MNDNR

INVESTIGATION OF TREMATODES AND FAUCET SNAILS RESPONSIBLE FOR LESSER SCAUP DIE-OFFS

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SUMMARY OF FINDINGS

The spring of 2013 was very late, with lakes being ice-covered when migrating lesser scaup (*Aythya affinis*) arrived, forcing the birds onto rivers for open water. Ice-off on Winnibigoshish occurred after scaup departed, but the edges were opening and available to the birds just before their departure the second week of May. We were able to access Winnibigoshish from resorts on the Mississippi River, but could not access Bowstring or Round lakes while the birds were here. Five lesser scaup were suspected to have trematodiasis at Winnibigoshish in the spring of 2013, but the birds could not be captured for confirmation.

During the fall of 2013, few birds were suspected of trematodiasis at Winnibigoshish, Bowstring, and Round lakes. Five birds were collected from Winnibigoshish and confirmed to have had trematodiasis. The number of sick and dying birds in 2013 was very low this year but was not due to a lack of use by migrating scaup.

We sampled faucet snails at all sites where they were known to occur in interior Minnesota; Lake Winnibigoshish, Upper and Lower Twin lakes, the Shell River, First Crow Wing Lake, the Crow Wing River, Second Crow Wing Lake, Bowstring Lake and several ponds on the White Earth Nation. We also sampled Round Lake for faucet snails, because it is known to be important to migrating lesser scaup and sick birds have been previously reported here.

We are currently analyzing data. A final report will be prepared in September.

INTRODUCTION

During the autumns of 2007 and 2008, thousands of lesser scaup and hundreds of American coots died on Lake Winnibigoshish in north-central Minnesota. These deaths were attributed to trematodiasis caused by non-native intestinal trematodes (*Cyathocotyle bushiensis*, *Sphaeridiotrema spp.,* and *Leyogonimus polyoon)* and concerned both waterfowl hunters and non-consumptive users.

The trematode species responsible for the die-offs have a complex life cycle that involves two intermediate hosts. The faucet snail (*Bithynia tentaculata*), a non-native species from Europe (Sauer et al. 2007), is the only known first intermediate host of these trematodes in the Midwest and also serves as the second host for *C. bushiensis* and *Sphaeridiotrema spp.* The second host of *L. polyoon* is one of a variety of larval aquatic insects, including damselflies (Zygoptera) and dragonflies (Odonata) (US Geological Survey, National Wildlife Health Center (NWHC), unpubl. data). Adult trematodes develop in waterfowl after they consume infected snails and in American coots (*Fulica americana*) and common moorhens (*Gallinula chloropus*) after consumption of infected insects. Parasite eggs are then defecated by sick birds and later ingested by snails, continuing the cycle. Because of this complex life cycle, the dynamics of faucet snail distribution and transmission of these parasites to lesser scaup and other birds are poorly understood.

The first U.S. detection of the faucet snail was in Lake Michigan in 1871 (Mills et al. 1993). It has since been documented in the mid-Atlantic states, the Great Lakes Region, and

Montana, and undoubtedly will continue to spread (Sauer et al. 2007). In 2002, the faucet snail was detected in the Upper Mississippi River. Since then, trematodiasis has killed an estimated 52,000-65,000 waterbirds, primarily lesser scaup and American coots, but also dabbling ducks such as blue-winged teal (*Anas discors*), Northern shoveler (*Anas clypeata*), mallard (*Anas platyrhynchos*), American black Duck (*Anas rubripes*), and Northern pintail (*Anas acuta*); diving ducks such as ring-necked ducks (*Aythya collaris*) and redheads (*Aythya americana*); and other waterfowl such as ruddy ducks (*Oxyura jamaicensis*), buffleheads (*Bucephala albeola*), and tundra swans (*Cygnus columbianus,* R. Cole, NWHC, pers. comm.).

The faucet snail was detected in Lake Winnibigoshish in the spring of 2008, following the loss of 7,000 Lesser Scaup and a few hundred coots to trematodiasis the previous fall (Lawrence et al. 2008). In 2008, 2,000 more birds died (Lawrence et al. 2009). The severity of the outbreaks seems to have lessened in Lake Winnibigoshish over time. This may be because fewer birds are stopping over on the lake during migration or there may be another explanation related to the disease cycle. In any event, these outbreaks are highly visible and attract the media, which can spur public concern and a desire for action.

In recent years, new areas have been designated as infested with faucet snails in north central Minnesota. The faucet snail was first detected in Upper and Lower Twin lakes and the Shell River in 2009. In 2010, the Crow Wing River was designated as infested with faucet snails, and in 2011, First Crow Wing Lake and Second Crow Wing Lake were added to the list of waters infested with faucet snails. In 2012, several new ponds were designated as infested on the White Earth Nation. These newly designated sites may afford us additional opportunities to learn about this disease cycle.

We examined the factors associated with faucet snail abundance and distribution, parasite prevalence within snails, and the influence of snail densities and site attributes (e.g., water depth, distance from shore, substrate composition) on lesser scaup foraging. For example, depth influences the amount of work that scaup have to do against buoyancy. Shallow depths are thus important to foraging scaup (Jones and Drobney 1986, Mitchell 1992). If such depths are also preferred by faucet snails, then the potential for exposure will be much higher than if snails prefer dissimilar water depths. The profitability of food items will vary as a function of depth, density, and prey type among other things (Lovvorn and Jones 1991, Lovvorn et al. 1991, Beauchamp et al. 1992, de Leeuw and van Eerden 1992, Lovvorn 1994).

OBJECTIVES

1- Improve understanding of lesser scaup foraging as it relates to faucet snail and other food source distribution and density, including water depth, distance from shore, and substrate composition
2- Examine factors (e.g., temperature, substrate, vegetation, other snail species) that are associated with the distribution and movement of faucet snails
3- Examine the factors that influence the prevalence of the parasites in faucet snails (e.g., snail density, temperature, microhabitat, time of year)
4- Examine how faucet snail distribution varies during spring, summer, and fall

METHODS

During 2013, we sampled faucet snails at the same locations sampled in 2012 (Roy 2013). We sampled during spring, summer, and fall at the same points within a lake or river (Table 1a,b). In small lakes (<405 ha), we used transects that traversed the entire length of the lake and across a range of depths. In large lakes, we used index areas with points stratified by depth for sampling. In Lake Winnibigoshish, we had 2 index areas, the West Winni Index Area and the East Winni Index Area, which were 5-6 km along the longest dimension and approximately 2 km in width. In rivers, we sampled points at regular intervals (500 m) along the infested corridor for a maximum length of 10 km. In small ponds, we placed sample points ~100 m apart in such a way as to attempt to maximize the number of sampling locations in each pond (diameter 75-320 m).

We used 2 sampling methods; we used a bottomless sampling cylinder (0.2 m^2) at 30 and 60 cm depths for comparisons with an ongoing study on the Upper Mississippi River, and we also sampled with a benthic sled to standardize our protocol for all depths. We dragged the sled a distance of 1.2 m at deeper depths to examine how snail distribution varied within a water body. We collected data on microhabitat variables at each point to examine relationships to snail distribution, the snail community, and parasite prevalence. These included substrate (e.g., silt, rock, sand, vegetated, mud), temperature (C^o), water depth (cm), and a secchi depth (cm) reading was taken 8 times (4 times on the way down and 4 times on the way up) from the shaded side of the boat and averaged. At each snail collection site, we determined pH, dissolved oxygen (mg/L), conductivity (µS/cm), and salinity ($^o/_{oo}$) with a Hach Company (Loveland, Colorado) HQd portable meter that was calibrated daily for pH and weekly for conductivity. Flow (mps) was measured at 60% of the total depth (from the surface) with a Global Water Instrumentation (Gold River, California) flow probe when flow was detectable and averaged over a 40 s interval (the USGS "6 tens method").

Invertebrate samples were stored in the refrigerator until processed. We used a magnifying lens and microscope as needed to identify all invertebrates to Order and noted their presence in each sample. We identified all snails to genus and counted their numbers in each sample. We determined the size of *B. tentaculata* and similarly sized *Amnicola* spp. with calipers, as measured along the central axis from the apex. Parasite prevalence was determined for all samples possessing at least 50 *B. tentaculata* (R. Cole, NWHC, unpubl. data). For samples possessing 10-49 *B. tentaculata,* we collected additional snails while in the field from the same location at the same time to increase the number of samples for which we could do prevalence. These additional snails were not used in the determination of snail abundance at the site. Trematode stages (cercariae or metacercariae), species (*C. bushiensis, Sphaeridiotrema spp., L. polyoon*), and numbers were also recorded in the lab.

Each season, we collected a water sample at each sample pond, lake, or river and sent it to the Minnesota Department of Agriculture for analysis. Total phosphorus (ppm), nitrite plus nitrate nitrogen (ppm), chlorophyll a (ppb), total alkalinity (ppm), ammonia nitrogen (ppm), and calcium (ppm) were quantified.

We also attempted to identify sites where lesser scaup foraged and collected benthic samples at these locations. These sites were identified through observations of birds from shore or from a boat. We determined the location of rafts of scaup using a compass from 2-3 observation points, which was plotted in ArcMap version 10 (Environmental Systems Research Institute, Inc., Redlands, California) to determine the area occupied by the birds. We then placed a transect through this area and sampled at 100 m intervals. Food densities, water depths, distance from shore, lake size, and substrate composition at these foraging locations were recorded using the same techniques as snail sampling.

We also collected scaup carcasses during die-offs at study lakes for confirmation of trematodiasis by the NWHC in Madison, Wisconsin. Additionally, Bowstring and Round lakes are known for having large number of scaup, particularly in the fall, and have been the sites of trematodiasis die-offs in the past. We monitored Bowstring and Round lakes for scaup die-offs during the fall only, because we were unable to access the lakes in the spring due to ice-cover. Staff from the Minnesota Department of Natural Resources-Grand Rapids office also made regular visits to Winnibigoshish, Round, and Bowstring lakes throughout the fall season to check for sick birds. Scaup sightings at focal lakes during DNR Fall Waterfowl Migration Surveys were also noted.

RESULTS

Faucet snails

We detected faucet snails at both index areas on Lake Winnibigoshish, Upper and Lower Twin lakes, the Shell River, First Crow Wing Lake, Crow Wing River, Bowstring Lake, and the White Earth Ponds (Tables 1a,b).

Trematodes

Both *C. bushiensis* and *Sphaeridiotrema spp.* were detected on Lake Winnibigoshish, Lower Twin Lake, the Shell River, First Crow Wing Lake, the Crow Wing River, and the White Earth ponds. Samples from Bowstring and Upper Twin lakes did not include sufficient numbers of faucet snails to determine prevalence and intensity of infection this year. *Sphaeridiotrema spp*. has been detected at Upper Twin Lake in previous years of this study. Samples from Second Crow Wing Lake contained *C. bushiensis* only, but few samples contained faucet snails at this location. Prevalence (proportion of snails infected) of *C. bushiensis* was generally higher than that of *Sphaeridiotrema spp.* within a water body. Prevalence of *C. bushiensis* was generally highest at Winnibigoshish, Shell River, and the White Earth ponds. Prevalence of *Sphaeridiotrema spp.* was highest at West Winni Index Area and the Shell River. The intensity (number of parasites in infected snails) of parasite infections was also very high at these locations.

Scaup

The spring of 2013 was very late, with lakes being ice-covered when migrating lesser scaup (*Aythya affinis*) arrived, forcing the birds onto rivers for open water. Ice-off on Winnibigoshish occurred after scaup departed, but the edges were opening and available to the birds just before their departure the second week of May. Five lesser scaup were suspected to have trematodiasis at Winnibigoshish in the spring of 2013, but the birds could not be captured for confirmation (Table 2). We were unable to monitor Bowstring and Round lakes in the spring of 2013 because the boat accesses were iced-up.

During the fall of 2013, few lesser scaup were suspected of trematodiasis at each of Winnibigoshish, Bowstring, and Round lakes. Five lesser scaup were collected from Winnibigoshish and confirmed to have had trematodiasis by the National Wildlife Health Center. An American coot was collected from Upper Twin Lake and also confirmed to have died of trematodiasis. The number of sick and dying birds in 2013 was very low this year and was not due to a lack of use by migrating scaup (Table 2).

DISCUSSION

This report summarizes activities for the third year of field work (spring, summer and fall 2013). Fall 2010, a pilot season, and the 2011 and 2012 field seasons were included in earlier reports. Data entry and analysis are preliminary and still underway. A final report will be prepared in September for the funding agency, with publications to follow in peer-reviewed journals.

LITERATURE CITED

Beauchamp, G., M. Guillemette, and R. Ydenberg. 1992. Prey selection while diving in common eiders, *Somateria mollissima*. Animal Behaviour 44:417-426.

de Leeuw, J. J., and M. R. van Eerden. 1992. Size selection in diving tufted ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. Ardea 80:353-362.

Jones, J. J., and R. D. Drobney. 1986. Winter feeding ecology of scaup and common goldeneye in Michigan. Journal of Wildlife Management 50:446-452.

Lawrence, J. S., S. D. Cordts, R. A. Cole, and P. Loegering. 2008. Determining gastropod hosts of trematodes and monitoring lesser scaup and coot mortality in north central Minnesota. Unpublished Phase 1 Proposal, Minnesota Department of Natural Resources, Wildlife Research.

Lawrence, J. S., P. Loegering, R. A. Cole, and S. D. Cordts. 2009. Scaup and coot die-off at Lake Winnibigoshish-2008 Update. Minnesota Department of Natural Resources, Section of Wildlife, unpublished report, Minnesota Department of Natural Resources, Wildlife Research.

Lovvorn, J. R., and D. R. Jones. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks. Canadian Journal of Zoology 69:2879-2887.

Lovvorn, J. R., D. R. Jones, and R. W. Blake. 1991. Mechanics of underwater locomotion in diving ducks: Drag, buoyancy and acceleration in a size gradient of species. Journal of Experimental Biology 159:89-108.

Lovvorn, J. R. 1994. Biomechanics and foraging profitability: An approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 279/280:223-233.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Seacor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19(1):1–54.

Mitchell, C. A. 1992. Water depth predicts Redhead distribution in the Lower Laguna Madre, Texas. Wildlife Society Bulletin 20:420-424.

Roy, C. 2013. Investigation of trematodes and faucet snails responsible for lesser scaup die-offs. Summaries of Wildlife Research Findings 2012, Minnesota Department of Natural Resources, http://www.dnr.state.mn.us/publications/wildlife/index.html.

Sauer, J.S., R. A. Cole, and J. M. Nissen. 2007. Finding the exotic faucet snail (*Bithynia tentaculata*): Investigation of water bird die-offs on the Upper Mississippi River National Wildlife and Fish Refuge. U.S. Geological Survey Open-File Report 2007–1065, 3 p.

Table 1a. Regular sampling sites for faucet snails in infested northern Minnesota water bodies during spring, summer, and fall 2013. Number of points refers to the number of points sampled each season of sampling.

Location	**No. seasons sampled**	**No. sample points**	**Faucet snails detected**
East Winnibigoshish Index Area	3	80	Yes
West Winnibigoshish Index Area	3	80	Yes
Upper Twin Lake	3	24	Yes
Lower Twin Lake	3	39	Yes
First Crow Wing Lake	3	37	Yes
Second Crow Wing Lake	3	18	Yes
Crow Wing River	3	18	Yes
White Earth Ponds	3	24	Yes
Shell River	3	22	Yes
Total		1026	

Table 1b. Sampling sites for faucet snails associated with lesser scaup in northern Minnesota water bodies during spring and fall 2013. Number of points refers to the number of points sampled each season of sampling.

Location	**Season sampled**	**No. sample points**	**Faucet snails detected**
Lake Winnibigoshish	Spring	9	Yes
Bowstring Lake	Fall	7	Yes
Round Lake	Fall	7	No
Total		23	

Table 2. Reports of scaup observed by Minnesota Department of Natural Resources staff on lakes in northern Minnesota during spring and fall 2013. Scaup that failed to escape approach or had drooping heads were considered to be sick; dead birds were typically found along the shoreline.

Location	Date	Total no. of scaup observed	No. of sick or dead scaup observed
SPRING			
Mississippi River near west Winnibigoshish	4/29/13	100	None
Mississippi River near west Winnibigoshish	5/3/13	330	None
Mississippi River near west Winnibigoshish	5/6/13	585	~5 suspect[a]
Dam on Winnibigoshish	5/8/13	168	None[a]
Winnibigoshish	5/16/13	0	0
FALL			
Kenogama	10/8/13	200	Lake not infested, from flight[b]
Twin Lakes	10/16/13	350 coot	1 dead coot[c]
Round	10/18/13	1,450	None
Bowstring	10/18/13	3,000	Sick hen scaup[a]
Bowstring	10/28/13	2,000	7 suspect[d]
Round	10/28/13	2,000-5,000	One sick hen scaup[d]
Winnibigoshish	10/29/13	600-800 coot	Two dead scaup, 5 dead coot[d]
Winnibigoshish	10/29/13	1,000	Determined from flight[b]
Bowstring	11/2/13	8,700	None[a]
Round	11/2/13	4,100	None[a]
Bowstring	11/5/13	3,100	Sick birds noted[d]
Round	11/5/13	3,000-4,000	None[d]
Winnibigoshish	11/7/13	100-200	2 sick, 5 dead, other sick birds noted[c,d]
Bowstring	11/7/13	2,600	None[a]
Winnibigoshish	11/14/13	3	None, but hunters left 3 dead scaup on DNR vehicles[d]
Round	11/15/13	Frozen	None
Bowstring	11/15/13	200	2 sick, unable to fly

[a]Benthic samples collected below scaup.
[b]From flight during DNR Waterfowl Migrations Surveys.
[c]Collected and sent to the National Wildlife Health Center to be tested. Trematodiasis confirmed.
[d]Reported by Grand Rapids Area Wildife staff.

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SHALLOW LAKES: ASSESSING QUALITY AND PREDICTING FUTURE CHANGE

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SUMMARY OF PROPOSAL

Lake managers face unprecedented challenges to surface and groundwater quality. Minnesota's 4000 shallow lakes are especially vulnerable to degradation because they often occur in close proximity to intensive agriculture, they are highly interconnected allowing nutrient/chemical inputs and exchange of aquatic species, and because they can quickly transition from clear-water to turbid-water conditions with accompanying poor water quality. Future conservation and management practices for shallow lakes will require special attention as resource managers respond to increasing pressures from agriculture, shoreland development, expanding drainage networks, invasive species, and changing precipitation and temperature patterns. With the recent advent of dedicated funding through the Outdoor Heritage Account, funds are available for shallow lake management, but tools are needed to help prioritize management projects. Prior DNR-and LCCMR-funded studies and other research have identified factors associated with deterioration of water quality, wildlife habitat, and ecological characteristics of Minnesota shallow lakes. Our goal is to use this information to develop a modeling framework that links shallow lake quality to specific drivers of shallow lake condition, including characteristics of individual lakes and features of lake watersheds, along with future changes that may result from increased shoreland development, climate transitions, and other factors.

Previous research has identified important associations between fish, plants, nutrients, and shallow lake quality. Yet, ecological theory suggests that shallow lakes are dynamical systems, and that simple statistical models of associations may not be sufficient for predicting lake condition or for guiding management decisions. Rapid shifts from clear- to turbid-water conditions (or regimes) reflect complex non-linear relationships between predictors and water quality, with multiple interactions among key variables likely to be the norm. Further, thresholds that describe transitions away from clear-water states may vary regionally and conditions that describe transitions from turbid- back to clear-water regimes may differ from those favoring opposite shifts. We propose to develop a data- and model-based framework to guide decisions and management strategies for shallow lakes in Minnesota. This effort will use existing operational resources within the Shallow Lakes Program (DNR Wildlife), build on previous research done by DNR Fish and Wildlife staff and collaborators, and extend our current knowledge regarding the consequences of present and future conditions for shallow lakes in Minnesota. Our broad project goal is development of a modeling context for predicting future shallow lake conditions in Minnesota's changing landscapes which will be useful for managers as they try to identify where to invest existing and newly available resources.

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INTRODUCTION

Minnesota has approximately 4,000 lakes characterized by mean depth $\leq$ 15 ft and surface area > 50 acres (Nicole Hansel-Welch, personal comm.) and many thousands of smaller waters technically classified as large "prairie wetlands" yet functionally indistinguishable from the larger analogues. These shallow lakes are an international resource, providing critical waterfowl habitat and ecological benefits within Minnesota and the Mississippi Flyway. Currently, only about 48 of these lakes (> 50 acres) are formally designated for wildlife management, yet many others are focus areas for lake rehabilitation and other habitat and conservation practices. Motivated by concerns over shallow lake water quality, seasonal duck abundance and habitat use, and hunter satisfaction, MN DNR recently proposed a collaborative plan to Recover Ducks, Wetlands, and Shallow Lakes (http://files.dnr.state.mn.us/outdooractivities/hunting/waterfowl/duck_plan_highlights.pdf), with a future goal of rehabilitating 1,800 shallow lakes in Minnesota. Lake rehabilitation efforts are logistically difficult, extremely costly, and time consuming. In addition, lake responses are sometimes disappointing and usually short-lived (< 5-10 years, for example see Hobbs et al. 2012). Conservation planning for shallow lakes will require improved tools that managers can apply to many questions such as the following: Which management actions have the highest probabilities of improving lakes in a given region (inducing shifts to a clear state)? Which lakes within a given area have highest rehabilitation potential? What are the specific management actions that optimize the chances for successful rehabilitation given features of an individual lake in a particular watershed? Managers would also benefit from planning tools that can identify management actions that are likely to increase stability or resilience to change in shallow lakes presently in the clear regime, as well which clear lakes that might be candidates for ongoing management efforts. Anecdotal evidence indicates that it is far less costly to preserve clear-regime lakes with high water quality than to respond to deteriorated conditions once they develop, and tools we describe here should help managers develop such forward-looking approaches.

Unfortunately, data on typical baseline conditions and regional variability are not always available, especially for northern Minnesota lakes. Managers are often unsure of the current shallow lake status and whether ecological characteristics of these areas may be limiting use by waterfowl and other wildlife. Despite major advances in shallow lake monitoring, inventory, and research, managers still receive little guidance for improving condition of shallow lakes on a regional scale, or for predicting consequences of future changes such as decreasing CRP, increased drainage, accelerated shoreland development, and other anthropogenic influences in these areas.

Ecological characteristics of shallow lakes, along with their suitability for ducks and other wildlife, result from influences of climate, hydrology, and in-lake biological processes operating simultaneously at multiple scales. Lakes may respond to factors operating at considerable distance from affected basins, and lake responses to these influences probably vary regionally and throughout the state. Ecologists have shown that prairie wetlands (and "shallow lakes") are strongly influenced by gradients of hydrology (or hydrogeomorphic setting) and climate (especially precipitation) (Euliss et al. 2004). Yet within these boundaries biological interactions in a given lake, especially those resulting from planktivorous and benthivorous fish communities, also exert major structuring influences on lake communities and characteristics of shallow lakes (Hanson et al. 2005). Previous research in Minnesota and elsewhere indicates that water clarity and quality in shallow lakes often differs dramatically in response to fish presence, density, and community structure in these sites. Fish - especially planktivorous and benthivorous species such as fathead minnows and black bullheads - influence invertebrate community structure, nutrient dynamics, water transparency, and other lake features in Minnesota's Prairie Pothole Region (PPR) and elsewhere (Bendell and McNicol 1987; Hanson and Riggs 1995, Zimmer et al. 2000, 2001 and many others). Recent work shows that fish presence in shallow lakes has greater influence on major groups of aquatic invertebrates than does abundance or taxonomic composition of fish communities (Hanson et al. 2012). Herwig et al. (2010) recently showed that surface connectivity among lakes, rivers, and other waters is a major determinant of fish presence in shallow Minnesota lakes. Along with influences of fish on aquatic communities, this illustrates potential consequences of increased ditching, flooding, and factors influencing surface water connections among shallow lakes, and points toward importance of managing both site- and landscape-scale factors for maintaining and improving quality of shallow lakes.

Shallow lakes are distinct from their deeper counterparts because limited average depth allows greater light penetration to the substrate over most of these basins. With relatively clear water, these lakes often "fill" with lush stands of submerged vascular macrophytes (SAV), contributing to further reductions in turbidity, lower water-column nutrient levels, lower phytoplankton biomass, and favorable conditions for waterfowl and other wildlife (Moss et al. 1996, Scheffer 2004, Moss et al. 2013). Healthy SAV communities may be the most ubiquitous goal of shallow lake management worldwide (Moss et al. 1996, Scheffer 2004), pointing to the central role of these plant communities in maintaining high water quality and wildlife suitability in these sites.

Ecologists have proposed conceptual models to explain dynamics in which shallow lakes alternate between two alternative conditions, either clear-water (macrophyte- dominated) or turbid-water (phytoplankton-dominated) regimes (Scheffer and Carpenter 2003, Scheffer 2004). These shifts are known for shallow lakes world-wide and have been specifically shown to occur in Minnesota lakes (Hanson and Butler 1994; Zimmer et al. 2001; Zimmer et al. 2009). Here and elsewhere, shallow lake management activities usually strive to achieve and maintain clear-water regimes, and stable clear-water conditions with abundant SAV are usually the goal of lake rehabilitation projects.

A major goal of our previous shallow lake studies was to develop conceptual and empirical models linking watershed and site-level features to ecological characteristics of shallow lakes. An overarching finding of the prior work was that regional gradients were major sources of variance in characteristics of shallow Minnesota lakes. Regional differences in nutrient levels are most obvious, yet extent of surface-water connectivity, fish community composition, dissolved organic matter and other processes may also vary consistently among ECS regions in Minnesota and may affect lake-regime responses. For example, we know that combinations of increased benthivorous fish mass and/or decreased abundance of submerged macrophytes will often induce regime shifts in shallow lakes, and these changes probably portend shifts to turbid-water states. However, we speculate that increased fish mass is much less likely to induce turbid-states in north-central Minnesota lakes, and turbid states may not even be possible in northern lakes where low ambient nutrient levels prevail. Additional data synthesis is needed to document extent and patterns of regional variation in occurrence and frequency of turbid regimes in shallow lakes, and to assess how regime dynamics respond to key influences such as surface connectivity, fish community characteristics, stability of phytoplankton- and macrophyte-dominated states, and proportion of lakes in clear- vs. turbid-water states.

Models for quantifying transient, nonlinear transitions in response to major drivers have been developed for grasslands and other ecosystems, but rarely for shallow lakes, despite the fact that these approaches seem to hold great promise as forecasting tools for managers who need frameworks for relating present and future changes to quality of shallow lakes. We believe understanding of lake-regime dynamics, data availability, and analytical methods has reached a point where the modeling framework we propose is possible and it would improve understanding of factors associated with shallow quality. Such a model framework would provide a useful conceptual and practical tool for lake managers in Minnesota and elsewhere.

GOALS AND WORKING HYPOTHESES

Our overall project goal is two-fold; the first is hypothesis oriented, but the second is mostly predictive. Based on results of previous studies, we have already constructed environmental variable models testing various hypotheses about factors that influence shallow lake communities and characteristics. In a sense, the proposed effort extends this hypothesis testing, but also refines earlier efforts to solidify the basis for the second modeling framework described below. Broadly, we have two objectives. First, we propose to test region-specific hypotheses using models relating shallow lake regime dynamics to fundamental drivers, these being environmental variables responsible for variation in lake characteristics in Minnesota (and elsewhere depending on data availability). For example, we hypothesize that seasonal temperature patterns, increased sedimentation and nutrient levels, fish abundance and community type, loss of grass cover in watersheds, and lake morphometric features all influence probability of lakes being in clear-water, turbid-water, or transitional regimes in a given landscape setting. Lake responses to combinations of these factors are non-linear, synergistic, and will vary regionally based on ambient nutrient levels and other factors. Models must incorporate these multiple factors to identify isoclines delineating combinations of variables and their associated values where lake-regime characteristics, resilience, and transitions are most likely to occur. Other factors such as inter-annual variability in precipitation and temperature will have strong influences on shallow lakes, and this inter-annual variability may need to be incorporated in predictive models.

Our second project goal is to develop a 2-state (clear/turbid) Markov model (hereafter transition model), where the transition probabilities between states are informed by results of environmental variable models mentioned above, but also using published relationships from shallow lakes in North America and worldwide. For example, probabilities of transitioning from clear to turbid may depend on fish colonization rates (or lake connectivity), increases in nutrient loads, or changes in other key drivers. Initially, we expect to model transitions between states using rule- or frame-based formats described in various applications by Starfield et al. (1989), Starfield (1990), and Starfield and Chapin (1996). An example of a simple rule could be:

$$P(\text{transition from clear to turbid}) = \begin{cases} 0.1 \text{ if total phosphorus (TP) is } < x_1 \\ 0.4 \text{ if } x_1 \leq \text{TP} < x_2 \\ 0.9 \text{ if TP} \geq x_2. \end{cases}$$

More complex rules may be defined using multiple state variables (e.g., TP and fish abundance). These additional state variables may themselves be influenced by other state variables (e.g., fish abundance may be influence by lake connectivity) as well as additional rules. An advantage of rule-based models is that they require only reliable qualitative (not quantitative) understanding of variables influencing complex relationships (in our case, factors influencing whether shallow lakes are in turbid- or clear-water regimes). Results from our earlier studies of Minnesota shallow lakes, along with data compiled by DNR Shallow Lakes Program staff, should provide a solid foundation to help guide development of rules governing transitions between states and also how watershed variables may influence these transition probabilities.

Our proposed framework can be viewed as a derivative of the dynamical system models suggested by Scheffer and Carpenter (2003) and Scheffer et al. (2001) which are now well known in aquatic ecology and do an excellent job of describing (and making sense of) catastrophic responses of shallow lakes to high densities of undesirable fish, increased nutrient loading, and perhaps other environmental influences. Such shifts are known from shallow lakes across North America and Europe, but occur in coral reefs, other ocean populations, and terrestrial ecosystems including grasslands and deserts (Scheffer et al. 2001). Dynamical systems models are useful not only as theoretical constructs, but have very practical applications helping managers understanding historical changes in Lake Christina and other shallow waters in Minnesota (Hanson and Butler 1994, Zimmer et al. 2009, Hobbs et al. 2012).

In the dynamical systems models developed for shallow lakes (Scheffer and Carpenter 2003, and others), transitions between states are not explicitly defined; rather they are an emergent property of these models. These transitions and also the equilibrium state of the system depend on how the model is formulated, including the number of key state variables (fish, nutrient levels, SAV, etc), the types of interactions among these state variables, and the specific parameters that govern the strength of these interactions. By contrast, we propose to explicitly model transitions between states using empirically derived rules. The main advantages of our proposed approach is that: a) the model will be considerably easier to parameterize and apply; 2) it will be easier for managers to understand; and 3) it will provide a simple framework for linking individual shallow lakes and within-lake variables to characteristics of adjacent watershed uplands or regional landscapes; these links are currently lacking in the dynamical systems models developed for shallow lakes.

Model Building Process

We intend to use rapid prototyping (Starfield et al. 1994, Nicholson et al. 2002) to quickly explore a variety of simple models from start to finish (where, “finish” includes a summary of conclusions as well as a careful examination of assumptions and a sensitivity analysis to evaluate the effect of parameter uncertainty); a rule-based approach seems ideally suited to this goal. This important first step should help to further define key research objectives that focus efforts on the most pressing questions and problems facing managers, while also helping to elucidate the relative importance of different model components. Additional complexity can then be introduced as needed to capture missing features or to better fit the qualitative dynamics of the system. We expect significant regional variation in system dynamics, and this regional variation (and data) can provide a rich medium for adaptive model building. For example, models may be initially ‘tuned’ using data from one region and then tested by comparing model predictions to empirical data from another region. Lastly, we expect that the iterative process of model-building and testing may serve to motivate the need additional data collection efforts; if so, we anticipate that the participating graduate student, staff from the DNR Shallow Lakes Program, and our research team would work together to address these data needs.

Objectives and Hypotheses

Presently, dynamical shallow lakes models (Scheffer and Carpenter 2003 and others) provide only generalized views of shallow lake behavior and, in a sense, stop short of linking shallow lakes to characteristics of adjacent watershed uplands or regional landscapes. For example, it is not yet possible to estimate likelihood of lake-regime shifts in response to changing extent of native upland cover (grass or CRP) in lake watersheds, to increased ditching in lake watersheds, or to increased mean annual precipitation and temperature. Such refinements should be possible with sufficient data linking lake-regime to watershed and landscape characteristics, lake-level variables, and regional variation. For example (and as a step in this direction), Zimmer et al. (2009) linked inter-annual changes in fish mass and ambient nutrients levels (total phosphorus in lake waters) to regime shifts in Minnesota lakes, suggesting that these dynamics may be predicted in more detail using factors not entirely accounted for in original catastrophic models. We believe a major information gap exists between Scheffer's dynamical systems models of lake-regime behavior and various environmental "predictors", or factors that may affect these regime dynamics and are known for shallow lakes in Minnesota landscapes. Our approach points to a qualitative framework that relates site- (lake) and watershed-scale variables to regime status of shallow lakes (clear- and turbid-water states) in Minnesota. Empirical data from research in Minnesota lakes, along with other appropriate information, will provide an underlying basis for qualitative rules required for the model building process. Conceptually our project includes two general aspects:

- Part I: Develop statistical models linking factors associated with turbid, clear, and shifting lakes, to environmental variables, and (if possible) evaluate whether these key drivers of lake regimes vary across the state (Figure 1A,B). This requires a series of refinements to earlier analyses (and publications) relating lake- and watershed-scale variables to shallow lake communities and characteristics. Examples of previous efforts include reports linking surface water connectivity to fish presence in shallow lakes (Herwig et al. 2010), importance of fish abundance and guild composition on phytoplankton abundance (Friedrichs et al. 2010), comparing influences of lake- and watershed-scale variables on aquatic invertebrate community abundance patterns among lakes (Hanson et al. 2012), and predicting phytoplankton abundance in shallow lakes in response to watershed cover types, background nutrients, and in-lake fish abundance (Gorman et al. 2014). We propose further modeling with additional data (developed since these publications) to clarify relationships, better account for variability in lakes among ECS regions (Figures 1A, 2), and to fill in data gaps where they exist. As indicated above, this step will emphasize modeling responses of lake characteristics to environmental factors. Relationships are almost certain to be non-linear, synergistic, and variable according to regional gradients in ambient nutrient levels and other factors. Models must identify relationship isoclines (such as indicated in Figure 3), and delineate combinations of variables and their associated values having greatest influence on lake-regime characteristics and transitions.

- Part II: Formulate rules and develop a frame-based transition model for predicting status and changes in water-clarity regimes in shallow lakes in response to present lake- and watershed-scale conditions; model implications to shallow lake regimes resulting from future changes in Minnesota (e.g. climate change, increased agriculture in watersheds, more extensive ditching) (Figure 1C). We propose an approach that melds catastrophic-regime models of Scheffer et al. (2001, 2003) and Scheffer (2004) with rule- and frame-based modeling efforts such as those developed by Starfield and Chapin (1996). Preliminary discussions with Dr. Tony Starfield confirmed that frame-based models (Starfield and Chapin 1996, Hahn et al. 1999) seem especially appropriate for predicting regime shifts in shallow lakes in response to changes in key environmental variables. Subsequent analyses may suggest better modeling approaches, but we anticipate using rule- or frame-based models as a starting point. Final models will incorporate environmental variable relationships (described in approach 1 above). This requires complex modeling approaches so as to incorporate influence isoclines, account for likely hysteresis in relationships between lake regime and environmental variables, incorporate influences of regional gradients (Figure 2), and include interactions among important variables. An example of theoretical frame-based lake model is shown in Figure 1C.

Logistics and Approach

Our effort consists primarily of integrating existing data resources, using these to model (and refine) relationships between environmental variables and regime dynamics in shallow lakes, then incorporating these relationships into frame-based models to predict lake regime status and transition. Initial modeling will be based primarily on data resources derived from shallow lake studies conducted in Minnesota during 2005-2011 by research staff from DNR Fish and Wildlife Research Units, Dr. Kyle Zimmer (University of St. Thomas, St. Paul), and other collaborators and funded by DNR, the Natural Resources Environmental Trust fund (through LCCMR), Ducks Unlimited, National Science Foundation (through a grant to Dr. Zimmer), and other sources. In practice, this will require a combination of several approaches including evaluation of existing data from Minnesota studies and elsewhere, possible data gathering to meet additional information needs (especially if this is needed to clarify regional patterns), and actual model development. Data summary, evaluation, and possible data gathering will be conducted by primarily by Hanson, Herwig, Zimmer, and Hansel-Welch, along with staff from DNR Shallow Lakes Program, DNR Wildlife staff, and perhaps managers from other resource agencies in Minnesota. Model development will be primarily the responsibility of Fieberg, Starfield, and Johnson, along with a graduate student enrolled in Fish, Wildlife, and Conservation Biology at UM (with Fieberg serving as major advisor).

First, along with collaboration of DNR Shallow Lakes Program staff, we will review and synthesize data resources available to assess extent of shallow lake regime status by major ECS regions (Figure 1A). Previous LCCMR-funded research helped to clarify relationships between environmental variables and shallow lake quality, but also showed a need for a more extensive geographic sampling across the state. We anticipate utilizing Shallow Lake Program staff and other collaborators to fill in existing data needs, especially in north eastern and north western areas of Minnesota where relatively few shallow lake surveys have been completed. Expanded regional data gathering may be necessitated by extreme variability among shallow lake conditions across ECS regions (Figure 2) and because this variability is likely to influence complex responses of lake regimes to environmental gradients (Figure 3).

Second, we propose to expand and refine efforts to connect shallow lake characteristics known to reflect lake regime status (turbidity, phytoplankton biomass, extent of submergent macrophytes, and other variables) to key environmental variables, those being factors that are especially likely to influence lake regime status. This will include variables measured at lake- and watershed (landscape)- scales. We expect to expand environmental variable modeling at a large geographic (ECS Section) scale. This activity will improve our understanding of the factors responsible for lake quality, improve understanding of regional patterns, and aid in conservation planning. Ultimately, data availability may determine extent to which regional analyses are plausible and broader geographic modeling may be required.

Third, collaborating biometricians and modelers (Fieberg, Starfield, Johnson) will work toward development of transition models useful for forecasting regime status and future changes in Minnesota shallow lakes in response to the suite of factors identified as key drivers of lake regimes (or identified as important environmental variables in our second objective, above). We anticipate that likely drivers of regime status and changes in shallow lakes will be loss of grasslands and riparian areas (such as CRP) in lake watersheds, and changes in temperature, precipitation patterns and hydrologic conditions (climate fluctuation), and other anthropogenic factors such as shoreland development, ongoing ditching among surface waters, further loss of temporary and seasonal wetlands and other factors.

MANAGEMENT IMPLICATIONS

We anticipate that our products (transition models) will be useful on two levels. First, proposed "future lake-condition models" should be extremely useful for DNR Area Wildlife Managers, Shallow Lake Program staff, and other lake managers and conservation planners responsible for making informed policy decisions that impact water quality at regional scales in Minnesota. Our expectation is that this broad transition model framework will be especially useful as a conservation tool for those who need to forecast influences of complex changes in Minnesota's landscape including transitions in upland cover types (such as loss of CRP), extent of ditching (or surface-water connectivity), transitions in precipitation and temperature (climate change), shoreland development, or other likely trends. We know from shallow lake survey data that over half of the shallow lakes surveyed in the prairie are poor condition. The transition models will help us forecast how many more lakes may be in jeopardy of decline with potential changes in landscapes or climate and serve as planning tools to potentially try to mitigate for some of these changes.

Second, the modeling framework described above will also help clarify expected lake-specific outcomes, integrating the best available information for assessing the relative effectiveness of alternative management actions as a function of within-lake conditions, landscape setting, connectivity, current conditions, and expected changes to the landscape/climate. In a sense, this means a manager should be able to refine expectations for individual lakes based on results of our transition models. If possible, we will also develop a lake manager's model such as those developed previously by Starfield within Excel (unpublished data) that allows predictions of likely outcomes for a specific lake, given landscape setting, connectivity, current conditions, and expected changes to the landscape/climate.

PLANNED OUTREACH

Models will help policy makers and lake managers identify primary causes of poor shallow lake water quality and health, more clearly evaluate future threats to shallow lakes, and determine where management actions have most potential to mitigate or minimize impacts and favor high water quality in these sites. The proposed frame- (or rule-) based modeling, while linked to empirical data, is qualitative and will be far easier to understand than more quantitative approaches. We expect our modeling framework will lead to original insights from new data analyses, but will also lend itself to practical applications by DNR lake managers and others. Frame-based models we describe should lead to observable, discrete lake outcomes (turbid- or clear-water lakes) based on sets of rules that will be easily applied to the specific conditions and anticipated changes. If appropriate, and to encourage development of these applications, we plan to meet with DNR managers and others to distribute and discuss project models and results.

LITERATURE CITED

Bendell, B.E., D. K. McNicol. 1987. Fish predation, lake acidity and the composition of aquatic insect assemblages. Hydrobiologia 150: 193-202.

Friederichs, S. J., K. D. Zimmer, B. R. Herwig, M. A. Hanson, and J. R. Fieberg. 2011. Total phosphorus and piscivore mass as drivers of food web characteristics in shallow lakes. Oikos 120: 756-765.

Euliss, N. E. Jr., J. W. LaBaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: a conceptual framework for interpreting biological studies. Wetlands 24: 448-458.

Gorman M. W., K. D. Zimmer, B. R. Herwig, M. A. Hanson, R. B. Wright, S. R. Vaughn, and J. A. Younk. 2014. Relative importance of phosphorus, fish biomass, and watershed land use as drivers of phytoplankton abundance in shallow lakes. Science of the Total Environment 466-467: 849-855.

Hahn, B. D., R. D. Richardson, and A. M. Starfield. 1999. Frame-based modeling as a method of simulating rangeland production systems in the long term. Agricultural Systems 62: 29-49.

Hanson, M. A., and M. G. Butler. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Canadian Journal of Fisheries and Aquatic Sciences 51: 1180-1188.

Hanson, M. A., and M. R. Riggs. 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. Wetlands 15: 167-175.

Hanson, M. A., K. D. Zimmer, M. G. Butler, B. A. Tangen, B. R. Herwig, and N. H. Euliss, Jr. 2005. Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. Wetlands 25: 764-775.

Hanson, M. A., B. R. Herwig, K. D. Zimmer, J. Fieberg, S. R. Vaughn, R. G. Wright, and J. A. Younk. 2012. Comparing effects of lake-and watershed-scale influences on communities of aquatic invertebrates in shallow lakes. PLoS ONE: 7(9): e44644. Doi:10.1371/journal.pone.0044644.

Herwig, B. R., K. D. Zimmer, M. A. Hanson, M. L. Konsti, J. A. Younk, R. W. Wright, S. R. Vaughn, and M. D. Haustein. 2010. Factors influencing fish distributions in shallow lakes in Prairie and Prairie-Parkland regions of Minnesota, USA. Wetlands 30: 609-619.

Hobbs, W. O., J. M. Ramstack Hobbs, T. LaFranchois, K. D. Zimmer, K. M. Theissen, M. B. Edlund, N. Michelutti, M. G. Butler, M. A. Hanson, and T. J. Carlson. 2012. A 200-year perspective on alternative stable state theory and lake management from a biomanipulated shallow lake. Ecological Applications 22: 1483-1496.

Moss B., J. Madgwick, and G. Phillips. 1996. A Guide to the Restoration of Nutrient-Enriched Shallow Lakes. WW Hawes, UK.

Moss B., E. Jeppesen, M. Sondergaard, T. L. Lauridsen, and Z. Liu. 2013. Nitrogen, macrophytes, shallow lakes and nutrient limitation: resolution of a current controversy? Hydrobiologia 710: 3-21.

Nicolson, C. R., A. M. Starfield, G. P. Kofinas, and J. A. Kruse. 2002. Ten heuristics for interdisciplinary modeling projects. Ecosystems 5:376-384.

Scheffer, M., S. R. Carpenter, J. A. Foley, C. Folk, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413: 591-596.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18: 646-656.

Scheffer, M. 2004. The ecology of shallow lakes. Kluver Academic Publishers, Dordrecht, The Netherlands.

Starfield, A.M., K. A. Smith, and A. L. Bleloch. 1994. How to Model it: Problem Solving for the Computer Age. 2nd edition. Burgess International Group, Edina, MN.

Starfield, A. M. 1990. Qualitative, rule-based modeling. Bioscience 40: 601-604.

Starfield, A. M., B. P. Farm, and R. H. Taylor. 1989. A rule-based ecological model for the management of an estuarine lake. Ecological Modeling 46: 107-119.

Starfield, A. M., and F. S. Chapin, III. 1996. Model of transient changes in arctic and boreal vegetation in response to climate and land use change. Ecological Applications 6: 842-864.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. Canadian Journal of Fisheries and Aquatic Sciences 57: 76-85.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. Ecosystems 4: 346-357.

Zimmer K. D., M. A. Hanson, B. R. Herwig, and M. L. Konsti. 2009. Thresholds and stability of alternative regimes in shallow prairie-parkland lakes of central North America. Ecosystems 12: 843-852.

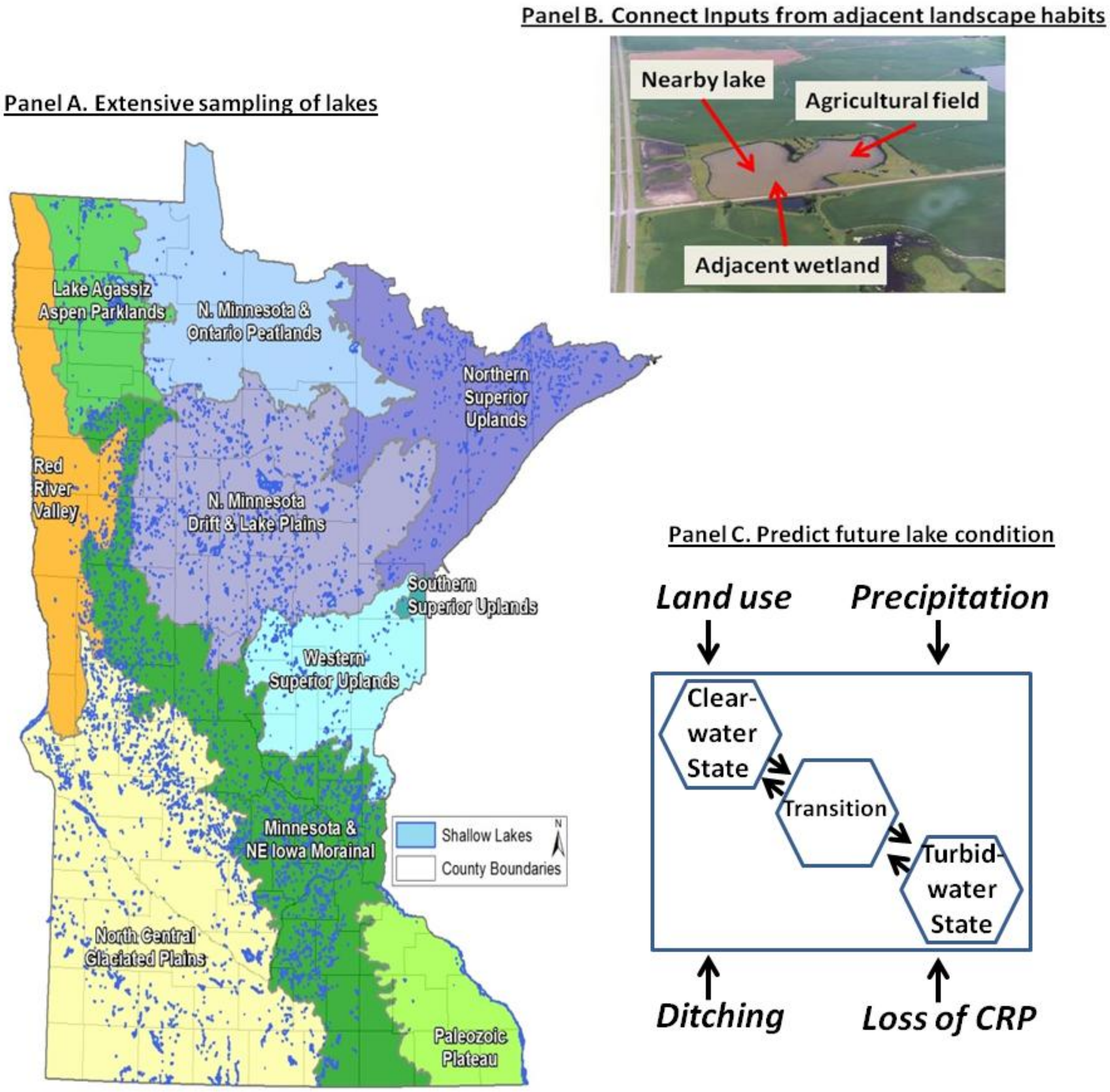

Figure 1. Overall study strategy. **Panel A** shows extent of Ecological Sections and distribution of shallow lakes in Minnesota. P**anel B** indicates connections between landscapes inputs and imbedded lakes; these connections (arrows) will be modeled in **part I**. **Panel C** illustrates frame-based modeling approach (**Part II**) we plan to use to predict predominant future lake conditions. Predictions will be based on lake responses to potential landscape modifications and other changes within the Ecological Sections.

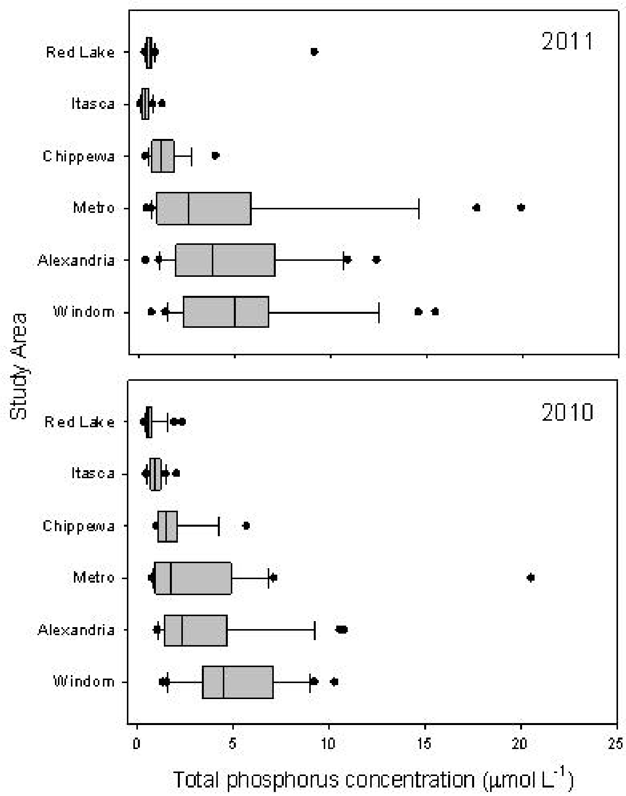

Figure 2. Box plots showing mean abundance of total phosphorus (TP) for 127 shallow lakes sampled within 6 study regions during 2010 and 2011. Vertical lines within boxes depict median TP values for each study region; extent of shaded boxes depict 25th and 75th percentiles. Whiskers show 10th and 90th percentiles, with dots indicating more extreme values.

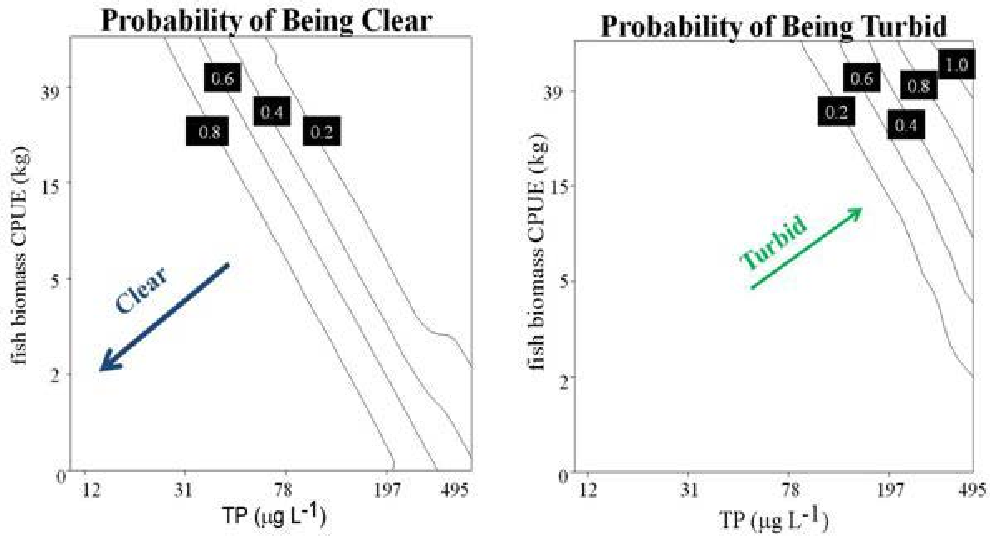

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Figure 3. Isobars in panels indicate probability of lakes exhibiting characteristics of clear (left) or turbid regimes. Probabilities of turbid regime show positive relationship to TP concentrations and are based on data from 127 Extensive Lakes

REHABILITATING SHALLOW MINNESOTA LAKES: EVIDENCE FROM SHORT-TERM RESPONSES

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SUMMARY OF FINDINGS

Shallow lake management is complex and rehabilitation efforts often produce unexpected-even disappointing-results. Relatively few strategies are available to lake managers and general strategies have changed little during the past 50 years. Most common approaches are drawdown, removal of undesirable fishes, or combinations of both. Both the application of these efforts and the interpretation of lake responses are complicated by multiple factors. For example, inducing drawdown can be confounded by high precipitation, extensive surface water connectivity, and expectations of recreational lake users. Fish removal is logistically difficult, often requires in-lake use of chemical toxicants, and fish typically re-colonize lakes within a few years after treatment. To maximize project results, managers often apply multiple treatments, but this makes it nearly impossible to identify causal relationships that would inform future projects. Restoration of grasslands or other native vegetation within lake watersheds also favors improved water quality in shallow lakes, but these projects are extremely costly and benefits are slow to develop. We reviewed results of 12 shallow lake rehabilitations in Minnesota and compared communities of these lakes to those of regional shallow lakes in clear- and turbid-regimes. Results indicated that rehabilitated lakes showed a pattern of increased similarity to clear-regime lakes in terms of phytoplankton, nutrients, and submerged aquatic plants. In general, lakes treated by drawdown and fish removal appeared to show stronger rehabilitation responses than did sites where only fish removals were applied.

INTRODUCTION

Shallow lake management is especially challenging because these sites are often highly altered and frequently occur in close proximity to intensive agriculture, roadways, and other unnatural features. Combined effects of increased nutrients, sedimentation, and agricultural chemicals along with altered hydrology may directly limit ecological integrity and wildlife suitability of these lakes. Watershed- and local-scale factors, along with mild winters, favor high densities of planktivorous and benthivorous fishes, and these populations contribute further to water quality and habitat declines. For lake managers, reducing nutrient inputs is often difficult or impossible. In the past 50 years, controlling dense, undesirable fish communities has been a core strategy of shallow lake managers in Europe and the United States (Lammens 1999). Research in recent decades shows potential improvements resulting from controlling undesirable fish communities (including species like bullheads, fathead minnows, and others) rather than

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just eradicating carp (Shapiro and Wright 1984, Hanson and Butler 1994, Moss et al. 1996, Zimmer et al. 2001, Scheffer 2004, Potthof et al. 2008, and many others).

Research in North America and Europe has shown that water-level fluctuations (WLF) influence virtually all aquatic vascular plants in freshwater wetlands (Squires and van der Valk 1992, Wilcox and Meeker 1992, van der Valk et al. 1994, Murkin et al. 2000, Euliss et al. 2004, van der Valk 2005, Wantzen et al. 2008, and many others). It is not surprising that WLF also affect submerged macrophytes (SAV), nutrient cycling, and other properties of shallow lakes, and that natural WLFs are essential for maintaining lake processes and communities (Coops et al. 2003, Chow-Fraser 2005, Leira and Cantonati 2008). Sustained high-water levels are almost certain to favor loss of SAV and may induce transitions to turbid regimes, especially in lakes with high nutrient levels and benthivorous or planktivorous fish (Blindow et al. 1992, Coops et al. 2003, Scheffer and Jeppesen 2007, Hobbs et al. 2012). Alternatively, intermittent periods of lower water levels increase light availability at sediments and favor increased abundance and diversity of submerged aquatic plants, ultimately favoring transitions to clear-water regimes.

In Minnesota, drawdown and fish removal are often used simultaneously (or sequentially) to improve water clarity, light available for SAV, and to enhance zooplankton and other invertebrates, usually for the benefit of waterfowl and other wildlife species (Hansel-Welch and Kudelka 2010). Efforts combining drawdown with fish removal are intended to maximize favorable responses by eliminating undesirable fish populations, favoring re-establishment of SAV, and stimulating germination of emergent macrophytes in lake margins. Rotenone is often applied during late fall or winter periods after lake volumes are reduced, and target fish populations may be concentrated and stressed by seasonal hypoxia. In nearly all cases, shallow lake rehabilitation aims to improve lake water clarity and ultimately induce shifts to clear-regime conditions (Moss et al. 1996, Scheffer 2004, Zimmer et al. 2009). Combination approaches certainly improve likelihood of favorable outcomes, but factors responsible for lake improvements are extremely difficult to identify. In addition, lake management may induce unexpected disturbances and surprising responses in shallow lake communities. For example, equivocal – even contrasting - responses may result from sediment dessication, physical disturbance by wind and ice, re-colonization and variable survival of fish species following rotenone treatment, or other factors. In a sense, use of combined management techniques creates a conundrum; even if lake rehabilitation is successful, managers may not be able to identify which activity worked best and favored lake improvements.

To better understand responses to current management, we evaluated characteristics of 12 shallow lakes in Minnesota following rehabilitation of these sites during 2007-2011. We gathered post-treatment data from rehabilitated (managed) lakes and then assessed lake responses by comparing features of managed sites to those of similar untreated lakes within adjacent areas. We used two approaches to compare managed and untreated lakes. First, we summarized data on fish communities, SAV, and average total phosphorus, nitrogen, and phytoplankton abundance (as chlorophyll a, Chla) comparing these levels in rehabilitated and untreated sites. Second, we used ordination methods to compare limnological variables and SAV mass in managed sites with values from similar untreated lakes exhibiting clear- and turbid-water regimes. Our approach illustrates patterns among managed and unmanaged lakes, identifies challenges associated with evaluating shallow lake rehabilitation efforts, and we summarize what we believe are important considerations for shallow lake managers.

METHODS

Selection of lakes

During 2010-2011, we gathered data from 12 shallow lakes in Minnesota, all of which were managed between 2007 and 2010 (Table 1). Lakes were rehabilitated using combinations of water- level reduction (drawdown) and fish removal with 4 lakes managed by drawdown, 4 treated with rotenone, and 4 sites subjected to combinations of both approaches. In several cases, piscivorous walleye were also added (as fry) to suppress fathead minnows (*Pimephales promelas*) and increase zooplankton (Potthoff et al. 2008). In all cases, the management objective was re-establishment of clear-water conditions as described by Scheffer (2004), Zimmer et al. (2009). We included only managed lakes for which we could obtain at least one year of pre-management data, and we required that rehabilitation had been completed within the past 4 years. All lakes (managed and untreated comparison sites) lay within two ECS Ecoregions, Northern Glaciated Plains (N=7) and Western Corn Belt Plains (N=5, Omernik 1987). We made no attempt to evaluate cause-and-effect relationships, only to assess lake characteristics following management (most often including both fish removal and drawdown).

Fish Communities

All fish sampling was done during July and August in 2010 or 2011 to estimate composition and abundance (biomass per unit effort) using a combination of gear deployed overnight. Three mini-fyke nets (6.5 mm bar mesh with 4 hoops, 1 throat, 7.62 m lead, and a 0.69 X 0.99 m rectangular frame opening into the trap) were set overnight in the littoral zone of each lake. One experimental gill net (61.0 mm multifilament net with 19.0, 25.0, 32.0, 38.0, and 51.0-mm bar meshes) was deployed along the deepest depth contour in lakes less than 2 m deep or along a 2 m contour in lakes with sufficient depth. The approach has been effective in shallow lakes in Minnesota (Herwig et al. 2010) and in small lakes from other regions (Tonn and Magnuson 1982; Rahel 1984). Fish were sorted by species, rated (counts per unit weight), and weighed in bulk. Data were summarized as the total biomass of each feeding guild (planktivores, benthivores, piscivores) collected in all four nets.

Nutrients, phytoplankton, and submerged macrophytes

Surface (dip) water samples were taken from central locations of each lake once during July and concurrent with other sampling. Samples were frozen and transported to the University of St. Thomas (St. Paul, MN) for analysis of phytoplankton abundance (Chla), total nitrogen (TN), and total phosphorus (TP) using methods of APHA (1994) and Zimmer et al. (2009). Abundance of submerged macrophytes (SAV) was measured using modified techniques of Jessen and Lound (1962), and Deppe and Lathrop (1992). During July (2010) or August (2011) SAV was sampled at 15 stations in each lake, equidistant along four transects running the width of each basin. A single cast with a weighted plant rake was made at each location, and plant samples were gathered along 3 m of lake bottom. Plants recovered on each cast were weighed using spring scales (wet weight) and percent composition was recorded for each species. SAV data were summarized as average total mass of all rake samples (mean mass across the total number of rake casts) for each lake.

Framework for Evaluating Lake Responses

Management activities at each of the 12 study lakes are summarized in Table 1 along with lake names, sizes, and other project information. Our evaluation was limited by lack of pre-rehabilitation data from 8 of these 12 sites. We were able to obtain a single year of pre-treatment data from an additional 4 managed lakes because these sites were subjects of another study. Also, as part of concurrent research in Minnesota and within these ECS regions, we gathered identical data from 48 similar but unmanaged shallow lakes during comparable periods in 2010 and 2011. We reasoned that this larger group of unmanaged lakes would provide biological benchmarks for comparing characteristics of managed sites, allowing us to illustrate similarity and patterns among lakes with contrasting management histories. Going one step further, we assigned unmanaged lakes to clear- or turbid-regime categories using Chla threshold values following classification of Zimmer et al. (2009). Use of these defined groups allowed us to assess whether characteristics of managed lakes resembled clear- or turbid-water regional counterparts. While less informative than pre- and post-treatment comparisons, data from unmanaged regional lakes did provide a means of broadly assessing lake rehabilitation success if positive outcomes could be inferred from similarity with clear-regime regional lakes (supporting dense SAV, relatively lower levels of Chla, TP, and TN).

We used non-metric multidimensional scaling (NMS; McCune et al. 2002) to compare characteristics of 12 managed and 48 unmanaged regional lakes. NMS is useful for exploring data patterns in cases like this because resulting plots emphasize similarity relationships among groups of study units (lakes in our case). The method also relaxes requirements for normal data distributions and linear relationships to environmental gradients. To identify factors responsible for underlying relationships, we calculated correlations between final NMS axes and variables in the original ordination matrix. We used Sorenson (Bray-Curtis) distance measures and preliminary models based on a 6-dimensional solution, with significance of axes assessed by Monte Carlo permutation (250 permutations). Axes in final ordinations models were based on stress reduction and were adjusted with varimax rotation to align axes and aid interpretation of patterns (McCune et al. 2002). All NMS procedures were conducted using PC-ORD v. 5 (McCune and Mefford 1999) and followed guidelines of McCune et al. (2002).

RESULTS AND DISCUSSION

Trends in Fish Populations, SAV, and limnological features

In general, details of drawdown responses varied widely among lakes and ranged from relatively brief and partial-, to full-basin de-watering lasting more than a single growing season. Use of drawdown and/or application of rotenone was only marginally effective in removing fish populations from managed lakes and planktivorous and benthivorous fish were well established in managed lakes by 2010 and 2011. Abundance of planktivores (such as fathead minnows) and benthivores (bullheads, carp) varied dramatically among rehabilitated lakes, but standard errors (SEs) indicated that mean mass levels could not be distinguished from those observed for unmanaged turbid-water sites (Figure 1A). Presence of fish in Leverson and Froland by August suggested that fish either survived rotenone treatments during fall 2010, or quickly immigrated back into the lakes following management.

Mass of SAV remained relatively low in all managed lakes during 2010-2011 and values fluctuated only modestly between these study years. In only one managed lake (Teal lake) did SAV reach levels within the range of our regional unmanaged clear-water sites in 2010, and here SAV declined sharply by the following year (2011, data not shown). SAV data seemed to indicate marginal responses and low abundance in most managed lakes, with levels similar to those observed in turbid regional sites (Figure 1B). An important point is that variability in fish and SAV abundance (mass) among lakes and classes (rehabilitated, regional clear- and turbid-regime) were so high (during 2010-2011) that general trends among these categories were difficult to discern.

Chla (phytoplankton abundance), along with levels of TP and TN, also varied widely among lakes, but mean values in managed sites were intermediate between managed lakes and regional turbid-state sites (Figure 2A,B,C) although SEs overlapped among lake classes. TN levels showed higher overall variability than TP, but average TN values in managed lakes were generally similar to those in regional clear-regime lakes (Figure 2B,C) and this may be related to modest improvements in SAV (and resulting increases in denitrification rates) in managed sites.

Similarity Patterns Between Managed and Unmanaged lakes

Overall patterns identified using NMS suggested that rehabilitated lakes had improved since management, but stopped short of transitioning solidly to conditions observed in regional clear-regime sites. Two significant dimensions (axes) in NMS explained approximately 95% of the variability in Chla, TP, TN, and SAV mass among lakes classified as rehabilitated, regional turbid-, and regional clear-regime sites (Table 2). Broadly, this suggests that managed lakes showed greater similarity with regional clear-regime lakes, yet managed sites remained somewhat intermediate between regional clear and turbid counterparts (Figure 3).

To clarify possible responses to “fish removal only” management, we included four lakes for which we had both pre- and post-treatment data. Comparing patterns for these lakes before and after management (rotenone treatments only) shows improvement, but scores remained in close proximity to those of regional turbid-regime lakes (Figure 3). We also examined correlations between Chla, TP and TN, and SAV and values showed that TN and Chla were most strongly associated with significant underlying NMS axes (R^2 values on axis 1 = 0.82 and 0.54, respectively; Table 2).

CONCLUSIONS

Our analysis indicates that shallow lake management (rehabilitation) via drawdown and/or fish removal often favors short-term improvements in water quality in shallow Minnesota lakes. Patterns also suggest that management favors conditions more like those noted for lakes in clear-water regimes, but we think these lake improvements should be viewed cautiously. First, results here depict only constellations among lake characteristics during one or two seasons within 3-5 years following lake management. Second, planktivorous and benthivorous fish were widespread in these lakes shortly after management and increases in these fish are known to trigger transitions to turbid-water regimes (Zimmer et al. 2009). Finally, while ordinations show evidence of modest lake improvements in terms of limnological variables and SAV, overall patterns suggested that lake responses typically stopped short of solid transitions to clear-water regimes.

Experiences of lake managers with these and other projects in Minnesota show that shallow lake improvements often persist no more than 5-10 years after management. Recent paleolimnological studies at shallow Minnesota lakes (Lake Christina and Blakesley WPA) help clarify reasons for this and indicate that sediment nutrients may be responsible for resilience of turbid-water conditions (Hobbs et al. 2012, 2014). In both Lake Christina and Blakesley WPA, historical lake sediments showed evidence of greatly increased nutrient loading since European settlement. While restoration of upland cover within lake watersheds has many beneficial effects, shallow lake characteristics are only loosely linked with present-day watershed land cover (Bayley et al. 2012, Hanson et al. 2012). This means that efforts to improve shallow lakes by conversion of uplands from row crops to grass may not be enough to trigger lake transitions to clear-water regimes, or to improve conditions for waterfowl and other shallow lake wildlife, at least on short time scales. Given the present uncertainty about triggering and sustaining long-term improvements in shallow lakes, we suggest lake managers consider the following. First, accelerated monitoring of shallow lakes is critical if we hope to improve understanding of what does (and does not happen) in response to lake management in Minnesota and elsewhere. Second, lake management approaches should continue to include methods favoring short-term improvements (like drawdown and fish removal) along with efforts to eliminate non-point nutrient inputs (by runoff from adjacent row crops). Third, high priority should be given to preserving clear-water shallow lakes with intact communities of SAV and limited surface-water connectivity. Fourth, lake managers and policy makers must realize that favorable lake responses to management are categorically successful, even if improvements persist for only several years. Managers should expect that drawdown, fish removal, or other efforts will need to be repeated if shallow lakes are to be maintained in clear-water regimes in highly altered landscapes. Finally, we need to refine models and forecasting tools to allow lake managers to anticipate implications of changing land-use patterns, temperature and precipitation, and economic fluctuations. An initial attempt to develop such a modeling approach is described in the accompanying research summary entitled: *Shallow lakes: assessing quality and predicting future change.*

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Table 1. Summary narrative of management activities applied to 12 shallow lakes in Minnesota during 2007-2011.

Lake	Size (acres)	Rehabilitation Strategy	Evaluation Chronology
Augusta	**499**	**Full drawdown in 2008; lake re-flooded in 2009. Water control structure and fish barrier on adjacent waters.**	**2 yrs post-trt**
Froland	**15**	**Rotenone treatment during fall 2010**	**1 yr pre-& post-trt**
Hjermstad	**60**	**Partial drawdown implemented in 2008; rotenone-treated under the ice during 2008-09. Stocked with piscivores (walleye fry) in 2009 to reduce planktivores. Water control and fish barrier in place.**	**2 yrs post-trt**
Leverson	**27**	**Rotenone treatment during fall 2010.**	**1 yr pre-& post-trt**
Maria	**425**	**Full drawdown implemented from fall 2006 through fall 2007. Rotenone applied to remaining flooded areas under the ice in winter 2007. Water level remained low through 2010. Water control weir with stop logs and electric fish barrier in place.**	**3 yrs post-trt**
Nora	**60**	**Full drawdown implemented in 2007, reflooded by 2009. Began to refill in 2008, 40-50% open water by 2009. Metal half-riser structure with stoplogs functions as a fish barrier.**	**3 yrs post-trt**
Sedan	**62**	**Partial drawdown in 2007, full drawdown in 2008. Began to refill in 2009. Water control structure in place.**	**2 yrs post-trt**
Spellman	**300**	**Drawdown from 2006-08; full reflooding by 2009. Water control structure and fish barriers in place.**	**2 yrs**
Teal	**91**	**Partial drawdown during 2008; rotenone-applied under the ice during winter 2008-09. Water control structure in place.**	**2 yrs**
Todd N	**35**	**Rotenone treatment during fall 2010**	**1 yr pre-& post-trt**
Todd S	**23**	**Rotenone treatment during fall 2010**	**1 yr pre-& post-trt**
Wilts	**55**	**Natural partial drawdown during 2008; rotenone-treat of remaining standing water during fall 2008.**	**2 yrs post-trt**

Table 2. Summary of R^2 values from linear associations between limnological variables in shallow Minnesota lakes during 2010 and 2011. Both axes significant ($P<0.05$) and cumulative R^2 for both = 0.95. Values show relationships between variables in main matrix and final fitted axes following non-metric multidimensional scaling with varimax rotation (details discussed in McCune et al. 2002).

	R^2 values	
	Axis 1	**Axis 2**
ChlaAve	**0.535**	**0.217**
TPAve	**0.368**	**0.002**
TNAve	**0.817**	**0.002**
SAVAve	**0.327**	**0.006**

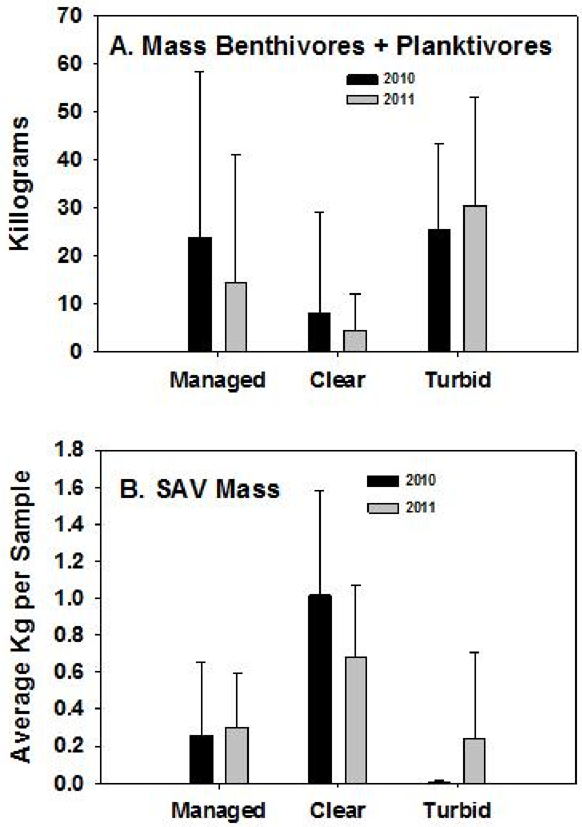

Figure 1. Relative abundance of planktivorous and benthivorous fish (average mass per lake) in study lakes during 2010 and 2011. Bars indicate means and SEs in regional unmanaged regional lakes in clear- and turbid-water regime, along with managed (rehabilitated) lakes as described in text (lake categories based on threshold values established following approach of Zimmer et al. 2009).

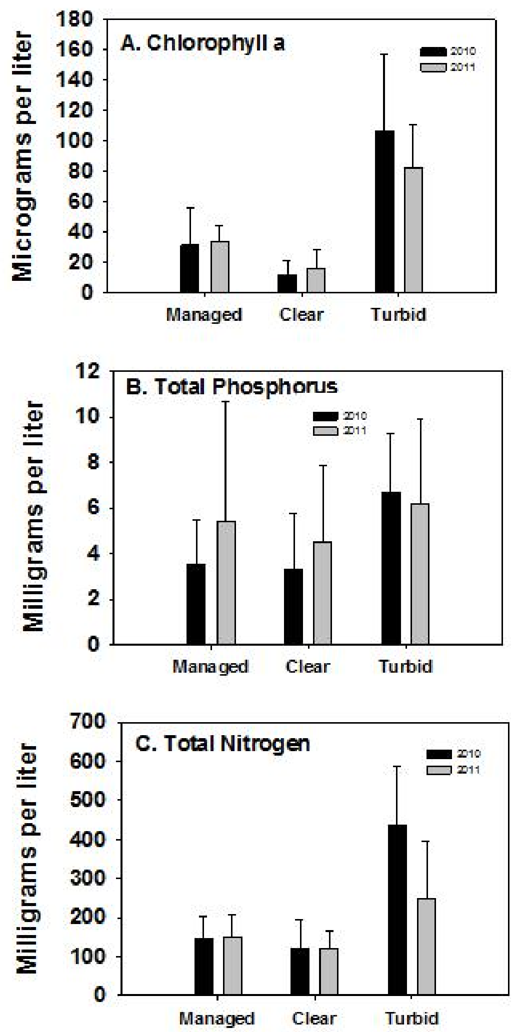

Figure 2. Bars depict chlorophyll a, total phosphorus, and total nitrogen concentrations in study lakes during 2010 and 2011. Values indicate means and SEs in regional unmanaged regional lakes in clear- and turbid-water regime, along with managed (rehabilitated) lakes as described in text (lake categories based on threshold values established following approach of Zimmer et al. 2009).

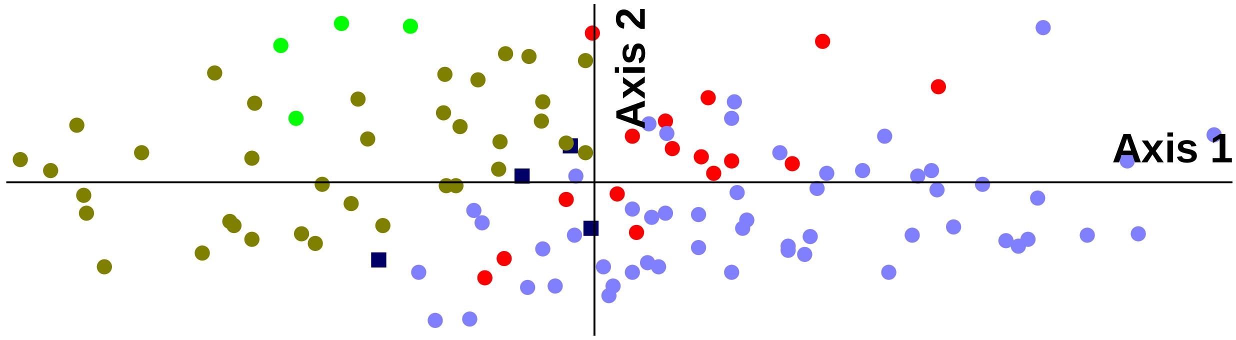

Figure. 3. Two-dimensional NMS summary of final non-metric multidimensional scaling model with varimax rotation using Chlorophyll a, total phosphorus, total nitrogen, and total SAV mass measured in 112 shallow Minnesota lakes during 2010 and 2011 (details discussed in text). Symbol color indicates lake rehabilitation status: regional clear lakes (blue), regional turbid lakes (olive), rehabilitated within 3-4 yr (red) lakes, 1-yr pre-rehabilitation (green), 1-yr post-rehabilitation (black box).

REFERENCES

APHA. 1994. Standard methods for the examination of water and wastewater. Washington, DC: American Public Health Association.

Bayley, S. E., A. S. Wong, and J. E. Thompson. 2012. Effects of agricultural encroachment and drought on wetlands and shallow Lakes in the boreal transition zone of Canada. Wetlands 33: 17–28.

Blindow, I. 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biology 28: 15–27.

Chow-Fraser, P. 2005. Ecosystem response to changes in water level of Lake Ontario marshes: lessons from the restoration of Cootes Paradise Marsh. Hydrobiologia 539: 189–204.

Coops, H., M. Beklioglu, and T. L. Crisman. 2003. The role of water-level fluctuations in shallow lake ecosystems – workshop conclusions. Hydrobiologia 506-509: 23–27.

Deppe, E. R., and R. C. Lathrop. 1992. A comparison of two rake sampling techniques for sampling aquatic macrophytes. Wisconsin Department of Natural Resources, Findings #32, PUBL-RS, 732-92. Madison, Wisconsin.

Euliss, N. H., J. W. LaBaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: A conceptual framework for interpreting biological studies. Wetlands 24: 448–458.

Hansel-Welch, N., and S. Kudelka. 2010. Shallow Lakes – Minnesota’s Natural Heritage. Water Resources Center, Minnesota State University, Mankato, MN.

Hanson, M. A., and M. G. Butler. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Canadian Journal of Fisheries and Aquatic Sciences 51: 1180-1188.

Hanson, M. A., B. R. Herwig, K. D. Zimmer, J. Fieberg, S. R. Vaughn, R. G. Wright, and J. Younk. 2012. Comparing effects of lake- and watershed-scale influences on communities of aquatic invertebrates in shallow lakes. PloS One, 7(9), e44644.

Herwig, B. R., K. D. Zimmer, M. A, Hanson, M. L. Konsti, J. Younk, R. W. Wright, and M. D. Haustein. 2010. Factors influencing fish distributions in shallow lakes in prairie and prairie-parkland regions of Minnesota, USA. Wetlands 30: 609–619.

Hobbs, W. O., J. M. Hobbs, T. LaFrançois, K. D. Zimmer, K. M. Theissen, M. B. Edlund, N. Michelutti, M. G. Butler, M. A. Hanson, and T. J. Carlson. 2012. A 200-year perspective on alternative stable state theory and lake management from a biomanipulated shallow lake. Ecological Applications 22: 1483–1496.

Hobbs, W. O., K. M. Theissen, S. M. Hagen, C. W. Bruchu, B. C. Czeck, J. M. Ramstack Hobbs, and K. D. Zimmer. 2014. Persistence of clear-water, shallow-lake ecosystems: the role of protected areas and stable aquatic food webs. Journal of Paleolimnology 51: 405–420.

Jessen R., and R. Lound. 1962. An evaluation of a survey technique for submerged aquatic plants. Minnesota Department of Conservation. Game Investigation Report 6. St. Paul, MN.

Lammens E. H. 1999. The central role of fish in lake restoration and management. Hydrobiologia 395/396: 191-198.

Leira, M., and M. Cantonati. 2008. Effects of water-level fluctuations on lakes: an annotated bibliography. Hydrobiologia 613: 171–184.

McCune, B.,J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities (Vol. 28). Gleneden Beach, OR: MjM software design.

McCune, B., and M. J. Mefford. 2002. PC-ORD: multivariate analysis of ecological data; Version 5 for Windows [User's Guide]. MjM software design.

Moss, B., J. Madgwick, and G. Phillips. 1996. Guide to the Restoration of nutrient-enriched shallow lakes. W. W. Hawes, UK.
Murkin, H. R., A. G. van der Valk, and W. R. Clark. 2000. Prairie wetland ecology: the contribution of the Marsh Ecology Research Program. Iowa State University Press. Ames, IA.
Omernik, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American geographers 77: 118-125.
Potthoff, A. J., B. R. Herwig, M. A., Hanson, K. D. Zimmer, M. G. Butler, J. R. Reed, B. G. Parsons, and M. C. Ward. 2008. Cascading food-web effects of piscivore introductions in shallow lakes. Journal of Applied Ecology 45: 1170-1179.
Rahel, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology 65: 1276-1289.
Scheffer, M. 2004. Ecology of shallow lakes. Kluver Academic Publishers, Dordrecht, The Netherlands.
Scheffer, M., and E. Jeppesen. 2007. Regime Shifts in Shallow Lakes. Ecosystems 10: 1–3.
Shapiro, J. S., and D. I. Wright. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biology 14: 371-383.
Squires, L., and A. G. van der Valk. 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. Canadian Journal of Botany: 1860-1867.
Tonn, W. M., J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 64: 1149-1166.
Wantzen, K. M., K.-O. Rothhaupt, M. Mörtl, M. Cantonati, L. Tóth, and P. Fischer. 2008. Ecological effects of water-level fluctuations in lakes: an urgent issue. Hydrobiologia 613: 1-4.
Wilcox, D. A., and J. E. Meeker. 1992. Implications for Faunal Habitat Related to Altered Macrophyte Structure in Regulated Lakes in Northern Minnesota. Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. Wetlands 12: 192-203.
van der Valk, A. G., L. Squires, and C. H. Welling. 1994. Ecological Applications 4: 525-534.
van der Valk, A. G. 2005. Water-level fluctuations in North American prairie wetlands. Hydrobiologia 539: 171–188.
Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. Ecosystems 4: 346-357.
Zimmer, K. D., M. A. Hanson, B. R. Herwig, and M. Konsti. 2009. Thresholds and stability of alternative regimes in shallow prairie–parkland lakes of central North America. Ecosystems 12: 843–852.