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ORIGINAL RESEARCH

Changes in Wetland Vegetation in Regulated Lakes in Northern Minnesota, USA Ten Years after a New Regulation Plan Was Implemented

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Abstract

Lake-level regulation alters wetland plant communities and their role in providing faunal habitat. Regulation plans have sometimes been changed to restore ecosystem function; however, few studies have shown the effects of such changes. In 2000, a new plan was implemented for regulation of Rainy Lake and Namakan Reservoir in northern Minnesota, USA. We had studied wetland plant communities under the previous 1970 regulation plan in 1987 and used those data to evaluate changes during 2002–2006 and 2010 resampling efforts using the same methods. Ordinations showed that plant communities changed little on Rainy Lake, where regulation changes were minor. However, on Namakan Reservoir, substantial changes had occurred in both vegetation and faunal habitat within two years, as plants favored by dewatering were replaced by submersed aquatic plants favored by year-round flooding under the new 2000 regulation plan. After ten years, Namakan showed greater similarity to unregulated Lac La Croix but still differed overall. Longer-term studies may be needed to determine if the regulation-plan change continues to alter Namakan plant communities. The speed at which changes began suggests that studies on other regulated lakes should begin in the first growing season following implementation of a new regulation plan and should continue periodically for a decade or longer.

Keywords Lake-level regulation · Rule-curve change · Wetland vegetation · Growth form · Faunal habitat

Introduction

Regulation of lake levels has a long history of altering wetland plant communities (Nilssen 1981, Rorslett 1989, Hill et al. 1998, Shay et al. 1999, Wilcox et al. 2008). As a result, changes in initial water-level-regulation plans have sometimes been requested or suggested by management agencies, citizen groups, and the scientific community (e.g., Wilcox and Whillans 1999, Grosshans et al. 2004, Wilcox 2011) to restore ecosystem functions. However, implementation of revised regulation plans has been rare, and few studies have been performed to determine the effects of such changes. What is the response to altered hydroperiod, changing from flooded to dewatered conditions and vice versa, and duration of such changes? How many years are required to show a response, and how long will changes continue to occur? We had the opportunity to address these questions in a previously studied regulated lake system in northern Minnesota, USA through ten years after a new regulation plan was enacted.

Voyageurs National Park lies along the United States-Canadian border in northern Minnesota (Fig. 1). There are 30 lakes in the park, and water levels of the largest lakes that form a chain along the Rainy River are controlled by dams. A hydroelectric dam constructed in 1909 between International

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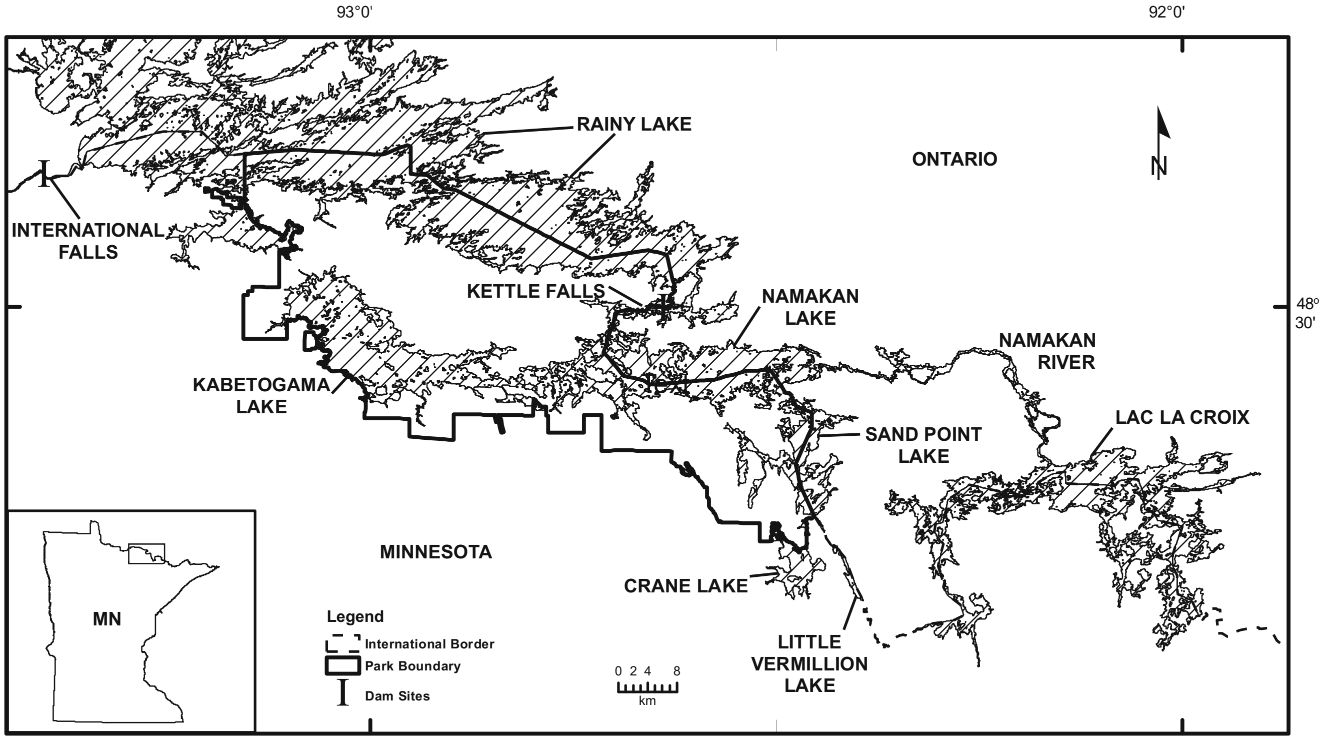


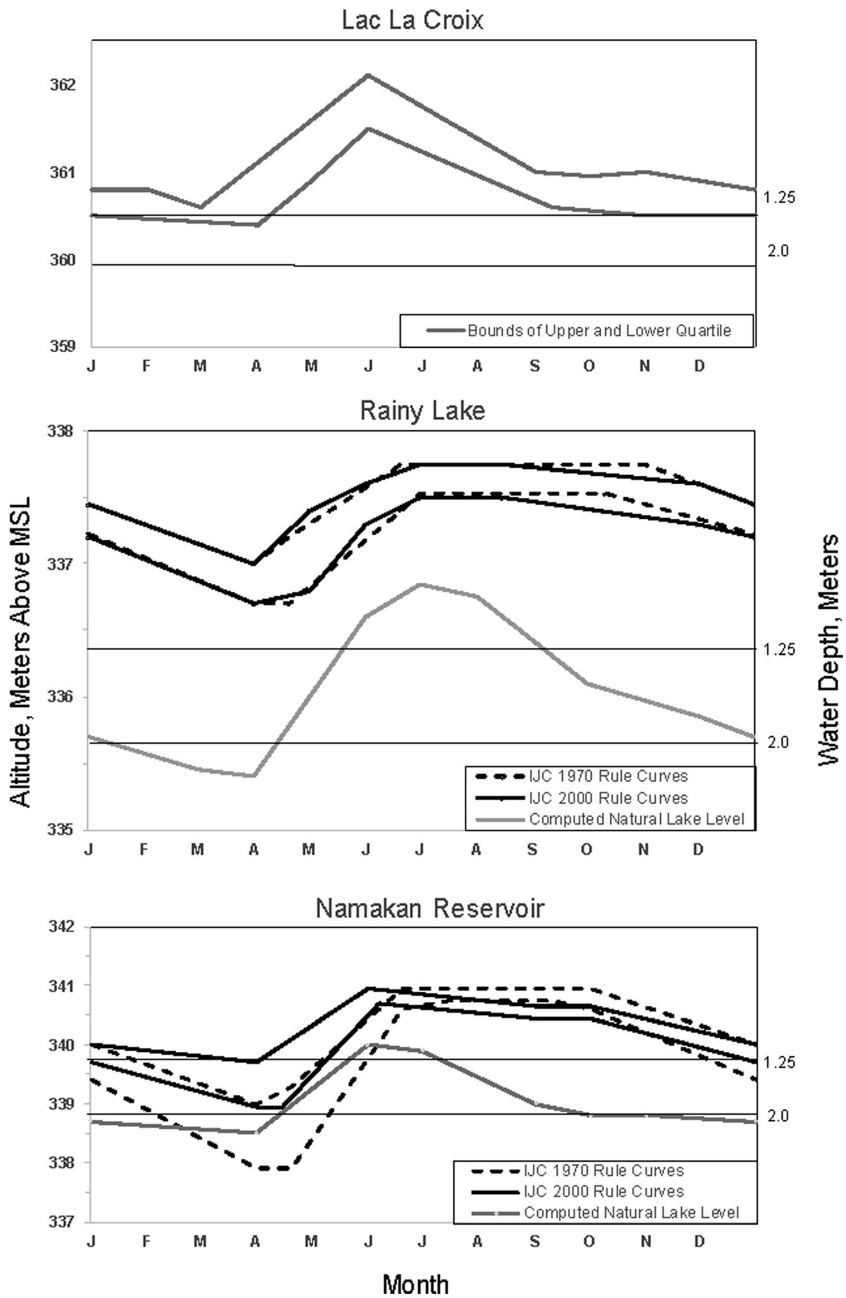
Fig. 1 Map of study area in northern Minnesota showing the study lakes (Lac La Croix, Rainy Lake, and Namakan Reservoir), other major lakes, dam sites, and boundary of Voyageurs National Park. The international border and park boundary coincide from Rainy Lake to Little Vermilion Lake

Falls, Minnesota and Fort Francis, Ontario controls downriver Rainy Lake (89,357 ha; 14,600 ha in park). Upriver Namakan, Kabetogama, Sand Point, Crane, and Little Vermilion lakes are controlled by two dams constructed in 1914 at the natural outlet of Namakan Lake at Kettle Falls to form Namakan Reservoir (18,400 ha in park). Water levels are regulated by the U.S.-Canadian International Joint Commission because the lakes cross the border. A water management program was established in 1970 that set acceptable high and low lake levels (termed rule curves) throughout the year. Mean annual fluctuations in Rainy Lake were reduced from 1.9 m to 1.1 m; Namakan Reservoir fluctuations increased from 1.8 m to 2.7 m, as water storage and release were controlled to assist in regulating Rainy Lake (Flug 1986, Wilcox and Meeker 1991). Under the 1970 rule curves, peak lake levels were reached in late June or early July, rather than following spring runoff a month earlier. Instead of decreasing gradually after the peak, lake levels were held stable until autumn and then drawn down through winter, as shown in Fig. 2.

A new regulation plan was implemented in 2000 that reduced the spring/summer drawdown in Namakan Reservoir such that the mean annual fluctuation under the new rule curve is less than 1.8 m (Fig. 2). The annual peak is reached in late May, and levels then recede gradually through the growing season. However, the entire range of fluctuations is about 0.8 m higher in elevation than computed natural levels based on water supplies with no regulation (Fig. 2) (Flug 1986, Wilcox and Meeker 1991). Few changes were made in the Rainy Lake rule curve, but a slight decrease in summer levels reduced the mean annual fluctuation from 1.1 m to 1.05 m, and drawdowns begin in early September rather than November (Fig. 2).

Wetland and aquatic vegetation was sampled in 1987 by Wilcox and Meeker (1991) to assess differences in plant communities in Rainy Lake and Namakan Reservoir resulting from differing non-natural hydroperiods brought about by regulation. As a control, Lac La Croix, an unregulated natural lake in Boundary Waters Canoe Area upriver from Namakan Reservoir (Fig. 1) was also sampled. Mean annual fluctuations in Lac La Croix are 1.6 m; peak levels are reached in late May or early June, and levels then decrease gradually until spring runoff occurs the following April (Fig. 2). However, extreme year-to-year seasonal variability can range from 0.3 m to 3.0 m (Appendix A; Gutreuter et al. 2013), while deviations from the ranges of the rule curves have been infrequent at Rainy Lake and Namakan Reservoir since regulation began. Sites on all three lakes were resampled in 2002–2006 and again in 2010 to assess changes in plant communities and resultant faunal habitat brought about by the change in rule curves.

Fig. 2 Water-level regimes for Lac La Croix, Rainy Lake, and Namakan Reservoir showing bounds of variation under both 1970 and 2000 rule curves, computed natural water levels (Flug 1986), and altitudes of mid-deep and deep transects



Methods

Study Sites

Thirty-one sites were chosen for sampling in 2002–2006 by Meeker and Harris (2009) and were resampled in 2010. Ten sites were located in each of Rainy Lake and Lac La Croix, and 11 sites were in Namakan Reservoir, including the two sites at each lake that were sampled in 1987 by Wilcox and Meeker (1991). A set of potential sites in Rainy Lake and Namakan Reservoir was identified from the Voyageurs vegetation database (Hop et al. 2001) and used for random selection of the remaining sites on those lakes that had not been sampled in 1987. Wetland polygons containing submersed aquatic vegetation, wild rice marsh, deep marsh, and northern water lily vegetative cover-types were included in the set, with a minimum size of one hectare. Because vegetation mapping was unavailable for Lac La Croix, sites in close proximity to the 1987 sampling sites were initially selected based on aerial photographs and field reconnaissance. In 2005, new aerial photography and Ikonos imagery for Lac La Croix were used to select more sites randomly within a region approximately 10 km west of the initial Lac La Croix sites.

All potential sites were visited in the field to assess their suitability. Suitable sites were not heavily influenced by human activity (e.g., former or existing cabins, landings) and were not dominated by floating mat vegetation, which would likely not be affected by changes to the rule curves. All sites chosen are listed in Appendix B.

Field Sampling

Two transects were sampled at each site in 2002–2006 and again in 2010. The transects represented the mid-deep submersed zone and deep-water zone defined by Wilcox and Meeker (1991). Although a third transect representing the shoreline at 0.0 m was sampled in 2002–2006 (Meeker and Harris 2009), those data are not included here because longer-term 2010 sampling focused on the two transects where the greatest vegetation changes were occurring.

The mid-deep zone transect followed a depth contour of 1.25 m (based on mean high water, MHW) in unregulated Lac La Croix that is flooded in April, remains flooded throughout the growing season, and is often dewatered again in February (Fig. 2). It should contain aquatic species that can tolerate late-winter drawdown. Under both 1970 and 2000 rule curves, this zone is always flooded in Rainy Lake. Under the 1970 rule curve, this zone in Namakan Reservoir was dry February to April and flooded May to January (Wilcox and Meeker 1991); however, under the 2000 rule curve, it may be flooded year-round but can be dewatered February to April in low water years.

The deep-water zone transect was established along a depth contour of 1.75 m by Wilcox and Meeker (1991) for sampling in 1987 – a contour that is always flooded in Lac La Croix and should contain aquatic species capable of tolerating deep water. It remains flooded year-round in Rainy Lake also. This deeper transect was shifted to a 2.0 m depth starting in 2002, which retained sampling under the same flooding conditions in La La Croix and Rainy Lake but ensured that sampling in Namakan Reservoir would remain in the year-round flooded zone also, thus capturing the intended effects of the new rule curve to avoid unnatural dewatering (Fig. 2).

The sampling methodology devised by Wilcox and Meeker (1991) was employed, in which all transects were laid out with floats using depth soundings relative to lake levels (accessed at the time of each sampling event from the Lake of the Woods Control Board website http://www.lwcb.ca/waterflowdata.html, which was also the source of long-term hydrologic data). Sampling was conducted in late July to late August 2002–2006 and again in 2010 – a period when the vegetation was fully developed. Not all sites were sampled in each year from 2002 to 2006 due to access problems sometimes created by high or low waters, as well as the later addition of new sites. Rainy Lake was not sampled in high water year 2002, and only three of ten sites were sampled in low water year 2003 (Appendix A). No sites were sampled in Lac La Croix in low water year 2003. Twenty 1 m × 1 m quadrats were sampled on each newly laid-out transect in each year according to a stratified random design, re-randomized for each sampling event. The total length of each transect was estimated, the transect divided into 20 equal segments, random quadrat locations selected within each segment, and each quadrat location marked with a float attached to a sinker. At each quadrat, we listed all taxa and estimated absolute percent cover. Taxa covering less than 1% of a quadrat were systematically recorded as 0.1%. Since plants may occupy space at different strata, the sum of individual cover estimates could exceed 100%. Nomenclature follows Flora of North America (http://www.Efloras.org).

Data Analyses

To give equal weight to frequency and cover, Importance Values (IV) were calculated as the sum of relative frequency and relative mean cover on each transect at each site and were used to assess floristics on both transects in all lakes. Importance Value vs. transect matrices for each elevation were analyzed separately by non-metric multi-dimensional scaling ordinations (NMDS) (McCune and Grace 2002) using data restricted to taxa occurring on three or more transects across all water bodies. The axis 1 and axis 2 scores were graphed to show similarities and dissimilarities in species composition and dominance among lakes and years.

The first set of ordinations focused on site-specific changes in vegetation at each elevation following enactment of the new regulation plan in 2000 by including only the two sites at each lake that were sampled in 1987 by Wilcox and Meeker (1991). Those sites were also sampled after the 2000 change in regulation plan and data included in the ordinations: Lac La Croix in 2002 and 2010; Rainy Lake in 2003 and 2010; and Namakan Reservoir in 2002, 2004, 2006, and 2010. To get a broader perspective on plant community changes under the new regulation plan, a second set of ordinations for each transect included all sites at all lakes in all years. To demonstrate changes through time, the graphed ordination results for each transect were then assessed separately by identifying and circling sites in each lake sampled during the intermediate time period (2002–2006) and again in 2010. Some visually obvious outliers were not included in circled sites.

To assess changes in potential faunal habitat provided by plants found in each lake and compare with 1987 results from Wilcox and Meeker (1992), we categorized prominent taxa found in 2002–2006 and 2010 into the five different life forms they used – thin-stem emergents, mat formers, low rosettes, low-growth aquatics, and erect aquatics – by matching their taxa in each category (Appendix C). We added erect aquatics *Ceratophyllum demersum, Elodea canadensis,* and *Utricularia vulgaris*, which were more prominent in 2002–2006 and 2010 than in 1987. The IVs of all taxa in each category were then summed for the mid-deep and deep transects of each lake.

Results

Floristics

Sampling across many sites in different years sometimes made identification of all specimens to species level difficult. Therefore, some taxa were combined at genus level for presentation. However, most *Isoetes* were likely *I. echinospora, and Sparganium* were *S. fluctuans. Sagittaria* were typically rosettes that could not be identified further. The terms "dominant" and "prevalent" are used in a descriptive sense and do not relate to wetland delineation indicators.

Mid-Deep Transect (1.25 m)

Based on IV, the 1.25 m mid-deep transect at two sites in Lac La Croix was dominated by *Najas flexilis, Nymphaea odorata, Myriophyllum* spp., and *Bidens beckii* in 1987 (Table 1). *Najas flexilis* remained dominant in 2002–2006 sampling of 10 sites, joined by *N. odorata*, with the addition of *Sagittaria* spp. Reductions were observed in *B. beckii* and *Myriophyllum* that continued in 2010 sampling. In 2010, this transect was also dominated by *N. flexilis* and *N. odorata*. The differences among years appear to be due to the numbers of sites sampled (e.g., *B. beckii* and *Myriophyllum* were dominant at only one of the two 1987 sites).

In 1987 sampling of two Rainy Lake sites, the mid-deep transect was dominated by *Vallisneria americana, Isoetes* spp., and *Sparganium* spp. (Table 1). *Vallisneria* and *Isoetes* remained dominant in ten 2002–2006 sampling sites, with the addition of *N. flexilis. Sparganium* spp. was reduced in 2002–2006 and remained low in 2010 sampling. *Vallisneria* was clearly most dominant in 2010, as reductions from 1987 through 2010 were seen in *Sparganium, Isoetes*, and also in less common species *Eleocharis acicularis* and *Potamogeton robbinsii* – again likely due to differences in the number of sites sampled, as there were no major changes in the Rainy Lake rule curve.

In 1987, the two Namakan Lake sites were dominated by *Ranunculus reptans, E. acicularis,* and *Crassula aquatica* at the mid-deep transect (Table 1). However, *E. acicularis* was much reduced in 2002–2006 and 2010 sampling of 11 sites expanded across the larger Namakan Reservoir, and *R. reptans* and *C. aquatica* were not found. Instead, this transect was dominated by *V. americana* and *N. flexilis* in both later sampling periods, with *Potamogeton gramineus* also prevalent in 2010.

Deep Transect (1.75 or 2.0 m)

At the deep transect, Lac La Croix was dominated by *N. flexilis, N. odorata, Myriophyllum* spp., *Potamogeton amplifolius*, and *V. americana* in two 1987 sites (Table 2). In 2002–2006 sampling, *Isoetes* spp. was also dominant, as were *N. flexilis* and *V. americana* when 10 sites were sampled. In 2010 sampling, *U. vulgaris* was also prevalent.

The deep transect at Rainy Lake was overwhelmingly dominated by *V. americana* in 1987, with *Potamogeton richardsonii* also prevalent and only two other species observed (Table 2). When 10 sites were sampled in 2002–2006 and again in 2010, *V. americana* and *P. robbinsii* were dominant, and more than 20 taxa were found in a broader sampling effort.

Namakan Lake sampling in 1987 found *Chara* spp. and *P. richardsonii* dominant at the deep transect, with *V. americana* also prevalent (Table 2). *Vallisneria* was much more dominant when 11 sites were sampled in both 2002–2006 and 2010 across broader Namakan Reservoir. *Chara* remained dominant but decreased successively from 1987 through 2010, while *N. flexilis* increased and was also dominant by 2010.

Ordinations

Mid-Deep Transect (1.25 m)

Ordination of the two sites per lake from the 1987 study by Wilcox and Meeker (1991), but including all years in which they were later sampled, showed that the plant community at the mid-deep transect differed by lake in 1987, with Lac La Croix to the right, Rainy in the center, and Namakan toward the top (Fig. 3). The Lac La Croix and Rainy communities remained similar in 2002 and 2010 sampling. However, the 2002 Namakan community at one site plotted with Rainy; in ensuing years (2004, 2006, 2010), both sites plotted between Rainy and the 1987 Namakan sites. These results suggest that vegetation at the mid-deep transect in Namakan had already changed by 2002.

To verify this observation, we conducted a full ordination of all mid-deep transect data from all sites in each lake across all years. The full ordination is shown in Fig. 4a with the 2002–2006 sampling sites for each lake circled. In this grouping, Lac La Croix plots separately from Rainy and Namakan. The Namakan sites are spread more widely and overlap with Rainy sites. The only outlier is one Rainy site from low water year 2003. However, the other two Rainy sites from 2003 were within the circled grouping. Figure 4b shows groupings by 2010 sampling sites. Lac La Croix remains different from Rainy and Namakan. Rainy sites remain in the center of the plot, and Namakan sites continue to overlap with Rainy but have outliers plotting closer to Lac La Croix.

Table 1 Importance values of 20 most prominent taxa on the mid-deep (1.25 m) transects at Lac La Croix, Rainy Lake, and Namakan Reservoir in northern Minnesota in 1987, 2002–2006, and 2010

Taxa	Lac La Croix			Rainy Lake			Namakan Reservoir		
	1987	2002–2006	2010	1987	2002–2006	2010	1987	2002–2006	2010
Bidens beckii Torr.	11.9	2.3	1.5	0.4	0.6	1		1.2	3.1
Ceratophyllum demersum L.		0.1			1.2	0.1		2.3	0.4
Chara spp.	6	2.4	0.4	1.4	1.4	0.8	2.4	2.4	2.3
Crassula aquatica L.							12.3		
Elatine minima (Nutt.) Fisher & C. Meyer			1.6		2.6	0.7	3.5	1.6	1.4
Eleocharis acicularis (L.) K. & S.		0.3	5	7.2	5.3	2.7	21.4	1.7	2.9
Eleocharis palustris (L.) Roem. & Schult.		6.5	5	2.9	1.4	3.8			
Elodea canadensis Michx.		0.5	0.1		3.2	0.7		2	3.4
Eriocaulon aquaticum Druce		2.1	3.6			0.3			1.1
Glyceria borealis (Nash) Batchelder		2.5	3.3			2.7	7.4	0.8	0.3
Isoetes spp.		3.3	2.3	18.8	11.8	8.4	5	7.6	3.2
Lemna trisulca L.								1.8	2.3
Myriophyllum spp.	16.6	4	6.8	0.7	1.1	1.7		0.8	2
Najas flexilis (Willd.) Rostik & Schmidt	21.6	20.4	15.1	4	14.6	9	2.1	21	18.5
Nitella spp.	2.2								
Nuphar variegata Durand	1.2	0.9	0.1		0.6				
Nymphaea odorata Aiton	19.5	8.6	11.6		0.2	5.4		3.5	2.2
Persicaria lapathifolia (L.) Delarbre							5.4		
Potamogeton foliosus Raf.	0.5			4.6					
Potamogeton gramineus L.		2.5	6.3	4.3	6.5	7.5	2.4	6.4	14.3
Potamogeton natans L.		0.2	0.3		3.7	0.1			
Potamogeton richardsonii (Benn,) Rydb.	4	0.4	1.2	4	1.4	1.5	0.5	1	1.8
Potamogeton robbinsii Oakes	0.5	0.4	0.1	4.3	2.9	0.2			
Potamogeton spirillus Tuckerman	3.5		6.1			6.7	1		1.3
Potamogeton zosterifomis Fern.	2.7	0.6	0.1		0.3			1.4	
Ranunculus longirostris Gordon	1.9	0.4	0.4		0.7	1.2	0.1		2.17
Ranunculus reptans L.							21.5		
Sagittaria spp.		14.4	6.8	9.5	5.6	8	5.7	6.1	5.2
*Shoenoplectus subterminalis (*Torr.) Sojak		3.3	0.5					0.3	
Sparganium spp.		5.3	3.5	14.1	6.1	6.8	0.3	0.6	0.6
Utricularia vulgaris L.	1.6	2.8	5		0.1			1.4	0.4
Vallisneria americana Michaux	5.1	1.6	1.3	25.5	16	26.5	5.3	21	13.6

In summary, it seems that Namakan Reservoir did respond to change in regulation plan and, although still resembling Rainy Lake, it is perhaps headed toward Lac La Croix. Additionally, this change seems to have occurred prior to the 2002–2006 sampling period.

Deep Transect (1.75 or 2.0 m)

The deep transect ordination of two sites per lake sampled by Wilcox and Meeker (1991) with all years for those sites included (Fig. 5) also showed that plant communities differed by lake in 1987. However, Lac La Croix site 9–87 was a clear outlier far removed from 2002 and 2010 Lac La Croix plots, which grouped near each other to the left. Rainy sites plotted in the upper right in all years, with the exception of outlier 7–10. Although the same two sites were sampled in each year, Namakan sites were spread across a wide range on Axis 2 from year to year. Namakan 5–02, 7–02, 5–06, and 5–10 resembled Rainy, while Namakan 7–06 more closely resembled Lac La Croix.

To explore these discrepancies further, we again conducted a full ordination of all deep transect data from all sites in each lake across all years. The full ordination is shown in Fig. 6a, with the 2002–2006 sampling sites for each lake circled. In

Table 2 Importance values of 20 most prominent taxa on the deep transects at Lac La Croix, Rainy Lake, and Namakan Reservoir in northern Minnesota in 1987, 2002–2006, and 2010

Taxa	Lac La Croix			Rainy Lake			Namakan Reservoir		
	1987	2002–2006	2010	1987	2002–2006	2010	1987	2002–2006	2010
Bidens beckii	0.6	4.9	4.6		6	6		3.4	4.5
Ceratophyllum demersum		0.6	0.6		0.9	0.4		5	0.7
Chara spp.	8.1	6.7			1.2		28.6	13.5	10.9
Crassula aquatica.							7.5		
Elatine minima	8.1	6.7		1.2			28.6	13.5	10.9
Eleocharis acicularis			0.1		0.2	0.3	4.4	0.4	2.9
Eleocharis palustris		0.3	0.4		1.7	3.9		5.1	4.9
Elodea canadensis		15.5	11.7		1.1	1.8	7.2	0.6	1.4
Eriocaulon aquaticum		1.6	0.9		0.1				
Heteranthera dubia (Jacq.) MacMill.			2.5		4	1.8			
Isoetes spp.		15.5	11.7		1.1	1.8	7.2	0.6	1.4
Juncus pelocarpus Meyer		1.6	0.9		0.1				
Myriophyllum spp.	14	1.8	6.4		5.3	5.5	1.7	2.9	6.6
Najas flexilis	15	10.9	16.2		4	6.2	5	9.3	16.2
Nitella spp.	7.8		9.8			3.4			0.7
Nymphaea odorata	14	9.1	8.5		0.3	0.4	2.9	3.5	2
Potamogeton amplifolius Tuckerman	13	0.1			0.2				
Potamogeton epihydrus Raf.	1.3	0.4	0.8		0.9	0.6			
Potamogeton foliosus	3.9			2.3			4.4		
Potamogeton gramineus.		2.5	2.1	3	0.6	0.5	1.8	1.6	3.4
Potamogeton robbinsii	9.7	1.4	1.4		14.2	15			0.3
Potamogeton spirillus	2.5		2.7			1.4	1.4		2.2
Potemogeton vaseyi Robbins			0.2				5.3		2.1
Potamogeton zosterifomis	3.5	1.3	1.1		0.5	0.3	0.5	1.7	0.4
Ranunculus longirostris		1.2	1.7		5.2	2.6	1.5	0.2	1.3
Ranunculus reptans							0.9		
Sagittaria spp.		4.7	2		0.7	0.3	0.5	0.5	1.8
Shoenoplectus subterminalis		6.2	0.8						
Sparganium spp.		4.7	2.1		0.6	1.4			1
Utricularia vulgaris		7.1	10.5		0.3	2.8		0.3	0.5
Vallisneria americana	11.3	11.2	8.3	78.7	40.9	36.5	9.5	36.2	20.6

this grouping, all water bodies plotted near the center, but with little overlap, each was distinct. The outliers were for Lac La Croix in 2005 and Namakan in 2002 – neither related to extreme water levels. When grouped by 2010 sampling dates (Fig. 6b), each lake expanded in range, with Lac La Croix and Rainy remaining distinct from each other and Namakan overlapping more with Lac La Croix. Two outliers were for Namakan in 2010 and thus did not relate to water levels.

Overall, the ordinations show that, with only minor changes in the regulation plan, Rainy Lake changed little from its 1987 composition to 2002–2006 or 2010 composition and showed little resemblance to unregulated Lac La Croix. As hydrologic conditions became more similar and additional sites were sampled, plant communities of Namakan Reservoir and Lac La Croix showed changes from those in 1987 and became more similar by 2010, as seen with the considerable overlap between these water-bodies.

Aquatic Growth Forms

Mid-Deep Transect (1.25 m)

In Lac La Croix, prevalence of thin-stem emergents, mat formers, and low rosettes increased at the mid-deep transect during low water years in 2002, 2006, and 2010 from non-existent in 1987 (Table 3). In contrast, low-growth aquatics and erect aquatics were both reduced in the later time periods in which water levels were low. In Rainy Lake, low rosettes were

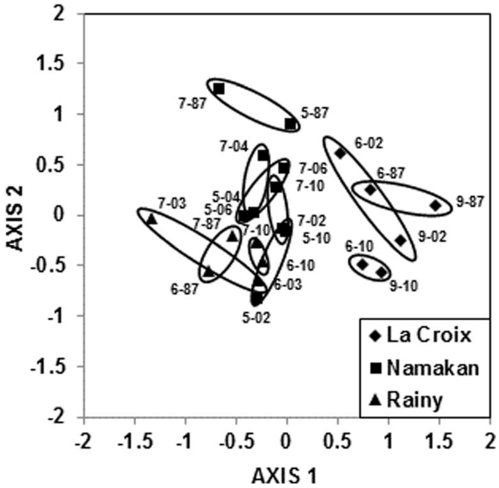


Fig. 3 Two-dimensional plot of NMDS ordination of the Importance Value vs. transect matrices for the mid-deep transects in all years at Lac La Croix, Rainy Lake, and Namakan Reservoir sites sampled in 1987 by Wilcox and Meeker (1991). Points plotted are site number-year (e.g., 7–87) labeled by lake. Autopilot on, Sorenson distance, no species weighting, final stress = 14.58, final instability = 0.0000, number of iterations = 88

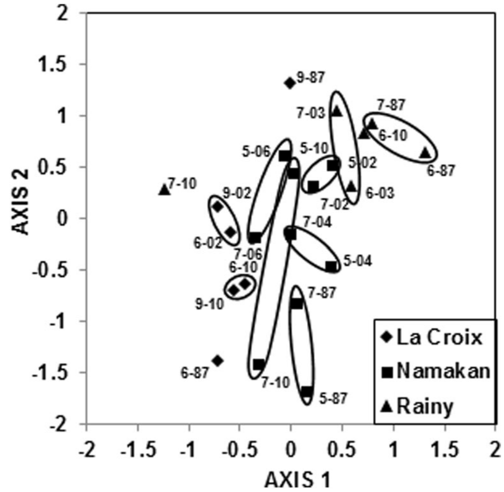


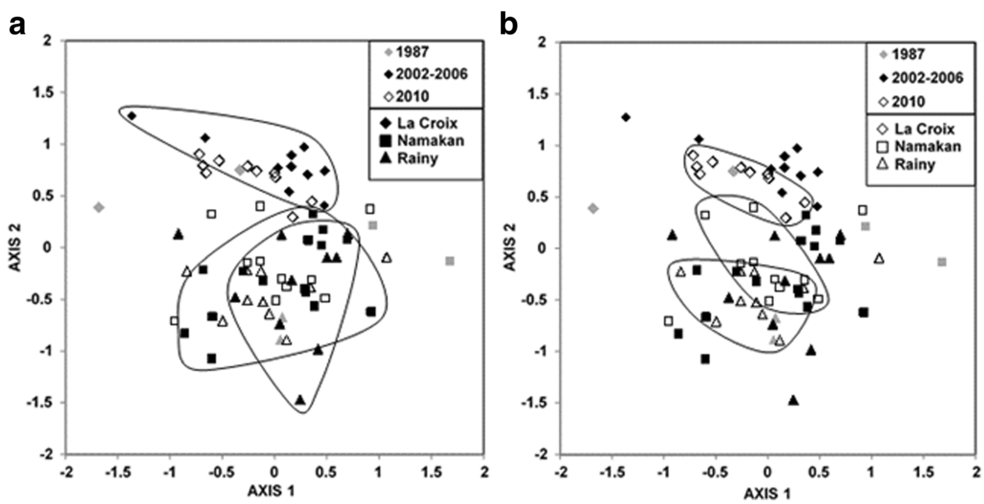
Fig. 5 Two-dimensional plot of NMDS ordination of the Importance Value vs. transect matrices for the deep transects in all years at Lac La Croix, Rainy Lake, and Namakan Reservoir sites sampled in 1987 by Wilcox and Meeker (1991). Points plotted are site number-year (e.g., 9–87) labeled by lake. Visually obvious outliers were not included in circled groupings. Autopilot on, Sorenson distance, no species weighting, final stress = 13.68, final instability = 0.0000, number of iterations = 94

reduced and low-growth aquatics increased from 1987 levels at both later times. The most obvious change in prevalence of life forms was in Namakan Reservoir, where the new rule curve produced changes in flooding/dewatering conditions. Thin-stem emergents, low rosettes, and especially mat formers were already greatly reduced in 2002–2006 from those in 1987 under the old rule curve and remained low in 2010. Low-growth aquatics and erect aquatics both increased greatly following the change in regulation plan. In 2002–2006, potential faunal habitat in Namakan Reservoir, as determined by life forms of aquatic vegetation, bore some resemblance to Rainy Lake, but by 2010, it more closely resembled that of Lac La Croix at the mid-deep transect, with the exception of some thin-stem emergents appearing in Lac La Croix. Namakan and Rainy were less similar, and Rainy differed from Lac La Croix.

Deep Transect (1.75 or 2.0 m)

Low rosettes appeared at the deep transect in Lac La Croix in 2002 and 2006 when water levels were low (Appendix A), and low-growth aquatics were reduced from 1987 (Table 3). In Rainy Lake, low-growth aquatics increased in 2002–2006 and 2010, while erect aquatics seemed to have decreased; however, the 1987 value for erect aquatics was greatly influenced by dense stands of *V. americana* in one of the two sites sampled that year. Following the change in rule curve, mat formers and low rosettes were greatly reduced in both 2002–2006 and 2010 in Namakan Reservoir, while erect aquatics increased greatly. Across all life-form categories in 2002–2006, aquatic growth forms in Namakan were quite similar

Fig. 4 Two-dimensional plot of NMDS ordination of the Importance Value vs. transect matrices for the mid-deep transects at all sites in Lac La Croix, Rainy Lake, and Namakan Reservoir in all years. Points plotted are identified by year and lake. Groupings are shown for 2002–2006 data (**a**) and 2010 data (**b**). Visually obvious outliers were not circled. Autopilot on, Sorenson distance, no species weighting, final stress = 16.59, final instability = 0.0000, number of iterations = 112



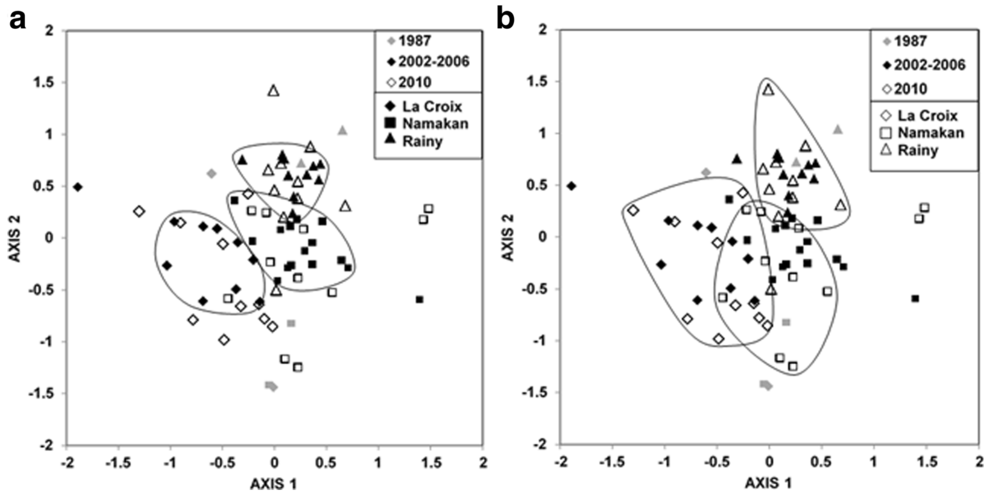


Fig. 6 Two-dimensional plot of NMDS ordination of the Importance Value vs. transect matrices for the deep transects at all sites in Lac La Croix, Rainy Lake, and Namakan Reservoir in all years. Points plotted are identified by year and lake. Grouping are shown for 2002–2006 data (**a**) and 2010 data (**b**). Visually obvious outliers were not circled. Autopilot on, Sorenson distance, no species weighting, final stress = 14.27, final instability = 0.0000, number of iterations = 82

to Rainy at the deep transect, but by 2010, Namakan low-growth and erect aquatics were similar to Lac La Croix. Namakan and Rainy differed in the extent of erect aquatics in 2010 but were similar in other growth forms. Rainy differed from Lac La Croix in both low rosettes and erect aquatics in 2010.

Discussion

Plant Species Changes Vs. Habitat Requirements

Mid-Deep Transect (1.25 m)

The most obvious changes in species occurrence at the mid-deep transect were in marked decreases at Namakan Reservoir for *E. acicularis, R. reptans*, and *C. aquatica*. All are short, bottom-dwelling species favored by drawdown (Ashton and Bissell 1987, Renman 1989, Rorslett 1989) that formed dense mats during regulation under the 1970 plan when this elevation was typically dewatered from February to April (Wilcox and Meeker 1991). This elevation was under water when ice formed, but dewatering allowed ice to settle onto the substrate. Rhizomes of *E. acicularis* break into fragments upon freezing, allowing each piece to grow vegetatively to form a mat (Renman 1989). *Ranunculus reptans* is a clonal perennial (Odland and del Moral 2002) that aborts stolons upon freezing to reduce mass, which may allow it to withstand frost heave and become dominant (Renman 1989). *Crassula aquatica* is an annual plant favoring muddy shores that can get established during drawdown (Chadde 2012). Also decreasing at the mid-deep transect under the new regulation plan were *Elatine minima*, a small mat-forming annual often found on mudflats, *Glyceria borealis,* a perennial grass also common to

Table 3 Sum of Importance values for taxa in each of five life-form categories (Wilcox and Meeker 1992) on mid-deep (1.25 m) and deep (1.75, 2.0 m) transects at Lac La Croix, Rainy Lake, and Namakan Reservoir in northern Minnesota in 1987, 2002–2006, and 2010

	Lac La Croix			Rainy Lake			Namakan Reservoir		
	1987	2002–2006	2010	1987	2002–2006	2010	1987	2002–2006	2010
1.25 m transects									
Thin-stem emergent	0	9	8.3	2.9	1.4	6.5	13.3	0.8	0.3
Mat-formers	0	0.3	6.6	7.2	7.9	3.4	46.4	3.3	4.3
Low rosettes	0	17.7	9.1	28.3	17.4	16.4	22.8	13.7	8.4
Low-growth aquatics	33.8	23.2	21.7	8.3	18.9	16.7	5.4	23.4	22.1
Erect aquatics	54.1	25.6	31	49.1	29.8	43.7	0.5	33.8	27.5
1.75–2.0 m transects									
Thin-stem emergent	0	0	0	0	0	0	0	0	0
Mat formers	0	0	0	0	0.4	0.3	12.4	0.6	3.3
Low rosettes	0	20.2	13.7	0	1.8	2.2	13.6	1.1	3.2
Low-growth aquatics	43	19	30.1	0	19.4	26	34.9	22.8	30.3
Erect aquatics	52.1	41.6	49.4	96.8	63.3	63	29.2	59.3	45.6

mudflats, and *Persicaria lapathifolia*, a common mudflat annual (Chadde 2012). Under the 2000 regulation plan, winter drawdowns no longer dewater the mid-deep transect, thus minimizing ice formation in the sediments and exposure of mudflats that promoted those species. As might be expected, the reduction or loss of these species occurred soon after the change in regulation plan, as noted by sampling in 2002–2006.

Without dewatering in the growing season in most years, the mid-deep transect at Namakan Reservoir became suitable habitat for submersed aquatic plants under the 2000 regulation plan, with *N. flexilis, P. gramineus*, and *V. americana* becoming dominant. *Bidens beckii, Elodea canadensis, Myriophyllum* spp., *Potamogeton natans*, and floating *N. odorata* were also found under the new plan. Again, the changes were already observed in 2002–2006 sampling.

The 2000 regulation plan did little to change plant habitats at Rainy Lake, but reductions in *E. acicularis, Isoetes* spp., and *Sparganium* spp. were noted in both post-2000 sampling periods. Perhaps this can be explained by unusually low water levels in 1987 (Wilcox and Meeker 1992) that provided suitable habitat at that transect elevation in Rainy Lake that year. Many more taxa were found in 2002–2006 and 2010 than in 1987, which was likely the result of sampling many more sites. Similar increases in total taxa sampled were found at unregulated Lac La Croix in 2002–2006 and 2010, likely due to increased sampling sites; however, low water levels in 2002 may have resulted in appearance of more taxa.

Deep Transect (1.75 or 2.0 m)

Elatine minima, E. acicularis, and *C. aquatica* were less prevalent at the deep transect elevation than the mid-deep transect in 1987 in Namakan Reservoir because winter drawdown to the sediment was more limited under the 1970 regulation plan. However, coverage of these plants was also reduced under the 2000 regulation plan, as early as in 2002, likely for similar reasons as at the mid-deep transect. Submersed aquatics *E. canadensis, Myriophyllum* spp., *N. flexilis,* and *V. americana* responded with increases under the 2000 regulation plan when dewatering no longer occurred. Again, the increase began by 2002.

Only four species were present at the deep transect plots of Rainy Lake in 1987. When more extensive sampling under the 2000 regulation plan was conducted in 2002–2006 and 2010, species richness increased substantially but was likely related to more sampling, not the regulation plan. At Lac La Croix, species richness also increased with greater sampling effort, but the only notable difference between 1987 and later sampling efforts was appearance of substantial amounts of *Isoetes* spp., which may have been present in 1987 but not sampled.

Potential Effects on Fauna

Invertebrates

Wilcox and Meeker (1992) suggested that the occurrence of only erect aquatic plants at the 1.75-m deeper elevation of Rainy Lake under the 1970 rule curve should result in reduced diversity of aquatic invertebrates (Brown et al. 1988). However, Kraft (1988) reported greater diversity of invertebrate species at both 1- and 2-m depths than in deeper waters of Rainy Lake in 1984–1985 sampling. The presence of other growth forms in 2002–2006 and 2010 sampling of more sites at the deeper transect, with no effective change in hydrology, supports Kraft's conclusion if those additional sites had greater plant diversity than the two 1987 sites of Wilcox and Meeker (1992). In Namakan Reservoir, Kraft (1988) found the greatest diversity of invertebrates at depths greater than 3 m that were never dewatered. Wilcox and Meeker (1992) attributed this to near lack of low-growth and erect aquatics at the 1.25 m mid-deep transect. By 2002–2006 and again in 2010, the plant structural groups at the mid-deep and especially the deep transect of Rainy and Namakan were more similar than in 1987.

Sampling by McEwen and Butler (2010) in 2004–2005 found changes in macroinvertebrate community structure at 1–2 m depths in Namakan Reservoir. A before-after study by Ferrington and McEwen (2015) conducted in 2012–2013, with sampling targeted to vegetation beds, concluded that invertebrate communities at 1–2 m had progressively become more similar between lakes since the 2000 rule curve was implemented. They also found that Simpson's diversity index was higher in Namakan than Rainy in 2013. Based on our data, we attribute those results to increased similarity of habitat provided by plant structural groups at both transects following the change in regulation plan.

Aquatic Birds

Physical structure of vegetation is important to marsh-nesting birds (Weller 1978). In 1983–1986, Reiser (1988) found 14 bird species in Rainy Lake and Namakan Reservoir with affinities for aquatic vegetation and concluded that some were likely affected by depauperate nesting sites related to alterations of plant communities. Many birds feed on foliage, shoots, tubers, and seeds of aquatic vegetation, as well as the invertebrates that inhabit the vegetation (Weller 1981). Thus, Wilcox and Meeker (1992) concluded that vegetation at 1.75 m in Rainy Lake and 1.25 m in Namakan Reservoir was likely of reduced habitat value under the 1970 rule curve. The changes we found in both structure and diversity of aquatic plant communities at the 1.25-m mid-deep transect at Namakan Reservoir following the change in regulation plan thus likely improved nesting and feeding habitat for birds. A follow-up study by Grabas et al. (2013) was unable to draw conclusions due to relatively low water levels in 1995–1997 and unusually high water levels in 2008 that affected plant communities.

Fish

At least 12 of the 48 fish species found in the lakes of Voyageurs National Park are known to use wetland or aquatic plant communities in one or more life-history stages (Wilcox and Meeker 1992). Plants provide spawning habitat for fish species such as northern pike (*Esox lucius* L.) and yellow perch (*Perca flavescens* Mitchell) that were studied by Kallemeyn (1987) in Rainy Lake and Namakan Reservoir in relation to water-level regulation under the 1970 rule curve. Yellow perch prefer to spawn on submersed aquatic vegetation (Krieger et al. 1983), which was in low supply at the mid-deep and deep transects of Namakan Reservoir under the 1970 rule curve (Wilcox and Meeker 1992). Although no post-2000 rule curve data have been collected to replicate the Kallemeyn (1987) study for perch, the increase in submersed aquatic vegetation in Namakan Reservoir provided greater areas of preferred spawning substrate and likely affected perch populations. Northern pike prefer to spawn on flooded grasses and sedges (Becker 1983, Pierce 2012), but they are forced to use other habitats, with less success, when regulated water levels in springtime are low (Farrell et al. 2006), as was found in Namakan Reservoir by Kallemeyn (1987).

Larval northern pike were sampled by Timm and Pierce (2015a) following implementation of the 2000 rule curve. They used quatrefoil light traps for sampling in Rainy Lake and the Kabetogama Lake portion of Namakan Reservoir in the spring of 2012 and 2013 as part of a long-term study. No significant differences were found in catch rates across the 2004–2013 long-term data set, suggesting that perhaps any changes related to the new rule curve could have occurred soon after its implementation, although this conclusion may be confounded by other reasons for differences in year-class strength. Across lakes, the catch rates were greatest in the available *Typha* x *glauca* Godr., *Sparganium* spp., *Carex* spp., and *Zizania palustris* L. that, unlike newly emerging submersed aquatic taxa, provided flooded plant biomass from the previous year for spawning substrate. In Namakan Reservoir, that dead emergent vegetation at higher elevations typically had not been flooded in the spring under the 1970 rule curve.

Minnesota DNR conducted long-term sampling of young-of-the-year (YOY) northern pike from 1983 to 2014 in Rainy Lake and Kabetogama Lake using seines (Timm and Pierce 2015b). Although variable by year, post-2000 rule curve catches were consistently greater at both lakes, and Timm and Pierce (2015b) concluded that those increases in mean catches were significant. At Kabetogama Lake, the increased catches were significantly correlated with May and June water levels.

Timm and Pierce (2015b) also set trap nets in preferred vegetation types in the summer of 2012 and 2013 in Rainy Lake, Kabetogama Lake, and Namakan Lake to collect YOY northern pike. The plants with the greatest frequency of occurrence in the vegetation types where trap nets were set included *T.* x *glauca, Potamogeton* spp., *Z. palustris, C. demersum,* and *V. americana*. In our study, *Vallisneria* was shown to be the most dominant species at both mid-deep and deep transects in Rainy Lake in 1987 under the 1970 rule curve and also in 2002–2006 and 2010 under the 2000 rule curve. In Namakan Lake, mat formers and low rosettes that dominated both transects in 1987 were replaced by *Vallisneria* in post-2000 rule curve sampling (as well as *Potamogeton* at the mid-deep elevation), thus providing an increase in erect aquatic submersed vegetation from that available under the 1970 rule curve. According to previous research, this type of vegetation is preferred by northern pike YOY (Holland and Huston 1984, Cook and Bergersen 1988).

Response Time and Future

Changes in the rule curve for Rainy Lake were not great, but they were substantial for Namakan Reservoir. How long did it take for plant communities to respond to the 2000 rule curve in Namakan Reservoir, are changes still occurring, and what might be expected in the future?

At the mid-deep transect, the Namakan plant community had already changed and was more similar to Rainy by 2002, but bore little resemblance to Lac La Croix (Fig. 3). Across all 2002–2006 sampling dates, Namakan and Rainy were very similar (Fig. 4a). Potential faunal habitat in Namakan had also changed and showed similarities to both Rainy and Lac La Croix in 2002–2006 (Table 3). However, those changes were not stable. Sampling in 2010 showed the plant communities of some Namakan sites to resemble Lac La Croix (Fig. 4b), as did potential faunal habitat (Table 3). At the deep transect, the Namakan plant community had also changed by 2002, with some sites resembling Rainy (Fig. 5). However, across the 2002–2006 sampling period, the Namakan plant community was more distinct from those of the other lakes, although some sites more closely resembled Lac La Croix and others resembled Rainy (Fig. 6a). Life forms at the deep transect in Namakan resembled Rainy in 2002–2006 but had similarities to Lac La Croix by 2010 (Table 3). By 2010, the resemblance of the Namakan plant community to Lac La Croix also became greater (Fig. 6b).

Thus, it seems that within two years, conversion of dewatered sediment to standing water habitat at the mid-deep transect in Namakan Reservoir had reduced thin-stem emergents (*G. borealis, P. lapathifolia)*, mat-formers

(*E. minima, E. acicularis, R. reptans*), and low rosettes (*C. aquatica*) and increased low-growth aquatics (*N. flexilis*) and erect aquatics (*B. beckii, C. demersum, E. canadensis, N. odorata, V. americana*). Ten years after the change in rule curve, there was little further change in the species with reduced coverage, but *N. flexilis, C. demersum,and V. americana* decreased from 2002 to 2006 levels, while *B. beckii, P. gramineus,* and additional submersed aquatics continued to increase. Some of the changes shown in 2010 suggest that the mid-deep transect at Namakan may be progressing toward La La Croix in plant community composition.

Within two years, conversion of dewatered sediment to standing water at the deep transect in Namakan also reduced *E. minima, E. acicularis*, *C. aquatica, Isoetes* spp., and *Chara* spp., accompanied by increases in *B. beckii, C. demersum, E. canadensis, N. flexilis,* and *V. americana*. Following ten years, *V. americana* showed a decrease but *B. beckii, C. demersum, E. canadensis, N. flexilis,* and other submersed aquatics continued to increase, also suggesting that Namakan may be progressing toward Lac La Croix.

The ultimate goal of the change in rule curves was to restore ecosystem functions in the regulated lakes. The rule curve and presumably function for Rainy Lake changed little. However, indications that Namakan Reservoir is becoming more like Lac La Croix suggest progress toward that goal, but changes in function may still be happening, and future studies may be warranted. The speed at which changes began to occur also suggests that studies to track vegetation change on other regulated lakes should begin in the first growing season after new regulation plans are enacted and should continue periodically for a decade or longer.

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