Hydrobiologia **395/396:** 19–28, 1999.
D.M. Harper, B. Brierley, A.J.D. Ferguson & G. Phillips (eds), The Ecological Bases for Lake and Reservoir Management.

Lake restoration: capabilities and needs

Stephen R. Carpenter[1] & Richard C. Lathrop[1,2]
[1]*Center for Limnology, 680 North Park Street, University of Wisconsin, Madison, WI 53706, U.S.A.*
[2]*Bureau of Integrated Science Services, Wisconsin Department of Natural Resources, 1350 Femrite Drive, Madison, WI 53716, U.S.A.*

Key words: eutrophication, lake, management, restoration, Wisconsin

Abstract

Lake degradation results from excessive nutrient inputs, toxic substances, habitat loss, overfishing, species invasions and extirpations. The scientific basis of lake degradation is generally well understood, although each restoration project requires some level of new site-specific research. Remediation may require management actions which are difficult to implement for social or institutional reasons. Even where large-scale remediations are attempted, it is difficult to sustain scientific assessments for long enough to evaluate success. Collaborations of scientists and managers have sometimes succeeded in overcoming limitations to lake restoration, and produced important advances in our capability to restore lakes.

Introduction

Lakes provide humankind with many services: esthetic enjoyment, recreation, fish, transportation, water for irrigation, drinking and dilution of pollutants (Postel & Carpenter, 1997). These services are impaired by exploitation of lakes and the lands of their catchments. The goal of management is to balance the uses of lakes with conservation measures to sustain ecosystem services over time. Research can provide understanding of lakes, their catchments and the mechanisms that sustain ecosystem services; the causes of lake degradation; and methods and technologies for lake restoration. This brief paper summarizes the state of scientific knowledge relevant to lake restoration, and discusses some of the linkages between research and management.

Complex problems with multiple causes

In relatively undisturbed lakes, water quality is maintained by several mechanisms, each acting at different scales of space and time (Carpenter & Cottingham, 1997). In these lakes, impacts of climate fluctuations or terrestrial ecosystem changes are damped in many ways. Riparian vegetation and wetlands delay or prevent the transport of nutrients to lakes from eroding upland soils. Wetlands release humic substances which reduce the response of algae to nutrients. Zooplankton prevent the buildup of algal biomass and efficiently transfer nutrients to higher trophic levels. The water remains clear enough for macrophyte growth, and considerable amounts of nutrients are stored in macrophytes. Food web structure is regulated by large piscivorous fishes, which use the habitat provided by macrophyte beds, wetlands and trees fallen from riparian forests. The resilience of lake water quality thus depends on mechanisms which have similar effects at different scales.

Eutrophication is a syndrome that develops when several resilience mechanisms are broken down (Harper, 1992; National Research Council, 1992). Agriculture and urban development increase nutrient inputs. Loss of riparian vegetation and wetlands increases the efficiency of nutrient transport to lakes. Humic inputs decline, and humic constraints on algal growth are less effective. Piscivorous fish abundance is reduced by overfishing, so planktivorous and benthivorous fishes become more abundant and the large zooplanktonic grazers are reduced. Consequently, incoming nutrients accumulate in phytoplankton biomass, especially blue-green algae which are no longer controlled by grazing. Macrophyte beds decline with losses of water clarity. Loss of crucial habitat – macrophytes, wetlands, fallen trees – leads to further breakdown of the food web. The result is a lake with few piscivorous fishes, abundant planktivorous and benthivorous fishes, few large herbivorous zooplankton, few macrophytes, dense algal blooms, and risks of anoxia and algal toxins. Species invasions, losses of biodiversity, and toxic pollutants also degrade lakes, and may interact with effects of nutrient enrichment, habitat loss and overfishing.

Status of lake restoration

Lake degradation is a syndrome with multiple causes. For some restoration problems, proven solutions exist (National Research Council, 1992; Cooke et al., 1993, chapters in this volume). For other restoration problems, methods are insufficient. Gaps occur in scientific knowledge, institutional mechanisms, or both. Here we briefly note some major needs in lake restoration.

Excess nutrient input has received more attention than the other causes of lake degradation. Point sources of nutrient input can often be controlled by sewage treatment plants. Nonpoint sources of nutrients result from erosion, livestock waste, overfertilization of crops and urban wastes (Carpenter et al., 1998). These sources account for most of the water pollution in the United States (National Research Council, 1992). Control of nonpoint pollution requires improvements in land use that are difficult to implement for economic and political reasons (National Research Council, 1992). The best treatment for excess nutrient problems is reduction of nutrient input. However, a number of methods exist for removing or inactivating nutrients after they have entered lakes (Cooke et al., 1993). These methods can succeed where input reductions are slow or insufficient, and where recycling of nutrients from bottom sediment maintains eutrophication, even after inputs are reduced (National Research Council, 1992).

Prediction of phosphorus inputs from land use data is a complex interdisciplinary problem, for which many solutions have been proposed (Poiani & Bedford, 1995; Soranno et al., 1996). Existing approaches leave considerable room for improvement, and research toward better non-point pollution assessments deserves greater effort. Also, management practices designed to control non-point pollution are rarely tested at the large scale of actual applications. Non-point pollution control projects should be operated as large-scale experiments to determine whether the management actions have any effect on nonpoint pollution (Carpenter et al., 1997).

The fundamental policy problem in lake restoration is that those who cause non-point pollution do not benefit from reduced pollution, especially in large agricultural catchments. Conversely, the beneficiaries of non-point pollution control are not those who cause the pollution, except in some urban lakes. This mismatch between polluters and beneficiaries is the root of institutional shortcomings that prevent the success of non-point pollution control programs.

Toxic substances, such as metals, organochlorine compounds and acid, have been managed most successfully by reducing inputs at their sources. However, non-point inputs of toxins can be large. Examples are airborne inputs of mercury and PCBs to lakes (Swackhamer & Armstrong, 1986; Driscoll et al., 1994). Once they are added to lakes, persistent toxins like mercury and organochlorine compounds are difficult to remediate (National Research Council, 1992). Cleanups can be successful when pollution is concentrated in a restricted area. In some cases, sediment-bound pollutants can be removed by localized dredging. In other cases, however, resuspension of these sediments would exacerbate problems and it is better to leave the sediment undisturbed. Lakewide pollution may dissipate very slowly even after point-source inputs have ceased (Stow et al., 1995). Cleanup of persistent toxic pollution at large spatial scales poses enormous technological and fiscal challenges, and may be impossible in many cases (National Research Council, 1992).

Restoration of habitats – wetlands, macrophytes and fallen trees – is a crucial aspect of self-sustaining lake restorations. Wetland restoration is the subject of substantial and ongoing research effort (National Research Council, 1992; Zedler 1996). Restoration of macrophytes in shallow lakes has yielded some notable successes (Scheffer et al., 1992; chapters in this volume). Restorations that target particularly desirable species of macrophytes are an important priority for further research.

Fallen trees are a critical, but vanishing, habitat element in both lakes and streams (Maser & Sedell, 1994; Christensen et al., 1996). Losses of woody habitat are caused by declining riparian forests and deliberate removal of fallen trees from the littoral zone. In some Wisconsin lakes, it will take centuries to restore wood habitat to its former abundance (Christensen et al., 1996). Effects of these habitat losses on fish production in lakes are potentially large but not yet well quantified (Heck & Crowder, 1991). Although artificial structures have long been used in fish management (Johnson & Stein, 1979), the extent to which these structures mimic the invertebrate production and shelter afforded by fallen trees is not known. Further research is needed on the effects of littoral woody habitat on fishes. Managers need to consider new mechanisms for preserving riparian vegetation and littoral woody habitat in lakes.

Overfishing affects water quality by reducing populations of large piscivorous fishes, thereby increasing populations of zooplanktivores (which consume grazers) and benthivores (which resuspend sediments and recycle nutrients). Angling has powerful effects on fish populations (Johnson & Carpenter, 1994; Carpenter et al., 1994). Kitchell & Carpenter (1993) argued that fishing increases the temporal variability of lakes by increasing the probability of recruitment events, stock collapses, and their reverberations through the food web. Although anglers have strong effects on sport fish populations and lake food webs, relatively few studies have examined the interactions of sport fishers and their prey. Anglers can respond rapidly and creatively to changes in the resource (Johnson & Carpenter, 1994). If anglers do not agree with the need for regulation, then regulations are not likely to work. Hilborn et al. (1995) argued that management has largely failed to preserve commercial fisheries, and suggest that sustainable management of commercial fisheries is impossible. Sport fish management may face similar institutional limitations.

Species invasions and extirpations have been addressed only occasionally by lake restoration projects (National Research Council, 1992). Our abilities to anticipate or predict invasions are limited (Lodge, 1993). Removal of exotic species has succeeded only rarely, although exotic species can sometimes be reduced to tolerable levels. There have been few successful re-introductions of extirpated species to lakes.

A case study: Lake Mendota, Wisconsin

Because lake degradation has multiple causes, lake restoration usually requires multiple interventions. Here we summarize past and continuing efforts to restore Lake Mendota, Wisconsin. Lake Mendota has all of the problems described above, with the exception of toxic pollution. The lake has been the subject of substantial research and management programs conducted by agency and university staff over the past century. Efforts to restore Lake Mendota exemplify the current state of the art.

Lake and catchment description

Bordered by Wisconsin's capital city and leading university, Lake Mendota is symbolic of the quality of life in a state with more than 15 000 lakes and a multibillion dollar per year recreation industry centered on lakes (Figure 1). Management of the lake is highly visible to government officials.

The lake (A_0=40 km^2, $Z_{\max}$=25.3 m) is located in a rich agricultural region, and its eutrophic state derives largely from agricultural runoff (Lathrop, 1992b; Lathrop et al., 1998). At present, the 601 km^2 catchment is 80% agriculture, 9% urban, and 11% wetlands, forest and lake area. The urban area is expected to increase to 15% by the year 2020 (Soranno et al., 1996). Although most of the catchment is prime agricultural land, the lake's urban setting attracts a heavy use of the lake. Fishing, boating and swimming are important, but scenic enjoyment undoubtedly is the lake's most popular use. The amenities of Lake Mendota contribute to the region's high property values and burgeoning population growth.

Nutrient enrichment

Most of Madison's sewage effluents were discharged downstream from Lake Mendota after a sanitary sewer collection system and treatment facility were first built in the early 1900s (Lathrop 1992b; Lathrop et al., 1992). However, sewage from small communities in the lake's catchment began entering the lake via inflowing streams in the 1920s. Dissolved phosphorus (P) concentrations in these streams increased substantially after the end of World War II (Figure 2). The sewage effluents continued entering the lake until the sewage was diverted in late 1971. This diversion reduced biologically available phosphorus loading to the lake by about 30% (Lathrop, 1990).

Over the past century and a half, however, nutrients from nonpoint pollution have probably been more important than sewage inputs (Lathrop, 1992b; Lathrop et al., 1992). Urban runoff has been adding increasing amounts of nutrients to the lake, especially from construction site erosion, as urban population growth has increased steeply in recent decades. Agriculture, however, accounts for most of the non-point inputs. While the arable land of the catchment was farmed by 1870, an increase in corn (maize) production occurred soon after World War II. Because corn

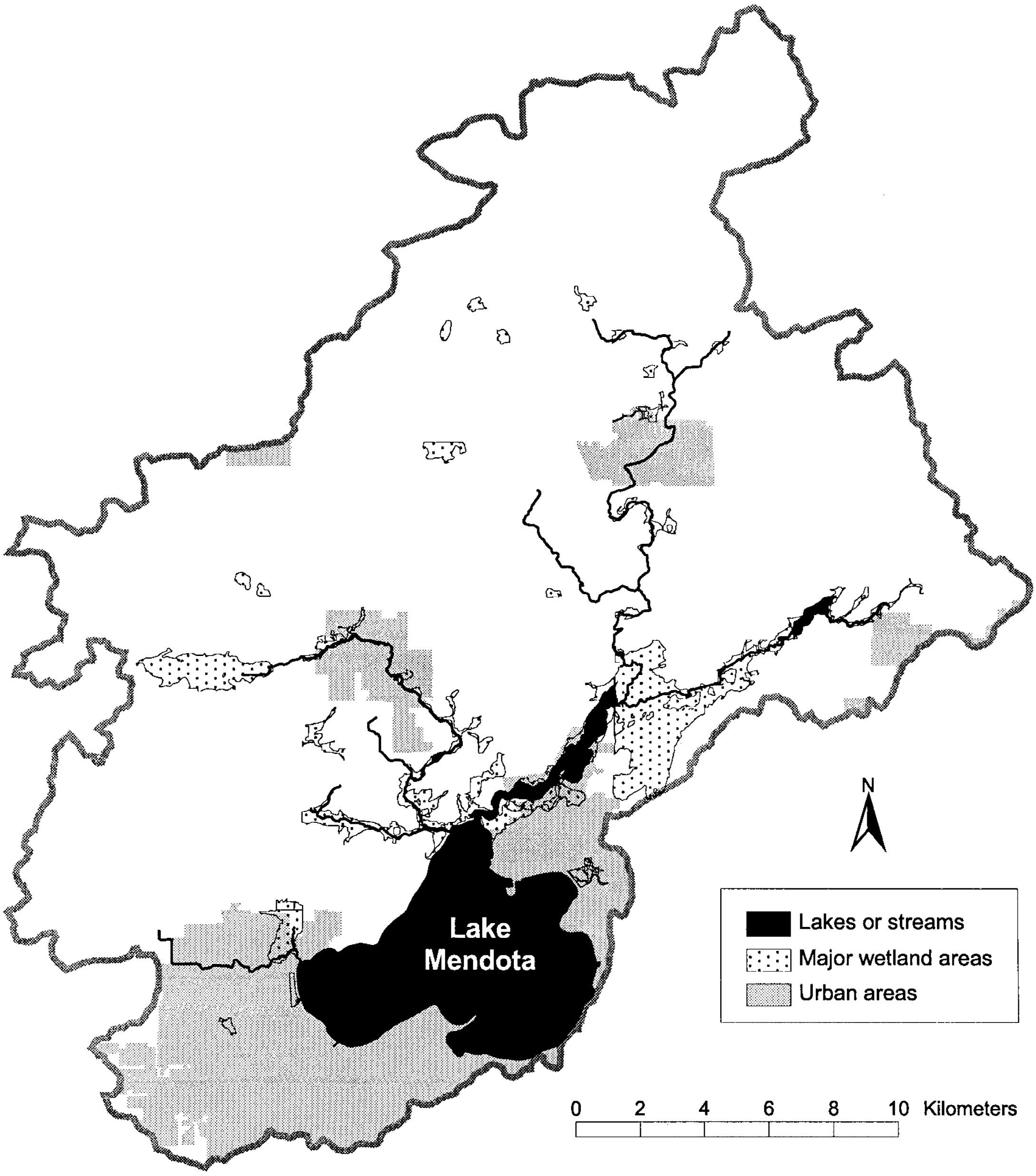

Figure 1. Lake Mendota Watershed, Dane County, Wisconsin, U.S.A.

exposes soil to erosion for longer periods of time than other grains, nutrient loadings also increased at that time. In addition, the use of artificial fertilizers increased after the war. As a consequence, phosphorus concentrations of soils susceptible to runoff have increased in recent years. The numbers of cattle and hogs (pigs) on farms have also increased. Nutrients leached from manure enter the lake in greater amounts, especially during times when manure is being spread on frozen ground. These changes in agriculture have significantly increased nutrient inputs from non-point sources.

Water quality problems apparently first became an issue in Lake Mendota by the mid-1940s. While summer cyanobacterial blooms were common since at least the late 1800s (Brock, 1985; Lathrop & Carpenter, 1992a), algal blooms became severe enough during the mid-1940s that a special study was com-

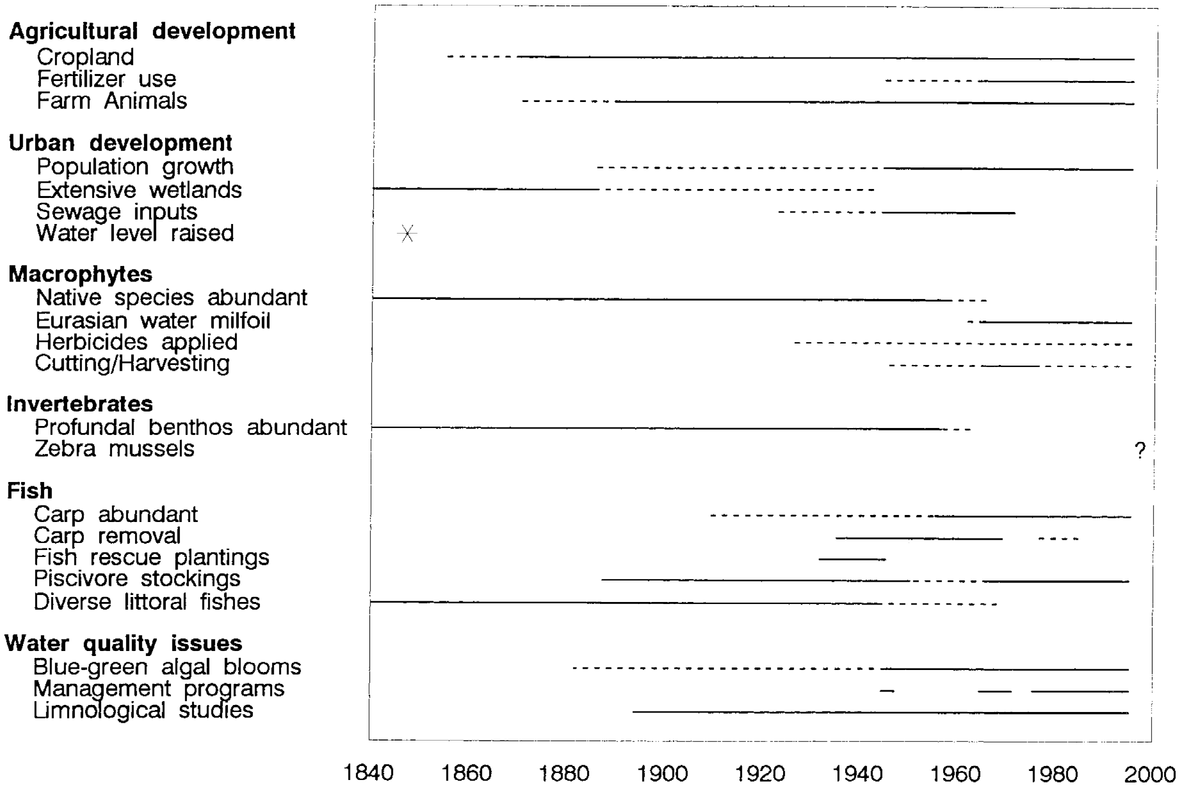

Figure 2. Time line of major human disturbances and management programs for Lake Mendota, Wisconsin from 1840 to present. Solid lines indicate major activity, dashed lines indicate minor activity. Asterisk denotes the time of water level increase. Question mark indicates that zebra mussel invasion is deemed likely to occur in the near future.

missioned to address the causes for these blooms. However, little was done to control the nutrient inputs to Lake Mendota. Rather, attention was focused on diverting Madison's sewage effluents out of the downstream lakes, which had much worse water quality problems. This diversion was extremely controversial, both economically and politically. Because of lawsuits related to the new discharge channel that carried the sewage around all the lakes, the diversion was not completed until 1958.

Concerns about the sewage going into Lake Mendota was not a major concern until the mid-1960s, when serious water quality problems coincided with the invasion of Eurasian water milfoil (*Myriophyllum spicatum*). In 1965, the Lake Mendota Problems Committee (LMPC) was formed, bringing together university and governmental scientists and managers to work on various aspects of lake management. As a result of that work, the sewage was diverted out of the lake in 1971. The LMPC also addressed the importance of reducing non-point pollution to Lake Mendota from agricultural sources, but no action was taken.

Beginning in 1975, the Dane County Regional Planning Commission began preparing a plan with the assistance of local and state government agencies to reduce nonpoint pollution to Lake Mendota and other area waters. This plan was prepared under the provisions of the federal government's 1972 Water Pollution Control Act Amendments and the 1977 Clean Water Act. While many sources of nonpoint pollution were identified, corrective measures were voluntary with some limited cost-sharing money available for implementation.

Further efforts at reducing non-point pollution from drainage basins in the western half of the lake's catchment were conducted during the early to mid-1980s, when the Wisconsin Department of Natural Resources (WDNR) designated the area a 'Priority Watershed Project'. However, because the project was the first to be conducted in the state, and because corrective measures were voluntary, there was little participation in the program by area farmers. Also, many of the 'best management practices' implemented were untested and later proved ineffective at reducing phosphorus loads to the lake.

Recognizing that only an aggressive non-point pollution abatement program would improve water quality in Lake Mendota, the WDNR designated the entire watershed as a Priority Watershed Project in 1993 (Betz et al., 1997). This designation allows state funds to identify significant sources of pollution and to cost-share with both rural landowners and local municipalities, to apply management practices that will reduce phosphorus loads to the lake. Approximately 9 million U.S.$ of state monies have been committed for implementation of the management practices. Local sources (mostly municipalities) are asked to spend an equal amount for cost-sharing practices and other pollution control activities. To date, the project has produced inventories of pollution sources (Betz et al., 1997), and determined the phosphorus load reductions that will be needed to reduce the frequency and severity of cyanobacterial blooms in the lake (Lathrop et al., 1998). The implementation phase of the project began in 1998 and will continue for 10 years. Because much experience has been gained since the early nonpoint source priority watershed projects in Wisconsin, and because mechanisms are now in place for regulating severe pollution sources, expected reductions of agricultural and urban nonpoint pollution to Lake Mendota are significant. This project will be monitored closely by scientists and managers. It is viewed as a long-term experiment by both university and agency staff, who plan to monitor the effects of the program for up to 20 years.

Overfishing

A biomanipulation project begun in 1987 established a strong connection between Lake Mendota's water quality and the fishery (Kitchell, 1992). The experiment employed massive stockings of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) to decrease planktivorous fish populations and increase zooplankton grazing on phytoplankton in Lake Mendota. These piscivores were protected by size limits and bag limits that (at the time) were the most restrictive in Wisconsin (Johnson & Staggs, 1992). However, angling effort increased substantially in response to publicity about the project. Increased angler effort resulted in a four-fold increase in exploitation on walleyes, even with the restrictive fishing regulations (Johnson & Staggs, 1992; Johnson & Carpenter, 1994).

Angler response to the biomanipulation has heightened managers' concerns about overfishing. Technologically advanced fishing gear, the proximity of large urban centers with effective media dissemination of fishing hot spots and the increase in power boat usage, have made anglers rapidly responsive to changes in fishing conditions (Johnson & Staggs, 1992). Overfishing has depleted populations of panfish such as yellow perch (*Perca flavescens*) and bluegill (*Lepomis macrochirus*), as well as predators such as walleye, northern pike and largemouth and smallmouth bass (*Micropterus salmoides* and *M. dolomieu*). Maintenance of these species at high densities may require special fishing regulations – shorter open seasons, larger size limits, and smaller bag limits – to offset increasing fishing effort (Johnson & Staggs, 1992). Additional options include restoring habitat for piscivores and educating anglers about reasonable exploitation rates to sustain viable fisheries.

Habitat loss

Significant losses of wetland habitat from Lake Mendota's catchment have occurred since the area was first settled by Europeans. In 1847, the water level was raised approximately 1.5 m by a dam constructed at the outlet (Lathrop et al., 1992). The increase altered littoral habitat, flooded the upstream wetlands and created new wet areas up the tributary streams. In later years, approximately 50% of the original wetlands in the lake's catchment were either filled for urbanization or ditched and drained for agricultural use. The remaining wetlands are now protected by state laws and local zoning ordinances, but urbanization near wetlands continues to have negative impacts, particularly from sediments eroded from construction sites. Local ordinances for construction site erosion standards are now in place county-wide, but enforcement has been lacking. One of the primary objectives of the Mendota Priority Lake Project is to provide money to enforce these erosion standards.

The decline in area, density and species richness of aquatic macrophytes is another important loss of habitat (Lathrop et al., 1992; Nichols et al., 1992; Nichols & Lathrop, 1994). Surveys and other accounts of macrophytes from the late 1800s into the 1950s indicate that as much as 25% of the total lake area was covered with a diverse community of macrophytes, with plants growing to water depths of 5 m and more.

Major plant species included wild celery (*Vallisneria americana*), various pondweeds (*Potamogeton* spp.), coontail (*Ceratophyllum demersum*), and native milfoil (*Myriophyllum* spp.). By the early 1960s, the submersed macrophyte community changed drastically. At the same time that native species were declining, Eurasian water milfoil invaded and spread rapidly in dense stands throughout Lake Mendota. However, plant growth became restricted to water depths less than 3 m.

Before and during the early years of the milfoil invasion, primitive weed cutters were used to manage nuisance macrophytes. The cut plants were removed by work crews on barges after the plants had floated to shore. This practice undoubtedly aided in the rapid spread of Eurasian milfoil throughout the area's lakes, because milfoil can grow readily from vegetative fragments. To solve this problem, university engineers developed and tested prototype mechanical harvesters that removed the cut plants from the lakes (Livermore & Wunderlich, 1969). A program of harvesting nuisance aquatic macrophytes continues to this day, although Eurasian milfoil no longer attains the same biomass levels as in former years (Carpenter 1980; Nichols & Lathrop 1994). In more recent years, native aquatic macrophytes have been slowly increasing, but the littoral habitat is still not as extensive as it was before the milfoil invasion (Deppe & Lathrop 1993; Nichols & Lathrop 1994).

Invading species

A number of other species, in addition to Eurasian milfoil, have successfully invaded Lake Mendota. The invasion of European common carp (*Cyprinus carpio*) also had significant impacts. This species was introduced intentionally to lakes throughout southern Wisconsin in the late 1800s (Lathrop et al., 1992). It proliferated rapidly and was soon recognized as a cause of poor water clarity. While commercial fishing of carp began in the early 1900s, carp became so numerous in the state that in 1934 Wisconsin established a major carp removal program that was active until 1969. Since 1969, commercial fishing has been minimal due to low demand and poor market prices for carp.

Although studies conducted during the 1940s and 1950s indicated that carp were harming aquatic macrophytes and associated fish communities in many southern Wisconsin lakes, Lake Mendota was perceived to be relatively unaffected by carp through those years (Lathrop et al., 1992; Magnuson & Lathrop 1992). However, after nutrients increased in the mid-1940s (Lathrop, 1992b), carp densities also increased. Increased carp populations may have caused the hundred-fold decline in profundal zoobenthos densities that occurred between the mid-1950s and the mid-1960s (Lathrop, 1992a). The depauperate profundal zoobenthos may have had negative impacts on native fish species, such as yellow perch.

Other species have invaded Lake Mendota, although impacts have been less pronounced than for Eurasian water milfoil and carp. Invading fish species include the freshwater drum (*Aplodinotus grunniens*) and the yellow bass (*Morone mississippiensis*) (Lathrop et al., 1992; Magunson & Lathrop, 1992). Yellow bass were inadvertently introduced to local waters from fish 'rescued' from shallow sloughs of the Mississippi River during the 1930s–1940s. They first were recorded in Lake Mendota in 1957, and were common until a major die-off occurred in 1976 when they became rare. Freshwater drum were not present in Lake Mendota and other area lakes in the early 1900s. Drum may have been introduced from fish rescue operations or they may have migrated into the lakes from the Mississippi River. Freshwater drum were uncommon in Lake Mendota during the mid-1900s, but have reached moderate densities since the mid-1970s. A few other fish invasions have occurred, but their impact on the lake apparently has been minimal. Other exotic or non-native fish currently found in the Great Lakes or the Mississippi River are likely to spread to Lake Mendota.

Records of pelagic zooplankton species do not show any significant change in dominant species between the early 1900s and more recent years (Lathrop & Carpenter, 1992b). *Eubosmina coregoni*, a European exotic that invaded the Great Lakes in the early 1960s, was found in the recent sediment record of Lake Mendota (Kitchell & Sanford, 1992). It achieved modest abundances during the fall months of the mid-1980s (Lathrop & Carpenter, 1992b), but has virtually disappeared from the plankton in more recent years. Other exotic species such as the zooplankton *Bythotrephes* sp. and the benthic zebra mussel (*Dreissena polymorpha*) have colonized nearby Lake Michigan, but have yet to invade Lake Mendota. Impacts of zebra mussel on the lake's food web will likely be substantial, but at present no policy exists that can prevent their introduction to Lake Mendota from other lakes.

Extirpations and loss of genetic diversity

Extirpations of many different plants and animals have occurred in Lake Mendota during this past century. The species diversity of aquatic macrophytes declined after the mid-1950s. Many species of the genus *Potamogeton*, including the once abundant *P. amplifolius*, are no longer present (Nichols & Lathrop, 1994). Declining numbers of migratory waterfowl may be related to declines of favored forage such as wild celery (*Vallisneria americana*) and sago pondweed (*Potamogeton pectinatus*). While some plant species are slowly returning to the lake, it is unknown whether the macrophyte community structure in Lake Mendota will return to its former diversity, now that Eurasian milfoil is no longer growing in dense monotypic stands.

A less noticeable extirpation has been the fingernail clam (*Pisidium* sp.) that once was found in moderate densities throughout the profundal sediments until the mid-1960s when other zoobenthos densities declined (Lathrop, 1992a). Its ecological importance in reprocessing detrital organic matter in Lake Mendota is unknown.

Finally, extirpations of many small littoral-zone fishes have occurred in Lake Mendota since the early 1900s (Lyons, 1989). Most of these fish species are intolerant of environmental degradation. Some species may have declined because they prefer habitat with extensive, diverse macrophytes – a condition that changed around the time of the invasion of Eurasian milfoil in the early 1960s. Another factor that may have contributed to their decline is greater predation due to an increase in piscivore stocking in the 1960s (Magnuson & Lathrop, 1992). These fish may have been an important food source for piscivorous fish, particularly in the spring before the young-of-the-year panfish are available. Now a single species, the brook silverside (*Labidesthes sicculus*) dominates the littoral fish community. Abundance of silversides fluctuates considerably, and effects of these fluctuations on recruitment of the larger fish species is unknown.

While the loss of species diversity has occurred through extirpations, the loss of genetic diversity in some piscivorous fish has occurred through the massive stockings in Lake Mendota (Lathrop et al., 1992). Concerns have been raised about hatchery strains of fish being planted in the state's waters. Low survival of walleye fry and fingerlings stocked during the biomanipulation project on Lake Mendota was attributed to the unsuitability of stocking northern Wisconsin strains of these fish (Johnson & Staggs, 1992). Northern strains were stocked because most of the state's hatchery production of walleyes was from that area. However, future stockings will use local strains more suited for southern Wisconsin's warmer, more eutrophic waters.

Summary

Lake Mendota exemplifies the status of research and management for many eutrophic lakes of agricultural and urban regions. Non-point phosphorus pollution is the keystone cause of the lake's problems. Non-point pollution has been difficult to control. The principal reason is that farmers lack the incentives to manage phosphorus appropriately. At present, hopes are high that the Priority Lake Project possesses the regulatory capabilities and the financial incentives needed to solve the problem. Biomanipulation can substantially improve the lake's water clarity (Lathrop et al., 1996), but intensive angling has made it difficult to sustain the large piscivore populations needed for biomanipulation (Johnson & Staggs, 1992; Johnson & Carpenter, 1994). More restrictive harvest regulations could potentially sustain adequate levels of piscivory in the lake. Restorations of wetlands, native macrophytes, riparian forests and woody habitat of the littoral zone are needed to improve fish habitat. Riparian forests and wetlands also contribute to nonpoint pollution control. Zebra mussels are likely to invade Lake Mendota in the next few years. Their effect on the food web is likely to be strong, but more specific predictions are highly uncertain.

Collaboration of scientists and managers

Lake restoration involves unprecedented manipulations of large, complex systems. Consequently, restoration projects often yield surprising results. While the particular surprises cannot be forecast, we should expect the need to change tactics as restorations develop and new scientific information becomes available.

Successful lake restoration projects have often involved collaborations of scientists and managers (Gulati, 1990; Kitchell, 1992; National Research Council, 1992; Moss et al., 1996; chapters in this volume). In our experience, successful collaborations have certain characteristics. These are:

1. Scientists and managers are involved in the design, implementation and assessment of the project. There is clear communication of goals and expect-

ations among participants. Public outreach is an effective component of the program.

2. The partners agree on the scope of the project. Generally, this means that scientists must work on spatial units larger than those studied by many ecologists. Managers must work at the temporal scale of ecosystem responses, which is long in comparison to typical agency processes.
3. The restoration is conducted as an experiment (Carpenter et al., 1995). Both premanipulation and postmanipulation studies are performed. If possible, a reference ecosystem is studied in parallel with the manipulated ecosystem. Replicate reference and manipulated ecosystems are included, if possible. The manipulation is strong, sustained and consistent. Confounding factors and alternative explanations are carefully evaluated.

Several advantages of collaboration are discussed in Kitchell (1992). These include the new and promising ideas that come from interactions of scientists and managers; opportunities for funding and career advancement that derive from collaboration; academics and students who are better informed about the challenges of environmental management; and managers who are better informed about current scientific understanding (Rudstam & Johnson, 1992; Staggs, 1992). Such collaborations are very successful at overcoming scientific limitations to lake restoration, and have produced important advances in our ability to restore lakes. They have been less successful at overcoming political, institutional and economic constraints to the success of restoration projects.

Acknowledgements

We are grateful for the support of the North Temperate Lakes Long-Term Ecological Research Program, the Pew Foundation and the Wisconsin Department of Natural Resources. We thank Michelle Richardson, Dane County Land Conservation Department, for preparation of the map.

References

Betz, C. R., M. L. Lowndes & S. Porter, 1997. Nonpoint source control plan for the Lake Mendota Priority Watershed Project. Wisconsin Department of Natural Resources, Madison, Wisconsin, U.S.A., Publication number WT-481-97.

Brock, T. D., 1985. A Eutrophic Lake: Lake Mendota, Wisconsin. Springer-Verlag, New York.

Carpenter, S. R., 1980. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Can. J. Bot. 58: 527–535.

Carpenter, S. R., D. Bolgrien, R. C. Lathrop, C. A. Stow, T. Reed & M. A. Wilson, 1998. Ecological and economic analysis of lake eutrophication by nonpoint pollution. Australian Journal of Ecology 23: 68–79.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley & V. H. Smith, 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8: 559–568.

Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler & R. F. Wright, 1995. Ecosystem experiments. Science 269: 324–327.

Carpenter, S. R. & K. L. Cottingham, 1997. Resilience and restoration of lakes. Conservation Ecology 1. Internet at http://www.consecol.org/vol1/iss1/art2.

Carpenter, S. R., A. Muñoz del Rio, S. Newman, P. Rasmussen & B. M. Johnson, 1994. Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. Ecological Applications 4: 822–832.

Christensen, D. L., B. J. Herwig, D. E. Schindler & S. R. Carpenter, 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. Ecological Applications 6: 1143–1149.

Cooke, G. D., E. B. Welch, S. A. Peterson & P. R. Newroth, 1993. Restoration and Management of Lakes and Reservoirs. Lewis Publishers, Boca Raton, Florida, U.S.A.

Deppe, E. R. & R. C. Lathrop, 1993. Recent changes in the aquatic macrophyte community of Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 81: 47–58.

Driscoll, C. T., C. Yan, C. L. Schofield, R. Munson & J. Holsapple, 1994. The mercury cycle and fish in Adirondack lakes. Envir. Sci. Technol. 28: 137–143.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. van Donk (eds), 1990. Biomanipulation – Tool for Water Management. Developments in Hydrobiology 61. Kluwer Academic Publishers, Dordrecht, 628 pp. Reprinted from Hydrobiologia 200/201.

Gunderson, L. H., C. S. Holling & S. S. Light (eds), 1995. Barriers and Bridges to the Renewal of Ecosystems and Institutions. Columbia University Press, New York, U.S.A.

Harper, D. M, 1992. Eutrophication of Freshwaters. Chapman & Hall, London, England.

Heck, K. L. & L. B. Crowder, 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. In S. S. Ball, E. D. McCoy & H.R. Mushinsky (eds), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman & Hall, London: 281–299.

Hilborn, R., 1992. Can fisheries agencies learn from experience? Fisheries 17: 6–14.

Hilborn, R., C. J. Walters & D. Ludwig, 1995. Sustainable exploitation of renewable resources. Ann. Rev. Ecol. Syst. 26: 25–44.

Johnson, B. M. & S. R. Carpenter, 1994. Functional and numerical responses: A framework for fish-angler interactions? Ecol. Applic. 4: 808–821.

Johnson, B. M. & M. D. Staggs. 1992. The fishery. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 353–375.

Johnson, D. L. & R. A. Stein (eds), 1979. Response of Fish to Habitat Structure in Standing Water. American Fisheries Society Special Publication Number 6: Columbus, Ohio, U.S.A.

Kitchell, J. F. (ed.), 1992. Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York.

Kitchell, J. F. & S. R. Carpenter, 1993. Variability in lake ecosystems: Complex responses by the apical predator. In M. J.

McDonnell & S. T. A. Pickett (eds), Humans as Components of Ecosystems. Springer-Verlag, N.Y., U.S.A.: 111–124.

Kitchell, J. F. & P. R. Sanford, 1992. Paleolimnological evidence of food web dynamics in Lake Mendota. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 31–47.

Lathrop, R. C., 1990. Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and the effect on downstream lakes. Verh. int. Ver. Limnol. 24: 457–463.

Lathrop, R. C., 1992a. Decline in zoobenthos densities in the profundal sediments of Lake Mendota (Wisconsin, U.S.A.). Hydrobiologia 235/236: 353–361.

Lathrop, R. C., 1992b. Nutrient loadings, lake nutrients and water clarity. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 71–98.

Lathrop, R. C. & S. R. Carpenter, 1992a. Phytoplankton and their relationship to nutrients. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 99–128.

Lathrop, R. C. & S. R. Carpenter, 1992b. Zooplankton and their relationship to phytoplankton. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 129–152.

Lathrop, R. C., S. B. Nehls, C. L. Brynildson & K. R. Plass, 1992. The fishery of the Yahara lakes. Tech. Bull. No. 181. Wis. Dep. Nat. Resour., Madison, Wis.

Lathrop, R. C., S. R. Carpenter & L. G. Rudstam, 1996. Water clarity in Lake Mendota since 1900: Responses to differing levels of nutrients and herbivory. Can. J. Fish. aquat. Sci. 53: 2250–2261.

Lathrop, R. C., S. R. Carpenter, C. A. Stow, P. A. Soranno & J. C. Panuska, 1998. Phosphorus loading reductions needed to control blue-green algal blooms in Lake Mendota. Can. J. Fish. aquat. Sci. 55: 1169–1178.

Livermore, D. F. & W. E., Wunderlich, 1969. Mechanical removal of organic production from waterways. In G. A. Rohlich (ed.) Eutrophication: Causes, Consequences, Correctives. National Academy of Science, Washington, D.C.: 494–520.

Lodge, D. M., 1993. Biological invasions: lessons for ecology. Trends in Ecology & Evolution 8: 133–137.

Lyons, J., 1989. Changes in the abundance of small littoral-zone fishes in Lake Mendota, Wisconsin. Can. J. Zool. 67: 2910–2916.

Magnuson, J. J. & R. C. Lathrop, 1992. Historical changes in the fish community. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 195–231.

Maser, C. & J. R. Sedell, 1994. From the Forest to the Sea: The Ecology of Wood in Streams, Rivers, Estuaries and Oceans. St. Lucie Press, Delray Beach, Florida, U.S.A.

Moss, B., J. Stansfield, K. Irvine, M. Perrow & G. Phillips, 1996. Progressive restoration of a shallow lake: a 12-year experiment in isolation, sediment removal and biomanipulation. J. appl. Ecol. 33: 71–86.

National Research Council, 1992. Restoration of Aquatic Ecosystems. National Academy Press, Washington, D.C.

Nichols, S. A. & R. C. Lathrop, 1994. Cultural impacts on macrophytes in the Yahara lakes since the late 1800s. Aquat. Bot. 47: 225–247.

Nichols, S. A., R. C. Lathrop & S. R. Carpenter, 1992. Long-term vegetation trends – a history. In J. F. Kitchell (ed.), Food Web Management: a Case Study of Lake Mendota. Springer-Verlag, New York: 153–173.

Poiani, K. A. & B. L. Bedford, 1995. GIS-based nonpoint source pollution modeling: considerations for wetlands. Journal of Soil & Water Conservation 50: 613–619.

Postel, S. & S. R. Carpenter, 1997. Freshwater ecosystem services. In G. Daily (ed.), Ecosystem Services. Island Press, Washington, D.C.

Rudstam, L. G. & B. M. Johnson, 1992. Development, evaluation, and transfer of new technology. In J. F. Kitchell (ed.), Food Web Management: A Case Study of Lake Mendota. Springer-Verlag, New York, USA: 507–524.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution 8: 275–279.

Soranno, P. A., S. L. Hubler, S. R. Carpenter & R. C. Lathrop, 1996. Phosphorus loads to surface waters: A simple model to account for the spatial pattern of land use. Ecological Applications. 6: 865–878.

Staggs, M. D., 1992. Benefits on a larger scale. In J. F. Kitchell (ed.), Food Web Management: A Case Study of Lake Mendota. Springer-Verlag, New York, USA: 525–538.

Stow, C. A., S. R. Carpenter, C. P. Madenjian, L. A. Eby & L. J. Jackson, 1995. Fisheries management to reduce contaminant consumption. BioScience 45: 752–758.

Swackhamer, D. L. & D. E. Armstrong, 1986. Estimation of the atmospheric and nonatmospheric contributions and losses of polychlorinated biphenyls for Lake Michigan on the basis of sediment records of remote lakes. Envir. Sci. Technol. 20: 879–883.

Zedler, J. B., 1996. Ecological issues in wetland mitigation: an introduction to the Forum. Ecol. Applic. 6: 33–38.