Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project

R. C. LATHROP,*,† B. M. JOHNSON,‡ T. B. JOHNSON,§ M. T. VOGELSANG,* S. R. CARPENTER,†
T. R. HRABIK,† J. F. KITCHELL,† J. J. MAGNUSON,† L. G. RUDSTAM¶ and R. S. STEWART*
*Wisconsin Department of Natural Resources, Madison, WI, USA
†Center for Limnology, University of Wisconsin-Madison, Madison, WI, USA
‡Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO, USA
§Lake Erie Fisheries Station, Ontario Ministry of Natural Resources, Wheatley, Ontario, Canada
¶Cornell Biological Field Station, Cornell University, Bridgeport, NY, USA*

SUMMARY

1. A total of 2.7×10^6 walleye fingerlings and 1.7×10^5 northern pike fingerlings were stocked during 1987–99 in eutrophic Lake Mendota. The objectives of the biomanipulation were to improve sport fishing and to increase piscivory to levels that would reduce planktivore biomass, increase *Daphnia* grazing and ultimately reduce algal densities in the lake. The combined biomass of the two piscivore species in the lake increased rapidly from < 1 kg ha^{-1} and stabilised at 4–6 kg ha^{-1} throughout the evaluation period.

2. Restrictive harvest regulations (i.e. increase in minimum size limit and reduction in bag limit) were implemented in 1988 to protect the stocked piscivores. Further restrictions were added in 1991 and 1996 for walleye and northern pike, respectively. These restrictions were essential because fishing pressure on both species (especially walleye) increased dramatically during biomanipulation.

3. Commencing in 1987 with a massive natural die-off of cisco and declining yellow perch populations, total planktivore biomass dropped from about 300–600 kg ha^{-1} prior to the die-off and the fish stocking, to about 20–40 kg ha^{-1} in subsequent years. These low planktivore biomasses lasted until a resurgence in the perch population in 1999.

4. During the period prior to biomanipulation when cisco were very abundant, the dominant *Daphnia* species was the smaller-bodied *D. galeata mendotae*, which usually reached a biomass maximum in June and then crashed shortly thereafter. Beginning in 1988, the larger-bodied *D. pulicaria* dominated, with relatively high biomasses occurring earlier in the spring and lasting well past mid-summer of many years.

5. In many years dominated by *D. pulicaria*, Secchi disc readings were greater during the spring and summer months when compared with years dominated by *D. galeata mendotae*. During the biomanipulation evaluation period, phosphorus (P) levels also changed dramatically thus complicating our analysis. Earlier research on Lake Mendota had shown that *Daphnia* grazing increased summer Secchi disc readings, but P concentrations linked to agricultural and urban runoff and to climate-controlled internal mixing processes were also important factors affecting summer readings.

6. The Lake Mendota biomanipulation project has been a success given that high densities of the large-bodied *D. pulicaria* have continued to dominate for over a decade, and the

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Correspondence: Richard C. Lathrop, UW Center for Limnology, 680 N. Park St., Madison, WI 53706, U.S.A.
E-mail: rlathrop@facstaff.wisc.edu

diversity of fishing opportunities have improved for walleye, northern pike and, more recently, yellow perch.

7. Massive stocking coupled with very restrictive fishing regulations produced moderate increases in piscivore densities. Larger increases could be realised by more drastic restrictions on sport fishing, but these regulations would be very controversial to anglers.

8. If the lake's food web remains in a favourable biomanipulation state (i.e. high herbivory), further improvements in water clarity are possible with future reductions in P loadings from a recently initiated non-point pollution abatement programme in the lake's drainage basin.

Keywords: biomanipulation, *Daphnia* grazing, Lake Mendota, piscivore stocking, trophic cascade

Introduction

Shapiro, Lamarra & Lynch (1975) first proposed 'biomanipulation' as a lake restoration technique where fish populations would be manipulated to produce reductions in algal densities. In the strictest sense, we refer to the technique where smaller planktivorous fish are reduced directly (e.g. by seining) or indirectly by increasing the density and biomass of piscivorous fish, the effect of which then cascades to lower trophic levels allowing more herbivorous *Daphnia* to graze on algae. This technique incorporates the earlier discoveries of Hrbáček *et al.* (1961), Brooks & Dodson (1965) and others, and has since been extensively evaluated both experimentally and theoretically (Carpenter, Kitchell & Hodgson, 1985; McQueen, Post & Mills, 1986; Benndorf, 1990; Reynolds, 1994; Hansson *et al.*, 1998; Meijer *et al.*, 1999; Carpenter *et al.*, 2001; Benndorf *et al.*, 2002; Mehner *et al.*, 2002). Special symposia have been convened to synthesise experiences for a variety of lake systems (Gulati *et al.*, 1990; Kasprzak *et al.*, 2002) and guidelines have been written that review the technique (e.g. Cooke *et al.*, 1993; de Bernardi & Giussani, 1995). However, a majority of the biomanipulation projects reported to date have been conducted in shallow unstratified lakes where major short-term successes have been achieved if nutrient levels are not excessive (Benndorf, 1990; Jeppesen *et al.*, 1990; Gulati, 1995; Meijer *et al.*, 1999).

In this paper, we report the results of a long-term biomanipulation project on Lake Mendota, a relatively large, stratified eutrophic lake (Table 1) located near major population centres in southern Wisconsin, USA. The project planning began in early 1986 and the piscivore stockings started in 1987. The early results of the project through 1989 have been reported elsewhere

(Kitchell, 1992), but a complete synthesis of the long-term data set has not been conducted because of the need to wait until the stockings of the long-lived piscivores – walleye (*Stizostedion vitreum* Mitchell) and northern pike (*Esox lucius* L.) – had their full impact in the lake.

Because the Lake Mendota biomanipulation project and its evaluation in such a relatively large stratified lake was projected to be expensive, a number of reasons for initiating the project were identified to garner support within governmental agencies, local fishing clubs, and the general public before commencing biomanipulation. The reasons were:

• Algal blooms continued to be a problem in Lake Mendota even after sewage diversion and the implementation of non-point source pollution control programmes (Lathrop, 1992; Lathrop *et al.*, 1998; Carpenter & Lathrop, 1999).

• Other studies (e.g. Shapiro *et al.*, 1975; Carpenter *et al.*, 1987) have shown that biomanipulation could reduce algal densities in certain lakes, although uncertainty existed about whether it would work in eutrophic lakes (e.g. McQueen *et al.*, 1986; Benndorf, 1990).

• Federal monies for fishery projects in the state had recently increased and as such uncommitted state funding was available within the Wisconsin Depart-

Table 1 Characteristics of lake Mendota

Characteristic	Value
Surface area (ha)	3985
Maximum depth (m)	25.3
Mean depth (m)	12.7
Catchment area (km^2)	604
Water residence time (year)*	4.6
Phosphorus loading (g P m^{-2} year^{-1})*	0.85

*From Lathrop *et al.* (1998).

ment of Natural Resources (WDNR) to conduct the expensive project, thus avoiding the difficult problem of reallocating existing fishery management monies in the agency (Addis, 1992).

- Long-term data on fish, zooplankton, algal densities and nutrients for Lake Mendota were available to evaluate the effect of biomanipulation (Kitchell, 1992).

- A strong partnership existed between the WDNR and the University of Wisconsin–Madison Center for Limnology (UW-CFL) to conduct such a large research/management project (Addis, 1992).

Specific fishery management objectives were identified to justify the stocking programme. To enhance the sport fishery in Lake Mendota, fishing opportunities had to be diversified. This included increasing the overall size and catch rates of walleyes and northern pike, increasing the catch of trophy-size northern pike, and increasing the growth rate of popular planktivorous fish, especially yellow perch (*Perca flavescens* Mitchell). Another objective was to sustain the piscivore enhancement by fostering natural reproduction. More restrictive harvest regulations were needed to protect the stocked piscivores to build up spawner populations. Thus, public education for sustainable management was a key component of the project. The fishing public needed to recognise that Lake Mendota was impaired, sacrifices and support were required to carry out the biomanipulation project, and water quality was valuable to all lake users including anglers. Specifically, blue-green algal blooms were not only noxious and unaesthetic, but also impaired the sports fishery.

Thus, biomanipulation of eutrophic Lake Mendota was deemed an important opportunity to test the biomanipulation theory in a real world setting where the outcome could not only be fully evaluated scientifically, but where it was hoped that the project would produce significant, long-lasting water quality and fishing benefits for a heavily used urban lake. The objective of this paper is to synthesise our insights from monitoring the long-term dynamics in Lake Mendota from both a scientific and management point of view.

Methods

Piscivore stocking

A total of 2.7×10^6 walleye fingerlings were stocked into Lake Mendota during the biomanipulation
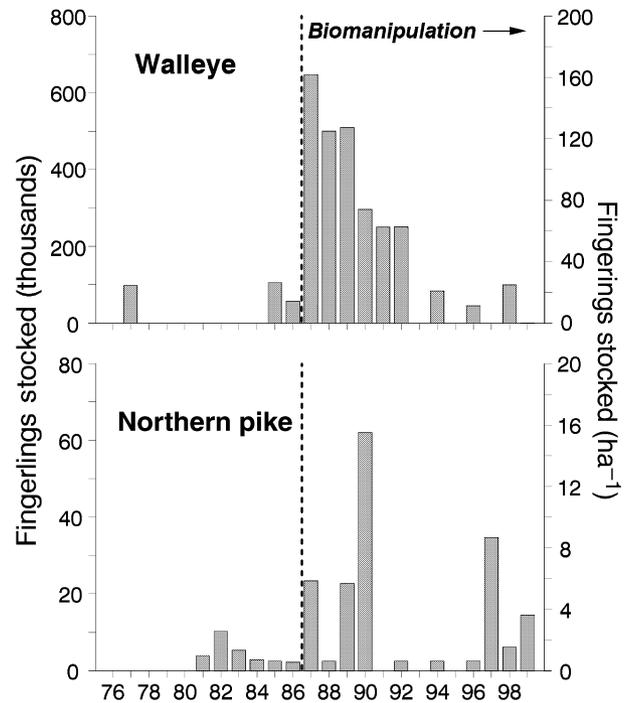

Fig. 1 Walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) fingerling stockings to Lake Mendota in thousands of fish (left axis) and number of fish stocked per hectare of lake area (right axis) 1976–99.

project between 1987 and 1999 (Fig. 1). Prior to biomanipulation, few walleyes had been stocked throughout the 1970s and early 1980s, although a local fishing club had raised and stocked modest numbers of walleye fingerlings in 1985–86 to improve fishing. During 1987–89 – the first 3 years of the biomanipulation project – about 500 000–650 000 (125–162 ha^{-1}) walleye fingerlings were stocked each year. In addition, 20 million walleye fry were stocked each spring, but their survival was considered negligible and therefore the fry stocking was not continued. In 1990–92, the heavy stocking rates were reduced to half, corresponding to about 250 000–300 000 fingerlings year^{-1}. In subsequent years, an alternate-year stocking programme at relatively low rates was instituted; no walleyes were stocked in 1993, 1995 and 1997, and only a very few fingerlings were stocked in 1999. Walleyes were generally stocked during June and early July at a total length of about 50 mm throughout the project.

Managers hoped that the heavy stocking of walleye fingerlings in 1987–92 would build up the adult spawner population sufficiently to allow for natural reproduction to sustain the population at high densities. The

alternate year stocking schedule in later years allowed for assessment of the young-of-the-year fish stocks by electrofishing in autumn, which indicated whether natural reproduction was occurring in years without stocking. Natural reproduction apparently was not extensive for most years without stocking; only in the fall of 1993 were modest numbers of small fish recorded.

Stocking rates of northern pike fingerlings (1.7×10^5 fingerlings between 1987 and 1999) were much less than for walleyes (Fig. 1), because the supply of hatchery-raised northern pike was very limited. Before biomanipulation started, the WDNR stocked relatively low numbers of northern pike fingerlings throughout the 1980s. The heaviest stocking in the early years of the biomanipulation was in 1990 (62 000 fingerlings, 16 ha^{-1}); over 20 000 northern pike fingerlings were stocked in 1987 and 1989. In 1987–89, 10 million northern pike fry were also stocked each year, but similar to the walleye fry stocking, the northern pike fry survival was determined to be very low and was later discontinued. No northern pike fingerlings were stocked in 1991, 1993 and 1995; fall surveys indicated natural reproduction was poor in the lake.

In 1996, a wetland rearing pond for northern pike was built on one of the major river tributaries to Lake Mendota. The addition of northern pike fingerlings to the lake has been relatively high since then, and may increase in future years because of plans to develop more wetland rearing sites in the lake's drainage basin (K. Welke, WDNR Fisheries Manager, personal communication). Northern pike fingerlings raised in hatchery ponds were usually stocked in late summer at a mean size of about 250 mm total length. Fingerlings released from the wetland rearing pond were stocked in the spring at about 50 mm.

Harvest regulations

Restrictive harvest regulations were implemented on Lake Mendota beginning in 1988 to protect stocked walleye and northern pike for the biomanipulation and to rebuild adult spawner populations of both species (Table 2). These regulations included both an increase in the minimum size limit and a reduction in the daily bag limit of fish permitted to be harvested from the lake (i.e. three walleyes, one northern pike). The minimum size limit was further increased in 1991 and 1996 for walleye (46 cm total length) and northern

Table 2 Harvest regulations for walleye and northern pike in Lake Mendota during four time periods

Period	Species	Minimum size limit (cm)	Daily bag limit
Before 1988	Walleye	None	5
	Northern pike	None	5
1988 to April 1991	Walleye	38	3
1988–95	Northern pike	81	1
May 1991 to present	Walleye	46	3
1996 to present	Northern pike	102	1

pike (102 cm total length), respectively, to further protect adult populations. In the case of northern pike, the regulations were also implemented to promote a 'trophy' fishery.

Piscivore assessment

We used a variety of approaches to assess fish populations and sports fishery dynamics in Lake Mendota. Adult walleye and northern pike abundances were estimated by mark–recapture techniques (Ricker, 1975). Fyke nets were used for marking during spring, and creel survey and gill nets to obtain recapture samples during the following summer and fall (Johnson *et al.*, 1992a; WDNR, unpublished fish management progress reports). Abundance estimates were computed within size classes to minimise gear selectivity bias. Biomass variances were computed from variances of abundance estimates and the mean weight of fish in each size class (Ricker, 1975); variance was not estimated for northern pike because of small recapture sample sizes. Age–length and length–weight relationships, and size structure were assessed using fyke nets, electrofishing, gill nets, and creel surveys (Johnson *et al.*, 1992a). A combination of stratified-random gill net surveys and radio-telemetry were used to determine seasonal depth distributions and thermal experience of walleyes and northern pike (Johnson *et al.*, 1992a).

Piscivore diets were determined by stomach analysis of fishes sampled from the electrofishing, gill net and creel catches (Johnson *et al.*, 1992a). Prey consumption by age 2 and older walleye and northern pike was estimated with a bioenergetics model (Hewett & Johnson, 1987; Hanson *et al.*, 1997). Energy density of predators and fish prey were assumed to be 5 kJ g^{-1} wet weight (Johnson *et al.*, 1992b).

Average prespawn weights-at-age (males and females combined) for simulations of bioenergetics were estimated from scales during 1987–93 as growth increments, assuming an average loss of 13 and 10% of body mass during spawning for walleyes (Colby, McNicol & Ryder, 1979) and northern pike (Diana, 1983), respectively. Natural mortality rates were estimated from the literature (walleye: Colby *et al.*, 1979; northern pike: Kempinger & Carline, 1978; Snow, 1978) and fishing mortality rates were estimated from the mark-recapture abundance estimates and numbers of fish harvested estimated from creel surveys (Johnson & Staggs, 1992).

Planktivore assessment

Population abundances of planktivorous fish for 1981–95 were estimated with a 70-kHz Simrad EY-M echo sounder during night hydroacoustic surveys using methods described in Rudstam, Lathrop & Carpenter (1993). Returning acoustic signals were recorded on audio (1981–87) and digital audio tape (1988–95) and analysed with Hydroacoustic Data Acquisition Software (Lindem, 1990). From 1997 to 1999, a split beam, Hydroacoustic Technologies 120 kHz system was used. The software settings for the sounder included depth strata defined at 1-m intervals, pulse duration of 0.4 ms, and a pulse rate of two per second. Standard target calibration was performed shortly before each sampling date, and maximum target strength never varied significantly from the known target strength of the calibration sphere. Analysis procedures included eliminating any bottom anomalies using Echoscape postprocessing software (Hydroacoustic Technologies Inc., Seattle, WA, USA, v. 1.51) and estimation of fish density at each depth strata using echo integration and mean target strength after correcting for system configuration. All acoustic estimates were conducted during August or early September when the fish were restricted to the upper one-half of the water column because the hypolimnion was anoxic. Transducer signal noise prevented recording fish in the upper top metre of the water column, because the transducer was located just below the lake surface. However, vertical gill net data (see below) indicated few fish stay near the surface, especially at night.

The vertical distribution and species composition of fish caught in a suite of vertical gillnets placed near the transects were used to estimate the proportion of each species at each depth. This information allowed us to assign species to the targets observed in the hydroacoustic data set for each year. The graded-mesh vertical gillnets were 4 m wide, 23 m deep, and with 25, 38, 51, 64, and 89-mm stretch mesh. Cisco (*Coregonus artedi* Lesueur), yellow perch, white bass (*Morone chrysops* Rafinesque) and freshwater drum (*Aplodinotus grunniens* Rafinesque) comprised 94–100% of the offshore fish community between 1981 and 1999 (UW-CFL, unpublished data). Adult freshwater drum are benthivorous, while all life stages of the other three species are almost exclusively zooplanktivorous in Lake Mendota (Johnson & Kitchell, 1996). Further, drum rarely comprised more than 10% of the abundance (median value 1.8%), so our remaining analyses will focus on cisco, yellow perch and white bass.

Whole lake fish biomass for each species of fish was determined by comparing species, size and depth distribution of all fishes captured in gillnets with corresponding depth strata from the acoustics abundance estimates. Species-specific biomass in each year was converted to age-specific biomass using expected growth and age composition information. Whole-lake biomass estimates are conservative as acoustic data could not be collected in shallow waters of the littoral zone. Detailed description of the population characteristics can be found in Johnson & Kitchell (1996).

Bioenergetic models (Hanson *et al.*, 1997) were used to estimate predation by cisco, yellow perch and white bass using species- and site-specific information on diet, energy density of fish and prey, temperatures to which the fish were exposed and growth rates. Diet of fishes was determined by gut content analyses conducted during 1987–89 (Luecke, Rudstam & Allen, 1992) and 1993 (Johnson & Kitchell, 1996). General characteristics of the diet (proportion of planktivory relative to other feeding modes) did not change between the two periods and was considered unlikely to change over the years of our analyses (Rudstam *et al.*, 1993; Johnson & Kitchell, 1996). Energy density of fish was determined from water content of tissues, while energy densities of most prey items were determined by bomb calorimetry (Hewett & Johnson, 1987). Temperatures experienced by the fishes throughout the year were estimated from thermal profiles recorded about every 2 weeks from ice-off until freeze-up each year (WDNR & UW-CFL,

unpublished data). Based on the thermal preferences for fish in Lake Mendota (Rudstam & Magnuson, 1985), we assumed adult fish would be distributed close to their preferred temperature (15.8 °C for cisco, 23 °C for yellow perch and 27.8 °C for white bass), although low hypolimnetic oxygen concentrations (< 4 mg L^{-1}) could force fish into warmer water during the summer and early fall. Temperature regimes to which larval and juvenile fishes had been exposed were estimated from temperatures recorded at 1-m depth and the water surface, respectively. A more comprehensive description of the energetic modelling can be found in Johnson & Kitchell (1996).

Daphnia biomass

The abundance and biomass of *Daphnia* species were estimated from vertical tow samples collected with conical zooplankton nets during 1976–99 (Lathrop, 1998). Sampling was conducted biweekly during the open water period and at least once through the ice at the deepest region of the lake in water depths of about 23–24 m. In 1976–94, zooplankton samples were collected using a net with a 15-cm diameter opening (small net) lowered to within 0.5 m of the lake bottom. Beginning in 1991, samples were collected using a 30-cm diameter closing-style net (large net) to a standardised depth of 20 m. The nets were made of Nitex screening with a mesh size of 75–80 μm for all years except for 1976 when the mesh size was 153 μm. Direct comparisons showed that *Daphnia* density, biomass and species composition determined by the large and small nets were not significantly different (Lathrop, 1998). For our analyses, *Daphnia* data for the small net were used for the period 1976–94; large net data were used for 1995–99.

Daphnia in each zooplankton sample were counted and measured to the nearest 0.01 mm under a microscope. Dry weights (dw, μg) for both juveniles and adults were computed from the average length data (Length, mm) based on equations given in Lynch, Weider & Lampert (1986) for *D. galeata mendotae* (dw = 5.48 Length$^{2.20}$) and *D. pulicaria* (dw = 10.67 Length$^{2.09}$), the two major *Daphnia* species encountered in Lake Mendota. The average weights were then multiplied by their respective densities to compute raw biomass concentrations (mg dw L^{-1}). Biomass concentrations for the summer and early fall stratification periods when the hypolimnion was anoxic were

adjusted to the tow depth that was above a dissolved oxygen threshold concentration of 1 mg L^{-1}.

Another factor that affects *Daphnia* biomass concentrations was zooplankton net efficiency, that is the reduction in organisms entering the net because of hydraulic resistance as the fine-meshed net is towed through the water. Both the small and large nets used for sampling *Daphnia* had reduced net efficiencies when algal densities were high (because of mesh clogging) compared with periods of clear water (Lathrop, 1998). During clear water periods, net efficiencies for the two nets were about 0.6–0.7, based on comparative analyses with flexible tube samplers. Net efficiencies declined to about 0.4 during periods of summer algal blooms. Because these differences are small compared with the very large range in *Daphnia* biomasses that we observed, and because we did not quantitatively analyse *Daphnia* biomass data in the analyses presented in this paper, we did not correct biomasses for net efficiency.

Results

Piscivores and piscivory

Walleye biomass increased steadily from a little over 1 kg ha^{-1} in 1987 to over 3 kg ha^{-1} in 1993 and reached a peak of 3.5 kg ha^{-1} in 1998, the last year when population estimates were made (Fig. 2). The standard error of biomass estimates averaged 0.37 over 1987–98. Because the 1993 and 1998 estimates were similar and piscivore biomass generally changes rather slowly, walleye biomass probably was stable during 1993–98 at a level about two to three times the 1987 biomass.

Northern pike biomass increased rapidly in the initial years of the study to over 4 kg ha^{-1} (Fig. 2), apparently because of excellent survival and growth of fingerlings stocked in 1987. Subsequent year-classes did not appear to fare as well. Stocking rate dropped greatly in 1991, and despite very restrictive harvest regulations, recruitment and survival were not adequate to maintain the population biomass achieved early in the study. Biomasses stabilised at 2.5 kg ha^{-1} through 1993, then dropped in 1998. Mean length of adult northern pike in spring sampling increased only modestly from 58 cm in 1987 to 71 cm in 1998.

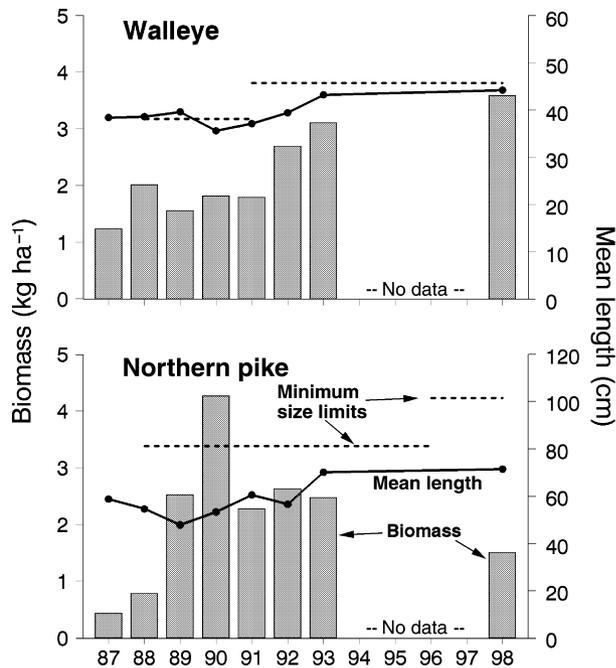Estimated biomass of prey consumed by walleye and northern pike populations increased rapidly

Fig. 2 Walleye and northern pike biomass estimates, and mean fish lengths and minimum size limit regulations for Lake Mendota, 1987–99.
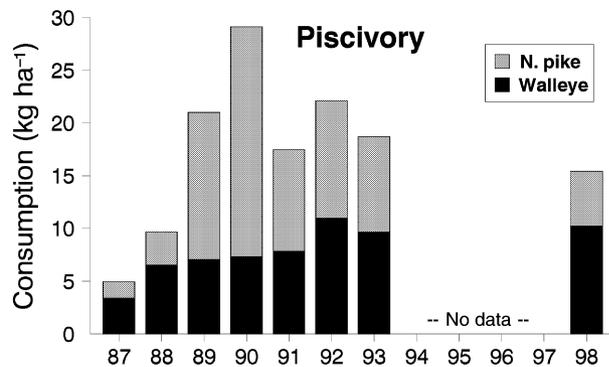

Fig. 3 Bioenergetic estimates of piscivory consumption on planktivorous fish for Lake Mendota, 1987–99.

during 1987–90 (Fig. 3), particularly as a result of the large increase in northern pike biomass (Fig. 2). Prey consumption declined somewhat in 1991 and remained relatively stable through 1998 (Fig. 3), but at levels much higher than prior to the period of heavy stocking of piscivores. We estimated that walleye and northern pike together consumed an average of 17 kg ha^{-1} of prey fishes year^{-1} during the biomanipulation years.

Sport fishing

Fishing effort directed at walleyes in Lake Mendota increased more than sixfold during 1987–89 and remained high ($\sim$2 angler-hours ha^{-1} month^{-1}) for most years through the 1998 creel survey (Fig. 4). This increase in angler interest was in response to the publicity about the massive stocking programme that began with the fishing club efforts in 1985–86 followed by the biomanipulation project (Johnson & Carpenter, 1994). The density (number ha^{-1}) of walleyes >28 cm in length increased from the stockings and did not decline by 1998 (Fig. 4). Angler catch rates (both kept and released fish) generally increased with walleye density. In 1991 and 1998, anglers were less successful at catching walleyes, probably because large year-classes of prey fishes were present in those years, although angling effort remained high.

Despite restrictive bag and size limits, walleye harvest rates (fish kept and not released by anglers) were so high by 1990 that project managers and investigators were concerned that the build-up of piscivore biomass in the lake would be prevented (Johnson & Carpenter, 1994). Walleye harvest rates dropped precipitously in 1991 following the increased minimum size limit (46 cm length) that was imposed to prevent the smaller fish from being harvested before they reached their adult spawning size (about 43 cm length for females; Johnson & Staggs, 1992).

Catch rates of northern pike also tracked increases in northern pike abundance, increasing rapidly during 1987–90 in response to the stocking efforts (WDNR,
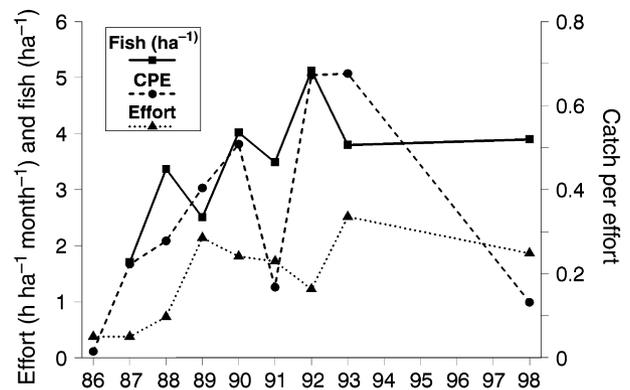

Fig. 4 Walleye density (fish ha^{-1}), fishing effort by anglers specifically seeking walleyes (angler-hour ha^{-1} month^{-1}), and catch per effort (CPE) by those anglers (walleyes caught per hour of fishing for walleyes) in Lake Mendota, 1986–99.

unpublished data). Catch rates decreased rapidly after 1990, as northern pike biomass (Fig. 2) and abundance declined when stocking was reduced.

Planktivores and planktivory

Cisco and yellow perch were the dominant planktivores in Lake Mendota prior to biomanipulation (Fig. 5). An unusually large year-class of crappies (*Pomoxis* spp.) also contributed to planktivory in the lake in the early 1980s (Lathrop *et al.*, 1992), but population densities of crappies have been low since then. Because large adult crappies are not captured by gill netting, they were not part of the biomass and planktivory estimates in those years. White bass had been abundant in the lake prior to a major die-off in 1976. They reappeared in low densities in the early 1990s and represented a minor increase in planktivory in 1992 (Fig. 5).

For many decades, cisco populations had been very low in the lake until populations increased dramatic-

For many decades, cisco populations had been very low in the lake until populations increased dramatically in the late 1970s (Fig. 5). This increase was attributed to good recruitment in 1976 and especially 1977 (Rudstam *et al.*, 1993). As a result, total planktivory increased to very high levels by 1978, until rates declined sharply following a massive cisco die-off in the summer of 1987, 1 year before biomanipulation started (Fig. 5). A minor decrease occurred in 1983 resulting from a smaller die-off.

Planktivory in the late 1970s and early 1980s was also augmented by yellow perch. Perch populations declined by the mid-1980s and remained low until a strong year-class occurred in 1997, which led to a pronounced increase in their biomass by 1999 (Fig. 5), the last year of our evaluation. Planktivory rates also increased in 1999, but the bioenergetic estimates were lower compared with situations when a similar biomass of cisco was present, because yellow perch has a lower *Daphnia* consumption rate (Johnson & Kitchell, 1996).

In summary, total planktivore biomasses and planktivory rates had changed greatly during 1976–99. The rapid increase in total planktivory after the strong 1977 year-class of cisco was apparent, followed by the sharp decrease in planktivory recorded in the late summer estimate of 1987. However, the 1977 increase in planktivory most probably occurred too late in the season to affect the spring and early summer *Daphnia* community that year. Likewise, the 1987 drop in planktivory occurred later in the summer; the spring and early summer *Daphnia* community was subjected to planktivory rates characteristic of the previous year. This 1987 drop in planktivory would also have occurred 1–2 years before piscivory increased as a result of the massive stocking programme. In subsequent years, extremely low planktivore biomass and planktivory were maintained, suggesting that piscivory could have been controlling densities of planktivore populations. However, the large increase in yellow perch in 1999 from the 1997 year-classes indicated that with a combination of the right conditions (i.e. low competition from other planktivores, ample zooplankton food resources, and favourable weather conditions for spawning), a strong year-class of planktivores can develop even with the relatively high piscivore biomass that was attained in the lake.
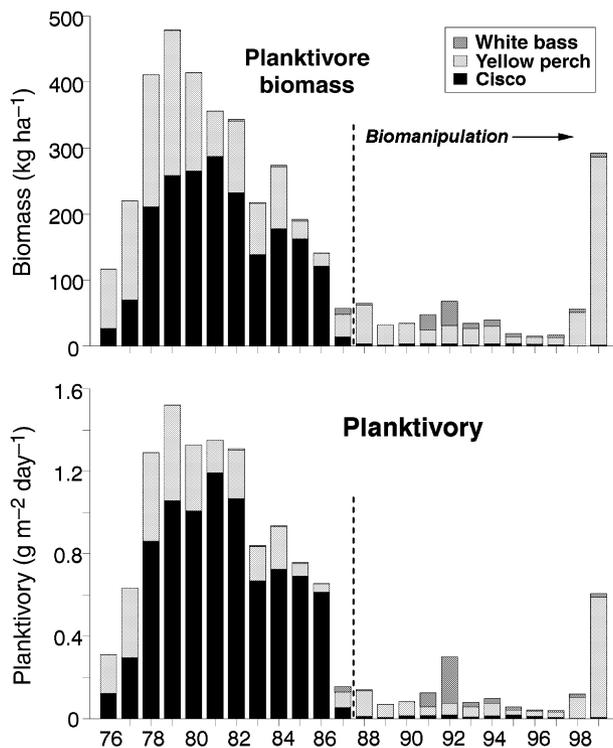
Daphnia

Daphnia pulicaria Forbes and *D. galeata mendotae* Brooks were the main *Daphnia* species in Lake

Fig. 5 Biomass estimates for planktivorous cisco (*Coregonus artedi*), yellow perch (*Perca flavescens*) and white bass (*Morone chrysops*), and bioenergetic estimates of *Daphnia* consumption in Lake Mendota, 1976–99. The biomanipulation effect is marked to begin in 1988, 1 year after the piscivore fingerling stocking was initiated.

Mendota during the pre- and post-evaluation years of the biomanipulation project, which is consistent with historical records (Kitchell & Sanford, 1992; Lathrop, Carpenter & Rudstam, 1996). They are the dominant *Daphnia* found in many lakes throughout the region (Kasprzak, Lathrop & Carpenter, 1999). The only other species recorded was *D. retrocurva* during the early 1980s in late summer and fall, but in minor densities (Lathrop & Carpenter, 1992).

While *D. pulicaria* and *D. galeata mendotae* can attain the same total body length in Lake Mendota, *D. pulicaria* has a much larger body mass (Fig. 6) and thus can reach significantly greater algal grazing potentials than *D. galeata mendotae* (Kasprzak *et al.*, 1999). Consequently, zooplankton grazer length distribution has not been a good predictor of plankivory or herbivory effects in Lake Mendota (Lathrop & Carpenter, 1992), whereas *Daphnia* biomass has produced insightful results of the trophic cascade effects from planktivory (Rudstam *et al.*, 1993; Johnson & Kitchell, 1996) and responses to herbivory (Lathrop, Carpenter & Robertson, 1999).

In most years, the spring and early summer *Daphnia* populations were dominated by only one species

Fig. 6 Photograph of the larger-bodied *Daphnia pulicaria* and the smaller-bodied *D. galeata mendotae*, the two main species of *Daphnia* that dominated the crustacean zooplankton in Lake Mendota throughout the 1900s including the biomanipulation project years.

(Fig. 7). In 1976–77 and in 1988–99 (except for 1994), the larger-bodied *D. pulicaria* dominated ('*D. pulicaria*' years) when spring planktivory levels were low. In 1978–84 and again in 1987, the smaller-bodied *D. galeata mendotae* dominated ('*D. galeata*' years) when spring planktivory levels were high. Only in 1985–86 and in 1994 did both species codominate, but biomass density of neither species was high. In general, *Daphnia* biomass increased earlier in the spring, reached greater densities, and lasted longer into the summer in *D. pulicaria* years than in *D. galeata* years. In *D. galeata* years, the increase in biomass usually occurred in June and declined again to very low densities by early July. The relatively high *D. pulicaria* biomass in July and August of many *D. pulicaria* years would have resulted in a much greater grazing impact on algal communities in those years.

Water clarity

Secchi disc readings as a measure of water clarity were highly variable during spring turnover, early stratification and summer periods of 1976–99 in Lake Mendota (Fig. 8). (Secchi readings are highly correlated to chlorophyll concentrations, because abiotic seston is relatively unimportant in Lake Mendota; R. Lathrop, WDNR, unpublished data.) During spring turnover in many but not all years dominated by *D. pulicaria*, mean and maximum Secchi disc readings were greater than in *D. galeata*-dominated years. Minimum readings, which often occurred early in the spring when water temperature was still low, were similar between years before and after the start of biomanipulation, indicating that *Daphnia* grazing had not yet occurred. A large increase in water clarity during spring turnover occurred in *D. pulicaria* years because this species can grow and reproduce in much colder water than *D. galeata mendotae* (Burns, 1969; Threlkeld, 1980).

During the early stratification period when both *Daphnia* species reached their peak biomasses, relatively high Secchi disc readings (>8 m) were recorded in some but not all the *D. pulicaria* years (Fig. 8). In general, mean readings were greater in *D. pulicaria* years after biomanipulation began. The lowest Secchi disc readings during the late spring/early summer period occurred in 1979 and 1990. In 1979, a very low biomass of *D. galeata mendotae* occurred during a year of very high planktivory (Fig. 5). In 1990, *D. pulicaria*
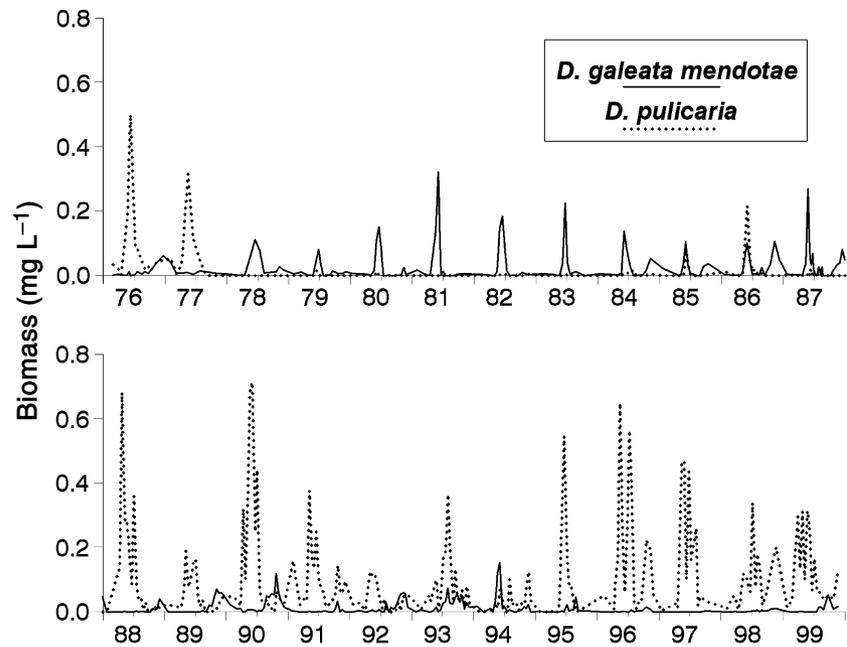
Fig. 7 Biomass concentrations of *Daphnia pulicaria* and *D. galeata mendotae* in Lake Mendota, 1976–99. Concentration data have not been corrected for net efficiency such that actual concentrations are higher (see text).

biomass was very high, coincident with a very dense bloom of the blue-green alga, *Aphanizomenon flos-aquae*.

During the mid-summer months, Secchi disk readings were generally greater in the biomanipulation years, although a few years in the mid-1980s prior to biomanipulation also had rather high water transparency (Fig. 8). Exceptionally good clarity occurred during the summer of 1988 with a mean Secchi depth of 3.5 m and a maximum >4 m. Similar maximum readings also occurred in 1989 and 1997. Even in 1990 when *Aphanizomenon* blooms were particularly prominent during the spring, the mean summer Secchi depth was similar to readings from other biomanipulation years and greater than summer readings of most previous years.

Nutrient levels

Changing nutrient levels in Lake Mendota as indicated by spring turnover phosphorus (P) concentrations (Fig. 9) complicated our evaluation of the biomanipulation effects on algal densities and water clarity. In the late 1970s, P concentrations were high, probably as a result of higher than normal runoff in previous years (Lathrop, 1990). Phosphorus concentrations steadily declined throughout the 1980s to a minimum in 1988 as a result of very low runoff during a 2-year drought in the region. Phosphorus

concentrations increased again after the biomanipulation commenced and reached very high levels resulting from large P inputs from runoff in 1993 (Lathrop *et al.*, 1998). Phosphorus concentrations have remained relatively high since then. Because spring P concentrations have been shown to be significant predictors of blue-green algal densities and water clarity during the summer months in the lake (Stow, Carpenter & Lathrop, 1997; Lathrop *et al.*, 1999), higher nutrient supply rates could have offset gains from increased algal grazing during the biomanipulation years.

Discussion

The heavy stocking rates of walleyes in the early years of the project represented a major share of the state's walleye hatchery production – a controversial commitment of resources that were diverted away from popular walleye stocking programmes in the northern regions of the state where many of the fish were raised (Johnson & Staggs, 1992). Northern pike stocking rates were almost an order of magnitude lower because of the difficulty in obtaining fingerlings from local hatcheries. Most of the walleyes were stocked in 1987–92; northern pike stockings were heaviest in the early and later years of the 1987–99 evaluation period. The survivorship of stocked fry for both species was
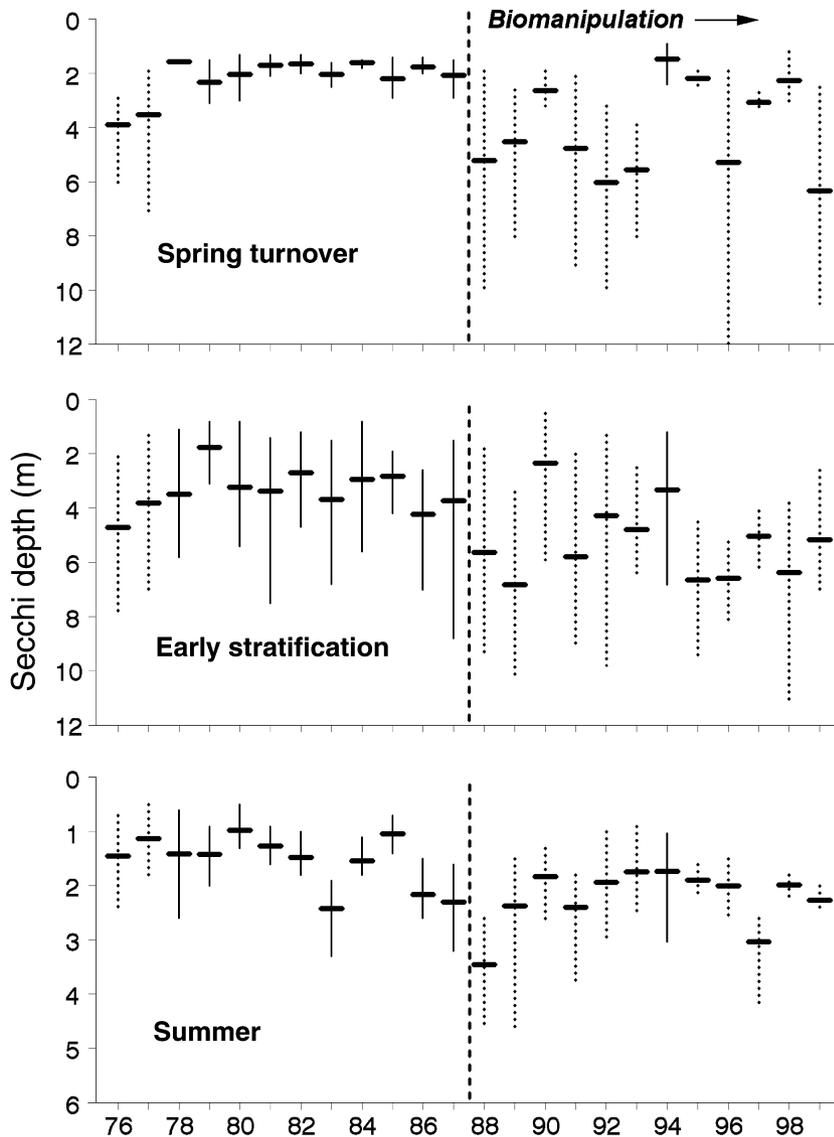
Fig. 8 Secchi disc readings as measure of water clarity and algal densities for three different time periods for Lake Mendota, 1976–99. (Spring Turnover = ice-out to 10 May; Early Stratification = 11 May to 29 June; Summer = 30 June to 2 September. Fat short horizontal bars are seasonal mean Secchi disc readings measured from the top of each graph. Vertical dotted lines are ranges of disk readings for years dominated by the larger-bodied *D. pulicaria*; vertical solid lines are ranges of disc readings for years dominated by the smaller-bodied *Daphnia galeata mendotae* or codominated by both species).

poor and was discontinued after the first 3 years of the project.

The biomass of both piscivore species substantially increased in the lake as a result of the stocking. In general, the combined biomass of both species ranged about 4–6 kg ha^{-1} from 1989 throughout the rest of the study years. While the combined piscivore biomass indicated a substantial increase compared with prebiomanipulation years (< 1 kg ha^{-1}), the levels are lower than those reported for other biomanipulation projects (e.g. >20 kg ha^{-1}; Benndorf, 1990). However, other piscivorous fish species (e.g. largemouth and smallmouth bass, *Micropterus salmoides* Lacepède and *M. dolomieu* Lacepède) are also found in Lake

Mendota and so would raise our piscivorous fish estimates to an extent.

The magnitude of the planktivorous fish changes in Lake Mendota is even more striking, decreasing from 300 to 600 kg ha^{-1} in prebiomanipulation years to 20–40 kg ha^{-1} after 1987 – an order of magnitude decline. Another indicator of fish conditions in lakes is the ratio of planktivore to planktivore plus piscivore biomasses. Jeppesen *et al.* (1990) found that this ratio was around 0.8–0.9 for shallow Danish lakes with high P concentrations ($P > 0.10$ mg L^{-1}), but dropped considerably for shallow lakes with lower P concentrations. While these ratios for shallow lakes are not directly comparable with deeper Lake Mendota, the
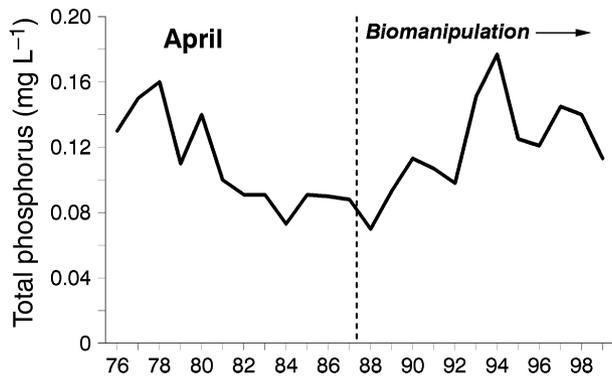
Fig. 9 Total phosphorus concentrations in the surface waters of Lake Mendota for mid-April, 1976–99.

ratio for the fish species summarised in our analyses changed from >0.99 before biomanipulation to approximately 0.85 after biomanipulation.

Of particular interest is whether a trophic cascade from piscivores to algae could improve water clarity in eutrophic Lake Mendota. Results from other biomanipulation projects suggested that lakes would not exhibit reduced algal densities following piscivore enhancement and/or planktivore reduction programmes if P loadings were high (McQueen *et al.*, 1986; Benndorf, 1990; Reynolds, 1994). Benndorf (Benndorf, 1990; Benndorf *et al.*, 2002) proposed a lake-specific P loading threshold ranging from 0.6 to 0.8 g P m^{-2} year^{-1}, above which biomanipulation measures would not reduce algal densities. Lakes with external P loadings below 0.6 g P m^{-2} year^{-1} had a high probability for biomanipulation to reduce algal densities. Lake Mendota has an average annual P loading rate of 0.85 g P m^{-2} year^{-1}, although annual loadings are highly variable (Lathrop *et al.*, 1998).

In 1988, the year following the sharp decline in planktivory caused by the cisco die-off, Lake Mendota experienced exceptionally good water clarity during summer coincident with high *Daphnia* biomass (Vanni *et al.*, 1990). This was also the year at the end of a prolonged drought with lower than average external P loadings (Lathrop *et al.*, 1998) and a hotter than normal summer with less internal loading because of greater water column stability (Lathrop *et al.*, 1999). The combined effect of lower P loadings and in-lake P concentrations plus increased *Daphnia* biomasses in 1988 supports Benndorf's (Benndorf, 1990; Benndorf *et al.*, 2002) proposed minimum P loading rate threshold for enhanced biomanipulation effects. In later

years when in-lake P concentrations and external P loadings were higher than the upper P loading threshold range of 0.8 g m^{-2} year^{-1} (Benndorf *et al.*, 2002), summer water clarity in Lake Mendota remained greater than in years before the fish die-off. A greater *Daphnia* biomass since 1988 conceivably was an important contributing factor.

It is debatable whether the increased piscivore densities (and hence increased piscivory) after the cisco die-off in 1987 directly suppressed planktivorous fish populations and prevented their resurgence until perch recovered in the late 1990s. However, sport fishing for walleye and northern pike improved greatly as a result of the biomanipulation programme. To protect the sport fishery, restrictive harvest regulations (increased size limits and reduced bag limits) were placed on Lake Mendota in 1988 for both stocked piscivore species, and then made even more restrictive in 1991 and 1996 for walleye and northern pike, respectively. These restrictions stabilised the fishery at the higher biomass levels. However, further increases in piscivore biomass probably were not achieved because fishing pressure remained high. The slight drop in northern pike biomass in 1998, if real, should be augmented again by increasing stocking of fingerlings from the wetland rearing pond on one of the lake's tributaries and possibly additional wetland rearing sites that are being proposed. The recent resurgence of yellow perch with rapid growth rates, apparently resulting from abundant zooplankton food, is further viewed as a positive response to biomanipulation in the lake. However, the full trophic cascade effect on *Daphnia* and ultimately water clarity needs to be evaluated as planktivory by perch continues to increase.

In summary, the Lake Mendota biomanipulation project has been a success in that high densities of the large-bodied *D. pulicaria* have continued to dominate for over a decade, and fishing opportunities have improved for walleye, northern pike and, more recently, for yellow perch. In addition, scientists and managers have learned to what extent a large eutrophic urban lake can be influenced by biomanipulation. Massive stocking coupled with very restrictive fishing regulations produced moderate increases in piscivore densities. Larger increases could be realised by more drastic restrictions on sport fishing, such as trophy regulations, mandatory catch-and-release programmes, or outright closures

of the fishery, accompanied by higher stocking rates or by habitat improvements to increase reproduction. However, many anglers, who now enjoy good fishing opportunities under the current stocking and harvest regimes, would undoubtedly be opposed to increased regulations.

Reduced planktivory in eutrophic Lake Mendota clearly did cascade to lower trophic levels, causing an increase in large *Daphnia*, reduced algal densities and increased water clarity. We are less certain whether the walleye and northern pike biomass (up to 6 kg ha^{-1}) attained in the lake directly controlled planktivory. After the cisco die-off 1 year before biomanipulation started, piscivory levels may have been high enough to suppress cisco and yellow perch recruitment for many years until conditions were favourable for perch to finally experience an exceedingly fast population growth. These perch are being heavily exploited by anglers; further perch recruitment will be needed to maintain their high biomass. Because yellow perch have lower planktivory rates on *Daphnia* than cisco (Johnson & Kitchell, 1996), the impact of the recent perch resurgence has not caused the larger-bodied *D. pulicaria* to be replaced by the smaller-bodied *D. galeata mendotae*. However, without the return of cisco, the lake's food web continues to be positioned (i.e. maintenance of high herbivory) to produce even further improvements in water clarity with future reductions in P loadings from a recently initiated drainage basin pollution abatement programme (Betz, 2000). Synergy between biomanipulation and non-point pollution control may be an important topic of future research and management initiatives in view of the increasing emphasis on controlling non-point nutrient loading of lakes in both Europe and North America.

Acknowledgments

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