

APPLIED ISSUES

The effects of water-level manipulation on the benthic invertebrates of a managed reservoir

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SUMMARY

1. Reservoir creation and management can enhance many ecological services provided by freshwater ecosystems, but may alter the natural conditions to which aquatic biota have adapted. Benthic macroinvertebrates often reflect environmental conditions, and this community may be particularly susceptible to water-level changes that alter sediment exposure, temperature regime, wave-induced sediment redistribution and basal productivity.
2. Using a before–after control–impact experimental design, we assessed changes in macroinvertebrate community structure corresponding with changes in water-level management in two lentic systems in the Voyageurs National Park, Minnesota, U.S.A. Littoral zone (depths 1–5 m) benthic macroinvertebrate assemblages were sampled in Rainy Lake (control system) and Namakan Reservoir (impact system) in 1984–85, and again in 2004–05 following a change in water-level management that began in January 2000. The new regime reduced the magnitude of winter drawdown in Namakan Reservoir from 2.5 to 1.5 m, and allowed the reservoir to fill to capacity in late May, a month earlier than under the prior regime. Rainy Lake water levels were not altered substantially.
3. We found changes in macroinvertebrate community structure in Namakan Reservoir relative to Rainy Lake at 1–2 m depths but not at 3–5 m depths. These shallower depths would have been most directly affected by changes in sediment exposure and ice formation.
4. In 2004–05, Namakan Reservoir benthos showed lower overall abundance, more large-bodied taxa and an increase in non-insect invertebrates relative to 1984–85, without corresponding changes in Rainy Lake.
5. Changes in the benthic community in Namakan may reflect cooler water in spring and early summer as well as lower resource availability (both autochthonous production and allochthonous inputs) under the new regime.

Keywords: BACI, macroinvertebrates, reservoir, Voyageurs National Park, water-level management

Introduction

Decisions related to the rate, magnitude and timing of water storage and release can have broad ecological consequences (Baxter, 1977; Petts, 1984; Haxton & Findlay, 2008; Wantzen, Junk & Rothhaupt, 2008). Reservoir creation and operation affect the physical

limnology of aquatic ecosystems, altering nutrient retention, sediment settling, shoreline development, depth profile, light attenuation, heat budgets and the dissipation of currents (Palomaki, 1994; Cyr, 1998; Furey, Mordin & Mazumder, 2004; Finlay, Cyr & Shuter, 2001). These abiotic impacts in turn have biological effects, via structuring influences on the

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diversity, density and the overall resilience of reservoir biota (e.g. Grimas, 1963; Kallemeijn, 1987; Kraft, 1988; Thurber, Peterson & Drummer, 1991; Wilcox & Meeker, 1991; Furey, Nordin & Mazumder, 2006). Biota can be particularly susceptible to impacts when the timing of water release or impoundment coincides with important life history events (Gregory, Beesley & Van Kirk, 2000; Durant *et al.*, 2007).

Benthic macroinvertebrate communities are important parts of aquatic systems and have historically served as good indicators of a variety of environmental conditions (Rosenberg & Resh, 1993). Positive associations have been recognised between benthic macroinvertebrate standing stocks and several limnological variables, including macrophyte diversity and vertical heterogeneity (Brown *et al.*, 1988), plankton standing stocks (Deevey, 1941; Rawson, 1942), fish abundance (Northcote & Larkin, 1956; Kalff, 2002) and waterbird use (Hanson & Butler, 1994; Hargeby *et al.*, 1994). Secondary production of invertebrates may be a better overall indicator of production in lakes compared to primary producers, since benthic invertebrates integrate all sources of available carbon, including phytoplankton, periphyton and allochthonous carbon; correlations have been made between the overall productivity of fresh waters and benthic animal productivity (Wetzel, 2001).

Water-level fluctuation can affect benthic macroinvertebrates directly where organisms become stranded when drawdown produces lower water levels (Benson & Hudson, 1975; Kaster & Jacobi, 1978; Hynes, 1980). Lower water levels can also reduce macrophyte populations indirectly leading to reductions in plant-dependent organisms (Grimas, 1965; Wilcox & Meeker, 1992). Fluctuating water levels enhance mechanical mixing of shoreline sediments, changing the properties of the sediments and presumably the types of organisms that inhabit those mixed sediments (Benson & Hudson, 1975). Given differing habitat requirements, physiological traits and life history characteristics among species, such changes in system characteristics, should differentially impact benthic taxa.

We assessed biotic impacts related to a January 2000 change in the water-level management regime of Voyageurs National Park, Minnesota (VOYA), on benthic macroinvertebrates inhabiting the soft sediments of the littoral zones of Rainy Lake and Namakan Reservoir. We repeated a study conducted during

1984 and 1985, testing earlier conclusions that the system with a more severe drawdown regime (i.e. Namakan Reservoir) had negative impacts on the benthic macroinvertebrate community (Kraft, 1988). We used a before–after control–impact (BACI) experimental design (Stewart-Oaten, Murdoch & Parker, 1986) with Rainy Lake as a ‘control’ system since its water-level regulation was not changed substantially.

Methods

Study site

The Voyageurs National Park is a system dominated by six major waterbodies that, for management purposes, are split into two different systems: Rainy Lake and ‘Namakan Reservoir’. The latter system is comprised of five connected waterbodies: Namakan, Sand Point, Kabetogama, Crane and Little Vermilion Lakes. The Rainy Lake – Namakan Reservoir system comprises 96% of the 34 000 hectares of water in VOA. Since the early 1900s, water levels in these large lake systems have been controlled by regulatory dams at Squirrel and Kettle Falls on Namakan Lake’s northwest end and a hydroelectric dam at the outlet of Rainy Lake (Fig. 1). Two natural spillways also occur, Bear Portage at the northcentral shore of Namakan Lake, and Gold Portage connecting Kabetogama Lake to Black Bay in Rainy Lake. These lakes once existed as natural waterbodies, but at present, they function as larger reservoirs that are regulated to satisfy a variety of water users. While the dams have always been owned and operated by private industry, these waters are shared by Canada and the United States, with the International Joint Commission (IJC) having regulatory authority. The IJC uses ‘rule curves’ or bands of permitted high and low water levels throughout the year to regulate this system of lakes.

Water-level manipulation

Rule curves in force between 1970 and 2000 allowed larger-than-natural lake level fluctuations on Namakan Reservoir to maintain less-than-natural fluctuations on Rainy Lake. The timing of water-level fluctuations under those rule curves differed substantially from what was found in natural lake systems, such that water levels in Namakan Reservoir rose later, and stayed higher longer, than would have been

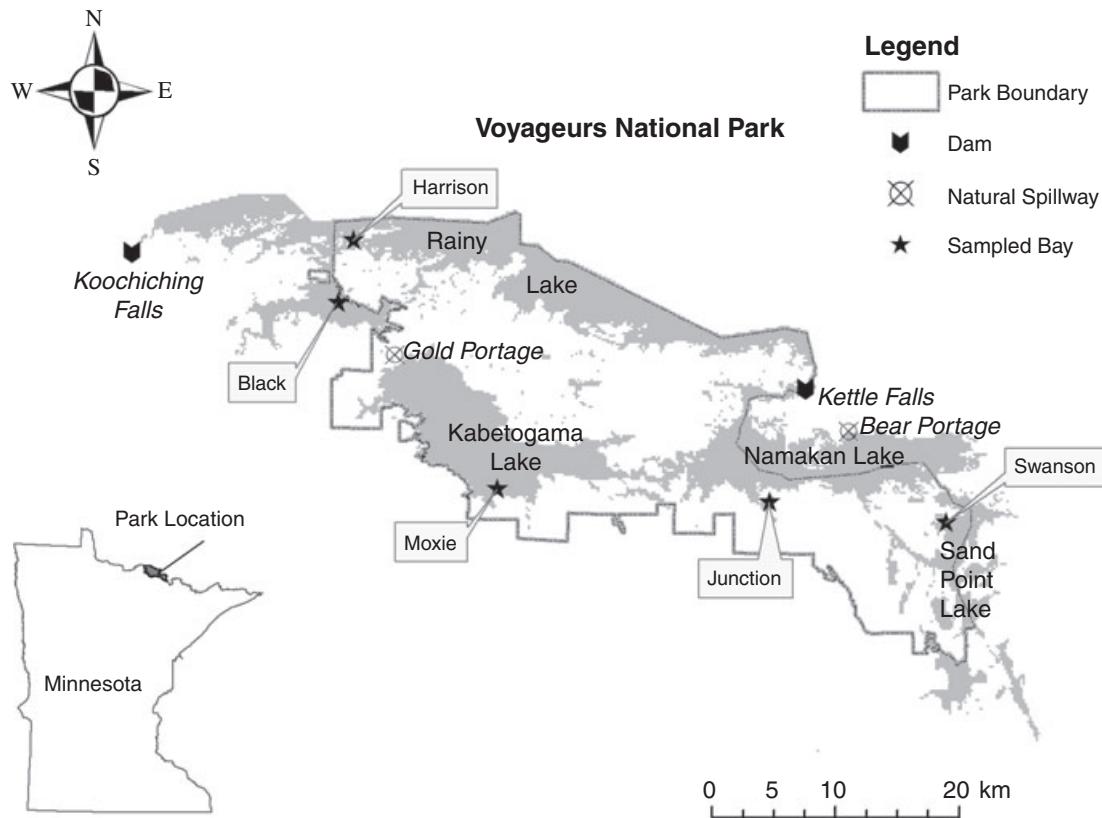


Fig. 1 Voyageurs National Park on the northeastern border of Minnesota. Water flows from Kabetogama and Sand Point lakes into Namakan Lake through control dams at Kettle and Squirrel Falls into Rainy Lake, where outflow is used for hydroelectricity generation at Koochiching Falls in International Falls, Minnesota. When water levels are high, flow can also occur through two natural spillways from Kabetogama into Rainy Lake at Black Bay via Gold Portage, and from Namakan into Rainy Lake through Bear Portage. Macroinvertebrate sampling sites in Rainy Lake: Harrison and Black Bays, and in Namakan Reservoir: Moxie Bay in Kabetogama Lake, Junction Bay in Namakan Lake proper and Swanson Bay in Sand Point Lake.

the case under a natural regime, according to historical modelling (Flug, 1986; Kallemeyn & Cole, 1990; Kallemeyn, 1992). In January 2000, the IJC issued a new supplementary order for management of the water levels in the Rainy–Namakan system, designed to reduce the negative environmental impacts associated with previous management programs. Rule curves in force since 2000 specify a winter drawdown in Namakan not exceeding 1.5 m, reduced from a previous maximum drawdown of 2.5 m, and call for refilling the reservoir to capacity by the end of May instead of the later part of June. In both Rainy Lake and Namakan Reservoir, a gradual summer drawdown was initiated in 2000, whereas previously, water levels were stable during the summer. The magnitude of drawdown and timing of spring refill remained essentially unchanged from the 1970 Rule Curves in Rainy Lake (Fig. 2). Thus, the relevant

parameters of interest, when comparing Namakan Reservoir and Rainy Lake, are limited to the change in the magnitude of winter drawdown and the timing of reservoir refill in the spring. We investigated whether this change positively affected the benthos in Namakan Reservoir by comparing benthic macroinvertebrate community structure in both systems during 2004–05 with that documented by Kraft (1988) two decades earlier.

Field methods

During 1984–85, Kraft (1988) sampled near-shore benthos in two bays of Rainy Lake (Harrison and Black Bays), and one bay in each of three lakes in Namakan Reservoir: Kabetogama (Moxie Bay), Namakan (Junction Bay) and Sand Point (Swanson Bay). Sampling was conducted in June (beginning

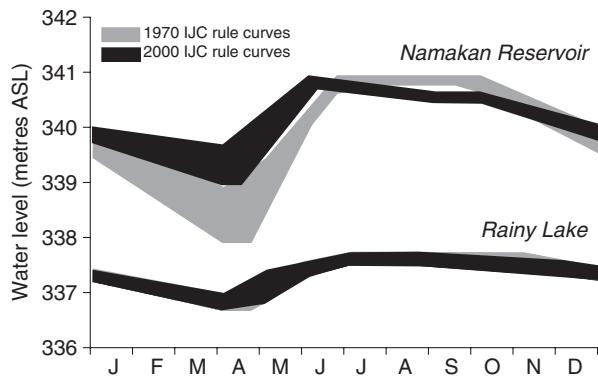


Fig. 2 Comparison of the 1970 and 2000 Rule Curves for water-level management at Voyageurs National Park, issued by the International Joint Commission (IJC). Rule curves set the allowable upper and lower water levels, and managers are directed to keep levels between these bounds. Under the 1970 rule curve ruling (gray), Namakan Reservoir had a winter drawdown of 2.5 m versus Rainy Lake at 1.5 m, with maximum water levels restored by the end of June for both systems. The 2000 rule curve ruling (black) reduced winter drawdown in Namakan to 1.5 m and allowed the reservoir to refill to capacity earlier, at the end of May.

7 June 1984 and 11 June 1985) and August (beginning 25 August 1984 and 26 August 1985). Within each bay, samples were collected along depth transects at one through 5 m depths, with the exception of Black Bay where 4 and 5 m depths did not occur. We sampled these same sites beginning 8 June 2004; 16 August 2004; 6 June 2005 and 21 August 2005. Both Kraft and we sampled all sites within 3–5 days of the starting date for each season/year.

We located the general vicinity of Kraft's original sites from maps in his report, then found the proper depth and recorded global positioning system (GPS) coordinates on our first sampling occasion during June 2004. These coordinates were used for subsequent sampling. Since water levels fluctuated on both an inter-annual basis and an intra-annual basis, water depth at a given set of coordinates was not constant. June sampling was undertaken near the annual high water levels for each year; on average, the water level dropped between June and August dates approximately 0.16 m in Rainy Lake, and 0.31 m in Namakan Reservoir. Consequently, during our return sampling visits, we selected sampling locations with the desired sampling depths (using a sonar depth finder) as close as possible to the targeted GPS coordinates.

In all, data from three bays at five different depths were available in Namakan Reservoir during eight

different sampling periods (four before and four after the implementation of the 2000 Rule Curves), giving 15 locations over eight sampling occasions. Within Rainy Lake, two bays were sampled. Five depths were sampled in one bay (i.e. Harrison Bay), and three depths were sampled in the other (i.e. Black Bay), giving eight locations over eight sampling occasions. Accounting for the total duration and spatial distribution of sampling events, more samples were obtained for Namakan Reservoir ($n = 120$) relative to Rainy Lake ($n = 64$).

Similar to Kraft (1988), we collected three subsamples from soft sediments at each bay-depth combination with an Ekman grab, and live-washed contents through a 0.59-mm mesh. We pooled these samples and did the same to Kraft's subsamples from his original dataset. We considered our sampling unit to be each depth-bay-time combination, which gave four repeated measures for each sampling unit in both the before and the after data sets. Each sampling unit was then multiplied by 11.33 in our case and 14.33 for Kraft's case to account for slight differences in the area covered by our respective grab samplers. This multiplication factor allowed us to express densities as numbers per square metre. Macroinvertebrates were identified to the 'lowest practicable level'.

Statistical methods

We placed our study within a BACI framework (Green, 1979; Stewart-Oaten *et al.*, 1986). We define before and after conditions with respect to the change in the implementation of the 2000 Rule Curves, in which Rainy Lake represents the 'control' condition and Namakan Reservoir represents the 'impact' condition. By using these terms, we do not mean to imply that Rainy Lake is entirely unaffected by alteration of the rule curves, or even disconnected from the response in Namakan Reservoir; rather, the 'treatment' in this case refers to both the magnitude of drawdown and the duration of spring refill, which changed under the 2000 Rule Curves in Namakan Reservoir but not in Rainy Lake, relative to the 1970 Rule Curves.

Multivariate ordination methods allowed us to examine the underlying structure of the benthic community. If communities in Namakan Reservoir and Rainy Lake relate similarly to environmental gradients in the 2004–05 dataset, but differently in the Kraft data from the 1980s, this would indicate that the

two systems became closer in ecological structure following the change in the rule curves. We caution that the only statistical decision that can be made from a hypothesis test, given rejection of the null, is that there is no evidence to support the hypothesis that the response variable in the two *locations* is the same (Hurlbert, 1984; Eberhardt & Thomas, 1991). There is no statistical connection between finding a difference in the control and impact locations, and attributing causation for that difference to the impact. There is only one treatment at one time (i.e. changing the drawdown regime only in one location – Namakan Reservoir). This is not to suggest that showing locational differences is unimportant. To argue for a causal link, we needed to first demonstrate there was a change *coinciding* with the treatment – even if we cannot show statistically that the change was *caused* by the treatment (Hargrove & Pickering, 1992).

Instead of using a statistical criterion to argue for causation, we adopt the logical approach suggested by Beyers (1998) of using Hill's nine criteria (i.e. strength, consistency, specificity, temporality, biological gradient, biological plausibility, experimental evidence, analogy and coherence; Hill, 1965). Hill's criteria are used by epidemiologists to evaluate causal associations for disease and have also been used in risk assessment and environmental toxicology studies conducted by the USEPA (Fox, 1991; USEPA, 1992). While decisions regarding the sufficiency of evidence for making a causal link are arbitrary, Hill suggested that the first three criteria (i.e. strength, consistency and specificity) are most important, and that where weaknesses exist, targeted research can be used to fill in gaps (Hill, 1965). While such an approach lacks statistical rigour, it is the best we can do with unreplicated experiments in which there are 'no simple solutions' (Stewart-Oaten, Bence & Osenberg, 1992).

We used distance-based redundancy analysis (db-RDA), with a Bray–Curtis distance measure, to test for the interaction term in the BACI design; db-RDA uses ordinary RDA on ordination scores produced through principal coordinates analysis (PcoA). RDA and the db-RDA extension are constrained ordination procedures that simultaneously estimate site scores and regression parameters using iteration to generate least squares estimates for regression coefficients related to environmental variables (Van den Wollenberg, 1977; Legendre & Anderson, 1999). Advantages to db-RDA over other direct-gradient

methods (e.g. canonical correspondence analysis, RDA) are (i) any semi-metric distance measure can be used (e.g. Bray–Curtis); (ii) interaction terms can be modelled and tested (necessitated by our BACI design) and (iii) db-RDA relies on permutation tests, which do not assume multivariate normality (Legendre & Anderson, 1999). PcoA scores were calculated using the log-transformed raw densities [i.e. $\ln(x + 1)$] to reduce the influence of abundant taxa. The PcoA was done in R using the Vegan Package, and the resulting scores were imported into CANOCO to perform the RDA (ter Braak & Smilauer, 2002; R Development Core Team, 2006; Oksanen *et al.*, 2007). Tests were performed using the split-plot design where bay/depth combinations represented whole plots ($n = 23$), and sampling periods ($n = 8$) were split-plots. Permutations were allowed freely among time periods within, but not across, bay/depth combinations. Bay/depth combinations were also permuted and freely exchangeable. Because actual water levels sometimes could not be maintained within the bounds of the rule curves, we wanted to account for periods of time when rule curves were violated so that statistical effects were limited to the management regimes. Preliminary analyses indicated that deviations from the rule curves were best accounted for by the cumulative metres that actual water levels deviated over or under the specified upper and lower bounds for the rule curves. We included, as covariates, depth, season (June or August), bay and deviations from the rule curves. We considered two basic models, one including a term for depth sampled and one that did not, along with *post hoc* comparisons of different depth groups if depth showed a structuring effect. *Post hoc* models were evaluated based on the residual error and *P*-value. Lower residual error and *P*-values were deemed to indicate better models. Statistical tests were performed using 9999 permutations. Taxa that could not be detected with 95% confidence were eliminated prior to the analysis (Green & Young, 1993).

To visualise community structure in ordination space, we used non-metric multidimensional scaling (NMDS) as an indirect gradient complement to db-RDA following Legendre & Anderson (1999). Solutions were accepted only where stress < 0.20 (McCune & Grace, 2002). Taxon scores were scaled to NMDS axes using the variance-weighted linear correlation method of Legendre & Gallagher (2001). Two separate NMDS ordinations were performed. In

the first ordination, we used each data point ($n = 184$; 23 bay/depths \times 8 dates) to generate site scores, while in the second, we ordinated the summed differences for each site ($n = 23$). While the first ordination gave a summary of whole system behaviour, the second ordination allowed us to visualise the individual responses of each site to the change in the rule curve. In both cases, the data matrix included the same log-transformed raw densities as used for the db-RDA described earlier.

For the first NMDS ordination, we used the Bray-Curtis distance matrix on the same community matrix used for the db-RDA followed by a summary of site scores by treatment: impact-after; impact-before; control-after and control-before, representing mean site scores and 95% confidence intervals. While individual taxa were used in the NMDS to generate site scores, to reduce the number of points related to taxa on the ordination diagram, we lumped individual taxon scores into groups based on size and trophy, since size has been determined to correlate with many environmental attributes, and trophy can be related to function (Peters, 1986; Brown, 2004). Size groups were defined using a cluster analysis based on literature values for maximum body size. Groups were further refined by dietary habits. We were left with groups defined by a break point of 15 mm for maximum length, where animals under and over this value were categorised as small and large, respectively. We separated taxa by dietary habits into two groups, one for animals that are primarily carnivorous and another, which we refer to as 'herbi-detritivores', for those that feed primarily on detritus and algae. We did not further divide the herbi-detritivores because few species feed exclusively on either live material or detritus. Small herbi-detritivore taxa were further divided into two life history groups with overlapping versus non-overlapping generations. Chironomidae were treated as a separate group because of their high relative abundance and diversity of size and feeding strategies.

Where these combined site groups indicated a treatment effect, we tested for differences using R package for non-parametric bootstrapping, where samples were drawn from the data subsets: control-after, control-before, impact-after and impact-before. We ignored non-independence because of space and time in these groups. This seems justified since the actual data were resampled, and we presume that

space-time influences did not differ among site groups. For each run, 50 000 samples were drawn with replacement. We then calculated the differences in the bootstrapped matrices between the control and impact sites, both before and after. Finally, we calculated the difference (before-after) of those differences (control-impact), along with means and confidence intervals based on these bootstrapped samples. If a 95% confidence interval included zero, we adjusted the confidence interval's size to the nearest percentage that did not include zero. We termed this the 'indicator confidence interval' and its interpretation is the percentage of resamplings whose CI did not include zero. This allowed us to make a judgment about the observed change in the value of each variable at any location, coinciding with the change in the rule curves. This method was also used to assess impacts on overall density and diversity.

For the second NMDS ordination, response variables for each bay/depth combination were derived by first summing densities for each taxon across all sampling dates in the singular categories of 'after' and 'before'. Then, we calculated before-after differences to generate a single score for each bay/depth combination (i.e. $n = 23$) where a positive value indicated an increase for the taxon and a negative value indicated a decrease in our samples relative to those taken by Kraft (1988). We produced a Euclidean distance matrix from these difference values, reflecting overall change in benthic community composition at each bay/depth, before versus after the change in the 2000 rule curve change. To more easily interpret relationships, we show only taxon scores for groups whose scaled correlation with one axis was greater than 0.10.

Following the NMDS, we determined groups of similarly responding sites based on a combination of cluster analysis and indicator species analysis (Dufrene & Legendre, 1997). Finally, we report summary statistics for densities and occupancy of dominant taxa for both systems under each rule-curve regime. We lumped taxa that could not be detected with 95% probability (Green & Young, 1993); a comprehensive list for these taxa can be found in McEwen & Butler (2008).

Results

We detected depth-specific changes at the impact sites relative to the control sites, coinciding with the

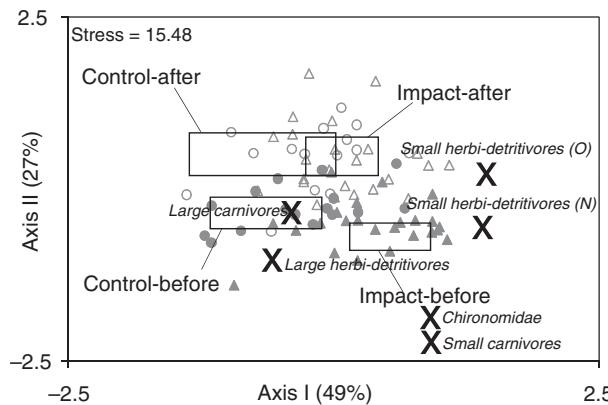


Fig. 3 Non-metric multidimensional scaling ordination plot of benthic communities at eulittoral depths (1 & 2 m) in Namakan Reservoir (Impact site) and Rainy Lake (Control site) using log-transformed densities [i.e. $\ln(x + 1)$]. Each sample represents one of the four conditions: \blacktriangle = Impact-Before; \triangle = Impact-After; \bullet = Control-Before; \circ = Control-After. Scores for taxon groups (X) are variance-weighted linear correlations against each axis. Small herbi-detritivores were separated on the basis of life histories with overlapping (O) versus non-overlapping (N) generations. Boxes were drawn on the 95% confidence interval for each group.

implementation of the 2000 Rule Curves. The db-RDA showed a significant change in benthic assemblages based on densities, but only when a term was included for an interaction with depth ($F = 1.678$, $P = 0.012$). The best model showed impacts when 1 and 2 m depths were combined, but not at the other depths or depth groupings.

For the first NMDS, based on the expanded community matrix, we display only the NMDS plot for the 1–2 m depths ('eulittoral' from this point forward), given that only these depths were statistically related to the change in the rule curve. We show the first two axes of a three-dimensional solution (Fig. 3). The first axis of the partial NMDS plot, representing most of the variance in the structure of eulittoral benthos, shows no overlap of the 95% confidence intervals for Rainy Lake and Namakan Reservoir under the 1970 Rule Curves. Under the 2000 Rule Curves, the intervals for the two systems do overlap, showing that their benthic communities had become more similar. Benthic community structure showed change in both Rainy Lake and Namakan Reservoir since Kraft's study, but the greater change occurred in Namakan Reservoir (i.e. the impact site). The change occurred at the impact sites in the form of a shift from smaller to larger animals. The second axis largely

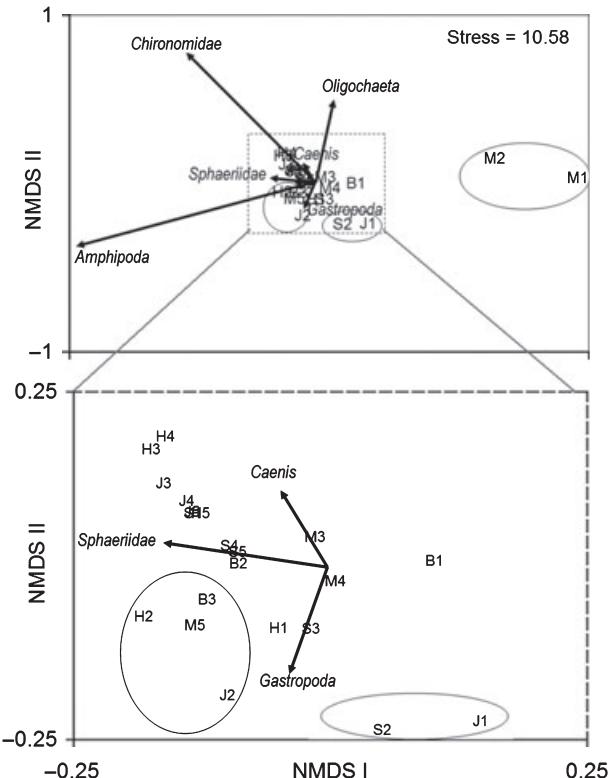


Fig. 4 Non-metric multidimensional scaling ordination plot of average differences between taxon densities at each site (after-before implementation of the 2000 Rule Curves). Labels for sites are a combination of bays (i.e. Rainy Lake: Black and Harrison; Namakan Reservoir: Junction, Moxie and Swanson) and depths (one through 5 m). Oval overlays are drawn around groups separated by cluster and indicator species analysis. The central zone of Fig. 4a is magnified in Fig. 4b to be able to differentiate relationships in the centre of the ordination.

captures changes because of time, not necessarily related to the two systems. We were unable to determine a pattern along the third axis and consequently do not show it.

The second NMDS (i.e. bay/depth-specific differences between after and before samples) also showed the greatest changes in bays of Namakan Reservoir at 1 and 2 m depths (Fig. 4). Indicator species analyses, along with cluster analysis according to Dufrene & Legendre's (1997) methodology for group separation, indicated four groups of sites in the NMDS ordination. Two groups, comprising samples from the eulittoral sites in Namakan Reservoir, occurred at the edges of the ordination diagram and thus showed the greatest community differences. Moxie Bay, 1 and 2 m depths (Group I), had the largest influence on the ordination, forming along the extreme positive fringe

of the first axis. Two sites comprised Group II: Swanson Bay at 2 m and Junction Bay at 1 m depth, while Junction Bay's 2 m depth was included in the third most-changed group, Group III. The only eulittoral site in Namakan that did not respond as predicted was Swanson Bay 1 m depth, which was included in Group IV. The ordination diagram shows that amphipods largely drove the separation of Group I: amphipod abundance was reduced in the 'after' data set at Moxie relative to the 'before' set. Group I also saw notable reductions in chironomids and sphaeriid clams. Changes at Junction 1 and 2 m depths and Swanson 2 m were largely driven by losses of chironomids and, to a lesser extent, oligochaetes.

Overall density, but not taxonomic richness in the eulittoral, was more different after the 2000 rule curve change relative to before between impact and control sites, and tests also indicated size-dependent shifts in community composition (Table 1). Mean density declined by 3 355 individuals per square metre in the impact system relative to the control system. While not suggesting statistical significance, all taxon categories did have a high probability (i.e. >90%) of non-zero change, with the exception of taxonomic richness, large carnivores and small carnivores. The overall tendency was for an increase in large primary consumers and a decrease in small primary consumers in the eulittoral impact areas relative to the control areas.

Table 2 gives a summary of responses (i.e. mean, median, standard deviation, maximum and per cent occupancy) for dominant taxa at Rainy Lake and

Namakan Reservoir for 1 and 2 m depths under the 1970 and 2000 rule curves. The highest taxon density recorded by Kraft (1988) was 22 059 amphipods square metre collected in one grab sample at Moxie Bay, 1 m depth; we collected a peak density of 5 524 amphipods per square metre at the same site. Our highest taxon density was 8 553 m⁻² chironomids, compared with Kraft (1988) who collected a maximum 9 960 chironomids per square metre in one sample. There was a higher average difference in the density of amphipods and chironomids after the 2000 rule-curve change relative to before between Namakan Reservoir and Rainy Lake. This change equated to a difference of 1763 and 1362 m⁻², respectively, for amphipods and chironomids; the next largest decrease occurred for Sphaeriidae, which showed a difference of 284 m⁻². There were increases by *Chaoborus*, *Oligochaeta* and *Hexagenia* in Namakan Reservoir relative to Rainy Lake. Oligochaetes occupied a higher number of sites in Namakan Reservoir under the 2000 rule curves but decreased in Rainy Lake. This pattern was reversed for Sphaeriidae, Gastropoda, Ostracoda, Oligochaeta, Hirudinea and *Mollana*, which occupied more sites in Rainy Lake but fewer sites in Namakan Reservoir under the 2000 rule curves.

Discussion

Depth-specific responses

The structure of the macroinvertebrate community changed in Namakan Reservoir more than in Rainy

Table 1 Relative change at 1 and 2 m depths for density, richness and predefined taxonomic groups in the impact system (Namakan Reservoir) relative to the control system (Rainy Lake) as a difference after and before the implementation of the 2000 rule-curve change. Means and confidence intervals were calculated from 50 000 non-parametric bootstrapped samples. Means are reported as absolute values with the direction of change given in the column for 'Change Direction'. Indicator confidence interval gives the largest CI where the difference does not include zero

Group	Change direction	Mean (95% CI)	Indicator CI (%)
Overall density	–	3355 (−7546, −375)	95
Taxonomic richness	–	1 (−4, 2)	71
Large carnivores	+	21 (−35, 80)	76
Large herbi-detritivores	+	411 (98, 750)	99
Small carnivores	+	53 (−152, 286)	66
Small herbi-detritivores (N)	–	759 (−1745, 212)	93
Small herbi-detritivores (O)	–	1718 (−4455, 512)	92
Chironomidae	–	1358 (−2811, −83)	96

Table 2 Summary responses for dominant taxon groups collected at Voyageurs National Park, Minnesota, correlated with the rule curve change in January 2000 for Rainy Lake (i.e. control system) and Namakan Reservoir (i.e. impact system). A single category for rare taxa included 35 individual taxonomic units that could not be detected with 95% certainty. Taxon groups are listed from most to least changed in Namakan Reservoir relative to Rainy Lake

	Rainy Lake					Namakan Reservoir				
	Mean	Median	SD	Max	Per cent occurrence	Mean	Median	SD	Max	Per cent occurrence
1970 Rule Curves										
Amphipoda	419	29	963	2942	75	2759	94	6117	22059	88
Chirononidae	1494	1120	1188	4334	100	3294	3007	2901	9960	100
Sphaeriidae	254	130	414	1579	75	529	201	1135	5411	92
Gastropoda	165	72	371	1536	75	216	144	283	1277	88
Ostracoda	0	0	0	0	0	233	7	354	1119	50
Chaoborus	208	50	446	1765	75	40	0	151	746	42
Oligochaeta	753	416	899	3157	100	520	0	1306	4650	25
Hexagenia	200	144	254	789	75	27	0	63	287	42
Nematoda	31	14	39	129	69	106	43	189	904	67
Caenis	288	58	706	2770	75	294	187	338	1177	88
Oecetis	14	0	33	129	38	63	43	63	244	83
Hirudinea	19	0	29	72	44	46	36	51	215	71
Ceratopogonidae	122	100	116	459	100	155	79	184	832	92
Hydracarina	13	0	24	72	38	34	22	43	158	63
Cernotina	25	0	48	186	38	22	0	43	187	42
Enattagma	5	0	18	72	13	19	0	44	172	21
Sialis	32	0	52	158	44	4	0	15	72	8
Spinicaudata	0	0	0	0	0	0	0	0	0	0
Rare	31	0	75	302	44	39	22	50	186	63
Mollana	1	0	4	14	6	15	0	25	100	46
Mystacides	5	0	15	57	19	13	0	25	100	33
2000 Rule Curves										
Amphipoda	127	51	166	568	63	704	139	1312	5524	83
Chirononidae	665	234	796	2706	100	1103	540	1762	8553	100
Sphaeriidae	244	129	242	702	94	235	78	346	1292	88
Gastropoda	485	234	770	3073	81	272	84	435	1938	92
Ostracoda	24	0	73	290	31	9	0	18	56	25
Chaoborus	33	6	53	178	50	26	0	58	245	42
Oligochaeta	272	206	231	802	94	162	89	178	668	92
Hexagenia	67	22	135	546	63	7	0	18	78	25
Nematoda	5	0	7	22	38	6	0	7	22	42
Caenis	26	0	68	200	25	76	11	242	1192	54
Oecetis	8	0	20	78	25	26	0	64	234	33
Hirudinea	12	11	17	66	56	10	11	15	67	54
Ceratopogonidae	10	0	16	45	38	15	0	25	100	46
Hydracarina	3	0	7	22	25	7	0	16	67	25
Cernotina	23	11	36	123	56	37	11	70	256	54
Enattagma	0	0	0	0	0	4	0	10	33	21
Sialis	21	0	50	200	38	0	0	0	0	0
Spinicaudata	3	0	11	45	6	0	0	0	0	0
Rare	24	6	32	100	50	29	11	46	189	63
Mollana	1	0	4	11	13	13	0	27	100	29
Mystacides	1	0	4	11	13	9	0	22	100	33

Lake when the water-level management regime was altered; however, the change was specific only to the two shallowest depths sampled (i.e. 1 and 2 m). Under the 1970 Rule Curves, the 2 m depth would

have been exposed in Namakan during the winter; in contrast, under the 2000 Rule Curves, the 2 m depth in Namakan was underwater for the duration of the winter. Since water levels drop over the course of the

winter, under the 1970 Rule Curves, some invertebrates settled in areas of Namakan that became exposed to the atmosphere by the end of the winter, probably leading to high mortality rates. Further, macroinvertebrates settling in areas where water froze to the sediment would have been at higher risk of mortality associated with shearing from ice crystal formation (Olsson, 1981).

We did not observe changes in the three to 5 m depths, which conflicts with some other studies (e.g. Grimas, 1961, 1963, 1965; Furey *et al.*, 2006). Change in sublittoral fauna has been attributed to redistribution of sediment particles associated with water-level fluctuation. We investigated impacts only 3 and 4 years following the rule curve change; too little time may have elapsed for sediments to be redistributed to a degree that affected the littoral zone taxa at deeper depths in VOYA (Cyr, 1998). Additional monitoring after more time may reveal impacts in these areas as well; however, there are currently no signs of impact to these depth areas.

Total density responses

The altered rule curves were associated with fewer total invertebrates in the shallow depths of Namakan Reservoir. While these results agree with findings by Furey *et al.* (2006), who found lower densities of littoral benthos in a natural lake than in a regulated reservoir, they are inconsistent with a number of other studies on impacts of water fluctuation on reservoir benthos, where lower macroinvertebrate densities were reported in regulated waters with more pronounced water-level fluctuations and higher magnitude drawdown (e.g. Nursall, 1952; Grimas, 1961, 1963, 1965; Paterson & Fernando, 1969a,b; Hunt & Jones, 1972; Benson & Hudson, 1975; Kraft, 1988; Richardson, Hanson & Locke, 2002; Valdovinos *et al.*, 2007). However, most of these studies do not report on manipulations consistent with the VOYA study, with most evaluating drawdowns of much greater magnitude, occurring at different times of the year, and in habitats different from those found at VOYA (e.g. dammed rivers instead of extant lakes).

There are plausible mechanistic explanations for lowered densities under the latest Rule Curves we observed. The lower macroinvertebrate densities observed in Namakan Reservoir relative to Rainy Lake since the implementation of the 2000 Rule

Curves may be related to overall decreases in both autochthonous and allochthonous productivity in Namakan Reservoir related to the 2000 Rule Curves. Under the more severe drawdown of the 1970 Rule Curve regime, photosynthetically active radiation would have penetrated into a greater percentage of the water column in the spring and early summer, allowing algae to be more highly productive. Further, greater drawdown probably increased the input of allochthonous material, as inundation pulses during spring refilling produced more energy over a larger area of the shore, displacing coarse woody debris (CWD) along with leaf litter and other organics into the littoral zone; high amounts of litterfall and CWD can make near-shore habitats more productive for invertebrates (France, 1997). Further, remineralised nutrients can be mobilised into the water of the littoral zone as waters recede, allowing for high rates of production (Bayley, 1991; Schindler & Scheuerell, 2002; Wantzen *et al.*, 2008).

Invertebrate life history events and overall productivity are tied to ambient water temperatures (Vannote & Sweeney, 1980, Finlay *et al.*, 2001). Lower mean water levels in the spring during the 1970 Rule Curves sped the warming in Namakan Reservoir shallows, as there was a lower volume of water to dilute incoming heat. This would have increased both the onset and the subsequent rate of invertebrate production. While thermal data do exist under both rule curves, they are not of sufficient quality to address whether there has been an alteration of the thermal regime in areas where invertebrates were sampled; however, mass balance constraints dictate that changes in water volume would impact heating.

Taxon-specific responses

Much of the change in community structure in Namakan Reservoir, over and above the background change observed in Rainy Lake, was driven by losses of amphipods and chironomids; two taxa often well represented in systems with unnatural water-level fluctuation (e.g. Vinson, 2001; Furey *et al.*, 2006). Amphipods had some of the highest densities at the 1 and 2 m depth sites in Namakan under the 1970 Rule Curves, without correspondingly high densities in Rainy Lake. Along with their relatively high mobility, certain life history characteristics make amphipods highly successful colonisers of new

habitats created during reservoir refill. Amphipods are capable of continuous reproduction and do not have to leave water to complete their life cycle, unlike many aquatic taxa that reproduce only once per year and must leave the water (Embody, 1912; Pickard & Benke, 1996; Smith, 2001). This allows amphipods to reproduce immediately in newly inundated areas and quickly saturate resources in newly refilled areas of a reservoir.

Chironomids were also much reduced in Namakan Reservoir at 1 and 2 m depth sites under the 2000 Rule Curves, without corresponding reductions in Rainy Lake. Finding lower chironomid densities following the change to a more naturally fluctuating water level in Namakan agrees with findings by Furey *et al.* (2006), who reported much lower densities of chironomids in a natural lake compared with a regulated reservoir. Small-bodied organisms with short life cycles that can complete their life cycle during the inundation period are probably favoured, relative to animals with longer generation times. For example, the chironomid *Procladius*, a dominant taxon in the VOYA system, produced three generations per year in the drawdown area of a reservoir studied by Sephton & Paterson (1986). Chironomids also have strong dispersal abilities, which probably allowed them to recolonise winter-exposed areas that are re-inundated in the spring before other taxa (Van de Meutter, Stoks & De Meester, 2006).

Chironomids and amphipods were replaced at shallow depths by larger-bodied insects as well as non-insect taxa. For example, both the burrowing mayfly *Hexagenia limbata* (Serville) and the predatory alderfly *Sialis* increased on average in Namakan eulittoral sites. Such large-bodied invertebrates did well in other drawdown studies, under either natural conditions or where drawdown was reduced (e.g. Grimas, 1961, 1963, 1965). Non-insect invertebrates are less mobile than most insects, and thus may be at greater risk of exposure in the drawdown zone. Most of the increases in relative densities for non-insect taxa were associated with gastropods and oligochaetes, and in a more localised case, sphaeriid clams, which increased only at Swanson 1 m depth. While amphipods, chironomids and other small-bodied organisms may have been superior colonisers, larger organisms may be superior competitors once they are given a chance to establish themselves (Levins & Culver, 1971; Hastings, 1980).

While density changes by other taxa were not as substantial as the losses of chironomids and amphipods, functionally these changes may be of equal or greater importance. Large taxa tend to be higher-level consumers which have a disproportionately large impact on system functioning through top-down (predatory) activities. Large-bodied predators are less species-rich, leading to little functional redundancy at higher trophic levels compared to smaller-bodied consumers. Strayer (1991) reviewed many of the potential effects of communities shifting to larger members, concluding there is an increased efficiency of energy and nutrient transfer to fish, and a larger effect on mixing sediments when communities are dominated by large, as opposed to small, members.

Causative argument

Our statistical evidence suggests that macroinvertebrate community structure and densities have changed in different ways for Namakan Reservoir than for Rainy Lake since 1984–85. While not providing a measure of probability for the cause of these changes, by using Hill's nine criteria, we can make a logical case relating observed changes in the eulittoral macroinvertebrate assemblages to the change in the water-level management regime.

Hill's (1965) first three criteria are *strength*, *consistency* and *specificity*. The criterion of *strength* suggests that a large proportion of individuals is affected in the exposed areas relative to reference areas, which we did find. While changes have occurred since Kraft's (1988) study in both Rainy Lake and Namakan Reservoir, changes were more pronounced and of a different nature in Namakan Reservoir. Most notably, there were large changes in the dominance structure with respect to amphipods and chironomids in the eulittoral of Namakan Reservoir relative to Rainy Lake. The second criterion, *consistency*, requires that similar responses be observed by other investigators, at other times and in other places. Our results did not always agree with those of other drawdown studies, but did in many respects, even though the experimental designs of some studies were questionable and their systems and impacts were much different from ours. We did find a high degree of consistency with the recent study of Furey *et al.* (2004). The third criterion, *specificity*, means that the effect is diagnostic of the exposure. Indeed, we think we did observe such

life history changes in populations of dominant organisms; however, we have no direct measurements of the temperatures these organisms experienced, or more importantly in a community context, no knowledge of how changes in life-history characteristics are further modified through interacting populations. Thus, our evidence is circumstantial and suggestive, but insufficiently clear to say that the specificity criterion has been satisfied.

The fourth, fifth and sixth criteria are *temporality*, *biological gradient* and *biological plausibility*, respectively. *Temporality* suggests that the exposure must precede the effect in time. This, of course, was the case with this study as time was a designed variable and the noted changes occurred after versus before the impact. The *biological gradient* requirement is that the risk of effect is a function of magnitude of exposure. Given that organisms in the 1 and 2 m depths were more affected than those in the 3–5 m depths, we believe we have cause to suggest that there indeed is a gradient of exposure. Organisms in shallow areas, which one would expect to be more influenced, were in fact most influenced. *Biological plausibility*, the sixth criterion, can be related to the effects that change the water-level regime should have on temperature and exposure (Olsson, 1981). Thus, while we failed to rigorously support the specificity criterion, we can appeal to this criterion to suggest that observed community-level differences are plausible responses to changes in temperature and exposure expected from the change in the rule-curve regime. The specific changes in chironomids and amphipods, compared with larger-bodied, slower growing invertebrates, are biologically plausible responses to the change in rule curve.

The seventh criterion is *experimental evidence*. To our knowledge, no field experiments have been carried out on communities by manipulating the variables potentially at work in VOYA; however, there has been experimental work on the effects of temperature on life history characteristics and on the effects of exposure and freezing on benthic animals. The majority of these studies are focused on populations, not communities; however, they do give some insights into community level dynamics that are not at odds with our findings (e.g. Brown, 2004).

Analogy, the eighth criterion, means that similar stressors cause similar effects. There is much research on thermal effects on aquatic invertebrates from

'thermal pollution' coming from power plants (Rosenberg, Danks & Lehmkuhl, 1986). It is within this context that the impact designs had their genesis (Green, 1979). Research on the effects of drought, flooding, 'natural' cycles of productivity in lakes (e.g. alternative-stable-states of shallow lakes), winter deoxygenation and sedimentation caused by shoreline development presents similar symptoms to water-level impacts on macroinvertebrate community dynamics. The final criterion is *coherence*, which requires that the causal hypothesis does not conflict with existing knowledge of biology or natural history. From a natural history perspective, we note that there is a developing literature on use of benthic invertebrate remains in sediment cores to trace cycles of water-level fluctuation, sometimes over periods of thousands of years (e.g. Hofmann, 1998; Itkonen *et al.*, 1999). This is suggestive that benthic communities are responsive to water-level fluctuation.

Conclusion

We are aware of no other drawdown impact study that takes an approach such as ours, in which (i) the response variables are differences between paired observations in both an impact system and a control system (i.e. Namakan and Rainy Lakes), (ii) data are analysed to detect locational differences correlated with a water-level management intervention, followed by (iii) an appeal to a logical criteria for causation (Stewart-Oaten *et al.*, 1986). Other studies either take a time-series approach within a single impoundment where drawdown is changed during the time series (e.g. Benson & Hudson, 1975; Richardson *et al.*, 2002), or compare regulated and unregulated lakes during the same time period (e.g. Grimas, 1961). A drawback of not using a BACI design is the assumption of an underlying stability to population numbers for macroinvertebrates in these systems. However, most macroinvertebrate taxa can be expected to exhibit long-term population fluctuations because of climatic irregularities, predator-prey and consumer-resource relationships and stochastic processes (e.g. Einarsson *et al.*, 2002; Cheke, 2007). The failure of impact assessment studies to take into account such 'extra-impact' factors influencing benthic macroinvertebrate populations can easily lead to erroneous conclusions. Having both before and after data on paired systems gave us a unique opportunity

to more rigorously evaluate changes in macroinvertebrate assemblages that might be attributed to altered water-level management, assuming there is reason to believe that Rainy Lake reflects background (i.e. stochastic) variability.

In conclusion, we were able to find a signal related to the change in water-level management despite sampling only the third and fourth year following the implementation of the new rule curves. Insufficient time may have elapsed to produce a more pronounced response by the benthic community. Further changes to benthic macroinvertebrate populations, plus interactions among these organisms and the rest of the lake ecosystem, may generate greater community change over time. Additional studies would help to determine whether the changes we report are sustained. We agree, in general, with Kraft's (1988) suggestion that benthic invertebrates in Namakan Reservoir under the more severe 1970 drawdown regime were negatively impacted.

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