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From: **Senator Kathy Bernier**

To: **The Senate Committee on Natural Resources and Energy**

Re: **Testimony on Senate Bill 725**

Relating to: biomanipulation projects to improve the water quality of lakes and impoundments and making an appropriation

Date: **January 29, 2020**

Chairman Cowles and members of the committee, thank you for hearing Senate Bill 725 today. This bill came out of the Speaker's Task Force on Water Quality and is one of many tools that we would hope to give the people of Wisconsin when addressing water quality issues in our many waterways.

Senate Bill 725 would create a grant program for the DNR to administer that would fund biolmanipulation projects in the state. Biomanipulation is the process of introducing or removing species in the lake's ecosystem in order to reduce algae blooms and other hazards that are harmful to water quality. The DNR is already able to do these projects under current law, this bill would just provide the Department with resources to help lake groups that want to use this method as a means of cleaning up their lake.

Everyone understands that biomanipulation is not the answer to water quality. If the source of the water quality issue is not addressed, biomanipulation will not solve the problem for very long. Biomanipulation is the last step in a process to clean up lakes and other waterways, but, it is an important and useful tool in that process. The more we can find out about it and its effectiveness, the more lakes can be rehabilitated.

For a relatively small investment, we can see what sort of results we can achieve using this scientific method to help lakes get healthy. I hope you will join me and Representative Summerfield in supporting SB 725 and ensuring that everyone has access to clean, healthy water in Wisconsin.

ROB SUMMERFIELD
STATE REPRESENTATIVE • 67th ASSEMBLY DISTRICT

January 29, 2020

Senator Cowles, Chair
Senator Olsen, Vice-Chair
Members of the Senate Committee on Natural Resources & Energy

Testimony on 2019 Senate Bill 725

Relating to: biomanipulation projects to improve the water quality of lakes and impoundments and making an appropriation

Dear Chairman Cowles, Vice-Chairman Olsen, and Committee Members:

Thank you for providing me with the opportunity to testify at today's public hearing on Senate Bill 725. I appreciate your time and consideration of this legislation.

Biomanipulation is the deliberate altering of an ecosystem by humans through adding or removing species; chiefly prey. This can cause a shift in predator/prey populations of an area which has an effect on the entire food chain and ecosystem.

Many of the impaired lakes and impoundments in Wisconsin have an excess amount of phosphorus and other nitrates. Bottom-feeding fish (ex: carp), and phytoplankton thrive in these conditions and create harmful algal blooms (HABs). Sedentary bodies of water rarely have their ecosystems change organically; thus, even if/when outside phosphorus/nitrate sources are reduced or eliminated, there can still remain a vicious cycle of ever-increasing bottom-feeding fish and phytoplankton populations.

In these situations, however, biomanipulation can be used as an ecological tool for water quality management when larger amounts of predatory game fish (ex: bass, pike) that feast on bottom-feeding fish are introduced into the lake or impoundment. As bottom-feeding fish decrease, rooted vegetation, beneficial zooplankton, and water clarity and quality increase.

This process has been successfully implemented before; such as with Lake Finjasjon in Sweden, Lake Vesijärvi in Finland, Big Wall Lake in Iowa, and Wingra Lake right here in Madison.

SB 725 creates a one-time, $150,000 competitive grant application process to fund water quality improvement projects using biomanipulation on impaired lakes and impoundments across Wisconsin. This type of eco-science has the potential to transform how our state addresses water quality issues moving forward, so I thank you again for your time and careful consideration of this impactful legislation.

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Rep.Summerfield@legis.wi.gov

Testimony in Support of SB 725

01-28-2020

Dear Senate Committee on Natural Resources & Energy Members,

My name is Dr. Scott McGovern I am a researcher in cyanobacteria mitigation and the public health concerns that these algae-like organisms can pose by the toxins these organisms produce. Most of the lakes that are stated as having an algae problem are in fact affected by cyanobacteria, a photosynthetic prokaryotic organism. Most watershed mitigation techniques mainly focus on the reduction of phosphate through the control of agricultural runoff to address problems such as cyanobacteria blooms.

However, research has shown that these techniques have often not achieved the desired results (Sharpley et.al., 2014). Consequently, I have been interested in an approach to watershed mitigation that implements multiple techniques. The scientific literature has demonstrated that using multiple techniques rather than a single approach to watershed mitigation has been significantly more successful and biomanipulation has been a common element in the majority of the studies (Anandotter, 1999).

Biomanipulation offers an inexpensive and effective addition to mitigate lakes infested with cyanobacteria caused by excessive nutrients. Biomanipulation is widely used in Europe and is becoming more common in the United States as well as other parts of the world. This bill introducing support for biomanipulation can provide an important tool for the reduction of harmful cyanobacteria and I strongly believe it to be an important step for water quality improvement.

Biomanipulation is really balancing a lake ecosystem so that the natural food webs that exist within a lake can alleviate an imbalance such as excessive cyanobacteria growth. Three aspects of the lake ecosystem must change to realize an improvement in water clarity, an increase in the number of zooplankton, increased coverage of the lake with macrophytes (large aquatic plants) and the fish population must change to a more balanced population. Zooplankton such as daphnia, copepods and seed shrimp consume photosynthetic organisms; therefore, increasing zooplankton reduces cyanobacteria improving water clarity. Benthivorous or bottom-dwelling fish destroy macrophytes and their young consume zooplankton making their reduction important for two reasons. Similarly, lakes have zooplanktivorous fish that can negatively impact a lake by also eating zooplankton. Predator fish stocking to reduce zooplanktivorous fish and benthivorous fish removal are techniques to stop the consumption of zooplankton. The root cause may be nutrient enrichment, however; managing the lake in such a way will allow less predation on zooplankton. As a result, the reduction of the green organisms is accomplished by increased grazing. In addition, reducing benthivorous fish will increase macrophyte growth. Consequently, increasing lake macrophytes, (large aquatic plants) will provide refuge habitat for zooplankton and a method of reducing nutrients making it unavailable for cyanobacteria. Nutrient reduction is important but this method reduces harmful cyanobacteria by direct consumption, macrophyte competition for nutrients and the removal of benthivorous fish through stopping their perturbation of the bottom sediment and macrophyte destruction. Macrophytes, therefore, increase when benthivorous fish are removed and if further increases of macrophytes are needed seeds and entire plants can be added to increase the coverage to further benefit the lake ecosystem.

Biomanipulation is said to work the best in shallow eutrophic lakes although it has been used extensively in all types of lakes. The method is inexpensive compared to many other lake remediation techniques, effective, it can use nets rather than toxic chemicals to remove fish and can be adjusted to fit individual lake ecosystems. The biomanipulation process will improve the fish populations and habitat of lakes. There really is not a negative side of using biomanipulation techniques.

I strongly support Representative Rob Summerfield's biomanipulation in SB 725 and can not emphasize enough that these techniques should be part of Wisconsin's efforts to improve water quality, public safety and recreation of affected lakes.

Sincerely,

Scott McGovern PhD
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Senate Bill 725 1/29/2020

Dear Members of the Senate Committee on Natural Resources and Energy,

My name is Dick Lamers and I reside on Tainter Lake in Dunn County. I have been active in water quality efforts since we obtained the property in 1981. We have watched a slow and continuing degradation of the entire Red Cedar Watershed since then.

Multiple, well meaning people have tried projects that were intended to solve the problem of Blue Green Algae Blooms and the associated toxins that occur each summer. The projects over the last ten years have included Barley straw bales to filter the algae, motors on docks to keep the water flowing, specialty pumps to aerate the water, dredging, alum treatments and now Bio manipulation studies. All of them had been attempted before and were shown that when applied to a River System like ours, they would have minimal or no impact on our significant Algae problem.

Any major/complex problem like the one experienced here, needs a leading organization to coordinate the process and a detailed root cause analysis to solve it.

The Leading organization in this case is the WI. Department of Natural Resources. They have qualified staff and expertise to lead this effort.

We already know the root cause. It has been proven to be the excessive loading of Phosphorus into our waters. It was verified over 8 years ago and included additional research to get our TMDL Plan approved by the EPA in 2012.

Attempting to use smaller marginal solutions just delay the results needed and continue the problems indefinitely. For us, all efforts should be focused on minimizing Phosphorus and keeping it on the land and out of all waterways.

Seven or Eight years ago, Wisconsin took Phosphorus out of lawn fertilizers, then out of dishwashing detergents. Our Land & Water Conservation departments have done a great job of developing Farmer Led and Producer Led Groups. No till and minimum till planting and the use of cover crops is gaining in acceptance across the state. Working together through field days and conferences for all citizens and land owners, we are all beginning to understand our individual roles in water Quality.

I am opposed to passing Bill 725.

Funding of Bio Manipulation projects are already covered in the current project management process. They should only be funded in lakes that are designated a priority and that have a high probability of success.

Respectfully submitted,

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WISCONSIN
DEPT. OF NATURAL RESOURCES

Senate Committee on Natural Resources and Energy

2019 Senate Bill 725
Biomanipulation projects to improve the water quality of lakes and impoundments and making an appropriation
January 29, 2020

Good morning Chairman Cowles and members of the Committee. My name is Meredith Penthorn, and I am the Fisheries Management policy specialist with the Wisconsin Department of Natural Resources. I am joined by Todd Kalish, Fisheries Management Deputy Bureau Director, and Tim Asplund with the Bureau of Water Quality. Thank you for the opportunity to testify, for informational purposes, on Senate Bill 725 (SB 725) relating to biomanipulation projects to improve the water quality of lakes and impoundments and making an appropriation.

This bill would provide an additional funding source for biomanipulation studies and activities with the overarching goal of improving water quality for lakes and impoundments on the impaired waters list. While the Department of Natural Resources periodically conducts biomanipulation projects for various purposes, including enhancing sport fisheries and rehabilitating aquatic ecosystems, this bill would create a new appropriation to assist local water improvement groups in conducting similar projects specifically for improving water quality under the oversight of the Department.

The new appropriation could benefit waters of the state by allowing more work to be conducted on certain impaired waters that the Department alone cannot accomplish with current funding or staffing levels. This would also allow local water improvement groups to assume a greater role in management of the waters in their communities. However, the Department cautions that biomanipulation may not be efficient or effective at improving water quality on waters with excessive nutrient or pollutant inputs, without concurrent reduction of those inputs. Biomanipulation may also be less successful on shallow waterbodies connected to flowing waters due to an increased risk of recolonization by detrimental fish species. In addition, anoxic conditions could limit the success of fish introductions aimed to control undesirable fish species.

Some biomanipulation projects, namely those involving the removal or addition of fish, could impact angler activity on the water. This could lead to a perception of user conflict if anglers feel excluded from any plans to remove fish by methods other than fishing, especially game fish that are considered to be detrimental in the waterbody, or if angler harvest pressure on stocked piscivorous fish is high. Outreach and education to anglers in the vicinity of the waterbody could help reduce any concerns and increase public buy-in.

The DNR estimates that the proposed one-time appropriation of $150,000 would fund biomanipulation projects on one to two waterbodies during the biennium. To ensure that the projects are feasible for meeting the goal of improved water quality, the Department could utilize an existing surface water grants program to administer these grants, which would draw from a pool of eligible applicants and would require a formal plan to be submitted with the application materials. Grants could also be solicited and awarded for surveys, studies, and developing plans for biomanipulation projects. The Department could publish an announcement soliciting applications for biomanipulation projects, including the screening process and procedures for monitoring grant activities specific to these grants, in its annual grant application guidance. These processes would entail collaboration between the Bureaus of Fisheries Management, Watershed Management, Office of Applied Science and potentially other DNR programs. Costs associated with implementing this bill would include staff time to create the needed guidance, review applications, process grants, and oversee grant project activities.

Finally, this bill states that activities allowed under the appropriation shall include comprehensive fish studies, removal of zooplanktivorous and benthivorous fish, and the introduction of piscivorous fish. Requiring all activities for each project would substantially limit the number of eligible grant applications. The DNR met with the bill authors and appreciated a discussion regarding the potential for allowing a combination of those activities and other types of ecological activities that may achieve water quality goals, such as water level management. To that end, the Department suggests incorporating additional flexibility into the bill language.

On behalf of the Bureau of Fisheries Management, I would like to thank you for your time today. We would be happy to answer any questions you may have.

January 28, 2020

Subject: Public hearing testimony on SB 725 and AB 798 in support of "Biomanipulation" lake management grants administered by DNR

Dear Senate and Assembly committee members:

My name is Richard Lathrop. I earned a PhD in Oceanography and Limnology from UW-Madison in 1998 and a M.S. in Natural Resources (Aquatic Ecology) at the Univ. of Michigan in 1975. I was a Research Limnologist for the Wis. DNR for 33 years until retiring in 2010. In that capacity I have studied and implemented techniques to improve lake water quality in nutrient-rich lakes including the Madison area lakes and Devil's Lake. For the past 21 years, I have also held an Honorary Fellow position at UW's Center for Limnology where I continue to collaborate on many research projects including the UW's North-Temperate Lakes Long-Term Ecological Research Project funded by NSF. Specific to the issues of this public hearing, I am very knowledgeable about "biomanipulation" – the manipulation of a lake's biota – to achieve improvements in lake water quality and/or overall ecosystem health.

I was a co-investigator on the DNR's and UW's collaborative Lake Mendota biomanipulation project from its inception in 1987, and I was the lead author of the project's peer-reviewed synthesis paper published in 2002. This project focused on increasing the lake's predator (piscivorous) fish population densities (i.e., walleye and northern pike) via stocking and harvest regulations in order to reduce the density of smaller zooplankton-eating (planktivorous) fish so that increased densities of large-bodied water fleas (*Daphnia*) would be able to reduce by grazing the free-floating algae (phytoplankton) in the open water area of the lake. The goal was to increase water clarity and reduce blue-green algae in the lake, which occurred in Lake Mendota. This type of biomanipulation project is considered a "top-down" approach to lake management via alternations in a lake's food web. Reviews of the technique indicate it has been most successfully applied to moderately fertile lakes.

I was also the lead DNR-UW researcher who spearheaded the biomanipulation of Lake Wingra by drastically reducing its overabundant bottom-feeding (benthivorous) carp population comprised of large long-lived individuals. In partnership with DNR fish management and the Friends of Lake Wingra, commercial seining of carp in 2008 caused the lake to completely switch from a turbid algal state with very poor water clarity and dense blue-green algae to a state of clear water that allowed sunlight penetration for aquatic plants to grow. This project was summarized in an article I published with co-authors in 2013 and has been a springboard for other such carp removal projects throughout Wisconsin. Such biomanipulations of shallow lakes have been widely conducted not only in the U.S., but throughout Europe and elsewhere.

In summary, I whole-heartedly support the Legislature providing $150,000 to the DNR for biomanipulation grants to improve lake water quality.

Sincerely,

Richard C. Lathrop

Carp Removal to Increase Water Clarity in **Shallow Eutrophic Lake Wingra**

Richard C. Lathrop, David S. Liebl, and Kurt Welke

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Introduction

In simplest terms, shallow eutrophic lakes typically have either of two alternative stable states – an algal-turbid state, or a clear-water/aquatic-plant state (Scheffer et al. 1993; Scheffer and van Nes 2007). The first state is characterized by very poor water clarity that restricts the growth of submersed aquatic plants (macrophytes) due to blue-green algal blooms and/or suspended sediments. The clear-water state has relatively good water clarity that allows macrophytes to grow throughout much of the lake. Scientists, managers, and lake users generally consider the latter state as having higher ecological and recreational value.

Shallow lakes can be stuck in the turbid-algal state because the top layer of the lakes' bottom sediments remain unconsolidated due to the feeding activities of dense populations of carp or other bottom-feeding fish (e.g., bullheads). Wind-induced water currents then can easily resuspend these "fluffy" sediments while enhancing nutrient recycling that promotes algae growth. In such lakes, carp populations dominated by large individuals of the long-lived fish can cause the stable state to persist.

When populations of carp and other bottom-feeding fish are significantly reduced through management efforts (or natural die-offs such as winterkill due to low dissolved oxygen levels), the water begins to clear. Increased water clarity allows aquatic macrophytes to grow more luxuriantly and in deeper water, resulting in improved conditions for sight-feeding fish as well as many prey fish species. The macrophytes dampen water current velocities, which in turn cause bottom sediments to consolidate making them even more resistant to resuspension while also reducing nutrient recycling. Water clarity further increases, creating a positive feedback loop that produces even lower water velocities, greater water clarity, and more macrophytes. Thus, this clear-water state is stable as long as carp densities remain low. Studies have shown that intensive feeding on carp eggs and fry by fish such as bluegills greatly reduces carp recruitment (Przemyslaw and Sorensen, 2010). If such fish predation is not present, then carp densities can quickly rebound.

To enhance desirable fisheries, lake managers in Wisconsin and elsewhere have used chemicals for whole-lake carp eradications since at least the 1950s. However, such chemical treatments are not always effective or long-lasting because of the size of the lake or the presence of interconnecting waters where carp can escape eradication. And in urban settings, chemically eradicating fish is not always possible due to public opposition. This article summarizes recent efforts to use large seines to reduce overabundant carp populations in Lake Wingra, a heavily-utilized shallow eutrophic lake located in Madison, Wisconsin.

Lake Wingra

Lake Wingra is a 140-hectare, shallow headwater lake with mean and maximum depths of 2.7 m and 3.8 m, respectively (Figure 1). The lake is fed by urban stormwater runoff and groundwater. Water flows from the lake's outlet over a low head dam (Figure 2) through Wingra Creek to much larger Lake Monona, one of the Yahara River chain of lakes. For years, Lake Wingra has supported mixed recreational opportunities including non-motorized and "no-wake" boating, fishing, and swimming. The typical warmwater fishery of bluegills, crappies, and largemouth bass was enhanced by heavy stocking of non-breeding muskellunge in the early 2000s. The resultant fishery has attracted a loyal following of muskie anglers from southern Wisconsin and beyond.

Soon after carp were introduced to the Yahara lakes in the late 1800s,

Figure 1. Aerial photo of Lake Wingra taken Sept. 22, 2007 showing dense blue-green algal bloom in the lake. Rectangular carp exclosure with clear water is visible along northern shoreline (photo: Emily Sievers, UW-Madison).

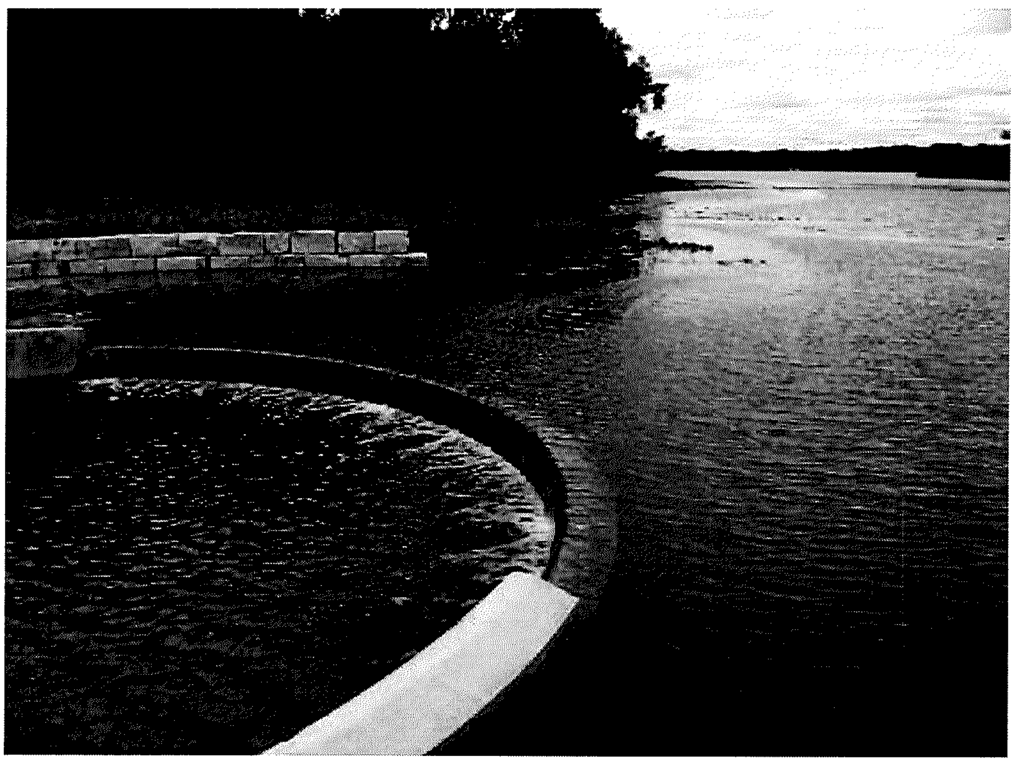

Figure 2. Photo taken July 28, 2013 shows low head dam at the outlet of Lake Wingra emptying into Wingra Creek, which flows with little elevation change to Lake Monona, one of the Yahara lakes. On that date, Lake Monona was approximately 1.3 feet higher than its normal summer maximum level, but one foot lower than the level reached in late June 2013 due to excessive precipitation (photo: R. Lathrop).

historical accounts indicate Lake Wingra became turbid with poor water clarity. In the mid-1950s, carp were removed by seining (Neess et al. 1957), but carp apparently repopulated quickly. Along with the establishment and proliferation of the invasive Eurasian watermilfoil (EWM) in the early 1960s, poor water clarity has persisted for many years as documented by a number of University of Wisconsin–Madison (UW) research studies including the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) project since 1996.

Following EWM's invasion, the plant reached extremely dense conditions in the 1970s; in subsequent years EWM has continued to dominate the lake's shallow waters although at somewhat reduced densities. However, a diverse community of submersed native macrophytes has persisted in shallow water along the lake shoreline even though water clarity has been poor. The native plants have likely survived because the lake has had little aquatic macrophyte management (herbicide treatments or mechanical cutting/harvesting) to control EWM because most of the lake's shoreline is natural habitat and in public ownership.

Since 1998, an active citizen's group called the Friends of Lake Wingra (FOLW, http://lakewingra.org/) has been working with local lake managers and scientists to improve the lake's overall ecological health (Lorman and Liebl 2005). One of FOLW's goals has been to increase water clarity and reduce blue-green algae blooms. Toward that end, much effort has focused on implementing watershed management practices for reducing phosphorus and sediment inputs to the lake.

Realizing that water quality improvements in Lake Wingra also required addressing an overabundant carp problem, two studies were initiated in late summer 2005. One study was a carp exclosure experiment to demonstrate the water clarity increase from reduced nutrient recycling and sediment resuspension while also testing the response of EWM and native macrophytes to clear water. The second study used radio-telemetry to determine when and where carp might be vulnerable to targeted removals by large seines. Results from these studies were so encouraging that carp removal by seining was conducted under the ice during March 2008 followed by a minor removal in March 2009 after ice-out. The exclosure demonstration, the telemetry study, the carp removal, and the lake's water clarity and aquatic macrophyte responses in five summer seasons (2008-2012) following reduced carp densities are described below.

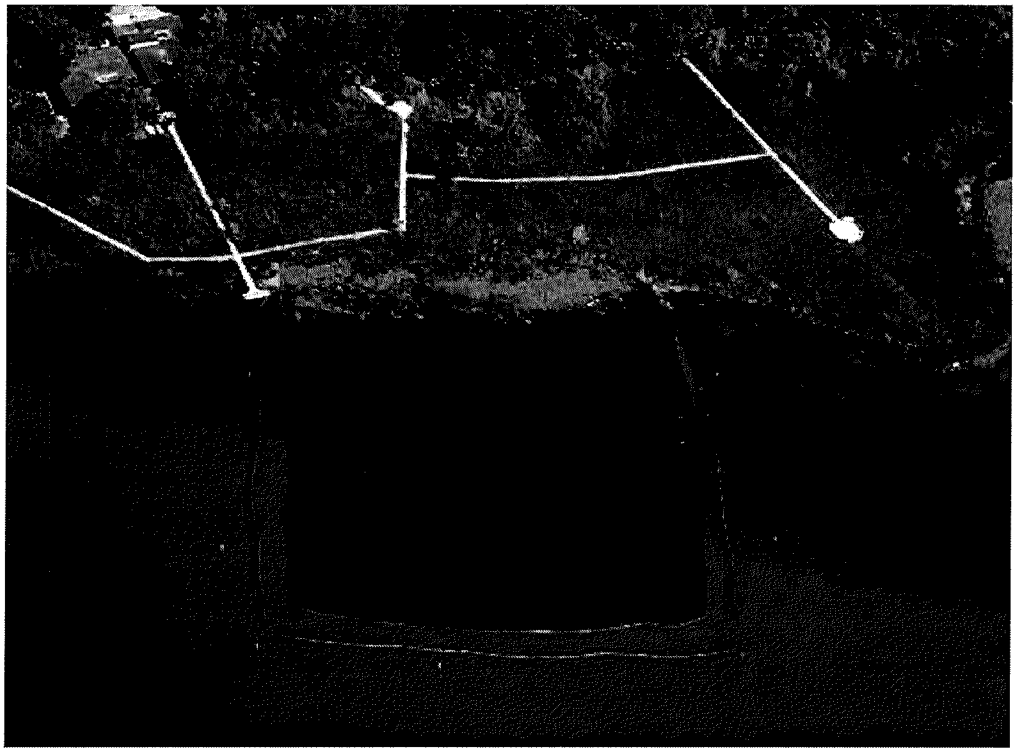

Figure 3. Aerial photo of 1-hectare carp exclosure in Lake Wingra taken July 7, 2007 showing clear water inside the exclosure contrasted with blue-green algal bloom in lake water surrounding the exclosure. Difference in growth extent of Eurasian watermilfoil inside and outside the exclosure is visible in the photo. Wave dissipater booms are also visible outside the exclosure walls (photo: Mike DeVries, *The Capital Times*).

Carp Exclosure Demonstration

The carp exclosure was a low risk demonstration project conducted for three years at a scale that allowed lake managers/researchers and especially the general public to evaluate whether a whole-lake restoration project centered on reducing carp densities would be worth pursuing. While recognizing that the exclosure experiment was not a true test of a whole-lake carp removal, the exclosure dampened water currents and stabilized bottom sediments quickly mimicking what would occur in the lake when macrophytes responded to clear water.

The exclosure was installed in the lake during August 2005, but the endwall was not closed until later in September when the carp were removed by electroshocking and seining. The few carp that remained inside the exclosure were later removed by trammel nets with the lack of carp verified by scuba divers.

Exclosure design/construction. The rectangular exclosure had an area of 2.5 acres (1.0 ha) with one endwall being the lake shoreline (Figure 3). The material of the exclosure was 2.5 mil vinyl plastic with a three-year UV exposure life expectancy. The exclosure's floatation collar consisted of ten-foot sections of Styrofoam tubes with a stainless steel tension cable in the wall underneath the collar. The two sidewalls of the exclosure were 340-380 feet in length and the lake endwall was 300 feet. The walls were fabricated to fit the depth profile of the lake with enough extra wall height added for minor fluctuations in lake level. The southwest and southeast exclosure corners had water depths of 2.7 m and 2.5 m, respectively. A ballast chain was fabricated in the bottom of each wall, and a three-foot skirt with an additional ballast chain was added to ensure a tight seal with the bottom sediments. *Environetics, Inc.* (Lockport, Illinois), a company specializing in water baffles and liners for various environmental engineering applications, fabricated the exclosure with design specifications provided by project leaders.

The corners of the exclosure were attached to heavy blocks with pipe driven into the cattail marsh shoreline, and to long heavy-duty galvanized iron pipe pushed deep into the lake's soft bottom sediments with the ends extending above the water line. The lake corners of the exclosure were attached to the pipes, which were connected by long cables to two sets of heavy concrete anchors placed far from each corner in line with the respective walls so that tension on the exclosure walls could be maintained. Side pipes (with outside anchoring) were attached every 50 feet along the three walls to help maintain the exclosure's rectangular shape.

Because the exclosure's walls were subject to strong water currents during periods of high winds, 300-foot long "wave dissipater booms" were installed to absorb some of the water current energy. The booms were constructed of 8 oz. Polypropylene Geotextile fabric with a Styrofoam boom collar, tension cable, and an 18-inch hanging curtain weighted with a ballast chain. Heavy anchors and cabling stretched each boom in a direction parallel to each exclosure wall with a separation of about 25 feet (Figure 3). Cement blocks were also attached along the length of each boom wall for further anchoring.

Exclosure experiment results. Water clarity increased rapidly once the exclosure was installed (Lorman and Liebl 2005), but the contrast between the lake and the exclosure was most dramatic during summer when blue-green algae growth was most abundant (Figures 1, 3). As expected, the density and depth distribution of aquatic macrophytes increased in response to the much clearer water, but most of the increased growth was due to EWM, which had completely colonized the exclosure by summer 2008 before the exclosure was removed in September. Native plants expanded their depth distribution slightly after 3 years of clear water and no carp browsing because dispersal rates are much slower for most native submersed macrophytes compared to EWM. However, in spite of the prospect of increased EWM growth, the exclosure's demonstration of how much clearer the lake water could become galvanized public support for removing carp even as early as August 2006 when one of Madison's local newspapers published a front-page article along with an aerial photo of the exclosure (similar to Figure 3).

Figure 4. Wisconsin DNR fish manager Kurt Welke implanting radio transmitters in anesthetized carp captured from Lake Wingra, September 2005 (photo: R. Lathrop).

Carp Radio-Telemetry Study

The carp radio-tracking study in Lake Wingra was initiated in the fall of 2005 because muskie anglers at an earlier public meeting had expressed their strong opposition to a whole-lake carp eradication with rotenone (a plant derivative used for fishing by indigenous Indians in Brazil) for fear that Lake Wingra's high density of stocked muskies would be harmed. From that public meeting it was obvious that a whole-lake carp eradication was not going to be possible; carp would have to be removed by other means such as commercial fishers using large seines. Thus, funding to partially support the tracking study was obtained from a local fishing organization (Madison Fishing Expo). After Wis. Dept. Natural Resources' fish managers implanted radio-transmitters in 14 carp captured from the lake (Figure 4), UW scientists regularly tracked the location of the tagged fish for two years (fall 2005 through summer 2007) until the transmitter batteries died (Figure 5).

Results of the tracking study indicated that carp spent most of the open water season in relatively shallow water around the perimeter of the lake with many carp exhibiting fidelity to the same location. One important finding, however, was that in mid-November immediately prior to the lake freezing over, carp congregated in the center region of the lake in water depths generally >3.0 m where they remained during most of the winter. This provided an opportunity for winter commercial seining to reduce carp densities.

Figure 5. Research staff from UW Center for Limnology recording locations of 14 radio-tagged carp in Lake Wingra (photo: UW Center for Limnology).

Carp Removal

During 2007, arrangements were made between project personnel and a commercial fisher to remove carp from the lake using long large-mesh seines deployed under the ice, a practice regularly used for fishing carp on other Wisconsin lakes. A subsidy was paid to the commercial contractor because the amount of fishing effort was significant for relatively small Lake Wingra where the profit from selling captured carp (and big mouth buffalo) was not enough incentive for doing the work. While the ideal time would have been earlier in the winter to seine carp based on the tracking study results, the lake was fished in mid-March 2008 shortly before the ice became unsafe.

That year 23,600 kg of carp were removed (Figure 6) while captured game fish were quickly returned to the lake by fish managers overseeing the seining. Captured carp and buffalo were shipped live via truck to eastern markets. A second carp removal arranged for March 2009 after ice-out netted only 1,500 kg more carp, although some carp may have been lost due to the net getting snagged while being pulled to shore. Together, the two seining efforts removed 6,722 adult-sized carp.

Observations of carp in the lake during subsequent summers indicated that carp densities were not abundant, and a 2009 winter survey of the lake using side-scanning sonar failed to identify significant numbers of carp. Carp recruitment has also been minimal as almost no small carp were captured during regular NTL-LTER fish samplings conducted during August 2008-2012. Following the 2008 carp removal, the dam was rebuilt in 2009 with a spillway design making it more difficult for carp to migrate into Wingra.

Nonetheless, high water in downstream Lake Monona during an intense period of rainfall in June 2013 allowed carp to move across the flooded dam and into Lake Wingra. At the time of this writing, it is too soon to tell whether enough migrants entered the lake to cause the lake to return to an algal-turbid state.

Figure 6. Commercial fishers removing carp captured by seining under the ice in Lake Wingra during mid-March 2008 (photo: D. Liebl).

Figure 7. Photo of Lake Wingra's popular Vilas Beach taken July 29, 2011 showing good water clarity (photo: R. Lathrop).

Water Clarity Responses to Carp Reduction

Water clarity in Lake Wingra increased soon after the March 2008 carp removal, which has resulted in noticeable improvements in water quality at the popular Vilas Beach (Figure 7). Informal interviews with life guards each summer indicated the beach has been one of the "nicest places to swim" in Madison since the carp removal, although beach closures still occurred periodically due to fecal coliform contamination due to goose droppings washed in during rainstorms. Since the carp removal, no summer beach closures due to excessive algae have occurred.

This increase in water clarity is well documented in NTL-LTER's Secchi disc record where recent readings have been consistently greater than the average seasonal readings for the 12 years (1996-2007) prior to the carp removal (Figure 8). In fact, many seasonal readings during 2008-2012 have been greater than the maximum seasonal readings observed during the pre-carp removal years, a condition that is particularly pronounced in the summer months when blue-green algal blooms have been historically dense.

Because of the improved summer water clarity, total phosphorus (TP) concentrations (reflective of blue-green algae and suspended sediment

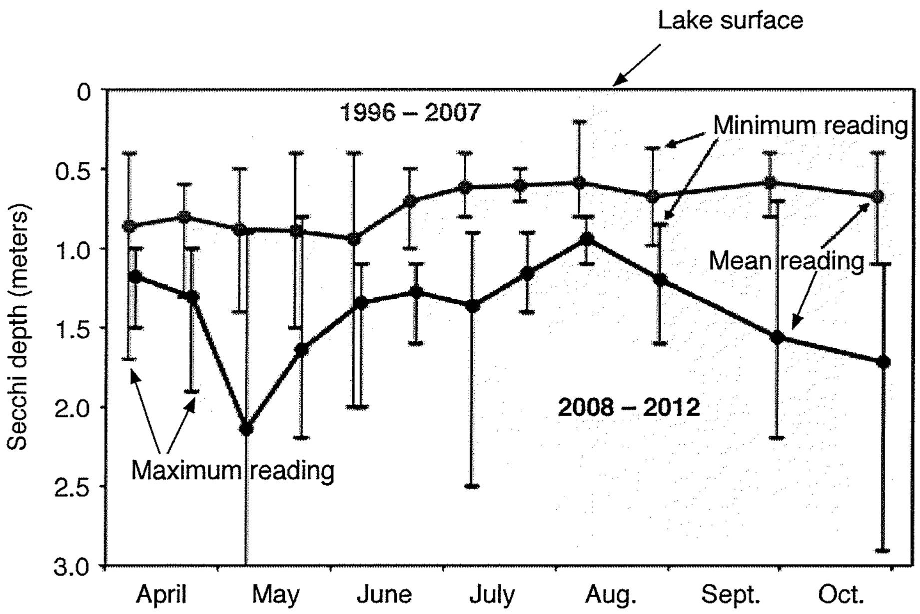

Figure 8. Secchi disc graph showing seasonal mean, maximum and minimum readings for 12 years (1996-2007) prior to the March 2008 carp removal (green line) and seasonal Secchi readings for 5 years (2008-2012) following carp removal (blue line). (Data source: UW Center for Limnology).

concentrations) in the lake's surface waters have also correspondingly responded. The median TP concentration for July-August 1996-2007 prior to the carp removal was 0.056 mg/L; median TP for July-August 2008-2012 was 0.033 mg/L.

Aquatic Macrophyte Response

Similar to the carp exclosure experiment, submersed aquatic macrophytes quickly began increasing their depth distribution in Lake Wingra with Eurasian watermilfoil (EWM) being the "first horse out of the gate," expanding into deeper lake regions where no plants grew before the 2008 carp removal (generally >1.8 m). Coontail, a native macrophyte that sometimes reaches nuisance levels in lakes, also expanded its depth distribution although not in densities as great as EWM. This expansion of EWM (and coontail) happened progressively during the growing seasons of 2008-2011 such that by 2012, most of the lake was filled with dense aquatic macrophytes (Figures 9-10). This caused some lake users to complain about the lack of boating opportunities (e.g., sailboating, motorized fish trawling), while other lake users appreciated viewing fish in the underwater "garden" while kayaking and canoeing. The EWM expansion motivated the county to conduct a public hearing on aquatic plant harvesting, with the outcome being that throughout much of the summer of 2012 the county harvesters tried to keep shore areas with fishing access free of milfoil as well as lanes for fishing from a boat (Figure 9).

Meanwhile native aquatic macrophytes (excluding coontail) have slowly increased their distribution throughout the lake (Figure 11). In many cases, the patches of native plants were occurring in locations where EWM no longer dominates. For the most part, the native plants have not posed a user access problem, and likewise are considered optimum habitat for fish.

Summary

Lake Wingra's water clarity increased rapidly and dramatically following the carp removal in March 2008 when a commercial fisher seined under the ice – a

Figure 9. Aerial photo of Lake Wingra taken July 7, 2012 showing harvester's cutting tracks through dense aquatic macrophytes (mostly Eurasian watermilfoil) growing over much of the surface area of Lake Wingra (Photo: Mike Kakuska).

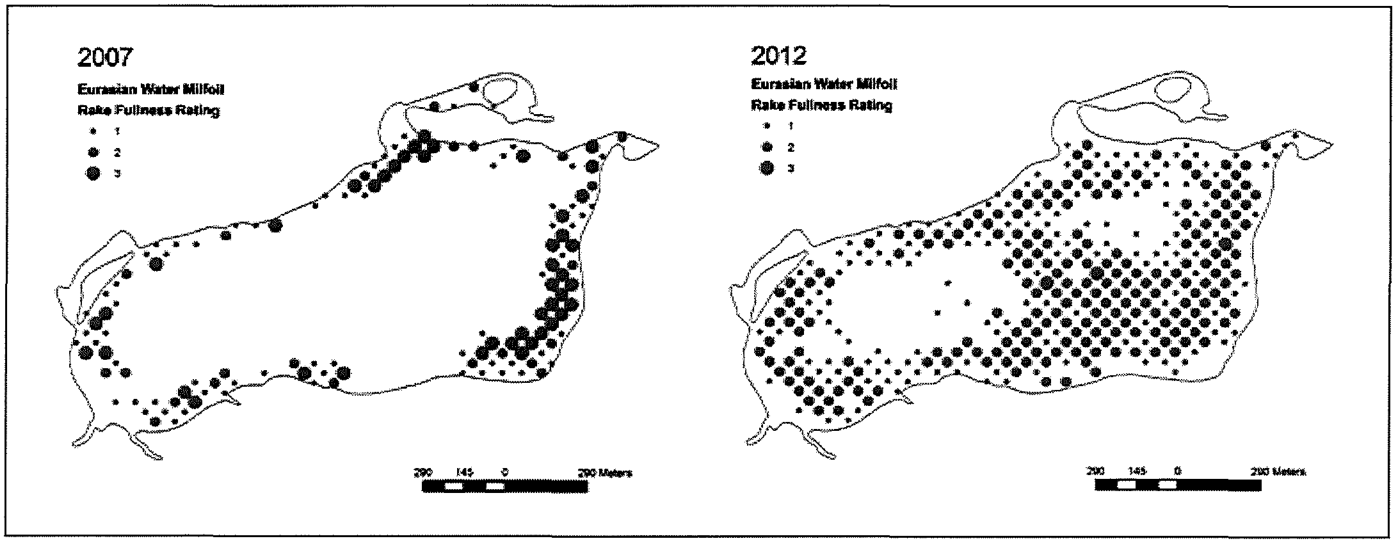

Figure 10. Distribution maps for Eurasian watermilfoil (EWM) in Lake Wingra for late summer 2007 and 2012 showing the spread of EWM after five growing seasons following the March 2008 carp removal. The density of EWM is indicated by rake fullness ratings from 1 to 3. The maps were created from rake surveys at grid points established every 50 m across the lake surface. (Map preparation: Martha Barton, WDNR)

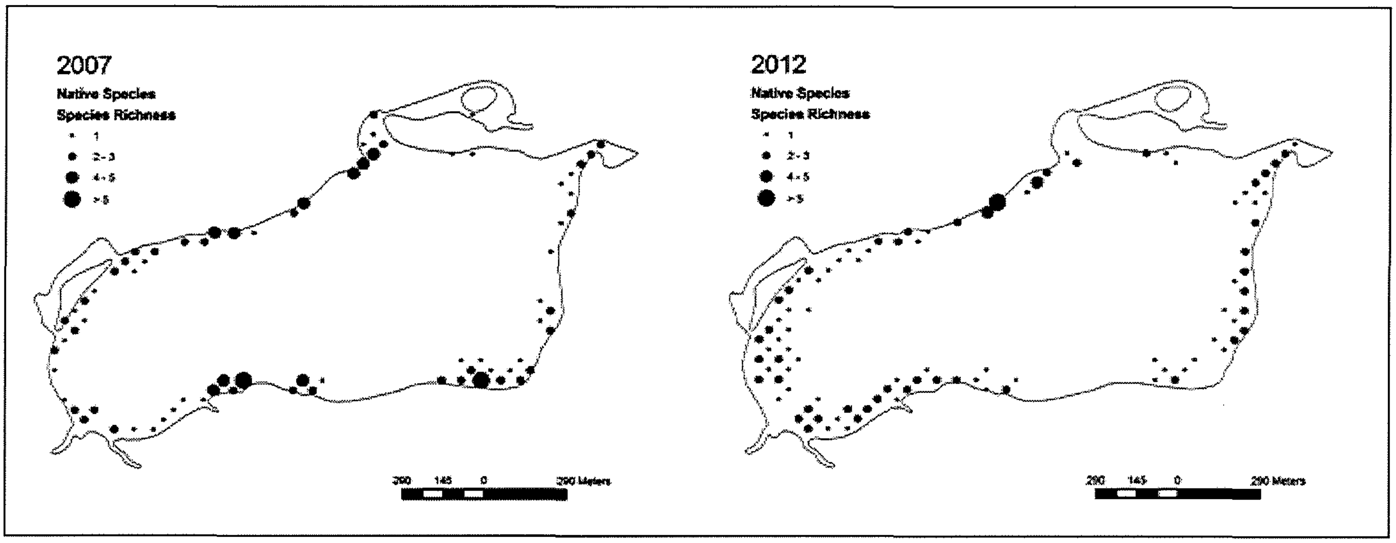

Figure 11. Species richness maps for native aquatic macrophytes (excluding coontail) in Lake Wingra for late summer 2007 and 2012 showing the location of native plant species after five growing seasons following the March 2008 carp removal. The maps were created from rake surveys at grid points established every 50 m across the lake surface. (Map preparation: Martha Barton, WDNR)

time that a radio-telemetry study indicated carp congregate in the deeper lake regions. This removal was not a whole-lake fish eradication, suggesting that carp densities need only be maintained at relatively low levels to keep the lake in its clear-water/aquatic-plant state rather than in its turbid-algal state typical of when carp densities were high. At least through 2012, carp populations have not rebounded in Lake Wingra since the seining, which suggests bluegills (known for their voracious appetite for carp eggs) may be suppressing carp recruitment as almost no small carp have been captured in August fish surveys.

Since the carp removal, Lake Wingra's aquatic macrophyte community has been in transition as the shallow lake has moved from the algal-turbid stable state to the clear-water/aquatic-plant state. During the summer of 2012, Eurasian watermilfoil became particularly dense throughout much of the deeper regions of the lake where aquatic macrophytes have not grown for almost a century (even before the early 1960s invasion of EWM). This EWM response required an aggressive aquatic plant harvesting effort to maintain areas open for fishing and boating.

Project leaders and other interested parties are hopeful that with time the native aquatic macrophytes will expand their depth coverage throughout the whole lake while EWM becomes less abundant. This will undoubtedly require aquatic plant harvesting to prevent EWM from forming a dense canopy at the lake surface that would otherwise prevent the expansion of native macrophytes in deeper water due to shading.

In conclusion, this project illustrates the complexities associated with managing shallow eutrophic lakes, and the tradeoffs associated with various management actions. While the algal-turbid state was undesirable for users, the clear-water/aquatic-plant state with the expansion of EWM has also incurred challenges for recreation. If EWM continues to grow densely throughout much of the lake in future years, then a discussion should occur about the trade-offs associated with how the lake is managed.

Conceivably, with continued recreational boating problems, the carp removal could be considered a "failed experiment" and the lake returned to an algal-turbid state by allowing the carp population to rebound. However, the public's desire to have waist-deep water clear enough to see their toes as well as have reduced exposure risk to blue-green algae toxins at the lake's popular swimming beach may dictate the clear-water/aquatic-plant state is worth "staying the course." If that is the case and enough carp find their way into Lake Wingra when its dam is periodically inundated during periods of flooding from heavy rains as occurred in June 2013, then another carp removal might be needed to maintain clear water in the lake.

Acknowledgments

We are thankful to the many unrecognized people who helped with the 2005 installation and subsequent maintenance of the carp exclosure in Lake Wingra. In that regard, special thanks are extended to Kelsy Anderson Frederico for her tireless efforts with the exclosure's installation effort. We also thank the many people who assisted with limnological sampling and aquatic macrophyte surveys.

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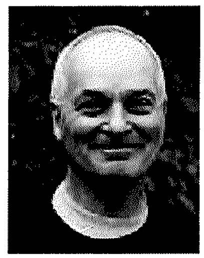

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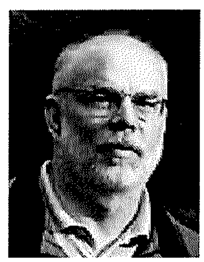

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Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project

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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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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 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.

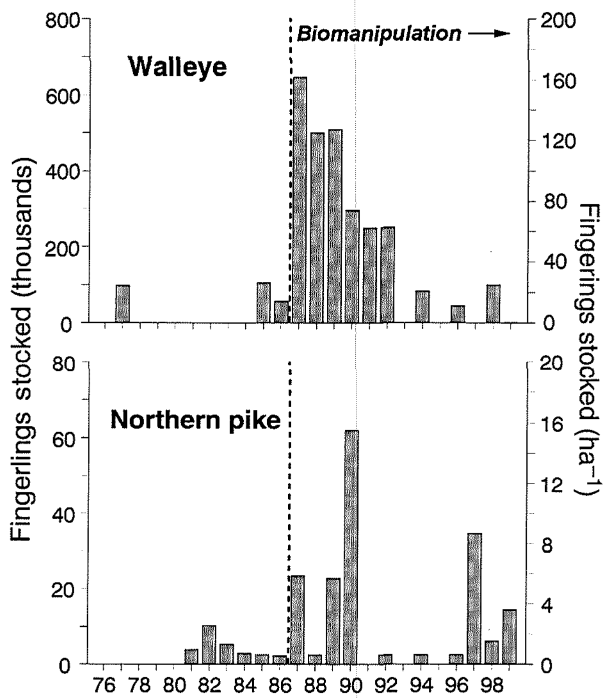

Fig. 1 Walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) fingerling stockings to Lake Mendota in thousands of fish (left axis) and number of fish stocked per hectare of lake area (right axis) 1976–99.

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 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.

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

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* ($\mathrm{dw} = 5.48\ \mathrm{Length}^{2.20}$) and *D. pulicaria* ($\mathrm{dw} = 10.67\ \mathrm{Length}^{2.09}$), 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

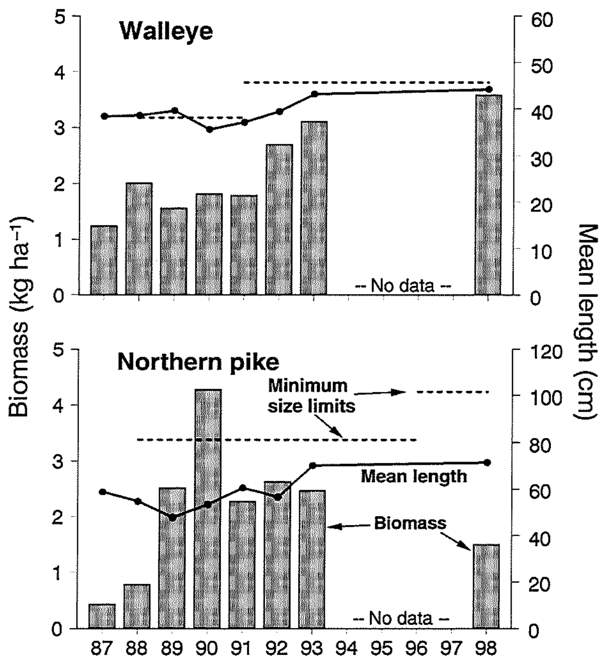

Fig. 2 Walleye and northern pike biomass estimates, and mean fish lengths and minimum size limit regulations for Lake Mendota, 1987–99.

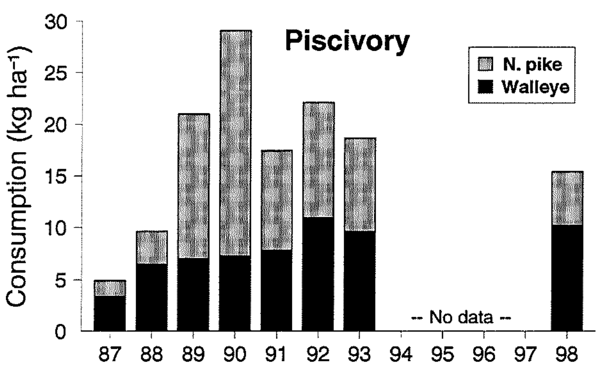

Fig. 3 Bioenergetic estimates of piscivory consumption on planktivorous fish for Lake Mendota, 1987–99.

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 (~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,

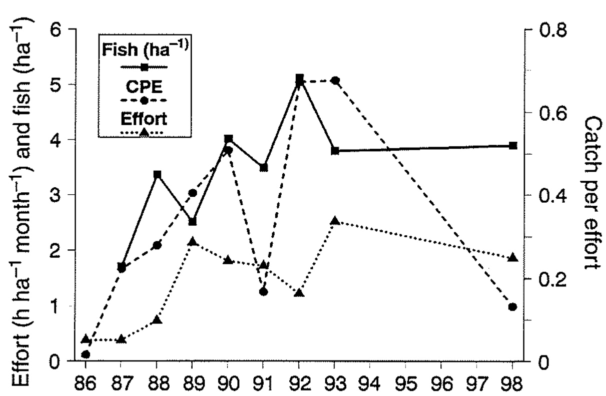

Fig. 4 Walleye density (fish ha^{-1}), fishing effort by anglers specifically seeking walleyes (angler-hour ha^{-1} month^{-1}), and catch per effort (CPE) by those anglers (walleyes caught per hour of fishing for walleyes) in Lake Mendota, 1986–99.

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 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.

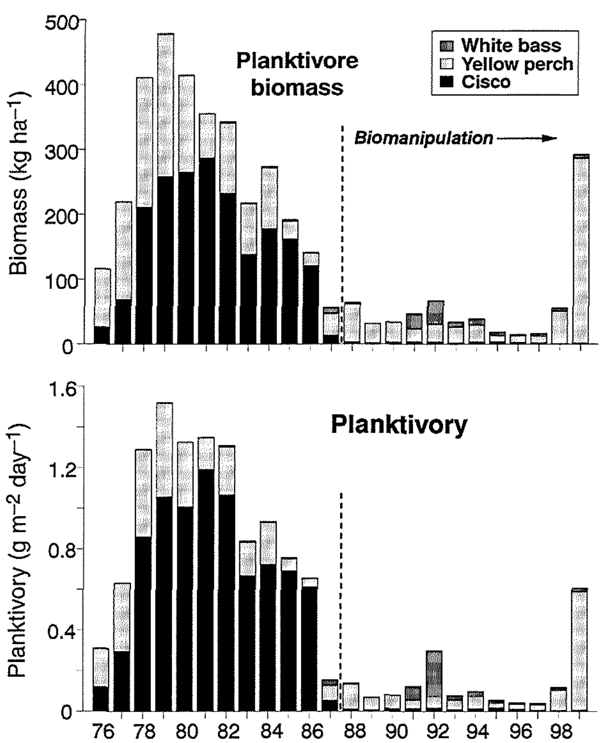

Fig. 5 Biomass estimates for planktivorous cisco (*Coregonus artedi*), yellow perch (*Perca flavescens*) and white bass (*Morone chrysops*), and bioenergetic estimates of *Daphnia* consumption in Lake Mendota, 1976–99. The biomanipulation effect is marked to begin in 1988, 1 year after the piscivore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

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

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

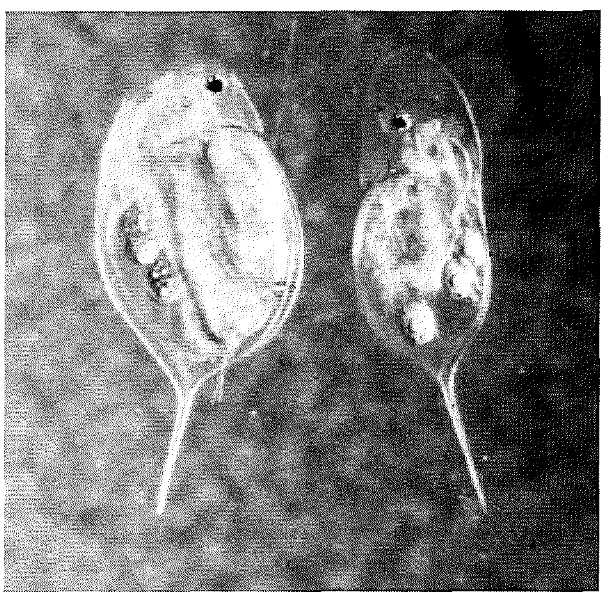

Fig. 6 Photograph of the larger-bodied *Daphnia pulicaria* and the smaller-bodied *D. galeata mendotae*, the two main species of *Daphnia* that dominated the crustacean zooplankton in Lake Mendota throughout the 1900s including the biomanipulation project years.

(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*

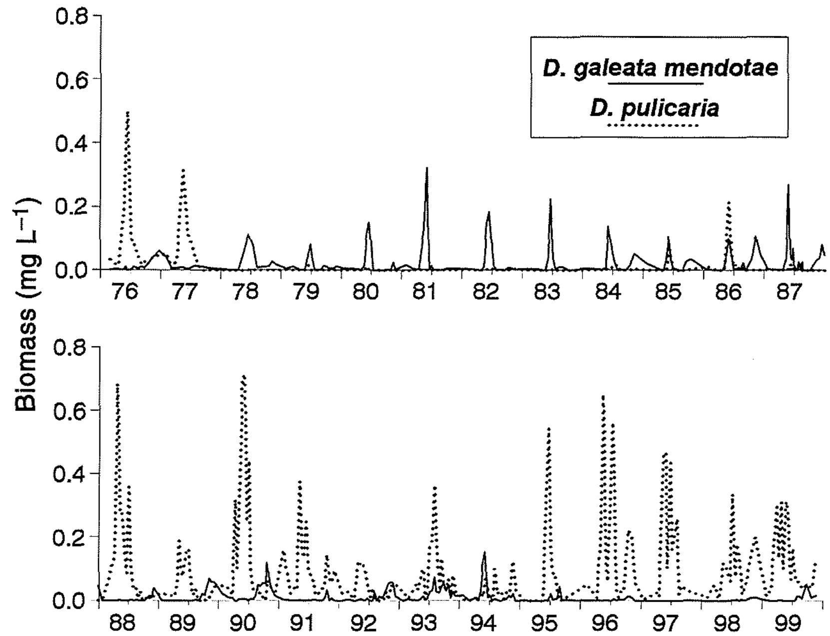

Fig. 7 Biomass concentrations of *Daphnia pulicaria* and *D. galeata mendotae* in Lake Mendota, 1976–99. Concentration data have not been corrected for net efficiency such that actual concentrations are higher (see text).

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

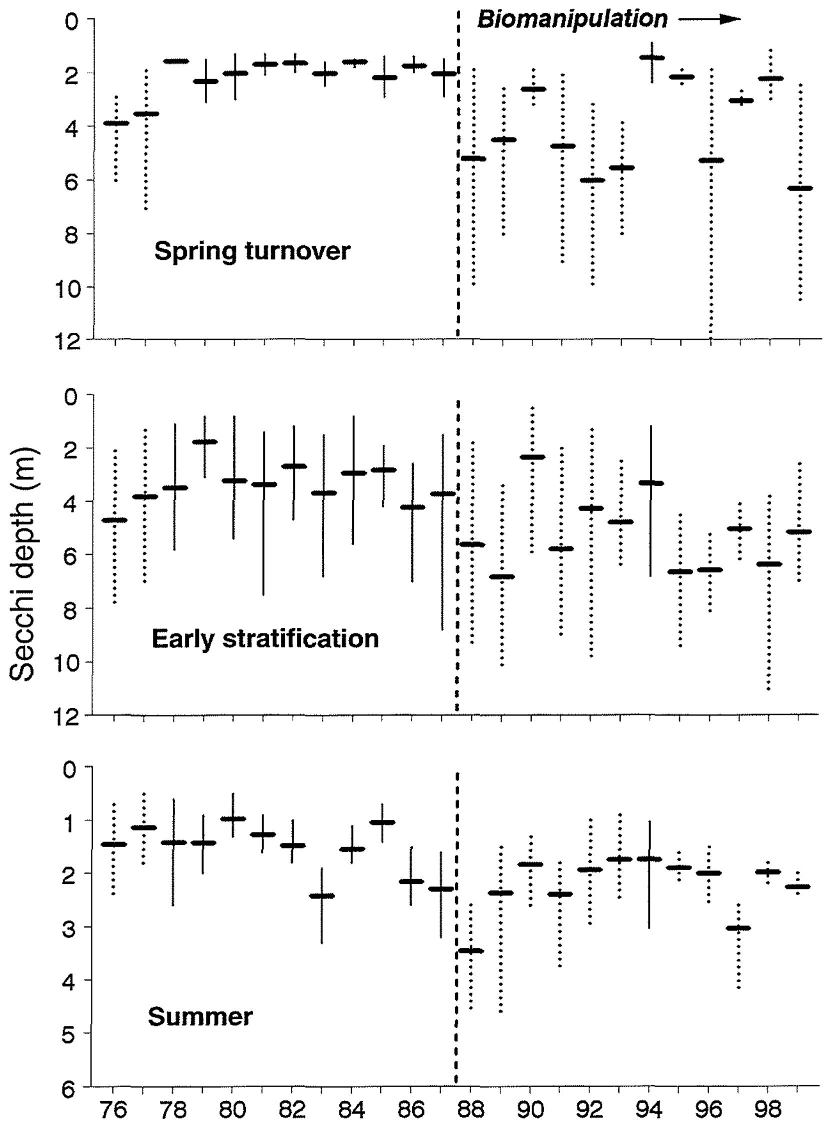

Fig. 8 Secchi disc readings as measure of water clarity and algal densities for three different time periods for Lake Mendota, 1976–99. (Spring Turnover = ice-out to 10 May; Early Stratification = 11 May to 29 June; Summer = 30 June to 2 September. Fat short horizontal bars are seasonal mean Secchi disc 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

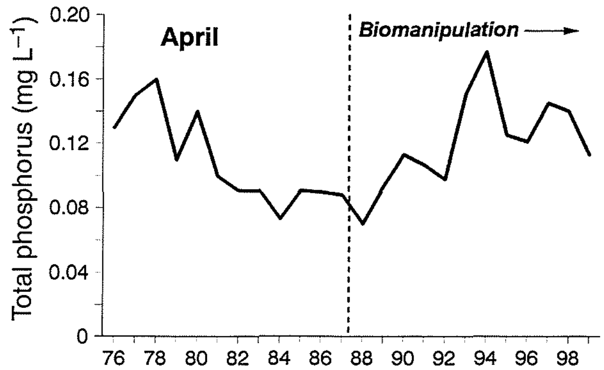

Fig. 9 Total phosphorus concentrations in the surface waters of Lake Mendota for mid-April, 1976–99.

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.

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January 29, 2020

TESTIMONY TO SENATE COMMITTEE ON NATURAL RESOURCES & ENERGY IN OPPOSITION OF SB725

Thank you for the opportunity to testify today in opposition of SB725. My name is Michael Engleson, and I am the Executive Director of Wisconsin Lakes, also known as the Wisconsin Association of Lakes. Wisconsin Lakes is a statewide non-profit conservation organization of waterfront property owners, lake users, lake associations, and lake districts who in turn represent over 80,000 citizens and property owners. We are the only statewide association of lake organizations.

It is not often that I appear to argue against the spending of money for a conservation practice, but that is exactly what I am here to do today. Biomanipulation is a well-studied tool for managing a limited number of shallow lakes in Wisconsin and is already adequately fundable through the surface water grant program of DNR, so long as it is part of an approved lake management plan. I am not encountering lake organizations asking for more funding or study of this strategy. In some cases, as described in a statement from Dick Lamers, a Wisconsin Lakes member who lives on Tainter Lake in Dunn County and which is included with my testimony, employing the practice can actually inhibit more comprehensive work being done to prevent the root causes of algae blooms.

Biomanipulation is a well studied and practiced lake management tool in Wisconsin. It works best in shallow lakes and even then it is often only a short-term solution for those waterbodies. Many factors, including whether phosphorus continues to flow into a lake system, can lead the lake to revert to the state it was in prior to the biomanipulation, leading to the need to repeat the process. This makes biomanipulation, over the long haul, potentially quite expensive and intensive.

In addition, biomanipulation does not necessarily remove phosphorus from a lake system, even if no new phosphorus is entering the waterway. Instead, by controlling the fish, other animals, and plants in a lake's ecosystem, it attempts to limit the conditions where algae could grow. It essentially "parks" the phosphorus in the system such that it could eventually contribute to new algae growths and spur yet more spending on additional biomanipulation efforts in the future.

Biomanipulation is more like taking ibuprofen to reduce a fever than a treatment that cures a disease. It may reduce that symptom (the algae) but does nothing to solve the root cause of the fever (often excess phosphorus flowing into the lake). And in the majority of lakes in the state its usefulness as a "fever reducer" is even questionable because of the greater complexity of the constantly changing makeup of larger, deeper lakes.

As Mr. Lamers' letter shows, highlighting and pouring funds into a marginal solution such as biomanipulation can take energy and focus away from getting at the root causes of surface water quality problems in lakes. In the Red Cedar River Basin, home to lakes Tainter and Menomin, considerable work is being done by partnerships and collaborations between citizen groups, local governments, the WI Dept. of Natural Resources, and local agricultural interests to limit the flow of phosphorus from the landscape into the river system that eventually reaches the lakes at Menomonie. Tools being used include a TMDL, the creation of producer led councils that promote the sort of sustainable agricultural efforts the Speaker's Water Quality Task Force is helping to promote in other legislation, and other efforts.

Biomanipulation was not a strategy that was likely to succeed in this complex, deeper-water riverine system and the special state funded biomanipulation project of several years ago resulted in little if any benefit to water quality and confusion in the public's understanding of the projects underway to create lasting change to the Red Cedar river basin.

To summarize, while biomanipulation may be a useful tool to help maintain a stable condition that limits algae blooms in shallow lakes, Wisconsin Lakes sees no benefit in the state earmarking any additional taxpayer funds for the practice. Where it is useful and appropriate, such projects are already able to receive funding, and are done so in conjunction with a larger lake management planning effort. If we are to spend money on water quality projects, we should ensure that they go to efforts to solve the root problems we face, the problems the Speaker's Water Quality Task Force wanted to address. More money for biomanipulation projects doesn't fit that bill.

Wisconsin Lakes therefore asks you to put this money to a better use, or at the least not spend it where it simply is not needed, and ask you to oppose SB725.

Senate Bill 725 1/29/2020

Dear Members of the Senate Committee on Natural Resources and Energy,

My name is Dick Lamers and I reside on Tainter Lake in Dunn County. I have been active in water quality efforts since we obtained the property in 1981. We have watched a slow and continuing degradation of the entire Red Cedar Watershed since then.

Multiple, well meaning people have tried projects that were intended to solve the problem of Blue Green Algae Blooms and the associated toxins that occur each summer. The projects over the last ten years have included Barley straw bales to filter the algae, motors on docks to keep the water flowing, specialty pumps to aerate the water, dredging, alum treatments and now Bio manipulation studies. All of them had been attempted before and were shown that when applied to a River System like ours, they would have minimal or no impact on our significant Algae problem.

Any major/complex problem like the one experienced here, needs a leading organization to coordinate the process and a detailed root cause analysis to solve it.

The Leading organization in this case is the WI. Department of Natural Resources. They have qualified staff and expertise to lead this effort.

We already know the root cause. It has been proven to be the excessive loading of Phosphorus into our waters. It was verified over 8 years ago and included additional research to get our TMDL Plan approved by the EPA in 2012.

Attempting to use smaller marginal solutions just delay the results needed and continue the problems indefinitely. For us, all efforts should be focused on minimizing Phosphorus and keeping it on the land and out of all waterways.

Seven or Eight years ago, Wisconsin took Phosphorus out of lawn fertilizers, then out of dishwashing detergents. Our Land & Water Conservation departments have done a great job of developing Farmer Led and Producer Led Groups. No till and minimum till planting and the use of cover crops is gaining in acceptance across the state. Working together through field days and conferences for all citizens and land owners, we are all beginning to understand our individual roles in water Quality.

I am opposed to passing Bill 725.

Funding of Bio Manipulation projects are already covered in the current project management process. They should only be funded in lakes that are designated a priority and that have a high probability of success.

Respectfully submitted,

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ENVIRONMENTAL EVIDENCE

SYSTEMATIC REVIEW

What is the influence of a reduction of planktivorous and benthivorous fish on water quality in temperate eutrophic lakes? A systematic review

Claes Bernes[1*], Stephen R Carpenter[2], Anna Gårdmark[3], Per Larsson[4], Lennart Persson[5], Christian Skov[6], James DM Speed[7] and Ellen Van Donk[8]

Abstract

Background: In recent decades, many attempts have been made to restore eutrophic lakes through biomanipulation. Reducing the populations of planktivorous and benthivorous fish (either directly or through stocking of piscivorous fish) may induce ecosystem changes that increase water transparency and decrease the risk of algal blooms and fish kills, at least in the short term. However, the generality of biomanipulation effects on water quality across lake types and geographical regions is not known. Therefore, we have undertaken a systematic review of such effects in eutrophic lakes in temperate regions throughout the world.

Methods: Searches for literature were made using online publication databases, search engines, specialist websites and bibliographies of literature reviews. Search terms were developed in English, Danish, Dutch and Swedish. Identified articles were screened for relevance using inclusion criteria set out in an *a priori* protocol. To reduce the risk of bias, we then critically appraised the combined evidence found on each biomanipulation. Data were extracted on outcomes such as Secchi depth and chlorophyll *a* concentration before, during and/or after manipulation, and on effect modifiers such as lake properties and amounts of fish removed or stocked.

Results: Our searches identified more than 14,500 articles. After screening for relevance, 233 of them remained. After exclusions based on critical appraisal, our evidence base included useful data on 128 biomanipulations in 123 lakes. Of these interventions, 85% had been made in Europe and 15% in North America. Meta-analysis showed that removal of planktivores and benthivores (with or without piscivore stocking) leads to increased Secchi depth and decreased chlorophyll *a* concentration during intervention and the first three years afterwards. Piscivore stocking alone has no significant effect. The response of chlorophyll *a* levels to biomanipulation is stronger in lakes where fish removal is intense, and in lakes which are small and/or have high pre-manipulation concentrations of total phosphorus.

Conclusions: Our review improves on previous reviews of biomanipulation in that we identified a large number of case studies from many parts of the world and used a consistent, repeatable process to screen them for relevance and susceptibility to bias. Our results indicate that removal of planktivorous and benthivorous fish is a useful means of improving water quality in eutrophic lakes. Biomanipulation tends to be particularly successful in relatively small lakes with short retention times and high phosphorus levels. More thorough fish removal increases the efficacy of biomanipulation. Nonetheless successes and failures have occurred across a wide range of conditions.

Keywords: Biomanipulation, Planktivore, Benthivore, Piscivore stocking, Fish removal, Lake restoration, Eutrophication, Water quality, Phytoplankton

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Background

Over the past century, many lakes in urban or agricultural regions of the world were eutrophied due to sewage discharges or nutrient runoff from land. Excess nutrients, especially phosphorus, stimulates the growth of phytoplankton, often to such an extent that the water becomes turbid [1]. The reduced light penetration and increased sedimentation of dead planktonic algae puts submerged macrophytes at a disadvantage, in some cases even eliminating them, often with strong impacts on ecosystem interactions and dynamics [2]. Certain species of phytoplankton – cyanobacteria in particular – can give rise to massive 'algal blooms' in the summer. The decomposition of dead plankton can lead to oxygen depletion and fish kills [3].

Problems of these kinds have often persisted even when nutrient supplies from the surroundings have been reduced, e.g. through sewage treatment. One important reason is that phosphorus stored in the sediments of eutrophied lakes can exchange with the water and thereby keep it nutrient-rich for decades [4]. There are indications that eutrophication has caused many lakes to shift from one state to another. In shallow unstratified lakes, one state is characterised by moderate abundance of phytoplankton, transparent water and vegetated bottoms, the other by high abundance of phytoplankton, turbid water and little or no submerged vegetation. In deep stratified lakes, one state is characterised by an oxygenated hypolimnion and low recycling of phosphorus, and the other by anoxia in the hypolimnion and rapid recycling of phosphorus. Once a lake has reached the latter state, it may tend to remain there even if nutrient concentrations in the water decrease.

The occurrence of 'alternative states' (stable turbid or clear-water states) of pelagic ecosystems can be a consequence of food web interactions [5,6]. Certain food web configurations lead to high abundances of planktivores, or fishes that eat zooplankton. Planktivorous fish species can feed intensively on zooplankton and thereby release phytoplankton from grazing, leading to turbid water. The predation by planktivorous fish can therefore sustain eutrophic conditions in the lake, conditions that are beneficial to the fish themselves, and this feedback may prevent the lake from returning to less eutrophic conditions despite reduced nutrient inputs.

In some cases where eutrophied lakes have failed to recover after a reduction of nutrient supplies, attempts have been made to remedy the problems through intervention in the lakes themselves. Several of the methods tried, including dredging, are very expensive but by no means always successful [7,8].

At least in the short term, however, notable improvements in water quality have been achieved through biomanipulation, usually in the form of decimating the planktivorous fish which typically dominate the fish fauna of eutrophic lakes [9,10]. In Eurasia, cyprinids such as roach (*Rutilus rutilus*) and bream (*Abramis brama*) are among the most common planktivores in nutrient-rich lakes. In North America, important planktivores of eutrophic lakes include sunfish (*Lepomis* spp.) and gizzard shad (*Dorosoma cepedianum*) as well as various cyprinid species.

Reducing the stocks of planktivorous fishes enhances survival of the zooplankton that such fish feed on, and this in turn can reduce the abundance of planktonic algae that serve as food for the zooplankton [11,12]. Another reason why removal of planktivorous fish may improve water quality is that the adults of some of these species (e.g. bream and gizzard shad) are also benthivorous. They search for food in the sediments, dispersing nutrient-rich silt and thereby adding to the turbidity and high phosphorus content of the water in eutrophic lakes [13]. Their feeding behaviour may also contribute to the lack of submerged vegetation in such lakes.

The dominance of planktivorous/benthivorous species in eutrophic lakes has been related to the possibility that such species induce an interspecific competitive bottleneck in the recruitment of juvenile predators to predatory (piscivorous) stages, thereby limiting the predation pressure by piscivores [14]. One factor that may induce such a bottleneck is the presence of resources (e.g. cyanobacteria) that are exclusively available to planktivorous/benthivorous species. Another is that many planktivorous/benthivorous species are less affected in their feeding by the low water clarity in eutrophic lakes than visually feeding piscivorous species [14,15].

Ideally, then, a reduction of the populations of planktivorous and benthivorous fish may shift a eutrophied lake back to a less eutrophic state, increasing transparency, allowing benthic vegetation to regain lost ground and decreasing the risk of disturbances such as algal blooms and fish kills. Such changes of lake ecosystem properties – and of the plankton flora in particular – may be driven both 'bottom-up' (i.e. by nutrient availability) and 'top-down' (via the upper parts of the food web) [11]. Numerous studies have indicated that aquatic ecosystems may have the potential of being controlled both ways, e.g. [16].

The persistence of biomanipulation effects will partly depend on whether the lake is likely to exhibit alternative stable states or not [17]. For example, this likelihood is greater in shallow lakes and lakes with warm hypolimnia [18]. If alternative states of water clarity do occur, the lake may remain in the new state induced by biomanipulation if it is not destabilised by some other event. If the lake has only a turbid stable state, the rate at which it returns to its previous condition after biomanipulation will among other things depend on the time scale at which the slowest component of its ecosystem operates.

In most lake food webs, piscivorous fish form the slowest component, with a time scale extending to a decade or more [19,20]. This time span is of the same order as that reported for the effects of many biomanipulation attempts.

Removal of planktivores and benthivores for the purpose of lake restoration is usually carried out through intensive fishing, although there are also cases where all fish have been eradicated for this purpose, e.g. through rotenone treatment or temporary emptying of ponds or reservoirs [21,22]. An alternative to removing planktivorous and benthivorous fish through direct intervention may be to reduce their dominance by stocking lakes with predatory fish (piscivores) such as pike (*Esox lucius*). These two approaches have frequently been used in combination – following removal of planktivores and benthivores, piscivores have been stocked in order to prevent zooplankton-feeding fish from regaining their former dominance [23,24]. In some cases, fisheries regulations aiming to increase piscivore biomass have also been used to support biomanipulation (e.g. [25]).

In recent decades, a large number of attempts have been made to restore eutrophic lakes through planktivore decimation or other forms of biomanipulation, not least in Denmark [26], the Netherlands [11] and Finland [27]. Interventions of these kinds have also been the subject of several reviews over the years, e.g. by Søndergaard *et al.* [7,16], Gulati *et al.* [8], Meijer *et al.* [11], Jeppesen *et al.* [12,28], Hansson *et al.* [29], Drenner & Hambright [30] and Hansson [31]. Their approaches and conclusions vary, but in general they have found the likelihood of successful biomanipulation to increase when a) internal and external nutrient loadings have been sufficiently reduced, b) post-manipulation abundance of submerged macrophytes has increased and c) substantial removals have been made of planktivorous fish, and of benthivorous fish in particular. Moreover, fish manipulation by direct removal of planktivorous and benthivorous fish has a higher success rate than stocking of piscivores as a means of controlling planktivores and benthivores [7,8,28,30]. Long-term studies are still not numerous, but they indicate that positive effects of biomanipulation generally last a relatively limited number of years, especially if attempts to reduce internal and external nutrient loadings have failed [7,8,28].

The efficacy of biomanipulation as a means of improving water quality is of considerable interest for lake and water management. In Europe, requirements for measures against eutrophication have become more stringent with the introduction of the EU Water Framework Directive [32]. While such measures mostly involve actions to reduce nutrient loads, biomanipulation has been suggested as an additional or alternative way of achieving 'good ecological status' in eutrophic lakes [33,34]. However, the generality of biomanipulation effects on water quality across different lake properties and geographical regions is not known.

Objective of the review

The purpose of this review is to clarify whether reduction of planktivorous and benthivorous fish may prevent eutrophication problems in lakes. A number of conventional literature reviews on this subject have reported on studies of particular sets of lakes, e.g. providing national overviews of biomanipulation efforts [11,16,27] or analyses based on relatively small international selections of lakes [12,28-30]. Here, instead, we widen the scope – using the 'systematic review' approach [35], we perform a quantitative synthesis of water-quality effects of biomanipulation in temperate eutrophic lakes throughout the world. Rather than reviewing a specific selection or random sample of such interventions, we have have sought to cover all available cases that fulfill our inclusion criteria.

Following an *a priori* protocol [36], we have thus assembled a large number of studies and screened them for relevance and susceptibility to bias. This has enabled us to extract a substantial amount of quality-assured data on how water quality is affected by biomanipulation. The rigour and transparency of the systematic approach is intended to avoid bias and permit quantitative and repeatable evaluation by means of meta-analysis. Our aim is that this review will provide a useful basis for deciding if and when biomanipulation is useful as a tool for improving water quality in eutrophic lakes.

The review examines full-scale applications of biomanipulation only. While small-scale experimental studies of such interventions can be valuable for clarifying the mechanisms involved, studies of whole-lake manipulation are more relevant when assessing the method as an instrument for environmental management.

In addition to deliberate attempts to improve water quality, we initially also considered unintentional water-quality effects of fish-community changes (caused e.g. by altered fish management practices). Only a few studies of the latter kind of effects were found, however (e.g. [37,38]). Moreover, since unintentional water-quality effects are more likely to have been reported in the scientific literature if they were appreciable than if they were insignificant, inclusion of such studies could increase the risk of publication bias. Therefore, this review covers deliberate biomanipulation efforts only.

Primary question

What is the influence of a reduction of planktivorous and benthivorous fish (performed directly or indirectly through stocking of piscivores) on water quality in temperate eutrophic lakes?

Components of the primary question

- *Subject (population):* Temperate eutrophic lakes anywhere in the world.

- *Intervention:* Reduction of populations of planktivorous and benthivorous fish.
  This includes removal of planktivorous and/or benthivorous fish, stocking of piscivorous fish and any combination of such interventions. Quantification of the intervention may be based on amounts of fish removed or stocked, and/or on estimates of standing fish stocks before, during and after the intervention.
- *Comparator:* No intervention.
- *Outcomes:* Changes of water-quality parameters such as Secchi depth, concentrations of nutrients and chlorophyll *a* and abundance of phytoplankton.
  If available, data on changes of community-structure parameters such as abundance of zooplankton and fish and coverage of submerged macrophytes have also been recorded.

Methods

Design of the review

The design of this systematic review was established in detail in an *a priori* protocol [36]. It follows the guidelines for systematic reviews issued by the Collaboration for Environmental Evidence [39].

As described in the protocol, we developed the review design in close cooperation with stakeholders, primarily in Sweden. Before submission, peer review, revision and final publication of the protocol, a draft version was open for public review at the website of the Mistra Council for Evidence-Based Environmental Management (EviEM) in December 2012 and January 2013. Comments were received from scientists, environmental managers and other stakeholders, and the protocol was revised appropriately.

Searches for literature

Searches for relevant literature have been made using online publication databases, search engines, specialist websites and bibliographies of literature reviews. Whenever possible, the search strings specified below were applied throughout the searches using online databases, search engines and specialist websites. In several cases, though, they had to be simplified as some sites can handle only a very limited number of search terms or do not allow the use of 'wildcards' or Boolean operators.

Full details of the search strings used and the number of articles found at each stage of the search are provided in Additional file 1.

Search terms

A scoping exercise had identified the following search terms as being capable of returning a satisfactory set of relevant articles:

- *Subject:* lake*, reservoir*, pond*, fresh$water
- *Intervention:* *manipulat*, remov*, restor*, stock*, introduc*, reduc*, addition
- *Target:* *planktivor*, *benthivor*, cyprinid*, piscivor*, "predatory fish*", *Rutilus, Abramis, Esox, Perca, Stizostedion, Micropterus, Dorosoma, Coregonus, Oncorhynchus, Salmo*, roach, bream, pike, muskellunge, perch, pike$perch, zander, sander, "*mouth bass", whitefish, cisco, minnow, "gizzard shad".

The terms within each category ('subject', 'intervention' and 'target') were combined using the Boolean operator 'OR'. The three categories were then combined using the Boolean operator 'AND'. An asterisk (*) is a wildcard that represents any group of characters, including no character, while a dollar sign ($) represents zero or one character. The full search string thus reads as follows:

- *English:* (lake* OR reservoir* OR pond* OR fresh$water) AND (*manipulat* OR remov* OR restor* OR stock* OR introduc* OR reduc* OR addition) AND (*planktivor* OR *benthivor* OR cyprinid* OR piscivor* OR "predatory fish*" OR *Rutilus* OR *Abramis* OR *Esox* OR *Perca* OR *Stizostedion* OR *Micropterus* OR *Dorosoma* OR *Coregonus* OR *Oncorhynchus* OR *Salmo* OR roach OR bream OR pike OR muskellunge OR perch OR pike$perch OR zander OR sander OR "*mouth bass" OR whitefish OR cisco OR minnow OR "gizzard shad").

Based on the English search string, the following Danish, Dutch and Swedish search strings were also developed:

- *Danish:* (sø* OR dam OR mose* OR ferskvand*) AND (*manipulat* OR opfisk* OR restau* OR udsæt* OR introduk* OR reduk*) AND (*planktivor* OR *benthivor* OR cyprinid* OR piscivor* OR rovfisk* OR fredfisk* OR skidtfisk* OR *Rutilus* OR *Abramis* OR *Esox* OR *Perca* OR *Stizostedion* OR *Coregonus* OR *Oncorhynchus* OR *Salmo* OR skalle OR brasen OR gedde OR sandart OR aborre OR *ørred OR helt)
- *Dutch:* (meer* OR plas* OR zoetwater*) AND (biomanipul* OR "actief biologisch beheer" OR afvissen OR restauratie* OR uitzetten*) AND (*planktivor* OR *benthivor* OR planktoneten* OR bodemomwoel* OR piscivor* OR visetende* OR roofvis* OR *Rutilus* OR *Abramis* OR *Esox* OR *Perca* OR *Stizostedion* OR brasem OR snoek OR ruisvoorn OR snoekbaars OR karper)
- *Swedish:* (sjö* OR insjö* OR *magasin* OR *damm* OR sötvatten* OR färskvatten*) AND (biomanipul* OR utfisk* OR reduktionsfisk* OR reducer* OR *restaurer* OR inplanter* OR utplanter* OR utsättning*) AND (*planktivor* OR *planktonäta* OR bent$ivor* OR bottenäta* OR bottendjursäta* OR cyprinid* OR karpfisk* OR piscivor* OR rovfisk*

OR *Rutilus* OR *Abramis* OR *Esox* OR *Perca* OR *Stizostedion* OR *Coregonus* OR *Oncorhynchus* OR *Salmo* OR mört OR brax* OR gädda OR abborre OR gös OR sik OR *lax OR *öring OR regnbåge).

No time, language or document type restrictions were applied during the searches.

In addition to searches using the main search string described above, a complementary search was made in a few of the sources mentioned below (Academic Search Premier, Aquatic Sciences and Fisheries Abstracts, Scopus, and Web of Science). The complementary search focused on potential mechanisms and outcomes of biomanipulation, using the following set of search terms:

- *Subject:* lake*, reservoir*, pond*, fresh$water
- *Target:* fish*
- *Mechanisms:* trophic, cascad*, foodweb, topdown, bottom$up, resuspen*, "stable state*", bistable, "regime shift*"
- *Outcomes:* water$quality, transparency, clarity, turbid*, secchi, "suspended solids", phosph*, nitrogen, oxygen, chlorophyll, phytoplankton

Publication databases

Searches were made in the following online databases:

1). Academic Search Premier
2). Agricola
3). Aquatic Sciences and Fisheries Abstracts
4). Biological Abstracts
5). BioOne
6). COPAC
7). Directory of Open-Access Journals
8). Forskningsdatabasen.dk
9). GeoBase
10). IngentaConnect
11). JSTOR
12). Libris
13). PiCarta
14). Scopus
15). SpringerLink
16). SwePub
17). Web of Science
18). Wiley Online Library.

Search engines

Internet searches were also performed using the following search engines:

Google (www.google.com)
Google Scholar (scholar.google.com)
Growyn
Scirus.

In each case, the first 100 hits (based on relevance) were examined for appropriate data. Potentially useful documents that had not already been found in publication databases were recorded.

Specialist websites

Websites of the specialist organisations listed below were searched for links or references to relevant publications and data, including 'grey literature'. Potentially useful documents that had not already been found using publication databases or search engines were recorded.

Broads Authority (www.broads-authority.gov.uk)
Danish Centre for Environment and Energy (dce.au.dk)
Environment Canada (www.ec.gc.ca)
European Commission Joint Research Centre (ec.europa.eu/dgs/jrc)
European Environment Agency (www.eea.europa.eu)
Finland's environmental administration (www.environment.fi)
International Union for Conservation of Nature (www.iucn.org)
IVL Swedish Environmental Research Institute (www.ivl.se)
Leibniz Institute of Freshwater Ecology and Inland Fisheries, IGB (www.igb-berlin.de)
National Institute for Public Health and the Environment (RIVM) (www.rivm.nl)
Netherlands Institute of Ecology (www.nioo.knaw.nl)
Norwegian Institute for Water Research (NIVA) (www.niva.no)
Swedish Agency for Marine and Water Management (www.havochvatten.se)
Swedish County Administrative Boards (www.lansstyrelsen.se)
Swedish Environmental Protection Agency (www.naturvardsverket.se)
Swedish River Basin District Authorities (www.vattenmyndigheterna.se)
UK Environment Agency (www.environment-agency.gov.uk)
United Nations Environment Programme (www.unep.org)
United States Environmental Protection Agency (www.epa.gov).

Other literature searches

Relevant literature was also searched for in bibliographies of literature reviews such as those mentioned in the Background section. Potentially useful documents that had not already been found in online sources were recorded. A few more articles were brought to our attention by stakeholders.

In addition, unpublished data were in some cases made available by e.g. study authors, consultants or local authorities involved in biomanipulation projects. Stakeholders had been asked to suggest suitable contacts.

Search update

An update to the literature searches was made in late 2013, about ten months after the main searches. The update involved searches in Web of Science and Google Scholar using the main English search string. Web of Science was also searched with the complementary search string.

Screening

Screening process

Articles found by searches in databases were evaluated for inclusion at three successive levels. First they were assessed by title by a single reviewer (CB). In cases of uncertainty, the reviewer chose inclusion rather than exclusion. As a check of consistency, a subset of 100 articles was assessed by all members of the review team. Since this check showed that the main reviewer was considerably more inclusive than the average team member, it seemed safe to proceed with the screening without modification or further specification of the inclusion/exclusion criteria.

Next, each article found to be potentially relevant on the basis of title was judged for inclusion on the basis of abstract, again by a single reviewer (CB) who in cases of uncertainty tended towards inclusion. A second reviewer (LP) assessed a subset consisting of 199 (10%) of the abstracts, and the agreement between the two reviewers' assessments was checked with a kappa test. Since the outcome, $\kappa = 0.71$, indicated a 'substantial' agreement [40] and since the inconsistency had chiefly been caused by the main reviewer being more inclusive than the second one, the screening was allowed to proceed without revision.

Finally, each article found to be relevant on the basis of abstract was judged for inclusion by a reviewer studying the full text. This task was shared by all members of the review team. The articles were randomly distributed within the team, but some redistribution was then made to avoid having reviewers assess studies authored by themselves or articles written in an unfamiliar language. Articles found using search engines, specialist websites, review bibliographies or stakeholder contacts were also entered at this stage in the screening process. Doubtful cases – articles that the reviewer could not include or exclude with certainty even after having read the full text – were discussed and decided on by the entire team.

A list of all articles rejected on the basis of full-text assessment is provided in Additional file 2: Table B together with the reasons for exclusion. This file also contains a list of potentially relevant articles that were not found in full text (Additional file 2: Table A).

Study inclusion criteria

Each study had to pass each of the following criteria in order to be included, either by providing all the required data itself or by referring to other articles where supplementary information was presented.

- *Relevant subjects:* Temperate freshwater lakes or reservoirs (with an area equal to or larger than 1 hectare) characterised by study authors as eutrophic (or hypertrophic) and/or having summer concentrations of total phosphorus (TP) exceeding 30 μg/l before biomanipulation.
- *Relevant types of intervention:* Removal of planktivorous or benthivorous fish, stocking of piscivorous fish and any combination of such interventions, provided that the intention was to improve water quality.
- *Relevant type of comparator:* No intervention.
- *Relevant types of outcome:* Change of Secchi depth, change of concentrations of chlorophyll *a*, total phosphorus, total nitrogen, oxygen or suspended solids, or change of total phytoplankton or cyanobacteria abundance.
- *Relevant types of study:* Any primary field study of water quality in lakes or reservoirs (or in artificially separated compartments with areas ≥ 1 ha in such water bodies) that had been subject to large-scale biomanipulation of any of the kinds described above. The study could be based on before/after comparisons or site comparisons or both (see Study quality assessment below).

During screening on full text, the following inclusion criterion was also applied:

- *Language:* Full text written in English, Danish, Dutch, German, Norwegian or Swedish.

Potential effect modifiers and reasons for heterogeneity

To the extent that data were available, the potential effect modifiers listed below were considered and recorded. This was done on a lake-by-lake rather than article-by-article basis.

Geographical coordinates
Altitude
Lake area
Mean and maximum lake depth
Retention time
Lake connectivity (whether the lake had tributaries and/or connections to other lakes)
Lake salinity
Water colour
Concentration of dissolved organic carbon (DOC)

Occurrence of stratification in the lake
Annual mean temperature
Presence of introduced species
Presence of grazing or piscivorous birds
Study duration and seasonality
History of biomanipulation (years and seasonality of interventions, amounts of fish removed or stocked, methods for fish removal, species, age and size of stocked fish, etc.).
History of other interventions and disturbances, e.g.

1) other in-lake attempts to mitigate eutrophication problems (such as dredging, aeration, improvement of recruitment habitats for predatory fish etc.);
2) external supplies of phosphorus (and other pollutants) from point sources and runoff, internal nutrient loading and any experimental nutrient additions to the lake;
3) land use in the surrounding area (including attempts to reduce nutrient losses by modifying the use of fertilisers, establishing buffer zones with permanent vegetation between fields and watercourses etc.);
4) damming, lake lowering and other hydrological disturbances;
5) special weather conditions (droughts, heat waves, storms);
6) fisheries and stocking not intended as a means of biomanipulation;
7) natural or unintended anthropogenic fish-kills.

Study quality assessment

In many cases, the biomanipulation of an individual lake has been described in several articles that cover different aspects of the intervention and its consequences. One article may focus on the stocking or removals of fish and how they have affected standing fish stocks, whereas details on how this intervention has influenced water quality may be found elsewhere.

For this reason, once the full-text screening of articles was completed, the review proceeded on a lake-by-lake rather than article-by-article basis – all articles with relevant data on a certain lake or biomanipulation project were considered together. Contrary to what was stated in the protocol [36], therefore, quality assessment of studies that had passed full-text screening was based on the entire evidence found on a certain lake biomanipulation, not on individual articles. A few articles that initially had been excluded due to absence of relevant water-quality data were re-entered at this stage, since they contained useful data on other aspects of a biomanipulation project.

The quality assessment was performed by the six ecologists in the review team (SRC, AG, PL, LP, CS and EVD) – again with care taken that reviewers would not assess articles authored by themselves – and double-checked by the seventh member of the team (CB). Doubtful cases were discussed and decided on by the entire team.

Exclusion criteria

If the combined evidence on a biomanipulated lake had any of the deficiencies listed below, it was considered to have high susceptibility to bias. In such cases, the lake was excluded from the review.

- *No (or insufficient) data on water quality before biomanipulation.* The available data were regarded as insufficient if they covered less than one full pre-manipulation summer season.
- *No useful quantitative data on fish removals or changes of standing fish stocks.*
- *Insufficient methodological description.*

A list of lakes rejected on the basis of quality assessment is provided in Additional file 3 together with the reasons for exclusion.

Additional quality criteria

For lakes that were not rejected based on the above exclusion criteria, the combined evidence was considered to have either low or medium susceptibility to bias. If any of the criteria listed below applied, susceptibility to bias was classified as medium. If none of them applied, susceptibility to bias was considered to be low (meaning that the quality of evidence was regarded to be high).

- *Confounding interventions or disturbances.* Interventions like aeration, dredging, aluminium treatment or sewage diversion (or disturbances like fish-kills) occurred just before, during or just after fish manipulation.
- *Insufficient data on potential effect modifiers.* Available lake metadata and data on lake history were so incomplete that they allowed no conclusions on whether other interventions or disturbances had occurred besides fish manipulation.
- *No useful data on within-year water-quality variation.* Available water-quality data consisted of only one observation per year or of annual means without standard deviations, standard errors, confidence intervals or similar measures of variation.
- *Multiple basins.* The lake or lake system consisted of at least two basins that were manipulated differently and/or had markedly different water quality.

Data extraction strategy

Annual means and variation of summer-season water-quality data have been extracted from tables and graphs in articles and reports, using image analysis software

(WebPlotDigitizer) when necessary. In some cases, study authors or database managers were asked to supply data in digital format. This was done where useful data had been published in graphs from which they were difficult to extract accurately enough, or when it was known or assumed that considerable amounts of relevant but unpublished data could be available in addition to the published results.

In cases where raw data were received, summary statistics have been calculated by us. Where individual water-quality data have been available, multi-year means and variation have been calculated based on these data rather than on annual averages.

The summer season has been defined differently by different authors, but 1 May – 30 September is the most common choice. This was also the period that we used ourselves when selecting relevant raw data (although our search for data was global, all biomanipulations found suitable for quantitative analysis had been performed in the northern hemisphere).

Data on potential effect modifiers and other metadata were extracted from the included articles whenever available, but data on annual means of the atmospheric temperature were downloaded from the WorldClim database [41].

Initially, outcomes and metadata were recorded in a separate Excel file for each included lake. Data to be used in meta-analysis were then transferred to an Access database.

Definitions of pre-, during- and post-manipulation periods

Most studies of biomanipulations have a Before/After ('BA') design – they compare data that have been collected prior to and following the intervention (or at least during different stages of the intervention). Since a biomanipulation may extend over several months or even years, BA studies often present data sampled not only before and after but also during the intervention. Due to the complexity of many biomanipulation projects, however, it is not always obvious when the main intervention started or ended. For instance, mass removals of fish may have been preceded or followed by less significant fish removals, and stocking may have taken place not only after periods of mass removal but also before or during them.

For intervention involving fish removal, we defined the *main biomanipulation period* as the years during which significant amounts of fish (at least 7–8 kg per hectare) were removed. Piscivore stocking performed within this period was normally seen as part of the main biomanipulation, but not if the fish removal resulted in complete eradication of the fish stocks. For interventions based on stocking only, the main biomanipulation period was defined as the years during which adult piscivores or significant numbers of young piscivores (at least 50–100 individuals per hectare) were stocked. A single year with insignificant or no fish removal or stocking was included in the main biomanipulation period if it was both preceded and followed by years with significant manipulation.

Building on these definitions, we applied the following rules to decide whether water-quality data sampled during a certain summer season represented Before, During or After conditions in the manipulated lake. Data that could not be included in any of these categories were not used.

The *Before* period was defined to stretch back as long as water-quality data were available and pre-manipulation summer conditions (concentrations of total phosphorus and chlorophyll *a*, Secchi depth etc.) were reasonably stable. If confounding interventions or disturbances (e.g. aeration, dredging, in-lake chemical treatment, significant increases or decreases of phosphorus inputs, or fish-kills due to oxygen deficiency) took place during the pre-manipulation period, the Before period was said to start after the last onset or end of such events. The Before period was defined to end with (and include) the last pre-manipulation summer. Periods without water-quality data were included in the Before period if they lasted no more than 5 years and were preceded by a year with water-quality data.

The *During* period was defined to begin with the first during- or post-manipulation summer and conclude with the last year with significant biomanipulation. This means that no summer season was categorised as 'During' if the manipulation was confined to a single autumn.

The *After* period was defined to begin with the first post-manipulation year and last as long as water-quality data were available and no additional interventions or confounding events began. Periods without water-quality data were included in the After period if they lasted no more than 5 years and were followed by a year with water-quality data.

Two biomanipulations of a single lake were regarded as distinct interventions (to be analysed individually) if they were separated by at least 8–10 years without significant manipulation. The last 3 years before the second biomanipulation were then defined as the Before period of that intervention.

Data synthesis and presentation

Meta-analysability and selection of a high-quality dataset

Although we have access to water-quality data for each of the biomanipulation projects included in this review, a considerable part of these projects do not appear in any of the meta-analyses described below. One reason is that for some biomanipulations, the available data do not include any of the water-quality parameters covered by the meta-analyses (Secchi depth, chlorophyll *a* concentration and cyanobacteria abundance). Another reason is that some of the data available to us are not meta-analysable due to absence of useful information on variation (such as standard deviations, standard errors or confidence intervals) or on the number of observations. Published data on water quality in manipulated lakes sometimes consist of single measurements per year or of summer averages without any information on within-year variation. In other cases, published summer means or medians are accompanied by fractiles or ranges, but there is no reliable way of converting such data to measures of variation that can be used in meta-analyses.

Where water-quality data were available for more than one year within a Before-, During- or After-manipulation period, calculation of interannual variation enabled us to include them in some meta-analyses even if there was no useful information on within-year variation. However, due to the large seasonal fluctuations of primary production and phytoplankton abundance that characterise most eutrophic lakes, within-year variation of water quality may be larger than the interannual variation, even if the analysis is restricted to data sampled during summer. If this is the case, we may introduce bias by using effect sizes with interannual variation only, since such data will then tend to have lower variance and hence be given higher weight in meta-analyses than if their within-year variation had been known and included too.

Another important quality aspect is the presence or absence of confounding interventions or disturbances. Biomanipulation has frequently been performed in combination with other efforts to improve water quality, such as aeration or artificial mixing of deep waters, dredging (sediment removal), sewage diversion or other reductions of external nutrient inputs, or in-lake phosphorus removal with aluminium or iron salts. In many eutrophic or hypertrophic lakes, moreover, fish-kills caused by oxygen deficiency may have water-quality effects resembling those of deliberate manipulations of the fish fauna.

For these reasons, much of our analysis uses a high-quality 'selected dataset' where effect sizes based on single data per year and/or confounded data have been excluded. An alternative way of identifying a high-quality dataset would have been to include effect sizes only for biomanipulations where data were categorised as having low susceptibility to bias. The classification of susceptibility to bias is somewhat coarse, however, being based on the combined evidence on a biomanipulation project rather than on individual effect sizes. Even for the same biomanipulation, some effect sizes may be based on confounded data or single data per year, while others are not.

Meta-analyses

The impacts of biomanipulation on water quality were mainly analysed using meta-analytical approaches. The meta-analyses were carried out using the metafor package [42] within the R environment v. 3.0.2 [43].

Most of the meta-analyses used water transparency (measured as Secchi depth) or chlorophyll *a* concentration as response variables. Since all data for these variables could be converted to the same units (m and µg/l, respectively), the comparisons were based on mean differences. The effect sizes were calculated as the difference between the mean response during or after the main biomanipulation period and the mean response before the manipulation. Positive effect sizes thus indicate that the response parameter was higher during or after intervention than before intervention. When analysing effect sizes based on the selected dataset, we also explored the consequences of exchanging mean differences for mean log ratios.

Moreover, a few meta-analyses were made of data on cyanobacteria abundance. Since these data were given in several incommensurable units, mean log ratios were used as effect sizes for the cyanobacteria meta-analyses.

Random effects models were developed for each response variable, comparing data acquired Before/During or Before/After manipulation. For the Before/After comparisons, models were developed for each of the first 7 years after manipulation, as well as the average of years 1–3 after manipulation. Random effects models were run using restricted maximum likelihood to estimate heterogeneity, and data are presented in forest plots showing mean effect sizes and 95% confidence intervals. Random effect models were also developed for separate subgroups of comparisons, covering various aspects of data quality and different types of biomanipulation.

To investigate to what extent lake properties and biomanipulation methods influence the effects of biomanipulation on Secchi depth and chlorophyll *a* concentrations, we performed meta-regressions on Before/During and Before/After comparisons (the latter covering years 1–3 after manipulation). The most relevant effect modifiers – lake area, mean depth, retention time, pre-manipulation total phosphorus (TP) concentration, mean annual atmospheric temperature, duration of fish removals, amount of fish removed (expressed as kg/ha or kg/ha/yr) and depletion of fish stocks – were used as co-variates.

Data were not plentiful enough to allow a complete analysis using all explanatory variables simultaneously. However, since lake area, mean depth and pre-manipulation TP concentration were highly correlated (see Additional file 4), we applied principal component analysis (PCA) to convert observations of these lake properties into a set of linearly uncorrelated variables (principal components, PC). We then used the first PC (PC1) as an explanatory variable in the meta-regressions.

PC1 explained 80% or more of the variation in the three selected lake properties, reflecting increasing lake area and decreasing pre-manipulation TP concentrations, whereas mean depth was mainly reflected in PC2 that only explained a minor part of the variation (see Additional file 5).

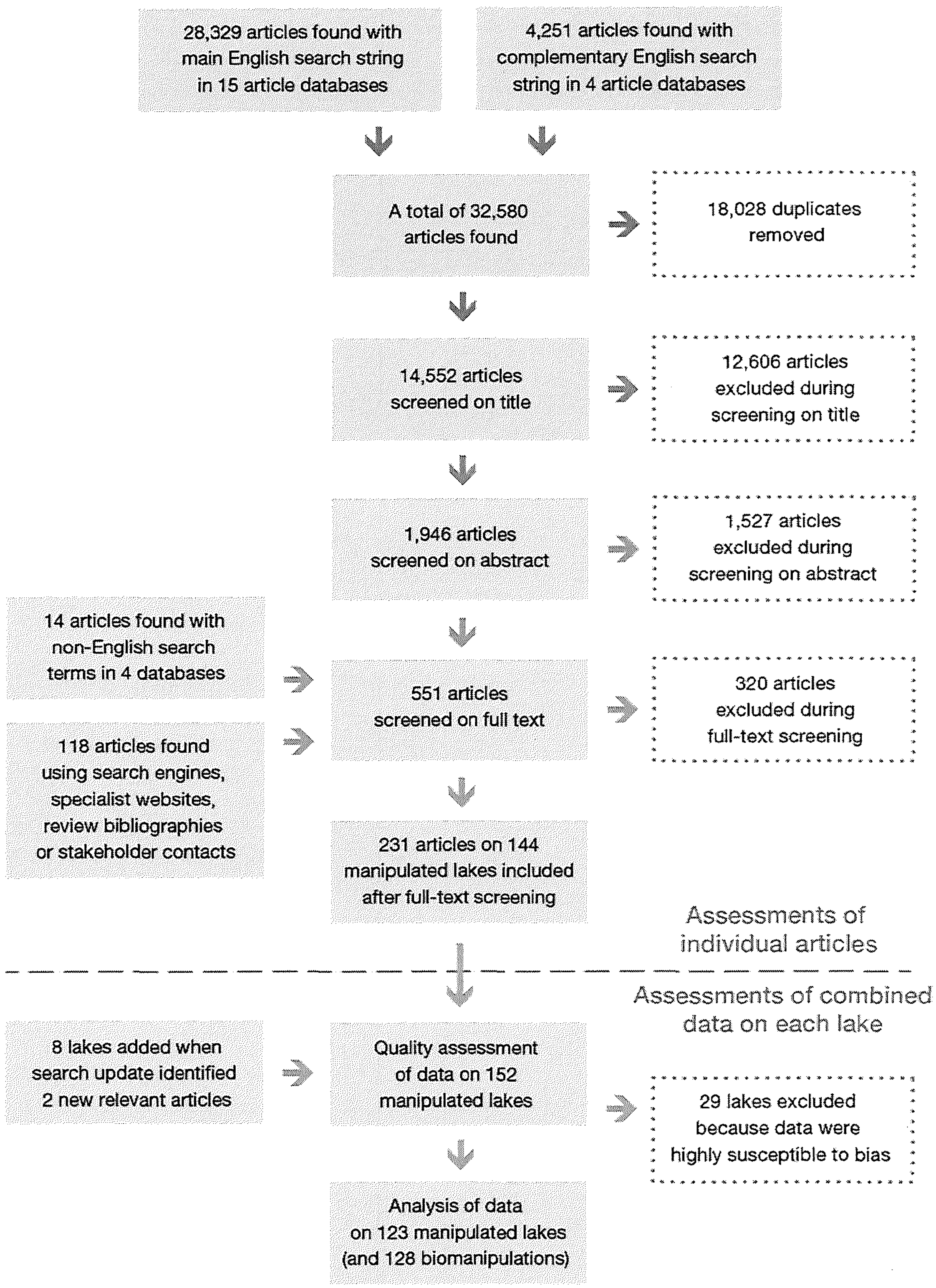

Figure 1 Overview of article inclusion, article screening and quality assessment of lake data.

Table 1 Susceptibility to bias of the evidence on included biomanipulations

	No. of cases
Low	53
Medium due to confounding interventions or disturbances	31
Medium due to insufficient data on potential effect modifiers	13
Medium due to absence of useful data on within-year water-quality variation	43
Medium since the lake consisted of multiple basins with different interventions or water quality	6

The evidence on some biomanipulations has medium susceptibility to bias based on more than one of the quality criteria.w

Meta-regression models were made using the combined 'lake-property' variable (PC1), a measure of intervention strength (fish removals expressed as kg/ha/yr), and the interaction between these two as explanatory variables. Selection between the models (including the intercept-only model) was based upon minimum Akaike's information criterion corrected for small sample size (AICc).

Since we were not able to test all effect modifiers listed above at the same time, we also performed meta-regressions with each of them separately.

All meta-regressions were based on the selected dataset, with stocking-only biomanipulations excluded (see Results). Due to skewness of the data, lake areas, mean depths, retention times, pre-manipulation TP concentrations and amounts of fish removed were log-transformed before analysis.

Finally, Secchi depth and chlorophyll *a* data (both from the selected set and from the entire set of meta-analysable data) were tested for possible publication bias using funnel plots.

Results

Review descriptive statistics

Literature searches and screening

The main searches for literature were conducted between 10 December 2012 and 4 March 2013, and an update was made on 26 October 2013.

Searches with the main English search terms in 15 publication databases returned a total of 28,329 articles (or 12,908 after removal of duplicates) – see Figure 1. Four of the databases (Academic Search Premier, Aquatic Sciences and Fisheries Abstracts, Scopus, and Web of Science) were also searched with the complementary search string, which returned a total of 4,251 articles (or 2,270 after removal of duplicates). Of these articles, 1,644 had not been found with the main search string.

After title screening of the 14,552 unique publications found by the main and complementary searches, 1,946 of them remained included. Screening based on abstract left 419 articles that still were considered as potentially relevant. Most of the excluded articles contained no relevant information on how water quality had responded to biomanipulation, or did not touch on reductions of planktivorous or benthivorous fish at all (see Additional file 6).

Searches with Danish, Dutch and Swedish search terms in national bibliographic databases yielded 4, 3 and 7 potentially relevant publications in these languages, respectively. Searches using search engines returned 33 potentially relevant articles (17 found with English search terms, 10 with Danish and 6 with Swedish ones) in addition to those that already had been identified. Similarly, searches on specialist websites located another 9 potentially useful publications (2 found using English search terms and 7 using Danish ones). An additional 38 articles were found in bibliographies of literature reviews, while 38 more were added by members of the review team or included as a result of stakeholder contacts or Google searches for the names of known biomanipulated lakes. A large part of the publications referred to in this paragraph can be characterised as grey literature.

In all, the searches resulted in 551 articles to be screened based on full text. After screening, 231 of them were still included. At this stage, the most common reason for exclusion was that studies contained no relevant primary data (see Additional file 6 and Additional file 2: Table B). In 22 cases, publications had to be excluded because they were not found in full text (see Additional file 2: Table A). When the search for publications was updated in late 2013, two new articles were included.

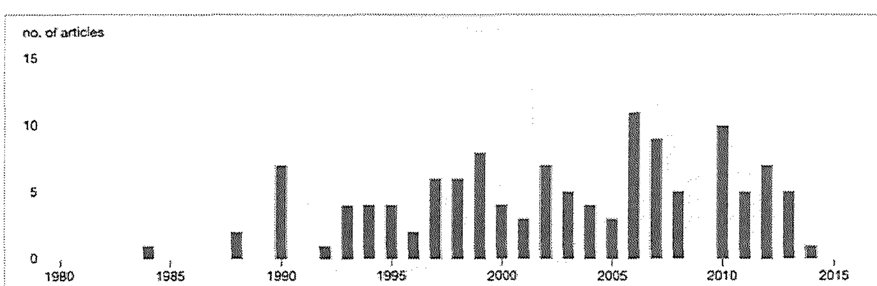

Figure 2 Year of publication of the 124 articles that were used for data extraction.

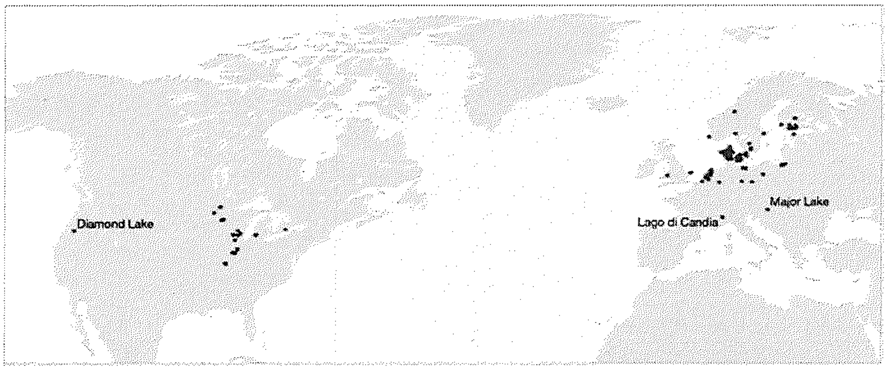

Figure 3 Locations of biomanipulated lakes included in the review. More detailed maps are available in Additional file 9.

Quality assessment

The 233 articles that had passed full-text screening described a total of 152 biomanipulated lakes. A single lake could be referred to in up to twenty different articles, while a single publication could describe a large number of different manipulation projects. Quality assessment of the available evidence was therefore performed per lake rather than per article.

This assessment led to the exclusion of 29 lakes from the review, since the evidence found on them was categorised as highly susceptible to bias. The most common reason for exclusion was that data on pre-manipulation water quality were insufficient or entirely absent (see Additional file 3).

In 5 of the 123 manipulated lakes that remained included in the review, interventions had been performed twice at sufficiently long intervals (8–10 years or more) that they could be regarded as independent of each other. Therefore, 128 individual biomanipulations have been considered in this review.

For 53 of the 128 biomanipulations we found the quality of the available evidence sufficient to have low susceptibility to bias. In the remaining 75 cases, we classified the susceptibility to bias as medium (see Table 1 and Additional file 7: Table B).

Sources of articles used for data extraction

Although 233 articles had been judged as relevant during full-text screening, only 124 of them were actually used for extraction of data. In some cases, the reason for not using an article was that it related to a lake that had been excluded during quality assessment, but the most common reason was that articles were redundant for the purposes of this review – they reported data that could also be found elsewhere (see Additional file 2: Table C and D). Many of them were reviews rather than sources of primary data.

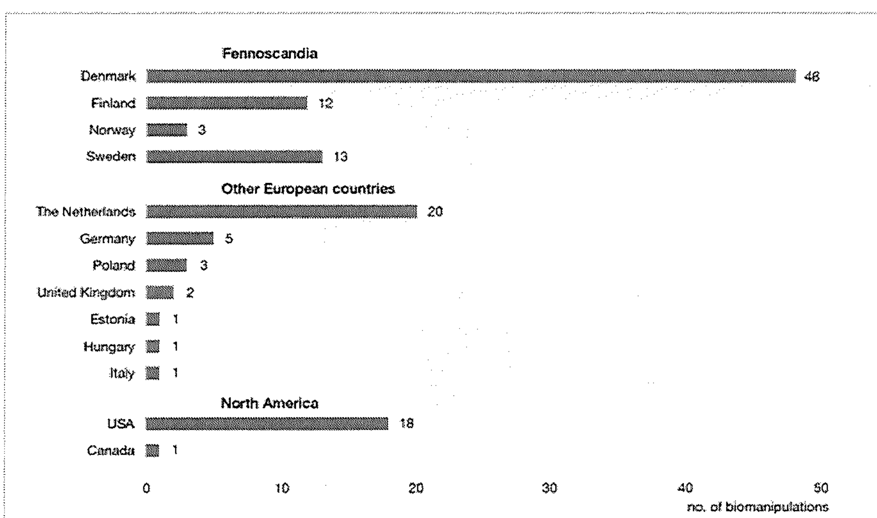

Figure 4 Number of included biomanipulations per country.

Table 2 Characteristics of included lakes

	Median	Min.	Max.
Mean depth (m)	2.1	0.7	13.5
Lake area (ha)	37	1.2	3985
Retention time (days)	220	1	3870
Total phosphorus concentration (pre-manipulation summer mean, μg/l)	133	25	1195
Mean annual atmospheric temperature (°C)	7.8	1.3	13.1

Of the 124 articles that were used for data extraction, 69 had been found in publication databases (see Additional file 8). Of these, 61 were identified using the main English search terms, while 5 others were found with the supplementary search string only and 3 with Dutch or Swedish search terms.

Of the remaining 55 articles used for data extraction, we had found 35 using search engines (mostly by searching for names of known biomanipulated lakes), 4 at specialist websites, 5 in review bibliographies and 3 through stakeholder contacts, whereas 8 had been provided by members of the review team. While 77 articles were written in English, 30 were in Danish, 3 in Dutch, 2 in German and 12 in Swedish.

Only 3 of the 124 articles were published before 1990. Years of publication of the more recent articles were distributed fairly evenly over the period 1990–2013 (see Figure 2).

Narrative synthesis

Overall characteristics of included lakes and biomanipulations

Most of the biomanipulations covered by this review were carried out in central or northern Europe – more than half of them in Fennoscandia alone – whereas the remaining 15% were performed in North America (see Figures 3 and 4 and Additional file 9). Our literature searches also identified a number of biomanipulated lakes in temperate parts of Asia, Australia and South America, but all of these cases were excluded during full-text screening or quality assessment.

The included lakes are typically shallow, small, and hypertrophic rather than merely eutrophic (see Table 2). Based on the available literature, 73 of them were categorised as natural lakes (although some of these have been lowered or modified in other ways), while 8 were characterised by study authors as artificial lakes, 11 as impoundments and 16 as former peat, sand or gravel pits (see Additional file 7: Table A).

Of the 128 individual lake biomanipulations in the review, 102 included fish removal. In 81 of these cases, stocks of planktivorous and/or benthivorous fish were decimated solely by fishing. Eleven other manipulations involved rotenone or other piscicides, while ten included partial or complete emptying of the lake or reservoir, often but not always in combination with fishing (see Additional file 7: Table C). Several of the latter interventions resulted in complete eradication of all fish species. In 35 cases where planktivorous and benthivorous fish were decimated, this intervention was combined with stocking of piscivores such as northern pike (*Esox lucius*), pikeperch (*Sander lucioperca*) or perch (*Perca fluviatilis*). The biomanipulations reviewed by us also include 26 cases solely based on piscivore stocking.

Details on the included biomanipulations are presented in three tables in Additional file 7. Table A in this file provides basic data on the manipulated lakes: location, lake type, lake area, mean depth, occurrence of stratification in summer, retention time, average pre-manipulation concentration of total phosphorus in summer, and mean annual atmospheric temperature. Table B presents study design, assessments of study quality, basic data on the main biomanipulation (type, timing and duration), and a selection of water-quality data (summer averages of Secchi depth and chlorophyll *a* concentration before and during the main biomanipulation and in the first three post-manipulation years). Table C provides details about fish removals and/or fish stockings included in the main biomanipulation, and also available data on changes of standing fish stocks.

Table 3 No. of biomanipulations with available effect sizes

	Before/During effect sizes			Before/After effect sizes*		
	All	Meta-analysable	Selected dataset	All	Meta-analysable	Selected dataset
Chlorophyll *a* concentration	87	75	30	73	65	26
Secchi depth	94	81	34	78	66	27
Total phosphorus concentration	106	81	28	92	71	27
Cyanobacteria abundance	35	27	13	23	13	5
Total phytoplankton abundance	39	29	13	24	13	4
Daphnia abundance	22	15	8	22	12	6
Cladocera abundance	24	15	8	23	13	7
Total zooplankton abundance	23	14	8	20	10	6

*Data available for at least one of the first three post-manipulation years.

Availability of water-quality data and other outcomes

The availability of water-quality data from different stages of each of the included biomanipulation projects is shown in Figures 5 and 6. This figure also indicates where available data have not been used due to confounding interventions or disturbances.

Of the 128 biomanipulations included in the review, 125 are covered by studies that – in a wide sense – have a 'BA'

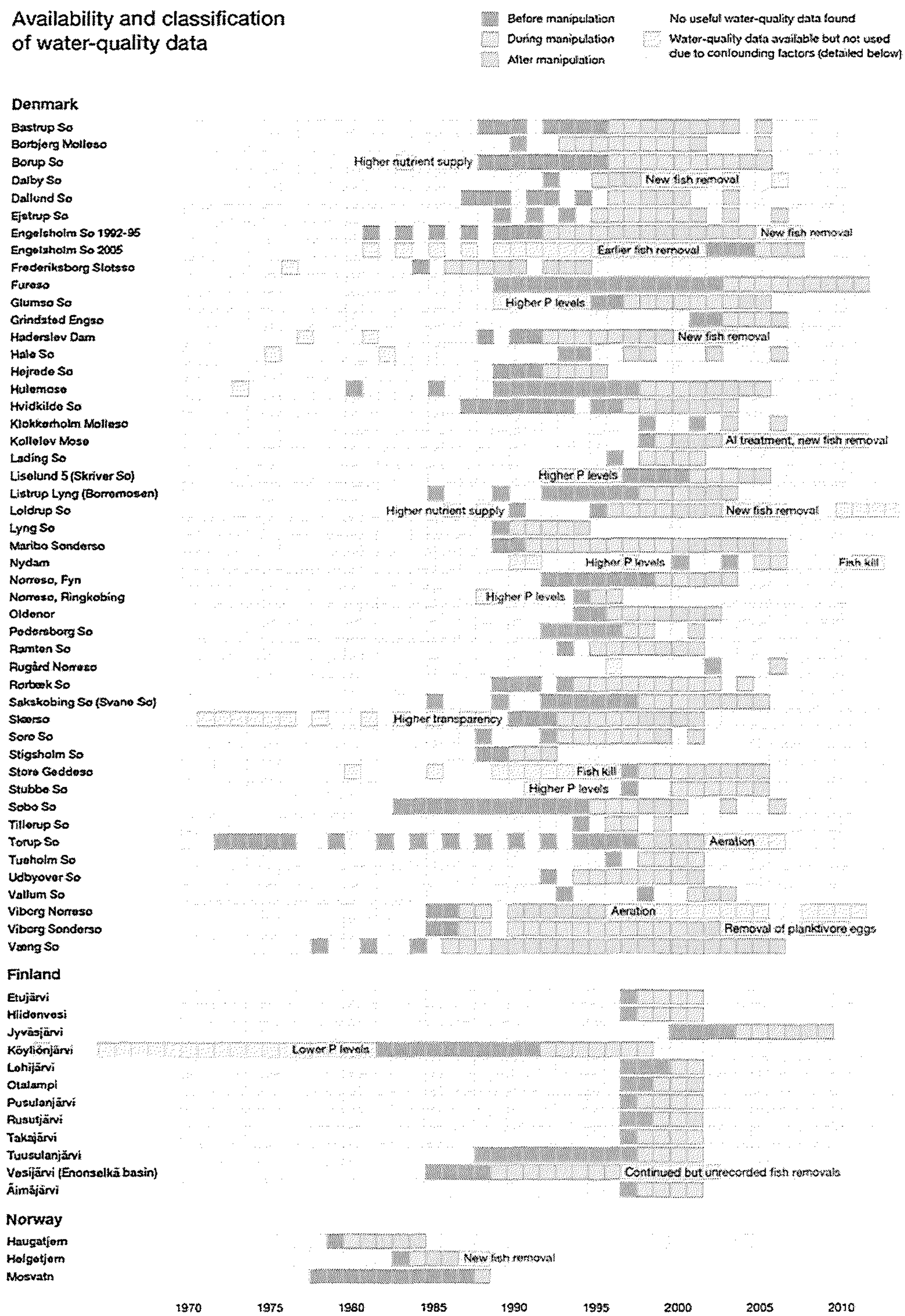

Figure 5 Availability of pre-, during- and post-manipulation water-quality data from the included lakes.

(Before/After) design. In 86 of these cases, we have access to water-quality data sampled not only before and after but also during the main biomanipulation, and we therefore refer to them as having a 'BDA' (Before/During/After) design (see the Methods section). In 27 other cases, we have data collected before and during the biomanipulation, but not afterwards. We refer to such cases as having a 'BD' (Before/During) design. The remaining 12 cases

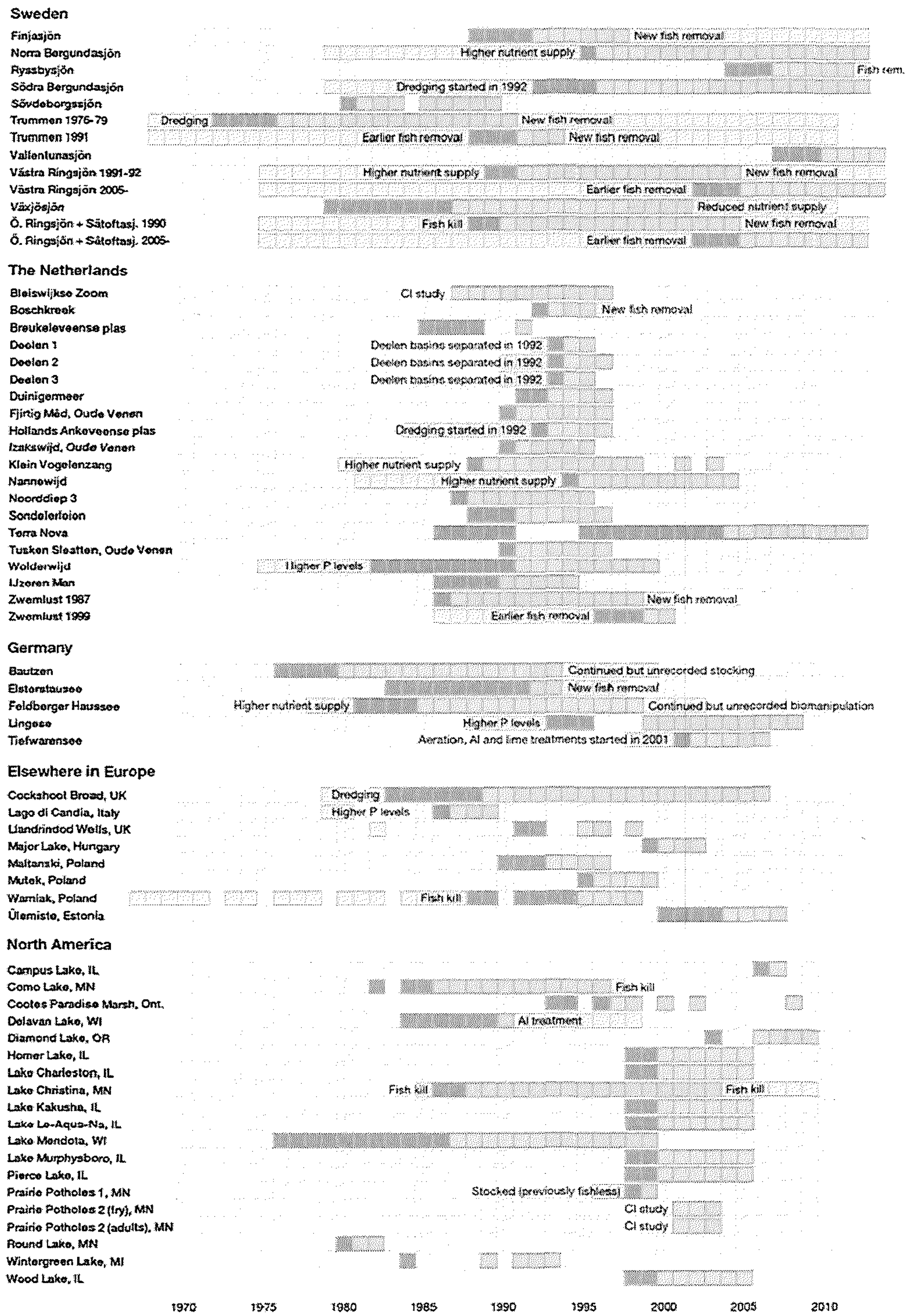

Figure 6 Availability of pre-, during- and post-manipulation water-quality data from the included lakes.

may be called 'true BA', since in these cases we have access to data collected before and after but not during the manipulation.

Three of the biomanipulations in the review – Bleiswijkse Zoom, Prairie Potholes 2 (adults) and Prairie Potholes 2 (fry) – are covered by studies that present no pre-manipulation data. Instead, these studies are based on comparisons between the manipulated lakes and similar lakes where no such intervention has taken place. This means that they have a 'CI' (Comparator/Intervention) design. In our quantitative synthesis, CI comparisons made during biomanipulation are included among Before/During comparisons, whereas CI comparisons made after biomanipulation are included among Before/After comparisons.

The outcomes that we have extracted from articles and databases are dominated by observations of Secchi depth, chlorophyll *a* and total phosphorus. We also extracted data on abundances of cyanobacteria, total phytoplankton, *Daphnia*, Cladocera and total zooplankton, although such information was found for relatively few of the biomanipulations (see Table 3). Data on oxygen levels, concentrations of suspended solids and cover of macrophytes were found to be too scarce and/or heterogeneous to be useful. We have also chosen not to use data on total nitrogen concentrations – such data are frequently available in the literature, but they have limited relevance to lake eutrophication.

An overview of all available Secchi depth and chlorophyll a data

The biomanipulations reviewed here include interventions of highly varying strength, ranging from very modest planktivore/benthivore removal (only 13–30 kg/ha/yr in some cases) or stocking of limited numbers of piscivores to complete eradication of the entire fish fauna. Moreover, they have been performed in a set of lakes that covers wide ranges of size, depth, trophic status and climatic conditions.

Yet, even a cursory inspection of the outcomes indicates that a clear majority of the interventions have had positive effects on water quality (see Figure 7 and Additional file 7: Table B). Secchi depths have in most cases increased, whereas concentrations of chlorophyll *a* have in most cases decreased. These effects usually appear both during biomanipulation and in the early post-manipulation phase. Nonetheless, we found a great deal of variability among case studies, and there are cases of lakes that did not improve.

Quantitative synthesis

Summary effect sizes based on datasets of different quality

Quantitative analysis of available data substantiates the observations that concluded our narrative synthesis. According to the meta-analyses summarised in Figure 8, biomanipulation leads to a significant ($p < 0.05$) increase of water transparency (measured as Secchi depth) and a significant decrease of phytoplankton abundance (measured as concentration of chlorophyll *a*) in summer, not only during years when such manipulation is carried out, but also during the first three post-manipulation years.

A large proportion – 85% or more – of all available Secchi depth and chlorophyll *a* effect sizes (i.e. the data presented in Figure 7) are meta-analysable in the sense that we have access to information on variation and sample sizes. Our meta-analyses of these data indicate that, on the average, Secchi depths are 0.22 m greater and chlorophyll *a* concentrations 22 μg/l lower during biomanipulation than before manipulation. The first three years

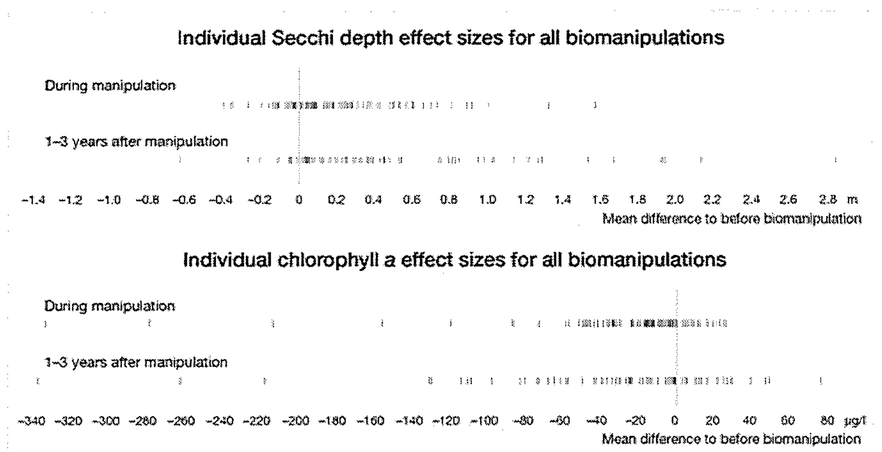

Figure 7 Effect sizes based on mean Secchi depth and chlorophyll *a* concentration. All biomanipulations with available data are represented in the diagram. 'Before' and 'During' periods have been defined as in Figures 5 and 6. All Secchi depth and chlorophyll *a* data in this and the following figures and tables are based on summer means.

Table 4 Summary effect sizes based on the selected dataset (mean differences to before manipulation)

	Mean	95% C.I.
Secchi depth during manipulation (m)	0.22	0.11 – 0.33
Secchi depth 1–3 years after manipulation (m)	0.47	0.23 – 0.70
Chlorophyll *a* during manipulation (μg/l)	−30	−42 – −17
Chlorophyll *a* 1–3 years after manipulation (μg/l)	−33	−52 – −14

after biomanipulation, Secchi depths are 0.46 m greater and chlorophyll *a* concentrations 30 μg/l lower than before manipulation, again based on averages of all meta-analysable data. All these summary effect sizes are statistically significant (see the topmost row in Figure 8 and pp. 1–4 in Additional file 10).

Calculation of interannual variation has enabled us to include some water-quality data in meta-analyses even in cases when there was no useful information on within-year variation (see Methods). However, there are indications that the within-year variation of water quality differs from the interannual variation. In 13 lakes where we have multiple data per summer season for at least 5 years within a pre-, during- or post-manipulation period, the within-year Secchi depth variation during these periods was on average 56% larger than the interannual variation. For chlorophyll *a* data, the corresponding difference was 68%. There are also some differences between summary effect sizes based on single vs. multiple data per year (i.e. data with interannual variation only and data with within-year variation over one or several years, respectively), as shown on rows 2 and 3 in Figure 8 (and pp. 5–8 in Additional file 10). The difference is statistically significant for Before/During comparisons of chlorophyll *a*, but while the summary effect size is smaller for single- than for multiple-per-year chlorophyll *a* data, the reverse applies to Secchi depth data.

Moreover, we have classified outcomes of about a quarter of the included biomanipulations as confounded since additional interventions or disturbances took place during, just before or just after the main biomanipulation (see Additional file 7: Table B). Confounded effect sizes tend to be smaller than non-confounded ones (see Figure 8, rows 4 and 5, and Additional file 10, pp. 9–12).

In order to reduce the risk of bias, we have based most of the further quantitative analysis on the 'selected dataset' from which single data per year and confounded data have been excluded (see the Methods section). Summary effect sizes calculated using the selected dataset are shown in Table 4, in Figure 8 (bottom row) and in Additional file 10 (pp. 17–18). For Secchi depth, they are almost identical to summary effect sizes based on all meta-analysable data, whereas for chlorophyll *a* they are somewhat larger, but not significantly so.

Alternatively, we could have defined a high-quality dataset by including effect sizes only for those biomanipulations where data were categorised as having low susceptibility to bias (see Methods). Summary effect sizes based on such data are very similar to those based on the selected dataset, as indicated by the two bottommost rows in Figure 8 (and pp. 13–16 in Additional file 10).

The Secchi depth and chlorophyll *a* effect sizes reported above are all based on mean differences. We also explored the consequences of exchanging mean differences for mean log ratios when analysing the selected dataset, but this did not alter the main results – Secchi depth increases and chlorophyll *a* decreases all remained significant.

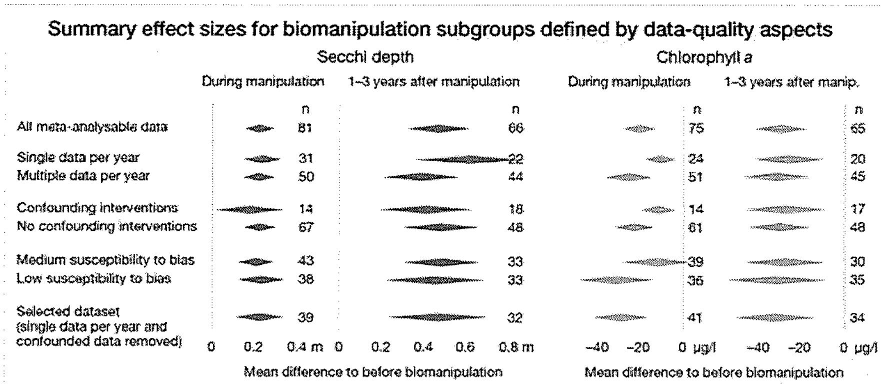

Figure 8 Summary effect sizes for biomanipulation subgroups defined by different aspects of data quality. The diamond-shaped symbols show means based on meta-analysable Secchi depth and chlorophyll *a* data (with 95% confidence intervals indicated by the widths of the symbols). The number of individual effect sizes (n) is indicated for each subgroup. 'Before' and 'During' periods have been defined as in Figures 5 and 6. Forest plots showing all individual effect sizes are presented in Additional file 10.

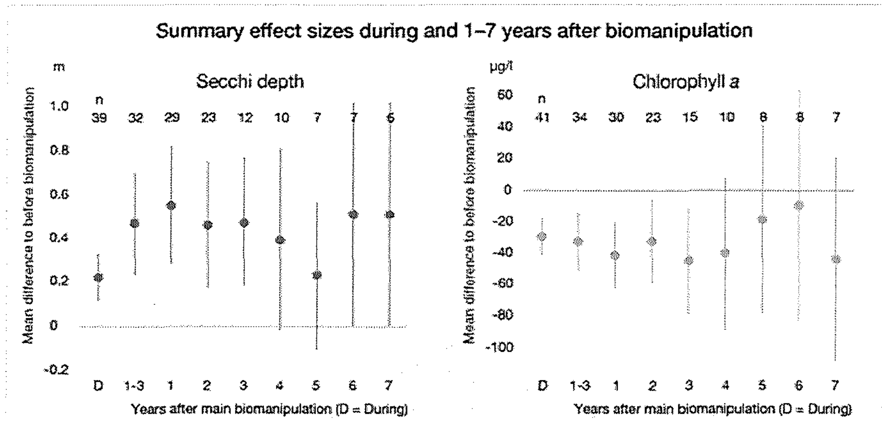

Figure 9 Summary effect sizes during and 1–7 years after biomanipulation. Means based on the selected dataset are shown during manipulation (D) and 1–3 years after manipulation, and also for each of the first 7 years after manipulation. Vertical lines indicate 95% confidence intervals. Numbers of biomanipulations with data are indicated in the upper part of the panels. 'Before' and 'During' periods have been defined as in Figures 5 and 6. Forest plots showing all individual effect sizes are presented in Additional file 10 (pp. 19–22).

Persistence of biomanipulation effects

Summary effect sizes for individual post-manipulation years show that four years or more after biomanipulation, the effects on Secchi depth and chlorophyll *a* are no longer significant, or just barely significant (see Figure 9). This may at least partly be due to the decrease of available information over time (see the number of observations in the upper part of Figure 9, and also the distribution over time of all individual meta-analysable effect sizes in Figure 10).

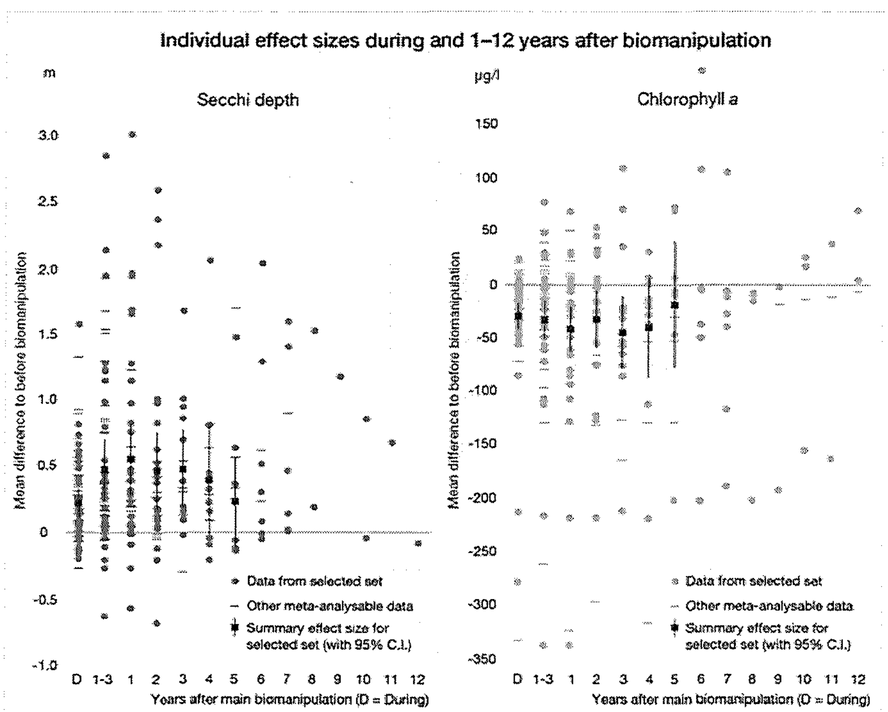

Figure 10 Individual effect sizes during and 1–12 years after biomanipulation. Here, distributions of effect sizes based on the selected dataset can be compared with those of other meta-analysable data. Individual effect sizes are shown during manipulation (D) and 1–3 years after manipulation, and also for each of the first 12 years after manipulation. Summary effect sizes based on the selected dataset are shown during manipulation and for the first 5 years after manipulation. 'Before' and 'During' periods have been defined as in Figures 5 and 6.

Another factor that most likely contributes to the variation of summary effect sizes in Figure 9 is that the data are based on different sets of manipulations in different years. In Figure 11, therefore, we present individual effect sizes for biomanipulation cases where long and more or less unbroken time series are available. These data, too, indicate that manipulation effects may last for a considerable number of years, in some cases ten years or more.

It is difficult to draw any general conclusions from these results, however, since a selection effect is involved. In this review, we followed the water quality of manipulated lakes only as long as no new mass removals of fish or other large-scale interventions were carried out. In many cases, though, lake managers repeated the biomanipulation after a few years since the water quality had then deteriorated. After the renewed intervention, such lakes no longer appear in our data. This means that lakes where manipulation effects have been more persistent than average are likely to be overrepresented in the set of biomanipulations for which we have data over many years.

Moreover, in 6 of the 13 cases represented in Figure 11 (panels at right), the main biomanipulation was followed up with other interventions (e.g. stocking or aeration) over several years, and this may have contributed to the persistence of the water-quality effects.

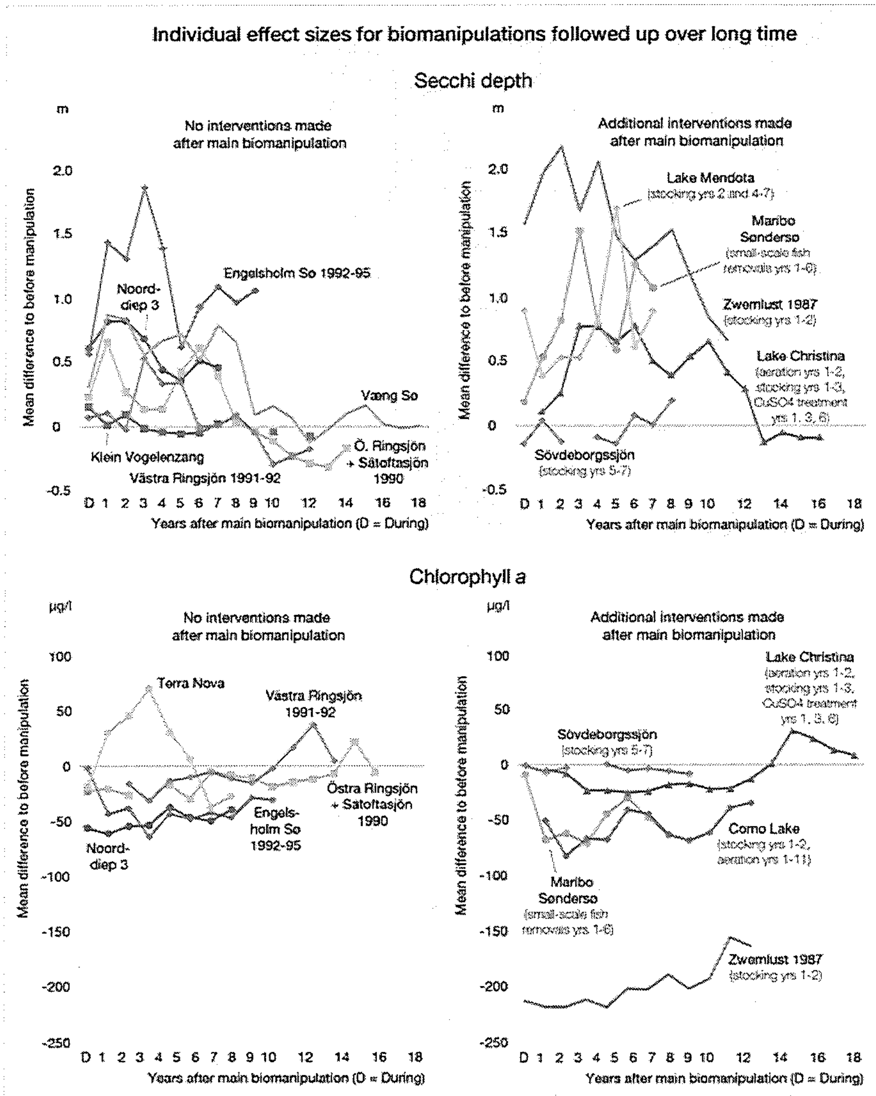

Figure 11 Individual effect sizes for biomanipulation cases where long time series are available. The effect sizes shown for Engelsholm Sø, Lake Christina, Maribo Søndersø, Væng Sø, Västra Ringsjön and Östra Ringsjön + Sätoftasjön are based on single data per year. The data in the panels at right may also have been influenced by interventions performed after the main biomanipulation, as detailed in the figure.

Effects on cyanobacteria abundance

Biomanipulation can also reduce the abundance of cyanobacteria (see Figure 12). Based on data for six biomanipulations in the selected set, the cyanobacteria abundance in summer decreased by an average of 84% from the pre-manipulation period to the first three years after manipulation. The available post-manipulation data is very limited, however, and the summary effect size remained significant only during the first year after manipulation.

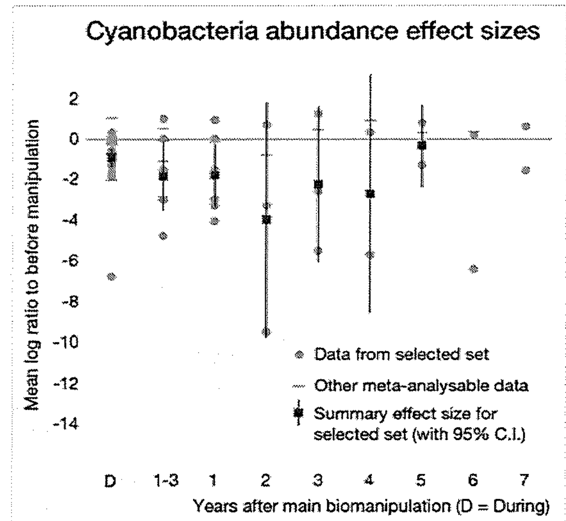

Figure 12 Individual and summary effect sizes of cyanobacteria abundance in summer. Shown here are individual effect sizes based on all meta-analysable data during manipulation (D) and 1–3 years after manipulation, and also for each of the first 7 years after manipulation. Summary effect sizes based on the selected dataset are shown during manipulation and the first 5 years after manipulation. 'Before' and 'During' periods have been defined as in Figures 5 and 6. Forest plots showing individual effect sizes from the selected dataset are presented in Additional file 10 (p. 23).

Effects of planktivore/benthivore removal vs. piscivore stocking

The biomanipulations that we have studied include removals of planktivorous and/or benthivorous fish as well as stockings of piscivorous fish, and also cases where these two approaches have been combined.

We have found clear contrasts between the water-quality effects of different kinds of biomanipulation (see Figure 13). Removal of planktivores/benthivores led to increased Secchi depth and decreased chlorophyll *a* concentration, both during intervention and in the first three post-intervention years, and regardless of whether the removal was combined with piscivore stocking or not. With one exception (Secchi depth 1–3 years after removal plus stocking), the effects were all significant. By contrast, manipulation based on piscivore stocking alone had no significant effect on Secchi depth or chlorophyll *a* concentration, neither during nor after the intervention.

Biomanipulation effects in relation to lake properties and intervention strength

The studies we have reviewed and analysed indicate that removal of planktivorous and/or benthivorous fish is capable of increasing water transparency and decreasing the amount of phytoplankton in lakes. However, the size of these effects varies both with lake properties and with intervention strength.

In Table 5, lakes that responded to biomanipulation (i.e. where water quality improved significantly) are compared with 'unresponsive' lakes (i.e. lakes where water quality did not change significantly, or even deteriorated). Lakes where water transparency was significantly larger after manipulation than before tended to be smaller and have shorter retention times than lakes where transparency did not improve. Similar tendencies can be seen in lakes where the chlorophyll *a* concentration was significantly lower after manipulation than before. These lakes also had higher pre-manipulation concentrations of total phosphorus (TP) than lakes where the chlorophyll level did not decrease.

We based this analysis on the selected dataset, but manipulations solely consisting of piscivore stocking were excluded, since we had found no evidence that such treatment improves water quality. This means that the analysis was based on a relatively limited amount of data, and none of the differences between responsive and unresponsive lakes was significant.

Meta-regression model selection showed that the effect of biomanipulation on chlorophyll *a* levels depends on the amount of fish removed, on the combination of the area and pre-manipulation TP concentration of the lake as represented by PC1 (see Methods), as well as on the interaction between these two variables (Table 6 and Additional file 11).

The selected models for chlorophyll *a* concentration during and after biomanipulation were both strongly supported (with AICc values more than 15 units less than the next best models; cf. [44]). The mean decrease of the chlorophyll *a* concentration was greater during biomanipulation in lakes where fish removal was more intense, and it was greater both during and after biomanipulation in lakes that were small and/or had high pre-manipulation TP concentrations (i.e. small values of PC1; Table 6). These relations also tended to reinforce each other – higher intensity of fish removal had a stronger effect on the chlorophyll *a* concentration in lakes that were small and/or had high pre-manipulation TP concentrations (as shown by the sign of the interaction term between between PC1 and fish removal; Table 6), both during and after biomanipulation.

Table 5 Comparison of responsive and unresponsive lakes

	Responsive lakes (significant improvement)			Unresponsive lakes (no significant improvement)		
	Mean	95% C.I.	n	Mean	95% C.I.	n
Response: Secchi depth 1–3 years after manipulation (vs. before manipulation)						
Lake area (ha)	18	10 – 32	19	40	14 – 119	8
Mean depth (m)	1.7	1.3 – 2.2	19	1.8	1.3 – 2.5	8
Retention time (days)	171	63 – 461	11	409	221 – 754	5
Pre-manipulation TP (μg/l)	144	93 – 223	19	127	62 – 260	6
Mean atmospheric temperature (°C)	8.0	7.0 – 9.0	19	7.8	6.4 – 9.2	8
Duration of main manipulation (yr)	2.1	1.6 – 2.5	19	2.4	1.5 – 3.3	8
Fish removal (kg/ha)	233	160 – 338	18	251	198 – 317	7
Fish removal (kg/ha/yr)	124	84 – 183	18	119	70 – 203	7
Fish stock depletion (%)	56	37 – 76	13	40	17 – 62	5
Response: Chlorophyll *a* 1–3 years after manipulation (vs. before manipulation)						
Lake area (ha)	12	5 – 36	12	35	14 – 86	15
Mean depth (m)	1.3	1.1 – 1.6	11	1.8	1.4 – 2.4	15
Retention time (days)	78	22 – 275	4	210	103 – 428	9
Pre-manipulation TP (μg/l)	196	120 – 322	12	126	83 – 190	13
Mean atmospheric temperature (°C)	8.1	7.1 – 9.1	12	8.2	7.5 – 8.9	15
Duration of main manipulation (yr)	2.0	1.4 – 2.6	12	2.0	1.5 – 2.5	15
Fish removal (kg/ha)	250	149 – 420	11	272	184 – 403	12
Fish removal (kg/ha/yr)	137	74 – 252	11	140	98 – 202	12
Fish stock depletion (%)	78	56 – 99	7	58	42 – 75	12

Data are based on the selected dataset, with stocking-only interventions excluded. Lake areas, mean depths, retention times, pre-manipulation TP concentrations and fish removals were log-transformed before calculation of means and confidence intervals, and then back-transformed.

Lake characteristics, in terms of area and pre-manipulation TP, clearly influence the effect of biomanipulation on chlorophyll *a* concentration both during and after manipulation, as the model with fish removal alone had a Δ AICc > 20 (Table 6).

High intensity of fish removal also corresponded to greater increases in water transparency (measured as Secchi depth) during biomanipulation (Table 6). In contrast to chlorophyll *a* concentrations, Secchi depth changes during biomanipulation were not related to lake properties (as the best model included only the intensity of fish removal). Several models of water transparency after biomanipulation received similar level of support (Table 6). The most supported model included only lake properties (PC1), but the support for the null (intercept only) model was almost as high (Δ AICc = 1.15). The model with only fish removal also had a Δ AICc < 2, showing that Secchi depth after biomanipulation may be explained either by lake properties or intervention strength.

For the purposes of exploration and illustration, we also performed meta-regressions with single effect modifiers (see Figure 14 and Additional file 12). These showed the improvement of water-quality caused by biomanipulation to decrease with lake area and to increase with pre-manipulation TP concentration (although not significantly so for Secchi depth after manipulation). Moreover, the effect of biomanipulation on chlorophyll *a* decreased significantly with increasing retention time. We also found that biomanipulation effects on water quality increased with fish removals as expressed per hectare and year (significantly so for Secchi depth and chlorophyll *a* during but not after manipulation; see Figures 14 and 15) and with the depletion of fish stocks (but significantly so only for Secchi depth after manipulation; see Figures 14 and 16).

Using effect sizes based on mean log ratios instead of mean differences produces similar results, although relations between Secchi depth changes and effect modifiers tend to become more significant, whereas the reverse applies to chlorophyll *a* changes.

Tests for possible publication bias

Earlier reviews have found certain evidence of publication bias in the literature about biomanipulation effects – seemingly, negative results have not been reported to the same extent as positive experiences [8]. In this review, we tested our selection of studies for publication bias using funnel plots (see Additional file 13). These plots do indicate that studies that have high precision (i.e. low standard error, usually due to a large number of

Table 6 AICc model selection

Intercept	PC1	Fish removal	PC1 x Fish removal	AICc	Δ AICc
Chlorophyll *a* during manipulation					
+1	−1	−1	+1	245.06	0.00
+1	+1	−1		260.91	15.85
+1		−1		267.20	22.13
−1	+1			271.04	25.98
−1				283.14	38.07
Chlorophyll *a* 1–3 years after manipulation					
−1	−1	+1	+1	201.11	0.00
+1	+1	−1		216.44	15.33
−1	+1			223.51	22.41
+1		−1		223.87	22.76
−1				234.28	33.17
Secchi depth during manipulation					
−1		+1		24.70	0.00
−1	−1	+1		27.67	2.97
−1	+1	+1	−1	27.81	3.11
+1	−1			28.94	4.24
+1				31.26	6.56
Secchi depth 1–3 years after manipulation					
+1	−1			44.71	0.00
+1				45.87	1.15
−1		+1		46.11	1.39
+1	+1	−1	−1	46.98	2.26
+1	−1	+1		47.18	2.47

The explanatory variables included in each model are indicated by +1 or −1, which shows the sign of their effects. AICc values are given, and also the difference in AICc between each model and the model with the lowest AICc. Models are arranged according to AICc value. Data are based on the selected set of effect sizes, with stocking-only interventions excluded. The output of the most supported models is presented in Additional file 11.

observations) generally report effect sizes closer to zero than studies with lower precision. This asymmetry, which suggests the possibility of publication bias, is clearly visible when all studies in the review are considered, especially among Secchi depth data, but it also appears in the selected dataset.

Discussion

Our review and meta-analysis show that biomanipulation of lakes increases Secchi depth and decreases chlorophyll *a* concentration (Figure 8, Table 4). Nonetheless, there is considerable variability among lakes, which is discussed further below. Within this variability some significant patterns are evident: (1) The effects of biomanipulation are significant during and 1–3 years after treatment (Figures 9, 10 and 11). (2) Removal of planktivores and benthivores, with or without stocking of piscivores, is capable of improving water clarity, but piscivore stocking alone has no significant effect of that kind (Figure 13). (3) Lakes that do not respond to biomanipulation tend to have longer water residence times and lower percentage depletion of stocks of planktivorous and benthivorous fish (Table 5). There is also a tendency for non-responding lakes to be larger in surface area, although there is a wide range in lake area for responding and non-responding lakes. (4) Effects of biomanipulation on chlorophyll *a* are significantly stronger in cases where fish removal is more intense and where pre-manipulation TP is higher and/or the lake area smaller.

Cyanobacteria are of special interest in lake management because of their potential toxicity and their capacity to form noxious scums on the lake surface. The case studies that reported responses of cyanobacteria were fewer than those that reported Secchi depth or chlorophyll *a*. Nonetheless, we found that biomanipulation significantly decreased cyanobacteria concentrations for up to three years after treatment (Figure 12).

Our review improves in several ways on previous reviews of biomanipulation. We obtained all of the literature that was available on a range of literature databases and systematically screened for useful studies. As a result our analyses included a large number of case studies from many parts of the world. We used a consistent, repeatable process to screen published reports for inclusion in further analyses. We then analysed the data using standard methods of meta-analysis [39].

Several previous reviews have concluded that biomanipulation is successful under some conditions [7,11,16,29,30,45,46]. These reviews reach various conclusions about the factors that lead to success or failure of biomanipulations. Some of the variability among reviews may be explained by differences in datasets available at the times the papers were written, or differences in the process for selecting papers for review.

As noted in Table 7, our findings are consistent with the conclusion of a number of previous reviews that substantial fish removals are needed for successful biomanipulation [11,16,29]. According to our meta-analysis, removal of benthivores and planktivores (with or without stocking of piscivores) has significant effects on water quality effects. By contrast, and in line with conclusions by Søndergaard *et al.* [7], our findings also suggest that piscivore stocking alone does not affect water quality as measured by Secchi depth and chlorophyll *a*.

On the other hand, our findings on the importance of lake properties differ from conclusions of some previous reviews (Table 7). Several authors point out that biomanipulation is mainly successful in shallow and/or small lakes [30,46], while our results show that successful and failed biomanipulations have occurred in overlapping ranges of

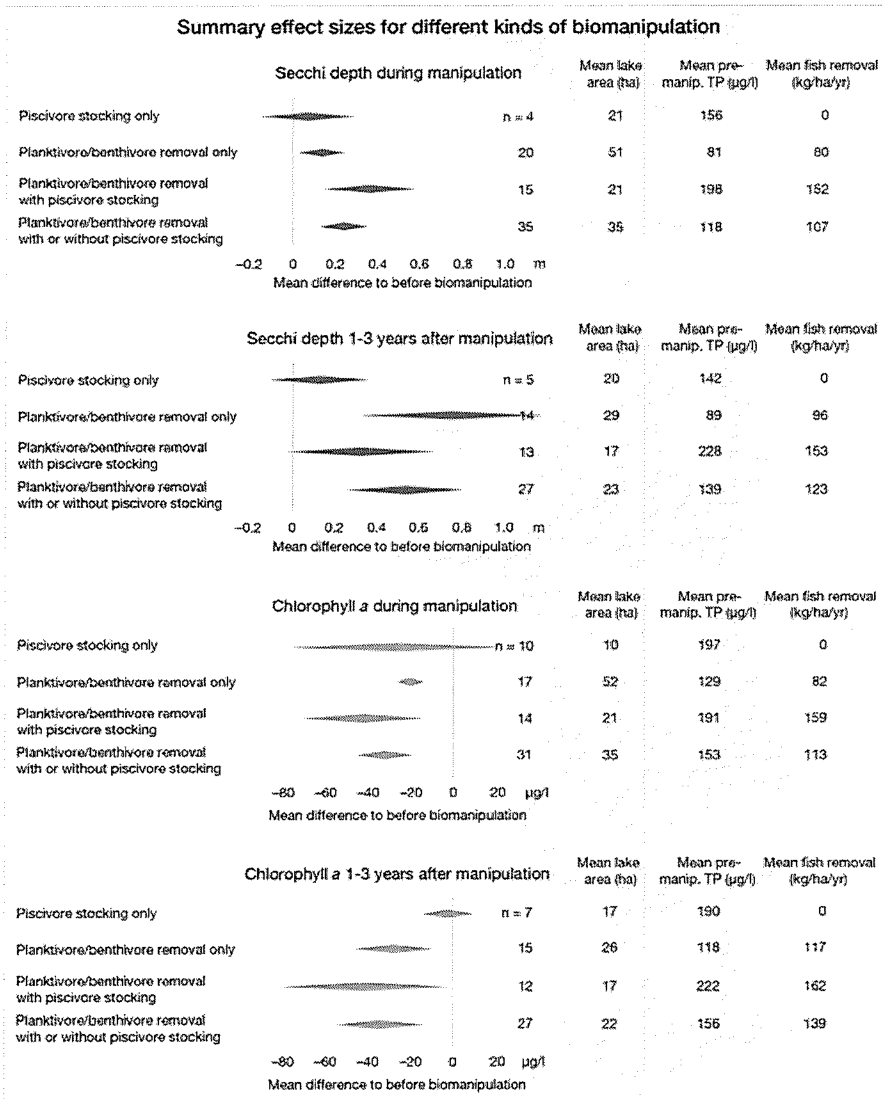

Figure 13 Summary effect sizes for biomanipulations based on piscivore stocking and/or planktivore/benthivore removal. The diamond-shaped symbols show means of Secchi depth and chlorophyll *a* data from the selected set (with 95% confidence intervals indicated by the widths of the symbols). In the bottom row of each panel, data presented in the second and third rows have been pooled. Forest plots showing all individual effect sizes are presented in Additional file 10 (pp. 24–27). Subgroup means of potential effect modifiers (lake area, pre-manipulation total phosphorus concentration (TP) and fish quantities removed per hectare and year) are shown at right. These data were log-transformed before the calculation of means, and then back-transformed.

lake mean depths and surface areas (Table 5, Figure 14). Nonetheless, we found that biomanipulation effect size declines with increasing lake area. We found that lakes with higher pre-manipulation TP respond more strongly to biomanipulation. Thus our findings do not support the conclusion that biomanipulation will not work if TP is too high [46].

Some of the studies included in this review reported on effects of biomanipulation that persisted even when the system would have been expected to return to initial conditions in the absence of alternative stable states [17,19]. The number of lakes with long-lasting biomanipulation effects was small, however (see next section), and data that would allow an analysis of mechanisms related to alternative stable states (such as the development of macrophytes over time) were lacking in most of these cases. We therefore refrain from attempting any such analysis in this report.

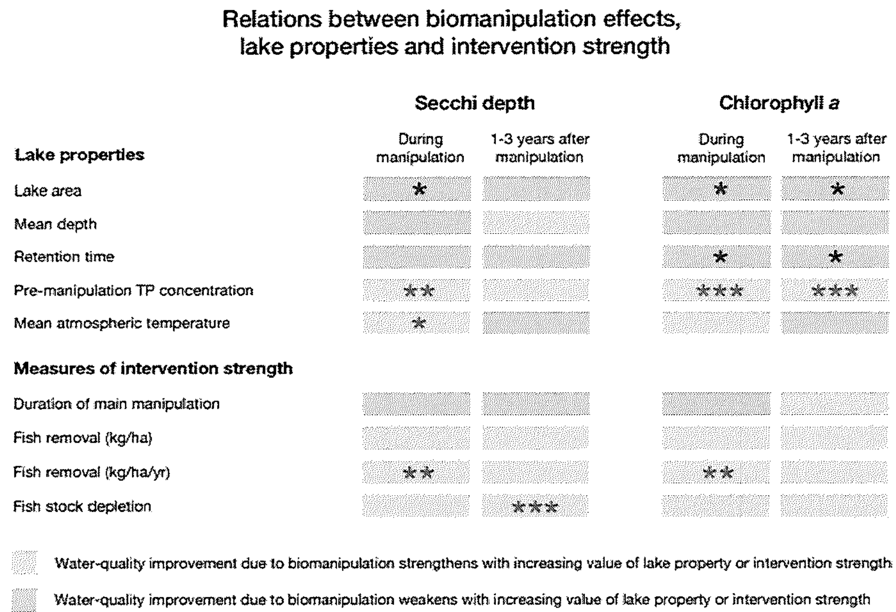

Figure 14 Relations between biomanipulation effects, lake properties and measures of intervention strength. Colours indicate whether changes of lake properties or intervention strength tend to strengthen or weaken the ability of biomanipulation to improve water quality (i.e. its ability to increase the Secchi depth or decrease the chlorophyll *a* concentration). Some of the meta-regressions summarised here are also presented in Additional file 12. The significance of the relations is indicated with one ($p < 0.05$), two ($p < 0.01$) or three ($p < 0.001$) asterisks. Lake areas, mean depths, retention times, pre-manipulation TP concentrations and fish removals were log-transformed. All analyses used the selected dataset with stocking-only biomanipulations excluded.

Reasons for heterogeneity

The variability among lakes in responses to biomanipulation has many dimensions, some of which can be illuminated using our dataset. It must be noted that no review of biomanipulation, including ours, has access to datasets in which important co-variates such as lake area, phosphorus loading, and magnitude of fish removal are statistically independent and sampled continuously from pre-manipulation until effect of the manipulation are no longer discernible. In the absence of such datasets, any evaluation of co-variate effects is provisional. Nonetheless, several statistically significant effects of co-variates should be discussed here.

Data quality appears to influence outcomes, especially the response of chlorophyll *a* (Figure 8). Therefore we focused on a high-quality 'selected' dataset that excludes studies based on a single datum per year and studies that confound biomanipulation with other types of manipulations.

Effects of biomanipulation are detectable statistically up to 3 years after the manipulation in the meta-analysis (Figures 9 and 10). Biomanipulation studies performed over longer periods are rare, however, and the variation of summary effect sizes increases as the number of lakes included in the meta-analyses goes down with the number of years elapsed after intervention (Figure 9). No statistically significant effect can therefore be found 4 years or more after biomanipulation, but the mean effect sizes show no obvious signs of diminishing even up to 7 years after intervention (Figure 9). In certain lakes the effects of biomanipulation last considerably longer, up to 10 or more years (Figure 11). Long-lasting effects were observed in deep stratified lakes (e.g. Mendota) as well as shallow well-mixed ones (e.g. Zwemlust). These results are in line with findings by Gulati and Van Donk [45] and Søndergaard *et al.* [7,16], which suggest that effects of biomanipulation can last up to 6–10 years but that water clarity eventually degrades in most cases.

Physical and chemical characteristics of lakes that affect biomanipulation success include lake area, water retention time, and pre-manipulation TP (Table 5, Figure 14). It is easier to remove large fractions of the benthivore and planktivore stocks from smaller lakes, which may be one reason why these tend to show stronger responses to biomanipulation. Lakes with longer retention times (i.e. slowly-flushed lakes) are less affected by biomanipulation, maybe because fish removal effects are counteracted by a higher degree of internal phosphorus loading. Lakes with high pre-manipulation TP show stronger responses to biomanipulation, especially when it comes to chlorophyll *a*. Initial chlorophyll concentrations are often very high in highly eutrophied lakes, which could mean that a large chlorophyll reduction (in absolute terms) is easier to achieve there than in less

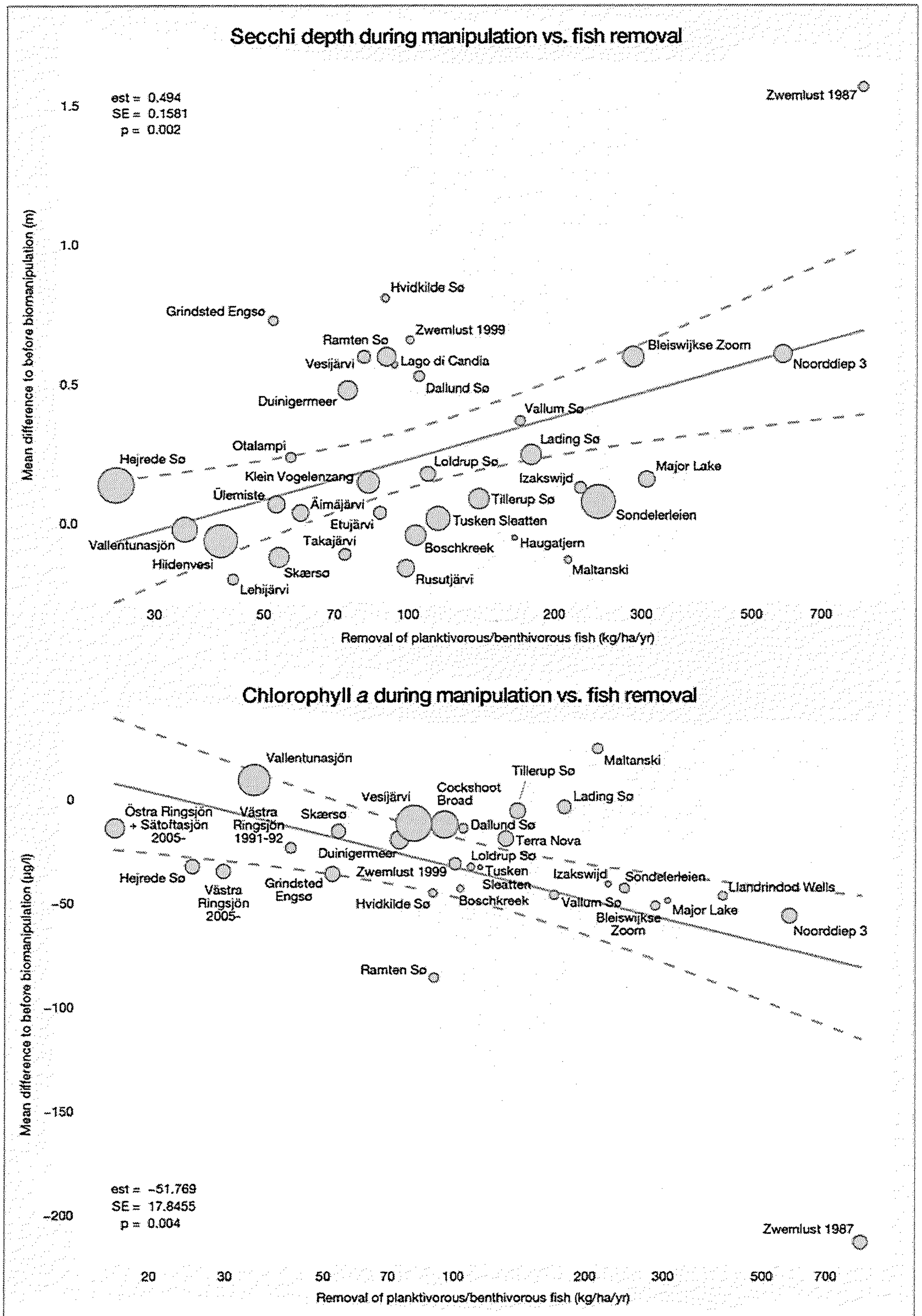

Figure 15 Meta-regressions of Secchi depth and chlorophyll *a* during manipulation vs. fish removal. Each symbol represents one biomanipulation. Symbol sizes indicate statistical weights based on inverse variances.

Table 7 Overview of conclusions in this and earlier reviews

Conclusions in earlier reviews	Ref.	Supported by this review
Planktivore/benthivore removal increases water transparency	[7,11,16,29]	Yes
Planktivore/benthivore removal decreases chlorophyll a	[7,11,16,29]	Yes
Planktivore/benthivore removal decreases cyanobacteria abundance	[16,29]	Yes
Increased planktivore/benthivore removal increases biomanipulation effects	[11,16,29]	Yes
Piscivore stocking is less efficient than planktivore/benthivore removal	[7,30]	Yes
Biomanipulation is more efficient in shallow lakes	[30,46]	No
Biomanipulation is more efficient in small lakes	[30]	Yes
Biomanipulation is less efficient in lakes with high pre-manipulation TP	[46]	No

eutrophic lakes with lower pre-manipulation chlorophyll levels. These speculations are interesting topics for future research but cannot be resolved here.

Intervention strength has variable but detectable effects on the response of lakes to biomanipulation (Table 5, Figures 14, 15 and 16). The high variance of fish population estimates may be a factor in the statistical analyses. Uncertainty in the x-axis will decrease the slope of a regression, for example (e.g. Figures 15 and 16). Nonetheless, there may be real effects of intervention strength as also noted in some earlier review papers [11,16,29,30]. Lake Zwemlust is an important case study in this regard. Removals of benthivores and planktivores from Zwemlust in 1987 were exceptionally high, and the response to biomanipulation was also large (Figure 15). As noted above, water quality improvements lasted for an exceptionally long time in Zwemlust.

Chlorophyll *a* and Secchi depth are widely-used measures of water quality. Secchi depth is largely determined by chlorophyll *a*, which is a proxy for phytoplankton abundance. The two variables are inversely related, but the correlation is never perfect. At a given chlorophyll *a* concentration, the Secchi depth can be higher or lower depending on the concentration of coloured dissolved organic matter, the concentration of inorganic particles suspended in the water, or the particle size distribution of phytoplankton. Therefore we should not expect to obtain completely consistent results for chlorophyll *a* and Secchi depth responses to biomanipulation. It is worthwhile to examine both indicators.

Review limitations

We were unable to analyse every aspect of biomanipulation due to limitations of the available data. For example, we were not able to evaluate relations between biomanipulation and biodiversity. Nonetheless it is clear that certain species, such as rooted submerged plants and large-bodied cladocerans such as *Daphnia*, play a critical role in many

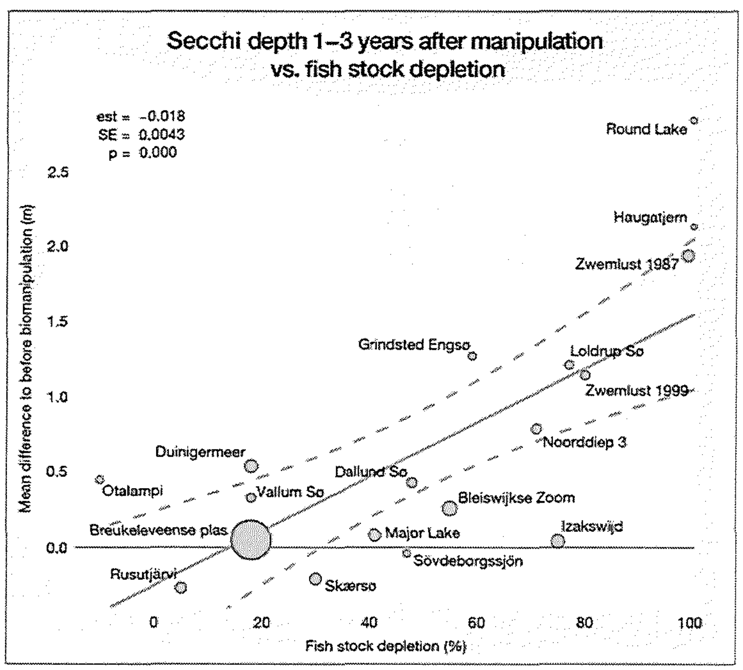

Figure 16 Meta-regression of Secchi depth 1–3 years after manipulation vs. fish stock depletion. Each symbol represents one biomanipulation. Symbol sizes indicate statistical weights based on inverse variances.

successful biomanipulations. Moreover, the dataset did not allow us to explore the outcomes of piscivore stocking in relation to the species or sizes of stocked fish, although this could have refined our overall conclusion that piscivore stocking alone has no impact on water clarity.

Of the 128 biomanipulations included in this review, more than half (68) were carried out in Denmark or the Netherlands, where most lakes are small, shallow and nutrient-rich. The median area, depth and pre-manipulation TP of the included Danish and Dutch lakes were 23 ha, 1.5 m and 162 μg/l, respectively, whereas the corresponding medians for included lakes in other parts of the world were 78 ha, 2.7 m and 86 μg/l, respectively. This means that the selection of lakes in this review may not be entirely representative of e.g. Swedish, Finnish, Norwegian or North American lakes where biomanipulation has been carried out or could be considered as a future option.

Conclusions

Implication for policy/management

Available evidence suggests that biomanipulation is a useful means of improving water quality in eutrophic lakes. Removal of benthivorous and planktivorous fishes (with or without stocking of piscivores) is effective, but piscivore stocking alone is not. More thorough removal of benthivorous and planktivorous fishes increases the effectiveness of biomanipulation in reducing chlorophyll *a* concentrations. Biomanipulation tends to be particularly successful in relatively small lakes with short retention times and high pre-manipulation phosphorus levels.

Since long-lasting studies are rare, it is difficult to draw conclusions regarding biomanipulation effects more than three years after intervention, but the duration of the effects clearly varies from case to case. In many cases re-treatment is necessary after a few years, but sometimes effects may last a decade or more.

Implication for research

Our review and meta-analysis uncovered several patterns worthy of further research. More research on the interactive effects of biomanipulation with other lake management tools would be useful and could reveal beneficial combinations of management interventions. The factors that lead to breakdown or persistence of biomanipulation effects in various types of lakes are not yet known. Better understanding could improve ecological theories related to stability and perhaps reveal new information useful for managers.

Our screening process excluded many biomanipulations that could have been analysed had authors provided appropriate data in their original publications. Researchers reporting on the outcomes of such interventions should always publish variances and sample sizes of water quality data, or provide raw data in an electronic appendix. The effects of biomanipulation cannot be assessed properly unless water quality data have been obtained prior to the intervention. Monitoring of water quality should also be continued for at least as long as effects remain evident. Quantitative measures of fish removal, stocking, or biomass changes are necessary and should always be reported.

Additional files

Additional file 1: Literature searches.
Additional file 2: Articles not used in the review.
Additional file 3: Lakes excluded on the basis of quality assessment.
Additional file 4: Correlations between potential effect modifiers.
Additional file 5: PCA diagrams.
Additional file 6: Reasons for article exclusions.
Additional file 7: Narrative tables.
Additional file 8: Sources of articles used for data extraction.
Additional file 9: Locations of included lakes.
Additional file 10: Forest plots.
Additional file 11: Output of the models most supported by AICc.
Additional file 12: Meta-regressions with single effect modifiers.
Additional file 13: Funnel plots.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
The team that was appointed by the Mistra Council for Evidence-Based Environmental Management to carry out this review consisted of CL, SRC, AG, PL, LP, CS, EVD. JDMS contributed by performing meta-analyses. All authors participated in the drafting, revision and approval of the manuscript.

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