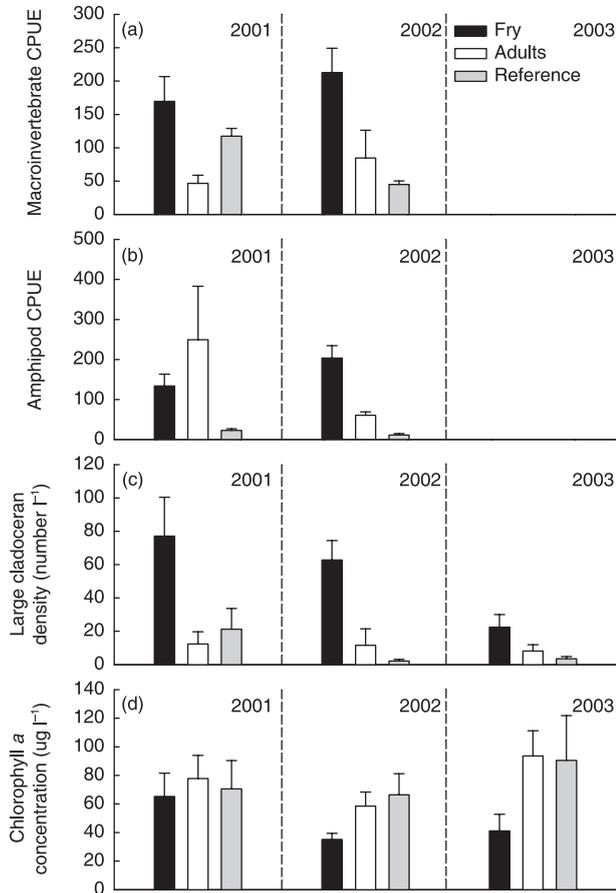


Fig. 3. Seasonal means among treatments (± 1 SE) during 2001–2003 for (a) macroinvertebrate abundance, (b) amphipod abundance, (c) large cladoceran zooplankton density (number L^{-1}), and (d) chlorophyll *a* concentrations ($\mu g L^{-1}$).

but indistinguishable in 2002 (LSMEANS_{adults vs. reference}: $P = 0.5593$). Amphipods, however, were more abundant in adult than reference lakes in both 2001 (Fig. 3b, LSMEANS_{adults vs. reference}: $P = 0.0056$; Table 1, effect size = 4.2) and 2002 (LSMEANS_{adults vs. reference}: $P = 0.0031$; Table 1, effect size = 4.7).

ZOOPLANKTON

R-ANOVA indicated overall treatment effects for large cladoceran densities in all 3 years (2001, $P = 0.0069$; 2002, $P < 0.0001$; 2003, $P = 0.0500$). Densities peaked at $> 100 L^{-1}$ in the walleye fry treatment, but remained $< 50 L^{-1}$ in the reference lakes during 2001 (Fig. 3c, LSMEANS_{2001, fry vs. reference}: $P = 0.0361$; Table 1, effect size = 3.0). Densities of large cladocerans remained significantly higher in fry lakes relative to reference lakes during 2002 (Fig. 3c, LSMEANS_{fry vs. reference}: $P < 0.0001$; Table 1, effect size = 15.4). By August and September 2002, densities declined sharply in the fry treatment lakes. Populations were again high in the fry treatment lakes during May–June of 2003 (Fig. 3c, LSMEANS_{2003, fry vs. reference}:

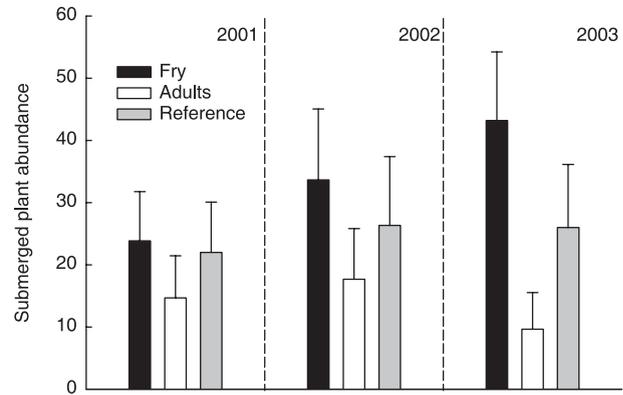


Fig. 4. Mean abundance of submerged aquatic vegetation in each treatment during 2001–2003 (± 1 SE).

$P = 0.0340$; Table 1, effect size = 2.7), but by July 2003, densities of large cladocerans declined to levels similar to those seen in reference lakes.

Stocking adult walleye had no significant effect on the abundance of large cladocerans, as densities in adult lakes remained relatively low ($< 61 L^{-1}$) and did not differ from reference lakes in 2001 (Fig. 4a, LSMEANS_{adults vs. reference}: $P = 0.1580$), 2002 (LSMEANS_{adults vs. reference}: $P = 0.7592$), or 2003 (LSMEANS_{adults vs. reference}: $P = 0.9152$).

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_{fry vs. reference}: $P = 0.0260$; Table 1, effect size = 2.6) and this continued throughout 2003 (Fig. 3d, LSMEANS_{fry vs. reference}: $P = 0.0236$; Table 1, effect size = 2.9).

Adult walleye stocking did not appear to influence Chl_a concentrations during 2001 (Fig. 3d, LSMEANS_{adults vs. reference}: $P = 0.5714$), 2002 (LSMEANS_{adults vs. reference}: $P = 0.9697$), and 2003 (LSMEANS_{adults vs. reference}: $P = 0.6476$). 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.

MACROPHYTES

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.

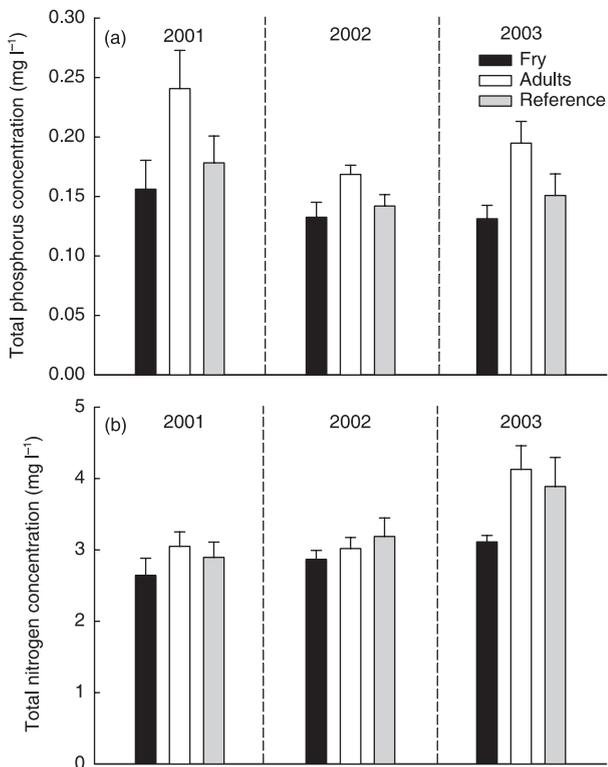


Fig. 5. Seasonal mean concentrations of (a) total phosphorus and (b) total nitrogen in fry, adult and reference lakes in 2001–2003 (± 1 SE).

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 phosphorus 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

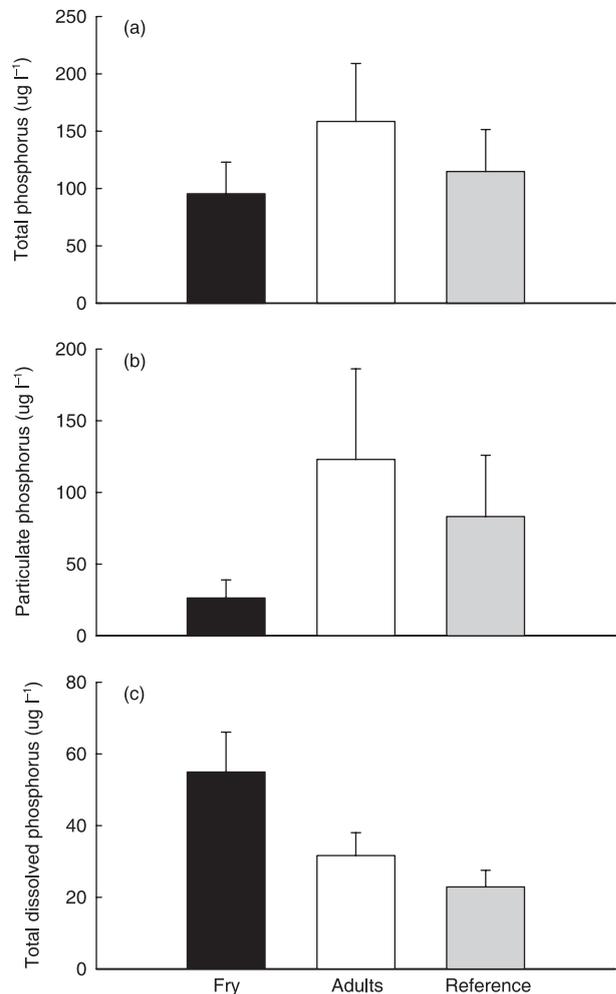


Fig. 6. Seasonal mean concentrations of (a) total phosphorus, (b) particulate phosphorus, and (c) total dissolved phosphorus in fry, adult, and reference lakes in 2002 (± 1 SE). Means were calculated from the subset of 16 lakes used for our detailed analysis of phosphorus partitioning.

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 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 (5–6–6.7 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 (Acreman *et al.* 2007; Jeppesen *et al.*

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 TP concentrations allowing either the clear or turbid state (approximately 50–150 µg L⁻¹, Jeppesen *et al.* 1997). Finally, as suggested by conceptual models of Angeler *et al.* (2003), low levels of hydrological disturbance (no flooding, drought, low connectivity) in our lakes probably increased the likelihood of favourable responses to walleye fry additions. However, as noted above, fathead minnows colonized one of our fry treatment sites as a result of flooding, and all improvements were immediately reversed. We also caution that positive effects we observed in response to walleye fry additions were short-lived, as many of the measured responses were no longer evident 1 or 2 years following walleye additions. Our results indicated that biomanipulation using walleye fry has the potential to induce trophic cascades, favouring transition to the clear-water state, but the short duration of these responses indicated that achieving long-term improvements may require repeated restocking of piscivores.

We believe that, in most cases, 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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References

- Acreman, M.C., Fisher, J., Stratford, C.J., Mould, D.J. & Mountford, J.O. (2007) Hydrological science and wetland restorations: some case studies from Europe. *Hydrology and Earth System Sciences*, **11**, 158–169.
- Angeler, D.G., Chow-Fraser, P., Hanson, M.A., Sánchez-Carillo, S. & Zimmer, K.D. (2003) Biomanipulation: a useful tool for freshwater wetland mitigation? *Freshwater Biology*, **48**, 2203–2213.
- Batzer, D.P. & Wissinger, S.A. (1996) Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology*, **41**, 75–100.
- Carpenter, S.R. & Kitchell, J.F. (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.
- Chow-Fraser, P. (1998) A conceptual ecological model to aid restoration of Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario, Canada. *Wetlands Ecology and Management*, **6**, 43–57.
- Cowardin, L.M., Carter, V., Golet, F.C. & LaRoe, E.T. (1979) *Classification of wetlands and deepwater habitats of the United States*. Northern Prairie Wildlife Research Center Home Page, US Department of the Interior, Fish and Wildlife Service, Washington, D.C. Jamestown, ND: <http://www.npwrc.usgs.gov/resource/1998/classwet/classwet.htm>
- Deppe, E.R. & Lathrop, R.C. (1992) *A Comparison of Two Rake Sampling Techniques for Sampling Aquatic Macrophytes*. Wisconsin Department of Natural Resources, Bureau of Research Findings Number 32, Madison, WI, USA.
- Duffy, W.G. (1998) Population dynamics, production, and prey consumption of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 15–27.
- Elser, J.J., Sterner, R.W., Galford, A.E., Chrzanowski, T.H., Findlay, D.L., Mills, K.H., Paterson, M.J., Stainton, M.P. & Schindler D.W. (2000) Pelagic C:N:P stoichiometry in a eutrophied lake: responses to a whole-lake food-web manipulation. *Ecosystems*, **3**, 293–307.
- Euliss, N.H. Jr., Swanson, G.A., LaBaugh, J.W., Nelson, R.D., Winter, T.C., Rosenberry, D.O. & Mushet, D.M. (2004) The wetland continuum: a conceptual framework for interpreting biological studies in the prairie pothole region. *Wetlands*, **24**, 448–458.
- Euliss, N.H. Jr., Wrubleski, D.A. & Mushet, D.M. (1999) Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management. *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (eds D.P. Batzer, R.P. Rader & S.A. Wissinger), pp. 471–512. John Wiley & Sons, New York.
- Fretwell, S.D. (1977) The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine*, **20**, 169–185.
- Greenberg, A.E., Clesceri, L.S. & Eaton, A.D. eds (1992) *Standard Methods for the Examination of Water and Wastewater, 18th Edition*. American Public Health Association, Washington, D.C.
- Hanson, M.A. & Butler, M.G. (1994) Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1180–1187.
- Hanson, M.A., Zimmer, K.D., Butler, M.G., Tangen, B.A., Herwig, B.R. & Euliss, N.H. Jr. (2005) Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. *Wetlands*, **25**, 764–775.
- Hansson, L.A., Annadotter, J., Berman, E., Hamrin, S.F., Jeppesen, E., Kairesalo, T., Luokkanen, E., Nilsson, P.A., Sondergaard, M. & Strand, J. (1998) Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems*, **1**, 558–574.
- Hansson, L.A., Brönmark, C., Nilsson, P.A. & Åbjörnsson, K. (2005) Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both? *Freshwater Biology*, **50**, 705–714.
- Havens, K.E., Fukushima, T., Xie, P., Iwakuma, T., James, R.T., Takamura, N., Hanazato, T. & Yamamoto, T. (2001) Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donhu (PR China), and Okeechobee (USA). *Environmental Pollution*, **111**, 263–272.
- Herwig, B.R. & Zimmer, K.D. (2007) Population ecology and prey consumption by fathead minnows in prairie wetlands: importance of detritus and larval fish. *Ecology of Freshwater Fish*, **16**, 282–294.
- Herwig, B.R., Hanson, M.A., Reed, J.R., Parsons, B.G., Potthoff, A.J., Ward, M.C., Zimmer, K.D., Butler, M.G., Willis, D.W. & Snook, V.A. (2004) *Walleye Stocking as a Tool to Suppress Fathead Minnows and Improve Habitat Quality in Semipermanent and Permanent Wetlands in the Prairie Pothole Region of Minnesota*. Minnesota Department of Natural Resources, Division of Fish and Wildlife Special Publication No. 159, Saint Paul, MN.

- Jeppesen, E., Jensen, J.P., Sondergaard, M., Lauridsen, T., Pedersen, L.J. & Jensen, L. (1997) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, **342/343**, 151–164.
- Jeppesen, E., Meerhoff, M., Jacobsen, B., Hansen, R., Søndergaard, M., Jensen, J., Lauridsen, T., Mazzeo, N. & Branco, C. (2007) Restoration of shallow lakes by nutrient control and biomanipulation – the successful strategy varies with lake size and climate. *Hydrobiologia*, **581**, 269–285.
- Jessen, R. & Lound, R. (1962) *An Evaluation of a Survey Technique for Submerged Aquatic Plants*. Minnesota Department of Conservation, Game Investigational Report 6, Saint Paul, MN.
- Kantrud, H.A., Krapu, G.L. & Swanson, G.A. (1989) *Prairie Basin Wetlands of the Dakotas: A Community Profile*. US Fish and Wildlife Service, Biological Report 85(7.28), Washington, D.C.
- Leppä, M., Hämäläinen, H. & Karjalainen, J. (2003) The response of benthic macroinvertebrates to whole-lake biomanipulation. *Hydrobiologia*, **498**, 97–105.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS Systems for Mixed Models*. SAS Institute, Cary, NC.
- Luecke, C. (1990) Changes in abundance and distribution of benthic macroinvertebrates after introduction of curthroat trout into a previously fishless lake. *Transaction of the American Fisheries Society*, **119**, 1010–1021.
- Mazumder, A. (1994) Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology*, **75**, 1141–1149.
- Merritt, R.W. & Cummins, K.W., eds. (1996) *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendall/Hunt, Dubuque, IA.
- Moss, B., Madgwick, J. & Phillips, G. (1996) *A Guide to the Restoration of Nutrient-Enriched Shallow Lakes*. Broads Authority and Environment Agency, Norwich, UK.
- Murkin, H.R., Abbott, P.G. & Kadlec, J.A. (1983) A comparison of activity traps and sweep nets for sampling nektonic invertebrates in wetlands. *Freshwater Invertebrate Biology*, **2**, 99–106.
- Muscha, M.J., Zimmer, K.D., Butler, M.G. & Hanson, M.A. (2001) A comparison of horizontally and vertically deployed aquatic invertebrate activity traps. *Wetlands*, **21**, 301–307.
- Northcote, T.G. (1988) Fish in the structure and function of freshwater ecosystems: a 'top-down' view. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 361–379.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.
- Pennak, R.W. (1989) *Fresh-Water Invertebrates of the United States: Protozoa to Mollusca*, 3rd edn. John Wiley & Sons, New York.
- Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S. (1992) Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist*, **140**, 59–84.
- Pierce, C.L. & Hinrichs, B.D. (1997) Responses of littoral invertebrates to reduction of fish density: simultaneous experiments in ponds with different fish assemblages. *Freshwater Biology*, **37**, 397–408.
- Price, C.J., Tonn, W.M. & Paszkowski, C.A. (1991) Intraspecific patterns of resource use by fathead minnows in a small boreal lake. *Canadian Journal of Zoology*, **69**, 2109–2115.
- Scheffer, M. (1998) *Ecology of Shallow Lakes*. Chapman & Hall, London.
- Scheffer, M., van Geest, G.J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M.G., Hanson, M.A., Declerck, S. & De Meester, L. (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos*, **112**, 227–231.
- Spencer, C.N. & King, D.L. (1984) Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1851–1855.
- Strayer, D.L. (1991) Perspectives on the size structure of lacustrine zoobenthos, its causes and its consequences. *Journal of the North American Benthological Society*, **10**, 210–221.
- Svensson, J.M., Bergman, E. & Andersson, G. (1999) Impact of cyprinid reduction on the benthic macroinvertebrate community and implications for increased nitrogen retention. *Hydrobiologia*, **404**, 1573–1517.
- Swanson, G.A. (1978) A plankton sampling device for shallow wetlands. *Journal of Wildlife Management*, **42**, 670–672.
- Ward, M.C. (2003) *Food habits and consumption estimates of walleyes stocked as a tool to suppress fathead minnow populations in west-central Minnesota wetlands*. M.S. thesis, South Dakota State University.
- Ward, M.C., Willis, D.W., Herwig, B.R., Chipps, S.R., Parsons, B.G., Reed, J.R. & Hanson, M.A. (2008) Consumption estimates of walleye stocked as fry to suppress fathead minnow populations in west-central Minnesota wetlands. *Ecology of Freshwater Fish*, **17**, 59–70.
- Zedler, J.B. (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Frontiers in Ecology and the Environment*, **1**, 65–72.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. (2000) Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 76–85.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. (2001) Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. *Ecosystems*, **4**, 346–357.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. (2002) Effects of fathead minnows and restoration on prairie wetland ecosystems. *Freshwater Biology*, **47**, 2071–2086.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. (2003a) Interspecies relationships, community structure, and factors influencing the abundance of submerged macrophytes in prairie wetlands. *Wetlands*, **23**, 717–728.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. (2003b) Relationships among nutrients, phytoplankton, macrophytes, and fish in prairie wetlands. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 721–730.
- Zimmer, K.D., Herwig, B.R. & Laurich, L.M. (2006) Nutrient excretion by fish and its potential to support algal production. *Limnology and Oceanography*, **51**, 197–207.

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