Changes in Wetland Vegetation Associated with Lake Level Management, Voyageurs National Park

Principle Investigators

James E. Meeker
Department of Natural Resources and Biology
Northland College
Ashland, WI 54806
USA
(715) 682-1550
jmeeker@northland.edu

Allan G. Harris
Northern Bioscience
363 Van Horne St.
Thunder Bay, Ontario, P7A 3G3
Canada
(807) 344-7213
aharris@tbaytel.net

Executive Summary

We present here the results from an additional year of research (2010) on the aquatic plant responses to the 2000 Rule Curves for Rainy Lake and Namakan Reservoir to provide the required data for the 2015 IJC review of the 2000 Rule Curves. Abundance and composition of nearshore aquatic plant communities were assessed at previously monitored sites to investigate how strongly any vegetative differences among water bodies are correlated with the effects of the 2000 Rule Curves and other environmental factors. Sites on two treatment water bodies (Rainy Lake and

Namakan Reservoir) and one control water body (Lac la Croix) were revisited to monitor changes in wetland plant communities. We employed similar sampling techniques as in two earlier studies (1987 and 2002-2005, with a few samples in 2006) to maintain methodological and taxonomic consistency in this ongoing assessment.

Findings

One of the main findings of this study was that we demonstrated an obvious difference in the vegetative composition and structure between the 2.0m and the 1.25m elevations. That is, the driving force influencing the composition and structure of vegetation in any water body is water depth resulting from the history of water-level fluctuations at each elevation and, of course, this is directly related to the rule curves (in the regulated water bodies). The results clearly indicate that there is a greater difference between elevations than any differences we observed over time, from time 1 (2002-2005) to time 2 (2010). This suggests that any further analyses comparing water bodies for changes over time should be conducted at each elevation separately.

In addition, there continued to be clear differences in aquatic vegetation *among water bodies* at both elevations. In 2002-2005 and in 2010, Lac la Croix appeared to differ in composition from the regulated Rainy Lake at both elevations, Lac la Croix differed from the Namakan Reservoir at the 1.25 elevation but only slightly at the 2.0m elevation, and Namakan more closely resembled Rainy at the 1.25 elevation. We may ask, had these assemblages been different prior to dam construction? Although we can never answer this for certain, it is likely that these water bodies had similar species pools, and some of the taxa still absent or at low abundance today in Namakan were likely put at disadvantage over years of reservoir-like conditions that exposed aquatic vegetation to desiccation and freezing on an almost annual basis.

Probably the most important question to be addressed is whether or not we noted changes in the abundance and composition of aquatic vegetation over the time period between the two recent studies (2002-2005 vs. 2010), as a means to assess empirically the vegetative response to the new rule curves. This comparison is notable in that, by 2005, we had added 8 -9 more sites in each water body, creating more statistically dependable analyses. We did document a few changes in total cover in Lac la Croix and Rainy, water bodies where we did not expect change, and noted little to no change in Namakan where we had predicted it.

Additionally, across all three water bodies, there was little indication that the abundance of individual dominant taxa differed much over time (2002-2005 vs. 2010). Of the ten most abundant taxa by cover at each elevation in 2010, eight taxa were also the most abundant in 2002-2005 for each water body at each elevation.

On the other hand, between 1987 and 2002, there appeared to be a 3- to 5-fold increase in the cover of tall submergent vegetation at both elevations of Namakan, in contrast to the Namakan comparison between 2002 and 2010, where no differences were detected. This is evidence that vegetative changes in Namakan probably took place between 1987 and 2002 as Namakan’s water-level regime began to approach that of the 2000 rule curve. The caveat in these analyses is that there were only two sites sampled in each water body in 1987. However, additional more robust evidence also indicating plant composition has changed since 1987 includes the ordination analyses. Ordinations using data from all three time periods (1987, 2002-6, and 2010) indicated change from 1987 at all three water bodies, but especially at Namakan at both the 1.25m and at 2.0m elevations.

In summary, it is clear that all three water bodies continue to differ in some aspects of their plant composition, as would be expected with their differences in annual highs and lows over the last 90 years. However, Rainy and Namakan are now more similar at the 1.25m elevation than they were in 1987, and Namakan and Lac la Croix are more similar at the 2.0m elevation. The 2000 changes in the rule curves in Namakan have now required a reduction in the fluctuation amplitude that was observed in the first 60-65 years of dam management. From an aquatic vegetation perspective, maintaining this more benign hydrological environment is critical in supporting the change we suggest began to occur in Namakan since the 1987 study. The fact that we did not note changes for the period 2002 to 2010 is most likely due to aquatic vegetation having already begun to respond by the mid-1980s and stabilized by 2000.

Purpose

The purpose of this study was to assess the possible changes in aquatic plant communities at Voyageurs National Park (VNP) since the initiation of the 2000 Rule Curves and to relate any noted change with water-level regulation. To accomplish this, abundance and composition of nearshore aquatic plant communities were assessed at previously monitored sites to investigate how strongly any vegetative differences among water bodies are correlated with the effects of the 2000 Rule Curves and other environmental factors.

The U.S. National Park Service funded monitoring of five indicators, including wetland vegetation, to facilitate their understanding of the effects of the 2000 Rule Curves. We present here an additional year of research on the aquatic plant responses to the 2000 Rule Curves to provide the required data for the 2015 IJC review of the 2000 Rule Curves. Sites on two treatment water bodies (Rainy Lake and Namakan Reservoir) and one control water body (Lac la Croix) were revisited to monitor changes in wetland vegetation communities.

We employed the same sampling techniques as in the 2002 to 2005 studies (Meeker and Harris 2009) and methods similar to a 1987 study (Wilcox and Meeker 1991) to maintain methodological and taxonomic consistency in this ongoing assessment. Sampling techniques used in this study and in the 2002 to 2005 studies are described below.

Background

Beginning about 1987-88, the middle, rather than the extremes of the previous rule curves (1970 rules), began to be targeted, resulting in a reduction of the extreme fluctuations in the Namakan Reservoir (Figure 1). Following a ruling by the International Joint Commission, new rule curves were established in 2000 (Figure 2). In 2002-2006, Voyageurs National Park (VNP) began to document vegetative response to the new rule curves by re-sampling the areas sampled in 1987 and starting a new, more robust, baseline assessment (Meeker and Harris 2009).

Changes under the 2000 Rule Curves

Changes under the 2000 Rule Curves include (Figure 2):

1. A considerable reduction of the drawdown in the Namakan Reservoir and the establishment of its annual peak in late May followed by gradual decline in water

level the rest of the growing months. Namakan's annual range was reduced from about 2.7m to less than 1.8m.

2. A slight increase in summer drawdown on Rainy Lake, changing the range from 1.1m to 1.05m.
3. Instructions for the dam operators to target officially the middle levels of the rule curve bands.

For reference, the mean annual range of Lac la Croix, the control lake, has been approximately 1.6m.

For Rainy Lake, these changes were minimal, but for the Namakan Reservoir, Meeker and Harris (2004) identified four distinct zones that characterized the difference between the 1970 and 2000 Rule Curves:

Zone 1: Areas that were formerly dewatered (i.e., exposed) in late winter should be now permanently covered. (Elevation relative to mean high water < 339.0 m).

Zone 2: Areas temporarily exposed under old and new curves. Flooding and dewatering cycle is similar under old and new rule curves, but the depths and time are shifted. Example: areas at 340.0 meters elevation were exposed under the old rule curve from mid-Dec. to end of May. Under the new curve, that area is exposed only until the beginning of May. Thus, the duration of exposure is reduced by approximately one month.

Zone 3: Areas formerly flooded throughout most of the growing season are now gradually dewatered through the growing season (Elevation approximately = 340.9 m to 340.7 m, the shoreline zone).

Zone 4: Shoreline fens that rise and fall with changing water level (for example, the west end of Kabetogama Lake). The vegetation is not rooted to mineral substrate but floats on a mat of organic material.

The recognition of these four zones allowed predictions of how the aquatic vegetation should have changed relative to the new regime and directed the 2002-2005 monitoring in the Namakan Reservoir efforts. These predictions included:

Zone 1: Aquatic vegetation (other than rosette-forming species) will increase in cover and frequency in Zone 1 on Namakan Reservoir. Maintaining water cover during the winter should reduce desiccation and freezing damage to plant tissues and reduce ice-scour of sediments.

Zone 2: Aquatic vegetation will show little net change in Zone 2 on Namakan Reservoir.

Zone 3: Cover of shrubs and other species intolerant of prolonged flooding through the growing season will increase in Zone 3 on Namakan Reservoir. Summer drawdown increases oxygen availability in the rooting zone and enhances vegetative reproduction of clonal species and germination of seeds of some emergent species.

Zone 4: Floating fen vegetation will show little change.

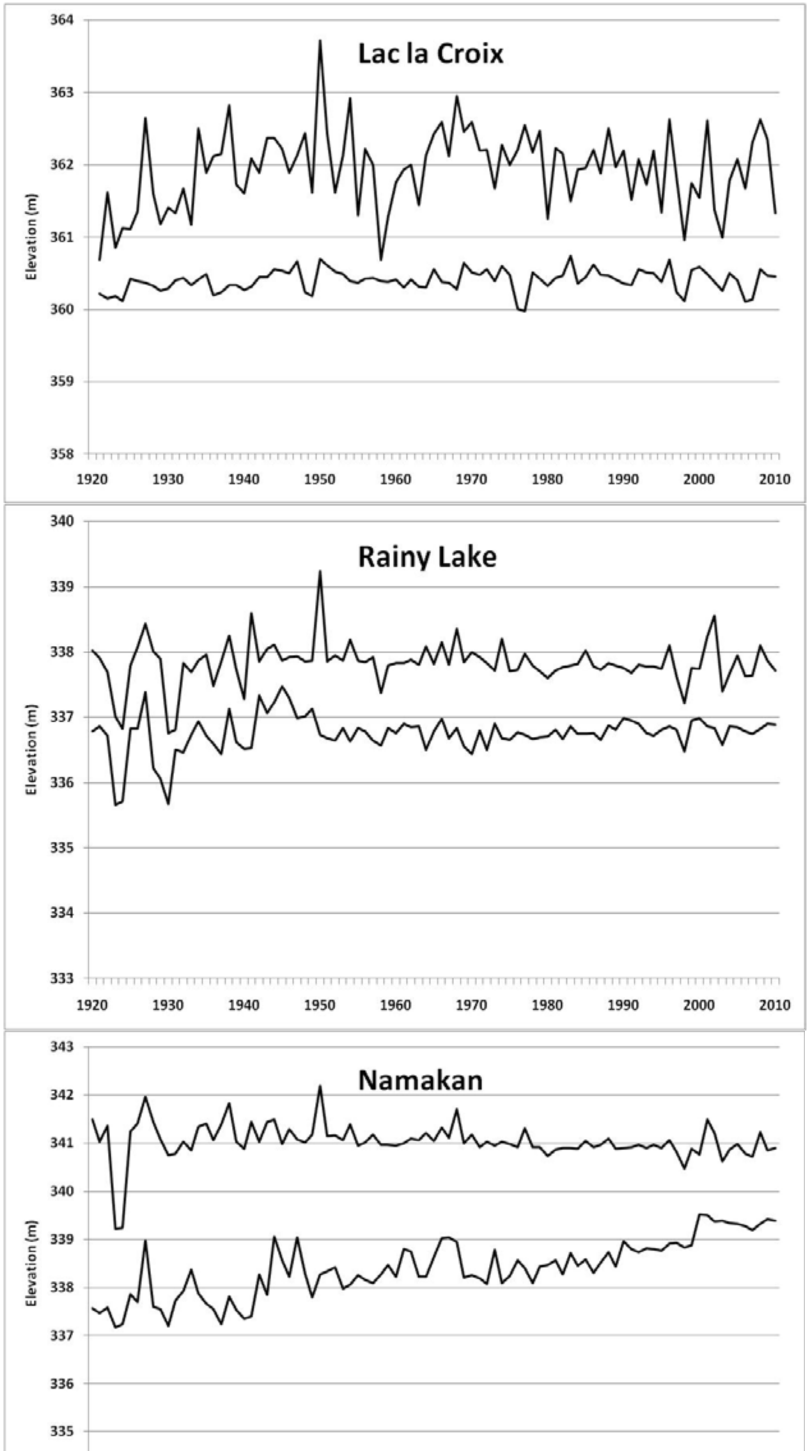
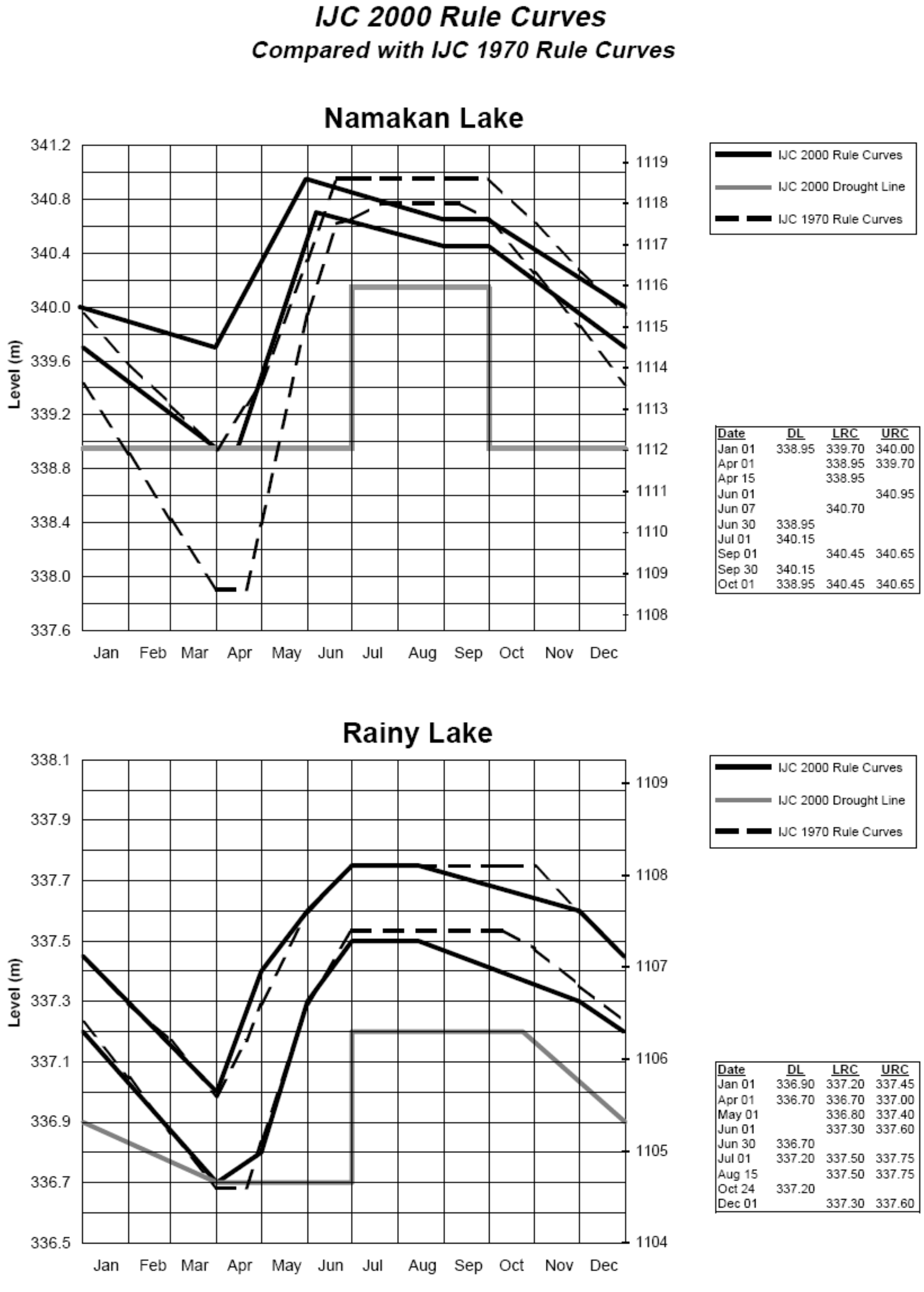


Figure 1. Annual extreme water levels for the period 1920 to 2010 for Lac la Croix, Namakan Reservoir, and Rainy Lake. Note differences in y axis scales.



Date	DL	LRC	URC
Jan 01	338.95	339.70	340.00
Apr 01		338.95	339.70
Apr 15		338.95	
Jun 01			340.95
Jun 07		340.70	
Jun 30	338.95		
Jul 01	340.15		
Sep 01		340.45	340.65
Sep 30	340.15		
Oct 01	338.95	340.45	340.65

Date	DL	LRC	URC
Jan 01	336.90	337.20	337.45
Apr 01	336.70	336.70	337.00
May 01		336.80	337.40
Jun 01		337.30	337.60
Jun 30	336.70		
Jul 01	337.20	337.50	337.75
Aug 15		337.50	337.75
Oct 24	337.20		
Dec 01		337.30	337.60

Figure 2. Rule curves for Rainy Lake and Namakan Reservoir. 1970 Rule Curves (dashed) and 2000 Rule Curves (solid) (adapted from Kallemeyn et al. 2003).

Studies and hydrology during the period 1987-2002

In 1987, as part of initial studies of lake-level effects at VNP, the aquatic vegetation of the three water bodies was assessed (Meeker and Wilcox 1989; Wilcox and Meeker 1991). These studies found differences in structure and composition among the three water bodies, especially among deep elevation aquatic macrophytes. Vegetation in the Namakan Reservoir was exclusively dominated by mat-forming species tolerant of extreme drawdowns, while that in Rainy was dominated by dense, erect aquatics; vegetation in Lac la Croix was intermediate to the other two lakes (Figure 3). These vegetative structural differences between the regulated lakes and Lac la Croix were implicated in the degradation of other biota that depend on the vegetation in the regulated lakes (Wilcox and Meeker 1992; Kallemeyn et al. 1993).

Partially in response to the 1987 study, water levels in Namakan Reservoir appeared to have been maintained closer to the middle of rule curve beginning in about 1987. Therefore, during the period 1987 to 2002, wetland vegetation should have begun to respond in the manner suggested by the above predictions. Analyses of the 1987 to 2002 data in Namakan (Meeker and Harris 2009) indicate that this may have been the case. For example, at the 1.75 m elevation in 1987 (Figure 3, adapted from Wilcox and Meeker 1991), the Namakan sites were dominated by mat-forming species that were favored by the extreme drawdown, whereas in 2002 these taxa were partially replaced by larger stature aquatic macrophytes (Meeker and Harris 2009).

Summary of 2002-2005 study

During 2002-2005, Meeker and Harris established sampling programs in Rainy Lake, Namakan Reservoir, and Lac la Croix at what were termed “intensive” sites (detailed floristic data). One component of the intensive effort was the repeat sampling of two sites in each of the three water bodies. This repeat sampling continued the initial work that was done in 1987. In addition to this repeat sampling, the total pool of wetlands was increased in the Namakan Reservoir to 11 sites, in Lac La Croix to 10 sites, and in Rainy Lake to 10 sites.

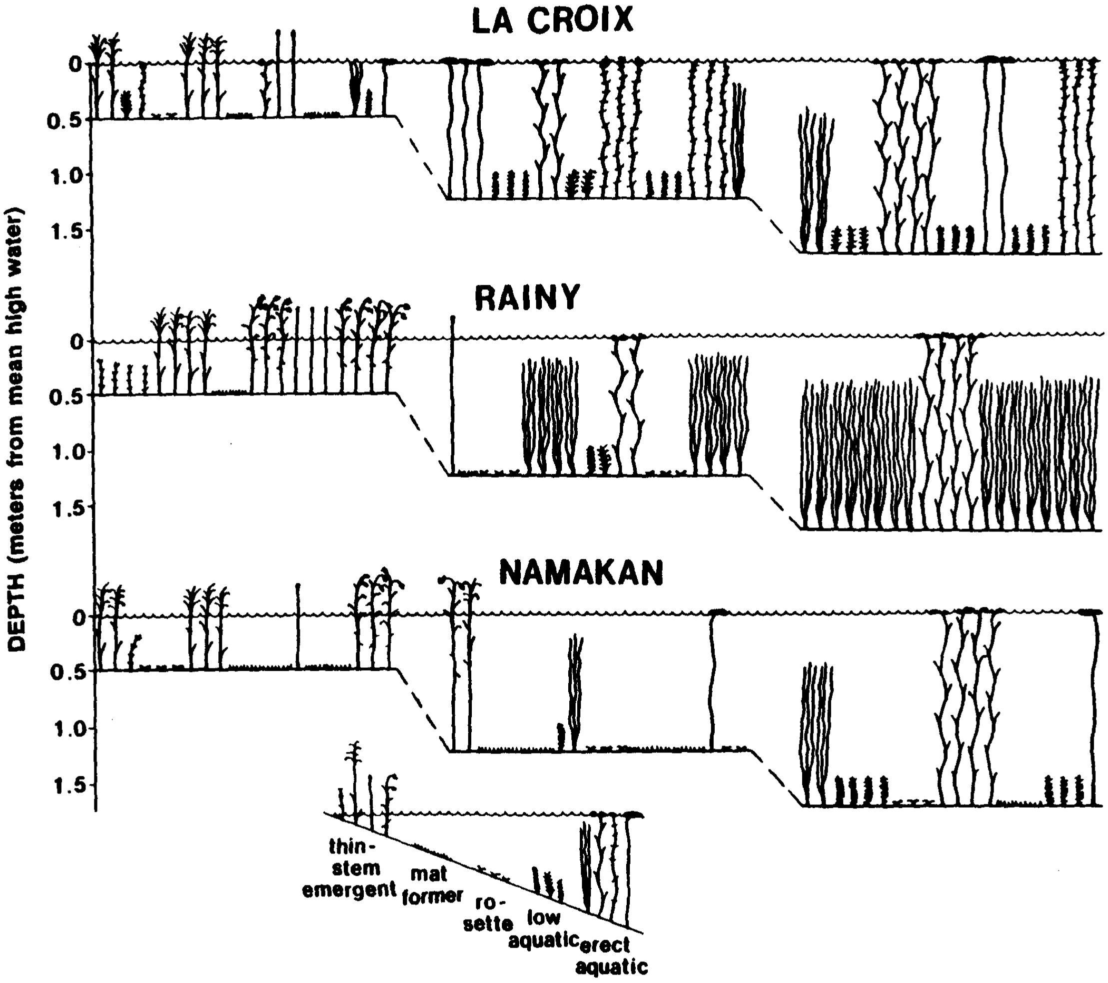


Figure 3. Schematic diagram representing the vegetation structure in 1987 at select elevations across two regulated water bodies, Namakan Reservoir and Rainy Lake, as compared to the unregulated Lac la Croix (adapted from Wilcox and Meeker 1991).

Again, the predictions for the future relative to the changes in rule curves would be that the Namakan Reservoir sites may increase in macrophyte abundance since, under the 2000 Rule Curves, these areas (Zone 1) will not be drawn down and exposed to winter/spring desiccation and freezing. Zone 1 in Rainy Lake would be unchanged and aquatic vegetation may not be altered, although all wetlands may change due to other factors.

Methods

Site Selection

Thirty-one sites were chosen for sampling, 10 each in Rainy and Lac la Croix (LLC), and 11 in Namakan. Prior to selecting the 25 additional sites (6 were already chosen in 1987), a pool of potential wetland sampling sites in the Rainy Lake and Namakan Reservoir was randomly chosen from the Voyageurs vegetation database (Hop et al. 2001). The area covered by vegetation mapping includes the southeast arm of Rainy Lake, the Namakan Reservoir, and Sandpoint Lake.

Wetland polygons of the midwest pondweed, wild rice marsh, deep marsh mosaic, and northern water lily vegetative cover-types were pooled, and potential sites were randomly chosen from this vegetation database. The potential pool was reduced to include only those polygons that were confluent with Rainy Lake or Namakan Reservoir and had a minimum size of greater than one hectare.

Vegetation mapping was unavailable for Lac la Croix. Due to travel limitations in 2002, sites were selected that were in close proximity to the 1987 sampling sites based on aerial photographs and field reconnaissance. In 2005, aerial photography from Lac La Croix and Ikonos imagery were used to select sites randomly within a region approximately 10 km west of the initial Lac la Croix sites.

Potential sites were visited in the field to assess their suitability. Suitable sites had zones 1, 2, and 3 represented, were not dominated by floating mat vegetation (since this vegetation was not expected to change with the new rule curve), and were not heavily influenced by human activity (former or existing cabins, landings, etc.). The few shorelines randomly chosen that were dominated by large cattail (*Typha* spp.) and common reed (*Phragmites australis*) stands were rejected since the behavior of these mat forming species appear to be less affected by rule curve changes. All sites chosen are listed in Meeker and Harris 2009, and included in this report as Appendix 1.

Sampling zones or elevations were located in the field by obtaining actual water-level measurements (Lake of the Woods Control Board website) at the time of sampling and comparing them to mean high water level (MHW). The mean high water levels served as the datum or reference elevations used in all the sampling and were as follows: Namakan Reservoir = 340.90 m, Rainy Lake = 337.75 m, Lac la Croix = 362.00 m. For example, when we sought the 1.25 m elevation in Namakan and the water level at the time of sampling was 340.75 m (or 0.15 m below MHW), we would establish the 1.25 m contour at actual water depths of 1.10 m.

Sampling of the 31 intensively studied sites took place between late July and late August in 2002-2005 (with some sites sampled in 2006) and again in 2010, during the weeks when the vegetation was fully developed. In 2002, water levels ranged from 10 to 30 cm above mean high water (MHW) in the Namakan Reservoir and from 20 to 30 cm below MHW in Lac la Croix. Due to extremely high water levels in Rainy Lake in 2002, we deferred the intensive vegetation sampling in that basin until 2003-2004; water levels in Rainy were 60 cm below MHW in 2003 and ranged from 15 to 20 cm below MHW in 2004. Sampling in Lac la Croix took place in 2002 and 2005 when water levels were 35-40 cm below MHW.

During the 2010 sampling season water levels in Namakan Reservoir were between 15 and 25 cm below MHW; in Rainy Lake, they were 25-30 below; and in Lac la Croix, 40 cm below MHW.

Field Methods

Sites established during the 2002-2005 study were sampled at three water-level elevations: 0.0 m, 1.25 m, and 2.0 m relative to MHW. It should be noted that Wilcox and Meeker (1991) used 1.75m as the deepest elevation sampled, whereas beginning in 2002 and ongoing, the deep transects were sampled at 2.0m. This minor change from the 1987 deep elevation was adopted to ensure that we sampled totally within zone 1, areas that were formerly exposed but now under the 2000 rule curve should not be drawn down.

In 2010, we sampled the aquatic vegetation only at the 1.25 m and 2.0 m depths, where the greatest vegetation change was expected to occur. Hence, any discussion concerning how shoreline vegetation may have changed only applies to the 2002-2005 study and is presented in Meeker and Harris (2009).

Twenty 1 m x 1 m quadrats were sampled on each of two elevation transects per site. Quadrat locations were distributed by first estimating the length of each transect, then dividing it into 20 equal segments. Within each of the 20 segments a quadrat location was randomly chosen. Each random quadrat location was marked with a foam float attached to a sinker. Snorkeling gear was used to sample the 1.25m and 2.0m depths. At each of these two elevations, we had 200, 220, and 200 quadrats for Lac la Croix, Namakan Reservoir, and Rainy Lake, respectively (i.e., 20 quadrats for each depth per site per water body).

At each quadrat, we listed all taxa and estimated their percent covers. Taxa covering less than 1% of a quadrat was systematically recorded as 0.1%. Since plants may occupy space at different strata, the sum of individual cover estimates could exceed 100%. Nomenclature follows Gleason and Cronquist (1991).

Data analyses

By design, we treated each elevation transect at each site as the experimental unit; hence, the quadrats are subsamples.

Metric development

Three main metrics were calculated from the quadrat data; these include **raw percent cover** for all taxa per transect, **frequency of occurrence**, and **relative importance value**, each described in more detail below. Total cover by plant life form was also calculated.

Raw percent cover was summed at the transect level: (i) for each taxon, (ii) by life forms, and (iii) summed for all taxa.

Another metric was calculated from the field data, and we refer to it as **frequency of occurrence** (sometimes referred to as frequency). This value can only be used at the transect scale and higher (e.g., water body). For example, a taxon has a frequency of 5 if it was found in 5 of the 20 quadrats along an elevation transect at a particular site. (It can also be reported as a percent, as 5/20 = 25%, but to minimize confusion with other percentile metrics, we will refer to it primarily as the number of times seen in a transect.)

Two other metrics were calculated as intermediate steps in calculating **relative importance value** (IV): namely, relative cover and relative frequency. Relative cover was calculated for each taxon as its percent cover divided by (or relative to) the sum of all other taxa found *in that transect*. Relative frequency was calculated for each taxon as its frequency of occurrence relative to the total frequency of all taxa *at a given transect*. Since each of these metrics is a measure of an individual taxon's abundance relative to all other taxa, the sum of all taxa's relative cover was 100%, and the sum of all taxa's relative frequency was 100%. Finally, to calculate **relative importance value** (IV, a composite of cover and frequency), each taxon's relative cover and relative frequency was averaged, and it too resulted in a total of 100% for all taxa at each transect. Since we sampled at 31 sites for each of two elevations and two times, the total relative importance value for all taxa at each elevation at each time was 3100% (100% x 31 sites).

ANOVAs on water body and time differences

We categorized all taxa found at any time into five different life forms (Meeker and Harris 2009, Table 3) and compared the differences for three measures: mean cover, frequency, and relative importance value (IV). Life-form groupings include emergent, floating leaf, isoetids, low submergent, and tall submergent.

Each sampling elevation was determined in the field relative to mean high water, referred to as either **1.25m** (**mid deep)**, or **2.0m** (**deep)**, and was analyzed separately below.

For each depth, a two-way analysis of variance (ANOVA), using the R environment (R Development Core Team 2011), was calculated for the main effects of water body (Lac la Croix, Namakan Reservoir, and Rainy Lake) and time (e.g., for Namakan, 2002, or time 1 vs. 2010, or time 2). For these analyses, each metric was transformed to address the assumptions of the test (cover = 4th root, frequency = square root, importance value = square root) and then restored to the original means for clarity. The significance of the year, water body, or their interaction was assessed with p-values computed from standard F statistics in two-way ANOVA table. Conservatively, P-values less than 0.01 were considered significant.

Multivariate Analyses

To summarize the floristic as well as the life form abundance differences among the three water bodies, we also created taxa x transect matrices and calculated non-metric multidimensional scaling (NMS) ordinations. These calculations were performed in PCORD (McCune and Mefford 1999) using either the cover, frequency, or importance value (IV) metrics on all taxa occurring in three or more transects across all water bodies.

We utilized four different types of ordinations for these analyses. First, we calculated *within water body ordinations* (individual ordinations for Lac la Croix, Namakan, and Rainy, respectively) as a means to compare the importance of both time and elevation in influencing vegetation composition and structure. These within water-body ordinations were calculated using Importance Values as the metric.

Following these analyses, we calculated *ordinations comparing all three* water bodies at each elevation separately across both time 1 and time 2. For Namakan, time 1 was 2002 and time 2 was 2010, for Rainy time 1 was 2003, 2004, 2005 vs. time 2 in 2010, and at Lac la Croix time 1 was 2002, 2005 while time 2 was 2010. These all-basin ordinations were calculated using first cover, then frequency, and finally Importance Values as metrics, as a means to gauge how different metrics may influence ordinations results.

Then, we calculated ordinations using the *1987 data* (Wilcox and Meeker 1991), available for *only two sites per water body*. These ordinations followed these six sites over three times (and in this case only, time 1 was 1987). Again, these 1987 data ordinations used cover, frequency, and Importance Values as metrics.

Finally, we calculated two ‘full’ ordinations, one for each elevation, using all sites and all times including both 1987 data and data of two Namakan sites that were sampled additionally in 2004 and 2006. (These two Namakan sites were then sampled in 1987, 2002, 2004, 2006 as a means to determine how sites may change over short time periods and reported in Meeker and Harris, 2009). These final ‘full’ ordinations were calculated using Importance Value as the metric and were then interpreted in different ways by grouping sites by both water body and time.

Multi-response Permutation Procedure (MRPP) and Blocked Multi-response Permutation Procedure (MRBP) pair wise comparisons of vegetation data were also conducted in PCORD to test for significant differences in vegetation composition among water bodies, between elevations, or between times (McCune and Mefford 1999).

Building Secondary Matrices for Ordinations

To determine how both environmental variables and the abundance of taxa life forms may influence, or are correlated with, ordination results, we developed secondary matrices to be used in conjunction with main matrix ordinations as prescribed by PCORD.

We intended to use these variables for the Akaike's Information Criterion analyses but were advised otherwise (D. Ogle pers. comm.) because these derived independent variables (e.g., growing degree days, years since drawdown, Julian day of ice-out) were nearly perfectly correlated with year or year-lake combination. For example, every observation for all Namakan Reservoir sites in 2010 would have the exact same annual growing degree days. Thus, adding the seemingly continuous variable of growing degree days to an Akaike model analysis was adding a factor to the model that was identical to having Namakan (water body) and 2010 (time) already in the model.

Environmental Variables of Secondary Matrices

We investigated available metrics, independent from our study, that were thought to influence the growth of aquatic vegetation in any given year. The environmental variables that we were able to assemble for each site, year, and depth included: 1) the actual water depth (m) at the time of sampling, 2) the range of water-level fluctuations (m) in the year of sampling, 3) the number of years since the site has last drawn down (i.e., exposed), 4) the number of drawdowns since 1927, 5) the estimated ice-out date for the water body of the year sampled, and 6) an estimate of spring-to-summer temperatures during the year of sampling. These variables are explained in more detail below and in Tables 1 and 2.

1) The actual water depth (m) at the time of sampling varied from 0.34 m to 1.85 m, depending on the elevational zone sampled (mid-deep = 1.25 m, deep = 2.0 m) and the water body/time sampled. The actual sampling depths for the

deep elevations generally varied from 1.25m to 1.85m, whereas the mid-deep elevations varied from 0.35 m to 1.1 m.

2) The range of water-level fluctuation (m) for each of the six years sampled varied from an average of 1.70 m on Namakan, to as little as an average of 1.06 m for Rainy. Lac la Croix appeared more variable (Table 1, and Figure 1).
3) The *number of years* since a site, at a particular elevation, last drew down (or was exposed) for at least three weeks in May was deemed to be a critical growth metric for vegetation (Table 2). This metric varied from zero (= a drawdown in the year of sampling) to 83 (no drawdowns since 1927, the year all three water bodies began to have consistent water-level measurements). In general, the deep sites in Rainy Lake and Lac la Croix have not been drawn down over the whole time period, whereas in 2010, the deep sites in Namakan Reservoir were last drawn down 23 years ago (the 1987 sampling year!). In 2010, the mid-deep sites in Namakan Reservoir, Lac la Croix, Rainy Lake were last exposed 12, 0, and 80 years ago, respectively.
4) The *number of times* sites have been drawn down for a least three weeks in May over the 83 years of measurement (Table 2) varied from as many as 23 for both the 2002 and 2010 Namakan Reservoir mid-deep elevations, 9 for the 2010 Lac la Croix mid-deep, and 6 for Namakan deep, to as few as 1 time at Rainy Lake 2010 mid-deep and never at 2010 Rainy and Lac la Croix deep.

5) The estimated ice-out date for the water body and year sampled was converted to Julian day (where April 1st = 91) and varied from 125 (May 5th), to as early as 94 (April 4th). (We only had observed data for Rainy Lake and Namakan Reservoir and assumed Lac la Croix ice out to be similar to that of Namakan, Table 2).
6) An estimate of spring to summer air temperatures for the year sampled from May to September in Growing Degree Days (GDD, Celsius) using a temperature base of 10 C is shown in Table 2.

Abundance of Taxa Life Forms of Secondary Matrices

In addition to the environmental variables described above, we also included in the secondary matrices an investigation of the degree that each of five life forms (emergent, isoetid, floating leaf, low submergent, and tall submergent) contributes to each site's plot in the ordinations for each of three metrics that we used to calculate ordinations. These metrics include raw cover, frequency and Importance Value (IV). For example, when an ordination of sites was calculated using individual taxa's importance values, the degree of correlation was calculated between the axis 1 and axis 2 scores of each site and the total percent IV of each life form. Similarly, if an ordination of frequency was calculated, axis scores were then correlated with the total frequency of each life form, and if raw cover was used, then axis scores were correlated with the total raw cover of each life form.

In general, the approach outlined above offers an estimate of which life forms or environmental factors more greatly influence the distribution and grouping of sites in ordination space. We used r = 0.5 as a cut off for indicating these correlation vectors on each ordination.

Results

Within water body comparisons between time and elevation using ordinations

Individual water body non-metric multidimensional scaling (NMS) ordinations suggest that elevation is a greater driver than time of site location in species space. For example, in an ordination of the Namakan Reservoir sites when labeled by elevation, the 1.25m sites generally plot apart from the 2.0m sites (Figure 4), whereas the same ordination labeled by either time 1 or time 2 shows little grouping with time (Figure 5). This ordination was strongly influenced by tall submergents (r= -0.723, axis 1), floating leaf taxa (r= 0.681, axis 2), and low submergents (r= 0.635, axis 1).

Ordinations for Lac la Croix (Figures 6 and 7) and Rainy (Figures 8 and 9) show similar results, with the two elevations in both cases plotting generally apart. Each of these ordinations (above) used relative Importance Value (IV) as the metric.

We also analyzed which taxa influenced the differences in elevation that we saw. Tables 3, 4, and 5 show comparisons between elevation of the 20 most abundant taxa in Lac la Croix, Rainy, and Namakan, respectively. In Lac la Croix, for example, four taxa (*Eleocharis palustris*, *Glyceria borealis*, *Eriocaulon aquaticum*, and *Eleocharis acicularis*) were only found at the 1.25 m elevation, while three others (*Isoetes* spp., *Vallisneria* *americana*, and *Chara* spp.) were 4x or more abundant at 2.0 m. These taxa were instrumental in influencing the ordination results we reported above.

On Rainy Lake (Table 4), there were eight taxa with abundance values 4x or more greater at the 1.25m elevation, including two that were also mid-depth indicators on Lac la Croix (*Eleocharis palustris* and *Eleocharis acicularis*). Rainy indicators of the 2.0m elevation include four submergent taxa (*Zosterella dubia, Ranunculus longirostis, Bidens beckii*, and *Potamogeton robbinsii*). It is interesting that *Isoetes* is more abundant at the 1.25m elevation in Rainy, while as noted above, it is a deep indicator at Lac la Croix (Table 4). This suggests that the frequency of drawdowns at mid-deep Lac la Croix (Figures 6 - 9, Table 2) may restrict *Isoetes* to the deep elevations in that basin (that have no drawdown), whereas it may be able to persist in Rainy Lake mid-deep due to lack of drawdowns in this basin.

1.25m indicators on Namakan Reservoir (Table 5) include *Eleocharis acicularis, Potamogeton gramineus*, *Sagittaria* rosette, and *Elatine minima,* as well as *Isoetes* that was a mid-deep indicator in Rainy. Deep indicators in Namakan include *Chara* spp. and *Lemna trisulca* (as sunken mats on the sediment surface). *Chara* was also a 2.0m indicator in Lac la Croix. In general, there were more taxonomic differences between elevations in Rainy, with 14 of the 20 abundant taxa acting as indicators.

Within water body comparisons between time and elevation using MRPP and MRBP

We also tested for within-water-body differences in elevation and time using two grouping multivariate tools, multi-response permutation procedures (MRPP) and blocked multi-response permutation procedures (MRBP). MRPP is a non-parametric analysis that tests for differences between or among groups (McCune and Mefford 1999) and indicates whether individual members within a group (in this case grouped by either elevation or time) are statistically more similar to one another than if they randomly belonged to other groups. In addition to IV (as in the ordinations above), we conducted these MRPP tests on raw cover and raw frequency to see if different metrics showed different results. Table 6 shows the results of nine runs of these analyses (3 water bodies x 3 metrics), and in 8 of 9 cases (excepting Namakan, using cover, at p=0.00375) sites at the same depth were relatively more similar than by chance, using the conservative cut- off level of p=0.001. (We used this cut-off level because, in our experiences with these grouping procedures, the visual grouping of sites as seen in ordinations only begin to appear consistent with the MRPP and MRBP tests at this cut-off level).

We used blocked procedures (MRBP) to test for differences between times (i.e., grouping by time, and blocking by sites, somewhat analogous to a paired t-test in controlling for variance among sites). Only in one case (Lac la Croix using frequency), was there any significant change from time 1 to time 2. (Table 7, p=0.00062).

In summary then, by first using NMS ordinations and then testing for differences between groups (time or elevation, using MRPP and MRBP), we conclude that ordinations meant to compare *among* water bodies should control for elevation, as it is the primary influence on plant distribution in these aquatic habitats. In addition, differences between times (= changes over time) were not generally observed.

Comparisons of water bodies through ordinations and MRPPs

Non-metric multidimensional scaling (NMS) ordinations were conducted using raw cover, frequency, and Importance Value at each of the 1.25m (mid-deep) and 2.0m (deep) elevations relative to mean high water. Rare taxa (seen in less than 3 transects across all 31 sites) were eliminated for the calculations as a means of reducing noise in the dataset and increasing the chance of detecting relationships between community composition and environmental factors (McCune and Grace 2002). In addition, secondary matrices factors (Table 2), with $r^2 > 0.250$ are plotted as vectors showing correlation to the ordination axes. Six MRPP procedures were also calculated for differences among water bodies across the three metrics and two elevations; these results are shown in Table 8, and significant differences are indicated among water bodies at p=0.001.

1.25m depth

Using the *cover* metric at the 1.25m depth, both ordination graphs (Figure 10) and MRPP tests (Table 8) suggest that regulated water bodies support different aquatic communities than Lac la Croix. In this case, using the cover metric, the MRPP test suggests that Lac la Croix is different from both Namakan Reservoir and Rainy Lake, while Rainy is not different from Namakan. In general, the LLC sites plotted higher on axis 1 while the Namakan and Rainy sites overlapped. Factors that correlate with axis 1 include the influence of tall submergent taxa (r= -0.581) and the number of years since the last drawdown (r= -0.523) at this elevation.

The NMS 1.25m ordination using *frequency* suggests a similar pattern, with a separation between LLC and the regulated water bodies and most all LLC sites plotting lower on axis 2. In general, emergent and floating leaf taxa were positively correlated with axis 1 scores and are more abundant at these LLC sites (Figure 11).

Using *IV* as a metric, LLC sites plotted apart from the regulated water bodies and greater on axis 2 (Figure 12), and there was considerable overlap between Rainy and Namakan. This ordination was greatly influenced by tall submergents (less represented on LLC, r= - 0.731), as well as emergent taxa (more on LLC, r= 0.594), and isoetids (r= - 0.530). MRPP results using IV also suggest differences among aquatic communities, excepting Namakan vs. Rainy at p=0.00459 (Table 8).

2.0m Depth

Using cover, the ordination of sites at 2.0m (Figure 13) again suggests that water bodies support different aquatic plant communities, with LLC site plotting higher on axis 2, but in this case, it appears that in addition, Rainy Lake sites are clustered apart from Namakan Reservoir sites as well (which are higher on axis 1); hence, there is a greater separation among water bodies at the deep elevation when compared to the 1.25m elevation. Both tall submergents (r= 0.509, axis 1) and low submergents (r= 0.684, axis 1) strongly influenced the ordination. MRPP results (Table 8) suggest that LLC sites are different from both Namakan Reservoir and Rainy Lake.

The NMS ordination using the frequency metric shows all water bodies plotting apart (Figure 14), with the number of drawdowns over time (r= 0.518, axis 2), floating leaf taxa (r= - 0.544, axis 2), and low submergents (r= - 0.521, axis 1) influencing the distributions of sites. MRPP frequency results also suggest that all water bodies are grouped apart (Table 8).

At 2.0m, the IV ordination again indicates a separation between LLC and the regulated water bodies that overlapped. This ordination was influenced by the abundances of floating leaf and tall submergent taxa (Figure 15). MRPP Importance Value results suggest all water bodies again grouped apart (Table 8).

In summary, using all three metrics, it appears that water bodies continue to support different aquatic vegetation communities at both elevations.

Comparisons among water bodies using Life Forms

In addition to the above-mentioned ordinations and grouping procedures that suggested similarities and differences among water bodies, we categorized taxa into different life forms (Meeker and Harris 2009, Table 2) and compared the differences for three measures, including mean cover, frequency, and relative Importance Value.

For each depth, a two-way analysis of variance (ANOVA) was calculated for the main effects of water body (Lac la Croix, Namakan Reservoir, and Rainy Lake) and time (for Namakan 2002 as time 1 vs. 2010 as time 2, for Rainy 2003, 2004, 2005 vs. 2010, and for Lac la Croix 2002 and 2005 vs. 2010).

1.25m elevation

Looking first at water-body differences along the 1.25m elevation (Table 9), Namakan has significantly less abundance of emergent vegetation compared to both Lac la Croix and Rainy *across all three metrics*. For example, the mean emergent cover at Lac la Croix was 72.2% (averaging both times), 95.0% for Rainy and only

18.3% for Namakan. This may still be a vestige of the extreme fluctuations in Namakan up through about 1999 (Figure 1).

For the floating leaf taxa, frequency was significantly greater at Lac la Croix, while cover and IV showed no differences. Similarly, low submergents were significantly more frequent on Lac la Croix but did not have significantly more cover. The reverse was true for tall submergents, which had more cover and IV on Namakan and Rainy when compared with Lac la Croix but were not significantly more frequent.

In only one instance, frequency of emergents, was there a significant difference between times, and in this case, emergents were more frequent in 2010 across all water bodies.

In general, these differences in significance among metrics support the use of multiple metrics, as species are often differentially abundant (i.e., some can be scattered frequently with low cover, while others can occur infrequently but with high cover). In essence, IV is an estimate of abundance that combines both frequency and cover. As an interpretation aide, a higher frequency generally would result from more taxa observed per quadrat.

2.0m elevation

At 2.0m (Table 10) LLC had significantly more abundant floating leaf and isoetid taxa than Namakan Reservoir and Rainy Lake across all three metrics, while the regulated water bodies had significantly more tall submergent as measured by cover and importance value. Again, there were no significant differences between times, except for slightly more ($p=0.02$) low submergents at time 2 for all water bodies.

In general, these life-form ANOVAs suggest that many aspects of the aquatic plant communities at the non-regulated LLC are different from the regulated water bodies, especially at the 1.25 elevation. It appears, however, that there were few significant changes in life form over time. However, at both depths, there were *some* significant differences among water bodies and between times in both *total* mean cover and *total* frequency (two–way ANOVAs, Table 11). For example, at 1.25m, Rainy had significantly more cover at time 1 (1293%) when compared to time 2 (612.7%) (Table 11), while LLC had higher total frequency of occurrence at time 2 (147.4) when compared to Rainy at time 2 (81.5) and Namakan at time 1 (101.6). At 2.0m, LLC had greater cover at time 2 (1783.5%) compared to the same sites at time 1 (742.5%) and Rainy at time 2 (746.7%). Overall, LLC had significantly greater frequencies of occurrence for most taxa than at Rainy (108.0 vs. 68.5, Table 11).

In summary, there were numerous differences among water bodies in the abundance of different life forms, with few changes in life-form abundance noted over time. There were, however, a few puzzling differences in total cover over time, with LLC increasing and Rainy decreasing. Namakan, the water body that may have been expected to change the most due to modification of the rule curves, showed little change over time (2002 vs. 2010).

Comparisons among water bodies using unique taxa

Ordinations, MRPP grouping, and ANOVAs comparing water bodies all suggest that the aquatic vegetation is different at different elevations among water bodies. Which taxa are driving these differences?

One comparison that would seemingly be fruitful relates to the presence or absence of taxa relative to the three water bodies. Combining the results over both time periods, we found that, at the 1.25m elevation, six taxa were uniquely absent in the 440 quadrats of Namakan, including two emergents, (*Eleocharis palustris* and *Zizania palustris*), several floating leaf taxa (*Nuphar* spp. and *Potamogeton natans*) and several submergent taxa (*Zosterella dubia* and *Potamogeton robbinsii*)(Table 12).

In addition *Zosterella dubia* and *Potamogeton epihydrus* were also absent at the 2.0m elevation in Namakan (Table 12). We surmise that these taxa were more abundant in the Namakan Reservoir prior to the reservoir management, but it appears likely that the early record of fluctuation (Figure 1) was quite extreme, and exposure to air and freezing temperatures probably took its toll.

Four taxa were also absent in Rainy 1.25m quadrats, including several that were rather frequent at LLC, including *Scirpus subterminalis* and *Callitriche hermaphroditica.*

On the other hand there were 9 taxa found at both elevations in LLC but not in the quadrats of either Rainy or Namakan, including two species of bladderwort (*Utricularia minor* and *Utricularia intermedia*) (Tables 12 and 13).

Comparisons among water bodies using abundant taxa

In addition to differences among water bodies driven by the presence or absence of unique taxa, differences can also exist due to the differential abundance of dominant taxa.

1.25m Elevation. The 10 most abundant taxa in each water body (combined over time) are listed for the 1.25m transects in Table

14. *Najas flexilis* is very abundant in all water bodies, contributing between 15 and 25% of the total cover and is the only taxa with that level of influence in all three water bodies. However, three taxa, including *Sagittaria* rosette, the narrow leaf *Potamogeton* group, and *Potamogeton gramineus*, were in the top ten most abundant in all three water bodies. The taxa that likely contributed to the differences seen in ordinations and the life form ANOVAs include *Nymphaea odorata, Scirpus subterminalis,* and *Eleocharis palustris,* which were in the top five in Lac la Croix but not in the top 10 in either Namakan Reservoir or Rainy Lake. Alternatively, *Vallisneria* was very abundant in Namakan and Rainy (approximately 20%) but contributed less than 1% in Lac la Croix.

Isoetes spp. have a particularly interesting mid-deep distribution. They are very abundant in Rainy Lake at the 1.25m elevation (10% of total), in the top ten in Namakan Reservoir (3%), and not listed in Lac la Croix's top ten, but as shown below (and in Table 15), they are the most abundant taxa (22%) at the 2.0m elevation in Lac la Croix and not listed in the 2.0m top ten at Namakan and Rainy. Hence, although both Lac la Croix and Rainy have not experienced a drawdown in the deep elevation during the last 83 years (Table 2), other factors (competition from *Vallisneria* in Rainy?) apparently favor the growth of *Isoetes* in Lac la Croix and work against it at the 2.0m elevation in Rainy).

Sparganium fluctuans was very common in Rainy (10% of all cover), in the top in Lac la Croix (3% cover), but not listed as an important taxa in Namakan, as it apparently does not do well in an environment of frequent drawdowns (Table 2).

2.0m Elevation. *Vallisneria* was the most common taxa on the 2.0m transects at both Namakan Reservoir (32%) and Rainy Lake

(49%)(Table 15); It was also common (5th most abundant at 5%) in Lac la Croix. Several taxa were common but not dominant across all three water bodies, including *Myriophyllum* sp., and *Bidens beckii*.

Of interest at the 2.0m elevation are the great abundances of *Chara* spp. (11% in Lac la Croix, 23% in Namakan Reservoir) and *Najas flexilis* (21% in Lac la Croix, 13% in Namakan) at both Namakan and Lac la Croix but not in Rainy Lake. This is counter-intuitive in that both Rainy and LLC have had no drawdowns at this elevation since 1927(Table 2), so they may be expected to have similar dominant taxa when compared to Namakan Reservoir that has had numerous drawdowns (23). In this case, however, it is Namakan and LLC that are more alike. Again, competition from *Vallisneria* may restrict the low submergent growth in Rainy.

Some other taxa likely drove the 2.0m elevation ordination differences shown and were in the top ten at Lac la Croix, the non-regulated water body, but not in Namakan Reservoir and Rainy Lake; these include *Nymphaea*, *Scirpus subterminalis,* as was seen at the mid-deep elevation, but at 2.0m also included *Sagittaria*. Other influential taxa were much more common in either Rainy Lake (e.g. *Potamogeton robbinsii*, 15%) or Namakan Reservoir (*Lemna trisulca*, 6%).

Multivariate Analyses of six sites that were first sampled in 1987

Six sites, two each from Lac la Croix, Namakan, and Rainy, formed the basis of Wilcox and Meeker's 1991 publication that suggested the aquatic communities differed among water bodies, especially at deeper elevations (Figure 3). In 2010, as we conducted the sampling discussed above, we again sampled these six sites, affording an opportunity to look at site changes at three times over a 23 year period (1987, 2002-5, and 2010). We conducted NMS ordinations at each elevation (1.25m and at 2.00m) using three different metrics: cover, frequency, and important value.

Ordinations and MRPP grouping of the six sites at 1.25m. Using cover, at mid depth (1.25m), water bodies appeared to separate in the ordination, with the Rainy sites (all times) plotting high on axis 1 and low on axis 2, apart from both Namakan (high on both axis), and Lac la Croix (high on axis 2, and low on axis 1) (Figure 16). Somewhat similar patterns are demonstrated with frequency (Figure 17) and importance value (Figure 18) but with much more variability among Namakan times, suggesting more change since 1987 in that water body. Conservative MRPP tests (Table 16 , p= 0.001) for groups suggest that Lac la Croix is different from Rainy, regardless of time, whereas there appears to be less differentiation between pairings of the other two.

Taxa that dominate the 1.25m elevation at these six sites over time are listed by cover in Table 17. Some appear dominant across all three water bodies and, hence, are not good indicators. These include *Potamogeton gramineus*, *Najas flexilis*, and the narrow leaf pondweed group. Other taxa are dominant in one water body only and, hence, influence the ordinations, including *Sparganium fluctuans*, *Isoetes* spp., *Eleocharis palustris*, and *Potamogeton robbinsii* found in the top ten on Rainy only. *Eleocharis acicularis*, *Ranunculus flammula*, and *Ranunculus longirostris* were dominant in Namakan only, while *Myriophyllum* spp., *Scirpus subterminalis*, *Bidens beckii*, and *Utricularia vulgaris* were common in Lac la Croix and not in the other two water bodies. In general, it appears that Namakan is still influenced by its past extreme drawdowns, being dominated more by taxa able to tolerate exposure in early spring. It is notable that *Vallisneria americana* is very abundant in the regulated lakes and only a minor taxon in Lac la Croix.

Ordinations and MRPP grouping of the six sites at 2.00m

NMS ordination of the 2.00m sites that were sampled three times over the 23 year period indicated no obvious trends for any of the three metrics (Figures 19-21), except that the Namakan sites moved considerably in ordination space over time (especially with cover as a metric), suggesting again, as at 1.25m, more change since 1987 in this water body. MRPP results for these 2.0m elevations support this conclusion, as there were no differences among water bodies at p=0.001 (Table 16), except for differentiation between Lac la Croix and Rainy using either frequency (p= 0.00494) or Importance Value (p=0.00447).

Again, as noted in Meeker and Harris (2009), any conclusions concerning changes over time only using the 1987 sites are tentative given the small number of sites per water body to be compared (2 for each water body) but suggestive in that each regulated water body pair plotted closely in 1987 (Figure 21).

Full Ordinations – all years, all sites, one for each elevation

Full Ordinations – 1.25m elevation

Another approach to interpret the ordination seen in Figures 18 (for 1.25m) is shown in Figure 22, which eliminated the successional vectors and grouped sites with similar vegetation. This approach clearly shows that the two Rainy 1987 sites started out different from Namakan and Lac la Croix and remained different from them up through 2010. The two Namakan sites started out very similar to each other in 1987 but were clearly different from Rainy and LLC. Then in 2002, N05 began to look like the Rainy sites and N07 plotted between the Rainy and Lac la Croix sites. Both Namakan sites plotted between Rainy and Lac la Croix in 2010. This analysis suggests that new regulations did not bring about much change for Rainy, but may have already caused changes to occur at Namakan by 2002. Since that analysis was based on only two sites per water body, we then calculated a ‘full’ ordination to see if the pattern seen in the 1987-only ordination is supported.

A full ordination was run for each elevation and included all sites over all the times they were sampled. This was calculated to gauge how sites may have changed over time. These were run using importance value as the metric, as it encompasses both aspects of plant abundance (frequency and cover). Each elevation’s ordination is shown four times, highlighting four different grouping of sites: 1) 1987 sites by water body, 2) all water bodies for the 2002-2006 sampling, 3) all water bodies for the 2010 sampling, and 4) all water bodies at all post-1987 times.

For the 1.25 elevation, Figure 23 indicated that the water bodies differed from each other in 1987 (as seen in the two site per water body ordination, Figure 22), even when all sites/times are included in the ordination. Figure 24 indicated grouping by water body during the middle years (2002-2006, which includes Nam05 and Nam07 that were repeatedly sampled in 2004 and 2006). In this grouping, LLC remains different from the regulated basins (low on axis one, mid-way on axis two, with one outlier, L07M02). Namakan did not group with LLC, and the Namakan 2002 points are well spread out and overlap with Rainy. When we group only the 2010 points by water body (Figure 25), a similar pattern is clear; LLC is tightly grouped with no outliers, and Rainy and

Namakan largely overlap, with two outliers (N03M10 and R04M10). In the last grouping of sites, including all years post 1987 (Figure 26), the results confirmed those seen above, with LLC plotting apart and the two regulated basins overlapping. In summary, it seems that Namakan did respond to change in regulation, but it now looks more like Rainy than control Lac la Croix. Additionally, given the similarity in groupings from 2002 (Figure 24) to 2010 (Figure 25), it seems that this change occurred prior to the 2002-2006 sampling.

Full Ordinations – 2.0m elevation

We repeated the 'full' ordination approach for the 2.0m elevation, first by eliminating the successional vectors from the 2.0m 1987 only ordination (Figure 21) and regrouping as shown in Figure 27. Then, as for the 1.25m elevation, we grouped the full, all sites/all times ordination four different ways (Figures 28-31).

Figure 27 indicates that LLC and Rainy grouped by water-body, but each had an outlier (L07D87 and R07D10 respectively), whereas the Namakan points were spread across the ordination. Adding the rest of the sites/times (Figure 28) showed the pairs of regulated 1987 sites (Namakan and Rainy) grouping closely by water body but apart from each other. There was considerable spread in the two 1987 LLC sites. It is notable that L0987 was an outlier at both elevations, absent of the dominance by mats of *Najas* spp. that were present at most other sites.

In 2002-2006, all water bodies plotted to the center of the ordination but Rainy overlapped very little with LLC and Namakan (Figure 29). A similar pattern is shown in Figure 30 for the 2010 groupings but with minor overlap of Rainy with LLC and Namakan, as well as for all sites and all times, as shown in Figure 31. Overall, it seems that Rainy changed slightly from its 1987 composition, as sites migrated slightly to the middle of the ordination over time, but showed little resemblance to LLC. Namakan and LLC both seemed to change considerably from the 1987 composition, but became more similar, as seen with the considerable overlap among these water-bodies (Figure 31).

Full Ordination Summary

In general there were differences among water-bodies at both elevations, but the pattern differed with elevation. At 1.25m, Lac la Croix was different from the regulated water bodies, which were similar to each other by 2002-2005 and remained so through 2010. However, these regulated water bodies appeared to have changed from the 1987 composition (especially at Namakan, less so with Rainy)(Figure 26). At 2.0m, Rainy showed little overlap with Lac la Croix and Namakan, while these two overlapped considerably (Figure 31), suggesting that Namakan had become more similar to Lac la Croix at that depth.

Discussion of Key Findings

Key Finding 1 – elevation relative to MHW is a major factor in aquatic plant development.

One of the main findings of this study continued to support the notion that elevation relative to mean high water (MHW) is a major factor in determining the aquatic vegetation at a particular site. That is, for this study, we found an obvious difference in the vegetative composition and structure between the 2.0m and the 1.25m elevations. The driving force is the history of water-level fluctuations at each elevation and, of course, is directly related to the rule curves (in the regulated water bodies). In this study, we continued to assess for change at elevations meaningful to the rule curves.

Wilcox and Meeker (1991) were aware of the importance of sampling relative to MHW, as opposed to merely using water depth at the time of sampling, and that approach was continued through the 2002-2005 study (Meeker and Harris 2009) and through this present study. As an example of following this concept, we sampled at 2.0m below MHW (Zone 1, described early on in this report), a zone that is greatly changed, mainly in Namakan, due to the new rule curve. Under the old rules this zone in Namakan was exposed to the elements (drawn down) for a duration of at least 3 weeks in May six times since 1927 and for much shorter durations almost annually over the same time period. This is in contrast to no drawdowns in May for at least three weeks in duration since 1987 (Table 2) and a marked reduction of the amplitude of fluctuations beginning in the mid-1980s (Figure 1).

The results of our individual water-body analyses (ordinations, Figures 4-9), clearly indicate that there is a greater difference between elevations than any differences we observed over time, from time 1 (2002-2005) to time 2 (2010). This was true for all metrics and for all three water bodies and suggested that any further analyses comparing water bodies for changes over time should be conducted at each elevation separately.

Key Finding 2 – There continued to be clear differences in aquatic vegetation among water bodies at both elevations.

Each of the three VNP aquatic vegetation studies, sampled in 1987 (Wilcox and Meeker 1991), 2002-2005 (Meeker and Harris

2009), and 2010 (this present study), noted differences in aquatic vegetation among water bodies.

At 1.25m in 2002-2005 and 2010, Lac la Croix appeared to differ from the regulated water bodies in composition (ordinations, unique taxa) and structure (ANOVAs). At both elevations, LLC had less tall submergent vegetation when compared to Namakan and Rainy. In other cases, Namakan appeared to differ from both LLC and Rainy, having fewer emergent taxa (Table 9) and a suite of taxa uniquely absent (Tables 12 and 13). Recognizing this, the question remains, had these assemblages been different prior to dam construction? Although we can never answer this for certain, it is likely that these water bodies had similar species pools, and some of the taxa still absent or at low abundance today in Namakan (wild-rice and some of the floating leaf taxa) were likely put at disadvantage over years of reservoir-like conditions that exposed aquatic vegetation to dessication and freezing on an almost annual basis. This suggests that any effort to have the species composition converge among the three water bodies in the future may require an active restoration effort by adding taxa, especially in zone 1 of Namakan.

Key Finding 3 – There is only slight evidence to suggest that aquatic plant communities changed substantially over the time period from time 1 (2002-2005) to time 2 (2010).

Probably the most important question to be addressed is whether or not changes were noted in the abundance and composition of aquatic vegetation over time, as a means to assess empirically the vegetative response to the new rule curves. This is especially true in Namakan, where the rule curve was modified considerably and where we might expect change, while any noted changes in LLC and Rainy may be related to other environmental factors.

In general, ordinations and MRBPs on individual water bodies did not group sites by time (Figures 5, 7, 9), suggesting little change in composition over time 1 (2002-2005) to time 2 (2010).

Contrary to expectations however, we did note some significant change in abundance at LLC at the 2.0m elevation with greater than a doubling of total cover from time 1 to time 2 (Table 11), as well as a slight increase in total cover at the 1.25m elevation. This was during the same period that Rainy at 1.25m experienced a 50% reduction in cover. In general, LLC water levels fluctuate more than Rainy (Figure 1), but this has been the case for much longer than the time period of the last two samplings, and perhaps not the best explanatory factor of these changes.

Again contrary to predictions (Background Section, above), in Namakan we found little to suggest that there were changes in either life form (ANOVAs Table 9-10) or total abundance (Table 11) since the 2002 sampling. Hence, we did document some changes in total cover in basins where we did not expect change and noted little change in Namakan where we had predicted it. As discussed below, it is likely that changes in Namakan took place prior to the 2002 sampling.

Across all three water bodies, there was little indication that the abundance of individual dominant taxa differed much over time. Of the ten most abundant taxa by cover at each elevation in 2010 (Tables 14-15), eight taxa were also the most abundant in 2002-2005, for each water body at each elevation (Meeker and Harris 2009, Tables 17 and 25).

The relation of Namakan to Rainy at the 1.25m elevation and to Lac la Croix at the 2.0m elevation changed little from time 1 to time 2, as shown in Figures 23-26 and 28-31.

Key Finding 4 – There is evidence to suggest that aquatic plant communities had already changed over the time period from 1987 to 2002-2005.

Between 1987 and 2002, there was a 3-5 fold increase in the cover of tall submergent vegetation at both elevations of Namakan and Rainy (Tables 43 and 45, Meeker and Harris 2009). This is in contrast to the Namakan comparison between 2002 and 2010 (Results above), where no differences were detected. This is the best evidence that the vegetative changes in Namakan probably took place between 1987 and 2002, which is consistent with the reduction in annual fluctuations and the concomitant reduction of reservoir-like conditions noted in Figure 2.

The caveat in these analyses is that there were only two sites sampled in each water body in 1987, which begs the question of "how representative are these two sites in Namakan in comparison to the additional nine?" Support for their representativeness can be garnered by noting that Namakan sites also sampled in 1987 (N05 and N07), grouped closely and plotted near the middle of the cluster of Namakan sites in our ordination figures 10 (1.25m) and 13 (2.0m).

In addition the full ordination analyses also indicate that plant composition may have changed since 1987 in all three water bodies, but especially at Namakan at 1.25m (Figures 23 and 26) and at 2.0m (Figures 28 and 31).

Summary of Findings and their relation to rule curves.

It is clear that water-level history at a site is the major determining factor in defining the structure and composition of aquatic plants. In addition, all three water bodies continue to differ in vegetation, as would be expected with their differences in annual highs and lows over the last 90 years (Figure 1). The 2000 changes in the rule curves (especially in Namakan) have codified, or made reliable, the reduction in fluctuation amplitude that can be observed when we compare the 1930s through the 1970s to the last 25 or so years (late 1980s through 2010). From an aquatic vegetation perspective, maintaining this more benign hydrological environment is critical in supporting the change we suggest began to occur in Namakan since the 1987 study. The fact that we did not note changes for the period 2002 to 2010 is most likely due to the fact that aquatic vegetation had already begun to respond by the mid-1980s and had stabilized by 2000.

Acknowledgments

Wil Schlager and Erin Adams (Northland College) assisted in the 2010 field work and data entry. Craig Treat of Voyageurs National Park (VNP) provided logistic and sampling support. Ryan Maki (VNP) provided advice, assistance, and reviews throughout, and Derek Ogle (Northland College) provided expertise with statistical analyses. Doug Wilcox provided the insight for the initial water-body comparisons and conducted an extensive review of this report.

References Cited

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Canada. Second Edition, New York Botanical Garden.

Hop, K., D. Faber-Langendoen, M. Lew-Smith, N. Aaseng, and S. Lubinski 2001. USGS-NPS Vegetation Mapping Program, Voyageurs National Park, Minnesota. U.S. Department of Interior, U.S. Geological Survey.

Kallemeyn, L., Y. Cohen, and P. Radomski, 1993. Rehabilitating the Aquatic Ecosystem of Rainy Lake and Namakan Reservoir by Restoration of a More Natural Hydrologic regime, U.S. Department of Interior, Biological Report 19.

Kallemeyn, L. W., K. L. Holmberg, J. A. Perry, and B. Y. Odde. 2003. Aquatic synthesis for Voyageurs National Park. U. S. Geological Survey Information and Technology Report 2003-0001.

McCune, B., and Grace, J.B. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon. 300 pp.

McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. Version 4. User's guide. MjM Software Design, Gleneden Beach, Oregon. 237 pp.

Meeker, J.E. and A.G. Harris. 2004. Voyageurs National Park Wetland Monitoring Final Report, 36 pp. plus Appendices.

Meeker, J.E. and A.G. Harris. 2009. Wetland Vegetation Monitoring: Voyageurs National Park. Natural Resource Technical Report NPS/NRPC/WRD/NRTR—2009/202. National Park Service, Fort Collins, Colorado. Report available at (http://www.nature.nps.gov/publications/NRPM).

Meeker, James E. and Douglas A. Wilcox. 1989. A comparison of Aquatic Macrophyte Communities in Regulated and Non-regulated Lakes, Voyageurs National Park and Boundary Waters Canoe Area, Minnesota. U.S. Department of the Interior, National Park Service, Research /Resources Management Report MWR-16. Midwest Regional Office, Omaha, Nebraska. 39 pp.

R Development Core Team. 2011. R: A language and environment for statistical computing. Version 2.12-1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Wilcox, D. A. and J. E. Meeker. 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota, Canadian Journal of Botany 69: 1542-1551.

Wilcox, D. A. and J. E. Meeker. 1992. Implications for faunal habitat related to altered macrophyte structure in regulated lakes in Northern Minnesota. Wetlands 12:192-203.