Impacts from Water-Level Regulation on Benthic Macroinvertebrate Community Structure in Namakan Reservoir and Rainy Lake

Voyageurs National Park

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Abstract

We investigated how changing the magnitude and timing of water release in a regulated reservoir impacted macrobenthic invertebrates communities within Voyageurs National Park (VOYA), Minnesota with a before-after control-impact approach, using both multi- and univariate response measures to simultaneously compare impacts on macroinvertebrates across both time and treatment. Under a management regime that went into effect in 1970, water-levels in VOYA were drawn down 2.5 meters in the winter in Namakan Reservoir and 1.1 meters in Rainy Lake. To investigate water-level management impacts on aquatic communities, macrobenthic invertebrates were collected from multiple sites in soft sediments of littoral zones in Rainy Lake (i.e., control system) and Namakan Reservoir (i.e., impact system) from 1984-1986. In that earlier assessment, it was concluded that invertebrates were especially vulnerable to desiccation and/or freezing in winter-exposed habitats in the shallows of Namakan, where Isopoda, *Caenis*, *Hexagenia*, and Gastropoda were supposed to be most susceptible. Chironomids seemed favored by the more severe drawdown and appeared to benefit from the high mortality rate of these other taxa at shallow depths. Further, overall faunal diversity was reported to be lower in winter-exposed habitats. Arguments were forwarded that a change in water-level management, particularly a reduction in drawdown magnitude for Namakan Reservoir, could help to alleviate some of these negative biological impacts. Beginning in 2000, the magnitude of winter drawdown in Namakan was reduced from 2.5 to 1.5 meters, and the reservoir was allowed to refill to capacity in late-May, about one month earlier than under prior management regimes. Water level regulation was unchanged in Rainy Lake. In 2003-2005, we revisited the same sites used in the earlier investigation, beginning three years after the change went into effect. We found lower densities of invertebrates in the impact site relative to the control site, with a shift from small to larger bodied invertebrates. Changes were most notable in Namakan Reservoir at 1m and 2m depths. Much of this change could be attributed to amphipods and chironomids, with both taxa greatly reduced following the change in water-level management regime. Of the taxa thought to be sensitive to extreme water-level fluctuation, only *Hexagenia*, Gastropoda, and *Sialis* responded as predicted, and we found insufficient evidence to conclude the same for *Caenis* or Isopoda. We also found lower abundance of chironomids at the impact sites, relative to data collected during the mid-1980s. We argue that observed changes likely resulted from cooler water and lower production under the new regime, coupled with a more stable environment with respect to physical processes involving wave energy and fluctuation. We recommend continued monitoring after several more years, as the system may still be resetting itself from this recent change in water-level management.

Introduction

Dams have been constructed for a wide variety of purposes throughout history, and while providing benefits such as flood abatement, power generation, recreational opportunities, and more, they have altered the natural flow of water, taking their toll on the world's water-related natural resources. Decisions related to the rate, magnitude, and timing of water storage and release can have broad ecological impacts. Reservoir creation and operation affects the physical limnology of aquatic ecosystems, altering nutrient retention, sediment settling, shoreline development, depth profile, light attenuation, heat budgets, and the dissipation of currents (Petts 1984). These abiotic impacts in turn have biological effects, via structuring influences on the diversity, density, and the overall resilience of reservoir biota. Resulting biotic changes can cascade from basal resources (e.g., phytoplankton, periphyton, dissolved organic carbon, etc.) to secondary production of heterotrophic bacteria, benthic and pelagic invertebrates, fishes, waterbirds, and aquatic mammals. Biota can be particularly susceptible to impact when the timing of water release or impoundment coincides with important life history events. Organisms have adapted through their evolutionary history to the natural timing and magnitude of water fluctuations. Consequently, reservoir operations have strong potential to modify the types and numbers of organisms that live in and below impounded areas (Baxter 1977).

Detrimental impacts on any biological community can serve as a proxy for the overall impact of reservoir operation on an aquatic ecosystem, but not all communities are equally useful for determining impacts. Good biotic indicators should be relatively immobile, easy to sample, and have intermediate turnover rates. Aquatic animals, including fish, mammals and birds, which are highly mobile and move through a three-dimensional habitat, are difficult to sample in a way that is representative of a specific area in a reservoir. Furthermore, mammals and birds generally do not inhabit aquatic ecosystems full time, being influenced by a broader range of environmental attributes, including those related to terrestrial habitats. Turnover rates that are too high (e.g., those related to primary producers, zooplankton, and bacterial communities) lead to high variability in response variables, and those organisms with low turnover (e.g., fish, mammals, and birds) will take a long time to integrate changing conditions. Consequently, these groups of organisms may not provide the best indication of the overall integrity of the aquatic system.

In contrast, benthic macroinvertebrate communities have historically served as good indicators of a variety of environmental conditions (Rosenberg and Resh 1993). Many benthic organisms are relatively immobile, and even those that do move, primarily move in two dimensions, whether on the lake bottom, rocks, plants or other debris. Their relative immobility makes them easier to sample than many other communities of aquatic systems. Turnover rates of benthos are, for the most part, intermediate to those of plankton and fishes. The majority of temperate zone benthic invertebrates have a one-year life cycle, although some have shorter (e.g., two or more generations per year) but very rarely longer ones (Butler 1982). Positive associations have been recognized 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 and Larkin 1956; Kalff 2002), and water bird use (Hanson and Butler 1994; Hargeby et al. 1994). Secondary production of invertebrates may be a better overall indicator of production in lakes relative to

primary producers, since they integrate all sources of carbon available, including phytoplankton, periphyton, and allochthonous carbon. Correlations have been made between the overall productivity of fresh waters and benthic animal productivity (Wetzel 2001).

We took advantage of the characteristics of benthic invertebrates to assess biotic impacts of a change in water-level management in Voyageurs National Park (VOYA), Minnesota. VOYA is a system dominated by six major water bodies that, for management purposes, are split into two different systems: Rainy Lake and "Namakan Reservoir." The latter system is comprised of five connected water bodies: 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 VOYA. 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 (Figure 1). Two natural spillways also occur, Bear Portage at the north-central shore of Namakan Lake, and Gold Portage connecting Kabetogama Lake to Black Bay in Rainy Lake. These lakes once existed as natural water bodies, 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.

Water–level fluctuation can affect benthic macroinvertebrates in the form of winter drawdown (Palomaki 1994), which has both direct and indirect impacts on this fauna. Directly, drawdowns may cause mortality in benthic communities by stranding organisms (Benson and Hudson 1975; Kaster and Jacobi 1978; Hynes 1980). Indirectly, low winter water levels reduce spring/summer macrophyte populations, leading to similar reductions in organisms that are dependent upon them (Grimas 1965; Wilcox and Meeker 1992). Sediment properties are also important in determining macroinvertebrate community structure. Drawdown allows for the mechanical mixing of shoreline sediments, changing the properties of the sediments and, presumably, the types of organisms that inhabit those mixed sediments (Benson and Hudson 1975). A selective advantage of winter drawdown for particular taxa, based on altered substrate type, was shown by Kaster and Jacobi (1978).

Macroinvertebrate communities can be influenced indirectly by water-level management via changes in biological interactions. In addition to density-dependent pressures on benthic macroinvertebrates, predators (mainly waterbirds and fish) will have an influence. If benthivorous fish dominate a system, benthic invertebrate population numbers will be reduced relative to systems with a different fish community structure (Wong et al. 1998). For example, brown bullheads (*Ictalurus nebulosus*) significantly reduce midge populations after they become abundant following larval recruitment (Batzer 1998). In lakes with limited fish forage, Northern Pike (*Esox lucius*), an abundant fish in VOYA, can significantly influence the structuring of benthic fauna in lakes where they occur (Jepsen et al. 2001). Even nonpredatory animals can influence the benthic fauna. For example, muskrat (*Ondata zibethicus*) lodge construction affects the diversity of macroinvertebrate populations (De Szalay and Cassidy 2001). Additionally, some evidence suggests that zooplankton compete indirectly with benthic organisms and that there is an inverse relationship in their abundance (Marshall and Ryan 1987).

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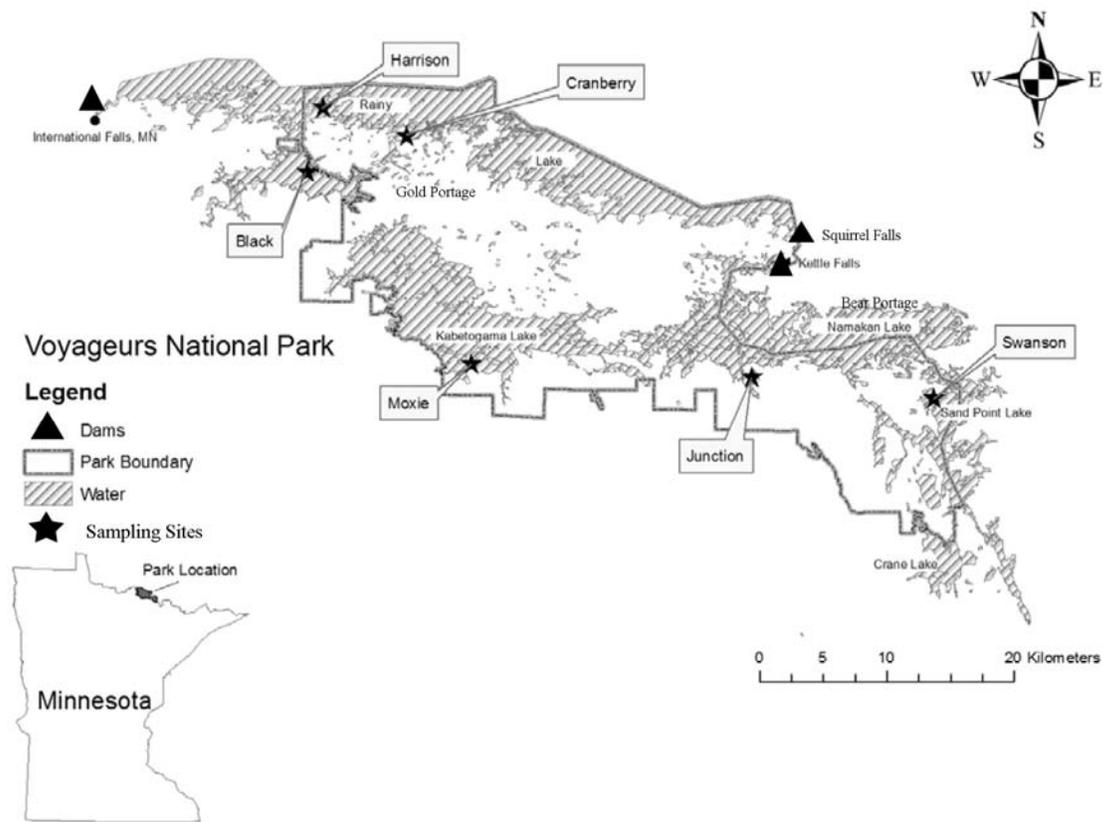
Figure 1. Locations of the six study areas. Rainy Lake sites include Harrison, Black, and Cranberry Bays, and Namakan Reservoir sites include Moxie Bay in Kabetogama Lake, Junction Bay in Namakan Lake proper, and Swanson Bay in Sand Point Lake.

The IJC uses "rule curves" or bands of permitted high- and low-water levels throughout the year to regulate this system of lakes. Rule curves in force between 1970 and 2000 allowed larger-than-natural lake level fluctuations on Namakan Reservoir in order 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 the case under a natural regime according to historical modeling (Flug 1986; Kallemeyn and Cole 1990; Kallemeyn 1992).

Concerns about the effects of lake-level fluctuations on aquatic ecosystems have been expressed repeatedly since the dams were constructed (Sharp 1941; Johnson et al. 1966; Chevalier 1977; Osborn et al. 1981) and were heightened by the establishment of VOYA as a National Park in 1975 (Kallemeyn et al. 2003). In the 1980s, VOYA initiated a comprehensive research program to address these concerns. Hydrologic models were used to develop alternatives to the water-level management program based on the 1970 rule-curve (Flug 1986; Kallemeyn and Cole 1990). A series of field studies documented widespread ecological problems, and researchers

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noted that the greater-than-natural fluctuations on Namakan Reservoir were particularly damaging (Kallemeyn and Cole 1990; Kallemeyn 1992).

Under the 1970 rule-curve, the effect of winter drawdown on benthic communities in VOYA was assessed by comparing Namakan Reservoir, with an average winter drawdown of 2.5 meters, with Rainy Lake, averaging a 1.1-meter winter drawdown (Kraft 1988). Both density and diversity of benthic invertebrates were reportedly higher in samples from Rainy Lake, where drawdown was less severe. Extreme winter drawdown in Namakan Reservoir showed greatest effects on communities at 1, 2, and 3 meters, compared with those at 4 and 5-meter depths. Ratios of invertebrate densities in June:August tended to be lower in the shallows of Namakan Reservoir relative to Rainy Lake, which was interpreted as a drawdown effect as high winter mortality would lead to low densities in June relative to August samples. These findings imply that the integrity of benthic invertebrate communities in VOYA lakes is linked to the severity of winter drawdown. Other studies have found a similar relationship between severity of a drawdown and reduction of zoobenthic biomass (Palomaki 1994). Taxa documented by Kraft (1988) as most negatively affected by extreme winter drawdown included the isopod genus *Asellus*, the phantom midge *Chaoborus*, snails (Gastropoda), the mayflies *Caenis* and *Hexagenia*, and the alder fly *Sialis*. Chironomidae, a large ubiquitous family of dipterans, tended to be more abundant in drawdown zones and appeared to be favored under the 1970 rule-curve.

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 (Figure 2). The IJC further indicated that the new order would be subject to review after 15 years based on environmental monitoring information collected by natural resource agencies. Thus, the IJC effectively called for extensive monitoring and research designed to document changes in biological communities because of their fundamental ecological importance and the central role biology played in the discussions leading to the change in water management. Since 2000, the new rule curves have reduced winter drawdown in Namakan from 2.5 to 1.5 meters and allow the reservoir to be refilled to capacity at the end of May instead of the later part of June; in both Rainy Lake and Namakan Reservoir a gradual summer drawdown was initiated instead of holding water stable during the summer (Kallemeyn et al. 2003). The magnitude of drawdown and timing of spring refill remained essentially unchanged from the 1970 rule-curve in Rainy Lake. For this reason, the relevant parameters of interest with respect to the change of rule curve in comparing Namakan Reservoir and Rainy Lake are limited to the change in the magnitude of winter drawdown and the timing for when the reservoir is filled to capacity in the spring. We investigated whether this change had positively affected the benthos in Namakan Reservoir by comparing the benthic community structure in both systems during 2004-2005 with that documented by Kraft (1988) a decade earlier.

IJC 2000 Rule Curves
Compared with IJC 1970 Rule Curves

Namakan Lake

Level (m)

— IJC 2000 Rule Curves
— IJC 2000 Drought Line
-- IJC 1970 Rule Curves

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

Rainy Lake

Level (m)

— IJC 2000 Rule Curves
— IJC 2000 Drought Line
-- IJC 1970 Rule Curves

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. Comparison of the 1970 and 2000 rule-curves issued by the International Joint Commission.

After giving a general description of the invertebrate community of VOYA, we will address the following questions with respect to the change in the rule curve in Namakan Reservoir relative to Rainy Lake:

1. Has the structure of the community been affected in terms of taxonomic composition, site occupancy and relative densities?

2. Has there been a change in the ratios of densities between June:August for individual taxa?

3. Is there an interaction between depth and the change in water-level management?

4. Which sites have shown the greatest amount of relative change?

5. Which taxa have shown the greatest amount of relative change?

6. Has overall benthic invertebrate density or diversity been affected?

7. Has the overall ratio of total number of organisms between June:August been affected?

8. Has the "stability" of communities changed in concert with the rule-curve change?

9. Have the abundance, density, and/or relative abundance of key taxa, identified by Kraft as being sensitive to water level regulations, been affected?

10. Which water-level variables are most closely associated with the structure of the benthic invertebrate community in VOYA?

Methods

Field Methods

Between 1984-1986, including three June dates, one July date, and two August dates, Kraft sampled in five locations, two bays in Rainy Lake (Harrison and Black Bays), and one each in the Namakan Reservoir lakes Kabetogama (Moxie Bay), Namakan (Junction Bay), and Sand Point (Swanson Bay) with previously reported morphometric and limnological descriptions (Table 1; Figure 3). We sampled these same sites, with the exceptions noted below, on June 8, 2004; August 16, 2004; June 6, 2005; and August 21, 2005. Hereafter, we will refer to samples from these dates as the AFTER data set. Kraft's (1988) data (hereafter referred to as the BEFORE data set) include samples from June 7, 1984; August 25, 1984; June 11, 1985; and August 26, 1985. Both Kraft and we sampled all sites within three to five days of the starting date for each season/year.

Table 1. Morphometric and limnological characteristics of the five Before-After Control-Impact (BACI) sites used in the benthic macroinvertebrate comparison between 1970 and 2000 rule curves. Littoral area (%) = proportion of lake < 4.6 m deep. Morphometric data from Kallemeyn et al. (2003). Limnological and trophic state data from Christensen et al. (2000) and Payne (1991, 2000).

	Junction	Moxie	Swanson	Harrison	Black
	Namakan	Kabetogama	Sand Point	Rainy	Rainy
Lake area (ha)	10170	10425	3580	92100	92100
Watershed to lake area ratio	193	197	567	42	42
Shore development	6.5	9.0	7.0	14.4	14.4
Maximum depth (m)	45.7	24.3	56.1	49.1	49.1
Mean depth (m)	13.6	9.1	12.0	9.9	9.9
Littoral area (%)	20	30	32	35	35
Volume ($m^3 x 10^6$)	1383	949	431	9118	9118
Renewal time (years)	0.6	0.6	0.6	1.0	1.0
Chl-a (mg/l)	1.6	6.4	1.7	1.6	5.8
TP (ug/l)	16	35	18	18	53
TN (ug/l)	497	697	616	436	786
N:P molar	31.1	19.9	34.2	24.2	14.8
Water temperature (ºC)	16.7	18.2	15.5	16.3	17.9
Secchi (m)	3.0	2.2	2.4	2.5	0.8
1970 Rule Curve Trophy	Oligo-mesotrophic	Eutrophic	Oligo-mesotrophic	Oligo-mesotrophic	Eutrophic
2000 Rule-Curve Trophy	Oligo-mesotrophic	Mesotrophic	Oligo-mesotrophic	Oligo-mesotrophic	Mesotrophic
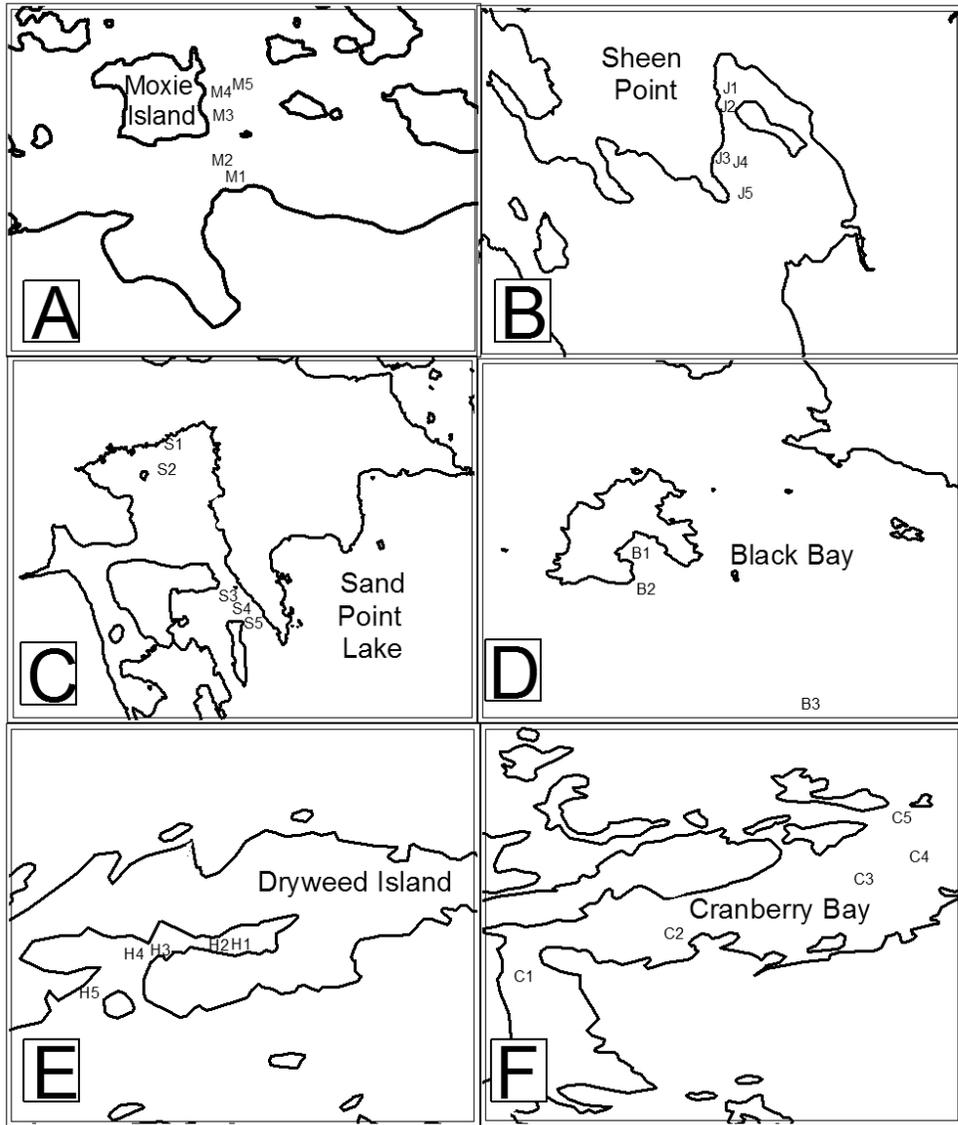
Figure 3. Locations of sampling sites. Letters correspond to the first letter of the name of the bay; numbers indicate depth. Inset A is Moxie Bay in Kabetogama Lake; B is Junction Bay in Namakan Lake; C is Swanson Bay in Sand Point Lake; D is Black Bay in Rainy Lake; E is Harrison Bay in Rainy Lake; and F is Cranberry Bay in Rainy Lake. Maps are not to same scale.

Since invertebrate abundances are likely structured by the season during the year, we did not use Kraft's July samples in our analyses. Kraft also sampled in June, but not in August, of 1986. Since there were no complementary August 1986 dates in the BEFORE set, and since we only sampled two years (2004 and 2005), we excluded the June 1986 data from our analyses as well. We were left with two years of data in the BEFORE set (i.e., June and August, 1984 and 1985) and two years of data in the AFTER set (i.e., June and August, 2004 and 2005).

In addition to revisiting all five of Kraft's sites, we sampled another site within Rainy Lake (Cranberry Bay). The extra data allowed a more robust description of the general macroinvertebrate community in the VOYA large lake systems at a finer taxonomic resolution than what Kraft provided. The additional site in Rainy Lake gave us a more nearly balanced data set for multivariate analyses aimed at relating environmental variables to taxa for implicitly assessing effects of water level manipulation on ecological communities using the AFTER data set alone. In other words, we related taxa to environmental variables that potentially could be impacted by water level management. We also used the Cranberry Bay data to assess whether Black Bay and Harrison Bay were representative of soft-sediment littoral communities in Rainy Lake. If representativeness cannot be demonstrated, then we should be cautious in making lake-wide inferences based on data collected from the sites chosen. Based on this test of exchangeability, we assigned bays as either fixed (i.e., Cranberry Bay was not exchangeable) or random (i.e., Cranberry Bay was exchangeable) in model construction.

We located Kraft's original sites by maps in his report. After locating the general vicinity and then finding the proper depth, GPS coordinates were taken on our first sampling occasion during June 2004; these coordinates were used for navigation purposes in the future (Table 2). Since water levels fluctuated on both an inter- and intra-annual basis, when we returned to sampling points, depths were not necessarily identical to what they had been when the original coordinates were taken. June sampling occurred 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 (Figures 4a and 4b). As a result, during subsequent sampling occasions we selected sampling locations with the desired sampling depths (using a sonar depth finder) as close as possible to the targeted GPS coordinates.

It is unclear from the Kraft report how he defined his sampling sites with respect to water level, and since he did not report exact coordinates there is no way to determine precisely where he took samples. Consequently, it is unlikely we sampled the exact same sites that he did; however, if we consider sites to be random factors for the general design of this "experiment," it is not necessary that the exact same points were sampled. We are not concerned with the similarity at the precise geographic point as Kraft but instead with the overall response at the particular bay-depth combination, or even more precisely, the system-depth response should bays be considered random factors. Furthermore, unless Kraft physically marked sampling sites, which does not seem probable, it is unlikely even he sampled the same exact sites throughout time. We matched depth instead of elevation, suspecting this was the most logical way that he selected a site.

Table 2. GPS coordinates taken June 2004 to establish sampling sites in bays of Rainy Lake and Namakan Reservoir.

Bay	Depth (m)	Symbol	Latitude	Longitude
		Rainy Lake		
Black	1	B1	48.56345968	-93.14401307
	2	B2	48.56228194	-93.14390293
	3	B3	48.55840640	-93.13857623
Harrison	1	H1	48.61280411	-93.12143583
	2	H2	48.61259004	-93.12361303
	3	H3	48.61274687	-93.12772905
	4	H4	48.61240639	-93.12937659
	5	H5	48.61063144	-93.13356419
Cranberry	1	C1	48.58493554	-93.06044600
	2	C2	48.58807893	-93.04831898
	3	C3	48.59254606	-93.03385491
	4	C4	48.59414784	-93.02945274
	5	C5	48.59739432	-93.03080600
		Namakan Reservoir		
Moxie	1	M1	48.42545953	-92.97622682
	2	M2	48.42657642	-92.97780555
	3	M3	48.43054265	-92.97808173
	4	M4	48.43209716	-92.97793211
	5	M5	48.43252321	-92.97607309
Junction	1	J1	48.42280271	-92.67654587
	2	J2	48.42204038	-92.67654771
	3	J3	48.42057749	-92.67653815
	4	J4	48.42054681	-92.67615066
	5	J5	48.41933847	-92.67539805
Swanson	1	S1	48.40916787	-92.48808204
	2	S2	48.40736652	-92.48835563
	3	S3	48.39976916	-92.48289188
	4	S4	48.39937571	-92.48214975
	5	S5	48.39917815	-92.48198907
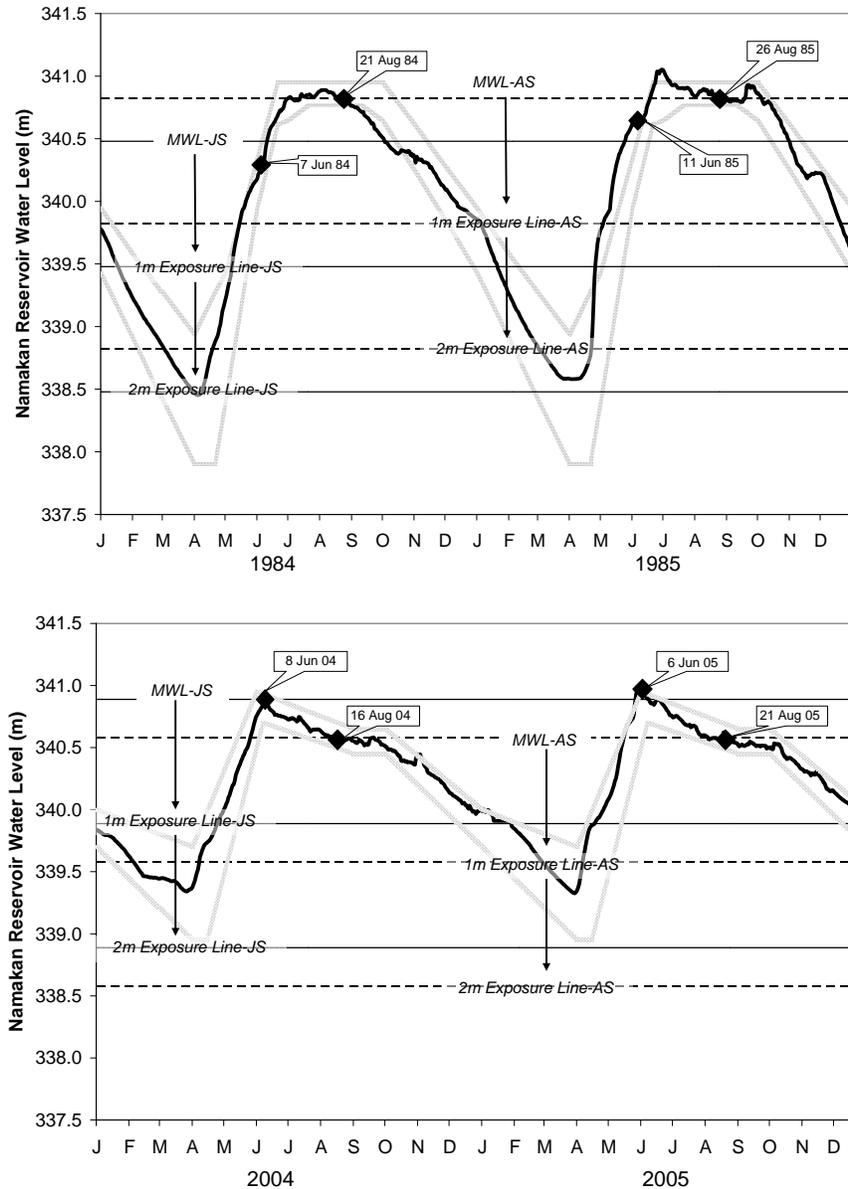
Figure 4a. Water levels in Namakan Reservoir for the duration of both study periods 1984-85 (upper) and 2004-05 (lower). Upper horizontal solid line indicates mean water levels during June sampling (MWL-JS), and the upper dashed line indicates mean water levels during August sampling (MWL-AS). Related horizontal solid and dashed lines show difference of one and two meters from mean water levels when sampling occurred. When the actual water levels (i.e., heavy solid lines) dip below these horizontal marks, it indicates the sites that were sampled would have been exposed in the winter. Solid diamonds (◆) and associated dates indicate actual water levels when sampling occurred. Thick gray lines show the upper and lower boundaries for the rule-curves under the respective 1970 and 2000 mandate for water level management by the International Joint Commission.

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Figure 4b. Water levels in Rainy Lake for the duration of both study periods 1984-85 (upper) and 2004-05 (lower). Upper horizontal solid line indicates mean water levels during June sampling (MWL-JS), and the upper dashed line indicates mean water levels during August sampling (MWL-AS). Related horizontal solid and dashed lines show difference of one and two meters from mean water levels when sampling occurred. When the actual water levels (i.e., heavy solid lines) dip below these horizontal marks, it indicates the sites that were sampled would have been exposed in the winter. Solid diamonds (◆) and associated dates indicate actual water levels when sampling occurred. Thick gray lines show the upper and lower boundaries for the rule-curves under the respective 1970 and 2000 mandate for water level management by the International Joint Commission.

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We were unable to find a four-meter depth in Black Bay for which Kraft recorded data. As a consequence, we did not use Kraft's data for Black Bay at four-meters. Only during 1985 did Kraft find a four-meter depth, where he sampled at a time when the water level was over the upper rule-curve. In contrast, our sampling sites were established during 2004 while the water level was within the rule-curve. Water was higher when we sampled during June 2005, so it is possible that a four-meter depth existed in Black Bay at that time. However, we returned to our June 2004 sites on subsequent visits (using GPS coordinates taken on the first sampling occasion), and thus we did not encounter a four-meter water depth in Black Bay even though it may have occurred in 2005. Given that we were not looking for four-meter depth and Kraft only had data for a single year at the four-meter depth for Black Bay, we did not include it in our sampling regime and subsequent analysis.

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), giving 15 locations over eight sampling occasions. Within Rainy Lake, two bays were sampled. Five depths were sampled in one bay, and three depths were sampled in the other, 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 ($n = 64$).

As did Kraft, we collected three replicate samples 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 as well as Kraft's original subsamples and considered our sampling unit to be each depth-site-time combination, which gave four repeated measures for each sampling unit in both the BEFORE and 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 compare densities between the two studies on a square-meter plot basis.

Our approach differs from Kraft's in that he considered each replicate grab as a sampling unit. If we used each individual grab sample, scaling it to square-meter plots, we would be assuming that the invertebrates were randomly distributed within the plots. If this were the case, we would expect nearly similar counts within each of the three individual grab samples per site, which did not occur. There was high variability among grabs taken at each site within a particular sampling occasion for both Kraft and the present study. This is consistent with the general understanding that invertebrate populations have an overdispersed (e.g., negative binomial, log-normal) distribution (Gray 2005). By pooling three grab samples together we could better account for this overdispersion and more closely approximate true density within a meter plot.

Washed samples were preserved in ethanol and sent to the Department of Entomology at the University of Minnesota for taxonomic identification. Macroinvertebrates were identified to the "lowest practicable level," which was different for samples collected by Kraft and those collected for the present study due to different investigators performing taxonomic identifications. Since taxonomic resolution differed between the two studies, it was necessary for some lumping of taxonomic groups for our data, which was more highly resolved, for direct comparison with Kraft's data. In particular, we identified organisms to a finer level resolution for Gastropoda, Sphaeriidae, Hirudinea, Pyralidae, and the dipteran families Ceratopoginidae and

Chironomidae. We calculated relative densities of the finer-scaled taxonomy within these clumped groups to give an indication of specific taxa that comprised the majority of membership in clumped groups (Table 3).

Additionally, we lumped Kraft's "Psychomyiidae" with our Polycentropodidae: *Phylocentropus.* Psychomyiidae and Polycentropopidae are two families of Tricoptera that are often misidentified and confused for one another (Wiggins 1996). Kraft found 52 individual Psychomyiidae for which he could not make a finer taxonomic determination. We found none of the members of this family, but we did find 217 *Phylocentropus* of the Polycentropodidae for which Kraft did not find any analogous representatives. We suspect that Kraft's Psychomyiidae were misidentified and are in reality *Phylocentropus,* and we proceeded in our analyses as if this were the case. An examination of voucher specimens from Kraft's study may be able to confirm this suspicion; however, these taxa are relatively rare compared to the rest of the animals in the communities and probably will not make much difference in the overall, final analyses.

We collected an additional sample at each site/depth for analysis of sediment characteristics (organic content, water content, and sediment particle size). We analyzed the organic content of the sediments following the loss-on-ignition protocol used by Kraft (1988). Sediments were separated into size fractions representative of sand, silt, and clay fractions (Kettler et al. 2001). While Kraft did not analyze sediment particle size, we used this information from our samples in our ordination analysis of taxon-environment relationships in the AFTER data set.

Semi-quantitative macrophyte data were also collected during the June and August sampling occasions during 2004. Four macrophyte rake pulls were taken at each one-meter and two-meter depth sites; macrophytes were identified to species when possible. Density was estimated on an ordinal scale from zero to five, where zero indicates not present and five indicates extremely abundant. The two-meter site in Black Bay was the only one of these shallow sites at which no plants were found during either June or August sampling. Only rarely were macrophytes observed at sites where the depth was greater than two meters. Summary variables for plant data included overall density, which was estimated as the maximum density index for any species within a site and species richness, which was the total number of species present at a site. Since we did not collect macrophytes in 2005, we evaluated only the macroinvertebrate/macrophyte relationship for 2004.

Table 3. Clumping of taxonomic units for common relatedness in BACI.

BACI Designation	Family	Genus	Fraction Total (%)[1]
Gastropoda	Physidae	*Physa gyrina*	4
Gastropoda	Planorbidae	*Gyraulus deflectus*	4
Gastropoda		*Gyraulus parvus*	15
Gastropoda		*Helisoma anseps*	3
Gastropoda		*Planorbella campanulatum*	1
Gastropoda		*Prominenetus exacous*	2
Gastropoda	Hydrobiidae	*Amnicola*	59
Gastropoda	Valvatidae	*Valvata lewsi*	2
Gastropoda		*Valvata sincera*	1
Gastropoda		*Valvata tricarinata*	<u>10</u>
			101
Sphaeriidae	Sphaeriidae	*Musculium*	26
Sphaeriidae		*Sphaerium*	18
Sphaeriidae		*Pisidium*	<u>56</u>
			100
Hirudinea	Erpobdellidae	*Erpobdella punctata*	27
Hirudinea		*Mooreobdella fervida*	2
Hirudinea		*Nephelopsis obscura*	1
Hirudinea	Haemopidae	*Haemopis*	2
Hirudinea	Glossiphoniidae	*Actinobdella inequiannulata*	1
Hirudinea		*Alboglossiphonia heteroclite*	3
Hirudinea		*Glossiphonia complanata*	2
Hirudinea		*Helobdella stagnalis*	57
Hirudinea		*Placobdella hollensis*	1
Hirudinea		*Placobdella monifera*	<u>1</u>
			97
Ceratopogonidae	Ceratopogonidae	*Bezzia/Palpomyia*	7
Ceratopogonidae		*Mallochohellea*	58
Ceratopogonidae		*Sphaeromias*	<u>35</u>
			100
Chironomidae	Chironominae	*Chironomus*	15
Chironomidae		*Cladopelma*	1
Chironomidae		*Cladotanytarsus*	3
Chironomidae		*Cryptochironomus*	1
Chironomidae		*Cryptotendipes*	1
Chironomidae		*Dicrotendipes*	3
Chironomidae		*Einfeldia*	1
Chironomidae		*Endochironomus*	1
Chironomidae		*Glyptotendipes*	0
Chironomidae		*Lauterborniella*	0
Chironomidae		*Microchironomus*	0
Chironomidae		*Micropsectra*	0
Chironomidae		*Nilothauma*	0
Chironomidae		*Pagastiella*	1
Chironomidae		*Paralauterborniella*	0
Chironomidae		*Paratnaytarsus*	1

Table 3. Clumping of taxonomic units for common relatedness in BACI (continued).

BACI Designation	Family	Genus	Fraction Total (%)[1]
Chironomidae		*Paratendipes*	0
Chironomidae		*Phaenopsectra*	0
Chironomidae		*Polypedilum*	4
Chironomidae		*Pseudochironomus*	8
Chironomidae		*Stempellina*	0
Chironomidae		*Stempellinella*	1
Chironomidae		*Stictochironomus*	0
Chironomidae		*Tanytarsus*	15
Chironomidae		*Undescribed*[3]	0
Chironomidae		*Xenochironomus*	0
Chironomidae		*Omisus*	0
Chironomidae		*Parachironomus*	0
Chironomidae		*Tribelos*	0
Chironomidae		*Harnischia*	1
Chironomidae		*Microtendipes*	1
Chironomidae		*Paracladopelma*	<u>0</u>
			58
Chironomidae	Diamesinae	*Protanypus*	<u>0</u>
			0
Chironomidae	Orthocladinae	*Acricotopus*	0
Chironomidae		*Corynoneura*	0
Chironomidae		*Cricotopus*	1
Chironomidae		*Epicocladius*	0
Chironomidae		*Heterotrissocladius*	0
Chironomidae		*Nanocladius*	0
Chironomidae		*Orthocladius*	0
Chironomidae		*Parakiefferiella*	0
Chironomidae		*Psectrocladius*	<u>1</u>
			2
Chironomidae	Tanypodinae	*Ablabesmyia*	6
Chironomidae		*Clinotanypus*	6
Chironomidae		*Labrundinia*	0
Chironomidae		*Larsia*	0
Chironomidae		*Natarsia*	0
Chironomidae		*Paramerina*	0
Chironomidae		*Procladius*	25
Chironomidae		*Tanypus*	<u>0</u>
			<u>37</u>
			97
Pyralidae	Pyralidae	*Acentria*	4
Pyralidae		*Crambus*	81
Pyralidae		*Parapoynx*	<u>15</u>
			100

[1] Fraction total does not always equal 100% due to rounding
[2] Chironomidae is further divided into Subfamilies
[3] Morphlogically similar to Stempellina/Constempellina

Analytical Methods

General Community Description

We developed a list of all taxonomic units that occurred in the park over the duration of both studies. We also assembled relative density and site occupancy curves for the description of community dominance overall using only the AFTER data because of its higher taxonomic resolution. We divided these data into two depth groups that will be referred to as the eulittoral (sites occurring at one and two-meter depths) and the sublittoral (sites occurring at three, four, and five-meter depths) as these depth separations will show the greatest structuring influences in community analysis. Relative density curves were constructed by ranking taxonomic units, with respect to density, in descending order and graphically displaying them with rank given along the abscissa and relative density given on the ordinate. Relative density scores (RD_i) for individual taxonomic units (TU_i) were computed as:

$$RD_i = \left(\frac{TU_i}{\sum_{i}^{p} TU_i} \right) * 100 \qquad \text{[Eq. 1]}$$

We calculated a standard error for relative density scores from combined spatial and temporal sources. We used the same mathematics to calculate site occupancy, but used a presence-absence matrix instead of a density matrix. These curves can reveal main patterns in community composition such that: (1) if a taxon has a high relative abundance and high site occupancy, it is both ubiquitous and locally abundant; (2) if a taxon has high relative abundance and low site occupancy, it is rarely found but locally abundant where it occurs; and (3) if a taxon has low relative abundance and high site occupancy, it is ubiquitous but sparse where it occurs. These descriptions will give an overall conceptual perspective with respect to which organisms are potentially important in these systems.

Before-After Control-Impact Experimental Design

We placed our study within the general Before-After Control-Impact (BACI) framework (Green 1979; Stewart-Oaten and Murdoch 1986). In the simplest implementation of the BACI design, paired samples are collected, one in the control site and one in the impact site, at several time points BEFORE and AFTER an impact. Differences are calculated at each time period for response variables AFTER-BEFORE and are compared using a paired *t*-test of a null hypothesis of no difference in the sample differences (C-I) BEFORE and AFTER. While there is a high probability that time series data for the original sites will suffer from autocorrelation, differences between the sites generally will not, provided that additivity occurs between the responses at impact and control sites (Stewart-Oaten and Murdoch 1986). Heuristically, additivity means that the "natural" trajectory of two systems will have an additive, as opposed to a multiplicative, relationship so that the difference at sampling period t_i for two systems is, on average, only of a constant.

The general idea of the BACI design is that some degree of background (i.e., not related to the impact) change will occur through time in populations being investigated, which can be captured by the response at the control site. The same trajectory is presumed to have occurred in the impact site in the absence of the impact (i.e., additivity). Any additional change observed in the impact but not in the control site is attributed to the impact.

While the general idea is appealing, it is important to note there is no statistical connection between finding a difference in the control and impact and assigning the difference causally to the impact; the only statistical decision that can be made from a hypothesis test, given the 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 and Thomas 1991). Taking multiple samples does not equate to "replication" but, instead, is subsampling. There is only one treatment at one time (i.e., changing the drawdown regime only in one location – Namakan Reservoir). To make statistical claims with respect to causation, we would need to take one of two approaches. If we wanted to make inferences on other similar reservoir-systems, we would be required to manipulate the drawdown regime of other reservoir-systems (e.g., other dams in other lakes), take samples from the replicated treatments and controls, and compare those using statistical tests. Alternatively, if we were only interested about the impact in the VOYA system, which seems to be the case for the present investigation, we would have to intersperse treatments, meaning we would have to find some way to randomly select sites within all areas of concern and randomly assign a treatment to those sites. For example, in Black Bay we would need to be able to change the drawdown regime at one site (e.g., B1) but leave it the same at adjacent sites (e.g., B2). Obviously, such an interspersion of treatments is impossible. We are left with the consequence that while we can apply statistical tests to subsamples within Namakan Reservoir and Rainy Lake, any observed difference will only indicate differences between locations and will not indicate differences due to the change in the rule curve. This is not to suggest that showing locational differences is unimportant. If we are to argue for a causal link, we need to first demonstrate there has been a change *coinciding* with the treatment even if we cannot show it is *caused* by the treatment (Hargrove and Pickering 1992). The follow up step requires a consideration of evidence supporting a causal link to the change in rule curve, including plausible alternative hypotheses, to attempt to explain the observed differences.

If locational differences are detected, we can then attempt to make causal connections to the treatment based on logical arguments, but not statistical ones (i.e., "weight-of-evidence" approach). We approximately follow Hill's criteria as summarized in Beyers (1998) in the discussion portion of the report. He suggested that we can build a logical case for causation based on the following:

1. Strength: a large proportion of individuals are affected in the exposed areas relative to reference areas
2. Consistency: the association has been observed by other investigators at other times and places
3. Specificity: the effect is diagnostic of exposure
4. Temporality: exposure must precede the effect in time
5. Biological gradient: the risk of effect is a function of magnitude of exposure
6. Biological plausibility: a plausible mechanism of action links cause and effect

7. Experimental evidence: a valid experiment provides strong evidence of causation
8. Analogy: similar stressors cause similar effects
9. Coherence: the causal hypothesis does not conflict with existing knowledge of natural history and biology

Hill's criteria are used by epidemiologists to evaluate causal association for disease and have also been used in risk assessment and environmental toxicology studies conducted by the USEPA (Fox 1991; USEPA 1992). While deciding whether enough evidence exists to conclude causal link is arbitrary, Hill suggested that the first three criteria 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 rigor, it is the best we can do with unreplicated experiments in which there are "no simple solutions" (Stewart-Oaten et al. 1992).

We define BEFORE and AFTER conditions with respect to the change in the implementation of the 2000 rule curve, in which Rainy Lake represents the "control" condition and Namakan Reservoir represents the "impact" condition. Reviewers of Kraft's study were critical of his use of Rainy Lake as a "control" to Namakan Reservoir (Kitchell and Koshinsky 1996). Due to their connectance, it would be naïve to assume that Rainy Lake would be unaffected by changes in the rule curve. In order to maintain nearly similar water-level management in Rainy Lake, management at the International Falls hydroelectric dam would also have to change to reduce outflow. This would mean that Rainy Lake would store water from Namakan Reservoir longer under the present rule curve.

The greatest similarity between Rainy Lake and Namakan Reservoir, with respect to our sampling sites, is Black Bay in Rainy Lake and Moxie Bay in Kabetogama Lake. Both Black Bay and Kabetogama Lake receive inflow from streams that drain watersheds with calcareous glacial drift south and west of the park, while the main basin of Rainy Lake, along with Namakan and Sand Point Lakes, receives water from the east of the park, largely draining thin, noncalcareous soils. The coupling of more minerals and nutrients from the more fertile watersheds, along with the relatively shallow nature of Black Bay and Kabetogama, can largely explain their generally higher productivity compared with other areas in the park (Table 1). Additionally, there is a natural spillway between Kabetogama and Black Bay, and when water levels are high in Namakan Reservoir, water flows from Kabetogama to Black Bay via Gold Portage. This likely links responses in Moxie Bay to Black Bay, and there appears to be higher temporal coherence between these two systems than among other lakes. In a study of system productivity in August 1999, four months prior to the implementation of the 2000 rule curve, Payne (2000) found that the trophic state in both Black Bay and Kabetogama had changed from eutrophic to mesotrophic relative to the period 1979-1983 (Payne 1991). The main basin of Rainy Lake and both Namakan and Sand Point Lakes remained meso-oligotrophic over the same period. A subsequent study in 2004 (the onset of our survey) showed that Black Bay and Kabetogama had remained mesotrophic. While it is implied in Christensen et. al's (2004) report that the change in the trophic state of Black Bay and Kabetogama correlates with the change in the 2000 rule-curve, we suspect that these systems had changed prior to the rule curve implementation based on the 1999 report (Payne 2000). Our comparisons between Namakan Reservoir and Rainy Lake, using sites from Black Bay and Kabetogama, are still legitimate if we explicitly take into consideration the similarities between the two bays Black and Moxie, which

we did by the use of covariables. At the same time, Black Bay still would not be exposed to the same drawdown in the winter, or the date when the systems are filled to capacity in the spring. Thus, with respect to the change in drawdown, Black Bay still provides a "control." As we want to make system-wide inference, it is fortunate that we have samples from both the main basin of Rainy Lake (represented by Harrison) and the shallow, more productive basin Black Bay. Thus Harrison can best be compared with Sand Point and Junction Bay sites in Namakan, and Black Bay can be compared to the Moxie Bay site in Kabetogama.

The use of the term "control" to address such natural experiments can easily lead to misunderstanding. We use the term not to mean that Rainy Lake is entirely unaffected, or even disconnected from the response in Namakan Reservoir. Rather, we apply the term "control" specifically to the dual "treatment" of changing both the magnitude of drawdown and the timing of the end of spring refill, which differed in Rainy Lake relative to Namakan Reservoir as the result of the 2000 rule-curve. We realize that Rainy Lake may be indirectly affected by the change, but the hypotheses we generate suggest a greater impact in Namakan compared to Rainy Lake, which in part satisfies Hill's fifth criterion (1965). Given that arguments with respect to the change in the rule curve will need to be made based on logical (as opposed to statistical) grounds, to what degree Rainy Lake serves as a statistical control may be trivial, should clear differences be found. Only if we are unable to find a BACI signal might we appeal to the lack of suitability of the comparison as one plausible explanation, although it would be difficult to determine with certainty. One might then hypothesize that Rainy was not sufficiently different to serve as a control and design an experiment to address this specifically.

Multivariate BACI
Community-level data from complex natural systems are sometimes difficult to evaluate rigorously with traditional univariate statistical approaches due to large numbers of response variables and complex interactions among treatments (ter Braak 1994). When using a series of univariate statistics to test for taxa responses individually, the implicit assumption is that each taxonomic unit acts independently with respect to the variable of interest, but that is not realistic, and often it is the case - such as in this analysis - that we explicitly want to know about interrelationships. If some taxa respond in a similar fashion to an environmental gradient, then a significant result for one taxon provides no new information apart from another significant result, while at the same time the extra tests increase the experimentwise error rate. Furthermore, univariate tests may be misleading; even when all individual ANOVAs produce nonsignificant results, it does not imply that a multivariate test will also be nonsignificant, because statistical power is increased in multivariate analysis when species vectors correlate with one another (Huberty and Morris 1989; Schmitz et al. 1998).

Multivariate ordination methods allowed us to examine the underlying structure of the benthic community. If communities in Namakan and Rainy relate similarly to environmental gradients in the 2004-05 data set, but differently in the Kraft data from the 1980s, this would indicate that the altered rule curve has brought the two systems closer in ecological structure. In addition, direct gradient analysis can be used to partition the variance in the benthic community among the major independent variables. This should allow us to assess the magnitude of change that may be attributable to the altered rule curve relative to other sources of variation in the benthic communities of these lakes.

Ordination methods can be divided into two complementary strategies: indirect gradient analyses (e.g., nonmetric multidimensional analysis, principal components analysis, correspondence analysis, etc.) and direct gradient analyses (e.g., redundancy analysis, canonical correspondence analysis). Indirect gradient analysis (IGA) is a two-step process where a matrix of sampling units by species is reduced to a matrix of sampling units by sites scores. The aim is to reduce the species component of these matrices to site scores because we presume that some species will behave in a similar fashion with respect to the environment. As such, much of the information in a species matrix is redundant. The goal is to reduce a large species matrix to a small number of dimensions, usually two or three, for visualizing the placement of sampling units (i.e., sites) along an implicit environmental gradient where sites are represented as points and the distance between two points, relative to two other points, is proportional to the similarity of their underlying fauna so that the closer two given points are to one another, the more similar their fauna. Plotting points along a Cartesian coordinate system produces sites separated by distances in Euclidean space, although this is not always most appropriate for ordination methods (see below). The second, optional step of indirect gradient analysis is to correlate environmental variables of interest with those reduced site-score dimensions. This provides the advantage of being able to consider any number of environmental variables because multicollinearity is not an issue since the environmental variables themselves are not used to order sites. In fact, IGA can reveal the nature of multicollinear relationships among a large set of environmental variables, which is often of interest.

While these reduced axes could then be used to assess the impact of treatments using traditional ANOVA designs, problems can arise if the first few reduced dimensions explain only a small amount of the variability or if the relationship between sites and an environmental variable of interest are not linear. Environmental variables important to the overall structure of the community may not be appreciated if they correlate linearly to residual dimensions or respond in a nonlinear fashion to any dimension. Direct gradient analysis directly addresses this problem. It adds an extra step in the initial, species-data reducing algorithm, using sites scores from all dimensions, regardless of their importance, in a regression analysis. The output provides a model of fitted values that reduces the overall total residual sums of squares. Thus, indirect gradient analysis considers environmental gradients implicitly and *a posteriori*, while direct gradient analysis considers the gradients explicitly and *a priori*. We use direct gradient analysis to test for a change in community structure that correlates in time with the impact of changing the rule curve. We then use indirect gradient analyses to visualize such change, as well as the explicit relationship of water-level variables on the structure of the invertebrate community before and after the change of the rule curve.

Legendre and Anderson (1999) introduced distance-based redundancy analysis (db-RDA) as a direct gradient analysis method to test for the interaction term in an experimental design such as BACI. Redundancy analysis is an iterative procedure in which sample scores are determined by alternately being regressed against coefficients for each taxonomic unit and environmental variable until predicted scores are the same for each. RDA is analogous to univariate multiple regression. The problem with RDA for community analysis is that forcing samples scores into a Euclidean framework is not appropriate for community data which consists of sparse matrices and many zeroes (Legendre and Gallagher 2001). It inappropriately considers two samples with zero values to be related; however, double-zeroes may indicate similarity or dissimilarity. If we

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presume a Hutchisonian niche and unimodel response to an environmental gradient, then a species' absence may indicate that it is at a point in the gradient that is either below or above its tolerance. If two species are simultaneously absent from a site, then one of three circumstances is true: (1) one species is below and one is above; (2) both species are above; and (3) both species are below. There is no analytic way to determine which is the correct view. Since these solutions conflict with one another (i.e., the sites are either very similar or very different), it is best to make no sort of conclusion based on the double absence of two taxa. Distance-based RDA uses the power of the redundancy analysis (RDA) framework without relying on the underlying assumption that sampling sites can be related using a Euclidean distance.

Distance-based RDA is a method that allows any distance matrix to be used in an RDA. Instead of importing a species matrix for RDA, db-RDA uses scores from a principal coordinate analysis (PcoA) on the distance matrix of choice as an input. Distance-based RDA is directly equivalent to RDA when the PcoA scores used as an input were derived from the Euclidean distance. The general idea of PcoA is that instead of using the taxa matrix directly, it uses the distance matrix for the taxa matrix of one's choosing and produces Euclidean coordinates for each sample while preserving the distances in the original matrix. At most, N-1 axes will be generated where N is the number of sites, and all are used as an input for RDA to ensure tests are not biased. Sometimes negative eigenvalues are produced because high-dimensional axes can be difficult to coerce into a Euclidean framework but they can be accounted for by adjusting the originally produced distance matrix (Legendre and Anderson 1999).

We chose the Bray-Curtis (BC) distance (a.k.a. Sorenson Coefficient) as an input for PcoA because it is one of the most ecologically meaningful and best-performing distance methods presently available. McCune and Grace (2002) give the interpretation of the BC distance as "shared abundance divided by total abundance." It is a distance measure that explicitly excludes double zeros for calculation. Legendre and Legendre (1998) term these distance measures asymmetrical coefficients (symmetrical coefficients explicitly use double zeroes in calculations of similarities). While it is appropriate for raw data, it can also be used on a transformed species matrix to allow rare taxa to have more of an effect, and rare taxa need special consideration in multivariate analyses. If a taxon is truly rare and sampling is adequate, then it should be given a high weight in the ordination; however, if the taxon is sporadically sampled and may or may not be more abundant, then giving rare taxa a high weight can lead to lower power to detect structure in a community (Legendre and Gallagher 2001). Further, simulations indicate that excluding taxa in less than 5-15% of sampling units improves the correlation between environmental variables and ordination axis scores (McCune and Grace 2002); however, to exclude rare taxa from impact studies means we consider that only the most abundant organisms are impacted, which is counterintuitive (Cao et al. 2001). Critical information is lost when excluding rare taxa from impact assessment (Cao et al. 1998). For this reason, we included rare taxa in the analyses, but we keep the caveat in mind for interpretation of results that using rare taxa sacrifices correlation strengths and that variance explained by the ordination would be higher if they were not used. Given that rare taxa would be most susceptible to impact because of low initial population levels, we believe their use is warranted even if statistical power is sacrificed. We attempted to ameliorate the negative impacts of rare taxa on ordination by using a log-transformation on the original data matrix. Thus, prior to computing the BC distance matrix we log (x+1) transformed taxon densities to reduce the influence of very abundant taxa.

We performed db-RDA by first calculating PcoA scores in R using the vegan package and importing the axes into CANOCO to perform the RDA (ter Braak and Smilauer 2002; R_Development_Core_Team 2006; Oksanen et al. 2007). CANOCO uses permutations to calculate a pseudo F statistic and accompanying P-value. Tests were performed using the split-plot design where sites were whole plots ($N=23$) and sampling periods ($N=8$) were split-plots. Permutations were allowed freely among time periods within, but not across, sites. Sites were also permuted and freely exchangeable. We included, as covariables, depth, season (June or August), bay, and deviations from the rule-curve. Preliminary analyses indicated that deviations from the rule curve were best accounted for by the cumulative meters that actual water levels deviated over or under the specified upper and lower bounds for the rule curves.

We considered four basic models: (1) BACI only; (2) BACI interacting with depth; (3) BACI interacting with one and two-meter depths as a group and three, four, and five-meter depths as another group; and (4) BACI interacting with one, two, and three-meter depths as a group and four and five-meter depths as a group. Models were evaluated based on the residual error and P-value. Lower residual error and P-values were deemed to indicate better models. We conducted the analysis both on density estimates and on density ratios of June:August samples to address Kraft's hypothesis that recovery from impact should show higher numbers to this ratio. For any significant effects, we also ran an additional test on the two water-level variables that changed: (a) the magnitude of drawdown and (b) the date by which the reservoir filled to capacity in the spring, as well as on the interaction of (a) & (b). These analyses were done both for significance and for attribution to variance components. Unless otherwise noted, 9999 permutations were used for each statistical test.

We followed db-RDA with an indicator species analysis (ISA) as a means to evaluate which taxonomic units could be best associated with any treatment (Dufrene and Legendre 1997). Indicator values are calculated as the product of relative abundance and relative frequency of a taxon in predefined groups. Results for ISA are given in two different ways: first, we give results for within system differences BEFORE and AFTER. We then proceed to give results for among system differences separately for the BEFORE and the AFTER data sets. The ISA are conducted separately for the eulittoral and sublittoral zones. We used this methodology in place of two single analyses where there would be four groups (i.e., NA, NB, RA, and RB) because an indicator taxa only can occur in one group per analysis, meaning that, for example, if a taxa were chosen as an indicator of the Rainy-Before group, it could not distinguish between Namakan-Before and Namakan-After, even though the taxa may give strong indication between Namakan BEFORE and AFTER. This approach will allow us to ask the following questions: (1) Are there taxa that give high indicator values for Namakan-Before versus Namakan-After? (2) Are there taxa that give high indicator values for Rainy-Before versus Rainy-After? (3) Were there taxa that could separate Namakan and Rainy Lake under the 1970 rule curve? (4) Are there taxa that can separate Namakan and Rainy Lake under the 2000 rule curve? High indicator values occur only when both relative abundance and relative frequency of a taxon is high for a particular group. Permutation procedures were used to test the significance of any taxonomic unit as an indicator of a group by randomly shuffling column data in the species matrix, calculating resulting indicator values, and then comparing these permuted ISA values to the values observed for the real data. For all ISA, 9999 permutations were used.

While direct gradient analysis is useful for statistical tests, its use as an ordination method can be misleading. This is because the ordination arranges sites only according to the linear model imposed upon the data (McCune 1997). If, as is generally the case, only a small amount of the variability one is interested in testing constrains the site scores, then the arrangement of sites is not the true relationship, but only shows the relationship with respect to the environmental variables used to constrain the analyses. For this reason we used db-RDA for statistical tests, but used indirect ordination methods (i.e., nonmetric multidimensional scaling) to describe the relationships in the data diagrammatically.

We visualized the relationships among sites in two dimensions using nonmetric multidimensional scaling (nMDS), one of the indirect gradient ordination methods least sensitive to data standardization, transformation, and distance measure (Jackson 1993; Legendre and Legendre 1998). The interpretation of nMDS ordination scores and diagrams is heuristically similar to metric methods such as principal components analysis (PCA) with a few exceptions. Dimensions are specified *a priori*, and unique solutions occur depending on the number of dimensions specified. Nonmetric multidimensional scaling allows for the use of different distance measures and is generally the recommended ordination method for ecological community data due to flexibility in distance measure choice and the relaxed requirement for data structure, as nMDS uses ranks of distances rather than the absolute distances used by its metric counterparts (Legendre and Legendre 1998; McCune and Grace 2002). No linearity assumptions must be made and as such, nMDS has been considered a robust ordination technique. Also, nMDS does not discard any of the information in a matrix (as do metric methods, which shuffle some variability to high dimension axes not visualized) but produces the best fit for a specified number of axes. Finally, nMDS makes intuitive sense as it is based on the ranks of distances between sites instead of absolute distances like its metric counterparts. We are generally more interested in site A's general relationship to sites B or C, than in site A's absolute distance from specific other sites (Clarke 1993).

We performed the nMDS with PCORD and then summarized site scores by treatment: Namakan AFTER (NA); Namakan BEFORE (NB); Rainy AFTER (RA); and Rainy BEFORE (RB), representing mean site scores and 95% confidence intervals (McCune and Mefford 1999). Species scores for ordinations can be generated in one of two ways for nMDS: (1) as a weighted-average based on each taxon's association with site scores or (2) as a correlation of each taxon with ordination axes. PCORD gives "species scores" as weighted-averages, but considers a given taxon to be represented by a single point in ordination space, ignoring its variability. For this reason, we used the correlations of taxa with an ordination axis, reflecting each taxon's increase or decrease along the gradient. We scaled taxa by multiplying the correlation for each taxon by its standard deviation and then dividing by the standard deviation of the scores for all taxa on the axis of interest (Legendre and Gallagher 2001). When using a large number of taxa, ordination diagrams can become uninterpretable. In order to more easily interpret relationships, we show only taxa whose scaled correlation has an absolute value greater than 1SD from the mean of all taxa.

The db-RDA and nMDS results describe the general pattern of responses by the benthic communities in both lake systems over the duration of the study, but the fine detail of site-specific impacts are compromised. Therefore, a final multivariate analysis on the species matrix was conducted to address site-specific impacts. This provides an indication of which sites and taxa changed most since Kraft's investigation. Response variables for each site were derived by first summing (across all sampling dates either BEFORE or AFTER) the densities for each taxon at a particular site-depth combination. We then obtained a difference by subtracting the value of the summed densities BEFORE from those AFTER, producing a matrix with both positive and negative values. As a result, the BC distance was inappropriate and since site-specific differences will be approximately normally distributed with a mean of zero, principal components analysis (PCA) is an appropriate method of analysis (McCune and Grace 2002). Following the PCA, we determined groups of similarly responding sites based on a combination of cluster analysis and indicator species analysis (Dufrene and Legendre 1997).

Univariate BACI

We tested differences in densities for each of the taxa described by Kraft as having been significantly impacted by the 1970 rule-curve in Namakan Reservoir. Average densities and standard errors were provided for *Caenis*, *Chaoborus*, Chironomidae, Gastropoda, *Hexagenia*, and *Sialis* under each regime group: Namakan-After, Rainy-After, Namakan-Before and Rainy-Before. We did not conduct a test for Isopoda, which, with a single exception, was absent for Namakan-Before and Namakan-After.

In addition to responses for taxa hypothesized by Kraft as being most affected by the extreme drawdown in Namakan Reservoir, we assessed six different univariate measures with the BACI design: (1) invertebrate density; (2) taxon richness; (3) Shannon-Weiner diversity; (4) Evenness; (5) community coefficient of variation; and (6) ratio of total macroinvertebrate density in June:August samples. Invertebrate density is simply the sum of all animals collected at each site. Taxon richness is the total number of taxonomic units in each sample. The Shannon-Weiner diversity index is given by:

$$H' = -\sum_{i}^{S} p_i * \log p_i \qquad \text{[Eq. 2]}$$

where S is the number of taxonomic units present and p_i is the proportion of individuals belonging to taxonomic unit $_i$ (McCune and Grace 2002). The measured unit for *H'* are "bits of information," but the direct application and meaning of such for populations and communities is not clear (Hurlbert 1971). We calculated this index to compare to Kraft's data set because he considered this measure to separate impaired communities in Namakan Reservoir from intact communities in Rainy Lake.

We calculated Evenness as Peilou's Evenness *J*, where evenness is defined as "the ratio of observed diversity to maximum diversity." It is calculated as:

$$J = \frac{H'}{\log S} \qquad \text{[Eq.3]}$$

where *H'* is the observed Shannon-Weiner Index and *S* is the average taxonomic unit richness within a given sample. The interpretation of this measure is difficult as well, but we use it as a comparison with Kraft's data set; in general we can interpret higher values as indicating samples that have a more even distribution of taxonomic units. Community coefficient of variation was computed by dividing the average density by the standard deviation for each group of sites (i.e., Namakan After, Namakan Before, Rainy After, and Rainy Before) and testing for their difference. Ratios were calculated as the ratio of total density of June samples to August samples within a year. Tests were computed in JMP using a repeated-measures analysis of variance with depth and bay as covariables (JMP 2002).

As with the multivariate analysis, for any significant effects we also ran an additional test on the two water-level variables that changed: magnitude of drawdown and the date for which the reservoir was finished filling to capacity in the spring, as well as their interaction. These analyses were done for both significance and for attribution to variance components, which could be accomplished with a random effects ANOVA.

Multivariate: Environmental Relationships (AFTER set only)
The 2004-05 (AFTER) data set is taxonomically more detailed than the BEFORE data set, and we measured more environmental variables than did Kraft. As a result, we were able to do a more robust ordination, with a finer scale of taxonomic resolution, on the AFTER set, but in doing so we needed to exclude the BEFORE data. The purpose of this ordination was to see which environmental factors were most highly correlated with invertebrate community structure. We can then discuss the probable effects of water-level fluctuation on those environmental variables.

Null Hypothesis Testing
Given that we cannot know, with the present experimental design, whether the treatment caused an impact, our statistical objectives become such that we desire to know (1) whether the benthic community changed in a different way for Namakan Reservoir than it did for Rainy Lake between sampling periods in the 1980's and 2000's; (2) how certain we can be of that change; and (3) how large in magnitude the change was, given that it occurred. Under the general framework of null hypothesis testing (NHT) objective (1) is a "silly null" because there is invariably a response. It is virtually impossible that we would measure the exact same response in the AFTER set relative to the BEFORE set. Really, what we are investigating is whether the magnitude of change and the sample size are large enough, given the variability, to detect the change (i.e., there is enough statistical power) (Cohen 1994; Nester 1996; Johnson 1999; Anderson et al. 2000). When one fails to reject the null hypothesis of "no difference," it means one of three things (or some combination of them): (i) the effect is too small to detect; (ii) sample size is too small; and/or (iii) the variance in the response variable is too large. It is impossible to determine which is true from a statistical test, but an examination of effect size, along with an estimate of variability, can give some indication. Without means and variances of response variables, *P*-values become "naked." We provide means and variances, typically the standard error of the mean, along with *P*-values to put our results in their proper context.

Null hypothesis testing does not address statistical objective (2) above. Rather, it provides a *P*-value representing the probability of observing a value as extreme, or more extreme, than the value actually observed, if (hypothetically) the research were conducted a large number of times on this system. Such a test cannot provide a probability statement with respect to the alternative hypothesis (i.e., that there actually is a difference between Namakan Reservoir and Rainy Lake over the time period sampled) if the study were hypothetically conducted a large number of times (Cohen 1994). Objective 3 is within the realm of NHT when a mean and variance are calculated and as such provides probably the most valuable results from traditional statistical methods (Colegrave and Ruxton 2002). Thus, producing a significant *P*-value shows only that statistical power is great enough to reject the silly null hypothesis of no difference. Statistical significance reflects only the probability structure and statistical structure of the data set and should not be confused with biological significance, which is what we are most interested in.

Some researchers would like to make stronger inference from a failure to reject the null at a specified error rate (i.e., α value, where α is the type I error rate) and to this end have advocated for publishing retrospective power analyses (Toft and Shea 1982). They argue that if one fails to reject the null but power is low, then the results would be less conclusive compared with a situation where one fails to reject the null but the power is high. The problem is that the latter circumstance is impossible; retrospective power analyses are logically in error and as such are misleading. Retrospective power calculations are meaningless because there is a 1:1 relationship between observed power and calculated *P*-values (Hoenig and Heisey 2001; Figure 5). The practical meaning of this is that a high *P*-value will ALWAYS be associated with low power and a low *P*-value will ALWAYS be associated with high power. The *P*-value is a reflection of the power of the statistical test as noted above. It is a misconception that one could have high power with a high *P*-value.

An additional complexity of NHT is that, traditionally, type I errors have been cautioned against more than type II errors, which may not be in accord with the goals of an environmental impact study. When an arbitrary α value is established, the researcher is implicitly declaring that it is more important to protect against falsely asserting that there is a difference when one does not exist over falsely asserting that there is no difference when a difference does in fact exist. When statistical power is low, this decision can lead to very high asymmetry in values favoring avoidance of type I errors relative to type II errors. For example, if we set *a priori* α to be the traditional 0.05 but our design only gives a corresponding power of 0.30, which is not unusual with the type of data we collected, then we are implicitly stating that protecting against type I error is 14 times more important than protecting against type II errors (type II/type I) (Mapstone 1995). This means that we are 14 times more concerned with declaring there is a difference when there really is not one than we are with declaring there is no difference when in fact there is one, which does not seem consistent with the goals of the National Park Service with respect to this study. Null hypothesis testing cannot simultaneously address both error types.
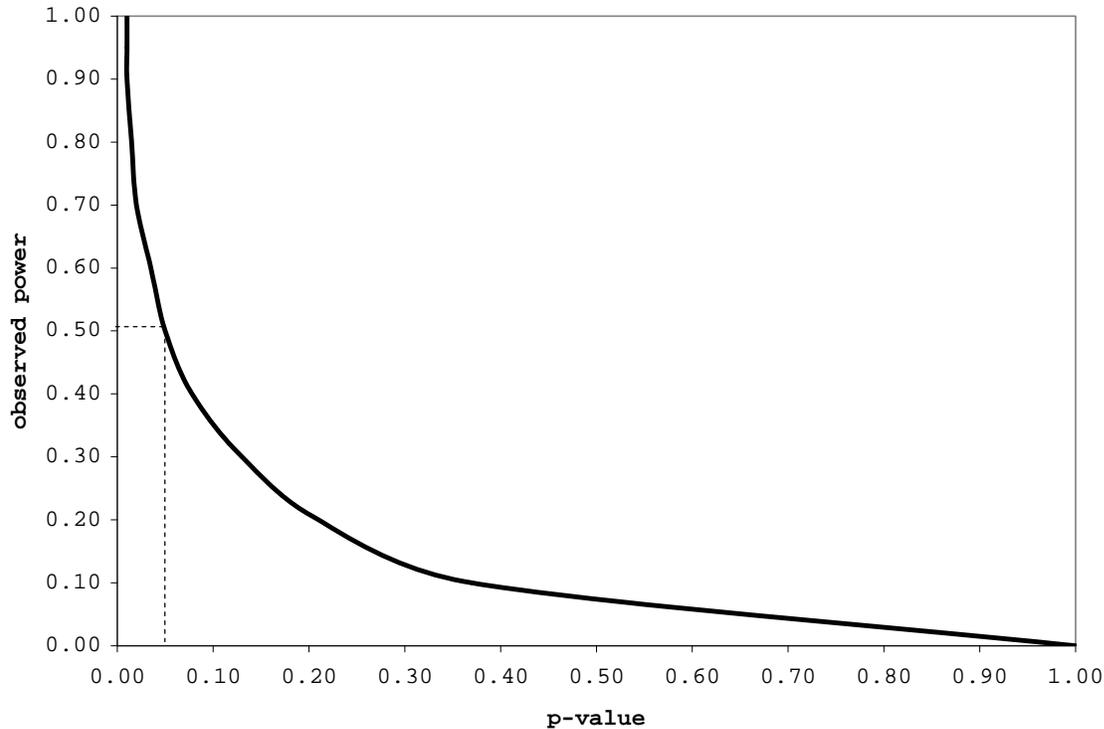
Figure 5. The relationship of calculated p-values to observed power, approximated from Hoenig and Heisey (2001). Dashed line indicates the relationship between observed power and the *p*-value when *p* is exactly 0.05.

Mapstone (1995) suggested that for environmental studies, when conducting *prospective* power analyses, arbitrary α values (i.e., 0.05) should not be used but scaled with respect to the probability of type II error (β) based on values participants ascribe to the different kinds of errors and predefined (and agreed upon) effect sizes. Naturally, a starting point would be to consider both error types to be equally important (i.e., $\alpha = \beta$). Unfortunately, we cannot retrospectively force this shell on the present study. We do provide value curves for type II/type I error for three different α values: 0.01, 0.05, and 0.10 (Figure 6). Because there is a 1:1 relationship between the power of a test and the *P*-value, we can use this relationship as a surrogate for power estimation for individual tests as a means by which we can make explicit associations of ascribed values to the different types of errors (Mapstone 1995; Hoenig and Heisey 2001).

With these caveats in mind, we do provide *P*-values as we recognize their role in decision making, but we caution that they should be interpreted thoughtfully and carefully. In general, it is much better to focus on parameter estimates of the mean and error when comparing response variables (Colegrave and Ruxton 2002). We stress that it is logically erroneous to conclude that there was not an effect on a given variable if the *P*-value is greater than the prespecified α. The correct interpretation of such an occurrence is that the data are inconclusive with respect to whether or not there was an effect. There may be or there may not have been an effect. The proper response under such circumstances is to evaluate results on a case to case basis by investigating means and errors and making nonstatistical judgments (Stewart-Oaten et al. 1992).

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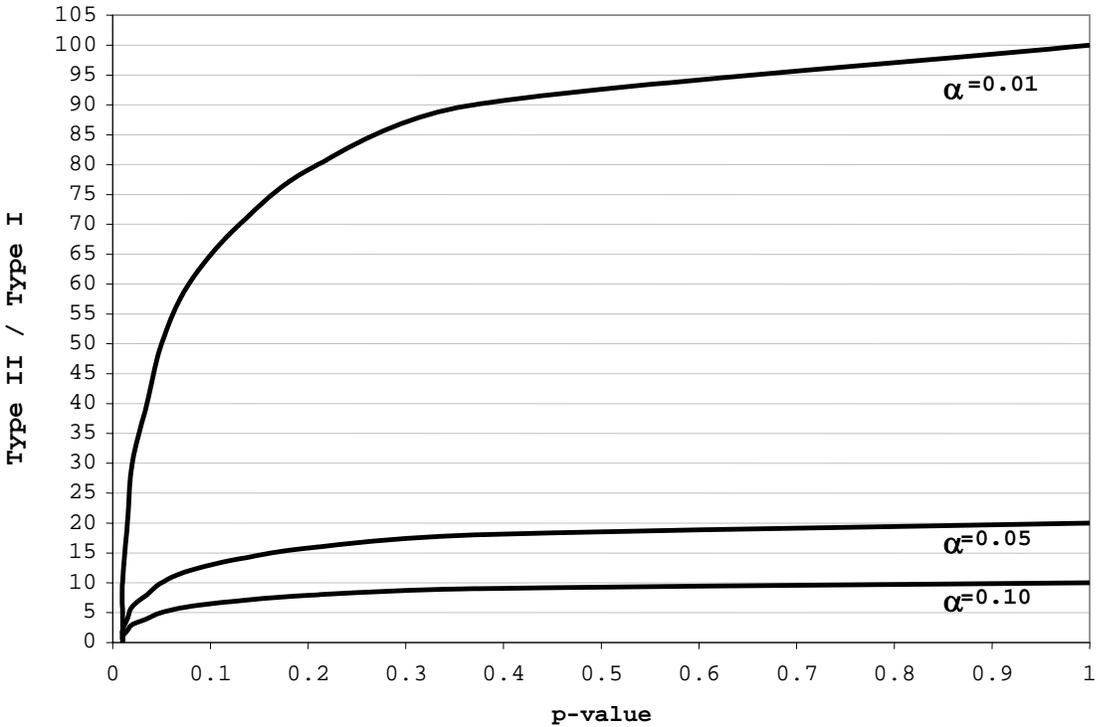
Figure 6. Relationship between type II and type I errors, determined by p-values under three common *a priori* determinations for type I error rate (α=0.01, 0.05, and 0.10) in ecological studies. Values indicated on the ordinate give the explicit ratio of how much more important it is to protect against making a type I error (i.e., determining there is an impact when there in reality is not one) relative to a type II error (i.e., determining there is not an impact when in reality there is one) for a given p-value. Values were approximated from data given in Hoenig and Heisey (2001).

For this report, we will use α=0.05, and report any *P*-value less than this to be "statistically significant." Where possible we always present the actual *P*-value for individual assessment.

We also recognize that the experimentwise type I error rate will be higher than α since we are running multiple tests. The experimentwise error rate can be calculated as:

$$1-\left(1-\alpha\right)^{N} \qquad \text{[Eq. 4]}$$

where α is the desired type I error rate for the individual test and *N* is the number of tests. The interpretation is that a researcher will find a significant test at a rate approximately equal to the calculated experimentwise error. Some researchers have corrected for this effect by lowering α using a sequential Bonferroni correction (Rice 1990). We do not provide this correction, but there are sufficient data in the report to calculate an adjusted α, should one desire. We agree

with Moran (2003) that the sequential Bonferroni correction is too conservative and will likely lead to important results not being appreciated. We emphasize the need to evaluate the results logically, instead in interpreting individual P-values. If several individual P-values are small, it is indicative that something is occurring. Some spurious results are going to appear as more tests are performed, but not all tests will be spurious (Moran 2003). Furthermore, provided effect sizes and confidence intervals are given, readers can make their own judgments with respect to individual test results reported in terms of P-values (Nakagawa 2004).

Results

General Community Description

Combining both the BEFORE and AFTER data sets for which the BACI was based, a total of 45,927 individual organisms were collected over a period of four separate years. On average, the lakes studied supported macrobenthos densities of 3,298 invertebrates per square meter (SD=4,418) based on a scaling multiplier for individual grab samples. Over 80% of the organisms belonged to one of five taxonomic units: Chironomidae (41%), Amphipoda (19%), Oligochaeta (11%), Sphaeriidae (7%), and Gastropoda (4%). Among the most ubiquitous invertebrates (those occurring in more than 50% of the grab samples) were Chironomidae (100%), Sphaeriidae (79%), *Hexagenia* (75%), Oligochaeta (70%), Ceratopoginidae (69%), *Chaoborus* (67%), Gastropoda (61%), and Amphipoda (57%). On average, the species richness was 10 (SD=4) per meter square, and there were no locations where no organisms were found.

There were 131 different taxa identified: 108 in Rainy Lake with 16 unique taxa found in Rainy Lake but not in Namakan Reservoir, and 113 taxa in Namakan with 21 unique taxa found in Namakan Reservoir but not in Rainy Lake (Table 4). At the taxonomic resolution of the present study, the majority of organisms (based on relative densities) were Amphipoda (15%), Oligochaeta (15%), and three Chironomidae: *Procladius* (9%), *Chironomus* (6%), and *Tanytarsus* (5%) (Figure 7). The most ubiquitous organisms were Oligochaeta (93%), *Procladius* (90%), *Hexagenia* (74%), *Clinotanypus* (65%), Amphipoda (63%), *Ablabesmyia* (62%), and *Pisidium* (61%) (Figure 8).

Multivariate BACI

Multivariate analyses showed a statistically significant change in benthic assemblages based on densities only when a term was included for an interaction with depth zone that distinguished the eulittoral zone (1m and 2m depths) from the sublittoral zone (3m, 4m, and 5m depths) $F=1.133$; $P = 0.038$). Other tests were inconclusive, including testing for a pure BACI effect, BACI interacting with each depth separately, or BACI interacting with alternative depth zones where the eulittoral was comprised of 1m, 2m, and 3m depths and the sublittoral of 4m and 5m depths (Table 5). No evidence was found to indicate the ratios of taxa in June:August changed in concert with the alteration of the rule curve under any of the three models tested (Table 6).

Given the significant result of BACI interacting with depth groups, we ran a model to explicitly test the two variables that differed between Namakan Reservoir and Rainy Lake with respect to the change in the rule curve: the minimum annual water level and the Julian date when Namakan Reservoir filled to capacity. We also included a term for the interaction of the two variables. We found the minimum annual water level to be highly multicollinear (VIF > 328); thus, we substituted the annual water level range as a surrogate for magnitude of drawdown with the result that none of the three variables showed a tendency for multicollinearity (VIF < 3). Variance inflation factors (VIF) for single environmental variables are the multiple correlations between that variable and the rest of the environmental variables in the data set; a VIF greater than 20 indicates multicollinearity (ter Braak and Smilauer 2002).This model accounted for 2% of the unconstrained (i.e., not accounted for by covariables) variation in the data, but was not significant ($F =1.081$, $P = 0.073$). We ran the same model using the forward selection procedure

Table 4. Inventory of benthic invertebrates at VOYA; Site occupancy and relative density reflect data only from the AFTER set.

ID	Group	Order	Family	Genus/Species	Common Name	Trophic role	Site Occupancy (%) Total	Eu-littoral	Sub-littoral	Relative density (%) Total	Eu-littoral	Sub-littoral	System
PORIFE	Porifera				Sponge	Detritivore	6	13	2	1	1	0	R,N
PHYGYR	Gastropoda	Basommatophora	Physidae	*Physa gyrina*	Snail	Herbivore	9	17	3	0	0	0	R,N
GYRDEF			Planorbidae	*Gyraulus deflectus*	Snail	Herbivore	1	0	2	0	0	0	R,N
GYRPAR				*Gyraulus parvus*	Snail	Herbivore	2	0	3	0	0	0	R,N
HELANC				*Helisoma anceps*	Snail	Herbivore	21	25	19	0	0	0	R,N
PLACAM				*Planorbella campanulatum*	Snail	Herbivore	6	2	9	0	0	0	R,N
PROEXA				*Prominenetus exacous*	Snail	Herbivore	5	6	5	0	0	0	R,N
AMNICO		Mesogastropoda	Hydrobiidae	*Amnicola*	Snail	Herbivore	58	65	53	5	5	4	R,N
VALLEW			Valvatidae	*Valvata lewsi*	Snail	Herbivore	12	10	13	0	0	0	N
VALSIN				*Valvata sincera*	Snail	Herbivore	4	4	3	0	0	0	R,N
VALTRI				*Valvata tricarinata*	Snail	Herbivore	32	48	20	1	1	0	R,N
SMUSCU	Bivalvia	Eulamellibranchia	Sphaeridae	*Musculium*	Fingernail Clam	Detritivore	41	58	28	2	3	2	R,N
SPHAER				*Sphaerium*	Fingernail Clam	Detritivore	45	56	36	2	2	2	R,N
SPISID				*Pisidium*	Fingernail Clam	Detritivore	61	77	48	5	6	5	R,N
NEMATO	Nematoda				Round Worm	Carnivore	34	48	23	0	0	0	R,N
NEMMOR	Nematomorpha				Horsehair Worm	Carnivore	3	2	3	0	0	0	R,N
TUBELL	Tubellaria				Flatworm	Detritivore	1	2	0	0	0	0	R
OLIGOC	Oligochaeta				Aquatic Earthworm	Detritivore	93	98	89	15	15	14	R,N
ERPPUN	Hirudinea	Arhynchobdellida	Erpobdellidae	*Erpobdella punctata*	Leech	Carnivore	2	0	3	0	0	0	R,N
MOOFER				*Mooreobdella fervida*	Leech	Carnivore	2	4	0	0	0	0	R,N
NEPOBS				*Nephelopsis obscura*	Leech	Carnivore	0	1	0	0	0	0	R
HAEMOP			Haemopidae	*Haemopis*	Leech	Carnivore	3	4	2	0	0	0	R,N
ACTINE		Rhynchobdellida	Glossiphoniidae	*Actinobdella inequiannulata*	Leech	Carnivore	1	2	0	0	0	0	R
ALBHET				*Alboglossiphonia heteroclita*	Leech	Carnivore	3	0	5	0	0	0	N
GLOCOM				*Glossiphonia complanata*	Leech	Carnivore	1	0	2	0	0	0	R
HELSTA				*Helobdella stagnalis*	Leech	Carnivore	1	0	2	0	0	0	R,N
PLAHOL				*Placobdella hollensis*	Leech	Carnivore	1	2	0	0	0	0	N
PLAMON				*Placobdella monifera*	Leech	Carnivore	1	0	2	0	0	0	N
AMPHIP	Crustacea	Amphipoda			Scud	Detritivore	63	69	59	15	15	14	R,N
ISOPOD		Isopoda	Asellidae		Aquatic Sowbug	Detritivore	10	10	9	2	3	2	R,N
OSTRAC		Ostracoda			Ostracod	Detritivore	28	29	27	2	1	4	R,N
SPINIC		Spinicaudata			Clam Shrimp	Detritivore	4	6	2	0	0	0	R
HYDRAC	Acarina	Hydracarina			Water Mite	Carnivore	21	40	6	0	0	0	R,N
CHRDON	Insecta	Coleoptera	Chrysomelidae	*Donacia*	Leaf Beetle	Herbivore	1	2	0	0	0	0	R,N
DYTHYD			Dytiscidae	*Hydroporus*	Predaceous Diving Beetle	Carnivore	18	19	17	0	0	0	N
DUBIRA			Elimidae	*Dubiraphia*	Riffle Beetle	Detritivore	5	4	6	0	0	0	R,N
GYRGYR			Gyrinnidae	*Gyrinus*	Whirligig Beetle	Carnivore	20	31	11	1	2	0	N
HALHAL			Haliplidae	*Haliplus*	Crawling Water Beetle	Herbivore	13	17	9	0	0	0	R,N
CERBEZ		Diptera	Ceratopogonidae	*Bezzia/Palpomyia*	No-See-Um	Carnivore	9	13	6	0	0	0	R,N
CERMAL				*Mallochohellea*	No-See-Um	Carnivore	34	54	19	1	0	0	R,N
CERSPH				*Sphaeromias*	No-See-Um	Carnivore	23	35	14	0	1	0	R,N
CHAOBO			Chaoboridae	*Chaoborus*	Phantom Midge	Carnivore	59	65	55	2	0	2	R,N
CHIRON			Chironomidae [1]				100	100	100	36	33	41	R,N
CHIR			Chironominae	*Chironomus*	Midge	Detritivore	34	27	39	15	9	21	R,N
CLAP				*Cladopelma*	Midge	Detritivore	13	8	17	1	0	1	R,N
CLAT				*Cladotanytarsus*	Midge	Detritivore	38	42	34	3	4	2	R,N
CRYC				*Cryptochironomus*	Midge	Carnivore	34	38	31	1	1	1	R,N
CRYT				*Cryptotendipes*	Midge	Detritivore	22	15	28	1	1	2	R,N
DICR				*Dicrotendipes*	Midge	Detritivore	39	31	45	3	2	4	R,N
EINF				*Einfeldia*	Midge	Herbivore	8	2	13	1	0	2	R,N
ENDO				*Endochironomus*	Midge	Herbivore	13	21	6	1	1	0	R,N
GLYP				*Glyptotendipes*	Midge	Herbivore	1	2	0	0	0	0	R,N
LAUT				*Lauterborniella*	Midge	Detritivore	0	0	0	0	0	0	R
MICC				*Microchironomus*	Midge	Detritivore	0	0	0	0	0	0	R

Table 4. Inventory of benthic invertebrates at VOYA; Site occupancy and relative density reflect data only from the AFTER set (continued).

ID	Group	Order	Family	Genus/Species	Common Name	Trophic	Site Occupancy (%)			Relative density (%)			System
							Total	Eu-littoral	Sub-littoral	Total	Eu-littoral	Sub-littoral	
MICP				*Micropsectra*	Midge	Detritivore	2	4	0	0	0	0	R,N
NILO				*Nilothauma*	Midge	Detritivore	0	0	0	0	0	0	R,N
PAGA				*Pagastiella*	Midge	Detritivore	29	27	31	1	1	1	R,N
PARA				*Paralauterborniella*	Midge	Detritivore	13	17	9	0	0	0	R
PARY				*Paratanytarsus*	Midge	Detritivore	0	0	0	0	0	0	
PARD				*Paratendipes*	Midge	Detritivore	14	4	22	0	0	1	N
PHAE				*Phaenopsectra*	Midge	Herbivore	1	2	0	0	0	0	R
POLY				*Polypedilum*	Midge	Herbivore	37	35	38	4	4	5	R,N
PSEU				*Pseudochironomus*	Midge	Detritivore	18	25	13	8	16	1	R,N
STEM				*Stempellina*	Midge	Detritivore	12	8	14	0	0	0	R,N
STEP				*Stempellinella*	Midge	Detritivore	11	13	9	0	1	0	R,N
STRI				*Stictochironomus*	Midge	Detritivore	0	0	0	0	0	0	R,N
TANT				*Tanytarsus*	Midge	Detritivore	59	56	61	15	15	15	R,N
STEN				*Undescribed* [2]	Midge	Detritivore	21	15	27	1	1	1	N
XENO				*Xenochironomus*	Midge	Carnivore	2	0	3	0	0	0	R,N
OMIS				*Omisus*	Midge	Detritivore	8	4	11	0	0	0	N
PARH				*Parachironomus*	Midge	Carnivore	12	13	11	0	0	1	R,N
TRIB				*Tribelos*	Midge	Detritivore	1	2	0	0	0	0	N
HARN				*Harnischia*	Midge	Detritivore	18	15	20	1	1	1	R
MICT				*Microtendipes*	Midge	Detritivore	29	29	28	1	1	2	R,N
PARL				*Paracladopelma*	Midge	Detritivore	3	2	3	0	0	0	R,N
PROT			Diamesinae	*Protanypus*	Midge	Detritivore	7	0	13	0	0	0	R,N
ACRI			Orthocladinae	*Acricotopus*	Midge	Detritivore	1	2	0	0	0	0	N
CORY				*Corynoneura*	Midge	Detritivore	3	6	0	0	0	0	N
CRIC				*Cricotopus*	Midge	Herbivore	14	25	6	1	1	0	R,N
EPIC				*Epicocladius*	Midge	Detritivore	8	6	9	0	0	0	R,N
HETE				*Heterotrissocladius*	Midge	Detritivore	0	0	0	0	0	0	R,N
NANO				*Nanocladius*	Midge	Detritivore	4	6	3	0	1	0	R,N
ORTH				*Orthocladius*	Midge	Detritivore	0	0	0	0	0	0	N
PARK				*Parakiefferiella*	Midge	Detritivore	0	0	0	0	0	0	R,N
PSEC				*Psectrocladius*	Midge	Detritivore	16	25	9	1	2	0	R,N
ABLA			Tanypodinae	*Ablabesmyia*	Midge	Carnivore	62	71	55	6	8	3	R,N
CLIN				*Clinotanypus*	Midge	Carnivore	65	58	70	6	7	6	R,N
LABR				*Labrundinia*	Midge	Carnivore	3	2	3	0	1	0	R,N
LARS				*Larsia*	Midge	Carnivore	2	4	0	0	0	0	R
NATA				*Natarsia*	Midge	Carnivore	1	0	2	0	0	0	N
PARM				*Paramerina*	Midge	Carnivore	9	17	3	1	1	0	R,N
PROC				*Procladius*	Midge	Carnivore	90	83	95	25	20	29	R,N
TANY				*Tanypus*	Midge	Carnivore	1	2	0	0	0	0	R
TABCHR			Tabanidae	*Chrysops*	Deer Fly	Carnivore	8	13	5	0	0	0	R,N
TEPHRI			Tephritidae		Fruit Fly	Detritivore	1	2	0	0	0	0	N
TIPULI			Tipulidae		Crane Fly	Detritivore	2	2	2	0	0	0	N
CALLIB		Ephemeroptera	Baetidae	*Callibaetis*	Minnow Mayfly	Herbivore	5	10	2	0	0	0	R,N
BAETIS			Baetiscidae	*Baetisca*	Armored Mayfly	Herbivore	1	2	0	0	0	0	R
BRACHY			Caenidae	*Brachycerus*	Square-Gilled Mayfly	Herbivore	3	6	0	0	0	0	R,N
CAENIS				*Caenis*	Square-Gilled Mayfly	Herbivore	33	58	14	2	0	0	R,N
EURYLO			Ephemerellidae	*Eurylophella*	Spiny Crawler Mayfly	Herbivore	0	0	0	0	0	0	N
HEXAGE			Ephemeridae	*Hexagenia*	Burrowing Mayfly	Herbivore	74	79	70	3	2	3	R,N
HEPMAC			Heptageniidae	*Macdunoa*	Flathead Mayfly	Herbivore	0	0	0	0	0	0	R
APHIDI		Hemiptera	Aphididae		Aphid	Herbivore	1	0	2	0	0	0	N
CORIXI			Corixidae		Water Boatman	Herbivore	12	17	8	0	0	0	R,N
ACENTR		Lepidoptera	Pyralidae	*Acentria*	Aquatic Moth	Herbivore	1	2	0	0	0	0	R
PARAPO				*Parapoynx*	Aquatic Moth	Herbivore	0	1	0	0	0	0	N
SIALIS		Megaloptera	Sialidae	*Sialis*	Alderfly	Carnivore	38	38	39	1	2	1	R,N

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Table 4. Inventory of benthic invertebrates at VOYA; Site occupancy and relative density reflect data only from the AFTER set (continued).

ID	Group	Order	Family	Genus/Species	Common Name	Trophic	Site Occupancy (%)			Relative density (%)			System
							Total	Eu-littoral	Sub-littoral	Total	Eu-littoral	Sub-littoral	
CLIMAC		Neuroptera	Sisyridae	*Climacia*	Spongillafly	Carnivore	1	2	0	0	0	0	R,N
ENALLA		Odonata	Coenagrionidae	*Enallagma*	Narrow-Winged Damselfly	Carnivore	3	6	0	0	1	0	R,N
TETRAG			Corduliidae	*Tetragoneuria*	Emerald Dragonfly	Carnivore	7	6	8	0	0	0	R,N
ARIGOM			Gomphidae	*Arigomphus*	Club-Tail Dragonfly	Carnivore	2	2	2	0	0	0	R
GOMDRO				*Dromogomphus*	Club-Tail Dragonfly	Carnivore	3	4	2	0	0	0	N
GOMGOM				*Gomphus*	Club-Tail Dragonfly	Carnivore	12	17	8	0	0	0	R,N
LEUCOR			Libelluidae	*Leucorrhinia*	Common Skinner Dragonfly	Carnivore	1	2	0	0	0	0	N
LIBUND				*Ladona*	Common Skinner Dragonfly	Carnivore	2	4	0	0	0	0	R,N
PERITH				*Perithemis*	Common Skinner Dragonfly	Carnivore	1	2	0	0	0	0	R,N
DIDYMO			Macromidae	*Didymops*	Stream Cruiser	Carnivore	1	2	0	0	0	0	R,N
HYDAGR		Trichoptera	Hydroptilidae	*Agraylea*	Micro Caddisfly	Herbivore	0	1	0	0	0	0	N
HYDOXY				*Oxyethira*	Micro Caddisfly	Herbivore	2	2	2	0	0	0	R,N
LEPMYS			Leptoceridae	*Mystacides*	Long-Horned CM [3] Caddisfly	Detritivore	11	15	8	0	0	0	R,N
LEPNEC				*Nectopsyche*	Long-Horned CM Caddisfly	Herbivore	2	2	2	0	0	0	R,N
LEPOEC				*Oecetis*	Long-Horned CM Caddisfly	Carnivore	27	48	11	0	0	0	R,N
LEPTRI				*Triaenodes*	Long-Horned CM Caddisfly	Herbivore	3	6	0	0	1	0	R,N
LIMLIM			Limnephilidae	*Limnephilus*	Northern CM Caddisfly	Detritivore	4	4	3	0	0	0	R,N
MOLMOL			Molannidae	*Molanna*	Hood CM Caddisfly	Herbivore	13	19	9	0	0	0	R,N
PHRBAN			Phryganeidae	*Banksiola*	Giant CM Caddisfly	Herbivore	5	4	6	0	0	0	R,N
PHRPHR				*Phryganea*	Giant CM Caddisfly	Herbivore	5	10	2	0	0	0	R,N
POLCER			Polycentropodidae	*Cernotina*	Trumpet-Net Caddisfly	Carnivore	39	35	42	1	0	2	R,N

[1]Chironomidae is further divided into Subfamilies: Chironominae,

[2]This is a previously undescribed genera of Chironomidae that is morphologically similar to Stempellina/Constempellina

[3]CM="Case-Maker"
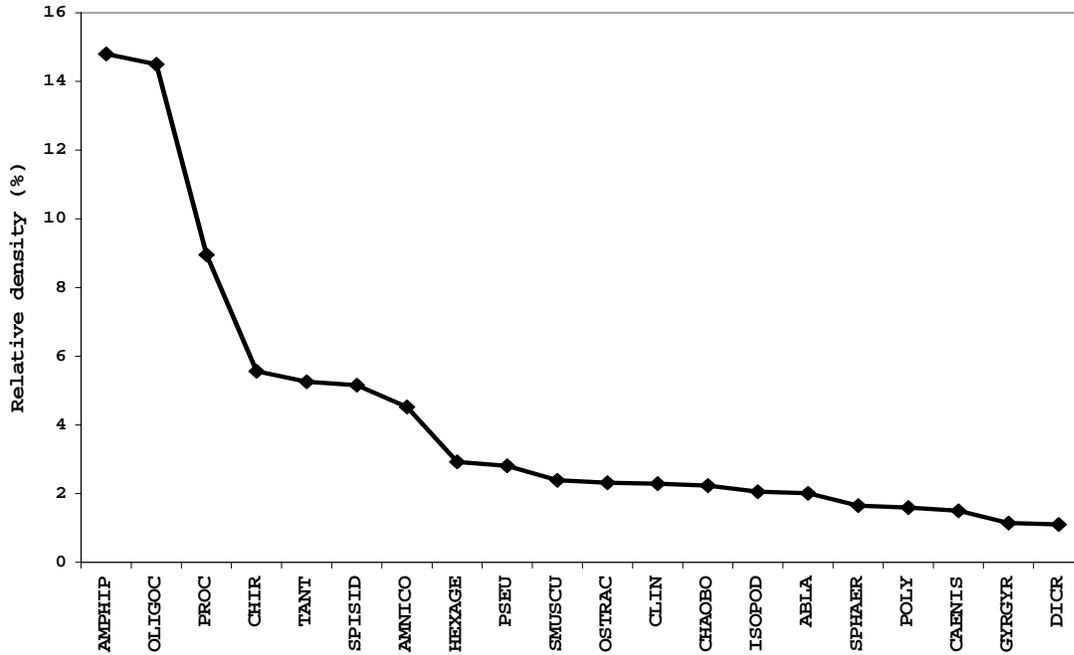
Figure 7. Relative density of taxonomic units for sampling occurring during the present study only. The 20 most abundant taxa are shown, which together represent approximately 85% of total individuals collected at all sites in both reservoirs.
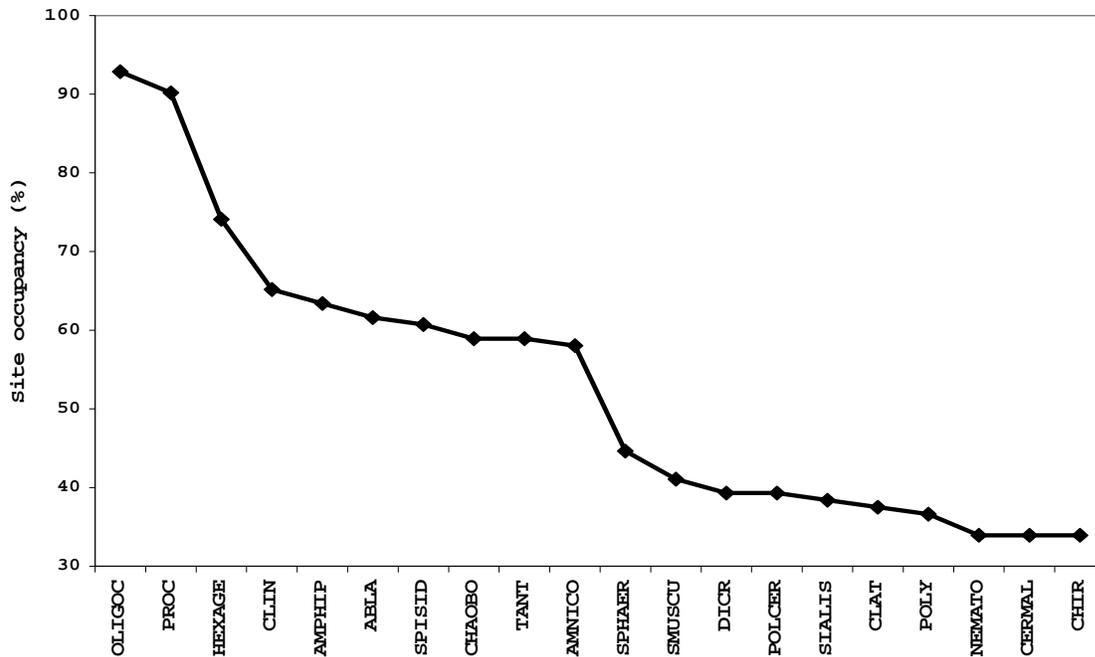

Figure 8. Site occupancy of taxonomic units for sampling occurring taken only during the present study. Compilation of data is over all sites from both reservoirs. Only the 20 most ubiquitous taxa are shown.

Table 5. Distance-based redundancy analysis using the Bray-Curtis distance computed from log(x+1) transformed taxonomic unit densities (samples = 184, taxonomic units = 57). The pseudo-F ratio was calculated with covariables including bay, depth, season, time, site, and cumulative meters above/below rule-curve. Permutations were carried out with CANOCO using a split plot design, where sites were whole-plots and sampling periods (t=8) were split-plots. Both whole-plots and split-plots were freely exchanged, but dependent across sites (i.e., time periods within sites moved together). 9999 permutations were used.

Model	Trace	$F^{\#}$	P
BACI	0.005	1.106	0.125
BACI*depth	0.010	1.093	0.087
BACI*1,2m	0.011	1.133	0.038
BACI*1,2,3m	0.010	1.057	0.176

Table 6. Distance-based redundancy analysis using the Bray-Curtis distance computed from taxonomic unit ratios (June:August; samples = 92, taxonomic units = 57). The pseudo-F ratio was calculated with covariables including bay, depth, season, time, site, and cumulative meters above/below rule-curve. Permutations were carried out with CANOCO using a split plot design where sites were whole-plots and sampling periods (t=4) were split-plots. Both whole-plots and split-plots were freely exchanged, but dependent across sites (i.e., time periods within sites moved together). 9999 permutations were used.

Model	Trace	$F^{\#}$	P
BACI	0.012	1.148	0.224
BACI*depth	0.023	1.114	0.222
BACI*1,2m	0.021	1.023	0.390
BACI*1,2,3m	0.022	1.092	0.249

in CANOCO, which selected the Julian date at which Namakan Reservoir filled to capacity as the best single variable; however, the results were still not statistically significant ($F = 1.157$, $P = 0.060$). The marginal variance by each of the three variables in the model indicated that each contributed equally to the variance explained.

Indicator species analyses showed that the eulittoral macrobenthos community of Namakan Reservoir was relatively weighted by Ceratopoginidae, Polycentropodidae, Chironomidae, *Caenis,* Hydracarina, Nematoda, *Oecetis,* Ostracoda, *and* Hirudinea under the 1970 rule-curve ($P < 0.05$, 9999 permutations). Under the 2000 rule-curve, only a single taxon (*Cernotina*) served as a significant indicator for the Namakan eulittoral community. Indicators for the sublittoral community in Namakan Reservoir included *Caenis*, Ceratopoginidae, Polycentropopidae, Chironomidae, *Chaoborus*, Hydracarina, *Sialis*, and *Hexagenia* BEFORE and only *Cernotina* AFTER (Table 7; $P < 0.05$, 9999 permutations).

Table 7. Indicator species analysis for Namakan Reservoir BEFORE and AFTER for both the eulittoral (1 and 2m depths) and the sublittoral (3,4, and 5m depths). Significant indicator taxa (*P*<0.05) are listed underlined and in **bold**.

Eulittoral

Taxa	Observed IV	Monte Carlo Mean	Monte Carlo SD	P
		BEFORE		
CERATO	83.7	43.2	6.82	0.000
POLYCE	41.7	16.8	5.21	0.001
CHIRON	74.9	57	5.17	0.002
CAENIS	69.6	44.1	6.78	0.002
HYDRAC	51.9	29.1	5.86	0.002
NEMATO	63.4	37.5	7.53	0.003
LEPOEC	58.9	36.6	6.04	0.003
OSTRAC	48.2	26.4	6.31	0.006
HIRUDI	58	39	6.1	0.009
PORIFE	29.2	12.6	4.38	0.009
AMPHIP	69.7	56.3	10.07	0.124
HEXAGE	32.6	24.7	6.48	0.131
HYDOXY	10.8	8.7	3.56	0.229
SPHAER	63.5	57.8	7.63	0.235
CALLIB	13.7	12.7	4.62	0.381
ENALLA	17.1	16.6	5.23	0.390
MOLMOL	25.3	25.7	5.71	0.430
TABCHR	11.7	12.6	4.37	0.475
SIALIS	8.3	5.8	2.42	0.484
DYTHYD	6	7.2	2.97	0.488
DUBIRA	8.3	5.2	3.12	0.491
LEPMYS	19.5	23.6	5.77	0.717
CHAOBO	25.1	32	7.55	0.789
HYDAGR	4.2	4.2	0.04	1.000
CLIMAC	3	5.6	2.66	1.000
DIDYMO	4.2	4.2	0.04	1.000
PERITH	4.2	4.2	0.04	1.000
PHRPHR	4.1	9.1	3.69	1.000
		AFTER		
POLCER	54.2	20.7	5.92	0.000
TETRAG	21.2	12.5	4.21	0.086
LIMLIM	12.5	7.2	3.07	0.233
EURYLO	12.5	7.2	2.94	0.235
PHRBAN	8.3	5.3	2.92	0.485
CHRDON	8.3	5.5	2.78	0.493
GASTRO	51	53.4	6.33	0.573
PYRALI	6.1	9.9	3.88	0.932
APHIDI	4.2	4.2	0.04	1.000
GOMGOM	4.2	4.2	0.04	1.000
GYRGYR	4.2	4.2	0.04	1.000
HALHAL	4.2	4.2	0.04	1.000
LIBUND	4.2	4.2	0.04	1.000
LEUCOR	4.2	4.2	0.04	1.000
LEPNEC	4.2	4.2	0.04	1.000
NEMMOR	4.2	4.2	0.04	1.000
OLIGOC	21.8	40.4	8.63	1.000
TEPHRI	4.2	4.2	0.04	1.000
TIPULI	4.2	4.2	0.04	1.000

Sublittoral

Taxa	Observed IV	Monte Carlo Mean	Monte Carlo SD	P
		BEFORE		
CAENIS	59.3	27.2	5.14	0.000
CERATO	67.7	39.5	4.85	0.000
POLYCE	36.1	13.5	3.74	0.000
CHAOBO	67.2	42.4	5.02	0.001
HYDRAC	39.8	21.6	4.58	0.002
SIALIS	50.9	37.6	4.58	0.013
CHIRON	63.3	55.3	3.95	0.040
HEXAGE	59.1	50.5	4.17	0.041
NEMATO	25.9	20.7	4.98	0.152
SPHAER	47	41.2	5.59	0.158
MOLMOL	12.4	9.2	3.08	0.192
DIDYMO	5.6	3.4	2.08	0.487
LEPMYS	5.6	3.4	2.08	0.491
HIRUDI	25	26.4	4.6	0.533
PHRPHR	2.8	2.8	0.03	1.000
PORIFE	2.8	2.8	0.03	1.000
		AFTER		
POLCER	36.1	13.3	3.52	0.000
OLIGOC	44.1	40.4	5.47	0.229
PYRALI	8.3	4.8	1.99	0.246
GASTRO	26.4	26.4	5.01	0.414
OSTRAC	22.8	24.2	5.35	0.537
AMPHIP	25.1	29.1	5.55	0.715
LEPOEC	17.6	21.3	4.27	0.793
PHRBAN	2.8	2.8	0.03	1.000
BRACHY	2.8	2.8	0.03	1.000
GOMDRO	2.8	2.8	0.03	1.000
HALHAL	2.8	2.8	0.03	1.000
ISOPOD	2.8	2.8	0.03	1.000
TETRAG	2.8	2.8	0.03	1.000
LEPTRI	2.8	2.8	0.03	1.000

Under the 1970 rule-curve, Rainy Lake eulittoral samples were structured by Ceratopoginidae, *Caenis*, Nematoda, Polycentropopidae, Chironomidae, Oligochaeta, and *Chaoborus*, while *Cernotina* and Ostracoda were significant indicators under the 2000 rule curve. The sublittoral in Rainy Lake was characterized by *Chaoborus*, Hydracarina, and *Hexagenia* BEFORE relative to AFTER, whereas Amphipoda were a more important faunal element at the deeper sites in Rainy under the 2000 rule curve (Table 8, *P* < 0.05, 9999 permutations).

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Table 8. Indicator species analysis for Rainy Lake BEFORE and AFTER for both the eulittoral (1 and 2m depths) and the sublittoral (3, 4, and 5m depths). Significant indicator taxa (*P*<0.0.05) are listed underlined and in **bold**.

	Eulittoral					Sublittoral			
Taxa	Observed IV	Monte Carlo Mean	SD	P	Taxa	Observed IV	Monte Carlo Mean	SD	P
	BEFORE					BEFORE			
CERATO	92.1	44.3	7.9	0.000	**CHAOBO**	80.9	53.7	7.43	0.001
CAENIS	68.7	40	9.97	0.004	**HYDRAC**	45.3	22.2	6.77	0.010
NEMATO	59.6	36.4	8.09	0.013	**HEXAGE**	62.5	52.6	4.35	0.029
POLYCE	37.5	17.1	6.23	0.019	LEPOEC	25	12	5.67	0.099
CHIRON	69.2	57.3	5.23	0.022	NEMATO	48.2	37.1	8.37	0.110
OLIGOC	73.5	58.2	7	0.031	SPHAER	49.1	44.3	8.92	0.263
CHAOBO	64.8	46.5	9.84	0.045	CERATO	44.1	45.5	7.55	0.486
HEXAGE	56.1	44.6	8.07	0.100	SIALIS	41.8	45.7	6.55	0.664
PORIFE	25	13.1	5.32	0.105	CHIRON	50.5	55.7	4.27	0.945
ISOPOD	31.2	24.8	7.66	0.193	CLIMAC	6.2	6.2	0.06	1.000
HYDRAC	29.4	24.2	7.38	0.215	POLYCE	6.2	6.2	0.06	1.000
AMPHIP	57.6	48.8	11.53	0.249	PORIFE	6.2	6.2	0.06	1.000
LEPMYS	14.9	15.1	6.11	0.345					
LEPOEC	24.4	24.9	7.55	0.451		AFTER			
CALLIB	11.3	11.2	4.83	0.481	**AMPHIP**	48.3	27.5	8.24	0.016
ENALLA	12.5	8.8	3.63	0.494	GASTRO	52.2	38	8.82	0.077
SIALIS	26.6	29.6	7.78	0.560	OLIGOC	56.5	50.7	7.94	0.217
HIRUDI	27	34.2	7.54	0.842	SPINIC	18.7	10.7	4.37	0.225
CLIMAC	6.2	6.2	0.06	1.000	POLCER	18.7	10.8	4.55	0.230
HYDOXY	6.2	6.2	0.06	1.000	CAENIS	26.2	26.2	8.38	0.406
PERITH	6.2	6.2	0.06	1.000	BRACHY	12.5	7.6	4.68	0.476
TETRAG	6.2	6.2	0.06	1.000	PYRALI	12.5	7.7	4.69	0.485
					HIRUDI	14	16.4	6.01	0.623
	AFTER				CALLIB	6.2	6.2	0.06	1.000
POLCER	56.2	22.9	7.31	0.001	HYDOXY	6.2	6.2	0.06	1.000
OSTRAC	31.2	16.3	6.16	0.042	LEPMYS	6.2	6.2	0.06	1.000
GASTRO	60.6	51.7	9.07	0.174	LEPTRI	6.2	6.2	0.06	1.000
PHRPHR	14.5	14.6	5.73	0.398	OSTRAC	7.4	13	5.63	1.000
PHRBAN	12.5	7.6	4.68	0.478	PHRPHR	6.2	6.2	0.06	1.000
ARIGOM	12.5	7.7	4.69	0.488					
CHRDON	12.5	7.7	4.69	0.490					
PYRALI	12.5	7.7	4.69	0.492					
SPHAER	45.9	51.9	7.37	0.751					
TABCHR	9.5	14.6	5.61	0.933					
BAETIS	6.2	6.2	0.06	1.000					
GOMGOM	6.2	6.2	0.06	1.000					
HALHAL	6.2	6.2	0.06	1.000					
HEPMAC	6.2	6.2	0.06	1.000					
MOLMOL	7.6	10.7	4.38	1.000					
LEPNEC	6.2	6.2	0.06	1.000					
SPINIC	6.2	6.2	0.06	1.000					
LEPTRI	6.2	6.2	0.06	1.000					
TUBELL	6.2	6.2	0.06	1.000					

We also compared Namakan Reservoir to Rainy Lake, both under the 1970 rule-curve and the 2000 rule-curve, in terms of indicator species analysis for eulittoral and the sublittoral. For the eulittoral communities, we found *Oecetis* and Ostracoda to be indicative of Namakan Reservoir, and *Hexagenia*, *Sialis*, Oligochaeta, and Isopoda in Rainy Lake, for the BEFORE set. *Molanna*, Amphipoda, and *Mystacides* were indicative of the eulittoral in Namakan AFTER, while *Sialis*, Isopoda, and *Hexagenia* were more important eulittoral taxa in Rainy Lake (Table 9). For the sublittoral, we found more *Caenis*, Chironomidae, Polycentropopidae, Hirudinea and Amphipoda in Namakan, but more *Hexagenia* in Rainy Lake BEFORE; *Oecetis* characterized Namakan AFTER, but more Oligochaetes, Spinacaudata and *Sialis* occurred in Rainy Lake AFTER (Table 10; *P* < 0.05, 9999 permutations).

Table 9. Indicator species analysis for eulittoral (1 and 2m depths) communities of Rainy Lake and Namakan Reservoir BEFORE and AFTER. Significant indicator taxa (*P*<0.0.05) are listed underlined and in **bold**.

	BEFORE					AFTER			
Taxa	Observed IV	Monte Carlo Mean	SD	P	Taxa	Observed IV	Monte Carlo Mean	SD	P
	NAMAKAN RESERVOIR					NAMAKAN RESERVOIR			
LEPOEC	62.3	38.5	8.31	0.013	**MOLMOL**	34.5	19.4	5.31	0.018
OSTRAC	44.4	22.6	7.68	0.017	**AMPHIP**	76.8	54	10.98	0.019
MOLMOL	34.3	22.1	7.21	0.080	**LEPMYS**	35.8	22	5.77	0.029
CHIRON	67.1	58.1	5.81	0.084	CAENIS	46.9	35.3	7.39	0.084
HIRUDI	43.5	37.3	7.38	0.187	ENALLA	24.1	16.1	5.15	0.089
AMPHIP	66.5	58.2	10.9	0.227	CHIRON	67	58.2	5.99	0.096
NEMATO	41.3	38.3	8.25	0.293	LEPOEC	37.5	28.6	6.28	0.098
HYDRAC	33.8	31.1	7.84	0.308	HYDRAC	29.9	25.2	5.96	0.199
PHRPHR	11.1	8.9	4.47	0.510	OSTRAC	27.9	23.1	6.55	0.213
TABCHR	11.1	13.7	5.62	0.665	TETRAG	15.8	13.4	4.56	0.231
CALLIB	9.6	11.3	5.38	0.696	LIMLIM	10	6.9	3.15	0.263
POLYCE	20.8	25.6	7.45	0.713	EURYLO	10	6.8	3.19	0.268
SPHAER	47.5	55.1	9.68	0.730	CERATO	36.5	35	6.56	0.347
GASTRO	46.3	54.4	9.42	0.765	HIRUDI	38.7	37.5	6.67	0.364
PORIFE	12.7	17.8	6.44	0.920	NEMATO	40.9	40.4	8.06	0.458
DUBIRA	5.6	6.7	1.36	1.000	DYTHYD	6.7	5.4	2.58	0.512
ENALLA	4.7	9.5	3.87	1.000	SPHAER	57.1	57.6	6.74	0.512
DYTHYD	5.6	6.7	1.36	1.000	HYDOXY	6.7	5.6	2.5	0.515
PYRALI	5.6	6.7	1.36	1.000	PYRALI	9	11	4.22	0.625
					POLCER	26.6	30.1	6.51	0.632
	RAINY LAKE				CALLIB	7.4	12.5	4.6	0.888
HEXAGE	69.5	38	9.16	0.004	HYDAGR	3.3	4	0.82	1.000
SIALIS	41.7	16.1	6.44	0.006	APHIDI	3.3	4	0.82	1.000
OLIGOC	64.5	37.9	9	0.010	PHRBAN	4.2	8.3	3.53	1.000
ISOPOD	33.3	14.5	6.31	0.019	CLIMAC	3.3	4	0.82	1.000
CHAOBO	60.7	46.1	10.79	0.103	DIDYMO	3.3	4	0.82	1.000
CERATO	48.1	56.9	7.29	0.910	DUBIRA	3.3	4	0.82	1.000
CAENIS	39.1	53.6	9.57	0.993	GYRGYR	3.3	4	0.82	1.000
CLIMAC	3.5	8.9	4.42	1.000	LIBUND	3.3	4	0.82	1.000
LEPMYS	10	17.9	6.8	1.000	LEUCOR	3.3	4	0.82	1.000
HYDOXY	5.1	11.2	5.16	1.000	NEMMOR	3.3	4	0.81	1.000
					TEPHRI	3.3	4	0.82	1.000
					TIPULI	3.3	4	0.82	1.000
						RAINY LAKE			
					SIALIS	36.4	16.2	5.12	0.002
					ISOPOD	30	11.5	4.58	0.003
					HEXAGE	53.5	30.6	6.87	0.005
					CHAOBO	40.2	31.1	7.05	0.117
					ARIGOM	10	5.4	2.59	0.158
					PHRPHR	15.5	12.4	4.52	0.244
					TUBELL	5	4	0.82	0.394
					BAETIS	5	4	0.82	0.401
					LEPTRI	5	4	0.82	0.401
					HEPMAC	5	4	0.82	0.402
					SPINIC	5	4	0.82	0.404
					OLIGOC	52.3	54.7	7.03	0.597
					GASTRO	48.3	52.5	6.86	0.669
					PORIFE	7.1	9.8	3.92	0.669
					POLYCE	8.5	11	4.21	0.743
					LEPNEC	3.8	5.4	2.69	0.751
					PERITH	3.6	5.4	2.63	0.761
					TABCHR	9.4	13.4	4.5	0.814
					CHRDON	5	8.3	3.47	1.000
					GOMGOM	3	5.4	2.56	1.000
					HALHAL	3	5.4	2.61	1.000

Table 10. Indicator species analysis for sublittoral (3, 4, and 5m depths) communities of Rainy Lake and Namakan Reservoir BEFORE and AFTER. Significant indicator taxa (*P*<0.0.05) are listed underlined and in **bold**.

	BEFORE					AFTER			
Taxa	Observed IV	Monte Carlo Mean	SD	P	Taxa	Observed IV	Monte Carlo Mean	SD	P
	NAMAKAN RESERVOIR					NAMAKAN RESERVOIR			
CAENIS	59.8	35.6	7.04	0.005	**LEPOEC**	33.3	18	5.52	0.023
CHIRON	70.9	56	4.44	0.005	OSTRAC	33.2	23.4	6.82	0.088
POLYCE	33.6	20	5.53	0.030	AMPHIP	47.5	37.7	8.05	0.127
HIRUDI	36.9	24.2	5.82	0.043	HIRUDI	29.1	24.9	6.36	0.234
AMPHIP	33.2	21.1	6.24	0.049	POLCER	24.1	22	5.6	0.307
OSTRAC	30.2	20.5	5.93	0.076	CHIRON	59	58.3	5.77	0.405
MOLMOL	16.7	10.8	4.24	0.156	SPHAER	41.1	41.3	7.55	0.449
CERATO	56	50	5.92	0.162	HYDRAC	10.7	12	4.65	0.516
SPHAER	47.8	45.5	7.21	0.325	MOLMOL	5.6	5.6	2.51	0.575
DIDYMO	5.6	5.6	2.19	0.566	PHRBAN	2.8	3.8	1.6	1.000
LEPMYS	5.6	5.7	2.23	0.571	GOMDRO	2.8	3.8	1.59	1.000
LEPOEC	19.6	21	5.62	0.572	HALHAL	2.8	3.9	1.61	1.000
PHRPHR	2.8	3.8	1.6	1.000	ISOPOD	2.8	3.9	1.61	1.000
					TETRAG	2.8	3.8	1.6	1.000
	RAINY LAKE								
HEXAGE	55.8	49	4.47	0.087		RAINY LAKE			
OLIGOC	41.6	33.6	6.99	0.135	**OLIGOC**	72.3	54.9	6.51	0.010
CHAOBO	58.7	54	5.19	0.175	**SPINIC**	18.7	6.6	3.44	0.022
NEMATO	32.2	27	6.5	0.193	**SIALIS**	52.4	39.2	5.9	0.033
CLIMAC	6.2	3.8	1.6	0.305	GASTRO	47.4	34	7.1	0.054
SIALIS	38.7	42.3	5.47	0.714	HEXAGE	60.2	53.8	4.35	0.094
GASTRO	20.8	26.9	6.38	0.864	CAENIS	25.6	18.9	6.01	0.137
HYDRAC	24.8	31.8	6.36	0.928	CERATO	39.1	33.5	6.14	0.169
PORIFE	4.3	5.7	2.24	1.000	BRACHY	10.2	6.7	3.53	0.216
					NEMATO	27.7	24.2	5.82	0.230
					PHRPHR	6.2	3.8	1.6	0.307
					CALLIB	6.2	3.9	1.61	0.310
					HYDOXY	6.2	3.9	1.61	0.310
					LEPMYS	6.2	3.9	1.61	0.313
					CHAOBO	36	38.9	6.96	0.593
					PYRALI	7.5	9.6	3.84	0.630
					LEPTRI	4.3	5.6	2.21	1.000

Given that there was a separation in the impact between the eulittoral and sublittoral, we display the nMDS plots separately for each of the depth groups by using a two-dimensional solution which recovered 78.1% of the original site relationships. On the partial nMDS plot for the eulittoral, there was no overlap between the 95% confidence ellipse between Rainy Lake and Namakan Reservoir structure under the 1970 rule-curve, but there was overlap between the two systems under the 2000 rule-curve, suggesting the communities have become more similar (Figure 9). Benthic community structure in both Rainy Lake and Namakan Reservoir showed change since Kraft's study, but the greater change occurred in Namakan Reservoir.

Ellipses on the nMDS plot for the sublittoral community did not show the same separation as did the eulittoral; Rainy Lake and Namakan Reservoir sites did not come closer together as hypothesized (Figure 10). There was overlap between Namakan Reservoir under the 1970 rule-curve and the 2000 rule-curve, indicating the sublittoral benthos did not change significantly in concert with the change in management regime. There was also overlap between the Rainy Lake samples BEFORE and AFTER. No overlap was observed between Namakan Reservoir and Rainy Lake BEFORE or AFTER, suggesting that the two lakes have distinct sublittoral communities even still.
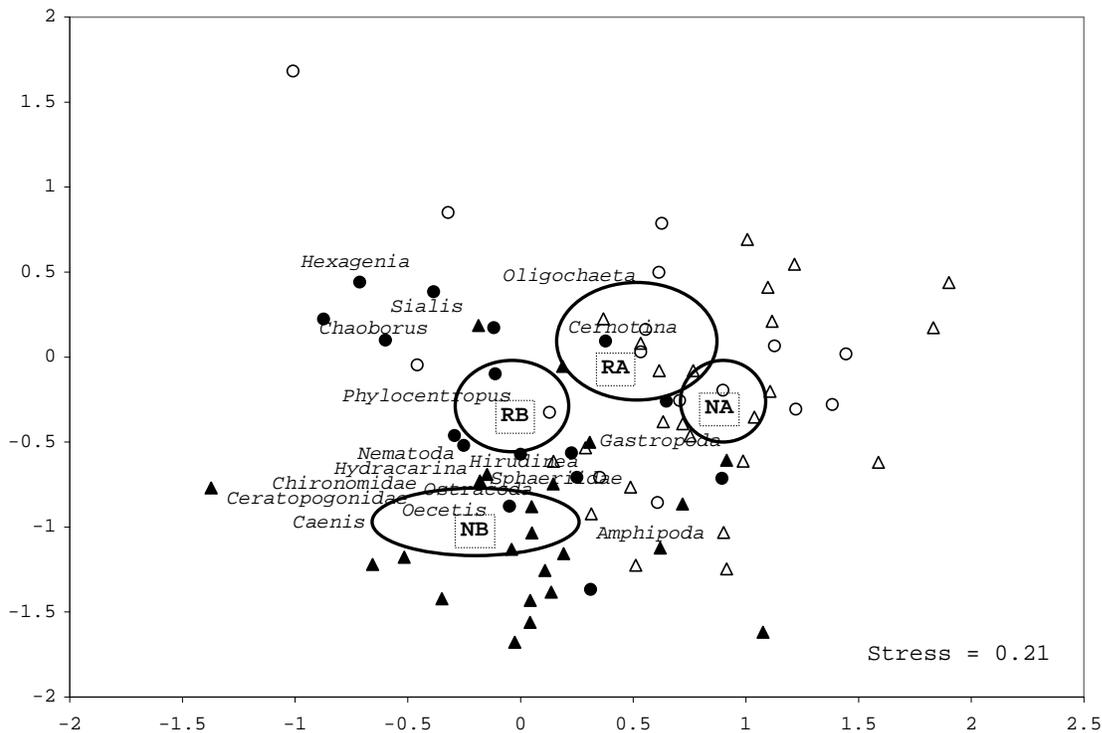
Figure 9. Two-factor nonmetric multidimensional scaling (nMDS) partial plot of assemblages in eulittoral depth samples, showing composite groups of time-space in samples from Rainy Lake under the 1970 rule-curve (RB) and under the 2000 rule-curve (RA) compared with Namakan Reservoir under the 1970 rule-curve (NB) and the 2000 rule-curve (NA). Ellipses were drawn on the 95% confidence interval for the two axes shown. Each sample represents one of the four conditions: ● = RB: ○ = RA: ▲ = NB: △ = NA Species scores are variance-weighted linear correlations against each axis. In order to more easily interpret relationships, we show only taxa whose scaled correlation has an absolute value greater than 1SD from the mean of all taxa. "Stress" is a measure of the relative amount of disagreement between the interpoint distance of nMDS and the original distance matrix. Generally, stress under 0.20 will give a reasonable representation of the original distances; however, stress is a function of sample size where it increases with increasing samples. This result is borderline but does give a configuration that is significantly different from a random configuration of points ($P < 0.05$, 20 permutations). Final configuration recovered 50.2% and 27.9% (total 78.1%) of the order of the original data matrix for the first and second axis, respectively. Original nMDS was a two dimensional solution conducted on Bray-Curtis distances of transformed data (log[1 + x]) with 184 samples and 57 taxonomic units.

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Oligochaeta

Amphipoda

Sphaeriidae Gastropoda

Chironomidae

Caenis

Ceratopoginidae   Cernotina

Sialis

Chaoborus   Hexagenia
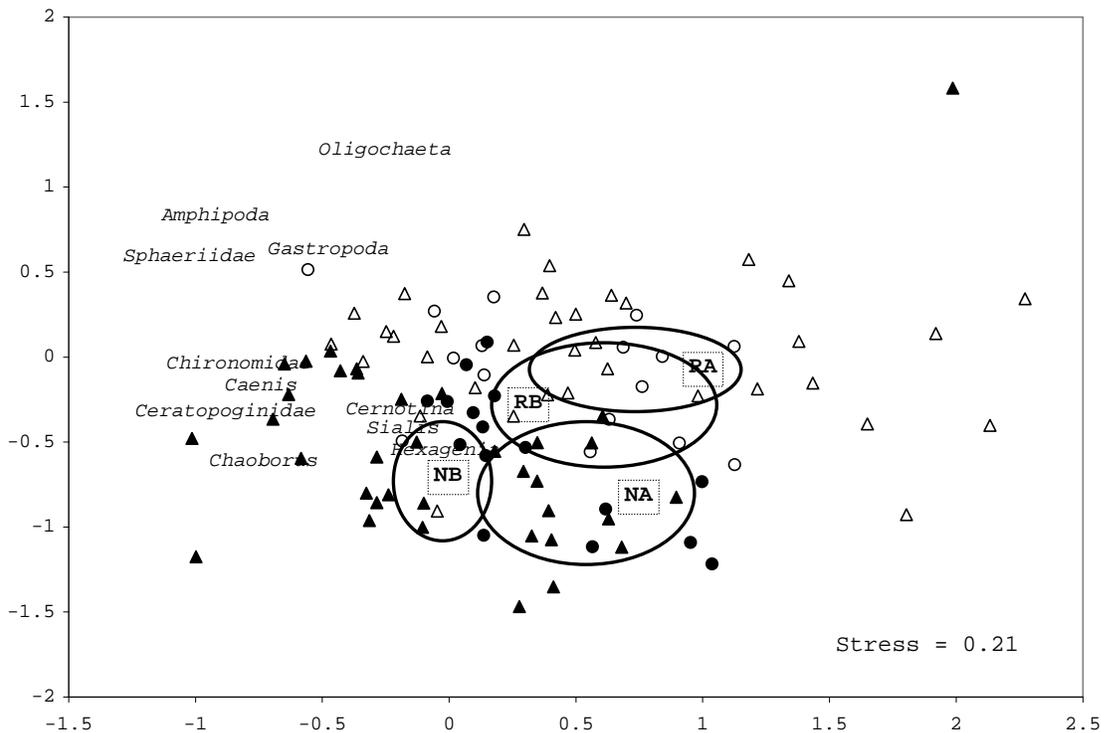
RA

RB

NB

NA

Stress = 0.21

Figure 10. Two-factor nonmetric multidimensional scaling (nMDS) partial plot of assemblages in sublittoral depth samples, showing composite groups of time-space in samples from Rainy Lake under the 1970 rule-curve (RB) and under the 2000 rule-curve (RA) compared with Namakan Reservoir under the 1970 rule-curve (NB) and the 2000 rule-curve (NA). Ellipses were drawn on the 95% confidence interval for the two axes shown. Each sample represents one of the four conditions: ● = RB: ○ = RA: ▲ = NB: △ = NA Species scores are variance-weighted linear correlations against each axis. In order to more easily interpret relationships, we show only taxa whose scaled correlation has an absolute value greater than 1SD from the mean of all taxa. "Stress" is a measure of the relative amount of disagreement between the interpoint distance of nMDS and the original distance matrix. Generally, stress under 0.20 will give a reasonable representation of the original distances; however, stress is a function of sample size where it increases with increasing samples. This result is borderline but does give a configuration that is significantly different from a random configuration of points (P < 0.05, 20 permutations). Final configuration recovered 50.2% and 27.9% (total 78.1%) of the order of the original data matrix for the first and second axis, respectively. Original nMDS was a two dimensional solution conducted on Bray-Curtis distances of transformed data (log[1 + x]) with 184 samples and 57 taxonomic units.

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There were apparent decreases in dominance by Chironomidae of eulittoral communities in both Rainy Lake and Namakan Reservoir, with corresponding increases in the relative densities of Sphaeriidae and Gastropoda AFTER relative to BEFORE (Figure 11, Figure 12). Ceratopoginidae, *Chaoborus*, *Caenis*, Polycentropopidae were all found at fewer sites overall AFTER compared to BEFORE, while *Cernotina* and Ostracoda became more ubiquitous in Rainy Lake (Figure 13). Ceratopoginidae, *Caenis*, *Oecetis*, Nematoda, Ostracoda, and Polycentropopidae were found at fewer sites, while Oligochaeta, *Tetragoneuria* and *Cernotina* were all found at more Namakan Reservoir eulittoral sites AFTER relative to BEFORE (Figure 14). Results for the sublittoral communities indicated a slight decrease in the relative density of *Hexagenia* and *Chaoborus* and an increase in Oligochaeta AFTER for Rainy Lake, with a corresponding decrease in *Chaoborus* and an increase in Oligochaeta for Namakan Reservoir. However, there was a drop in Chironomidae but no apparent decrease in *Hexagenia* in the subliottoral of Namakan, in contrast to the responses of these taxa in Rainy Lake (Figure 15, Figure 16). In terms of site occupancy, the Rainy Lake sublittoral showed decreased ubiquity of *Chaoborus*, Sphaeriidae, and Hydracarina, and an increase in Oligochaeta and Amphipoda (Figure 17). Namakan Reservoir had lower occurrence of *Chaoborus*, Ceratopoginidae, *Caenis*, Hydracarina, and Polycentropopidae but greater occurrence of Oligochaeta, Amphipoda, and *Cernotina* (Figure 18).
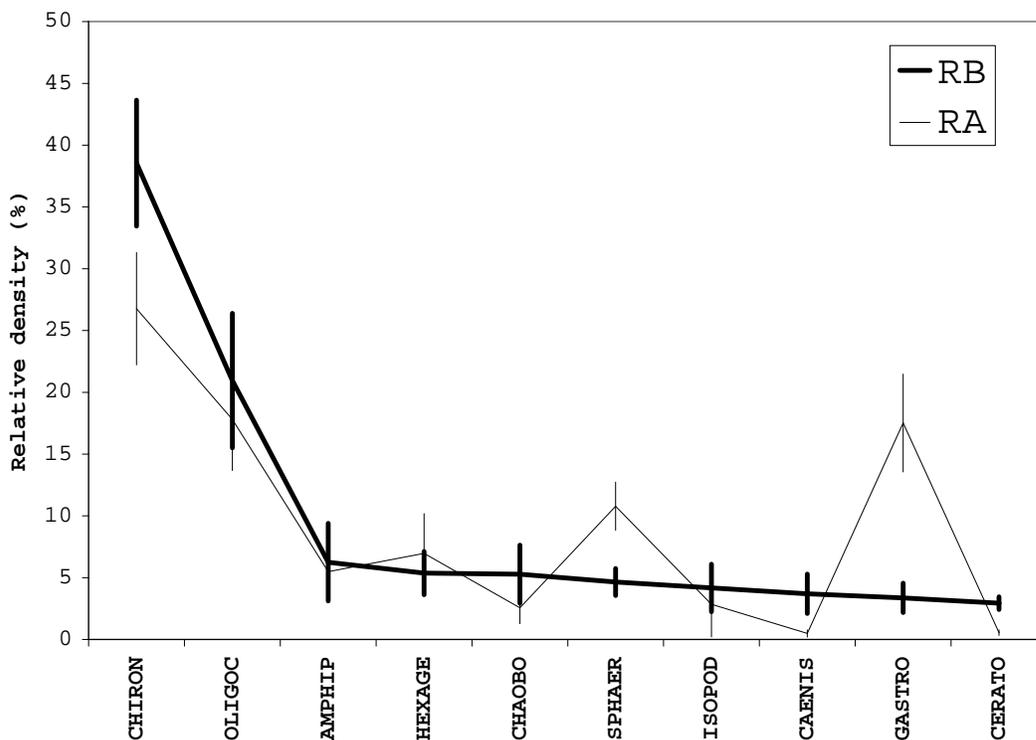

Figure 11. Change in relative density of taxonomic units in the eulittoral zone of Rainy Lake for sampling under the 1970 (Rainy-Before [RB]) and 2000 (Rainy-After [RA]) rule curves. Only the 10 most abundant taxa, as determined from the BEFORE data set, are shown. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
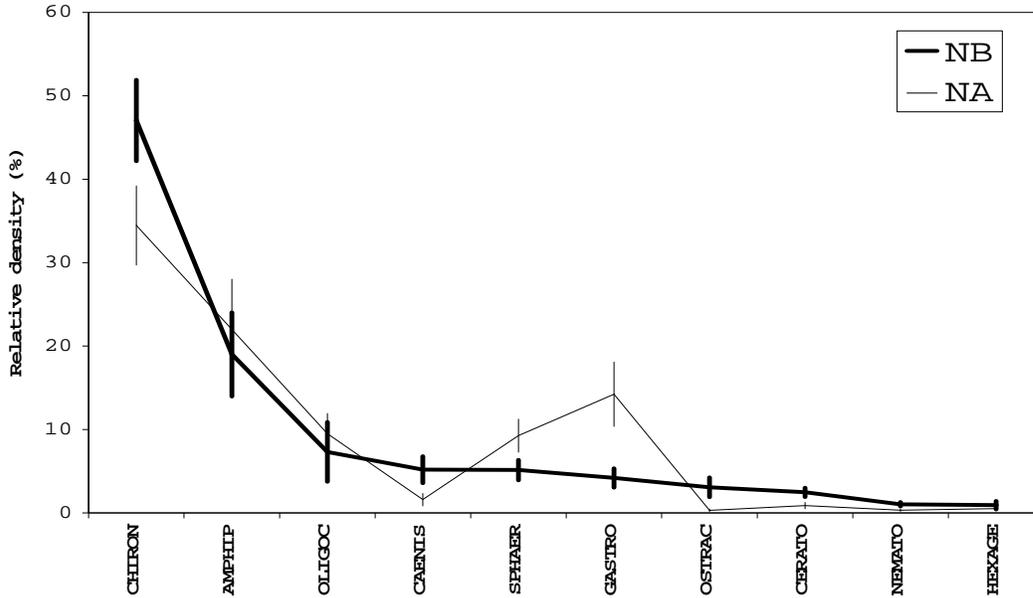
Figure 12. Change in relative density of taxonomic units in the eulittoral zone of Namakan Reservoir for sampling under the 1970 (Namakan-Before [NB]) and 2000 (Namakan-After [NA]) rule curves. Only the 10 most abundant taxa, as determined from the BEFORE data set, are shown. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
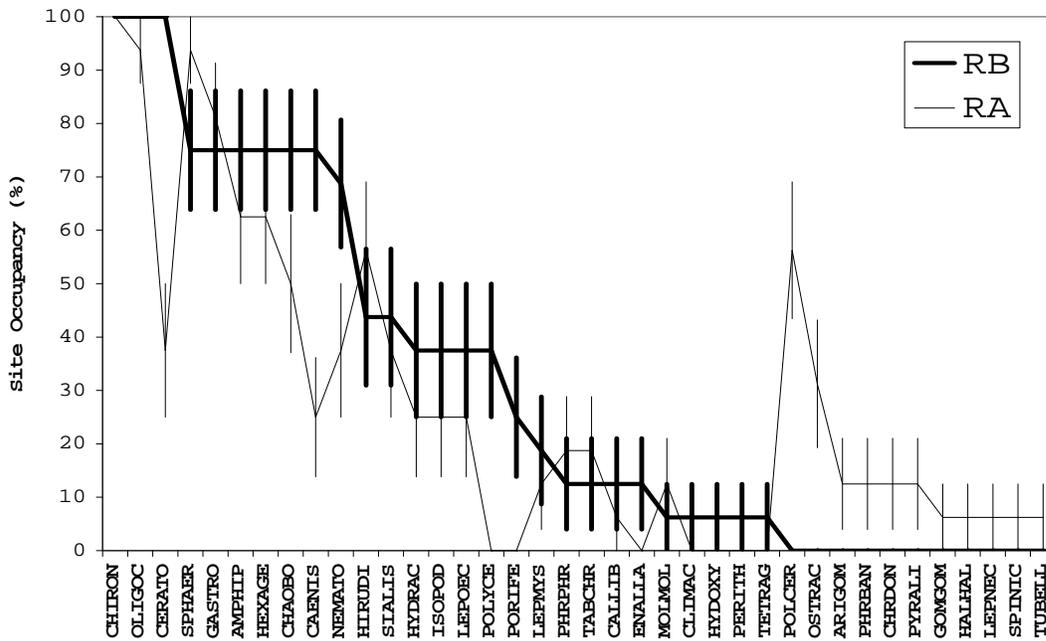

Figure 13. Change in site occupancy of taxonomic units in the eulittoral zone of Rainy Lake for sampling under the 1970 (Rainy-Before [RB]) and 2000 (Rainy-After [RA]) rule curves. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
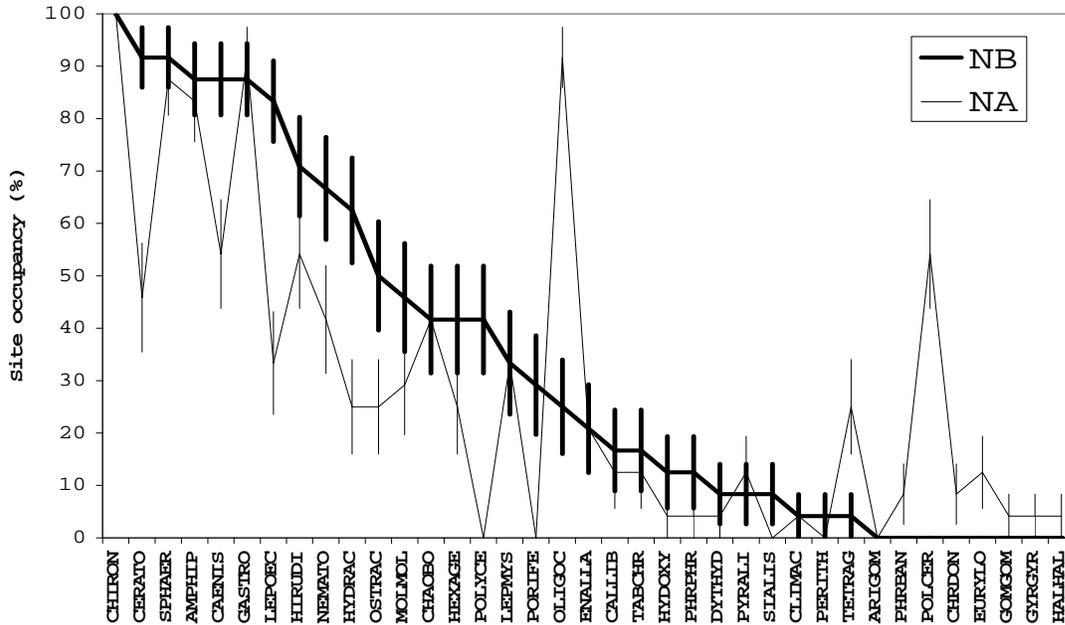
Figure 14. Change in site occupancy of taxonomic units in the eulittoral zone of Namakan Reservoir for sampling under the 1970 (Namakan-Before [NB]) and 2000 (Namakan-After [NA]) rule curves. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
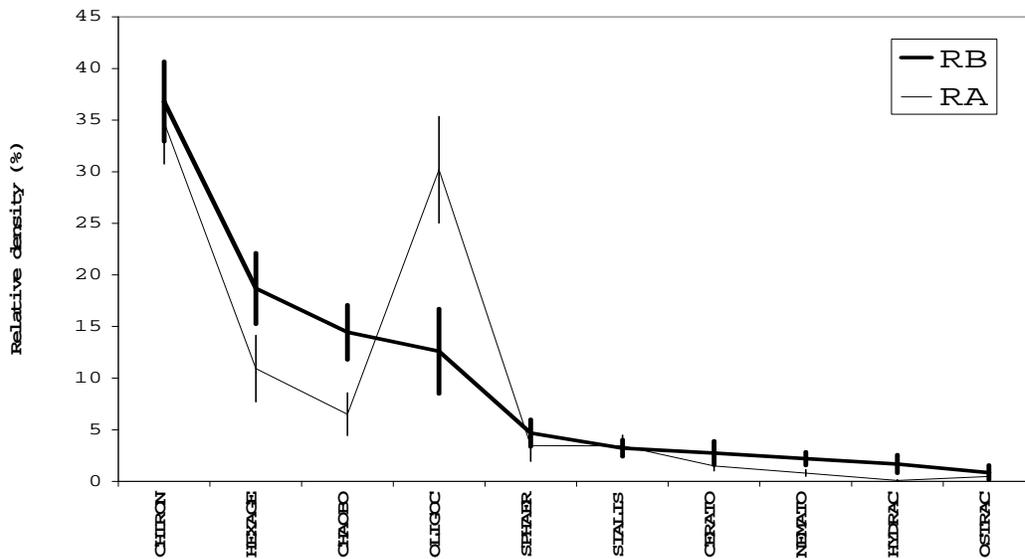

Figure 15. Change in relative density of taxonomic units in the sublittoral zone of Rainy Lake for sampling under the 1970 (Rainy-Before [RB]) and 2000 (Rainy-After [RA]) rule curves. Only the 10 most abundant taxa, as determined from the BEFORE data set, are shown. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
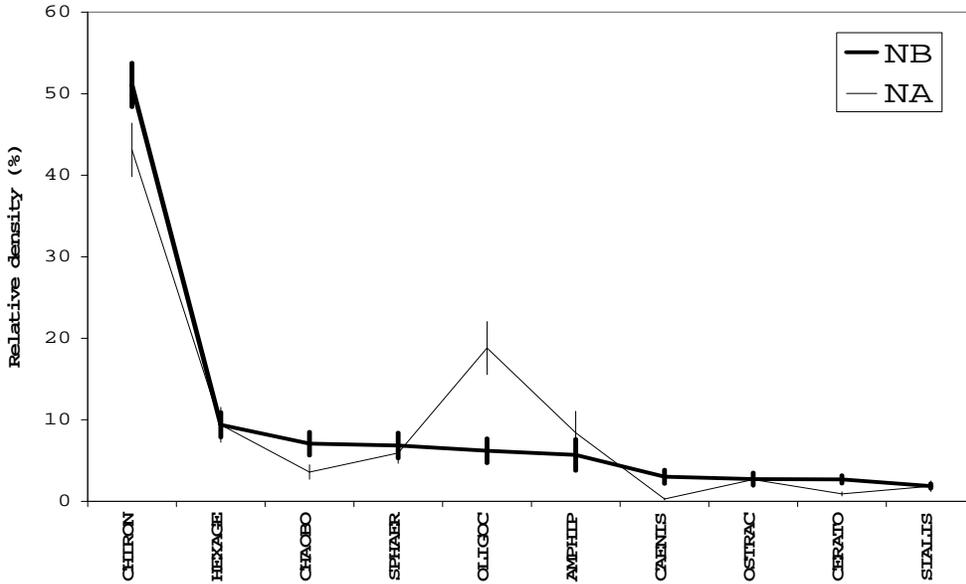
Figure 16. Change in relative density of taxonomic units in the sublittoral zone of Namakan Reservoir for sampling under the 1970 (Namakan-Before [NB]) and 2000 (Namakan-After [NA]) rule curves. Only the 10 most abundant taxa, as determined from the BEFORE data set, are shown. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
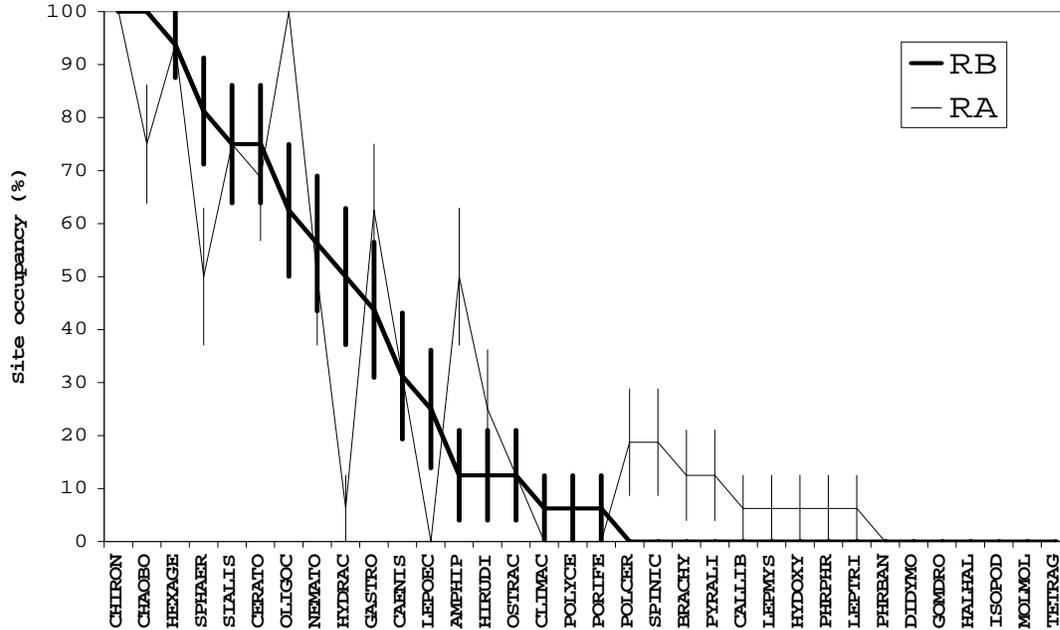

Figure 17. Change in site occupancy of taxonomic units in the sublittoral zone of Rainy Lake for sampling under the 1970 (Rainy-Before [RB]) and 2000 (Rainy-After [RA]) rule curves. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.
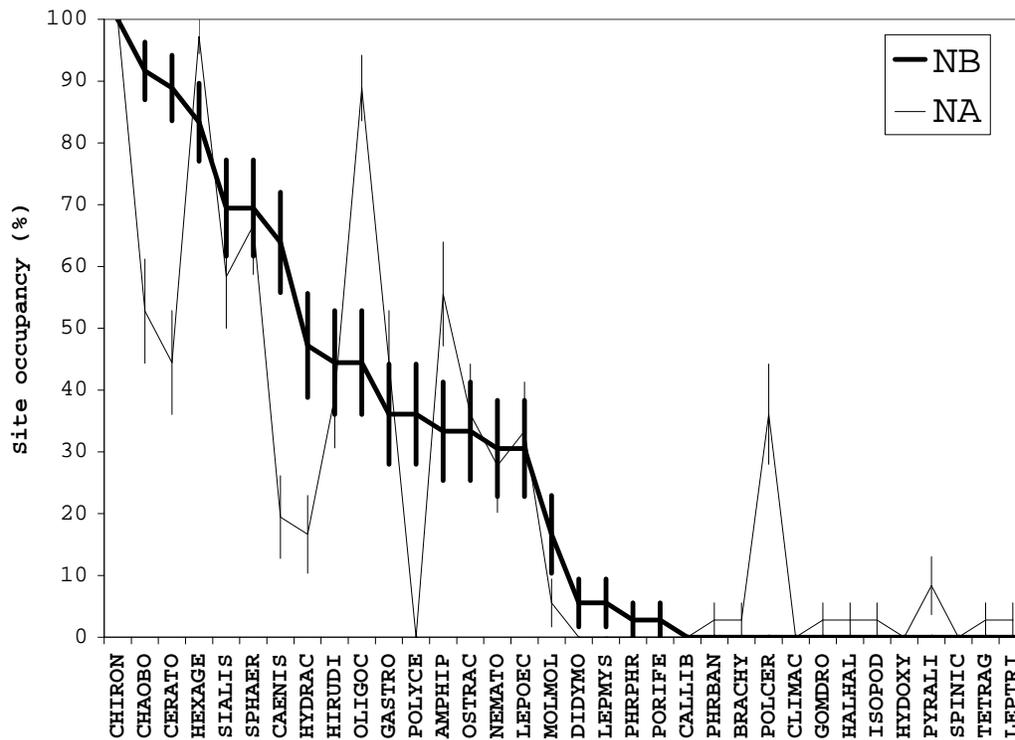
Figure 18. Change in site occupancy of taxonomic units in the sublittoral zone of Namakan Reservoir for sampling under the 1970 (Namakan-Before [NB]) and 2000 (Namakan-After [NA]) rule curves. Error bars indicate standard error of the mean, where variation is a composite of space, depth, and time.

Kraft did not do a comprehensive identification of Chironomidae, identifying genera only for Moxie and Harrison at 1m and 3m depths. Furthermore, it is difficult to ascertain from Kraft's report whether the chironomids he identified were from the samples he collected and used in his analyses of overall Chironomidae, or if they represent additional samples. If the former is true, we can compare Kraft's results to our samples from the same places. In the absence of that assurance, we can only make qualitative and descriptive comparisons. We were only able to describe proportional differences with these limited data, which seemed to indicate that detritivorous genera increased as a proportion of the chironomid fauna in Moxie 3m following the rule curve change (Table 11). The data also suggest that *Chironomus* replaced *Glyptotendipes* and *Tanytarus* at 3m depth in Moxie after the rule curve change. *Ablabesmyia*, a carnivorous genus, and the detritivore *Parakiefferiella* were found in the AFTER set in Moxie 1m, but were absent from the BEFORE set (Table 12).

Table 11. Chironomidae subfamily composition, feeding guild distribution, and body size before and after rule curve change. Kraft only identified genera for Harrison 1m and 3m and Moxie 1m and 3m; thus the comparison is restricted to those sites.

	One Meter Depth				Three Meter Depth			
	Rainy Lake, Harrison Bay		Namakan Reservoir, Moxie Bay		Rainy Lake, Harrison Bay		Namakan Reservoir, Moxie Bay	
	BEFORE	AFTER	BEFORE	AFTER	BEFORE	AFTER	BEFORE	AFTER
Percent Total Chironomidae in Subfamily								
Tanypodinae	23	57	7	11	8	50	35	19
Chironominae	67	43	77	82	92	46	64	81
Orthocladinae	10	1	16	6	0	3	1	0
Diamesinae	0	0	0	0	0	1	0	0
Percent Total Chironomidae in Feeding Guilds								
Carnivore	25	58	10	12	8	52	37	19
Detritivore	48	24	71	76	62	46	25	77
Herbivore	27	17	19	12	31	2	38	4
Weighted Average Size Category								
Size	3.80	3.93	3.20	3.18	3.08	3.57	4.00	4.00

Table 12. Relative abundance of Chironomidae genera expressed as a percentage. Kraft only identified genera for Harrison 1m and 3m and Moxie 1m and 3m; thus the comparison is restricted to those sites.

One Meter Depth

Rainy Lake, Harrison Bay				Namakan Reservoir, Moxie Bay			
BEFORE		AFTER		BEFORE		AFTER	
Polypedilum	20	*Procladius*	24	*Pseudochironomus*	16	*Cladotanytarsus*	20
Tanytarsus	20	*Polypedilum*	16	*Cladotanytarsus*	15	*Pseudochironomus*	20
Procladius	17	*Ablabesmyia*	16	*Glyptotendipes*	14	*Tanytarsus*	14
Psectrocladius	8	*Clinotanypus*	16	*Stictochironomus*	11	*Paratanytarsus*	10
Endochironomus	6	*Tanytarsus*	8	*Tanytarsus*	11	*Glyptotendipes*	8
Ablabesmyia	5	*Pseudochironomus*	7	*Parakiefferiella*	9	*Ablabesmyia*	8
Other	24	Other	13	*Procladius*	5	Other	20
				Other	19		

Three Meter Depth

Rainy Lake, Harrison Bay				Namakan Reservoir, Moxie Bay			
BEFORE		AFTER		BEFORE		AFTER	
Polypedilum	23	*Procladius*	42	*Glyptotendipes*	32	*Chironomus*	70
Cladotanytarsus	15	*Tanytarsus*	15	*Procladius*	26	*Procladius*	14
Cryptotendipes	15	*Cryptotendipes*	7	*Tanytarsus*	13	*Clinotanypus*	5
Procladius	8	*Ablabesmyia*	6	*Clinotanypus*	8	Other	12
Tanytarsus	8	Other	29	Other	21		
Endochironomus	8						
Pseudochironomus	8						
Nilothauma	8						
Stempellina	8						
Other	0						

We performed a PCA on the changes in benthic community data at each site, being satisfied that AFTER – BEFORE differences for sites were approximately multivariate normal (Mean$_{skew}$=1.87, SD$_{skew}$=1.35). Indicator species analyses, along with cluster analysis according to Dufrene and Legendre's (1997) methodology for group separation, indicated four groups of sites in the PCA ordination (Figure 19). Two groups, comprised of samples from the eulittoral sites in Namakan Reservoir, occurred at the edges of the ordination diagram and thus showed the greatest community differences AFTER – BEFORE. We found Moxie Bay 1m (M1) and 2m (M2) to have a very large influence on the ordination. Two sites comprised the second group: Swanson Bay 2m (S2) and Junction Bay 1m (J1), while Junction Bay 2m (J2) was included in the third most-changed group. The only eulittoral site in Namakon that did not respond as predicted was Swanson Bay 1m (S1), which was included in the fourth group. The ordination diagram shows that Amphipoda largely drove the separation of the M1 & M2 group, amphipods being reduced in the AFTER data set at Moxie relative to the BEFORE set. This site group also saw notable reductions in Chironomidae and Sphaeriidae. Changes at sites J1, J2, and S2 were largely driven by losses of Chironomidae and, to a lesser extent, Oligochaeta.
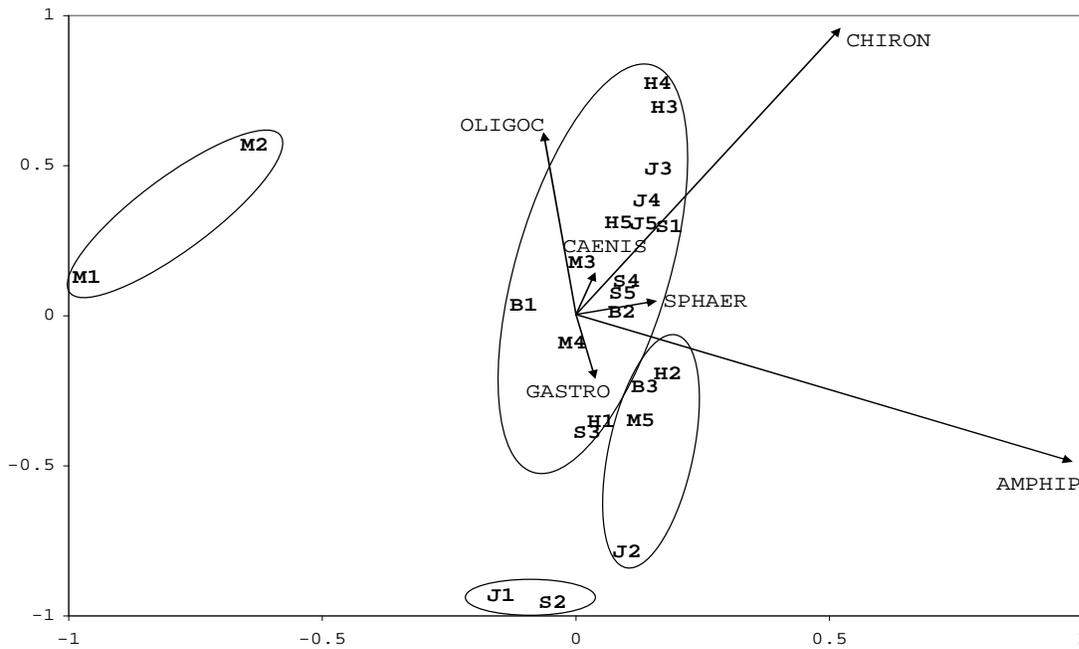

Figure 19. Principal component analysis using variance-covariance for centered untransformed average differences AFTER-BEFORE for each site. Sample scores and species scores were scaled by relativizing by the maximum so they shared the same scale. In order to more easily interpret relationships, we show only taxa whose scaled correlation has an absolute value greater than 1SD from the mean of all taxa.

Axis 1 explained 73% of the variance and axis 2 explained 13% (86% total) of changes in community composition. Elliptical overlay shows number and designation of site groups, using the method of Dufrene and Legendre (1997).

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Univariate BACI

All univariate skew was less than an absolute value of one, which indicated approximate normality for linear modeling; however, it was necessary to use a log (x+1) transformation on density data to achieve this result. Repeated-measures ANOVA indicated significant differences among treatment groups (NA, NB, RA, and RB) for overall density, Evenness, and Shannon-Weiner index in the eulittoral, and the community coefficient of variation in the sublittoral (Table 13).

There was a difference in the overall density of invertebrates among the four treatment groups: NA, NB, RA, and RB (F=5.757, P = 0.007). Post-hoc multiple comparison using Tukey HSD showed that NA formed a group that was significantly different from the other three groups ($P <$ 0.05). Overall density in the eulittoral decreased by 5,679 (SE =1,925) organisms per square meter in Namakan Reservoir in concert with the rule curve change, while Rainy Lake showed a reduction of 2,328 (SE = 949) organisms m^{-2}. A random effects model showed that 6.6% of total variance was associated with the date when the reservoir was filled to capacity, 2.1% was associated with the annual minimum water level, and 11.8% was associated with their interaction (R^2, F=5.475, P=0.002). There was no evidence to suggest that diversity in terms of species richness changed with respect to the rule curve. Both the Shannon-Weiner index (F=3.665, P=0.016) and Evenness (F=6.477, P = 0.001) increased for Namakan Reservoir and Rainy Lake AFTER relative to BEFORE, but increased more in Rainy Lake. The Shannon-Weiner index could be related to minimum water level for the year (8.9%), the date at which the reservoir was filled to capacity (2.0%), but not to their interaction (F=3.052, P = 0.034). Variation in Evenness was associated most with the minimum water level (12%) and only slightly to date of filling to capacity (2%) and their interaction (0.7%) (F=4.253, P=0.008). Community coefficient of variation (CCV) showed group separation in the sublittoral, and the Tukey HSD indicated that increased CCV occurred in NA, suggesting decreased stability in the sublittoral of Namakan Reservoir. The way CCV was calculated precluded its use in attempting to determine how the specific water levels were affecting response (Table 14).

We found an overall impact due to group relationships (i.e., NB, RB, NA, and RA) for *Caenis* densities in the eulittoral, but those differences were difficult to interpret; however, the nature of differences for *Caenis* were apparent in the sublittoral, where NB formed a group distinct from all other treatments (F=13.710, P = 0.001). *Chaoborus* densities were greatly reduced in both Rainy Lake and Namakan Reservoir in the sublittoral, but we could not directly associate a change between these systems with respect to the change in rule curves. Chironomidae were much reduced in Namakan Reservoir eulittoral relative to Rainy Lake, even though chironomid numbers were reduced in Rainy as well (F=7.851, P = 0.002). We also found group differences for *Sialis*, but the interpretation based on group separation was not clear, and *Sialis* numbers in the eulittoral were very low (F=3.768, P=0.032). Isopoda were excluded from statistical comparisons because they did not occur in Namakan Reservoir either BEFORE or AFTER, with a single exception.

Table 13. Univariate response variables under the 1970 rule curve for Rainy (RB) and Namakan (NB) and 2000 rule curve for Rainy (RA) and Namakan (NA). Values with an asterisk (*) indicate statistical significance ($P < 0.05$) using a repeated-measures ANOVA.

	NA		NB		RA		RB	
				Eulittoral				
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Density*	2748	549	8427	1845	2131	439	4459	841
June:August	2.04	0.68	1.10	0.31	2.79	1.04	0.89	0.20
Taxonomic richness	11	1	13	0	11	1	12	1
Eveness*	0.57	0.03	0.52	0.03	0.70	0.03	0.62	0.02
Shannon-Weiner*	1.32	0.08	1.28	0.07	1.59	0.06	1.51	0.07
Community CV	0.75	0.06	0.71	0.14	0.80	0.25	0.64	0.08
				Sublittoral				
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Density	1863	368	3063	443	1665	304	1824	376
June:August	2.79	0.71	3.24	2.22	1.39	0.36	1.01	0.25
Taxonomic richness	9	1	9	0	9	1	9	1
Eveness	0.66	0.03	0.64	0.02	0.66	0.04	0.73	0.03
Shannon-Weiner	1.31	0.04	1.38	0.06	1.41	0.06	1.51	0.08
Community CV*	0.78	0.07	0.55	0.04	0.63	0.05	0.42	0.04

Table 14. Response in density for select taxa hypothesized by Kraft (1984) to be particularly susceptible to drawdown regime in Namakan under the 1970 rule-curve implementation. Values are given for 1970 rule curve for Rainy (RB) and Namakan (NB) and 2000 rule curve for Rainy (RA) and Namakan (NA). Statistical significance ($P < 0.05$) was determined using a repeated-measures ANOVA on log(x+1) transformed densities. Values given are back-transformed.

Group	1 and 2 m depths					3,4, and 5 m depths				

Caenis

	$F=12.917,P < 0.001$					$F=13.710,P < 0.001$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	A	60	90	134		A	12	16	21
RB	AB	20	33	54		B	1	1	3
NA	BC	4	7	11		B	0	1	1
RA	C	1	2	3		B	1	2	4

Chaoborus

	$F=1.704,P=0.206$					$F=4.401,P=0.014$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	--	1	3	7		A	45	77	130
RB	--	14	31	67		A	74	162	356
NA	--	1	4	7		B	4	8	14
RA	--	2	6	13		AB	9	20	46

Chironomidae

	$F=7.851,P=0.002$					$F=1.603,P=0.217$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	A	1492	2020	2733		--	672	936	1304
RB	AB	778	1127	1633		--	254	354	493
NA	B	311	422	571		--	283	466	767
RA	B	181	262	380		--	242	399	656

Gastropoda

	$F=0.309,P=0.819$					$F=1.207,P=0.331$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	--	36	73	148		--	1	2	4
RB	--	13	33	80		--	1	3	5
NA	--	37	75	154		--	2	3	5
RA	--	43	104	247		--	5	10	18

Hexagenia

	$F=3.015,P=0.061$					$F=1.551,P=0.230$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	--	1	3	8		--	37	52	73
RB	--	19	44	102		--	84	140	233
NA	--	0	1	3		--	27	38	53
RA	--	5	12	28		--	36	60	100

Sialis

	$F=3.768,P=0.032$					$F=1.867,P=0.165$			
	Tukey HSD	-SE	Mean	+SE		Tukey HSD	-SE	Mean	+SE
NB	AB	0	0	1		--	9	12	17
RB	A	3	5	8		--	9	15	25
NA	B	0	0	0		--	3	5	7
RA	AB	1	3	5		--	8	13	21

Multivariate: Environmental Relationships (AFTER set only)

When controlling for time, there was not a significant difference in benthic community organization between Cranberry, Harrison, and Black Bays within Rainy Lake, which suggests we have no reason not to treat bays as random factors for this impact study (F=2.342, P=0.140).

We analyzed variance components using all environmental variables on the AFTER data set. Environmental variables were approximately divided into miscellaneous environmental variables, macrophyte variables (for this analysis site-specific macrophyte data collected during 2004 were used as surrogates for sites at 2005; a preliminary analysis showed this not to substantially alter partitioned variance while allowing for a more full comparison), lake sediment properties, and water level variables (Table 15). We calculated both marginal and conditional variances for the variable groups. For variance partitioning, in order to compute marginal variability when more than one variable was used, we maintained VIF < 20 so as not to inflate variance portioned. This led to the elimination of filamentous algae and maximum water level for the year. Location, macrophyte community, and water level variables all had high explanatory power when isolated (Table 16).

Based on these marginal variances, we constructed a model for conditional relationships to portion variance according to space, time, macrophytes, sediment, distance to shoreline, slope, and water level variables. It was necessary to eliminate maximum water level, *Myriophyllium*, *Zizania*, plant density, plant diversity, filamentous algae, and whether or not a site was exposed in the winter, to reduce the effect of multicollinearity (VIF > 20). The conditional model showed that space and time, together, accounted for 43% of the variance in the community. The structure of the macrophyte community accounted for 7%, and 5% of the variability in the community was explained by water levels (Figure 20). After fixing covariables, sediment characteristics, distance to shoreline, and slope explained only negligible variance and as a result were not included in the model. After setting space and time as covariables, macrophyte and water level variables showed a significant effect on structuring macroinvertebrate communities (F=1.124, P = 0.005). A total of 45% of the variability in the macroinvertebrate community structure could not be accounted for with the environmental variables we used.

The variability for the individual terms was not confined to the first two axes; as a result, we did not produce a biplot from the result of the db-RDA, but instead show correlations with the major underlying gradient using nMDS. This also allowed us to show collinear variables since they were not used in the production of actual site scores. Generally, water level variables were associated with the first axis and sediment characteristics with the second axis (Figure 21). Nearly all benthic taxa showed a strong relationship with respect to water level variables. In general, benthos taxa were most abundant when annual maximum and minimum water levels were high, summer and winter drawdown rates and spring refill rates were high, where the termination of winter drawdown occurred earlier in the year, when the summer drawdown period was short, when there was an earlier spring release, and when summer drawdown period was short. Several chironomids were strongly related to these water level variables including *Ablabesmyia*, *Procladius*, *Clinotanypus*, *Cladotanytarsus*, *Polypedilum*, and *Psectrocladius*. Besides these Chironomidae, all three genera of the Sphaeriidae found in the VOYA system also showed a strong relationship to the first axis. The second nMDS axis showed structure from sediment characteristics. Oligochaeta, *Hexagenia, Sialis,* and *Micropsectra* were favored in

Table 15. Environmental variables used for analyses of relationships to benthic macroinvertebrates for AFTER data set. We define "winter," for these purposes, to be the time when drawdown is initiated in autumn through to the point where low water is reached and refill begins. We define "filled to capacity" as the point during the year when the water first hits the top of the rule curve.

Code	Description
	Macrophyte Variables
PLDENS	Macrophyte density
PLDIVE	Macrophyte diversity
CERDEM	*Ceratophyllum demersum*
ELOCAN	*Elodea canadensis*
FILALG	Filamentous algae
LEMTRI	*Lemna trisulca*
MOSS	Moss
TYRSIL	*Myriophyllum sibiricum*
NITSPP	*Nitella*
NUPSPP	*Nuphar*
NYMSPP	*Nymphaea*
POTFOL	*Potamogeton foliosus*
POTRICH	*Potamogeton richardsonii*
POTROB	*Potamogeton robbinsii*
POTSPI	*Potamogeton spirillus*
UTRSPP	*Utricularia*
VALAME	*Vallisneria americana*
ZIZSPP	*Zizania aquaticus*
	Water Level Variables
min_wl	Annual minimum water level (m)
max_wl	Annual maximum water level (m)
drwdwn_rate	Rate of winter drawdown (m/day)
rfll_rate	Rate of spring refill (m/day)
summ_rate	Rate of summer drawdown (m/day)
sprng_rlse	Julian date for beginning of spring refill (d)
rls_end	Julian date for when reservoir was filled to capacity (d)
summer stable duration	Duration of summer drawdown (d)
dewat+ice	Duration of site exposure
dewaticedum	Site winter exposed: Yes or No
an_range	Annual range of water level fluctuation (m)
an_mean	Annual mean water level (m)
maxday	Julian date for when annual maximum water level occurred
minday	Julian date for when annual minimum water level occurred
	Lake Sediment Variables
Organic	Organic content of lake sediment (%)
Water	Water content of lake sediment (%)
Sand	Fraction of lake sediment particles greater than 0.02mm (%)
Silt	Fraction of lake sediment particles between 0.002mm and 0.02mm (%)
Clay	Fraction of lake semident particles less than 0.002mm (%)
	Miscellaneous Variables
depth	Depth (m)
d Shore	Distance from nearest shore (m)
Slope	Slope of lake basin at sampling site
spring	Season: June or August

Table 16. Marginal variance for environmental variable groups.

Variable Class	Variable	Marginal Variance (%)
Space	Lake	2
	Bay	6
	Site	34
Depth	All	5
	1,2 vs. 3,4,5	5
	1,2,3 vs. 4,5	4
Time		9
Plants	Taxa	18
	Summary	6
Sediment		9
Distance from Shore		2
Slope		2
Water levels		19
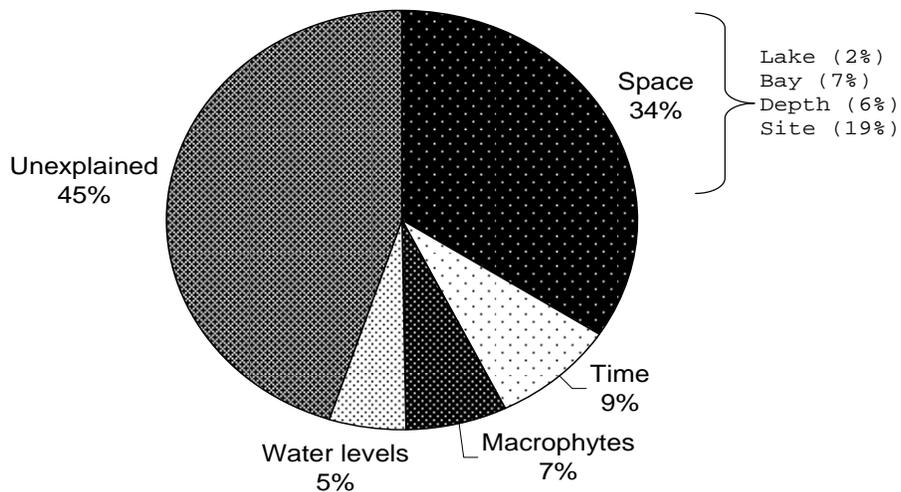
Figure 20. Variance partitioning of high resolution AFTER data set, based on dbRDA. Variance portioning of Space shows conditional variance attributed to each spatial dimension.

0.8

0.6

AMPHIP

0.4

MOLMOL   CHIR
POLCER   ACRI
HELSTA   BAEUND

0.2

CLAT   ERPPUN   minday summ rate   rfll rate
TANT   min wl
SPISID CLIN

summer stable
duration ABLA   max wl
        SMUSCU
PROC   Organic   drwdwn rate
sprng rlse   NILO
                        dewaticedum
CERMAL   Water
DICR CRYT
                    SIALIS
OLIGOC MICP

HEXAGE

-0.2

-0.4

-0.6

-0.8   -0.6   -0.4   -0.2   0   0.2   0.4   0.6
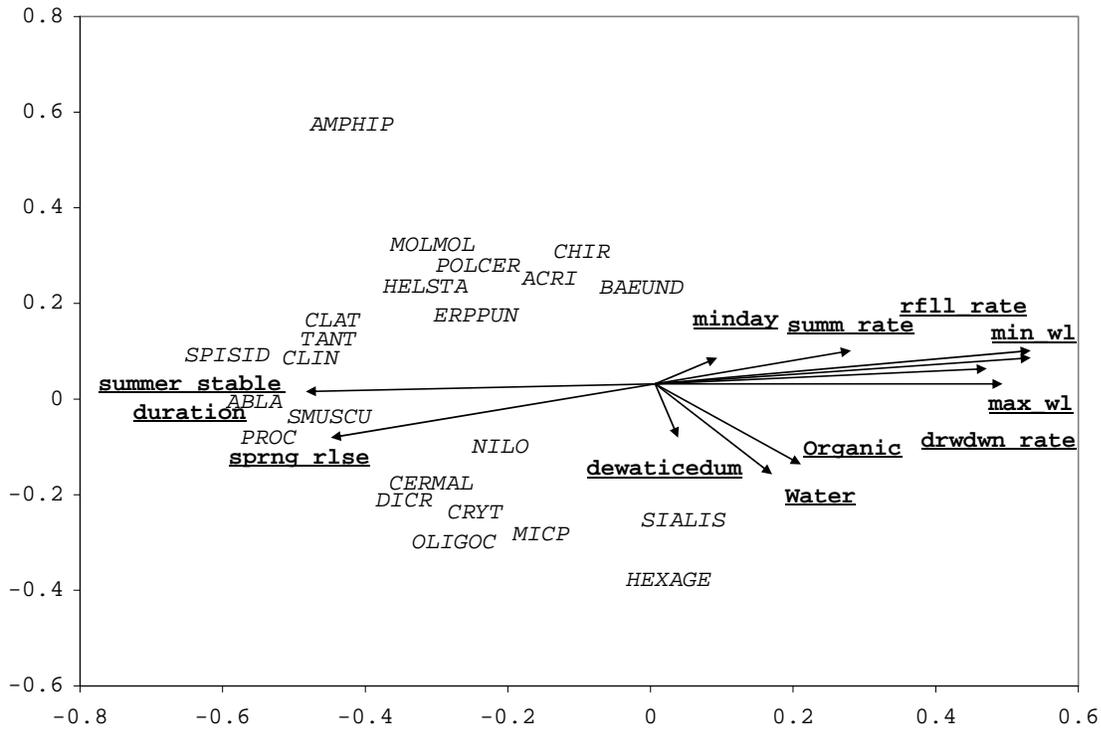
Figure 21. Pearson correlation of taxonomic units and environmental variables with nMDS axes generated from AFTER data set. In order to more easily interpret relationships, we show only taxa whose scaled correlation has an absolute value greater than 1SD from the mean of all taxa. Original site relationships recovered by the nMDS include 42% for the first axis and 28% for the second axis (70% total). Stress on original nMDS was 0.21.

sites with high organic and water content in sediments, while *Chironomus* and several trichopteran taxa were favored in areas with lower organic content. For the nMDS macrophyte plot, we only used data from 2004 and found *Potamogeton foliosis*, overall density, moss, *Elodea, Nuphar, Utricularia, Myriophyllium*, and *Lemna* related most strongly with nMDS axes (Figure 22).
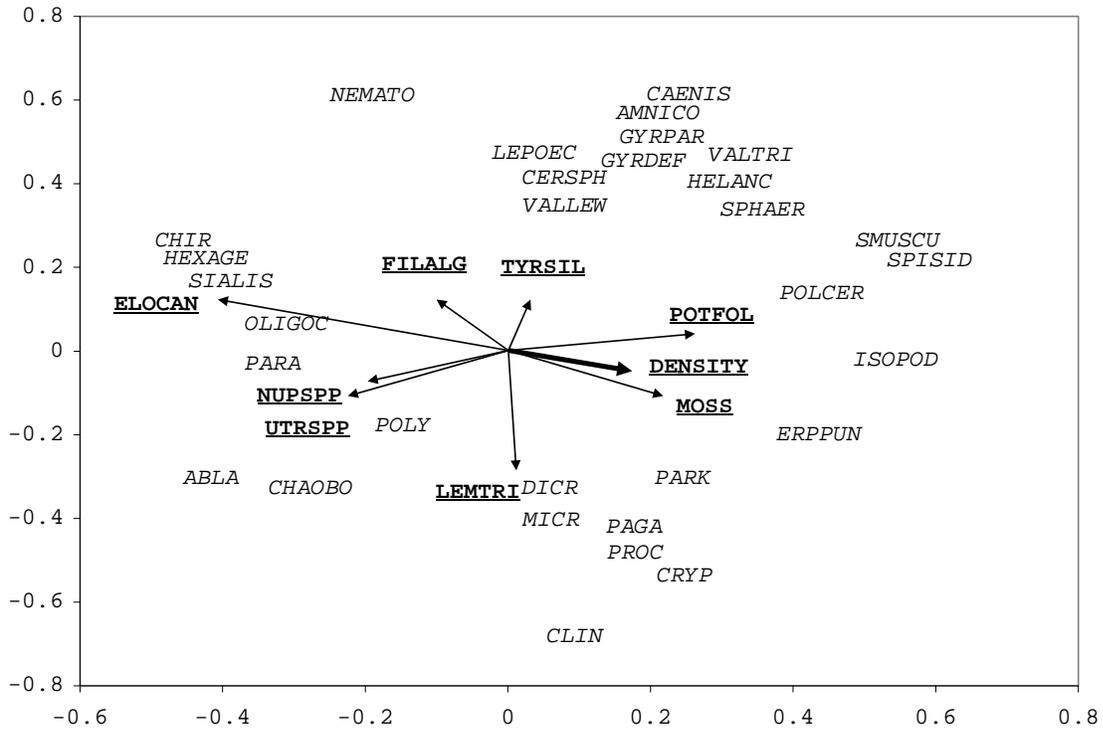
Figure 22. Pearson correlation of taxonomic units and environmental variables with nMDS axes generated from AFTER data set. Original site relationships recovered by the nMDS include 38% for the first axis and 30% for the second axis (68% total). Stress on original nMDS was 0.21. Underlined taxa are macrophytes.

Discussion

Community ecology is a science that suffers from a lack of central theory, such that much of what is known about community assembly and susceptibility to impacts is largely from isolated case studies such as the present research (Simberloff 2004). Biological communities are complex entities that interrelate to a myriad of factors, mostly outside of the control of an experimenter. The underlying presumption of the VOYA research is that macrobenthic invertebrate communities should respond in a predictable manner to alteration of a water-level management regime; however, we really have little theoretical basis for an expectation of how the system should respond. The best we can do is compare to other case studies that have addressed similar questions, including the report by Kraft (1988). We structure this discussion of our results by first summarizing our findings with respect to the hypotheses offered by Kraft in his 1988 report. Following that, we place our findings in the broader context of research conducted on biological communities. Finally, we offer conclusions and recommendations based upon our findings and within the general framework of Hill (1965).

Numerically, the soft-sediment littoral macrobenthos of VOYA is dominated by chironomids – particularly *Procladius*, plus amphipods, oligochaetes, sphaeriid clams, and snails, which together accounted for over 80% of all organisms collected. Chironomids were also the most ubiquitous organisms sampled based on site occupancy from presence/absence data. Other taxa that had high site occupancy percentages were sphaeriid clams, burrowing mayflies (*Hexagenia*), oligochaetes, biting midges (Ceratopogonidae), phantom midges (*Chaoborus*), snails, and amphipods. The basic community structure was thus highly skewed in terms of taxonomic representation, with few taxa comprising most of the numbers at most sites with sporadically-occurring or rare taxa filling out the communities.

The dominant taxa include those that Kraft hypothesized could be the most affected by the severe drawdown in Namakan Reservoir. Such dominant taxa may not necessarily be more strongly affected than less-abundant taxa, but they may serve as good statistical indicators due to their higher abundance than taxa that are found in only a few sites, as conclusions about their relationship to impact might be suspect. Dominant taxa are better candidates for statistical testing as their high numbers tend to lower variance, even though we might suspect rare taxa to have a more sensitive response due to low initial numbers (Cao et al. 1998; Cao et al. 2001).

We raise some questions about the validity of Kraft's analyses, with respect to his statistical methodology and his determination of "impacted taxa." The experimental design used both by Kraft and us has a highly structured error component, where a lack of independence of sampling units needs to be taken into account. We did this by first pooling replicate grabs at each site into a single experimental unit and then using site and time as covariables in a repeated measures design. Kraft, however, treated all grab samples in his analyses as independent replicates, while using nonparametric methods to account for departure from normality. There can be little doubt that repeated samples at a site, repeated samples within a bay, and samples collected within the same sampling period will be non-independent. While nonparametric methods can address deviations from normality, they do not address inherent problems of a lack of independence. The effect of not accounting for non-independent samples is an increase in the type I error rate (i.e., determining there is an effect when there really is none). A correlation factor must be added

in the term for the mean square error when sites are not independent, which was not done by Kraft (Kenny and Judd 1986). Accounting for this lack of independence would likely have led Kraft to different conclusions regarding which taxa were most affected by the magnitude of drawdown. Furthermore, univariate tests of any kind cannot account for interrelationships. Univariate tests and multivariate tests can potentially lead in the opposite direction (Huberty and Morris 1989). For example, univariate tests could show a reduction in the density of a given taxa, but if the whole community is reduced and a particular taxon is reduced less, that taxon would actually be shown to increase. For that reason, while we do provide univariate results to directly test Kraft's hypotheses, we rely mostly on multivariate results for our final conclusions when tests are in disagreement.

In terms of overall densities, between Kraft's survey in the mid-1980s and our recent reassessment, there have been decreases in both Rainy Lake (by 34%) and Namakan Reservoir (by 57%). The greater decrease in Namakan Reservoir indicates that the altered rule curve led to fewer total invertebrates in the reservoir. These results generally agree with findings by Furey et al. (2006), who found lower densities of littoral benthos in a natural lake than in a regulated reservoir sampled at the same time. However, our results are inconsistent with a number of other studies on impacts of water fluctuation on reservoir benthos, where lower benthos densities were reported in regulated waters with more pronounced water-level fluctuations (Nursall 1952; Grimas 1961, 1963, 1965; Paterson and Fernando 1969; Benson and Hudson 1975; Kraft 1988; Richardson et al. 2002; Valdovinos et al. 2007). For example, Grimas (1961) reported that regulation of Lake Blasjon led to density reduction of 70% in the regulated area and 25% elsewhere. Benson and Hudson (1975) reported a three-fold increase in invertebrate abundance in Lake Francis Case, a reservoir in Missouri River system, once annual drawdown was reduced from approximately 10 meters to six meters. Abundance and diversity both decreased in a North Wales reservoir, Llyn Tegid, under a large drawdown, but recovered when drawdown was minimized (Hunt and Jones 1972). We found densities in Namakan Reservoir to be reduced by 23% in relation to the change in the rule curve after taking into account the macroinvertebrate density decreases that occurred in Rainy Lake (i.e., 57% - 34% = 23%).

We suggest critical consideration of the literature on impact studies such as these for three reasons. First, while there is some degree of analogy, none report on manipulations even remotely consistent with the VOYA study, with most evaluating drawdowns of much greater magnitude occurring at different times of the year and in habitats very different from those found at VOYA (i.e., dammed rivers instead of extant lakes). Consequently, broad generalizations about drawdown effects should be avoided unless the underlying mechanistic explanation could plausibly affect the VOYA system in a similar manner. Second, these studies largely presume that there is an underlying stability to population numbers for benthos in these systems. However, most macrobenthic taxa can be expected to exhibit long-term population fluctuations due to climatic regularities, predatory-prey and consumer-resource relationships, and stochastic processes. For example, the chironomid *Tanytarsus gracilentus* in Lake Myvatn, a shallow Icelandic lake, exhibited an approximate 7-year population cycle where larval abundance fluctuated over 4 orders of magnitude. Longer periodicities for insects of decades to over 30 years have also been described, mainly explained by concomitant long-term climatic factors (Cheke 2007). Since a large number of consumer taxa will be limited by shared resources and similar climatic events, it is not difficult to imagine how community-wide densities act in concert

over long periods of time when impacts on basal resources (algae and detritus) cascade to higher level consumers (heterotrophs). The failure of impact-assessment studies to take into account such "extra-impact" factors influencing benthos populations can easily lead to erroneous conclusions. The design of the previously cited studies did not allow an explicit consideration of these extra-impact factors, but ours did. Although we are not able to rigorously quantify the effects of the change in rule curve compared to background or natural changes, we are aware of no other drawdown impact study that takes an approach such as ours, where response variables are differences between paired observations (i.e., Namakan and Rainy Lakes), thus involving a control to detect impact (Stewart-Oaten and Murdoch 1986). Other studies take either a time-series approach within a single impoundment where drawdown is changed during the time series (e.g., Benson and Hudson 1975; Richardson et al. 2002), or compare regulated and unregulated lakes during the same time period (e.g., Grimas 1961). Having both BEFORE and AFTER data on paired systems gave us a unique opportunity to more rigorously evaluate changes in macrobenthos 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 this way we consider the "extra impact" factors and suggest the much lower densities in both systems recently seem to indicate that natural variability in benthos populations has changed since Kraft's study.

Much of the community change over and above the background change was driven by amphipods and chironomids. Amphipods had some of the highest densities in the eulittoral zone under the 1970 rule-curve, without correspondingly high densities in Rainy Lake. For example, Kraft collected 20,566 m^{-2} and 22,059 m^{-2} amphipods in single grab samples at 1m and 2m depths in Moxie Bay during 1985, whereas the highest densities we observed were 5,594 m^{-2}, found at the 1m depth in Moxie during June 2004. These high BEFORE densities caused amphipods to show the greatest change following the 2000 rule-curve, mostly reflecting changes at shallow depths of Moxie Bay but also at Junction Bay (Figure 19). Swanson Bay showed a small increase in amphipods at all depths.

Apparently, amphipods were favored under the more extreme drawdown in Namakan Reservoir. Two amphipod species were present according to Kraft, including *Gammarus lacustris* and *Hyallela azteca*, the latter being the more abundant taxon. Amphipods may persist in stressed habitats due to of a number of life history traits. They are capable of continuous reproduction, unlike many aquatic taxa that reproduce only once per year (Pickard and Benke 1996). Brood size of female amphipods is related to body size, and size is related to ambient temperatures (Cooper 1965). Pickard and Benke (1996) reported that egg development time, egg density, and numbers of young per female all increased with temperature for *Hyalella azteca*. A single *H. azteca* female produces on average 15 broods over 152 days, which roughly corresponds to the ice-free period in VOYA lakes (Embody 1912; Smith 2001). Growth to maturation for these amphipods can occur in as little as 33 days if temperature is sufficiently high and increases dramatically from 98 days to 36 days as the temperature warms from 15 to 20 degrees. Egg production ceases in the winter when temperatures are below 15 degrees (Cooper 1965; Pickard and Benke 1996). Higher water temperatures resulting from shallower water under the 1970 rule-curve could facilitate amphipod dominance.

Amphipod dominance of the macrobenthos is often observed in regulated waters. For example, Furey et al. (2006) found amphipods to occur only in a regulated reservoir, being absent from natural lakes in their study. Fifty years of macroinvertebrate data revealed that downstream macroinvertebrate abundances increased after the implementation of water regulation at Flaming Gorge Dam in northeastern Utah (Vinson 2001). Amphipods dominated during impoundment but were replaced by mayflies when water levels were managed to more closely mimic natural hydrologic regimes. Vinson (2001) found *H. azteca* to be superior competitors with insects and suggested this is because amphipods do not need to leave the water for completion of life cycles, and that while all organisms have life history traits influenced by temperature, their development seems to rely less on temperature compared with insects. Further, amphipods have been shown to consume insect eggs and small instars (Embody 1912; Dick 1996). While this study differs from Vinson (2001), whose main focus was on the downstream instead of the upstream community, given that noted impacts were associated with a change in water levels and temperatures, there should be similar impacts. Vinson (2001) also reviews several studies showing that a decrease of insects and increase in amphipods occurs predictably after the construction of dams.

Chironomids were the next most impacted group of organisms, being much reduced in Namakan's eulittoral zone under the 2000 rule curve. The largest single-site decrease in Namakan was at Moxie one-meter, where chironomid larvae decreased by 3,924 (SE=2,055) m^{-2} following the rule curve change. Lower chironomid densities following the change in Namakan to a more naturally fluctuating water level agrees with findings by Furey et al. (2006), who reported much lower densities of chironomids in a natural lake compared with a regulated reservoir.

Many chironomids are tolerant of highly stressed habitats, having physiological and life-history characteristics that can give them an advantage over many other benthic organisms (Pinder 1986). For example, chironomid pupation is mainly signaled by light, whereas metamorphosis of many other insect taxa seems to be more temperature dependent. This would make chironomids less sensitive to variability in warming regimes during the early spring. In that temperature also has an effect on production, oxygen can become locally or temporally unavailable, yet many chironomids are tolerant of low levels of oxygen because of a form of hemoglobin in their blood that efficiently scavenges available oxygen molecules. Chironomid larvae have been found in areas with no detectable levels of oxygen. We argue that conditions under the 1970-rule curve would have favored higher production from high temperatures from lower water levels, which may have depleted oxygen locally, and hence, favored chironomids. While temperature in the reservoir varies inversely with discharge as cool water flows in (Kallemeyn, personal communication), since inflow to the reservoir was not manipulated in the implementation of the new rule curve, any effect from discharge on the temperature should be additive to changes brought about by the change in water-level management.

Most chironomids are uni- or bivoltine, but it is not unusual for some taxa to have three or four annual generations or continuous recruitment, as has been observed for some Orthocladiinae (Pinder 1986). Smaller-bodied chironomids with r-selected life history strategies have been found to thrive in drawdown zones of regulated lakes (Furey et al. 2006). Organisms that can complete their life cycle during the inundation period might be favored 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 and Paterson (1986).

Due to their strong dispersal abilities, chironomids likely have a competitive advantage in recolonizing winter-exposed areas that are re-inundated in the spring. Compared with 10 other families of aquatic invertebrates in a series of connected ponds, chironomids formed a single, significantly differentiated group with respect to dispersal abilities. Chironomids are able to disperse via aerial colonization, and their larvae migrate within the aquatic habitat by swimming at night (Van de Meutter et al. 2006). For most chironomids, overwintering occurs by building cocoons and can occur at any instar. Chironomids seem not to migrate during falling water levels, which may give them a head start when habitats are re-inundated, and larval populations quickly can become abundant (Pinder 1986).

Following the change in rule curve, there was a reduction in Namakan in the proportion of chironomids at all depths except 5m. In the study by Furey et al. (2006), chironomid diversity was greater directly below the drawdown zone in a reservoir compared to equivalent depths in a natural lake. The reservoir community included genera in the chironomid taxa Orthocladiinae, Chironomini, Tanytarsini, and Tanypodinae while the lake was dominated by Chironomini. Tanytarsini and Orthocladiinae were more prevalent than the Chironomini in regulated areas, probably due to oxygen being higher in the littoral zone – the part of the lake most impacted by water level regulation. Our results are consistent with the Furey et al. study, in that under the 1970 rule curve chironomids at the 3 meter depth in Moxie Bay were more diverse, with the dominant taxa being *Glyptotendipes* (32%), followed by *Procladius* (26%). After the implementation of the 2000 rule curve, chironomids at Moxie 3m were predominantly *Chironomus* (70%).

Spatial effects of drawdown have been well documented, with impacts varying between areas within, versus below, the drawdown zone, areas that approximately correspond to our eulittoral vs. sublittoral zones (Grimas 1961, 1963, 1965; Furey et al. 2006). Organisms within the drawdown zone (i.e., ~ eulittoral) must be able to adapt to pulse disturbance. For our analyses, we expected spatial effects to be greatest at Namakan 2m sites, which were exposed in winter-spring under the 1970 rule curve, but continuously inundated under the 2000 rule curve. To a lesser extent, 1m depths in Namakan remained exposed, but for a shorter time period under the new rule curve relative to the old. Exposure status did not change at other depths. As a result, the eulittoral zone should, and did, change the most.

Lower macroinvertebrate densities in the drawdown zone, following the change in rule curve, likely resulted from the dominance structure of the community. Under the 1970 rule curve, Namakan's shallow littoral zone was dominated by chironomids and amphipods, reflecting a general pattern in regulated water bodies (Grimas 1961; Furey et al. 2006). Such dominance can be linked to higher primary productivity coupled with an unstable habitat. In such circumstances, high populations of a few select taxa, able to cope with the unstable habitat, may develop in the drawdown zone. These animals utilize the available resources and prevent a diverse fauna from developing. Unstable habitats are created by drawdown when shallow sediments are exposed to higher wave energy, and potentially seasonal drying and freezing. Invertebrates better able to adapt physiologically to desiccation and cold temperatures should have a competitive advantage

in sites exposed during winter freeze (Kaster and Jacobi 1978). Taxa that produce desiccation-resistant eggs that can survive in sediments, and then hatch after inundation, could out-compete other taxa (Humphries and Baldwin 2003). Taxa with fast-developing life histories and multiple generations per year should also have a competitive advantage.

Higher density reductions in Namakan Reservoir relative to Rainy Lake since the implementation of the 2000 rule-curve may be related to overall decreases in both autochthonous and allochthonous productivity. Under the more severe drawdown of the 1970 rule curve regime, photosynthetically active radiation in Namakan Reservoir would have penetrated deeper into the water column, allowing phytoplankton and periphyton to be more highly productive. There is a general inverse relationship between phytoplankton and periphyton, and in VOYA lakes the highest phytoplankton biomass, as measured by chl-a, occurs in late July or August (Kepner and Stottlemyer 1988; Vadeboncoeur et al. 2003). Low phytoplankton densities and high light penetration early in the year would allow a large crop of periphyton to develop, serving as an early season resource for invertebrate growth.

Lower mean water levels likely also increased the overall temperature and the speed of warming in Namakan Reservoir, as there was less volume to be heated, thus increasing both the onset and subsequent rate of invertebrate production. Vannote and Sweeney (1980) developed a theoretical construct and provide empirical evidence, suggesting that there is an optimal temperature for any aquatic insect, at which both body size and fecundity are the highest. They argued that synchronous emergence demands that adult tissue maturation occur almost simultaneously in all larvae (size independent) when temperature first exceeds a given critical temperature. They suggested that at high temperatures, maintenance costs rise disproportionately to food assimilation rate leading to lower growth rates, early adult tissue maturation, and decreased adult body size and egg production due to a shorter time for growth. On the other hand, at temperatures below the optimum, there are reduced assimilation rates, but similar allocation to growth and development as at the optimum. This increases the duration of the larval stage and results in lower fecundity because of reduced body size and incomplete conservation of stored materials into eggs at low temperatures. Thus, temperature can have a large influence on a variety of invertebrate life history traits.

Changing the mean water level for the year would be expected to act synergistically with the already high temperature variability in the littoral zones compared to offshore areas. In that these effects are depth dependent, changing the mean water level, especially at critical times of the year, potentially can have large influences on temperatures in the littoral zones of lakes. Coupled with the geothermal equilibrium hypothesis of Vannote and Sweeney (1980), the change in magnitude and timing of drawdown and release potentially has a large structuring influence on the benthic communities in VOYA. Finlay et al. (2001) studied temperature at twenty-three different sites in four basins throughout the spring season in Lake Opeongo, Ontario, Canada. They found spatial variability to be only 2-4°C on average, but as high as 15°C during the same sampling period. Differential heating-cooling occurs between inshore and offshore areas, which causes convective heat currents.

Nutrient dynamics are probably being affected by the change in drawdown as well. Phosphorus, a limiting nutrient, can be made available (up to 70-fold) by drawdown exposure relative to continuously-inundated areas, especially in exposed zones that freeze (Klotz and Linn 2001). The phosphorus made available comes from the death of microorganisms killed by drying and freezing. It is difficult to determine whether or not this has occurred as a result of the rule curve because its effect was not directly measured. Measurements of total phosphorus (TP) from the water column may not reflect processes occurring in the benthos or the water-sediment interface. In other words, as phosphorus becomes available, organisms use it and it becomes part of the community pool, thus the released phosphorus is not sampled in pelagic components of the lake.

Additionally, with greater drawdown there is potentially more input of allochthonous materials, as inundation pulses during spring infilling produce more energy over a larger area of the shore, displacing course woody debris (CWD) along with leaf litter and other organics into the littoral zone. Litterfall and CWD can make near-shore habitats more productive for invertebrates. Greater areas of inundation resulting from drawdown and re-flooding may stimulate nutrient regeneration in riparian habitats that in turn, through litterfall, affect littoral communities (Schindler and Scheuerell 2002). Impoundment productivity can have a structuring effect on the littoral fauna. For example, Ephemeroptera and Odonata have been shown to decrease in impoundments where primary productivity is high, while Chironomidae increase (Michaletz et al. 2005). All these reasons give a plausible explanation as to why there were higher densities in the shallows of Namakan Reservoir under the old relative to the new rule curve.

Taking all these factors into account, a possible scenario for the observed change in amphipod and chironomids dominance is this: Under the old rule curve, newly-inundated habitat in the eulittoral zone warmed sooner in the spring allowing amphipods and chironomids to reproduce sooner and efficiently exploit the pulse of new algal production before other taxa could invade. Reduced winter drawdown could have broken chironomid/amphipod dominance in shallow zones of Namakan by decreasing primary productivity and temperatures, while at the same time increasing habitat heterogeneity and producing refuges for less-opportunistic taxa.

Chironomids and amphipods are likely being replaced by larger-bodied insects as well as non-insect taxa. Several trichopteran genera showed increased densities in the eulittoral after the rule curve change, including *Cernotina* and other members of the families Polycentropopidae, Leptoceridae, Molannidae, and Phryganeidae. Such large-bodied invertebrates also did well in other drawdown studies under either natural conditions or where drawdown was reduced (e.g., Grimas 1961, 1963, 1965). 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. Theory suggests that extinction is not a random process, and that higher trophic levels should be most impacted due to lower numbers, slower population growth rates, and more limited geographic range (Duffy 2002).

Non-insect taxa increased in relative density since the change in rule curve. These invertebrates are less mobile than most insects and thus may be at greater risk of exposure in the drawdown zone. Recovery by populations of non-insect taxa suggests that conditions are less harsh in the formerly exposed area under the 2000 rule curve. Our ordination showed that community structure in Namakan changed under the 2000 rule curve to favor non-insect taxa. Most of these responses were for gastropod and oligochaete taxa, and in a more localized case, sphaeriid clams, which increased only at Swanson one-meter. Kraft suggested that gastropods were negatively impacted by the more severe drawdown in Namakan, which generally agrees with our findings.

Some research has demonstrated that invertebrate densities below the drawdown zone (i.e., sublittoral) are higher than within the drawdown zone (i.e., eulittoral) of regulated reservoirs (Grimas 1961, 1963, 1965; Furey et al. 2006). Mechanistically, this deeper fauna may benefit from greater water-level fluctuation via the removal of fine sediments and organic materials from exposed areas, with transport to areas within the sublittoral (Cyr 1998). Sediment focusing happens when wave energy mixes and suspends littoral zone sediments, where heavier, coarser particles settle at a higher rate. Finer sediments remain suspended until they reach a zone where wave energy is below a critical threshold where they are deposited (Cyr 1998; Furey et al. 2004). This general process leads to a redistribution of lake sediments, with larger particle sizes at shallower depths. The sublittoral zone can also be affected by changes in light zonation, where lower mean water levels increase productivity via greater light penetration (Palomaki 1994; Hecky and Hesslein 1995).

While overall macrobenthos densities did decrease in the sublittoral, non-insect taxa increased most in the sublittoral, with oligochaetes leading the way, followed by gastropods and sphaeriid clams. While there was a general decrease in *Hexagenia* in the sublittoral (except at Moxie four-meter and five-meter depths), *Hexagenia* and *Chaoborus* were the only insect taxa showing overall density increases. Increases in these taxa replaced high densities of chironomids occurring in these zones during the 1970 rule curve. We also note a general change in the diversity of genera within the Chironomidae. Some taxa may be responding to shifts of the depositional zone, resulting from changes in rates and coverage of sediment focusing, altering the location where fine sediments and organic matter are being concentrated. For example, substrate type and volume influence gastropod diversity, with snails showing a preference for substrates of allochthonous organic materials. *Hexagenia* nymphs burrow into the sediment and show a preference for sandy or silty substrate. Burrowing taxa like *Hexagenia* may be aided by the deposition of soft sediments, providing greater availability of suitable substrate (Benson and Hudson 1975). Oligochaetes also are often associated with sediment of high organic content (Smith 2001; Thorp and Covich 2001).

We were unable to find evidence that the ratio of invertebrate densities in June relative to August increased. Kraft reported differences in Namakan Reservoir relative to Rainy Lake in terms of this ratio, suggesting that low June:August ratios were a result of high mortality of invertebrates over the winter. While Kraft reported stranding and death in some insects during the winter, it is unclear how he determined mortality, and his observations were limited. Olsson (1981) directly studied the impact of exposure and freezing on a benthic community both in the field and laboratory. He collected frozen substrate from a large, slowly moving river during the winter and allowed it to thaw for a period of two weeks. All invertebrates had a recovery of 82% to 100%

except the isopod *Asellus aquaticus,* which had a survival rate of only 2%. This may in part be the reason that isopods are not found in Namakan Reservoir. They may have been susceptible to exposure in the past and have not yet dispersed to Namakan from Rainy Lake. He also directly investigated mechanisms by which animals resisted mortality during the winter. Some snails formed an epiphragm, a thin closure of the shell aperture, during winter, something found in terrestrial snails during drought. Oligochaetes were able to form dehydration resistant cysts in which they remained coiled up. Trichopterans had closed their cases during the winter even though they were not in pupal or prepupal stages. Chironomids lay tightly coiled in winter cocoons. Olsson suggested that mayflies, stoneflies, and amphipods avoided freezing by moving to more moderate temperatures in the water body, as they were well represented in the summer littoral but completely absent from frozen samples in the winter. Apparently there is microhabitat that increases the survivability of some invertebrates over the winter. Olsson found that in many cases animals were aggregated in areas of thick ice, suggesting an attraction to depressions in the river bank. Other researchers have shown that some invertebrates have the ability to supercool to survive overwintering (Voituron and Mouquet 2002). In any respect, we think that Kraft may have overstated the impact of invertebrate stranding/exposure, and that the larger impact of the change in the rule curve came from the earlier refilling of Namakan Reservoir.

We did not detect any large patterns of changes in species richness (i.e., number of species), but did find increases in the littoral for both Shannon-Weiner index and the Evenness index. Kraft measured the Shannon-Weiner index and found there to be a large difference in Namakan Reservoir one, two, and three-meter depths compared to Rainy Lake. The Shannon-Weiner index is a measure of dominance, taking into account both the richness and the evenness of taxonomic units. While we did calculate this statistic, its interpretation is more difficult than simple species richness. The Shannon-Weiner index had its basis in information theory, and the score reflects the information in a sample, relative to a random sample from a particular area. High index values indicate less information, and thus greater diversity, but the actual scores are difficult to interpret. These results suggest that the community has become more evenly distributed with respect to taxa, which generally agrees with the finding that Namakan Reservoir under the 1970 rule-curve could be characterized by amphipod and chironomid dominance. Dominance by a single taxon, or few taxa, is typical of managed reservoirs (Hecky et al. 1984).

There are different types of diversity, and just because taxonomic richness is similar does not mean that the composition of the community did not change. In fact, results from our ordinations, at least in the eulittoral zone of Namakan Reservoir, suggest that community structure did change. In other words, the same number of taxa could have been present, but the organisms and distributions and relative densities did differ. Diversity can occur as species richness, as functional diversity, and as trophic diversity.

Kraft identified six taxa he believed to be of primary importance in monitoring effects of drawdown in these systems. While Kraft found that chironomids were abundant in the most severely drawn-down system, he listed six other taxa that were affected negatively to some extent by the more severe drawdown in Namakan Reservoir: *Asellus, Caenis, Chaoborus,* gastropods, *Hexagenia* and *Sialis*.

With respect to the eulittoral zone, univariate tests support Kraft's hypotheses only with respect to chironomids, in that chironomid larvae were much reduced under the 2000 rule-curve in Namakan Reservoir. There is suggestive evidence that *Chaoborus* and gastropods responded favorably to the change in rule curve, but there is no statistical significance for this claim. We found amphipods and *Caenis* to have responded in the opposite direction from Kraft's conjectures, having become much reduced in the AFTER, relative to the BEFORE, data sets in Namakan's eulittoral. When considering the nMDS partial plot for the eulittoral zone, we see that the ellipse for Namakan Reservoir moved in the positive direction along both axes, moving toward gastropods, suggesting that the rule curve change favorably affected them. There was a clear negative response by chironomids and *Caenis*, indicated by a general movement of Namakan away from these taxa. Results from the ordination for other taxa are inconclusive in that movements along the axes were in opposite directions, giving conflicting information (e.g., *Hexagenia*, *Sialis*, and *Chaoborus* responded favorably along the ordinate, but unfavorably along the abscissa). The site specific PCA of density differences showed amphipods to be much reduced in Namakan Reservoir's eulittoral, especially in Moxie Bay. Amphipods were not as influential in Junction or Swanson sites, which were more influenced by chironomids and oligochaetes. Indicator species analysis showed chironomids and *Caenis* to be indicators of the 1970 rule curve, suggesting that they had become a less important part of the Namakan community after the rule-curve change.

With respect to the sublittoral zone, univariate tests showed reductions in *Caenis* and chironomids in Namakan Reservoir compared with Rainy Lake. We also saw a reduction in the mean number of *Sialis*, although not sufficiently large to give a significant result. We saw apparent higher reductions of *Hexagenia* in Rainy Lake relative to Namakan Reservoir. The partial nMDS plot of the sublittoral showed movement of Namakan sites only along the first axis, indicating that amphipods, gastropods, chironomids, *Caenis*, and *Chaoborus* may not have been as important a part of the sublittoral community in Namakan after the change in the rule curve. From the site specific PCA plot, the sublittoral zone of Junction appeared to become enriched in chironomids and oligochaetes under the new curve relative to the old.

Kraft suggested that the isopod *Asellus* was the taxon most affected by drawdown, being entirely absent in Namakan, yet present in Rainy Lake samples. We found no strong evidence to suggest that isopods have colonized Namakan sites in response to the change in the rule curve, although we do report a single individual at the four-meter depth of Moxie Bay. However, we suspect the determination of that specimen may be in error, as isopods are not typically found at depths greater than one meter. Claims based on the absence of a taxonomic group (as opposed to its presence) ought to be critically considered, even though Kraft may have been correct in attributing the absence of this taxon to extreme drawdown. For example, habitat may be suitable in Namakan, but since *Asellus* is a poor disperser, stochastic factors may not have favored re-establishment of *Asellus* upstream in Namakan Lake. Isopods have no diapause stage or other adaptations to avoid desiccation, nor adaptations for transport by wind or phoresy; thus the probability of passive dispersal is low. With so little ability to actively disperse, isopod populations remain locally aggregated (Thorp and Covich 2001). Thus, Namakan Reservoir may lack isopod populations, despite the rule curve changes, because they have not yet arrived.

The overall response of the benthic community in concert with the recent rule-curve change supports Kraft's general hypothesis that the eulittoral zone in Namakan Reservoir was most highly affected by the 1970 rule-curve regime although our analyses did not place three-meter depths within this group as did Kraft's. Results of our BACI db-RDA did indicate that the eulittoral macrobenthos of Namakan Reservoir and Rainy Lake became more similar after the implementation of the 2000 rule-curve. Furthermore, our site-specific PCA on the community differences before and after the implementation of the 2000 rule curve indicated that sites at Moxie one and two-meters, Junction one and two-meters and Swanson two meters-changed the most since Kraft's study, and that these changes were largely due to reductions in numbers of amphipods and chironomids. There was not a similar change at the one and two-meter depths of Rainy Lake.

Swanson one-meter depth was the only Namakan eulittoral site under three-meters in depth not changing as predicted by Kraft. Change at the other eulittoral sites in Namakan was largely due to decreased abundance of chironomids. This did not occur at Swanson 1m depth, where Kraft found chironomid densities averaging 3535 larvae m^{-2} (SE=989) under the 1970 rule curve, while we found 3,310 larvae m^{-2} (SE=1,839) under the 2000 rule curve. At Swanson two-meter depths, chironomid density dropped from 3,811 m^{-2} (SE=2,130) to 944 m^{-2} (SE=237). It appears that Swanson 1m is a particularly high quality habitat for chironomids, and maintained overall high chironomid densities even after the change in the rule curve.

Our regression analyses indicate that minimum water level is not the most important variable impacting benthic communities in terms of the rule curve, but that a greater effect comes from the timing of spring release. The latter phenomenon explained more variance in macrobenthos densities and diversity. Coupled with the inconclusive results from statistical tests, we suggest that drawdown *per se* has a minimal direct effect on mortality, and that the greater response comes from the altered timing of the drawdown and the differential distribution of sediments as a result of wave action in the littoral zone.

Changes in community structure can have important ecosystem impacts in terms of the flow of energy and cycling of nutrients. High redundancy via diversity within functional feeding groups promotes stability in terms of ecosystem-wide processes (Duffy 2002). Functional diversity includes not only trophic relationships but also sediment movement. For example, chironomids, isopods, and oligochaetes affect the influx of oxygen into or out of sediment in various ways (Mermillod-Blondin et al. 2001). Chironomids and isopods move oxygen into sediments and decrease microbial activity, while oligochaetes do the opposite. Chironomids drive sediments downward; isopods homogenize sediments, and oligochaetes mix them throughout. These activities can have important consequences for redox conditions and the availability of nutrients.

Beneficial impacts in VOYA from restored macrophyte communities have been suggested as a possible mechanism for increasing littoral zone invertebrates (Wilcox and Meeker 1992). We found plant communities in the drawdown zone to have a strong structuring effect for many chironomid genera and amphipods. While feeding by freshwater invertebrates on live macrophyte tissue is extremely rare, plants do provide an important refuge from predators and a substrate for periphyton, as well as an important food source when they senesce (Newman 1991). Our ordination suggested that chironomids were most associated with *Potamogeton* species, and

amphipods were associated with *Nymphacea*, *Potamogeton spiralous*, and *Elodea canadensis*. If we consider chironomids and amphipods to be indicators of a stressed system, one might investigate whether plant taxa related to other invertebrate taxa, such as *Valliseneria*, *Zizania*, *Utricularia*, *Ceratophyllum*, *Lemna*, filamentous algae, and moss, have developed since the implementation of reduced drawdown.

Our results are consistent with other research showing strong relationships between invertebrates and macrophyte communities. For example, invertebrate abundance in a Wisconsin lake was compared in two contrasting plant beds, *Ceratophyllum demersum* and *Potamogeton nodosus,* as well as in open-water zones (Beckett et al. 1991). Overall benthic densities were up to 13 times higher in plant beds relative to open areas in the littoral zone. Gastropods were as much as 162 times more abundant in *Ceratophyllum* beds, where chironomids also predominated, while oligochaetes were found equally in both beds. No taxon was shown to prefer open-water habitats. There is some evidence that invertebrates preferentially choose some plant taxa over others. Abundance of a majority of benthic invertebrate taxa has been related to the overall abundance of macrophytes (Cyr and Downing 1988). Rooted macrophytes get most of their nutrients from sediments, whereas periphyton and phytoplankton compete for nutrients in the water; thus, macrophytes can benefit benthic communities indirectly by moving nutrients from the sediments, which eventually become available to invertebrates when the macrophytes die (Schindler and Scheuerell 2002).

Apparent overall reduction of macrobenthos in both systems may be confounded by an underestimation of total benthos by not adequately sampling the epiphytic fauna on macrophytes. There is no reason to suspect that Kraft did a better job of sampling epiphytic fauna than did we; however, if under the 1970 rule curve there were fewer macrophytes, given the same sampling effort, our samples would have been biased more low because we would have missed a higher proportion of total invertebrates given they would have been comprised of epiphytic fauna in comparison with Kraft's sampling. An appropriate, albeit more labor-intensive, method to sample macroinvertebrates associated with macrophytes would be by collecting macrophytes whole and rinsing macroinvertebrates from the plants. After drying and weighing both invertebrates and macrophytes, invertebrates per unit mass of macrophyte could be calculated. By regression, Rasmussen (1988) showed that as macrophyte biomass increased from 0 to 2.8 kg/m^2, the proportion of littoral zone benthos as a total decreased from 100% to less than 20%. If we had estimates for macroinvertebrate biomass on plants BEFORE or AFTER, it might be possible to use this regression to produce a correction factor to mitigate some of the bias from underrepresented invertebrates. The equation he gives is:

$$Arc\sin\left(\sqrt{P}\right) = 1.572 - 0.7518MB \qquad\qquad\text{[Eq. 5]}$$

where *P* is the proportion of littoral zoobenthos in the sediment and MB is macrophyte biomass (kg/m^2) (R^2=0.91, SE = 0.082). If macrophyte biomass estimates are similar between the two systems, then the bias becomes less important, but if there is a large difference, then estimates could be highly biased.

In a review of ecosystem effects on aquatic communities of Rainy Lake and Namakan Reservoir, Kitchell and Koshinsky (2002) discussed the need for data on macroinvertebrates to be tied more directly to the fisheries in VOYA. Evaluation of macroinvertebrate communities in the context of fisheries is important for two primary reasons. First, macroinvertebrates provide a food source, either directly or indirectly, to fish species of concern. Second, fish populations are relatively variable from year to year, and precise determinations of the success of the altered rule curves with respect to fish will be difficult to ascertain directly. However, changes in invertebrate populations have been predicted to quickly show any fish-related benefits derived from changing the rule curves. If no immediate benefit is seen for invertebrate populations, managers may infer that no benefit due to benthic prey has been passed along to the fish communities, even though fish may be positively impacted by other consequences of the rule-curve change (e.g., increased macrophyte beds necessary for spawning).

In general, greater drawdowns lead to a reduction in large-bodied organisms relative to smaller ones (Grimas 1963; Furey et al. 2006). We would expect fish to benefit from higher densities of larger-bodied, more mobile taxa relative to small-bodied, inconspicuous taxa. For example, in mesocosm experiments in the Canadian Experimental Lakes Area, pike fed preferentially on leeches and odonates which were largely eliminated, while less conspicuous taxa such as dipterans and caddisflies increased (Venturelli and Tonn 2005). Other evidence for fish preferring large-bodied taxa comes from research showing that fish can alter the size spectrum of macroinvertebrates (Blumenshine and Lodge 2000; Zimmer et al. 2001). An increase in larger-bodied invertebrates means that fish need to exert less energy in locating prey and feeding, and can spend more time on other life history efforts (e.g., growth and reproduction).

Further, if valuable prey species are patchy, fish will forage selectively in those sites that provide a rich source of energy. When their preferred prey is decimated, fish often turn to benthic energy sources, which are quantitatively more important than pelagic sources to fish (Schindler and Scheuerell 2002). In this sense, benthos help stabilize aquatic food webs. Schindler and Scheuerell (2002) suggest that benthic-pelagic linkages in most lake ecosystems involve a net flux of nutrients and energy from benthic habitats into the pelagic environment, largely facilitated by the relationship between fish and benthic invertebrates.

It is important to note that benthic community dynamics do not occur in a vacuum, but are part of an integrated lake system, acting and reacting to conditions and organisms across all trophic levels (Vander Zanden and Vadeboncoeur 2002). For example, while it looks as if macroinvertebrate density in Namakan Reservoir has decreased relative to Rainy Lake, it may be that production is just as high or higher, but is being utilized by predators such as fish. One of the driving factors behind adoption of the new rule curve was to increase fisheries, in part by fostering better conditions for recruitment. If stronger fish year classes have resulted from the change in the rule curve, and production of these fish has increased in Namakan relative to Rainy, it may be that a larger portion of invertebrate production is being utilized as food. In such a case, our measured densities could be underestimating benthic productivity. Response of the fisheries, as well as the other water-level components, will be a critical component in putting this present study in the correct context.

We now turn to a brief discussion of the current theoretical framework of community ecology as it relates to potential impacts in a community so that we can better argue that the change in rule curve produced some of the changes we observed that correlated with it. We reiterate that much of this theory is not well supported by empirical testing, even though there is circumstantial evidence to suggest that some of these mechanisms may be at work in community assembly.

Skewed frequency distributions of benthic organisms are typically seen in aquatic habitats. Why various taxa are not more equally represented in ecological communities has been long debated. and explanatory theories generally fall into two categories: neutral theory versus niche theory (Tilman 1982; Hubbell 1997). Neutral theory suggests that all taxa within a system should be considered as members of metacommunities, which might be thought of as patches within the lake. Within a trophic level, the composition of the overall community will remain relatively stable over time because it reflects the general make up of all component metacommunities at large. Over time, communities will change at random by ecological drift as individual taxa come and go. It is not that resource portioning does not occur, only that the effect of resource portioning is swamped by neutral ecological drift. This view is satisfactory if all taxa are considered to be equally competitive on all resources. Ecological impacts can be seen as events that drive the "evolution" of communities at a higher rate. This is because ecological drift is likely to occur at a higher rate when recolonization must occur frequently, even though changes in community structure may be very small.

The neutral theory of ecology ignores niche partitioning, in which community structure is thought to result from the competitive abilities of organisms. According to niche theory, taxa that are most adept at exploiting a given resource will be expected to occur at higher relative densities than less-competitive taxa. Niche theory and resource portioning predict that taxa vary in their abilities to utilize resources, thus under stable circumstances with a single limiting resource, the top competitor should out-compete all others, potentially leading to the extirpation of all other taxa. It is clear, however, that communities rarely devolve to a monospecific assemblage, and a set of supporting theories attempts to show why this is the case.

At least one recent paper has attempted to merge neutral and niche theories into a unified view in which taxon arrival is a neutral process, but niche portioning occurs once a species appears (Uriarte and Reeve 2003). One of the major contributions of this blended theory is the role of history in structuring a community, which has important implications for the present study. If something akin to the neutral theory is actually controlling community composition, then we should not expect to see widespread effects of environmental change on the benthic community, at short time scales, because differential niche advantages are slight.

Several competing ideas have been offered to explain how diversity is maintained in a community, if something akin to the niche partitioning is real. These ideas can be generally divided into two large categories: equilibrium explanations and nonequilibrium explanations (see Morin 1999 and references therein). By equilibrium explanations, we mean those that assume a given community do not depart from a single "basin of attraction" over time. That is, despite sources of variance, there is some stable global form to the overall biomass of a community. Those researchers who prefer nonequilibrium ideas consider it unlikely that community biomass ever approximates a state of global stability. Instead, nonequilibrium theory holds that

community biomass cycles through alternative stable states (i.e., varying configurations of local stability) or tends towards chaos in being inherently unpredictable from year to year (May 1974).

Most researchers agree that communities do not tend toward a global equilibrium, rather that community assembly occurs through other mechanisms than those mentioned above. Perhaps the most well-known explanation for nonequilibrium community structure is that of a gradually changing environment where multiple resources become limiting at different times. Hutchinson's resolution to his "paradox of the plankton" was that gradually changing environments prevented a single taxon from supplanting all others. Certainly in aquatic systems, with constant waxing and waning of variables like temperature and nutrient dynamics, which are likely influenced by water levels, this mechanism must be important.

Another way that benthos may be affected is through the storage effect (Warner and Chesson 1985). Carpenter (1988) suggested that there is periodicity transmitted through trophic levels of a lake that roughly correspond with the life cycle of the major piscivores in a lake. Variability in environmental conditions permits successful reproduction by long-lived animals only periodically. This "storage effect" allows organisms like fish to "store" the ability to reproduce until conditions are appropriate. For other organisms (many invertebrates), dormant stages can have the same effect. When certain favorable conditions coincide, large year classes of fish can be produced. During those years benthos may be highly impacted by fish predation, since a larger proportion of benthos is preyed upon by young-of-the year fishes (Mittelbach and Persson 1998). Should similar predator-prey dynamics be in effect for the VOYA system, responses by the benthos may be contingent on a synergy between year class strength in fish, water level variation, and probably climatic conditions.

Another ecological concept that directly relates to the VOYA study is the "intermediate disturbance hypothesis" (Connell and Slatyer 1977). This idea suggests that disturbance of an appropriate sort maintains diversity by preventing competitively dominant species from excluding others. Weak or infrequent disturbances are insufficient to alter the progress of competitive exclusion, and diversity declines. Intense or frequent disturbances so disrupt the community that species are actively excluded, leading to reduced diversity through the loss of particularly sensitive species. At some intermediate level, disturbance can promote the highest diversity by permitting frequent invasion/establishment of poor competitors with good dispersal, while not eradicating all species that thrive under more stable conditions.

Finally, we consider Hecky et al. (1984), who developed what they termed the "reservoir paradigm." Their study of Southern Indian Lake in northern Manitoba is especially pertinent for this VOYA study, since it is an example of an extant lake being turned into a reservoir, not the typical case of a river being dammed. They suggest that the major impact of converting a lake to a reservoir is shoreline erosion. The effect of shoreline erosion is to increase nutrients due to leaching from flooded soils and the decay of vegetation, leading to possible deoxygenation in shallow vegetated areas. While these factors were not directly assessed in the present study, dominance by chironomids in Namakan Reservoir prior to the change in the rule curve is suggestive that low levels of oxygen did occur in the shallows, which may have been the result of higher impacts on shorelines due to erosion. They also predicted overall decreases in benthos near eroding shorelines and in the sublittoral, but initial increase in productivity elsewhere. We

are unsure how erosion may have impacted benthic communities because we did not directly monitor it, but our results do agree that productivity was higher under the more severe drawdown in Namakan Reservoir. Sediments are suspended in the eulittoral and deposited offshore in the sublittoral. In their view, this redistribution of sediment has a negative impact on productivity of sublittoral invertebrates, linked to decreased phytoplankton production. We did find increased community instability in the sublittoral zone of Namakan after the change in the rule curve which seems to indicate that the more severe drawdown benefited offshore communities. Many of these organisms depend on fine sediments for burrowing, and we expect that higher rates of sediment focusing actually helps, not hurts, the sublittoral community. Phytoplankton production suffered from higher light attenuation caused by suspended materials, despite increased nutrient influx. The reservoir paradigm predicts an initial influx of nutrients, and increased productivity in all biotic components as a result. While we did not measuring production directly, we did find much lower densities, which would be in line with an overall reduction in production, but some of this reduction is due to background variability, evidenced from the lower densities in both Rainy Lake and Namakan Reservoir. When the mean depth of the lake increases, the temperature of the lake is affected as incoming heat is diluted. Newly inundated areas in Southern Indian Lake generally were first colonized by Chironomidae, followed by Oligochaeta and Mollusca, with dominance by a single taxonomic group as the rule. *Hexagenia* declined, amphipods increased, and sphaeriid clams remained unchanged in response to the damming of Southern Indian Lake and subsequent high rates of shore erosion (Rosenberg et al. 1986). Thus, while we found some similarities and agreement with the reservoir paradigm as provided by Hecky et al. (1984), there were some inconsistencies. Any attempt to determine exact causes of a response by benthos to a particular impact will depend on the theoretical context.

Conclusions

In conclusion, we have been able to tease apart the apparent major impacts to the benthic invertebrate communities of the VOYA large lake systems, related to the change in rule curves that began in January 2000. At the onset, our specific objectives were to answer the following list of questions with respect to this change. All of the following changes occurred in Namakan Reservoir. With the noted exceptions, changes in Rainy Lake were neither simultaneous, nor of the same magnitude.

1. **Has the structure of the community been affected in terms of taxonomic composition, site occupancy or relative densities?** Yes, in all respects. Communities have changed from domination by amphipods and chironomids, to include a greater contribution by larger-bodied insects plus non-insect taxa.

2. **Has there been a change in the June:August ratio of macrobenthos density for individual taxa?** No, we found no evidence to suggest that this ratio has changed since the Kraft study, in Namakan Reservoir in a different way than it did in Rainy Lake.

3. **Is there an interaction between depth and the change in water-level management?** Yes, we found evidence indicating that the one meter and two meter depths of Namakan Reservoir changed the most. This differs from Kraft's hypothesis that the three-meters depth should be included among the most-impacted sites.

4. **Which sites have shown the greatest amount of relative change?** All of the Namakan Reservoir sites at one-meter and two-meter depths (i.e.. M1, M2, J1, J2, and S2) with the exception of Swanson at two meters (S2).

5. **Which taxa have shown the greatest amount of relative change?** Amphipods and chironomids have both become much reduced in the eulittoral of Namakan Reservoir relative to Rainy Lake since the implementation of the new rule curve.

6. **Have overall benthic invertebrate density or diversity been affected?** Yes, overall density was reduced in both Namakan Reservoir and Rainy Lake but to a much greater degree in Namakan Reservoir since the implementation of the new rule curve. No, diversity in terms of species richness has not changed; however, there is some evidence to suggest that the Shannon-Weiner diversity index has increased in the eulittoral of Namakan Reservoir relative to Rainy Lake. However, interpretation of this index is problematic.

7. **Has the overall ratio of numbers of invertebrates in June relative to August been affected?** No, we found no evidence to suggest that the overall number of invertebrates in June relative to August is any different than it was before.

8. **Has the "stability" of communities changed in concert with the rule-curve change?** Maybe - we found no evidence of a change in stability for the eulittoral in Namakan Reservoir, but the sublittoral in Namakan became slightly less stable since the implementation of the 2000 rule curve.

9. **Have the abundance, density, and/or relative abundance of key taxa, identified by Kraft as being sensitive to water level regulations, been affected?** Yes and no - *Hexagenia*, gastropods, and *Sialis* showed evidence of higher numbers as predicted. *Caenis* responded in the opposite way as predicted (becoming less abundant), while isopods were unchanged. Chironomids responded as predicted by becoming less abundant.

10. **Which water-level variables are most closely associated with the structure of the benthic invertebrate community in VOYA?** Critical variables include the annual minimum and maximum water levels, the rates of winter drawdown and spring refill, the duration of the summer period of stability, and the Julian date when the reservoir begins refilling. Of the water-level variables manipulated and addressed by this study, the day by which the reservoir was refilled to capacity in the spring had a stronger structuring influence than did the magnitude of the actual drawdown.

As discussed above, the nature of this experimental design precludes our making *causal* claims about these changes being related directly to the change in water level management on *statistical* grounds. However, we can argue for causation on *logical* grounds, given that we have found sufficient evidence to suggest that there was a *correlative* response in the VOYA systems to the change in the rule curve. Here we summarize our arguments within the context of Hill's (1965) "criteria for causation."

Hill's first and second criteria are *strength* and *consistency*, respectively. With respect to the first criterion, *strength*, we note that while there are changes that have occurred since Kraft's 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 Namakan Reservoir relative to Rainy Lake. The criterion of *strength* suggests that a large proportion of individuals are affected in the exposed areas (i.e., Namakan eulittoral) relative to reference areas (i.e., Rainy Lake and, to a lesser extent, Namakan sublittoral). The second criterion, *consistency*, requires that there be similar responses observed by other investigators, at other times and in other places. A large portion of our discussion is devoted to showing how our results are consistent with many aspects of other studies investigating benthic responses to water level management. Where there were inconsistencies with other studies, we address these as well.

The third criterion, *specificity*, means that the effect is diagnostic of the exposure. We argue above that while there is no shortage of hypotheses in community ecology, there is no central, agreed-upon theory providing precise predictions as to what should happen when a water level management regime is changed. We have given a theoretical overview of some of the leading, current ideas in the field regarding impact-type research, but some of these ideas conflict with

one another and thus the issues are unsettled. While we might appeal to theories related to populations in isolation, which are better settled among the scientific community (e.g. exponential growth, temperature effects on birth and death rates, body size and life history traits, etc.), these theories cannot be directly applied to communities since they do not include mechanisms for interactions among populations. Consider as an example "exposure" of benthos to lower temperatures when the average water level is increased - as likely occurred when the drawdown regime was changed in Namakan Reservoir. We might be able to assign a change in a life-history parameter as a diagnostic response to a decrease in temperature (e.g., decreased intrinsic population growth, decreased individual growth rates, etc.). Indeed, we think we did observe such responses in populations of dominant organisms; however, we have no direct measurements of the temperatures these organisms experienced or, more important in a community context, no knowledge of how changes in life-history characteristics are further modified by interactions among populations. Thus, our evidence is circumstantial and suggestive, but not sufficiently clear to say that this criterion has been satisfied.

Hill's 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 true of this study, as time was a designed variable and the changes occurred AFTER versus BEFORE. The *biological gradient* requirement means that the risk of an effect is a function of the magnitude of exposure. Given that organisms in the eulittoral were more affected than those in the sublittoral, we believe we have cause to suggest that there indeed is a gradient of exposure as organisms in shallow areas, which are expected to experience a greater impact, were in fact most influenced. *Biological plausibility*, the sixth criterion, can be related to the effects that changing the water level regime should have on temperature and exposure. Thus, while we failed to rigorously support the specificity criterion, we can appeal to this criterion to suggest that there is plausibility in terms of community-level responses to a change in temperature and exposure from the change in the rule curve regime, especially as it relates to chironomids and amphipods compared with larger-bodied, slower growing invertebrates. We have reviewed the literature, reported on relevant research, and have thus provided evidence to suggest plausibility.

The seventh criterion is *experimental evidence*. While, to our knowledge, no field experiments have been done on communities by manipulating the variables that were potentially at work here, there has been experimental work on the effects of temperature on life history characteristics and on the effects of exposure and freezing on animals, including benthos. These studies are discussed above. Of course the great majority of these studies do suffer from being focused on populations, and not the entire community. Nonetheless, the studies cited in the discussion do give some insights into community-level dynamics.

Analogy, the eighth criterion, means that similar stressors cause similar effects. For this criterion, we can appeal to a number of other studies that investigate impacts of water level management on benthic communities. While these studies do not mimic ours exactly, they are analogous in many ways and report some consistent responses (e.g., the reservoir paradigm). Furthermore, there is much research on thermal effects on aquatic invertebrates related to "thermal pollution" from power plants. It is within this context that the original BACI designs had their genesis. We might also appeal to research on the effects of invertebrates to drought, flooding, "natural" cycles

of productivity in lakes (e.g., alternative-stable-states of shallow lakes), winter deoxygenation, sedimentation caused by shoreline development, and more to investigate how these different types of "exposures" affect macrobenthic communities. Such a comprehensive review of the literature is beyond the scope of the present project, but the references we do cite suggest that benthic communities respond consistently with respect to analogous "treatments."

The final criterion is *coherence*, suggesting that the causal hypothesis does not conflict with existing knowledge of biology or natural history. No responses that we saw were inconsistent with the current state of knowledge about aquatic invertebrate communities. From a natural history perspective, we note that there is a developing paleolimnological literature based on the use of benthic invertebrate remains in sediment cores to trace cycles of water level fluctuation, sometimes over periods of thousands of years. This is suggestive that over long time periods, benthic communities are responsive to water level fluctuation.

Thus, we believe we have a strong case for arguing that the changes we observed in concert with the altered rule curve can reasonably be viewed as cause and effect, having satisfied all but one of Hill's criteria.

Finally, we recommend sampling on a periodic basis in future years, as it certainly is possible that insufficient time has elapsed to produce a more significant response by the benthic community. In the present study, we sampled invertebrates during the fourth and fifth years following the change in the rule curve. Further changes to benthos populations, plus interactions among these organisms and the rest of the lake ecosystem, may generate greater community change over time. Additional studies, as funding is available, should help to determine how sustained are the changes we report and would provide better information about natural variation as well. It would also be prudent to do some sampling in an unconnected water body (e.g., Lac La Croix) should rule curves be changed in the future. An unconnected system would serve as a better "control," even if true replication cannot be achieved. Another, more direct approach for investigating the effect of water level regulation on benthos in these systems, would be to use transplant experiments. Enclosures could be placed at randomly selected coordinates across a spectrum of depths, sites, and lakes. Animals could be interchanged between Namakan Reservoir and Rainy Lake and impacts could be investigated directly on focal taxa by monitoring body size, fecundity, and population parameters (see Freilich, 1989 and references therein for methods of marking benthic organisms).While this type of study would not be a true community level experiment, it would place focal species in the broader context of the environment in which they must interact with other taxa. Environmental studies inherently involve a high degree of variability, and as such the conclusions in this report are made with caution. Further research and monitoring can help to ameliorate some of this uncertainty, but with respect to impact studies, there are indeed "no simple solutions."

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