

Paleolimnological reconstruction of cladoceran community reassembly following
experimental manipulation of two boreal shield lakes.

by

Lynn V. Frazer

A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg, Manitoba, Canada

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Abstract

Documentation of the recovery process from environmental impact can provide insight into the factors that drive community assembly. This study reconstructs the pattern of community reassembly following a perturbation, using cladoceran microfossils. The ability of cladoceran microfossils to indicate biological recovery was also assessed. The whole-lake experimental manipulations of Lake 302N (1972-1997) and Lake 223 (1976-1994) at the Experimental Lakes Area (ELA; Ontario, Canada) provided the opportunity to follow, from the sediment record, the trajectory of, and community state at, recovery. To put the recovery process into context, the trajectory of change, relative to the pre-manipulation state, was also evaluated. Comparison was made to reference Lake 377 (ELA) to estimate baseline conditions and natural community variability. Recovery trajectories were evaluated at both the species- and community-level, using univariate and multivariate metrics. Substantial hysteresis was observed in the recovery trajectories of the littoral and pelagic cladoceran communities. Up to fourteen years after cessation of acid addition, recovery of the Lake 302N and Lake 223 cladoceran communities had occurred not to the pre-manipulation condition, but to a state limited by biological resistance. In addition, a changing baseline appears to be present, with the appearance and increase of *Bosmina* (*Neobosmina*) *tubicen* in recent decades, in both the manipulated and reference lakes. Overall, both local and regional factors remained important in cladoceran community reassembly. Further exploration on the usefulness of cladoceran microfossils as indicators of lake ecosystem recovery is required.

Acknowledgements

I would like to thank my supervisor, Dr. Brenda Hann, for her guidance and support, as well as the fantastic opportunities she gave me throughout my Master's program. Thank you to my committee members, Dr. Mike Paterson and Dr. Lane Graham, for their valuable feedback and advice. Special thanks to Dr. Michael Turner, Ken Beaty and Mark Lyng (Freshwater Institute; Department of Fisheries and Oceans) for providing their expertise on this project. Assistance from Dave Findlay and Alain Dupuis in taking the freeze cores was much appreciated. Dr. Robert Flett provided me with background information on the ^{210}Pb dating and modeling process of the cores, which was completed by Flett Research (Winnipeg, MB). Dr. Dave Walker (University of Manitoba) and Dr. Bob Clarke (Plymouth Marine Laboratory) provided statistical advice. Jill Van Walleggem (Ontario Ministry of Natural Resources - Dryden Area) provided me with information on the historic forestry practices in the Experimental Lakes Area region. This research was funded by an NSERC Canada Graduate Scholarship, Experimental Lakes Area Graduate Fellowship and Dr. Ken Stewart Fish Futures Scholarship to Lynn Frazer, and an NSERC Discovery Grant to Dr. Brenda Hann. Most importantly, I would like to thank Alain Dupuis, my friends and wonderful parents for the love, strength and support they gave me throughout this journey.

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Introduction

Restoration ecology

Stressors, whether natural or anthropogenic, can induce drastic disturbances in community structure. How do communities recover to maintain stability with their environment? In restoration ecology, defining an achievable and appropriate endpoint for the restoration of a community that has been disturbed is a complicated task (Palmer, Ambrose and Poff, 1997). However, there are often legal requirements to have such endpoints defined explicitly (Battarbee *et al.*, 2005). A typical management objective is to return a community to its 'original' condition. Yet communities are dynamic systems, changing and evolving through time even in their natural state. Rather than attempting to restore a community to its 'original' condition, a more appropriate objective may be to return a community to its pre-disturbance condition (Cairns, 1989). Community theory, which describes the successional process as deterministic and leading to a stable climax condition, makes recovery to the pre-disturbance state seem probable (Cairns, 1989; Lockwood and Pimm, 1999). However, changing regional baseline conditions (e.g. climate change, or the invasion of an exotic species) may reduce the feasibility of a return to the pre-disturbance condition in long-term lake restoration efforts (Battarbee *et al.*, 2005).

Hysteresis, a term borrowed from physics (Frost *et al.*, 2006), indicates that the output of the system is not simply the inverse of the input (Scheffer *et al.*, 2001). As the explanatory variable varies cyclically, a system does not necessarily retrace its path (Gutschick and BassiriRad, 2003). In addition to changing baseline conditions, hysteresis implies that a return to the pre-disturbance state may be the exception, rather than the rule

(Power, 1999). Simply removing a stressor does not guarantee a return to the pre-disturbance state. Rather, communities are complex entities; therefore, even slight differences in community succession may lead to different recovery trajectories and different recovery states (O'Neill, 1999). Although the notion of multiple possible recovery states lies at the heart of community assembly theory, few steps have been taken to verify the theory in the realm of restoration ecology (Palmer, Ambrose and Poff, 1997). Following the recovery trajectories and states of a perturbed community first requires an understanding of the natural processes that structure a community (Chase, 2003).

Community assembly

The debate in restoration ecology, regarding the feasibility of a return to the pre-disturbance state, also exists in community assembly theory. Do communities, under similar environmental conditions, assemble to a single stable equilibrium or are multiple stable equilibria possible? Assembly rules are what prevent communities from being a random sample of the regional species pool (Diamond, 1975; Drake, 1990). Diamond (1975) initially proposed that, out of all combinations of species that can be formed from a regional pool, only certain combinations actually exist in nature. The 'rules' that guide the assembly of these combinations include competition, resource utilization, size of the regional species pool and characteristics of the abiotic environment, leading to assembly pathways that are highly deterministic and form a single, stable equilibrium. However, Diamond (1975) found that, even when similarity existed between these variables, communities often developed different structures. Although the species invasion order is

largely determined by chance, the historical order in which species invade is crucial as it guides assembly rules (Drake, 1990, 1991). For example, when initial invaders are given sufficient time to monopolize resources and sustain a faster growth rate, further colonization or dominance by alternative species may be prevented (Drake, 1991).

Known as priority effects, the structure of a community is dependent on the sequence in which it is assembled. This, therefore, leads to stochastic assembly trajectories and multiple stable equilibria, rather than a deterministic assembly trajectory and a single stable equilibrium. These multiple stable states may be persistent or transient, yet without knowledge of the invasion history, one cannot infer the mechanisms (i.e. competition, predation or sequence of assembly) that are responsible for the multiple stable states (Drake, 1991). Rather, Chase (2003) argues that it is better to ask under what conditions multiple stable states, rather than a single state, might occur. For example, communities with high levels of dispersal are more likely to develop to a single state, as there will be insufficient time for priority effects to occur (Robinson and Edgemon, 1988).

Both regional (e.g. rate of dispersal) and local (e.g. interspecific interactions) factors may be important in structuring communities (Havel and Shurin, 2004; Shurin, 2000), as well as guiding a successful restoration (Palmer, Ambrose and Poff, 1997). Communities with low rates of dispersal are more likely to be driven by regional scale processes, where poor dispersal capacity is a regulator of community composition, limiting interspecific interactions in depauperate communities (Jenkins and Buikema, 1998). Communities with high rates of dispersal, on the other hand, are more likely to be driven by local scale processes, by increasing the number of interspecific interactions (i.e. competition, predation) regulating community composition. In addition, as colonizing

species reach a quorum, or saturation of community structure, the relative importance of regional or local factors may shift through time. For example, Jenkins and Buikema (1998), in their study of early species colonization in experimental ponds, found dispersal ability to be the rate-limiting factor in the assembly of zooplankton communities. This led to different community structures being developed in environmentally-similar sites. Shurin (2000), on the other hand, in his study of invasion of permanent (>20 years old) zooplankton communities, found that when the effect of dispersal was controlled among species, interspecific interactions from the local community prevented successful colonization by new invaders. Finally, Louette, Vander Elst and DeMeester (2006), in their study of cladoceran colonization success in newly constructed ponds, observed a transition period after one year from communities regulated by regional factors (e.g. rate of dispersal) to communities that were regulated by local factors (e.g. interspecific interactions), as the community moved to quorum. From experimental ponds (Jenkins and Buikema, 1998) to newly constructed ponds (Louette, Vander Elst and DeMeester, 2006), to permanent ponds (Shurin, 2000), these three experiments demonstrate the shift over time from regional to local factors in regulating community assembly. As communities move towards a quorum over time, there are fewer opportunities to occupy empty niches. Therefore, such communities should be resistant to further invasion (i.e. dispersal at the regional scale) and structure can be further regulated at the local scale.

Interfering with the regional and local scale processes is dispersal limitation (e.g. physical barriers to dispersal, species vagility) and its influence on priority effects (Louette and De Meester, 2007). Dispersal limitation not only influences a species' colonization ability, but also the order in which species assemble. Therefore, although

dispersal exists at the regional scale, when limited it predetermines the timing and importance of local scale processes. The effects of dispersal limitation are often hard to extrapolate from experimentation to that which occurs in the natural environment. For example, in an experimental, three-species cladoceran community (*Daphnia obtusa*, *Daphnia magna* and *Simocephalus vetulus*), Louette and DeMeester (2007) found community structure to be strongly driven by species sorting of competitive ability. *D. magna* was the dominant species regardless of the invasion sequence treatment, except when *D. obtusa* was the first invader. In a natural setting, however, *D. obtusa* was generally found to be the first invader and dominated early communities (Louette and DeMeester, 2005). Louette and De Meester (2007) hypothesized that, in a natural setting, *D. obtusa* had a greater colonization capacity, even though it was not the superior competitor. Therefore, although the competitive ability of *D. magna* would have dictated, at the local scale, that it should be the dominant cladoceran species, its dispersal limitation allowed priority effects to favour dominance by *D. obtusa*. Overall, an understanding of whether local or regional scale processes structure a community is important when determining the trajectory and state of recovery (Chase, 2003).

Lake acidification and community recovery

Studies of lake acidification have made strong advancements in the understanding of the recovery process in affected lakes. Damage from acid precipitation has affected thousands of lakes in North America and Europe, due to the long-range transport of sulphur and nitrogen oxide emissions (Schindler, 1988). Whole-lake experiments on the effects of acidification, including Lakes 223 and 302 (Experimental Lakes Area, Ontario,

Canada) and Little Rock Lake (Wisconsin, U.S.A.), helped to quantify the changes that a decrease in pH could induce in aquatic biota (Schindler *et al.*, 1991). Some general trends include decreased species richness and diversity, increased water clarity, increased UV penetration, greater loading of toxic metals and species extirpation. In hopes of reversing the degradation of lakes and streams, governments in Canada, the United States and Europe legislated reductions in SO₂ emissions through the 1980s and 1990s (Stoddard *et al.*, 1999). As the resulting effects of decreases in acid deposition are now being seen, quantification of the recovery process of aquatic biota is essential in order to assess the efficacy of emissions abatement. Within the Sudbury, Ontario region, sufficient chemical recovery has occurred to allow the biological recovery process to be followed (Holt and Yan, 2003; Keller *et al.*, 2002; Arnott *et al.*, 2001; Yan *et al.*, 2004). From this knowledge base, and with an understanding of the key processes that drive recovery, a conceptual framework has been developed to determine the recovery trajectory and state that a community may follow (Yan *et al.*, 2003). We may therefore look to the acidification literature, in order to better understand the recovery process and apply it to community reassembly theory.

Defining community recovery

Determining the target at which to evaluate recovery is a difficult process, as a large amount of variability exists even in natural communities (Palmer, Ambrose and Poff, 1997). However, it is important to choose an endpoint from which to evaluate the recovery of the perturbed community. Targets for restoration may be the recovery of either community structure or community function. Dispersal limitation may prevent

certain species from returning following a disturbance and limit the feasibility of restoring community structure to its pre-disturbance state (Lockwood and Pimm, 1999). In this case, restoring community function may be more achievable. However, evaluating community function is a difficult process, and can be a less sensitive indicator of community change than structure, depending on the scale at which it is evaluated (Jenkins and Buikema, 1998). Schindler (1987), in whole ecosystem studies of the Experimental Lakes Area, found structural data to be a more sensitive indicator of community change than data on community function. Therefore, as there is considerable evidence for feedback between community structure and function (Palmer, Ambrose and Poff, 1997), a focus on the recovery of community structure should be a feasible starting point.

Recovery can also be evaluated at the species or community level. The extent of recovery of community structure can be identified using indicator species. Indicator species, which respond to low level changes in a stressor, provide an early warning of more widespread community change (Ford, 1989). For example, in acidified systems, an early indicator of recovery may be the disappearance of acid-tolerant species and the reappearance of acid-sensitive species (Holt and Yan, 2003; Locke *et al.*, 1994; Gunn and Sandøy, 2003; Walseng, Halvorsen and Sloreid, 2001). Once again, however, as dispersal limitation might prevent species from returning following a disturbance, complete species-level recovery might not be achievable. Rather, changes in community structure might provide a clearer indication of recovery (Arnott *et al.*, 2001).

When evaluating recovery at the community level, Keller and Yan (1998) suggest that there are four possible recovery states for acidified lakes: the pre-disturbance

community, an alternate natural community, a community limited by dispersal, and a community limited by biological resistance. With sufficient time and the recovery of habitat, there is greater likelihood for the progression to the pre-disturbance community (Niemi *et al.*, 1990). However, limiting factors may exist to prevent a return to the pre-disturbance state. For example, physical barriers to dispersal or a species' vagility might force recovery to a community that is limited by dispersal. Alternatively, biological resistance might determine the recovery state of the community, where continued dominance of an acid-tolerant species (competitor or predator) in the recovery phase prevents the re-establishment of key acid-sensitive species. Rather than a return to the pre-disturbance state, an alternate natural community may occur, included in states that exist in other similar but undisturbed communities (Keller and Yan, 1998). The range of natural community variability, both spatially and temporally, may therefore provide a recovery target for perturbed communities (Keller *et al.*, 2002). Of the four community states, none may be considered stable and each may be involved in a trajectory to recovery. To assess the state of recovery in a lake, however, knowledge of the pre-disturbance community is required.

Paleolimnology and lake restoration

In lakes, assessment of the recovery state is frequently limited by a lack of baseline information (Keller and Yan, 1998). With no knowledge of a community prior to its restoration, all that can be inferred is that the community has changed in some fashion (Chapman, 1999). A greater understanding of the recovery pathway requires knowledge of a set of reference conditions (Ford, 1989). Reference conditions not only provide a

baseline for the recovering community and the region, but also allow for the determination of natural community variability. By determining the natural range of variation, the deviation due to the perturbation can be quantified. Historical datasets, providing a temporal reference, are a strong source of baseline data; however, for most lakes, the data are rarely available (Smol, 1992). In addition, long-term environmental change is often obscured by seasonal and episodic variability in historic datasets (Battarbee, 1999). Comparison to similar unaffected lakes, as a spatial reference, is an alternative (Smol, 1992); however, the potential for confounding variables, such as contrasting altitude, latitude, morphometry and trophic status between lakes, is high. In addition, without knowledge of the invasion history, no inference can be made about mechanisms driving the current community structure. Paleolimnology, on the other hand, offers an inexpensive, fast and effective alternative to providing long-term baseline conditions (Smol, 1992). Although paleolimnology has only recently begun to be explored as a useful tool in following the lake recovery process, it provides great potential to quantify the pre-manipulation state, baseline conditions and natural variability of a community, in order to estimate its recovery trajectory and state (Battarbee, 1999).

Paleolimnology, the study of the sediment record of lakes, is a unique approach to evaluate changes over time. In the absence of long-term consistent sampling, the annual accumulation of organic and inorganic material in the sediment record can provide information from which to reconstruct the historic state of a lake. This can be particularly useful for ecosystem management, to determine potential trajectories for recovery of a damaged community (Schindler, 1987). Battarbee *et al.* (2005) recently demonstrated the

utility of combining paleo- and neo-limnological approaches, with respect to eutrophication, to identify current lake ecosystem status and the pre-manipulation condition, as well as to estimate future recovery endpoints and changing regional baseline conditions. Some groups of well preserved organisms (e.g. diatoms, cladocerans, pollen, chironomids) have proven invaluable in community and ecosystem reconstruction (Jeppesen *et al.*, 2001). Although paleolimnology has previously used biological indicators to track recovery patterns in acidified lakes (Smol *et al.*, 1998), its application has been through the use of transfer functions (i.e. diatoms and chrysophytes to infer pH), rather than changes in community structure, to infer chemical recovery. However, the potential of microfossil remains, including cladocerans, in lake sediments to define biological recovery targets has been recognized (Battarbee, 1999).

Cladoceran subfossils and community reassembly

Cladocera provide an exceptional test group of organisms from which to follow community assembly in the paleorecord. Their chitinous exoskeletons are well preserved in lake sediments, remains are identifiable to species, and species-rich communities characterize both littoral and pelagic zones of lakes (Hann, 1989). Within the Cladocera, species in the family Chydoridae are diverse, sensitive to changes in water chemistry and habitat type, preserve well in lake sediments, and are an important food source, making them particularly useful to infer large-scale changes in lakes. Although the usefulness of cladoceran microfossils in sediments is apparent, cladocerans have been underutilized for recounting community change. This is potentially due to the fact that, unlike other fossil groups, few reliable transfer functions to environmental variables exist (e.g. diatoms and

pH). Although many attempts have been made at developing reliable quantitative transfer functions for cladocerans, their covariance with multiple environmental variables makes such a task difficult. For example, although Korhola (1999) found cladoceran-based water temperature reconstructions from subarctic Fennoscandian lakes to be statistically significant, covariance with sediment organic content requires such a model to be treated with caution. The non-cosmopolitan nature and precise ecological and physiological requirements of chydorids also makes it difficult to develop quantitative transfer functions (Frey, 1986a). In addition to the lack of reliable transfer functions, cladocerans have been found to have a relatively low value as indicator species (Korhola and Rautio, 2001). When relating cladocerans to change in environmental conditions, the community should rather be considered as a whole. Overall changes in the cladoceran community should reflect responses to a stressor directly or indirectly through changes in diet or predation.

Although research has followed the recovery of the contemporary zooplankton community, with consideration of pelagic cladocerans as a portion of the zooplankton community (i.e. for recovery from acidification, see: Holt and Yan, 2003; Keller *et al.*, 2002; Arnott *et al.*, 2001; Yan *et al.*, 2004; Malley and Chang, 1994; Frost *et al.*, 2006), relatively few studies have followed the recovery of the littoral cladoceran community. Hann and Turner (2000), for example, in their study of the response and recovery of the littoral microcrustacean community to experimental acidification, found limited evidence of recovery seven years after minimum pH of 4.5 had been achieved, following chemical recovery to pH 5.9. Only one study exists that followed the recovery trajectory of the contemporary cladoceran community, from eutrophication and fish stocking, with

reference to community assembly theory (Louette *et al.*, 2008). Although the recovery trajectories of both sections of the partitioned Lake Kraenepoel (Belgium) were found to be highly deterministic, the communities did not recover to their pre-manipulation (1930) state. To the knowledge of this author, no study has used the paleorecord in order to follow cladoceran community reassembly. However, Louette *et al.* (2008) have recognized the important contribution that paleolimnological reconstruction may have in defining a reference state and following the recovery trajectory of the cladoceran community.

In terms of the reassembly of the cladoceran community, local rather than regional factors will likely be most influential on developing community structure. This is because the sediment egg bank is a stronger source for population establishment than the regional species pool (Jenkins and Buikema, 1998). However, in lakes where acidification has persisted for many decades, the viability of the egg bank as a source for colonization is unknown (Keller and Yan, 1998). In this case, where external sources are relied on for propagules, the dispersal and colonization capacities cannot be assumed to be uniform across all cladoceran species (Louette, De Meester and Declerck, 2008). However, the estimation of species-specific dispersal capacity in field studies is often confounded by their regional abundance and colonization success (Robinson and Dickerson, 1987). Overall, the relative importance of local versus regional factors in structuring the cladoceran community during reassembly will be dependent on the severity of the disturbance and its effect on colonist availability in both the local and regional species pool.

Research objectives

The purpose of this study is to follow the pattern of community reassembly, through the use of cladoceran microfossils. Although Schindler (1987) suggested the use of paleolimnology in studying anthropogenic stressors, in the absence of long-term contemporary datasets, he emphasized the necessity of calibrating methods in systems that have been experimentally modified and monitored for long periods of time. Therefore, this study will utilize three lakes where long-term contemporary data exist, in order to confirm results from the paleorecord.

Cladoceran community reassembly will be followed in two experimentally-manipulated lakes, with the use of a reference lake in order to estimate changing regional baseline conditions. Although the main focus of this study will be on acidification as the main stressor, the results should be generally applicable to the processes of community reassembly, following any disturbance, to a recovery state. It should not be the stressor type that guides recovery trajectories to stable states, but the underlying principles of community assembly, such as dispersal limitation and priority effects. However, to ensure that stressor type has a minimal effect on recovery trajectories and states, different types of experimental stressors will be observed (acidification by H_2SO_4 , HNO_3 and HCl ; epilimnetic fertilization and hypolimnetic nutrient injection). This increases the relevance and practicality of the study to environmental monitoring where baseline information on a perturbed lake is absent, as to whether the structure of a community over time can be reconstructed using paleolimnology.

The objectives of this study are based on Battarbee's (1999) and Battarbee *et al.*'s (2005) guidelines for using applied paleolimnology to define restoration targets,

including establishing baseline values and quantifying the direction and magnitude of community change. Using cladoceran microfossils, the objectives of this study are to reconstruct:

1) the trajectory of change in response to disturbance, relative to the pre-manipulation state:

Changes in community composition are difficult to detect without sufficient knowledge of the pre-manipulation state (Ford, 1989). Using paleolimnology, the deviation from the pre-manipulation state, due to the disturbance, can be detected. In addition, with an understanding of the trajectory of change in response to disturbance from the paleorecord, a potential path for cladoceran community reassembly to its pre-manipulation state can be inferred.

2) the trajectory of and community state at recovery:

Following trajectories of change to understand community dynamics must draw heavily on descriptive studies, due to the array of stochastic factors that may be involved in the assembly process (Ford, 1989). Using the paleorecord to reconstruct the trajectory of recovery may therefore aid in a better understanding of the process of cladoceran community reassembly. Although the complexity of the community assembly process might suggest a stochastic recovery trajectory, the findings of a deterministic trajectory in cladoceran community assembly (Louette *et al.*, 2008) can be confirmed from the paleorecord. In addition, through the observation of the recovery process in two experimentally-manipulated lakes,

the feasibility of the return to the pre-manipulation state, or an alternative stable state (i.e. state limited by dispersal, state limited by biological resistance or an alternative 'natural' state) will be evaluated. With knowledge of the assembly history from the recovery trajectory, the importance of regional versus local factors in driving cladoceran community structure in the recovered state may be inferred.

3) the trajectory of recovery, relative to baseline conditions:

Baseline values for a region may be used to assist in selecting a recovery target (Battarbee, 1999). However, depending on the duration over which a community has been perturbed, additional confounding factors, such as climate change and invasive species, may prevent recovery to the pre-manipulation state (Battarbee *et al.*, 2005). For example, the invasion of *Bythotrephes* into the Sudbury, Ontario region has changed the regional baseline and altered the trajectory and state to which acidified communities may typically recover (Strecker and Arnott, 2005). In order to determine if recovery to the pre-manipulation state is feasible, regional changes in baseline conditions will be quantified, through the use of a reference lake.

4) the degree of change, relative to natural variability:

Without knowledge of natural variability from a reference community, there is no way of knowing that the degree of change due to a perturbation falls outside the

range of natural variation (Ford, 1989). For example, in Lake 223, Experimental Lakes Area (ELA; Ontario), experimental acidification was found to increase water transparency (Schindler and Turner, 1982). However, upon further re-examination, an increase in water transparency in several other ELA lakes was found to coincide with the period of experimental acidification and was linked to a regional drought (Schindler, 1987). Although the increased transparency in Lake 223 due to acidification was later found to be significant, this example emphasizes the importance of quantifying natural variability. Natural cladoceran community variability will be quantified in a reference lake and during pre-manipulation conditions, in order to determine the degree of change that is in response to the manipulation.

Summary

Documentation of the recovery process has the potential of contributing to an increased understanding of processes that determine community structure (Keller *et al.*, 2002). However, Power (1999) stressed the critical importance in restoration ecology of relating the extent of recovery to both spatial and temporal reference systems, as well as separating the deviation due to a perturbation from natural variation. Restoration ecologists have lamented the difficulty in quantifying natural variability due to the lack of pre-manipulation data or reliable reference data (Palmer, Ambrose and Poff, 1997). Even within the realm of recovery of acidified lakes, the difficulty in assessing recovery, with respect to the pre-manipulation community, is frequently limited by a lack of baseline data (Keller and Yan, 1998). Paleolimnology has the potential to be an effective tool in

restoration ecology, by reconstructing baseline conditions and natural community variability in the absence of long-term contemporary data. This study hopes to strengthen the understanding of community reassembly following a disturbance, through paleolimnological reconstruction of community recovery using cladoceran microfossils.

Methods

Study sites

The study lakes are located at the Experimental Lakes Area (ELA), in northwestern Ontario, Canada (49°30' - 49°45'N, 93°30' - 94°00'W). Two manipulated lakes (Lake 302N and Lake 223) and one reference lake (Lake 377) were used for this study (Table 1).

Lake 302N is one half of the double basin Lake 302. Lake 302N was subjected to experimental hypolimnetic fertilization with phosphorus, nitrogen and carbon (1972-1976, 1978; Schindler, Rusczyński and Fee, 1980). In July of 1974, a vinyl-impregnated nylon curtain was installed to completely separate the two basins from each other. Following three years of recovery (1979-1981), a whole-lake acidification experiment was initiated. From 1982-1986, acidification by HNO₃ reduced the pH from 6.5 to 6.0 (Findlay *et al.*, 1999). HCl was then used to further decrease the pH over three years to 5.1 by 1989, where it was maintained at a minimum of pH 5.1 until 1993. From 1990-1993, NaNO₃ and Na₂SO₄ were also added in order to mimic naturally acidified lakes in eastern North America, which receive high nitrogen loading from the atmosphere (Findlay *et al.*, 1999). In addition, H₃PO₄ was added from 1992-1993 to stimulate algal productivity and internal alkalinity generation. Following 1993, three years of decreasing HCl additions were made in order to achieve increasing target pH levels for controlled recovery. Acid additions ceased in 1997. As the hypolimnetic nutrient injection experiment was not suspected to have had a significant effect on the cladoceran community, the main focus of this study will be on the acidification and epilimnetic

Table 1: Morphometric parameters for Lake 302N, Lake 223 and Lake 377
(Experimental Lakes Area, Ontario, Canada; Schindler, Ruszczyński and Fee, 1980;
Schindler et al., 1985).

	Lake 302N	Lake 223	Lake 377
Surface Area (ha)	12.8	27.3	26.9
Total volume ($\times 10^6 \text{ m}^3$)	0.73	1.95	2.47
Maximum Depth (m)	13.8	14.4	17.9
Mean Depth (m)	5.7	7.2	9.2

fertilization manipulation in Lake 302N. However, the time period of the hypolimnetic nutrient injection, and any observed changes in the cladoceran community, will be noted.

Lake 223 was subjected to experimental acidification by H_2SO_4 . From 1976-1983, the pH was gradually lowered on an annual basis from an initial value of pH 6.7 to pH 5.0, where it was held for three years (Findlay and Kasian, 1996). The lake then underwent a period of controlled recovery from 1984-1993, where gradually decreasing additions of H_2SO_4 were made to maintain pH at increasing target levels. Acid additions ceased in 1994.

Lake 377 was chosen as a reference lake due to its similarity in cladoceran species composition to the manipulated lakes (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data), as well as its un-manipulated history. Therefore, Lake 377 should be an accurate indicator of changing baseline conditions within the ELA region, as well as natural variability within an unmanipulated cladoceran community. Although Lake 377 has not been exposed to any experimental lake manipulations, logging has occurred within the catchment over the last century (K. Beaty, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication; J. Van Walleggem, Ontario Ministry of Natural Resources, Dryden, ON, personal communication). In addition, Lake 377 is located directly adjacent to Pine Road, a logging road built ca. 1980 that is now used as the main access road to the ELA field camp.

Throughout the analysis, three different periods are referred to in the experimentally-manipulated lakes. 'Pre-manipulation' is defined at the time period prior to the start of any experimental manipulation. 'Manipulation' is defined as the time

period for the duration of experimental manipulation (hypolimnetic fertilization, acidification and/or epilimnetic fertilization). This includes the process of controlled pH recovery, which were of different durations in Lake 302N (3 years of controlled recovery from minimum pH) and Lake 223 (10 years of controlled recovery from minimum pH). The 'recovery' time period is defined as the time following cessation of experimental manipulation, and does not refer to the state of the progression of chemical or biological recovery.

Sediment analysis

Sediment cores were collected from Lake 302N (October, 2006), Lake 377 (October, 2007) and Lake 223 (June, 2008) from the deepest portion of each lake. All cores were taken using a freeze corer (Shapiro, 1958; Crusius and Anderson, 1991). Frozen cores were sectioned into one centimetre increments from the sediment-water interface and placed in separate Whirl-Pak[®] bags. Sediments were dried and weighed prior to processing. Low resolution core sampling was done during key periods (pre-manipulation, acidification and recovery), at approximately every fourth centimetre. Due to the limited material available at certain core stratigraphic levels, some sediments (Lake 302N – 4 cm, 29 cm and 30 cm) were processed for counting of cladoceran microfossils from material that had been dried and ground for the ²¹⁰Pb dating process. At the time of processing, no bias was suspected to be caused by this method. Processing of sediment subsamples followed methods of Frey (1986b) and Hann (1989). Tared sediments were deflocculated in 10% KOH at 60°C by gentle heating of each subsample on a hot plate, while stirring with an acrylic rod, for 30 minutes. Sediments were then sieved through a

38 μm mesh. Residue retained on the screen was transferred to a vial and made up to a known volume (typically 10mL). A few drops of 10% formalin were added as a preservative. A measured aliquot of the fossil material (0.1mL), transferred by pipette, was mounted on each slide in glycerine jelly.

Cladoceran fossil remains were identified to species from large (i.e. headshields, carapaces, or postabdomens of chydorids) or small fossil fragments (i.e. postabdominal claws of *Daphnia* spp.). Sources used for identification included Smirnov (1974), Brooks (1965), Frey (1959), Frey (1980), DeMelo and Hebert (1994), Deevey and Deevey (1971), Dodson and Frey (2001) and the original species descriptions for verification, as well as a reference slide collection of intact organisms from the region (Hann, 1981; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data). For the Family Daphniidae, individuals were identified as belonging to a *Daphnia mendotae*-type group (spines of medial and distal pecten of similar size) or a *Daphnia pulex*-type group (spines of medial pecten stout, larger than distal pecten). For the Family Bosminidae, four taxa were found to be present (*Bosmina* (*Bosmina*) *longirostris*, *Bosmina* (*Eubosmina*) *longispina*, *Bosmina* (*Neobosmina*) *tubicen*, *Bosmina* (*Sinobosmina*) *liederi*); however, they were not able to be reliably separated based on carapace or headshield alone, due to large morphometric variation. The exception was *B. (N.) tubicen*, which was reliably separated based on the presence of dorsal incisures on the mucrone. Therefore, total abundance ($\text{No.} \cdot \text{g dry matter (DM)}^{-1}$) of certain Bosminidae spp. (including *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederi*) are presented separately from *B. (N.) tubicen*. Cladoceran exoskeletal components, both intact and fragmented, were counted only if a key distinguishing feature was visible (e.g.

headpores on headshield, post-ventral corner of carapace). Each cladoceran remain was then weighted by the number that could be contributed in one moult (e.g. number of carapace halves / 2; Frey, 1986b). The largest exoskeletal fragment count for each taxon was then used to estimate its relative population size. For each depth within the sediment core, all cladoceran microfossils were counted until over 100 chydorid whole animal equivalents had been examined. An exception to this was for the family Bosminidae, which were counted separately from the other cladoceran microfossils until over 100 bosminid whole animal equivalents had been examined. Identification and counting was done using a Nikon Optiphot binocular phase contrast compound scope (40-400X magnification). Final counts were presented as relative abundance (%), abundance (exuviae • g DM⁻¹) and accumulation rate (remains • cm⁻² • yr⁻¹). For counts that were presented as relative abundance (%), rare species (less than 2%) were removed from analysis. In addition, because *Bosmina* spp. contributed such a large proportion to total cladoceran population numbers, relative abundances of littoral and pelagic cladocerans were calculated separately. The planktonic to littoral cladoceran ratio was also calculated to determine if there were any shifts in dominance of the two groups over time. The planktonic to littoral cladoceran ratio can infer water level changes within a lake over time, depending on the morphometry of the lake basin (Mueller, 1964; Alhonen, 1970). In all three lakes, *Chydorus brevilabris* and *Chydorus sphaericus* were included in the ratio as littoral species.

²¹⁰Pb dating allowed for the estimation of sedimentation (g • cm⁻² • yr⁻¹) and accumulation (cladoceran remains • cm⁻² • yr⁻¹) rates, correlation of sediment depths (hereafter, 'depth' or 'sediment depth' is in reference to a sediment layer within a core)

with lake manipulation history, and verification that minimal physical and biological disturbance occurred within each of the cores. Additional ^{226}Ra dating was also completed to estimate background ^{210}Pb levels at the bottom of each of the cores. The chronologies and sedimentation rates were estimated by applying the linear regression model (Lake 302N, Lake 377 and Lake 223) and the Constant Rate of Supply (CRS) model (Lake 377 only) (Appleby and Oldfield, 1983). ^{210}Pb dating and modeling of the cores was completed by Flett Research (Winnipeg, MB). In the results section, age ranges given for core sections were estimated from the bottom of each sediment depth (e.g. 30-25 cm, ca. 1961-1971, where 30 cm is ca.1961 and 25 cm is ca. 1971). Therefore, it should be noted that age ranges for lower core stratigraphies, which may account for up to 10 years per centimetre of sediment, will be underestimated.

Contemporary samples

To confirm the change in cladoceran community structure inferred from the fossil record, particularly for those species that were underrepresented in the sediments (i.e. *Daphnia* spp., *Diaphanosoma birgei*, *Holopedium gibberum*; Frey, 1986b; Deevey, 1964; Krause, 1959), reference was made to contemporary pelagic cladoceran abundance data collected from the three study lakes (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data; Malley and Chang, 1994). Contemporary zooplankton samples were collected from each of the three lakes over different time periods. Lake 223 was sampled during the open-water season, biweekly or monthly, in 1974 and from 1977 to 2003 (Malley and Chang, 1986; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data).

Zooplankton were sampled using a 28.7L transparent Schindler-Patalas trap (1974), a four-barrel non-closing sampler (1977) or a two-barrel closing sampler (1978-2003), each with 53 μ m mesh nets. Zooplankton were collected at the deepest point of the lake, separately from the epilimnion, metalimnion and hypolimnion; however, strata were combined to represent animals $\bullet L^{-1}$ over the entire water column (see Malley and Chang, 1986; Chang and Malley, 1987). Lake 302N was sampled using similar methods as for Lake 223, from 1981-2005, either biweekly (1981-1991) or monthly (1992-2005). Lake 377 was sampled biweekly during the open-water season from 1988 to 1993 at multiple near-shore and open-water stations, using twin net and hose samplers (see Salki, 1993). Annual averages of contemporary pelagic cladoceran abundance (animals $\bullet L^{-1}$) were then used in the analyses. Littoral cladocerans were never quantitatively sampled from Lakes 302N, 223 or 377. However, qualitative sweepnet samples were taken in July, 2008 from the various littoral habitats (macrophytes, sand, sediment and rock) of each lake basin.

As *Daphnia galeata mendotae* has recently been re-classified, this species was renamed from the contemporary records to *Daphnia mendotae* (Hebert, 1995). In addition, due to the taxonomic reevaluation of the Family Bosminidae (De Melo and Hebert, 1994), the *Eubosmina* spp. group in the contemporary data is inclusive of *B. (E.) longispina* (recorded in the contemporary records as *Eubosmina longispina*) and *B. (N.) tubicen* (recorded in the contemporary records as *Eubosmina tubicen*).

Statistical analyses

As the choice of metric may affect the perception of recovery (Yan *et al.*, 1996), community structure was assessed using both univariate (i.e. species richness, diversity,

evenness) and multivariate (i.e. constrained cluster analysis, correspondence analysis, analysis of similarities) techniques. For the analysis of cladoceran community structure using species richness, diversity and evenness, focus was made solely on the Family Chydoridae to determine how community structure changed over time. Chydorids are diverse, preserve well in lake sediments, and have been found to be responsive to acidification (Hann and Turner, 1999; Hann and Turner, 2000; Paterson, 1994; Walseng, Yan and Schartau, 2003; Walseng *et al.*, 2008). Therefore, chydorids should be an accurate indicator of overall cladoceran community change. As species richness, diversity and evenness were expected to be biased by differential preservation, they were not calculated for the pelagic cladoceran community and the non-chydorid littoral cladocerans (Frey, 1986b; Deevey, 1964; Krause, 1959).

Species richness, diversity and evenness were univariate, quantitative measures used to characterize the cladoceran community structure in each lake examined. Species richness is the number of species within a community; however, it does not weight rare species differently than more common species. Therefore, species diversity was more useful to this study, as it is sensitive to the occurrence of rare species. The species diversity index used was the Shannon index (H' ; Krebs, 1999):

$$H' = - \sum_{i=1}^s p_i \ln p_i \quad (1)$$

where p_i is the proportion of the i th species to the total population, and s is the total number of species. The choice of the Shannon index over other diversity indices (e.g.

Simpson Index) was made because it is comparatively more sensitive to rare species, and is, therefore, particularly useful to a paleocladoceran study. Species evenness, which is a measure of the equality of species abundances in a community, allowed for comparison between lake communities, as it is not confounded by species richness. Pielou's evenness index (J ; Pielou, 1977) was used:

$$J = \frac{H'}{H'_{\max}} \quad (2)$$

where H' is diversity (as calculated using the Shannon index), and $H'_{\max}$ is the maximum value of H' , equal to:

$$H'_{\max} = -\sum_{i=1}^s \frac{1}{s} \ln \frac{1}{s} = \ln s \quad (3)$$

J has a range from 0 to 1, where a value of 0 indicates a community dominated by a single species and a value of 1 indicates a community with equal representation from all species present.

To determine the recovery status, state and trajectory of change in Lake 302N and Lake 223, in comparison to changes in the reference community (Lake 377) over time, additional multivariate data analyses were performed. Constrained cluster analysis was used to determine group structure in the cladoceran community over time for each lake, as well as to identify if different community structures existed during pre-manipulation, manipulation and recovery. Constrained cluster analysis was performed using the total

sum of squares method on percent species composition, which had been square root transformed (Grimm, 1987).

Correspondence analysis (CA) was used as an additional method to determine how cladoceran community structure in Lake 302N and Lake 223 changed over time in response to manipulation, as well as to compare the degree of change in the manipulated lakes, as compared to the reference Lake 377. By performing a reciprocal averaging on both sample and species data, the algorithm used in CA inherently standardizes the data and is, therefore, a robust method for data that are not normally distributed (Legendre and Legendre, 1998). Correspondence analysis was performed on the species abundance data (exuviae $\bullet$ g⁻¹ DM). Species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses, and no data transformations were performed. CA was performed both on the littoral cladoceran community, as reconstructed from fossil material, as well as the contemporary pelagic cladoceran data.

To determine how environmental and morphological characteristics of each of the study lakes may have influenced overall cladoceran community structure, a canonical correspondence analysis (CCA) was performed on abundance of littoral cladocerans, with environmental and morphological covariates for Lake 302N, Lake 223 and Lake 377. Both pre- and post-manipulation time periods were considered. Species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses. Annual means of the environmental and morphological variables (Schindler, Ruszczynski and Fee, 1980; Schindler et al., 1985; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data), including nitrate ($\mu\text{g} \bullet \text{L}^{-1}$), ammonium ($\mu\text{g} \bullet \text{L}^{-1}$), suspended phosphorus ($\mu\text{g} \bullet \text{L}^{-1}$), total dissolved phosphorus ($\mu\text{g} \bullet \text{L}^{-1}$

¹), dissolved organic carbon ($\mu\text{mol} \cdot \text{L}^{-1}$), chlorophyll a ($\mu\text{g} \cdot \text{L}^{-1}$), conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$), calcium ($\text{mg} \cdot \text{L}^{-1}$), pH and maximum depth (m) were log-transformed, with the exception of pH. For the pre-manipulation time period, the average of two years of environmental data were included for Lake 302N (1968, 1969), Lake 223 (1974, 1975) and Lake 377 (1978, 1982). The corresponding species abundance data from fossil material was averaged for all depths that occurred prior to the start of experimental manipulation. For Lake 377, the pre-manipulation community was classified as depths prior to the earliest start of experimental manipulation in all of the study lakes (1976 in Lake 223; depths 30, 26, 22 and 18 cm for Lake 377). For the post-manipulation, recovery time period, the average of two years of environmental data were included for Lake 302N (2004, 2005), Lake 223 (2003, 2004) and Lake 377 (2006, 2007). The corresponding species abundance data from fossil material was averaged for the top two, most recent core depths for each lake. Forward selection was performed on the environmental and morphological variables to retain only those that were important in describing the species data (ter Braak and Šmilauer, 1998). All ordinations were performed using CANOCO version 4.02 (ter Braak and Šmilauer, 1999).

To determine if there was a significant difference in littoral cladoceran community structure prior to and following experimental manipulation in the two manipulated lakes, and over a similar time period in the reference lake, an analysis of similarities (ANOSIM) was performed. ANOSIM is a non-parametric permutation procedure, analogous to an analysis of variance (ANOVA), which is applied to a rank similarity matrix (Clarke and Warwick, 2001). Unlike other multivariate analyses, it is

particularly useful for species abundance data as it does not assume a normal distribution and can handle datasets with an abundance of zero values.

To test the null hypothesis, that there was no difference between pre- and post-manipulation communities, the Bray-Curtis distance metric was applied to non-transformed, non-standardized littoral cladoceran species abundance data, from which rare species with less than 5% relative abundance had been removed. Sample depths within each time period (pre- and post-manipulation) were used as replicates. For reference Lake 377, the pre-manipulation community was classified as depths prior to the earliest start of experimental manipulation in the study lakes (1976 in Lake 223). This accounts for regional variation that may have been obscured over the period of experimental manipulation in Lake 302N and Lake 223. For Lake 302N, the sample depth corresponded to hypolimnetic fertilization was included as pre-manipulation, as this manipulation was suspected not to have had any strong effect on the structure of the littoral cladoceran community. The R statistic ranges from -1 to 1, however, will usually fall between 0 and 1. An R statistic of 1 indicates that within group replicates are more similar than between group replicates. An R statistic of 0 indicates that within and between group replicates are equally similar. The statistical significance of the R value is then calculated as a permutation test of the null hypothesis, that there is no difference between depths in the core. A significance level of $p \leq 0.05$ was chosen prior to the analysis. Following ANOSIM, similarity percentages (SIMPER) were used to identify the species contributing most to group dissimilarity. PRIMER version 6.0 (Clarke and Gorley, 2006) was used to perform both ANOSIM and SIMPER.

Results

²¹⁰Pb dating and sedimentation rates

Dry bulk densities increased exponentially with depth in each of the sediment cores collected (Figure 1). In Lake 223, however, significant decreases in dry bulk density, particularly at 16 cm ($0.85 \text{ g} \cdot \text{cm}^{-2}$ cumulative dry weight; ca. 1986), indicated potential input of sediment from other areas of the lake bottom.

In each of the three lakes, there was an exponential decrease in ²¹⁰Pb activity as a function of depth in the core (Figures 2, 3 and 4). A surface depression in ²¹⁰Pb activity was observed in Lake 302N and Lake 223, but not in Lake 377. Additional ²²⁶Ra measures indicated that, at the bottom of all cores, background ²¹⁰Pb levels had not been achieved; therefore, ²²⁶Ra activity was used to estimate background ²¹⁰Pb levels in the age-depth models (Oldfield and Appleby, 1984).

Overall, there was little variation in the shape of the activity profile over the length of each of the cores; therefore, linear regression model was used to estimate sediment accumulation rates over time (Figure 5). For Lake 223, however, the linear regression model was applied in two sections (0-14 cm; 14-30 cm) due to the varying rates at which sediments were deposited in the bottom half of the core. The CRS model was also applied to Lake 377 to account for changing sedimentation rates in the top half of the core (0-4 cm) and was calibrated from the linear regression model, as not all assumptions of the CRS model were satisfied (i.e. the core was too short to allow for background ²¹⁰Pb levels to be achieved). The age-depth profiles, calculated from both the linear regression model and the CRS model for Lake 377, were found to agree. The Lake 302N sedimentation rate was calculated to be $0.0366 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ and the bottom

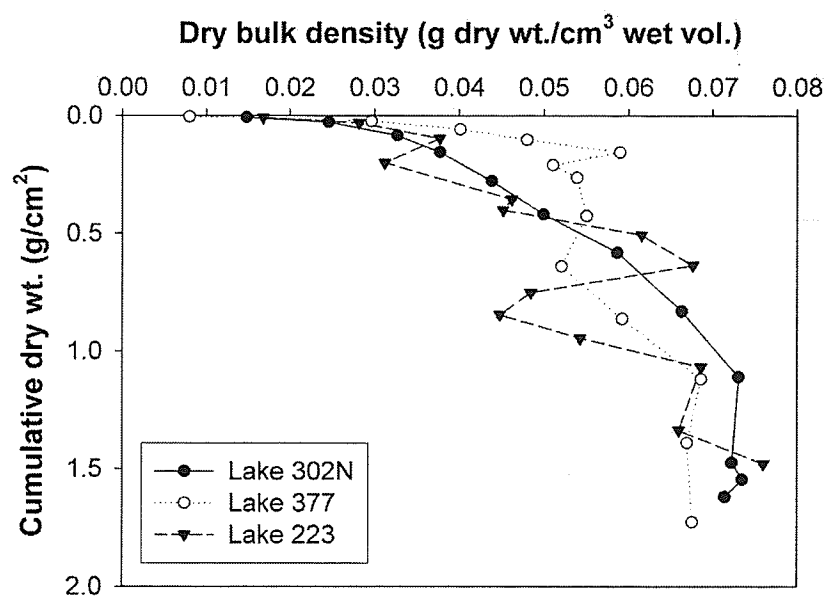


Figure 1: Dry bulk density (g dry weight/cm³ wet volume) as a function of depth (cumulative dry weight; g/cm²) for Lake 302N, Lake 377 and Lake 223.

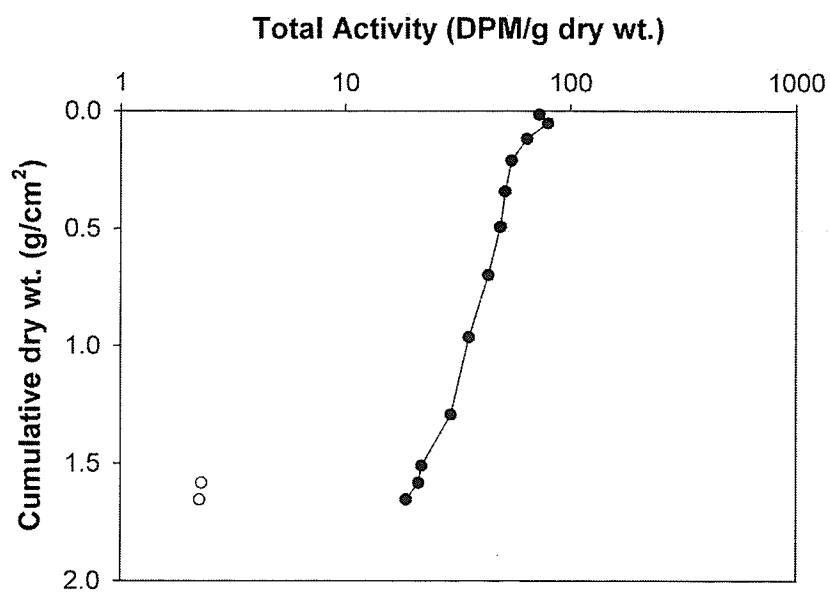


Figure 2: Activity profile of total ^{210}Pb activity (●; disintegrations per minute (DPM)/g dry weight) and ^{226}Ra activity (○; DPM/g dry weight) as a function of depth (cumulative dry weight; g/cm^2) for Lake 302N.

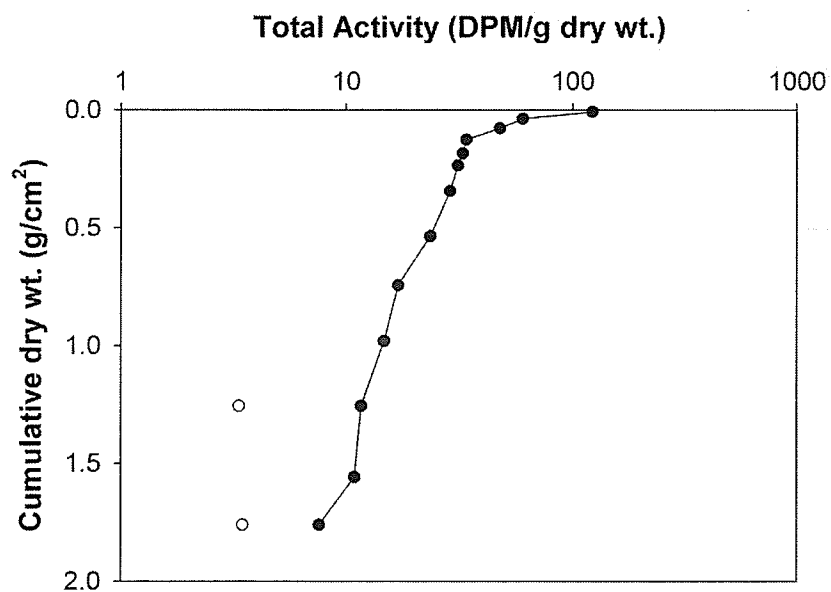


Figure 3: Activity profile of total ^{210}Pb activity (●; DPM/g dry weight) and ^{226}Ra activity (○; DPM/g dry weight) as a function of depth (cumulative dry weight; g/cm^2) for Lake 377.

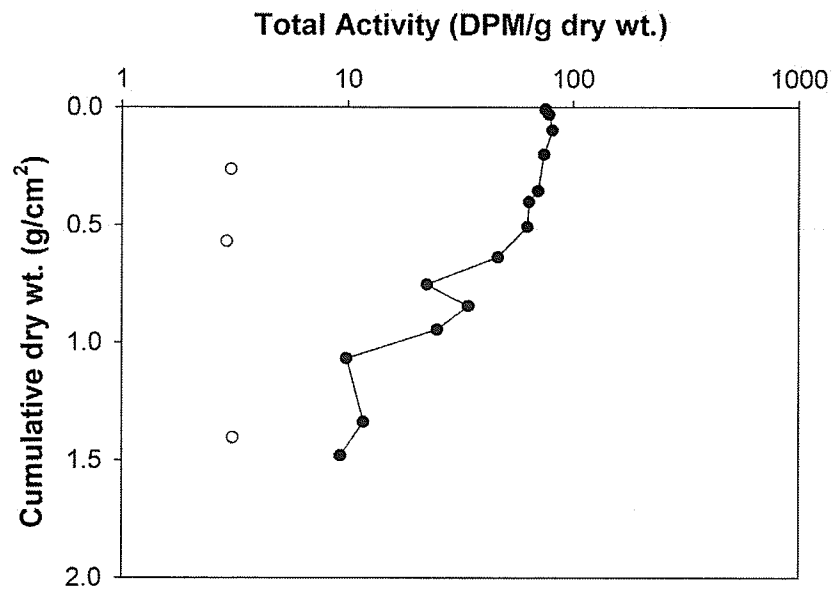


Figure 4: Activity profile of total ^{210}Pb activity (●; DPM/g dry weight) and ^{226}Ra activity (○; DPM/g dry weight) as a function of depth (cumulative dry weight; g/cm²) for Lake 223.

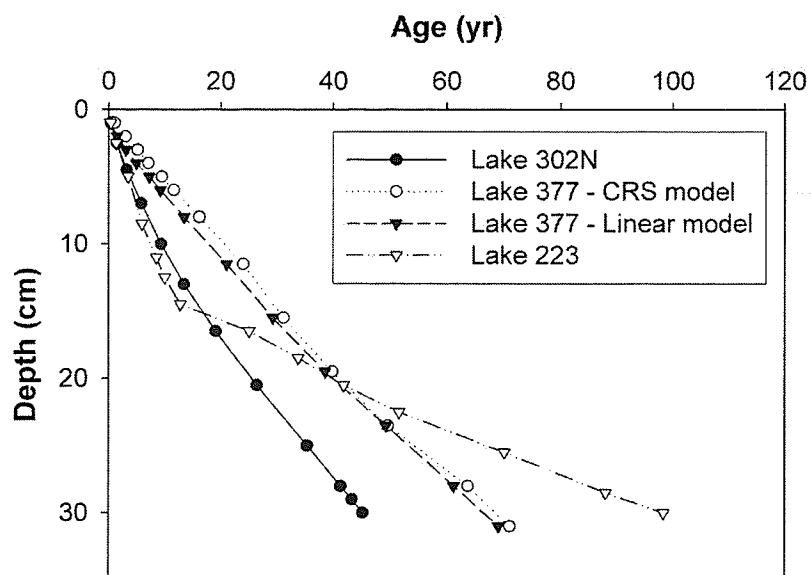


Figure 5: Age-depth profiles for Lake 302N, Lake 377 and Lake 223, calculated using the linear regression model (Lakes 302N, 377 and 223) and CRS model (Lake 377 only).

section of the core to be approximately 45 years old. The Lake 223 sedimentation rates were calculated to be $0.0444 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for the top half of the core (0-14 cm), and $0.0111 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for the bottom half of the core (14-30 cm). Due to the poorer regression fit for the bottom half of the Lake 223 core, and the potential sediment perturbations as inferred from the dry bulk density, the dating below 14 cm is thought to be less reliable. The age at the bottom section of the Lake 223 core was estimated to be approximately 100 years old. Using the linear regression model, sedimentation rates for Lake 377 were found to be $0.0255 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$. Sedimentation rates, estimated using the CRS model, can be found in Figure 6. The age at the bottom of the Lake 377 core was found to be approximately 69 years old.

Comparison was made to previously calculated sedimentation rates for Lake 302N and Lake 223 to confirm their accuracy (Anderson, Schiff and Hesslein, 1987). Sedimentation rates, calculated from ^{210}Pb dating, were found to agree for Lake 302N ($0.023 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$); however, sedimentation rates calculated for Lake 223 were found to differ by an order of magnitude from that of Anderson, Schiff and Hesslein (1987; $0.0034 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$). Although sediment cores for the Anderson, Schiff and Hesslein (1987) study were taken using a modified piston corer, an additional comparison made to an independent study of Lake 223 sedimentation rates, collected using a freeze corer (Davidson, 1984), was found to agree with that of Anderson, Schiff and Hesslein (1987). Therefore, the source for the discrepancy between sedimentation rates collected for this study, and historical records, is unknown.

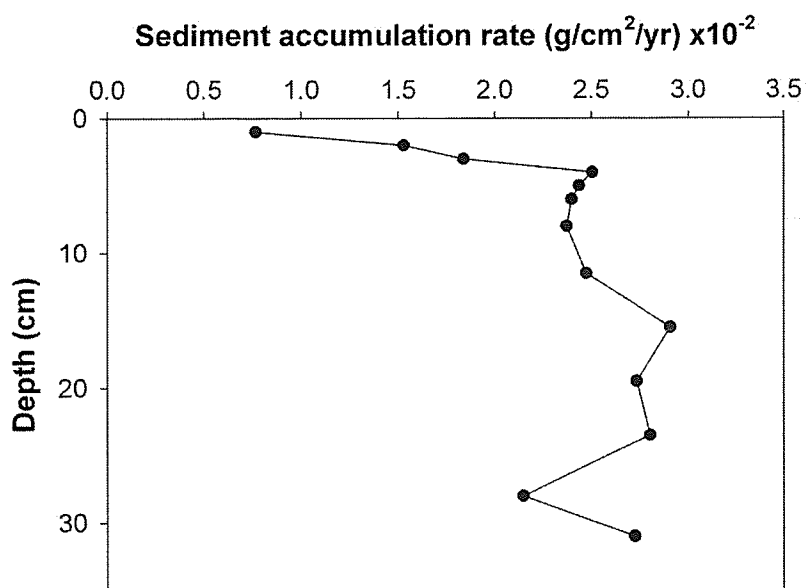


Figure 6: Sediment accumulation rate (g/cm²/yr) as a function of depth (cm) for Lake 377, as estimated using the CRS model.

Cladoceran community: The subfossil record

A diverse cladoceran assemblage was recovered from the subfossil record (Table 2). In total, the remains of 25 chydorid species were found from the three lakes studied. An additional 14 non-chydorid cladoceran species were recovered from fossil fragments. The dominant cladocerans represented in the subfossil record were from the Family Bosminidae. The only cladoceran that was not recovered from the subfossil record, yet was found in contemporary samples, was *Holopedium gibberum*.

Chydorid community structure: Species richness, diversity and evenness

In terms of species richness, diversity and evenness, there was relatively little change in Lake 302N and Lake 223 chydorid community structure in response to experimental manipulation (Figures 7, 8), compared to natural variability in the reference lake, Lake 377 (Figure 9). Throughout the length of the Lake 302N core, species richness remained within the range of that seen during pre-manipulation (Figure 7). During hypolimnetic fertilization, species richness was at maximum pre-manipulation levels (ca. 1961-1971). At the beginning of acidification, species richness decreased to a minimum of what was seen during pre-manipulation levels, and then increased slightly throughout the acidification period (ca. 1984-1997). The minimum species richness found throughout the core (approximately 45 years) occurred during the recovery phase (ca. 2003-2005), whereas maximum species richness found throughout the core was seen during pre-manipulation and hypolimnetic fertilization (ca. 1961-1977). Species diversity, on the other hand, increased outside of the range seen during pre-manipulation. During the

Table 2: Species list of cladoceran remains recovered from Lake 302N, Lake 377 and Lake 223 sediment cores (● – not found in Lake 223; ■ – not found in Lake 377; ▲ – not found in Lake 302N).

Family Chydoridae <i>Acroperus</i> cf. <i>harpae</i> <i>Biapertura affinis</i> <i>Alona barbulata</i> <i>Alona circumfimbriata</i> ● <i>Alona costata</i> <i>Alona guttata</i> <i>Biapertura intermedia</i> <i>Alona quadrangularis</i> <i>Alona rustica</i> <i>Alona setulosa</i> ▲ <i>Alonella</i> cf. <i>excisa</i> <i>Alonella exigua</i> ■ <i>Alonella nana</i> <i>Alonella pulchella</i> ■ <i>Chydorus brevilabris</i> <i>Chydorus sphaericus</i> <i>Chydorus faviformis</i> <i>Chydorus piger</i> <i>Disparalona acutirostris</i> <i>Eurycercus longirostris</i> <i>Graptoleberis testudinaria</i> <i>Kurzia latissima</i> <i>Monospilus dispar</i> <i>Pleuroxus denticulatus</i> ▲● <i>Rhynchotalona falcata</i>	Family Sididae <i>Latona</i> sp. <i>Sida crystallina</i> <i>Diaphanosoma birgei</i> Family Daphniidae <i>Daphnia pulex</i> -type group <i>Daphnia galeata mendotae</i> -type group Family Bosminidae <i>Bosmina</i> (<i>Bosmina</i>) <i>longirostris</i> <i>Bosmina</i> (<i>Sinobosmina</i>) <i>liederi</i> <i>Bosmina</i> (<i>Neobosmina</i>) <i>tubicen</i> <i>Bosmina</i> (<i>Eubosmina</i>) <i>longispina</i> Family Macrothricidae <i>Acantholeberis curvirostris</i> <i>Ophryoxus gracilis</i> <i>Ilyocryptus sordidus</i> ■ Family Polyphemidae <i>Polyphemus pediculus</i> ● Family Leptodoridae <i>Leptodora kindtii</i>
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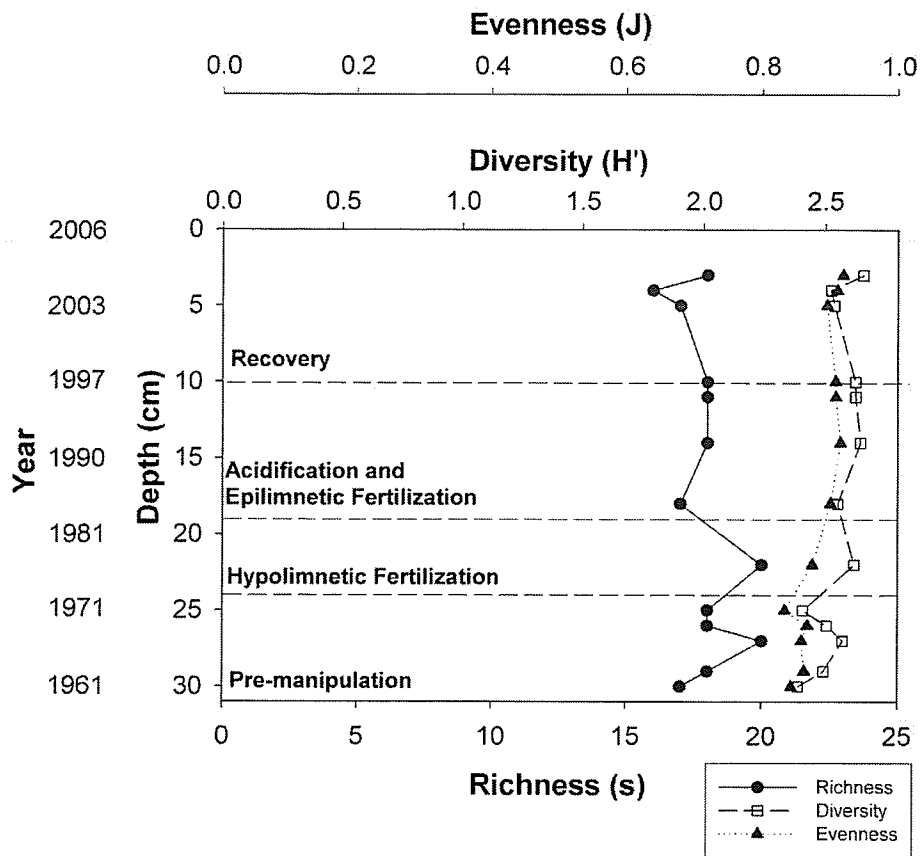


Figure 7: Vertical profiles of species richness (s), diversity (H'; Shannon index; Krebs, 1999) and evenness (J; Pielou's evenness; Pielou, 1977) for the Lake 302N chydorid community. Dashed lines separate periods of pre-manipulation, hypolimnetic fertilization, acidification and epilimnetic fertilization and recovery.

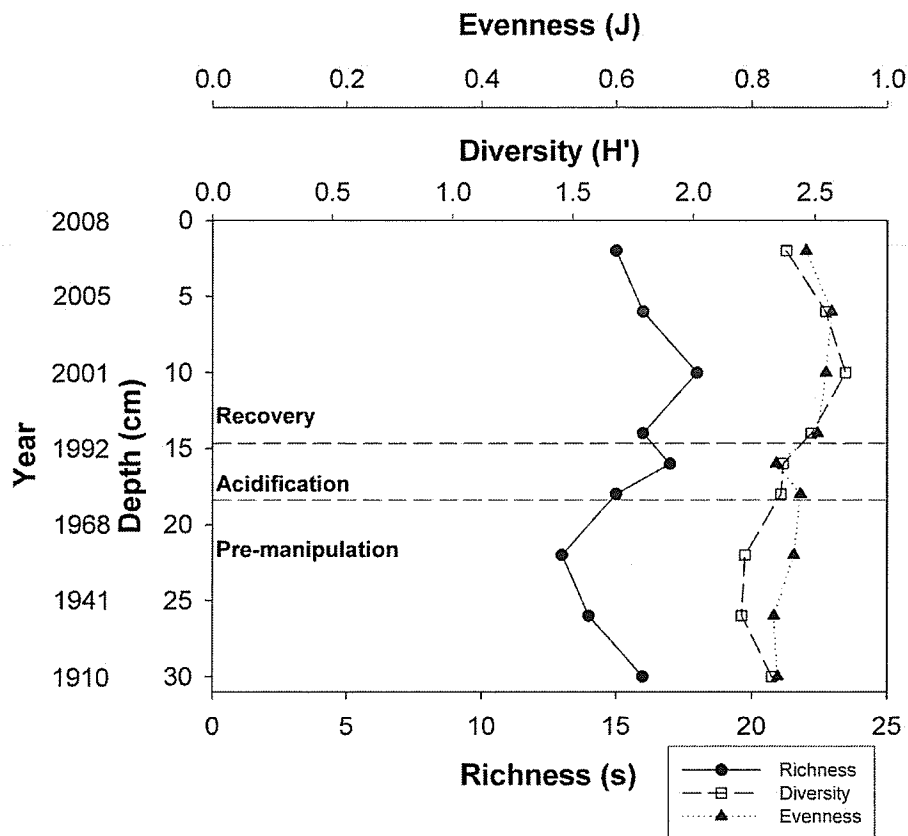


Figure 8: Vertical profiles of species richness (s), diversity (H'; Shannon index; Krebs, 1999) and evenness (J; Pielou's evenness; Pielou, 1977) for the Lake 223 chydorid community. Dashed lines separate periods of pre-manipulation, acidification and recovery.

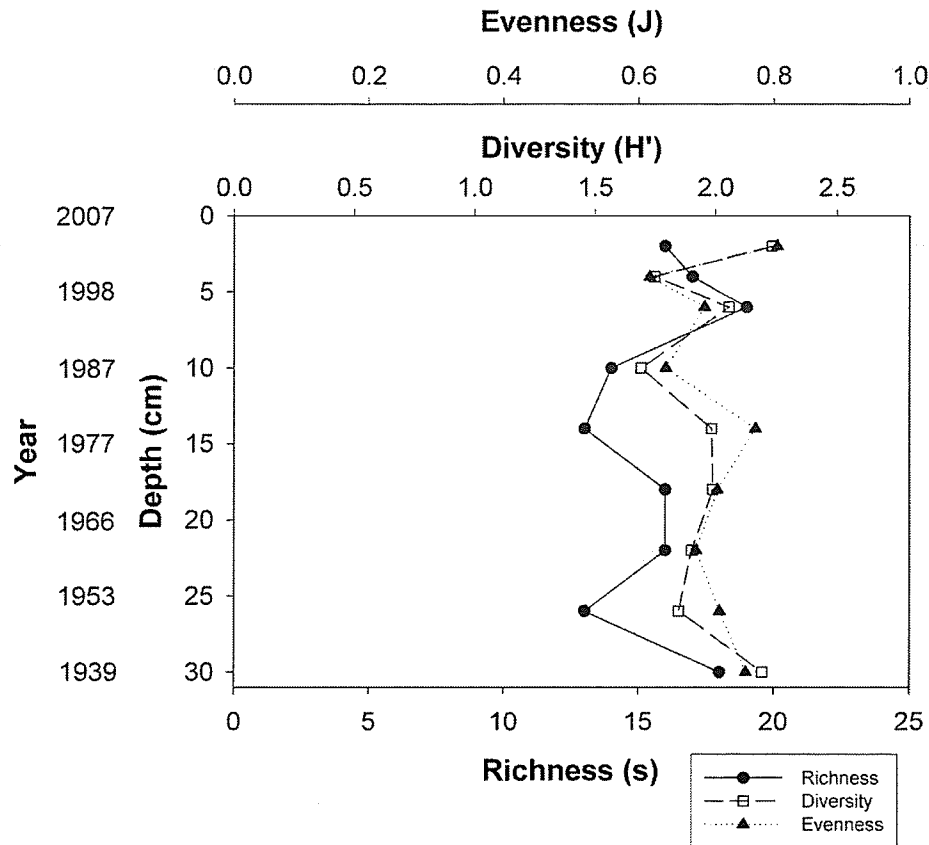


Figure 9: Vertical profiles of species richness (s), diversity (H'; Shannon index; Krebs, 1999) and evenness (J; Pielou's evenness; Pielou, 1977) for the Lake 377 chydorid community.

period of hypolimnetic fertilization, species diversity increased and continued to increase into the acidification and recovery phases. Maximum diversity was seen during the recovery phase, while minimum diversity was seen during pre-manipulation. Species evenness also increased from the pre-manipulation phase to hypolimnetic fertilization, and continued to increase during acidification and into recovery, where it achieved its maximum throughout the length of the core.

Chydorid species richness and diversity followed similar patterns in Lake 223, as compared to Lake 302N (Figure 8). During the pre-manipulation phase (ca. 1910-1956), there was a decrease in both species richness and diversity. Both species richness and diversity then increased during the period of acidification and into recovery (ca. 1976-1986), outside of the range of variability seen during pre-manipulation. In the top 10 cm of the core (ca. 2001-2007), species richness and diversity then decreased, but to values that were slightly higher than seen during pre-manipulation. Species evenness increased steadily from pre-manipulation, to acidification and recovery, with the exception of slight deflections at 16 cm (ca. 1986) and the top 6 cm of the core (ca. 2004-2007). Minimum richness, diversity and evenness occurred during pre-manipulation, whereas maximum richness, diversity and evenness occurred during acidification and recovery.

In the reference lake, Lake 377, there was no direction to changes in chydorid species richness and diversity over the approximately 70-year time period represented by the core (ca. 1939-2007; Figure 9). Species richness, diversity and evenness decreased within the bottom 5 cm of the core (ca. 1939-1950). Species diversity and evenness then increased over the following 30 years (ca. 1950-1979), before decreasing again at 10 cm (ca. 1987). Species richness also increased for 20 years (ca. 1950-1971), before

decreasing again ca. 1971-1980. In the top 6 cm of the core, (ca. 1987-2005), species richness decreased, whereas species diversity and evenness increased (with the exception of an inflection at 4 cm, ca. 2000). Overall, there were two periods of minimum species richness, diversity and evenness (ca. 1950 and ca. 1979-1987) and two maximum periods of species richness and diversity (ca. 1939 and ca. 1996-2005).

Throughout the entire length of each core, the greatest species richness, diversity and evenness for the chydorid community occurred in Lake 302N. Lake 223 had a similar average species richness to Lake 377, yet had a greater average diversity and evenness. Throughout the entire length of each core, species evenness was approximately 20% greater in the two manipulated lakes (Lake 302N and Lake 223) than in the reference lake (Lake 377).

Littoral cladoceran community structure: Relative abundance

The Lake 302N littoral cladoceran community consisted of a diverse assemblage of chydorid and non-chydorid species, with *Alonella nana* as the dominant species (Figure 10). In Lake 302N, there was no major species turnover or replacement throughout the length of the core (approximately 45 years). Little change in the relative abundance of the littoral cladoceran species occurred from the periods of pre-manipulation to hypolimnetic fertilization (ca. 1961-1977). During the periods of acidification and recovery (ca. 1984-2005), *Biapertura intermedia*, *Disparalona acutirostris* and *Monospilus dispar* all increased in relative abundance, whereas *Alona*

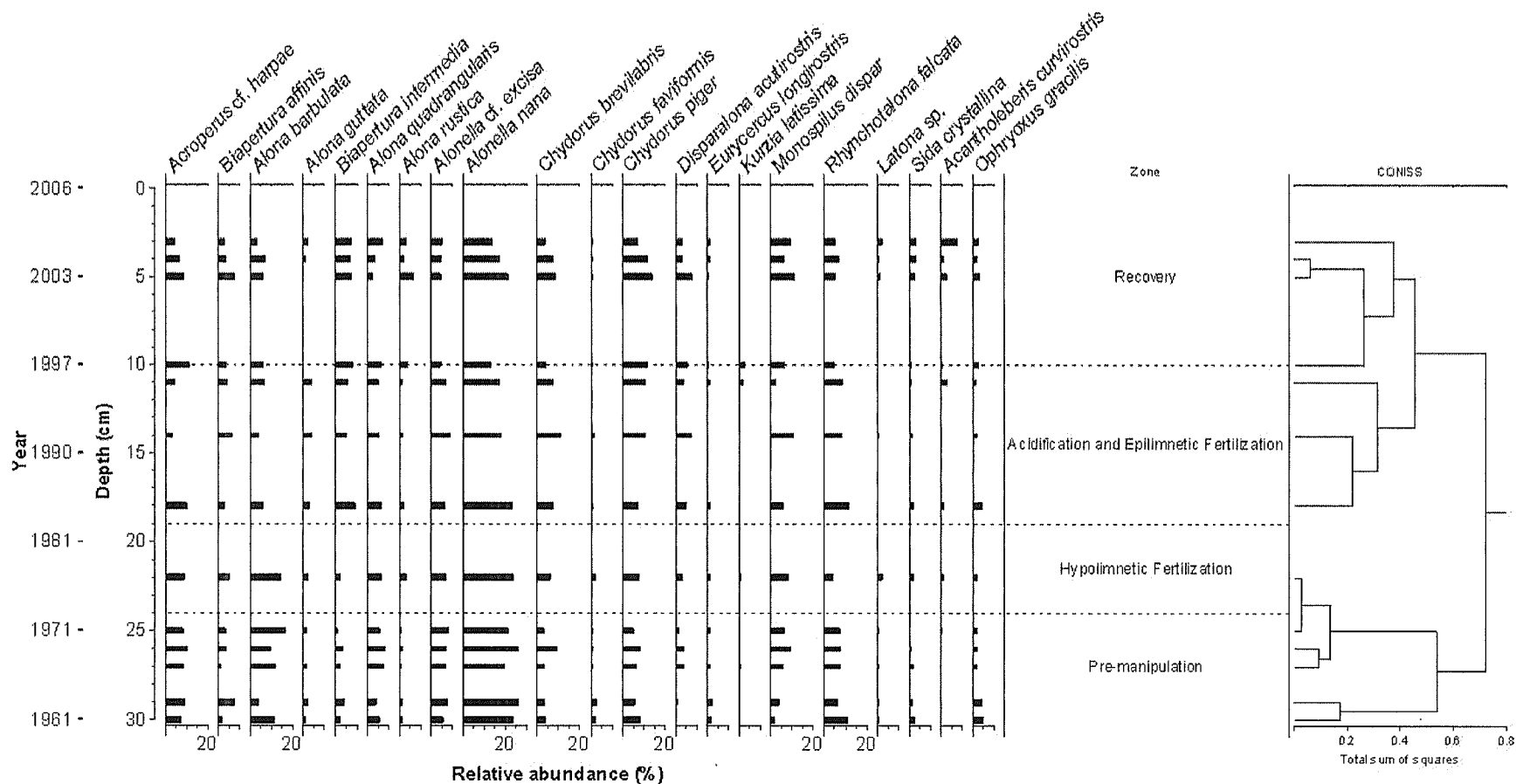


Figure 10: Vertical profiles of relative abundance (%) of littoral cladoceran species for Lake 302N. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differs, as compared to Figures 11-15).

barbulata, *Alonella* cf. *excisa*, *A. nana* and *Rhynchotalona falcata* all decreased in relative abundance. No changes, outside of those occurring during acidification, were apparent during the recovery period. Constrained cluster analysis of Lake 302N showed a clear partition between the pre-manipulation/hypolimnetic fertilization periods (ca. 1961-1977) and the acidification/recovery periods (ca. 1984-2005; Figure 10). With the exception of depths 4 cm and 5 cm, the pre-manipulation and hypolimnetic fertilization periods were most similar, clustering together first.

Overall, Lake 223 had a similar littoral cladoceran community structure as Lake 302N, with the most dominant littoral species throughout most of the core being *A. nana* (Figure 11). Once again, no major species turnover or replacement was observed. *Acroperus* cf. *harpae*, *C. brevilabris*, *Chydorus piger*, *C. sphaericus* and *Disparalona acutirostris* all increased in relative abundance from pre-manipulation to the acidification period (ca. 1910-1986). In addition, *C. sphaericus* and *D. acutirostris* were almost absent during the pre-manipulation phase, but appeared and increased during acidification. *A. barbulata*, *A. cf. excisa* and *A. nana* all decreased from pre-manipulation to acidification, and *Alonella pulchella* disappeared early in the acidification phase and did not re-appear in the rest of the core. With the exception of *C. brevilabris* and *B. intermedia*, species that changed in relative abundance during acidification did not return to pre-manipulation levels, following approximately two decades of recovery. *B. intermedia*, whose relative abundance had changed little during the period of acidification, increased during the period of recovery. Also, the relative abundance of *C. brevilabris* continued to increase into recovery, replacing *A. nana* as the dominant species. Constrained cluster analysis

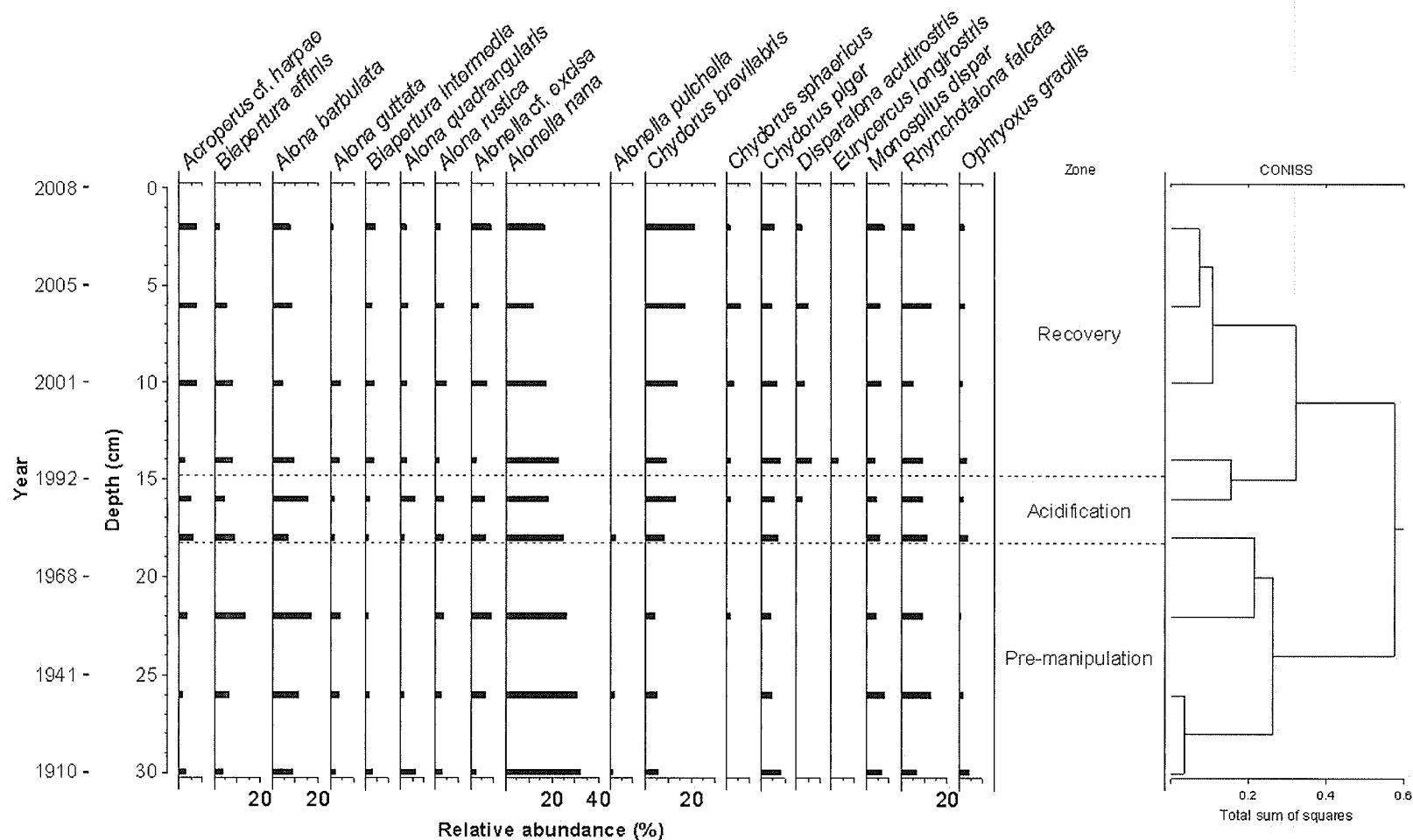


Figure 11: Vertical profiles of relative abundance (%) of littoral cladoceran species for Lake 223. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differs, as compared to Figures 10, 12-15).

showed a clear partition between the pre-manipulation period (ca 1910-1976) and the post-manipulation period (ca. 1996-2007; Figure 11). The two acidification depths, rather than clustering separately, clustered with the pre-manipulation period (18 cm, ca. 1976, early acidification) and the post-manipulation period (16 cm, ca. 1986, controlled recovery).

The overall structure of the littoral cladoceran community in Lake 377 differed from both Lake 302N and Lake 223. The community was dominated by *C. brevilabris* and *C. sphaericus* (Figure 12). Although the two species changed in proportion to one another throughout the core (ca. 1939-2004), there was no gradient over time to the changes. Similarly, less abundant species, including *Alona costata*, *Alona quadrangularis*, and *D. acutirostris*, disappeared and reappeared throughout the core; however, there appeared to be no gradient to these changes over time. *A. cf. excisa* and *A. nana* were the only littoral cladoceran species that appeared to have a gradient of change over time, with an increase in relative abundance at the top of the core (ca. 1996-2004). The constrained cluster analysis separated two zones within the core (ca. 1939-1961; 1971-2004) (Figure 12), with the oldest zone clustering together first. In comparison to the two manipulated lakes, Lake 377 depths clustered more closely together.

Pelagic cladoceran community structure: Relative abundance

The Lake 302N pelagic cladoceran community was dominated by Bosminidae spp. (including *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*; Figure 13). Prior to acidification, *B. (N.) tubicen* was present at a relative abundance of less than 10%;

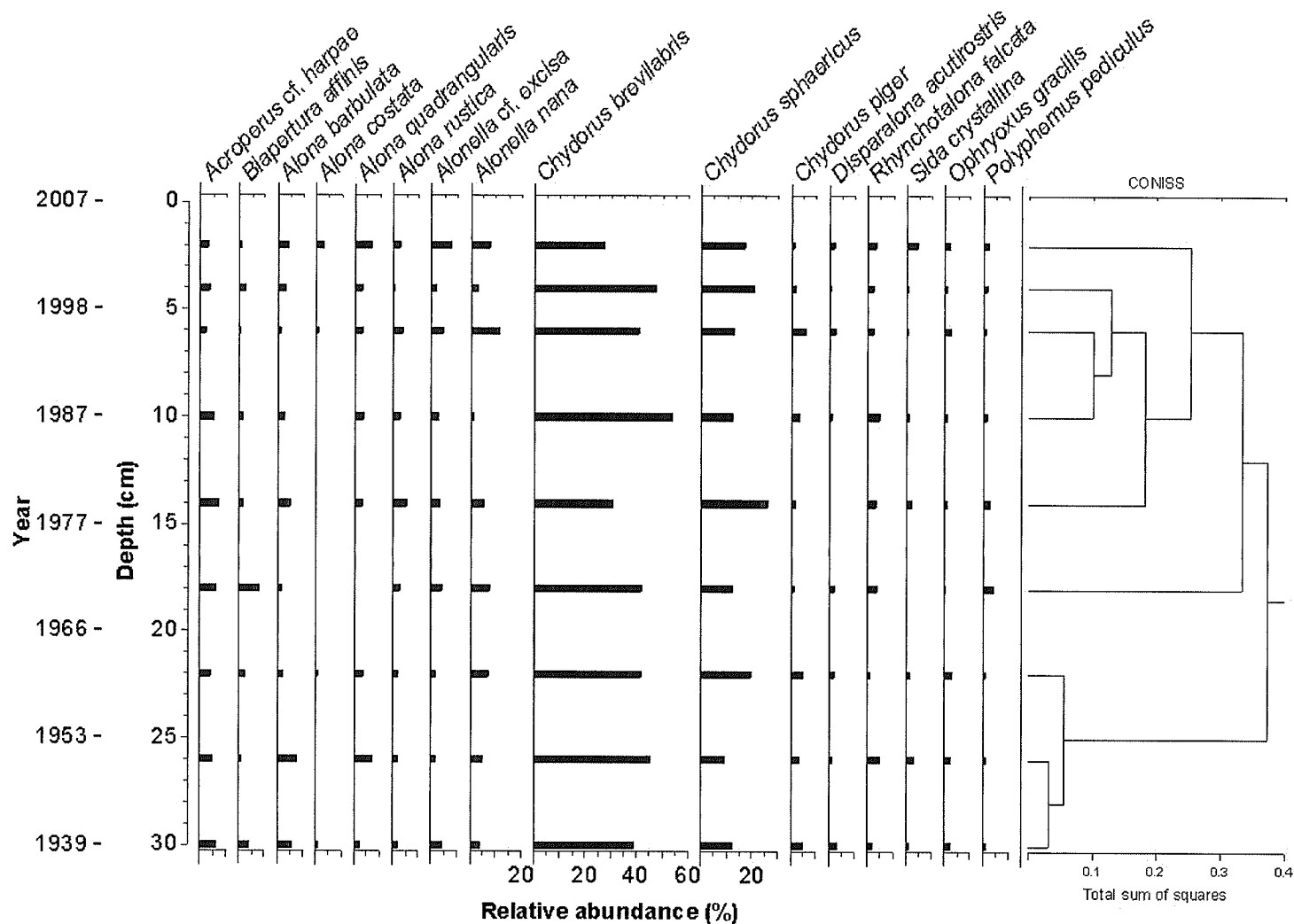


Figure 12: Vertical profiles of relative abundance (%) of littoral cladoceran species for Lake 377. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differences as compared to Figures 10, 11, 13-15).

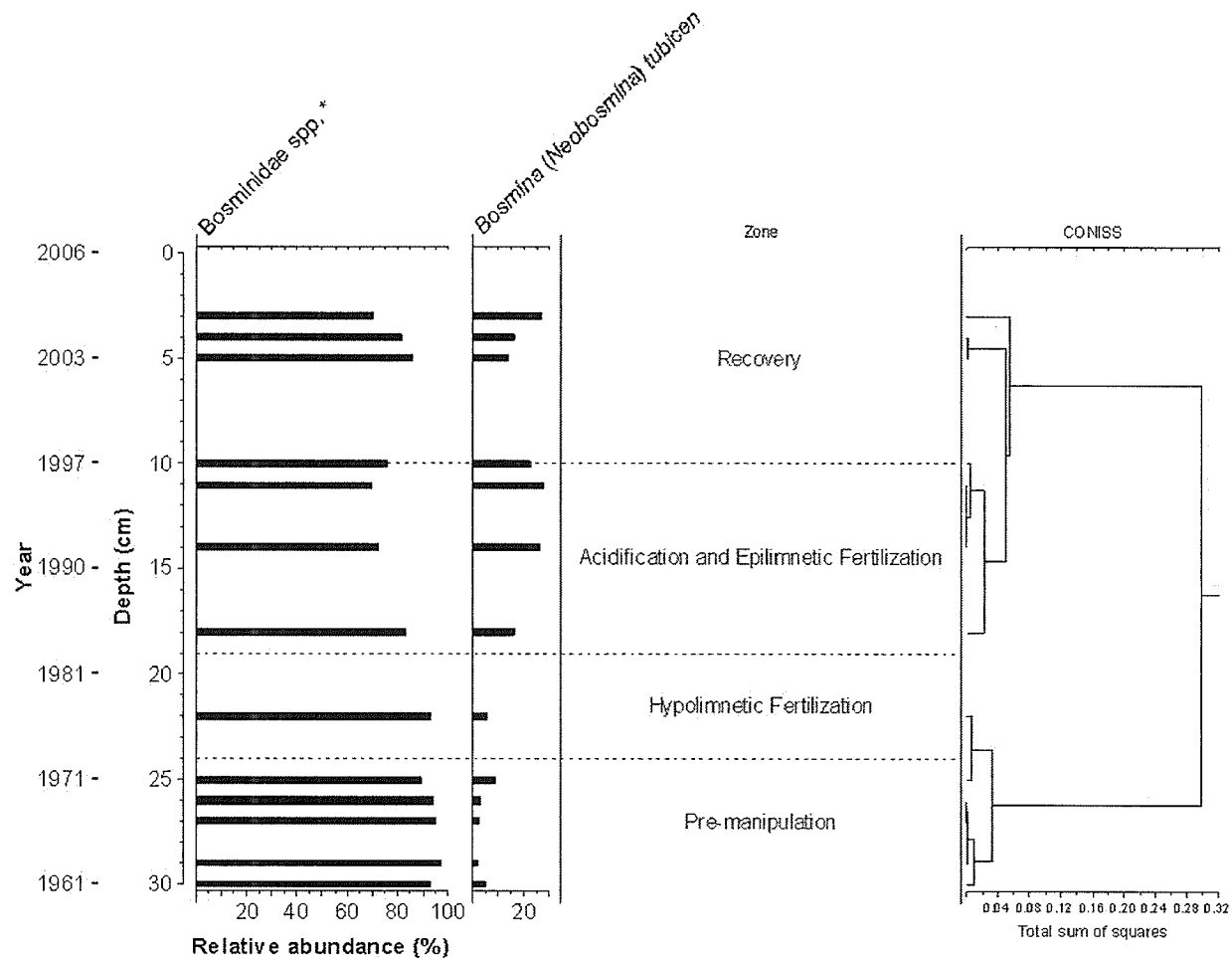


Figure 13: Vertical profiles of relative abundance (%) of pelagic cladoceran species for Lake 302N. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differs, as compared to Figures 10-12, 14-15). * - *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederi*.

however, *B. (N.) tubicen* increased during acidification and into recovery to a maximum relative abundance of almost 30% at depths 11 cm (ca. 1996) and 4 cm (ca. 2004). With the increase in the relative abundance of *B. (N.) tubicen*, there was a corresponding decrease in the relative abundance of the three other Bosminidae spp. (*B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*). A constrained cluster analysis showed a distinct separation of the pre-manipulation, acidification and recovery periods; however, the groups clustered more closely than the littoral cladoceran community in Lake 302N (Figure 10). The relative abundances of the *D. pulex*-type group, *D. mendotae*-type group and *Leptodora kindtii* did not increase above 2% throughout the entire length of the core.

The Lake 223 pelagic cladoceran community was also dominated by Bosminidae spp. (including *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*), but had a greater proportion of *Daphnia* spp. than seen in Lake 302N or Lake 377 (Figure 14). Prior to acidification, *B. (N.) tubicen* was present at a relative abundance of less than 2%. During acidification and into recovery, *B. (N.) tubicen* abundance increased to a maximum relative abundance of 22% at 2 cm (ca. 2007). There was a corresponding decrease in the relative abundance of the other three Bosminidae spp. (*B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*), reaching a minimum relative abundance of 56% ca. 2007. The *D. mendotae*-type group was the dominant daphniid group throughout the entire core, and the only daphniid group present prior to acidification. During acidification, the *D. pulex*-type group appeared; however, it reached a maximum relative abundance of only 3% ca. 1987. With the appearance of the *D. pulex*-type group, there was a corresponding decrease in the relative abundance of the *D.*

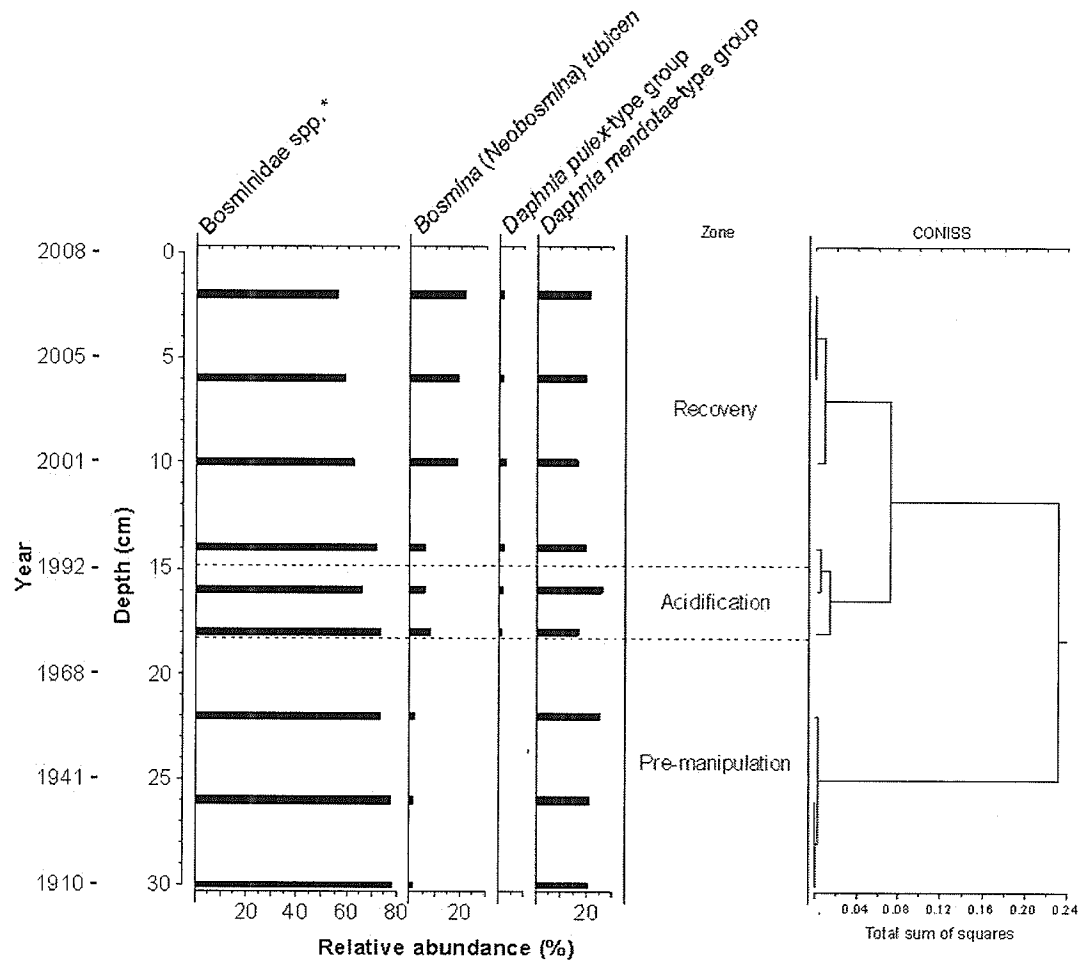


Figure 14: Vertical profiles of relative abundance (%) of pelagic cladoceran species for Lake 223. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differs, as compared to Figures 10-13,15). * - *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*.

mendotae-type group by approximately 5%, compared to its pre-manipulation relative abundance. A constrained cluster analysis showed a distinct separation of the pre-manipulation, acidification and recovery periods; however, the groups clustered more closely than the littoral cladoceran community in Lake 223 (Figure 11). *L. kindtii* was present, but at a relative abundance of less than 2% throughout the entire length of the core.

The Lake 377 pelagic cladoceran community was dominated almost entirely by Bosminidae spp. (including *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*) throughout the length of the core, at a relative abundance of approximately 98% (Figure 15). All other pelagic species (*B. (N.) tubicen*, *D. pulex*-type group, *D. mendotae*-type group and *L. kindtii*) were rare throughout the core. The exception to this was at 2 cm (ca. 2005). *B. (N.) tubicen*, which had existed at a relative abundance of less than 3% throughout the rest of the core, increased to 13%. In addition, the *D. mendotae*-type group, which had existed at a relative abundance of less than 2% throughout the rest of the core, increased to 8%. With the increase of these two species, there was a corresponding decrease in the relative abundance of the three dominant Bosminidae spp. (*B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederii*). Unlike the littoral cladoceran community (Figure 12), a constrained cluster analysis for the pelagic community was weakly clustered, showing only a clear separation of the top depth (2 cm; ca. 2005) from the rest of the core (Figure 15).

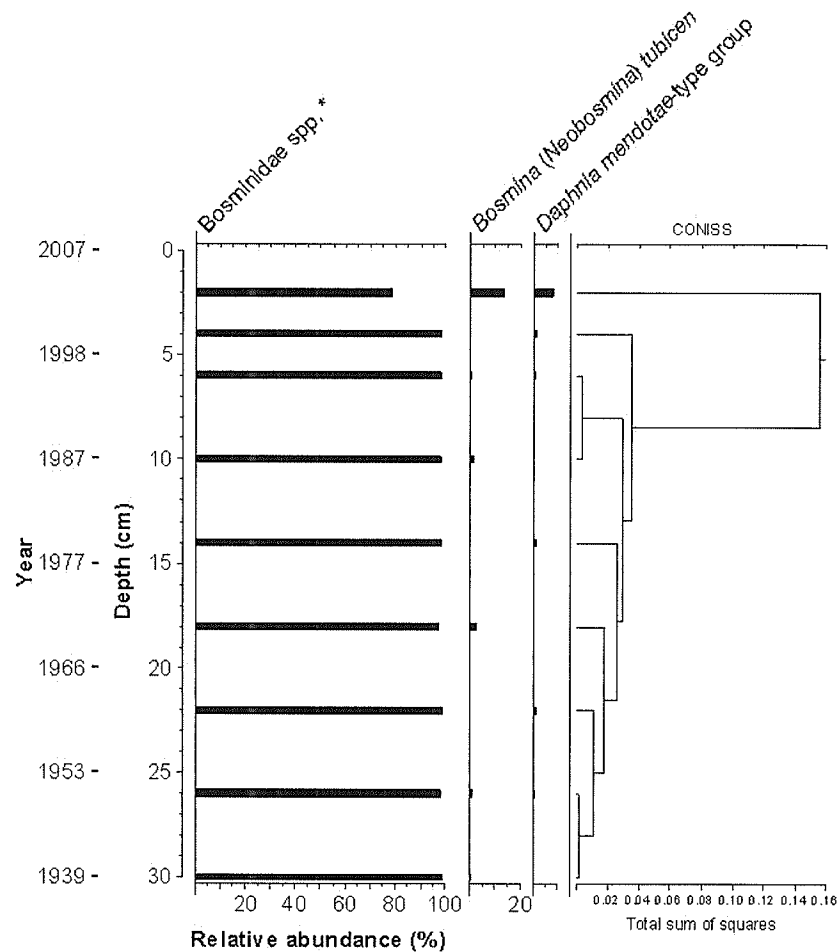


Figure 15: Vertical profiles of relative abundance (%) of pelagic cladoceran species for Lake 377. Rare species with less than 2% relative abundance in all sample depths were removed from analysis. Constrained cluster analysis presented at right (CONISS, Grimm, 1987; notice CONISS scale differs, as compared to Figures 10-14). * - *B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) liederi*.

Cladoceran abundance and accumulation rates

Littoral cladoceran abundance in Lake 302N varied little throughout the sediment core, and decreased only slightly from pre-manipulation to hypolimnetic fertilization, acidification and recovery periods (Figure 16). Pelagic cladoceran abundance, on the other hand, increased during pre-manipulation, remained stable during hypolimnetic fertilization, and then increased during the acidification and recovery phases. A large decrease in abundance was seen during the recovery phase (ca. 2004); however confounding factors, rather than a biological response, likely explain this decrease (see section on 'Methodology' below). Cladoceran accumulation rates for Lake 302N were calculated using a constant sedimentation rate of $0.0366 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$, as estimated from the ^{210}Pb linear regression model (Figure 17). Therefore, changes in accumulation rate throughout the core mirrored those changes seen in cladoceran abundance.

Similar to Lake 302N, Lake 223 littoral cladoceran abundance remained fairly stable throughout the sediment core (Figure 18.). Pelagic cladoceran abundance in Lake 223 showed a similar response during the period of acidification as seen in Lake 302N. Pelagic cladoceran abundance increased slightly during the pre-manipulation period and continued to increase into the period of acidification, showing a more drastic increase between 14 cm and 10 cm (ca. 1979-1987). During recovery, pelagic cladoceran abundance remained fairly stable, but above values seen during the pre-manipulation phase. Cladoceran accumulation rates for Lake 223 were also calculated based on estimates from the linear regression model ($0.0444 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for 0-14 cm; $0.0111 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for 14-30 cm; Figure 19). Higher sedimentation rates above 14 cm (ca. 1996)

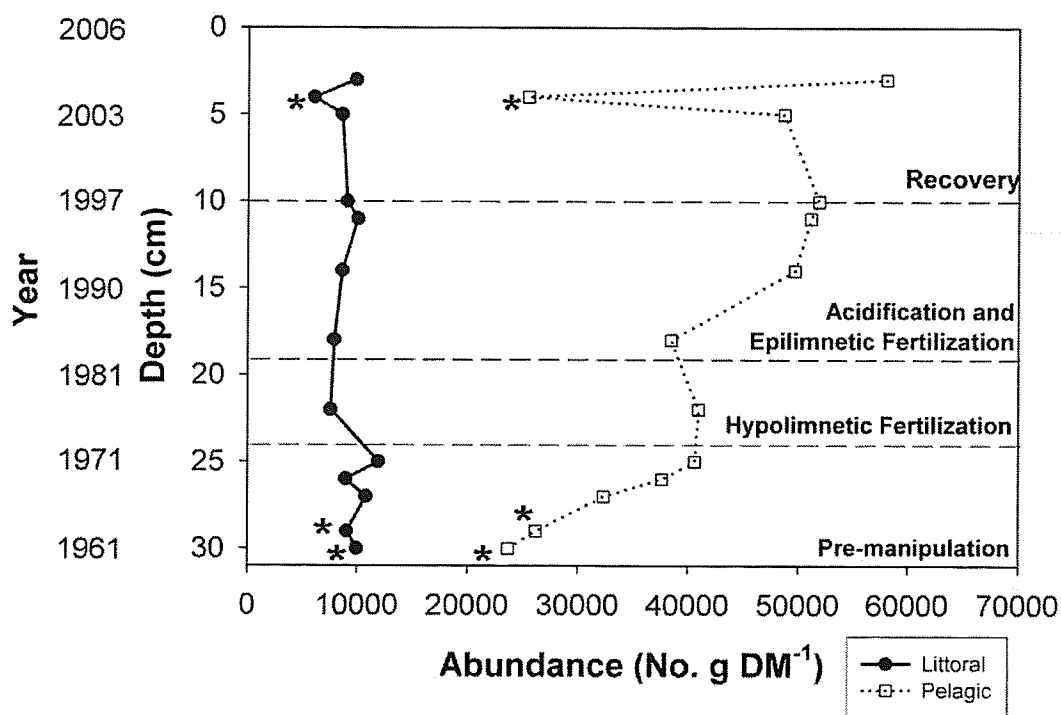


Figure 16: Vertical profile of abundance of pelagic and littoral cladoceran species (exuviae • g DM⁻¹) for Lake 302N. Dashed lines separate periods of pre-manipulation, hypolimnetic fertilization, acidification and epilimnetic fertilization and recovery. * - depths where sediment had been processed for ²¹⁰Pb dating prior to examination of fossil material (see results section on 'Methodology' for discussion).

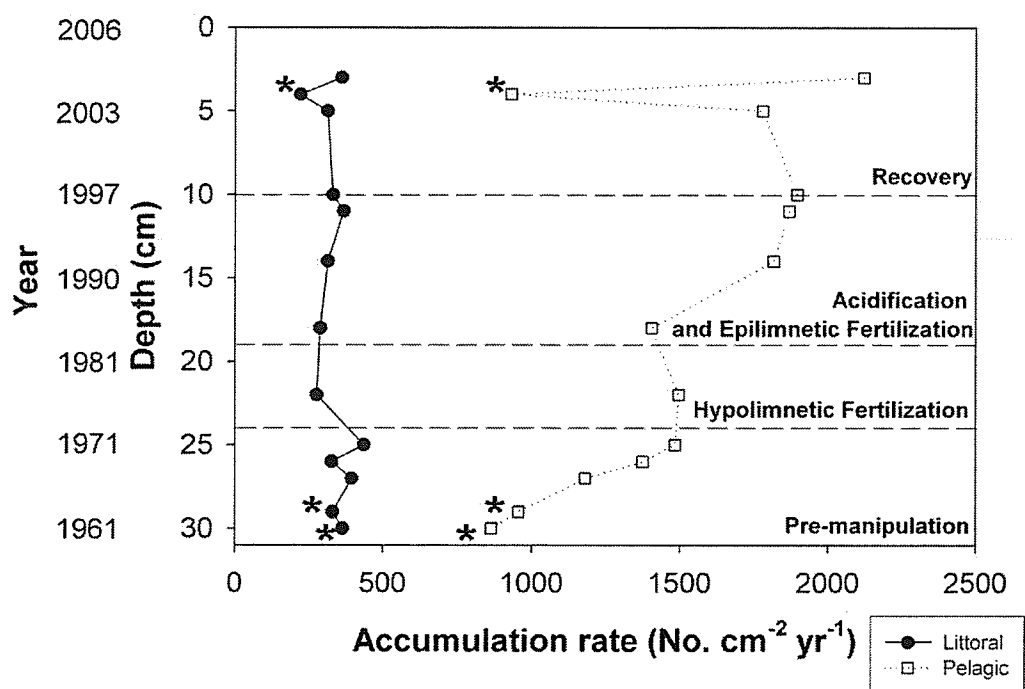


Figure 17: Vertical profile of accumulation rate of pelagic and littoral cladoceran species (No. • cm⁻² • yr⁻¹) for Lake 302N. Dashed lines separate periods of pre-manipulation, hypolimnetic fertilization, acidification and epilimnetic fertilization and recovery. * - depths where sediment had been processed for ²¹⁰Pb dating prior to examination of fossil material (see results section on 'Methodology' for discussion).

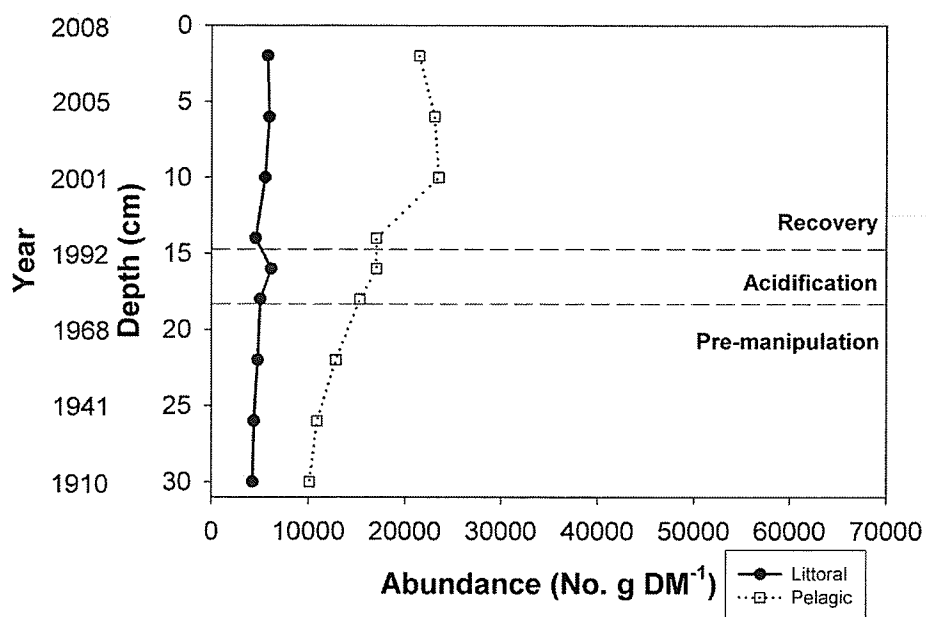


Figure 18: Vertical profile of abundance of pelagic and littoral cladoceran species (exuviae • g DM⁻¹) for Lake 223. Dashed lines separate periods of pre-manipulation, acidification and recovery.

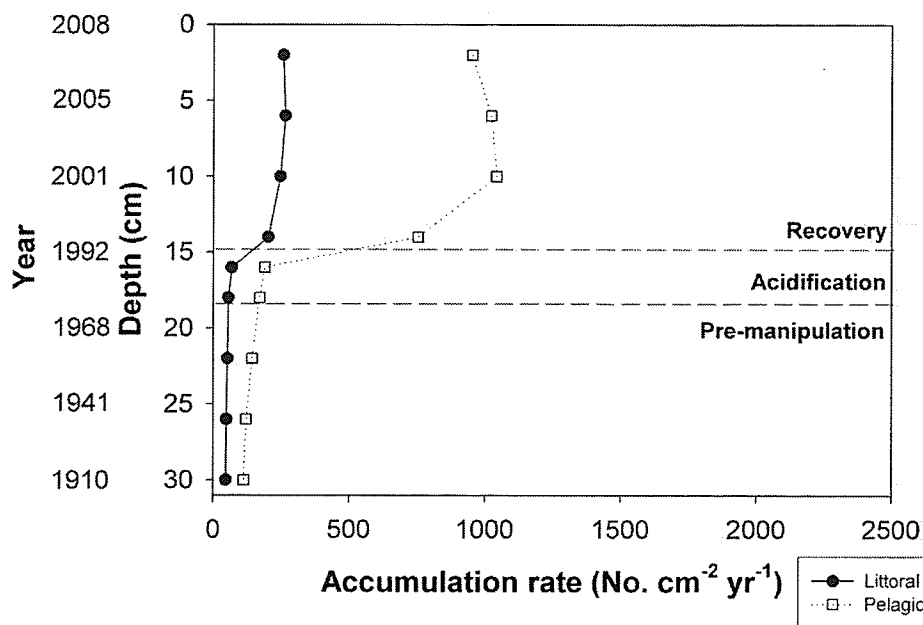


Figure 19: Vertical profile of accumulation rate of pelagic and littoral cladoceran species (No. • cm⁻² • yr⁻¹) for Lake 23. Dashed lines separate periods of pre-manipulation, acidification and recovery.

therefore magnify the increase in cladoceran abundance following acidification, as compared to pre-manipulation values.

Similar to Lake 302N and Lake 223, littoral cladoceran abundance varied little throughout the length of the Lake 377 core, with the exception of a decrease in recent sediments (ca. 1996-2004) (Figure 20). Pelagic cladoceran abundance in Lake 377 decreased at the bottom of the core (ca. 1939-1950), remained stable for a 30-year period (ca. 1950-1979) and then increased slightly (ca. 1979-1996) before a drastic decrease at the top of the core (ca. 1996-2004). With the incorporation of changing sedimentation rates throughout the core (as estimated using the CRS model, see Figure 6), two periods of decrease in pelagic cladoceran accumulation rates were seen (ca. 1940-1950; ca. 1996-2004), the greatest of which was in the most recent years (Figure 21). This decrease is a culmination of both decreasing pelagic cladoceran abundance and decreasing sedimentation rates.

Planktonic to littoral ratio

Sediments from each of the three lakes was dominated by remains of planktonic cladocerans (primarily Bosminidae spp.), making up approximately 80% of total abundance (Figures 22, 23 and 24). In Lake 302N, the proportion of littoral to planktonic cladocerans was variable throughout the core (Figure 22). However, there was a general increase in the proportion of planktonic cladocerans from pre-manipulation to the acidification and recovery periods. In Lake 223, the proportion of littoral to planktonic cladocerans was much more stable throughout the core, as compared to Lake 302N (Figure 23). However, there was a similar increase in the proportion of planktonic

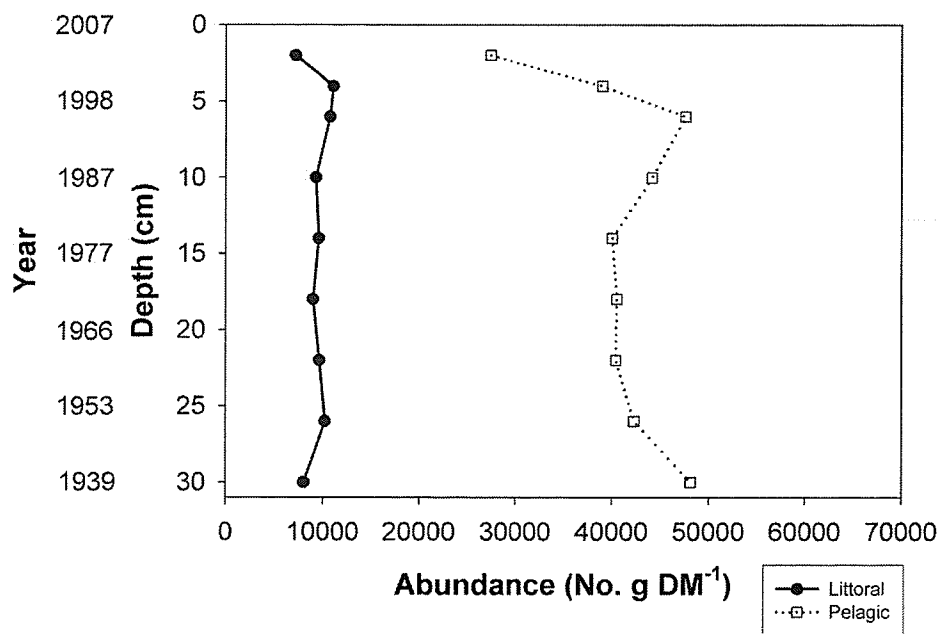


Figure 20: Vertical profile of abundance of pelagic and littoral cladoceran species (exuviae • g DM⁻¹) for Lake 377.

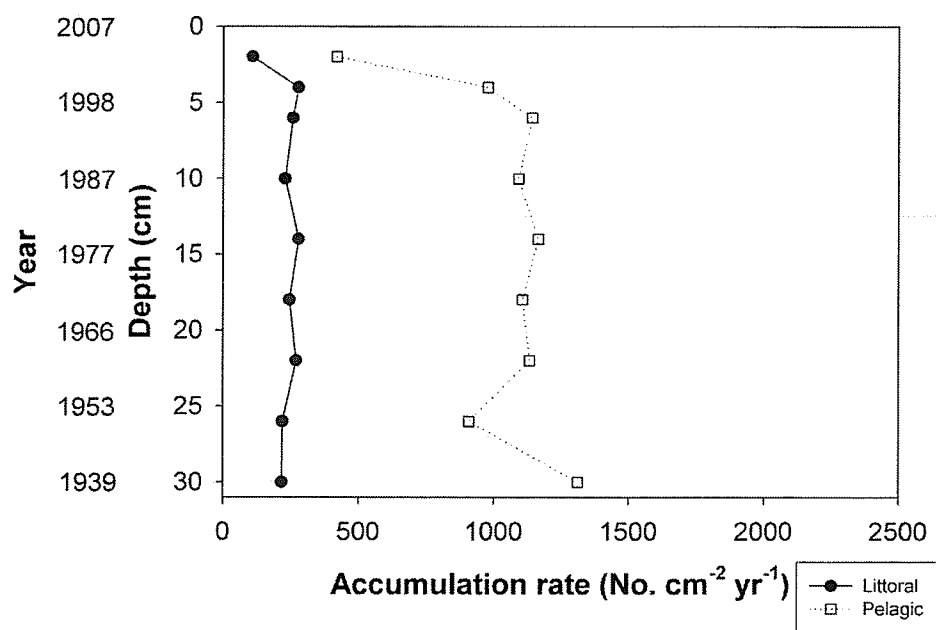


Figure 21: Vertical profile of accumulation rate of pelagic and littoral cladoceran species (No. • cm⁻² • yr⁻¹) for Lake 377.

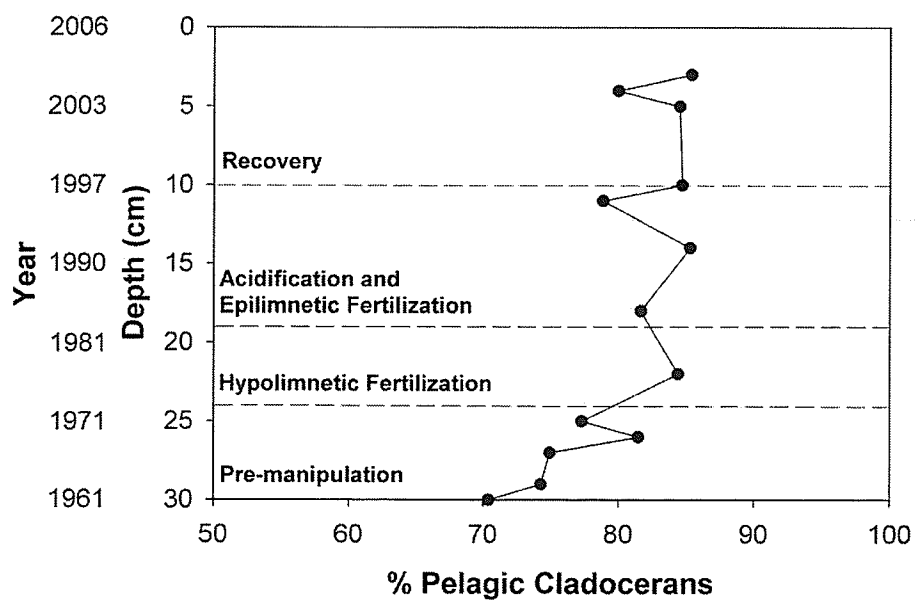


Figure 22: Stratigraphic profile of changes in the planktonic to littoral cladoceran ratio in Lake 302N. Dashed lines separate periods of pre-manipulation, hypolimnetic fertilization, acidification and epilimnetic fertilization and recovery.

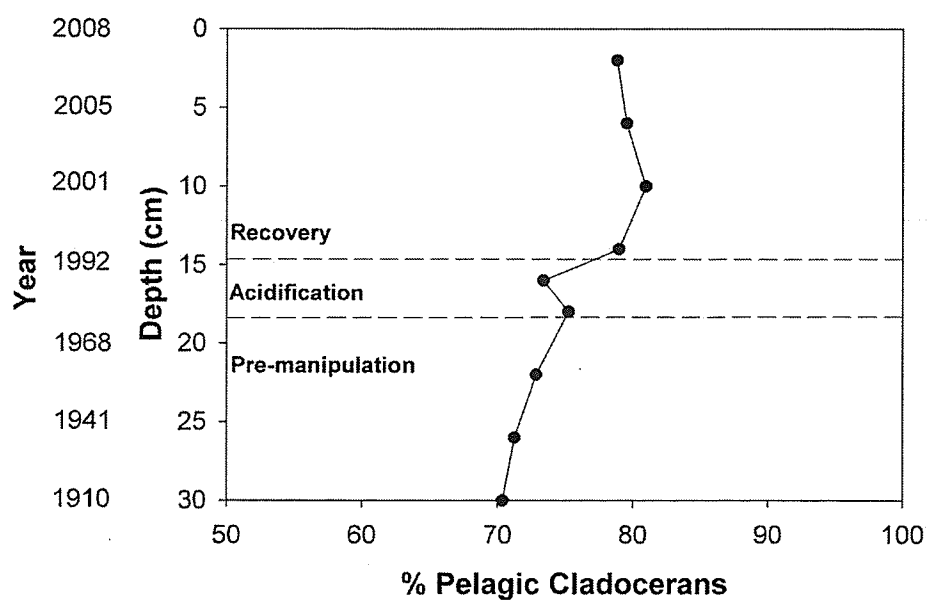


Figure 23: Stratigraphic profile of changes in the planktonic to littoral cladoceran ratio in Lake 223. Dashed lines separate periods of pre-manipulation, acidification and recovery.

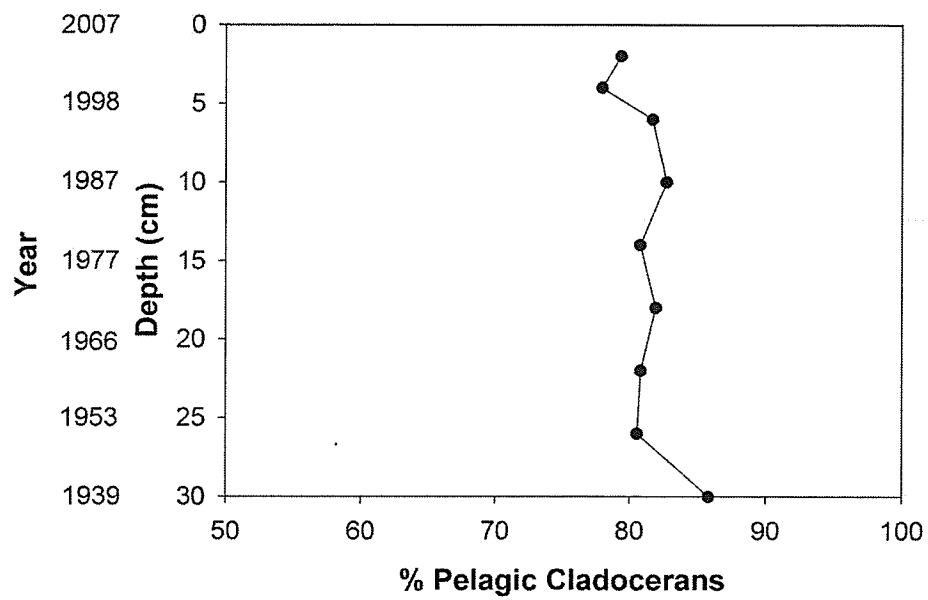


Figure 24: Stratigraphic profile of changes in the planktonic to littoral cladoceran ratio in Lake 377.

cladocerans from pre-manipulation to the acidification and recovery phases. In Lake 377, the planktonic to littoral ratio remained fairly constant throughout the core, with the exception of two periods of decrease, ca. 1939-1950 and following 1996 (Figure 24).

Methodology

An outlier in pelagic cladoceran abundance existed in Lake 302N at 4 cm, where abundance (mostly due to Bosminidae spp.) decreased drastically, as compared to the surrounding depths and the trend of increasing abundance from core bottom to top (Figure 16). This decrease could be due to a response in the Bosminidae spp. population to ecosystem change. However, it could also be attributed to a methodological artifact. A key confounding factor is that, due to limited availability of material, sediments from the 4 cm depth, as well as 29 cm and 30 cm, had been previously dried and ground for use in the ^{210}Pb dating process. This contrasts to the other depths from the Lake 302N, Lake 223 and Lake 377, which were processed for examination from dried material that had not been previously altered. Grinding of the sediment had the potential for fragmenting fossil exuviae, making identification difficult and increasing the proportion of small fragments lost during sieving.

To estimate the effect of grinding on the estimation of cladoceran abundance, a comparison of ground to non-ground sediment, from the same core depth in Lake 377, was made. A paired t-test on Bosminidae spp. counts from ground and non-ground sediment found a significant difference ($t=9.023$; $df=4$; $p\text{-value} = 0.001$) between the estimated abundances. Personal observation (L. Frazer) was also made of this increased fragmentation, as depths 4 cm, 29 cm and 30 cm had higher numbers of mucrones

separated from their carapaces, as compared to the other un-altered depths in Lake 302N. Overall, the estimated Bosminidae spp. abundance from the ground material was about 50% less than that estimated from the non-ground material. In the case of 4 cm (Lake 302N), an increase in Bosminidae spp. abundance of 50% would bring the outlier back within the range seen during recovery (Figure 16). However, an increase in Bosminidae spp. abundance of 50% at the two other altered depths (29 cm and 30 cm) would bring Bosminidae spp. abundances above the range seen in the other pre-manipulation depths. The effect of the grinding process on smaller cladoceran fossil fragments (e.g. Family Chydoridae) is unknown; therefore, results at these depths must be treated with caution.

Ordination: Correspondence analysis (CA)

A CA was performed to determine the trajectory of change in littoral cladoceran community structure over time in the two manipulated lakes, as compared to the reference lake, as well as to determine if the variation seen in the reference lake was greater than the response to acidification in the two manipulated lakes. After the removal of rare species with a relative abundance of less than 5% for all sample depths, 14 chydorids were included in the analysis. Overall, the dispersion in sample depths, from pre- to post-manipulation, in Lake 302N and Lake 223 was much greater than for Lake 377 throughout the entire core (Figure 25a-c). This suggests that change in chydorid community structure over time in the manipulated Lakes 302N and 223 was greater than in the reference Lake 377. In addition, there was a clear partitioning between the pre-

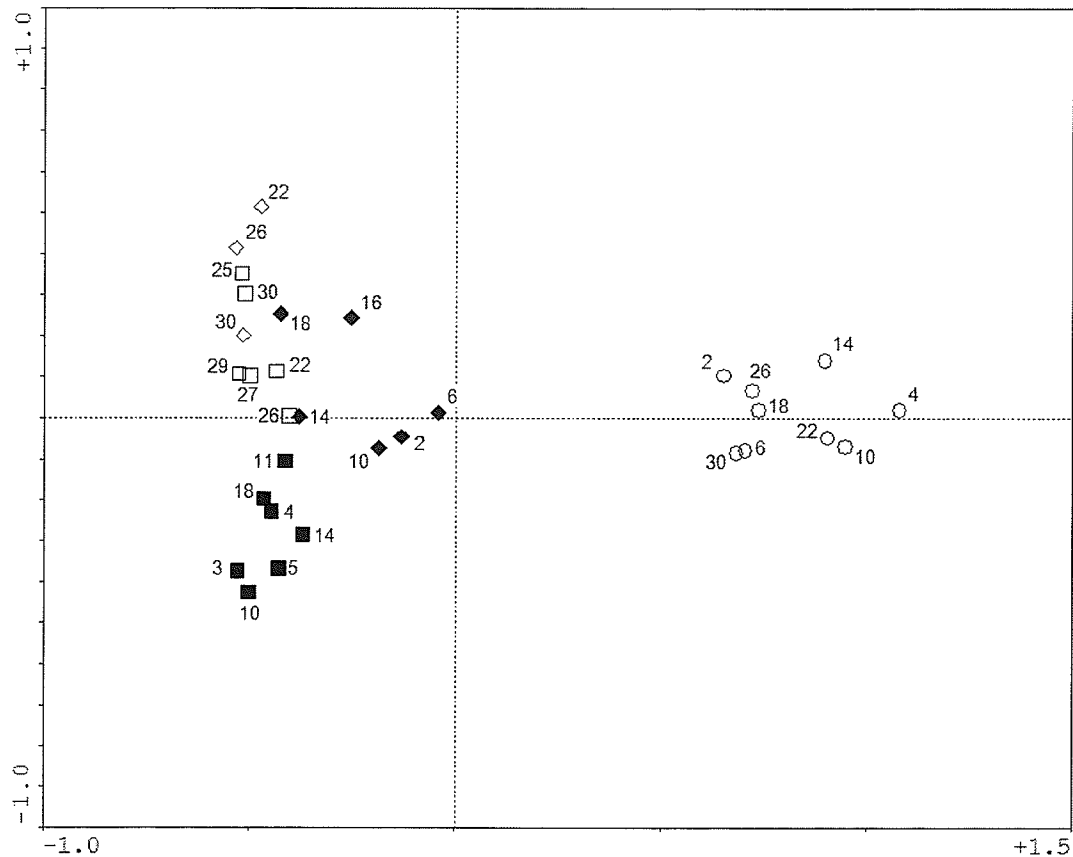


Figure 25a: Correspondence analysis (CA) of littoral cladoceran species abundance (exuviae $\cdot$ g⁻¹ DM) for Lake 302N (■, □), Lake 223 (◆, ◇) and Lake 377 (○). Open squares, diamonds and circles indicate pre-manipulation (Lake 302N, □; Lake 223, ◇) or reference (Lake 377, ○) sample depths. Filled squares and diamonds indicate manipulation and recovery sample depths (Lake 302N, ■; Lake 223, ◆). Numbers correspond to core sampling depth, in centimetres. Littoral cladoceran species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses. Note change in scale, as compared to Fig. 25b.

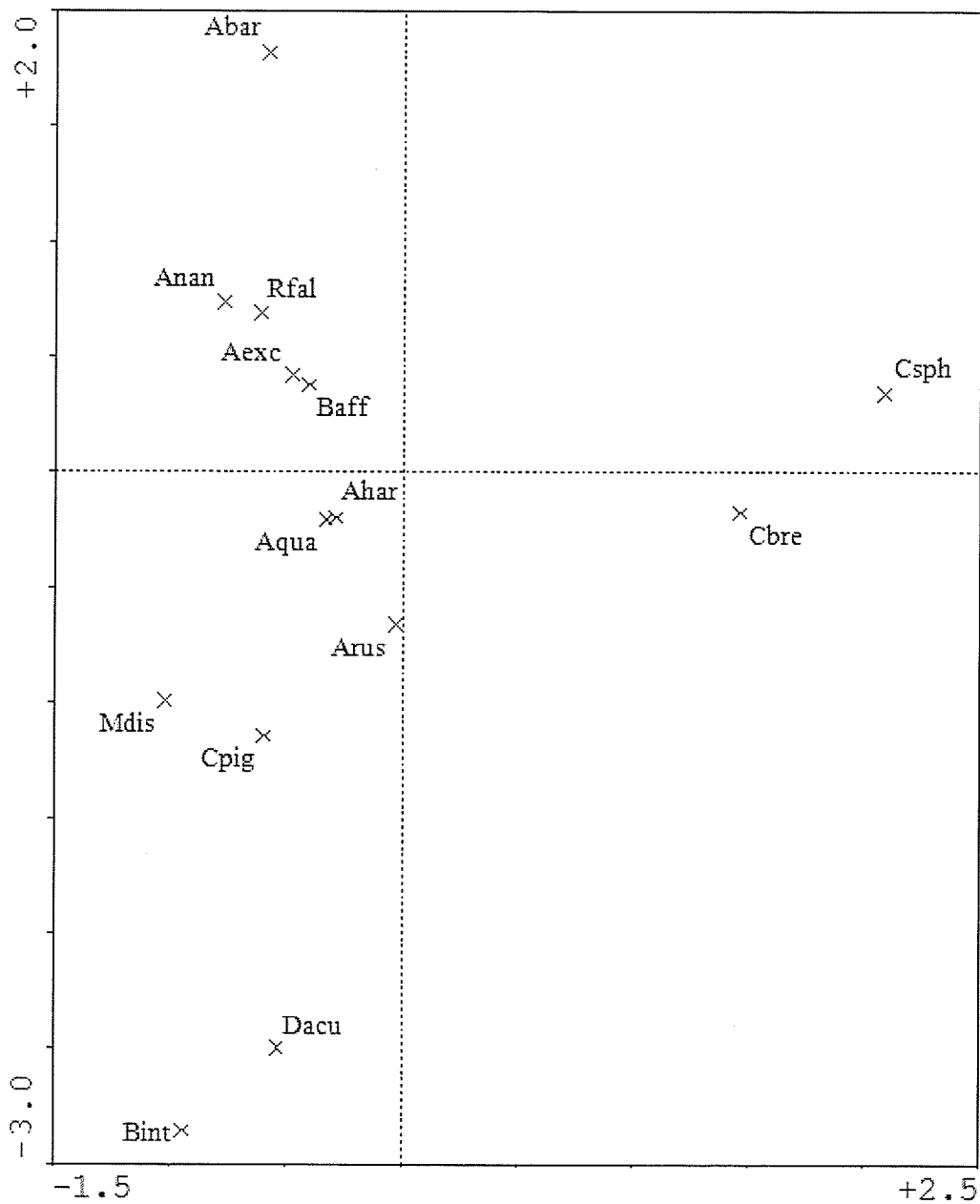


Figure 25b: Correspondence analysis (CA) of littoral cladoceran species for Lake 302N, Lake 223 and Lake 377. Littoral cladoceran species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses. Note change in scale, as compared to Fig. 25a, c. Species codes are: Ahar (*Acroperus* cf. *harpae*), Baff (*Biapertura affinis*), Abar (*Alona barbulata*), Bint (*Biapertura intermedia*), Aqua (*Alona quadrangularis*), Arus (*Alona rustica*), Aexc (*Alonella* cf. *excisa*), Anan (*Alonella nana*), Cbre (*Chydorus brevilabris*), Csph (*Chydorus sphaericus*), Cpig (*Chydorus piger*), Dacu (*Disparalona acutirostris*), Mdis (*Monospilus dispar*), Rfal (*Rhynchotalona falcata*).

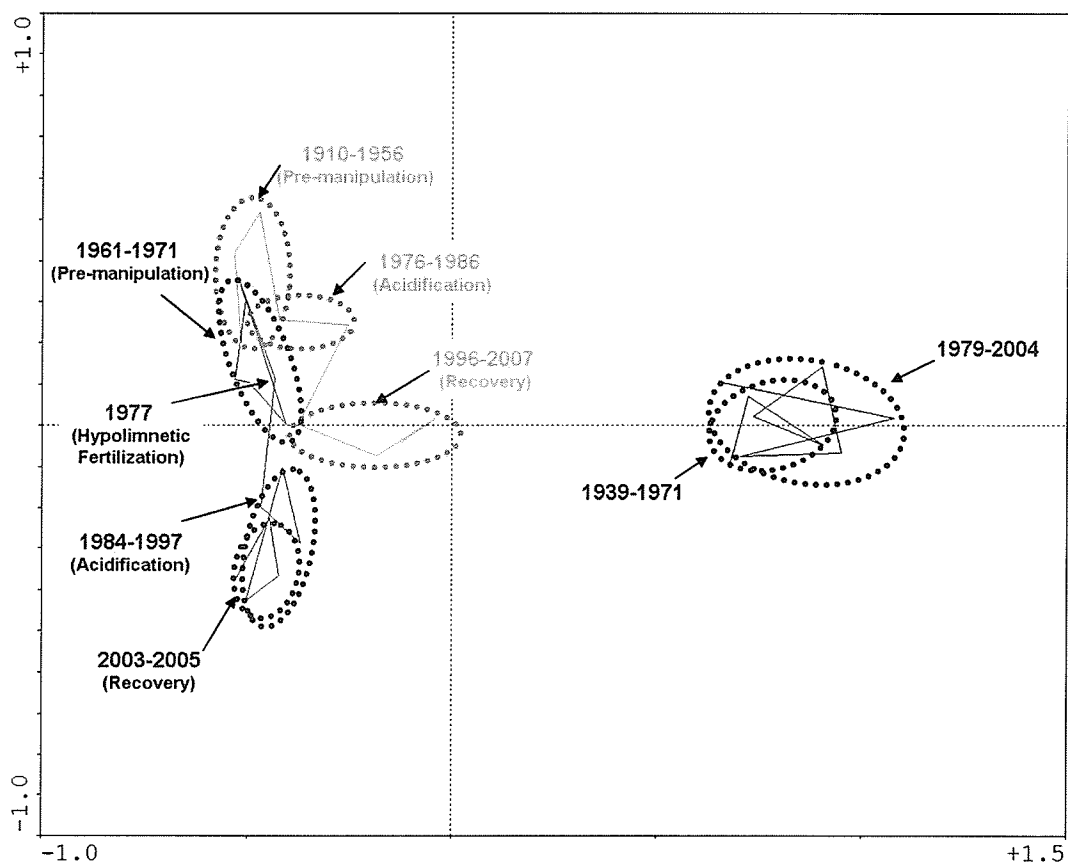


Figure 25c: Correspondence analysis (CA) showing trajectory of change in littoral cladoceran species abundance (exuviae $\cdot$ g⁻¹ DM) over time. Periods of pre-manipulation, manipulation and recovery are indicated for Lake 302N (red) and Lake 223 (green), with corresponding ²¹⁰Pb dating estimates. Pre- and post-1970 sample depths are indicated for Lake 377 (blue). Littoral cladoceran species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses. Note change in scale, as compared to Fig. 25b.

manipulation phases, and the acidification and recovery phases in both manipulated lakes, demonstrating a change in cladoceran community structure over time. The first axis (eigenvalue, $\lambda_1 = 0.362$), which accounted for 70% of the variance in species data, appeared to partition the two manipulated lakes and the reference lake by chydorid community type. Lake 302N and Lake 223 showed a more even chydorid community, whereas Lake 377 was dominated by *C. brevilabris* and *C. sphaericus*. The second axis ($\lambda_2 = 0.047$), which accounted for 10% of the variance in species data, partitioned the chydorid community along a pH gradient (pre-manipulation and reference depths, versus acidification and recovery depths).

For the manipulated lakes, the pre-manipulation chydorid community structure had positive loadings on the second axis, whereas the acidification and recovery community structure had negative loadings (Figure 25a). The exception to this was the acidification phase and early recovery for Lake 223, where the amount of change in littoral community structure, relative to the pre-manipulation state, seemed to be less than for Lake 302N. Key chydorid species driving pre-manipulation community structure in the CA included *A. barbulata*, *A. nana*, *R. falcata*, *A. cf. excisa* and *Biapertura affinis* (Figure 25b). Key chydorid species driving acidification and recovery community structure included *B. intermedia*, *D. acutirostris*, *C. piger*, *M. dispar* and *Alona rustica*.

The trajectory of recovery also differed between the two manipulated lakes (Figure 25c). The trajectory of recovery for Lake 223 moved primarily along the first axis, showing an increase in abundance of *C. sphaericus* and *C. brevilabris*. The trajectory of recovery for Lake 302N, on the other hand, moved primarily along the second axis, and was similar to the trajectory seen during the acidification phase. An

important point to note, however, is that the period of controlled recovery (increasing chemical recovery from the minimum pH) was much longer for Lake 223 (10 years), as compared to Lake 302N (3 years). Neither manipulated lake moved towards or returned to the pre-manipulation state during recovery.

For Lake 377, there appeared to be no direction in the trajectory of change in the chydorid community structure over time in the CA; however, the spread in the most recent 25 years (14 cm to 2 cm; ca. 1979-2004) was much greater than that seen at the bottom of the sediment core (30 cm to 18 cm; ca. 1939-1971; Figure 25a, c). This indicates an increase in variability of the chydorid community structure over time.

Ordination: Canonical correspondence analysis (CCA)

As the overall littoral cladoceran community structure of Lake 377 appeared to be very different as compared to Lake 302N and Lake 223, a CCA was performed on pre- and post-manipulation littoral cladoceran species abundance data and environmental variables from each of the three study lakes (Figure 26a, b). Similar to the results of the CA, Lake 302N and Lake 223 were separated along the first axis from Lake 377, which explained 83% of the variance in species and environmental data ($\lambda_1 = 0.359$). This is likely due to the fact that Lake 302N and Lake 223 showed a more even chydorid assemblage, whereas Lake 377 had a chydorid assemblage dominated by *C. brevilabris* and *C. sphaericus* (Figure 27b). The second axis, which explained 10% of the variance ($\lambda_2 = 0.042$), primarily separated the pre- and post-manipulation states of the experimental lakes (Lake 302N and Lake 223). After forward selection, key

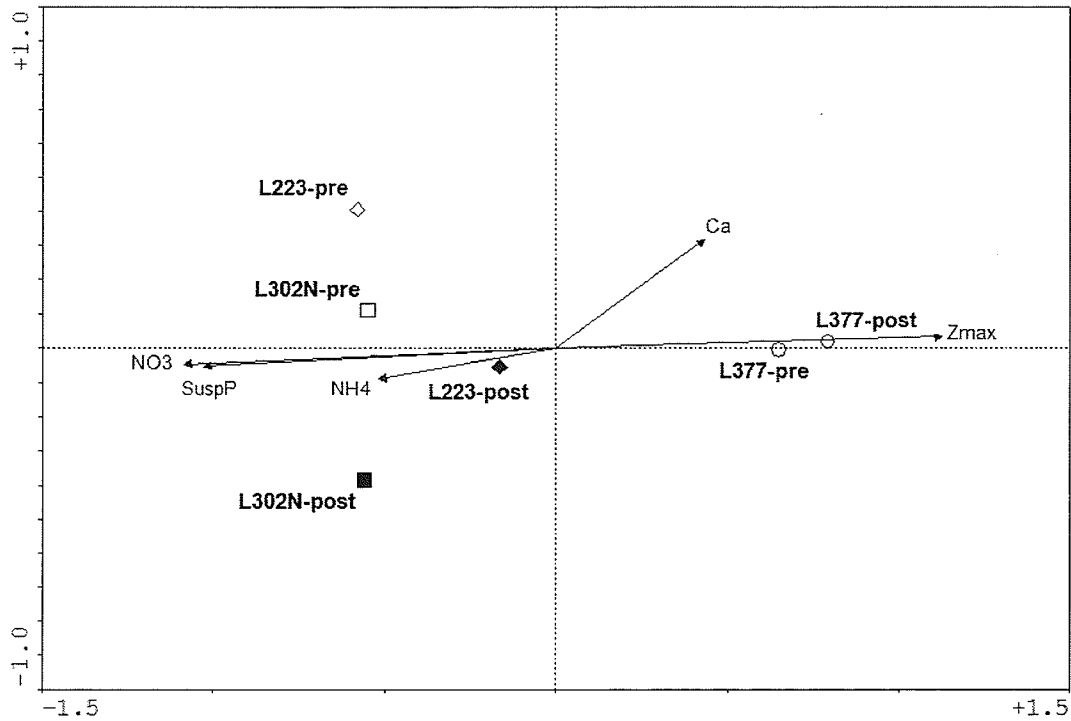


Figure 26a: Canonical correspondence analysis (CCA) of littoral cladoceran species abundance (exuviae $\cdot$ g⁻¹ DM) for Lake 302N (■, □), Lake 223 (◆, ◇) and Lake 377 (○). Open squares, diamonds and circles indicate pre-manipulation (Lake 302N-pre, □; Lake 223-pre, ◇) or reference (Lake 377-pre, -post, ○) sample depths. Filled squares and diamonds indicate post-manipulation depths (Lake 302N-post, ■; Lake 223-post, ◆). Littoral cladoceran species with a relative abundance of less than 5% for all sample depths were eliminated from the analyses. Environmental and morphological variable codes are nitrate (NO3), ammonium (NH4), suspended phosphorus (SuspP), calcium (Ca) and maximum depth (Zmax). Note change in scale, as compared to Fig. 26b.

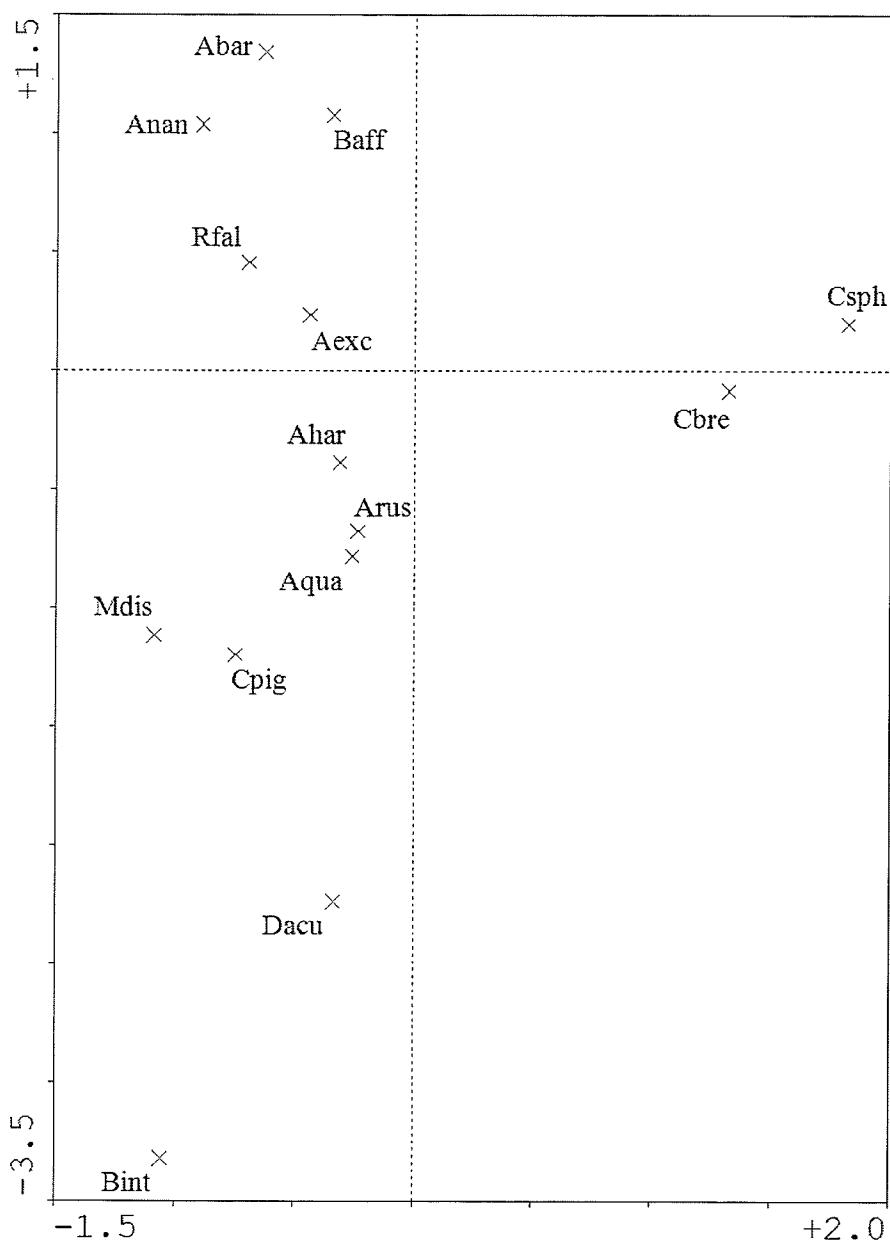


Figure 26b: Canonical correspondence analysis (CCA) of littoral cladoceran species abundance (exuviae $\cdot$ g⁻¹ DM) for Lake 302N, Lake 223 and Lake 377. Littoral cladoceran species with a relative abundance of less than 5% for all years were eliminated from the analyses. Species codes are: Ahar (*Acroperus* cf. *harpae*), Baff (*Biapertura affinis*), Abar (*Alona barbulata*), Bint (*Biapertura intermedia*), Aqua (*Alona quadrangularis*), Arus (*Alona rustica*), Aexc (*Alonella* cf. *excisa*), Anan (*Alonella nana*), Cbre (*Chydorus brevilabris*), Csph (*Chydorus sphaericus*), Cpig (*Chydorus piger*), Dacu (*Disparalona acutirostris*), Mdis (*Monospilus dispar*), Rfal (*Rhynchotalona falcata*). Note change in scale, as compared to Fig. 26a.

environmental and morphological variables that partitioned the lakes included $Z_{\max}$, nitrate, suspended phosphorus, ammonium and calcium.

Significance of community change: ANOSIM and SIMPER

For the ANOSIM, both Lake 302N and Lake 223 showed significant differences between their pre- and post-manipulation littoral cladoceran communities (Table 3). Lake 302N showed a greater change between its pre- and post-manipulation communities (R-statistic = 0.624; p-value = 0.002) than Lake 223 (R-statistic = 0.525; p-value = 0.024). Lake 302N and Lake 223 also shared key species contributing to the dissimilarity of the pre- and post-manipulation communities, showing a decrease in *A. nana* and *A. barbulata* from pre- to post-manipulation (Table 4). Lake 302N dissimilarity was also strongly characterized by an increase in *B. intermedia* and *M. dispar* abundance from pre- to post-manipulation, whereas Lake 223 dissimilarity was strongly driven by an increase in *C. brevilabris* abundance from pre- to post-manipulation. In addition, the post-manipulation communities of Lake 302N and Lake 223 were more similar to each other (R-statistic = 0.865; p-value = 0.002) than the pre-manipulation communities (R-statistic = 1; p-value = 0.012). Key species driving the differences in the pre-manipulation communities were *A. nana*, *A. cf. harpae*, *A. barbulata* and *A. quadrangularis*. Key species driving the differences between the post-manipulation communities were *C. piger*, *A. nana*, *B. intermedia*, *M. dispar* and *A. quadrangularis*. Differences between Lake 302N and Lake 223 pre- and post-manipulation communities were primarily due to higher abundances of each of these species in Lake 302N.

Table 3: ANOSIM results for Lake 302N and Lake 223 pre-manipulation (pre) and post-manipulation (post); and Lake 377 pre-1976 (pre) and post-1976 (post) littoral cladoceran communities. * indicates a significance of $p \leq 0.05$. ** indicates a significance of $p \leq 0.01$.

Group	n (a, b)	R	P-value
L302N pre ^a and post ^b	6, 7	0.624	0.002**
L223 pre ^a and post ^b	3, 6	0.525	0.024*
L302N pre ^a and L223 pre ^b	6, 3	1	0.012*
L302N post ^a and L223 post ^b	7, 6	0.865	0.002**
L377 pre ^a and post ^b	4, 5	-0.069	0.651

Table 4: SIMPER results for Lake 302N and Lake 223 pre-manipulation (pre) and post-manipulation (post); and Lake 377 pre-1976 (pre) and post-1976 (post) littoral cladoceran communities. Only species contributing a cumulative percent dissimilarity contribution of 50% for each grouping are shown. Species are ordered in decreasing contribution.

Group	Species	Average Dissimilarity	Dissimilarity / Standard Deviation	Contribution to Total Dissimilarity (%)
Lake 302N pre and post	<i>Alonella nana</i>	4.54	1.82	17.84
	<i>Alona barbulata</i>	4.00	1.64	15.71
	<i>Biapertura intermedia</i>	2.09	2.44	8.20
	<i>Acroperus</i> cf. <i>harpae</i>	1.83	1.62	7.18
	<i>Monospilus dispar</i>	1.76	1.46	6.94
Lake 223 pre and post	<i>Chydorus brevilabris</i>	5.73	1.89	20.70
	<i>Alonella nana</i>	3.52	1.80	12.73
	<i>Alona barbulata</i>	2.44	1.30	8.83
	<i>Acroperus</i> cf. <i>harpae</i>	2.37	1.99	8.57
Lake 302N pre and Lake 223 pre	<i>Alonella nana</i>	7.02	3.87	17.57
	<i>Acroperus</i> cf. <i>harpae</i>	5.53	7.83	13.85
	<i>Alona barbulata</i>	4.69	1.56	11.74
	<i>Alona quadrangularis</i>	3.81	2.65	9.55
Lake 302N post and Lake 223 post	<i>Chydorus piger</i>	4.29	3.24	13.56
	<i>Alonella nana</i>	3.78	1.75	11.95
	<i>Biapertura intermedia</i>	3.55	3.47	11.24
	<i>Monospilus dispar</i>	2.67	1.51	8.45
	<i>Alona quadrangularis</i>	2.47	1.68	7.82
Lake 377 pre and post	<i>Chydorus brevilabris</i>	7.21	1.57	31.41
	<i>Chydorus sphaericus</i>	3.83	1.34	16.68
	<i>Alonella nana</i>	1.80	1.31	7.84

Lake 377 did not show a significant difference in its pre- and post-1976 littoral cladoceran communities (R-statistic = -0.069; p-value = 0.651; Table 3). Although the R-statistic for Lake 377 is only slightly less than zero, a negative R-statistic indicates greater similarity between pre- and post-1976 replicates than within group (pre- or post-) replicates. Lake 377 dissimilarity was characterized by a decrease in *C. brevilabris* abundance and an increase in *C. sphaericus* and *A. nana* abundance from pre- to post-1976 (Table 4). Lake 377 was also found to be significantly different (R-statistic = 1; p-values from 0.001 to 0.029) from all pre- and post-manipulation community combinations with Lake 302N and Lake 223, with the exception of the Lake 223 post-manipulation community (R-statistic = 0.997; p-value = 0.002; not shown in Table 3).

Contemporary pelagic cladoceran community

Ordination: Correspondence analysis (CA)

To confirm the trajectory of change in cladoceran community structure inferred from the fossil record, a CA was performed on contemporary pelagic cladoceran abundance collected from the three study lakes (Malley and Chang, 1994; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data). Similar to what was found in the CA of the littoral cladoceran community, the amount of change in community structure, between pre-manipulation and acidification periods, was greater in the two manipulated lakes as compared to the amount of natural variability in the reference lake (Figure 27a-c). The first axis ($\lambda_1 = 0.530$) explained 41.5% of the variance in species data, while the second axis ($\lambda_2 = 0.286$) explained 22.5% of the variance in species data.

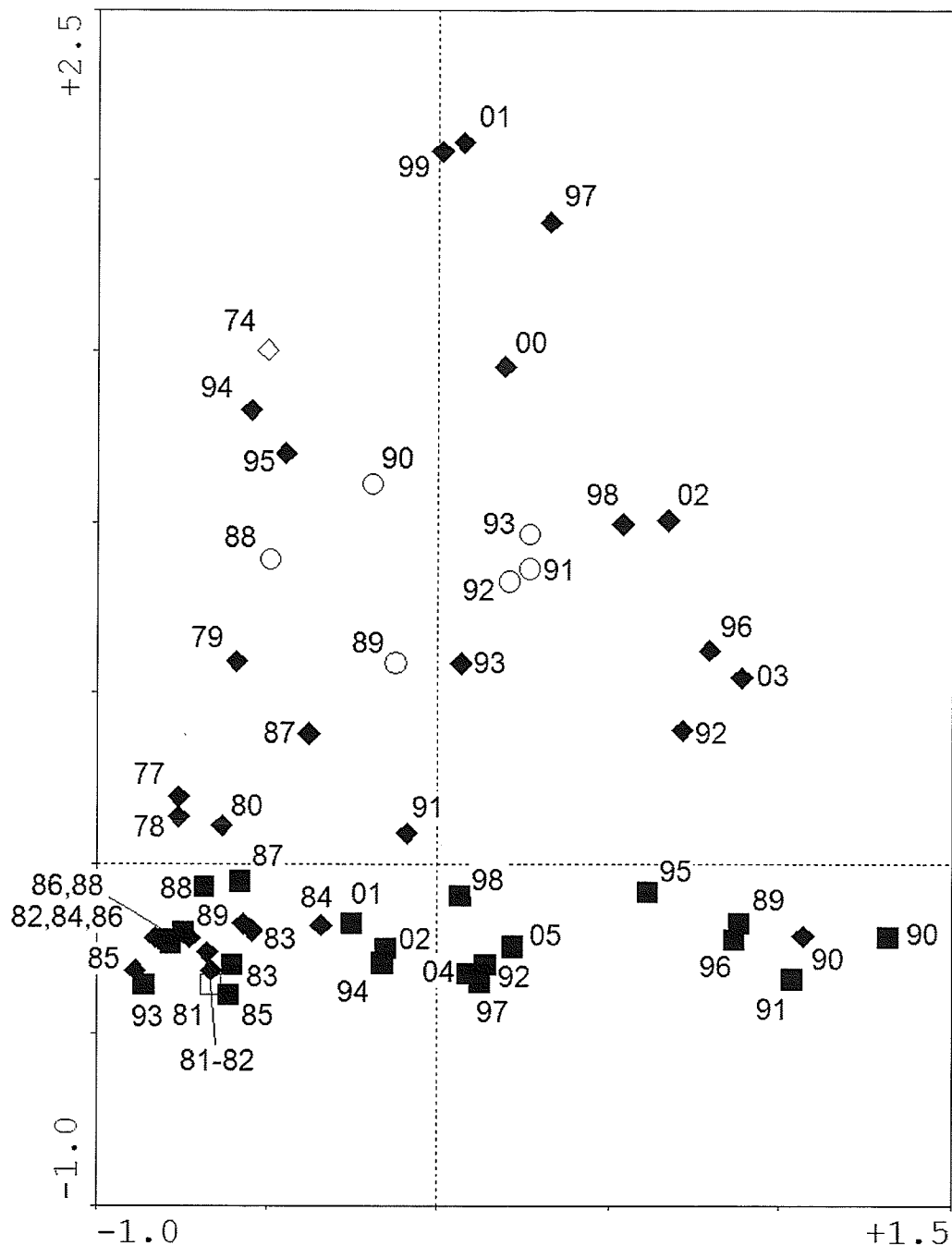


Figure 27a: Correspondence analysis (CA) of contemporary pelagic cladoceran species abundance (animals $\cdot$ L $^{-1}$) for Lake 302N (■, □), Lake 223 (◆, ◇) and Lake 377 (○). Open squares, diamonds and circles indicate pre-manipulation (Lake 302N, □; Lake 223, ◇) or reference (Lake 377, ○) years. Filled squares and diamonds indicate manipulation and recovery years (Lake 302N, ■; Lake 223, ◆). Numbers correspond to last two digits of the sampling year. Pelagic cladoceran species with a relative abundance of less than 5% for all years were eliminated from the analyses. Note change in scale, as compared to Fig. 27b.

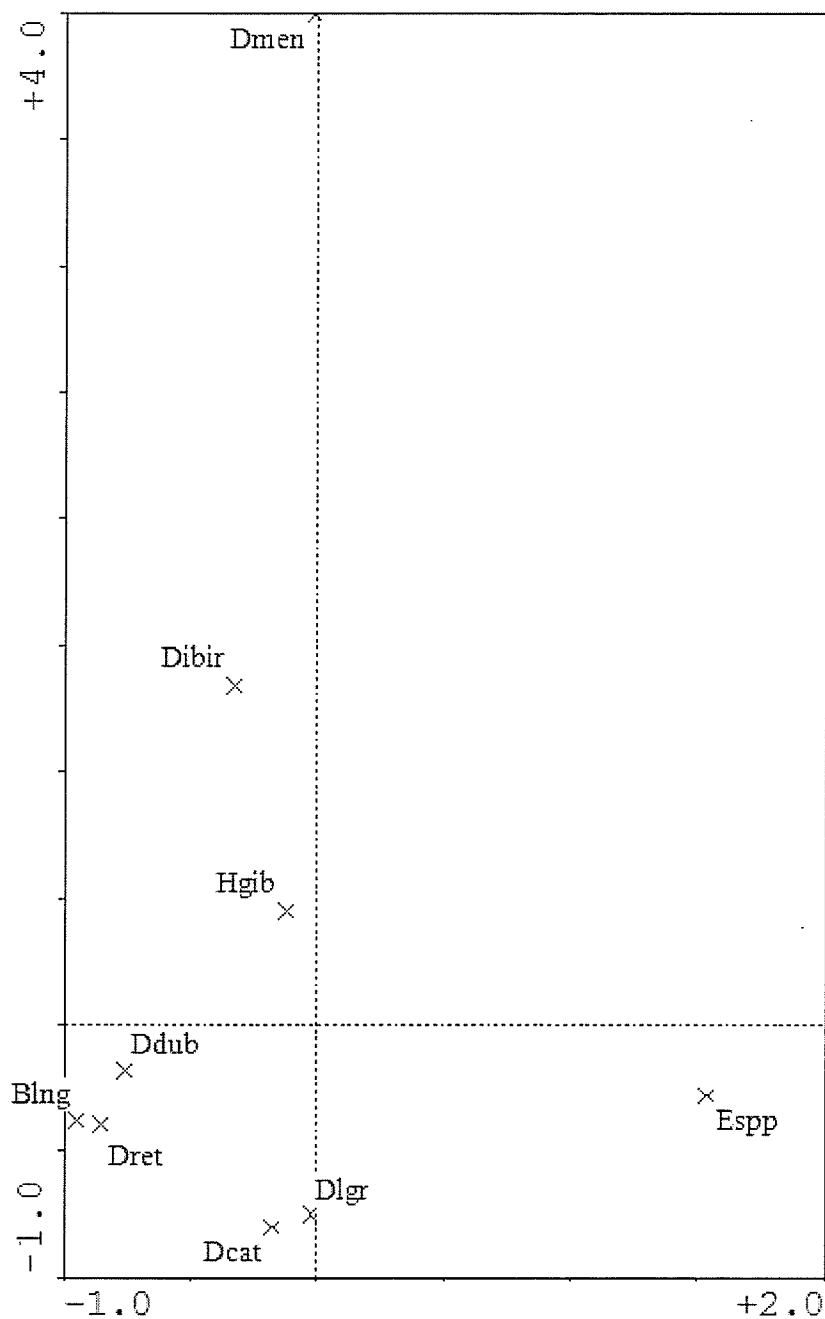


Figure 27b: Correspondence analysis (CA) of contemporary pelagic cladoceran species for Lake 302N, Lake 223 and Lake 377. Contemporary pelagic cladoceran species with a relative abundance of less than 5% for all years were eliminated from the analyses. Note change in scale, as compared to Fig. 27a, c. Species codes are: Blng (*Bosmina longirostris*), Ddub (*Daphnia dubia*), Dcat (*Daphnia catawba*), Dmen (*Daphnia mendotae*), Dlgr (*Daphnia longiremis*), Dret (*Daphnia retrocurva*), Dibir (*Diaphanosoma birgei*), Espp (*Eubosmina* spp.), Hgib (*Holopedium gibberum*).

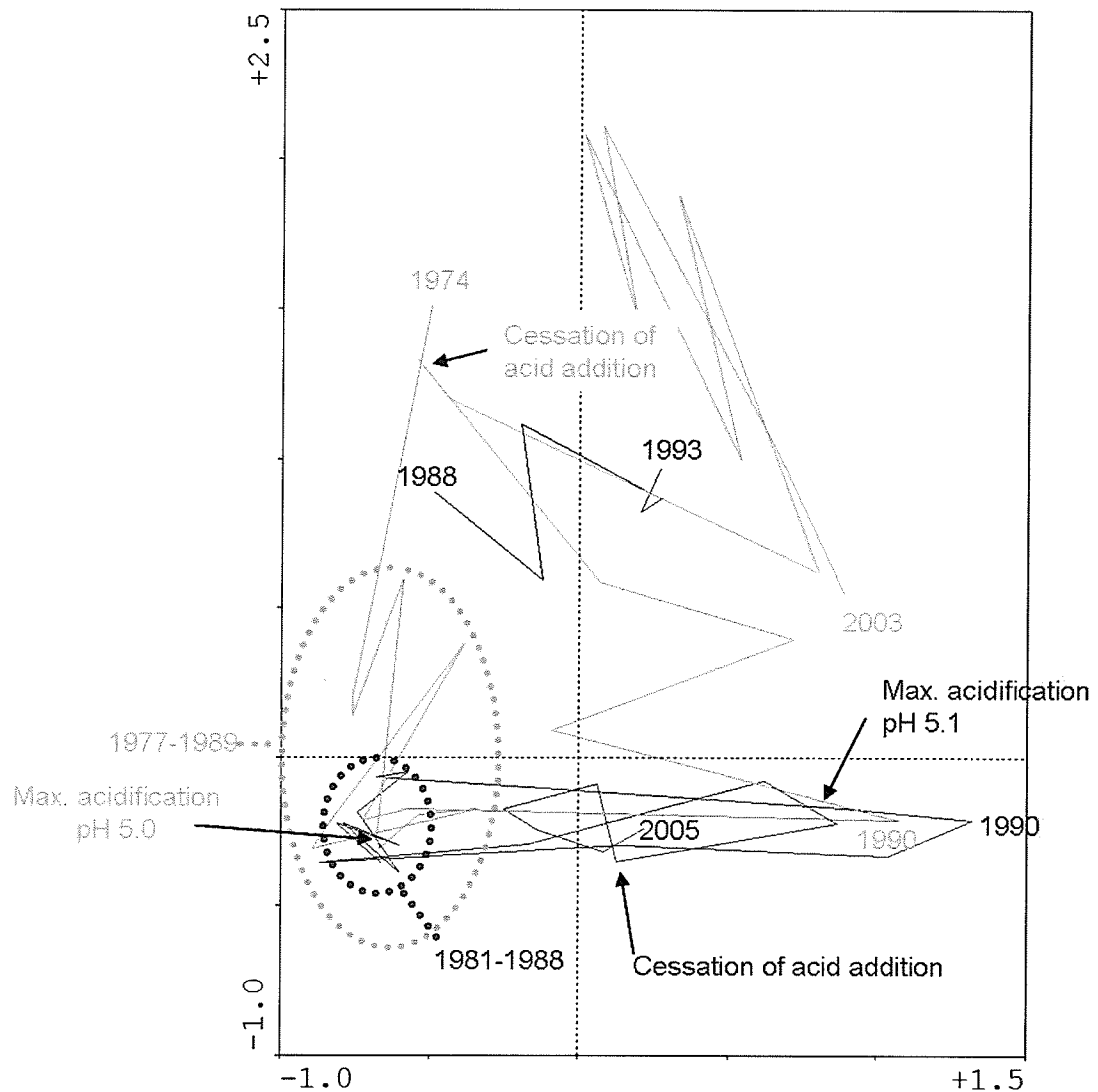


Figure 27c: Correspondence analysis (CA) showing trajectory of change in contemporary pelagic cladoceran species abundance (animals $\cdot$ L⁻¹) over time for Lake 302N (red), Lake 223 (green) and Lake 377 (blue). Pelagic cladoceran species with a relative abundance of less than 5% for all years were eliminated from the analyses. The years of maximum acidification and cessation of acid addition are indicated for Lake 302N and Lake 223, as well as the years of start and finish for the sampling periods presented for each lake. Note change in scale, as compared to Fig. 27b.

In Lake 302N, there was a shift in pelagic cladoceran community structure from negative to positive loadings on the first axis during acidification, over time (Figure 27a). From 1981-1988, the community was mainly dominated by *B. longirostris*, *Daphnia retrocurva* and *Daphnia longiremis*, all of which had a negative loading on the first axis (Figure 27b). Following 1988, when pH had dropped to the minimum of 5.1, the community switched back and forth between being dominated by *Eubosmina* spp. (1989-1992, 1995-1998, 2004-2005; positive loadings on first axis) and *B. longirostris* (1993-1994; 2001-2002; negative loadings on the first axis). After the cessation of acid addition (1997), pelagic cladoceran community structure did not recover to the range that was seen during pre-manipulation, but was less variable over time (Figure 27c). This was mainly due to the shift in bosminids from *B. longirostris* to *Eubosmina* spp. However, the daphniid community (primarily *D. retrocurva* and *D. longiremis*) had recovered to abundances seen during pre-manipulation.

In Lake 223, the only pre-manipulation date collected (1974) had a high positive loading on the second CA axis and was characterized by high densities of *Daphnia mendotae* (Figure 27a). This is in contrast to the early acidification dates (1977-1980), which had a low positive loading on the second axis, where *D. mendotae* was nearly absent. However, the main species that characterized the early acidification community, and had a negative loading on the first axis, was *B. longirostris* (Figure 27b). During the early period of acidification (1981-1989), movement was to more negative loadings along the second axis, mainly due to the appearance of *Daphnia catawba* and *Daphnia dubia*. Following 1989, dates with a positive loading on the first axis had higher densities of *Eubosmina* spp. The pelagic cladoceran community then switched back and forth

between a community that was dominated by *Eubosmina* spp. (positive loadings on the first axis) or *B. longirostris* (negative loadings on the first axis). The higher positive loadings on the second axis, after 1993, were due to the disappearances of *D. catawba* and *D. dubia*, and the reappearance of *D. mendotae*. Dates after the cessation of acid addition in 1994 did not recover to the range seen during pre-manipulation (Figure 27c). Similar to Lake 302N, this was mainly due to the shift in bosminids from *B. longirostris* to *Eubosmina* spp. In contrast, the daphniid community (primarily *D. mendotae*) had recovered to a structure seen during pre-manipulation.

In Lake 377, although there was lesser variability in pelagic community structure as compared to the manipulated lakes, there appeared to be a directional trajectory of change over the period sampled (1988-1993; Figure 27a). This is contrary to the results found from the fossil record, for the littoral community structure. From 1988-1990, the pelagic cladoceran community had a negative loading on the first axis, and was characterized by *B. longirostris*, *D. mendotae*, *D. longiremis* and *D. retrocurva* (Figure 27b). From 1991-1993, the pelagic cladoceran community then shifted to having positive loadings on the first axis, due to the shift in dominance from *B. longirostris* to *Eubosmina* spp. With this shift, the variability in pelagic cladoceran community structure appeared to be less from 1991 to 1993 than it was from 1988 to 1990 (Figure 27c).

There is an important point to note regarding the treatment of *Eubosmina* spp. In contemporary samples, the *Eubosmina* spp. recorded to be present in Lake 302N and Lake 223 was previously identified to be *B. (N.) tubicen*. In contrast, the *Eubosmina* spp. recorded to be present in Lake 377 was previously identified to be *B. (E.) longispina*. As the increase in *B. (E.) longispina* in Lake 377 appeared to be concurrent with the

appearance and increase of *B. (N.) tubicen* in other ELA lakes, both from the contemporary record and the fossil material, the contemporary samples were re-examined. Upon re-examination of the Lake 377 contemporary samples, the '*B. (N.) tubicen*' recorded in the fossil record was found to be present in Lake 377. In addition, the '*B. (N.) tubicen*' recorded in the fossil record resembled *B. (N.) tubicen* in Lake 302N and Lake 223. However, to preserve the original identifications until further confirmation of this author's (L. Frazer) re-identifications, *Eubosmina* spp. (inclusive of *B. (E.) longispina* and *B. (N.) tubicen*) will be referred to from the contemporary samples. However, it can be assumed that *B. (N.) tubicen*, as identified from the fossil record, was present in Lake 377, as well as Lake 302N and Lake 223.

Discussion

Although the focus of this study was to follow the pathway of cladoceran community reassembly, an understanding of what determines cladoceran community structure (i.e. local or regional factors), as well as the overall response of the cladoceran community to change, was necessary in order to put the recovery process into perspective. The results from the analyses of the cladoceran microfossils are explored according to: the trajectory of change in response to the disturbance, relative to the pre-manipulation state; the community state at recovery; the trajectory of recovery, relative to baseline conditions; and the degree of change, relative to natural variability. This process is based on the model of Batterbee *et al.* (2005) as a holistic approach for evaluating community recovery. This includes exploration of not only the theoretical but also the ecological knowledge base that might aid in explaining the trajectories of community change.

Yan *et al.* (1996) demonstrated that the choice of metric may affect the perception of recovery. Therefore, the response of the cladoceran community to experimental manipulation was evaluated at both the species and community level, using univariate and multivariate metrics, to ensure that an indication of community recovery was not overlooked. In addition, as the ecological relationships and habitat of the littoral and pelagic cladoceran communities differ (Dodson and Frey, 2001), their pathways to recovery were evaluated separately. Overall, careful observation and exploration of long-term changes using cladoceran microfossils might help illuminate the importance of regional versus local factors in the reassembly pathway, as well as their potential as biological indicators in defining recovery targets.

Trajectory of change in response to the disturbance, relative to the pre-manipulation state.

Without knowledge of a community's state prior to its restoration, all that can be surmised is that the community has changed in some fashion (Chapman, 1999). To be able to define the recovery state of the manipulated communities, it was essential that the pre-manipulation state be quantified. In addition, an understanding of the trajectory of change in response to the disturbance, for both the littoral and pelagic communities, might illuminate the necessary pattern of reassembly in order to restore the cladoceran community to its pre-manipulation state. By using the paleolimnological record to put the recovery process into context, the trajectory of change in response to the disturbance, relative to the pre-manipulation state, was defined for the Lake 302N and Lake 223 cladoceran communities.

The littoral community

Species-level indicators of change

At the species level, there was no major species turnover or replacement in the littoral cladoceran community for Lake 302N and Lake 223 in response to the manipulations. Rather, it was changes in the relative abundance of species that dominated the manipulation response. Key species that decreased in relative abundance during the acidification period in both lakes included *Alona barbulata*, *Alonella* cf. *excisa* and *Alonella nana*. Key species that increased in relative abundance in both lakes during the period of acidification included *Biapertura intermedia* and *Disparalona acutirostris*.

As recovery is often defined by the disappearance of acid-tolerant species and the return of acid-sensitive species (Holt and Yan, 2003; Locke *et al.*, 1994; Gunn and Sandøy, 2003; Walseng, Halvorsen and Sloreid, 2001), there have been attempts in the literature to characterize the acid tolerances of chydorids through regional surveys (Walseng and Schartau, 2001). Consistent results between these characterizations and the results of this study indicate potentially useful indicator species for acidification. For example, *A. nana* has been previously characterized as an acid-sensitive species (Walseng and Schartau, 2001; Walseng *et al.*, 2008; DeSellas *et al.*, 2008) and has been found to decrease in relative abundance in response to acidification (Paterson, 1994). More often than not, however, chydorid response to acidification is inconsistent among lakes. For example, *B. intermedia* has previously been considered to be an acid-tolerant species (Walseng and Schartau, 2001; DeSellas *et al.*, 2008), yet it has been found to both increase (Paterson, 1994) and decrease (Paterson, 1994; Hann and Turner, 2000) in response to acidification. Even between Lake 302N and Lake 223, certain species responded differently to acidification than others. Species that responded more strongly in Lake 302N than Lake 223 included *Rhynchotalona falcata* (which decreased in response to acidification) and *Monospilus dispar* (which increased in response to acidification). Unlike the Lake 302N community, *Chydorus brevilabris* and *Chydorus sphaericus* strongly increased in response to acidification in Lake 223.

Paterson (1994) hypothesized that the inconsistency in species responses to acidification in lakes of the Adirondack Mountains may be due to food-web effects, rather than a direct toxic response to acidification. In Lake 302N and Lake 223, the decrease in relative abundance of smaller chydorid species (i.e. *A. nana*, *A. cf. excisa*)

suggested a shift to invertebrate predation (Hann and Turner, 1999; Stenson and Eriksson, 1989). In response to acidification of Lake 223, however, *Mysis relicta* was extirpated, the abundance of small planktivorous fish decreased and *Chaoborus* remained rare (Malley and Chang, 1986). In Lake 302N, the *Chaoborus* response to acidification was not recorded, but it may have been maintained at low densities due to the persistence of lake whitefish, which preys on *Chaoborus* (Mills *et al.*, 2002; Bird, Mills and Schwartz, 1999). Therefore, food-web effects in the two manipulated lakes were not clear-cut at the species level.

In addition to food-web effects, Garrison and Webster (1988), in their companion mesocosm study to the Little Rock Lake (Wisconsin) acidification experiment, hypothesized that the observed increase in abundance of *A. excisa* and *Chydorus* sp. was likely an indirect response to an increase in habitat heterogeneity (with the development of benthic algal mats) rather than a direct acid response. However, in the study lakes, even species that prefer similar habitats did not respond similarly within the same lake. For example, *M. dispar* and *R. falcata* are thought to be associated with sediments and, therefore, should indicate changes in sediment habitat availability (Frey, 1986b). Yet, within Lake 302N, both of these species responded differently, in terms of relative abundance, during the acidification period. Depending on how habitat or the aquatic food web is altered due to acidification, the littoral cladoceran community may respond differently between lakes. This may be particularly applicable to Lake 302N and Lake 223, where the two manipulation histories have resulted in different ecosystem changes. Therefore, although it may be tempting to make generalizations of environmental tolerances of littoral cladocerans based on results from regional lake surveys, the results

of this study and the literature suggest factors influencing species responses are too complex to be confined in such a manner.

Community-level indicators of change: Univariate metrics

Species abundance, accumulation rates, richness, diversity and evenness were univariate metrics used to evaluate change at the community level. Similar to the species specific responses, there was relatively little change in these metrics, in comparison to the pre-manipulation state. One interesting response to note, however, was an increase in species diversity and evenness during the period of acidification in the two manipulated lakes. These results contrast with the results in most of the acidification literature, where a decrease in species diversity and evenness with decreasing pH is typically observed (Paterson, 1994; Hann and Turner, 2000; Walseng *et al.*, 2008; Davis *et al.*, 1983; Kenlan, Jacobson and Brakke, 1984; Brakke, Davis and Kenlan, 1984; Fryer, 1980). Although an initial increase in chydorid diversity was recorded in Speck Pond (Maine) with pH decline, no inference as to the cause was given (Brakke, Davis and Kenlan, 1984). A potential explanation for the observed increase in species diversity and evenness during the period of acidification was an increase in available habitat (Nilssen and Sandøy, 1990). With increasing habitat heterogeneity and complexity, so too does biological diversity (MacArthur, 1965). The increase in filamentous green algae with acidification, as observed in Lake 223 (Schindler *et al.*, 1985) and Lake 302N (Turner *et al.*, 1995a), may have been used as additional habitat, as a food source and as a refuge from the low lakewater pH and predation (Hann and Turner, 1999; Turner *et al.*, 1995b), leading to an increase in diversity and evenness.

Community-level indicators of change: Multivariate metrics

At the species level, and by using univariate metrics at the community level, only weak changes in response to the manipulation were detected. However, multivariate community metrics, including constrained cluster analysis and CA, revealed differences in community structure between the pre-manipulation and the acidified community. Unlike univariate metrics, which obscure individual species responses, multivariate metrics highlight interspecific covariation (Clarke and Warwick, 2001). As previously noted, since the littoral community response was mainly changes in relative abundance rather than species turnover or replacement, multivariate metrics are more suited to examine change in the littoral cladoceran community. Although the CA depicted similar pre-manipulation community structures in Lake 302N and Lake 223, the magnitude and the trajectory of change differed slightly between the two lakes. Both lakes moved along the second CA axis during the period of acidification; however, Lake 302N had negative loadings for all depths that occurred during acidification, whereas the second axis loadings of Lake 223 remained positive during acidification. Difference in the strength (i.e. distance in ordination space) of response may be due to the different strengths of the two manipulations. Lake 302N was held below pH 5.4 for two more years than Lake 223 (Findlay *et al.*, 1999; Findlay and Kasian, 1996). In addition, not only was Lake 302N acidified by HCl as well as HNO₃, it was also exposed to a period of epilimnetic fertilization, which induced additional changes in the phytoplankton (Findlay *et al.*, 1999) and the fish communities (Mills *et al.*, 2002). Therefore, the experimental manipulations

of Lake 302N may not only have been stronger, but may have elicited different responses than seen in Lake 223.

Not only the magnitude, but the trajectory of change also differed between the two manipulated lakes. Lake 302N moved mainly along the second CA axis during the period of acidification, while Lake 223 moved along both the second and first axis. This is mainly a result of the increase in *C. brevilabris* and *C. sphaericus* during acidification in Lake 223, which did not occur in Lake 302N. Although *C. brevilabris* and *C. sphaericus* are both considered to be littoral species, they are often transients of the pelagic zone, occupying the habitat not by swimming, but by attachment to large filamentous algal colonies (Fryer, 1968). During the period of acidification, an increase in abundance of transient *Chydorus* spp. in the contemporary zooplankton samples was noted in Lake 223 (Malley and Chang, 1994), but not in Lake 302N. Although the Lake 302N and Lake 223 pre-manipulation communities had a similar composition, without knowledge of the assembly history it is difficult to understand the factors responsible for driving the overall community structure and their vulnerability to new species invasions from the regional pool (Drake, 1991). How the assembly history may affect invasion success is not well understood, but whether species in the local community are increasing or decreasing in relative abundance, their current physiological state and environmental changes induced by species previously present in the community are all suspected to play a role. Therefore, differences in the historic assembly trajectories of Lake 302N and Lake 223 may have lead to the varying response of *Chydorus* spp. during acidification in each of these lakes. Further reasons hypothesized for this increase in Lake 223, as opposed to

Lake 302N, are considered below (see section on ‘Community state at recovery: Species-level indicators of recovery’).

The pelagic community

Species-level indicators of change

The pelagic cladoceran communities of the two manipulated lakes showed similar trajectories of change in response to the disturbance, relative to the pre-manipulation state, as observed at both the species and community level. These changes were also consistent with what has been observed in the literature. At the species level, the species specific responses to acidification between the two lakes were very similar. As depicted in the fossil record in both lakes, there was a decrease in the relative abundance of some of the Bosminidae spp. (*B. (B.) longirostris*, *B. (E.) longispina* and *B. (S.) lieder*) due to the corresponding increase in *B. (N.) tubicen* during the period of acidification. As the Bosminidae spp. group is an amalgamation of three species, it is difficult to infer meaning at the species level. *B. (N.) tubicen* has been characterized as a ‘weakly’ acid-tolerant species (Walseng and Schartau, 2001); however, what may have led to its increase, specifically, is unknown. Its long mucrone, compared to the mucrone lengths of *B. (B.) longirostris* and *B. (S.) lieder* (De Melo and Hebert, 1994), may have allowed it to resist changes in the food web structure of the two acidified lakes. For example, replacement of a smaller bosminid with a larger one might indicate a shift from planktivorous fish to predation by invertebrate predation (i.e. *Chaoborus*; Nilssen, 1978). However, in Lake 223, small planktivorous fish had decreased with acidification (Mills, Chalanchuk and Allan, 2000), while *Chaoborus* remained rare and *Mysis relicta* was

extirpated (Malley and Chang, 1986). This suggests that the increase in *B. (N.) tubicen* was not solely dependent on a predation shift (see section on the 'Trajectory of recovery, relative to baseline conditions' for further discussion). In addition to the increase in *B. (N.) tubicen*, the *Daphnia pulex*-type group appeared during the period of acidification in Lake 223, where the daphniid community was recorded in the fossil record. *Daphnia catawba* is a member of the *D. pulex*-type group and also invaded the lake based on the contemporary data (Malley and Chang, 1994). This species has previously been found to increase in response to acidification (Frost *et al.*, 2006); therefore, its disappearance might be a good indicator of recovery.

Community-level indicators of change: Univariate metrics

At the community level, pelagic abundance and accumulation rates, as inferred from the fossil record, were used as univariate metrics to quantify change. Both Lake 302N and Lake 223 showed an increase in abundance and accumulation rates from pre-manipulation to acidification. As the daphniid community and other key pelagic species tended to be underrepresented in the fossil record, due to their poor preservation (Frey, 1986b; Deevey, 1964; Krause, 1959), the recorded increase in pelagic cladoceran species was mainly due to the increase in some Bosminidae spp. (including *B. (B.) longirostris*, *B. (E.) longispina*, as well as *B. (S.) liederii* and *B. (N.) tubicen*). This mirrors what was recorded in the contemporary data; however, *Eubosmina* spp. (*B. (N.) tubicen*) was mainly responsible for the increase in pelagic cladoceran abundance in Lake 302N in response to acidification (data not shown; Malley and Chang, 1986; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data).

Frost *et al.* (2006) recorded an increase in pelagic cladoceran biomass in the experimentally-acidified Little Rock Lake (Wisconsin); however, Paterson (1994) recorded decreases in pelagic cladoceran accumulation rates in response to acidification in a set of atmospherically-acidified lakes in the Adirondack Mountains. In the paleorecord, increases in accumulation rates are indicative of increases in productivity, in that the larger the population, the more exuviae will be shed (Frey, 1986b). Although generalizations in response of community productivity to acidification cannot be made, inferences as to the lake-specific factors that may have driven these changes may be extrapolated. Paterson (1994), for example, found that historic records of the loss of trout from Deep Lake, allowing for a species shift and increase in *Chaoborus* predation, corresponded well with the decrease in pelagic cladoceran abundance. In Lake 223, the overall release of predation pressure (i.e. *Chaoborus*, *Mysis* and planktivorous fish) was attributed to the increase in abundance of cladocerans (Malley and Chang, 1986). In the case of Lake 302N, the *Chaoborus* response to acidification was not recorded, and no *Mysis* are known to be present; however, *Chaoborus* is thought to have increased strongly in abundance during acidification in the south basin of Lake 302 (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication). The persistence of lake whitefish in Lake 302N with epilimnetic fertilization (Mills *et al.*, 2002), as compared to Lake 302S (Vinebrooke *et al.*, 2003a), may have maintained *Chaoborus* populations at low densities (Bird, Mills and Schwartz, 1999), allowing the pelagic cladoceran population to increase. On the other hand, since the increase in abundance of pelagic cladocerans in Lake 302N can be attributed mostly to *B. (N.) tubicen*, then its competitive advantage has to be considered.

- Community-level indicators of change: Multivariate metrics

The multivariate metrics of the constrained cluster analyses and CA confirmed the trajectory of response, relative to the pre-manipulation state, as observed at the species level and at the community level, using univariate metrics. Although clustering more closely than seen for the littoral cladocerans, the pelagic cladoceran communities in both Lake 302N and Lake 223 were distinctly separated between a pre-manipulation state and an acidification state. This demonstrates that, even though the daphniid community and other pelagic species were underrepresented in the fossil record, a clear distinction could be made. To confirm that the response to the manipulation, as seen in the fossil record, matched what occurred in the extant community, a correspondence analysis was performed on the contemporary data. Although only a single pre-manipulation date was available, there was a clear trajectory of change to the acidified state. The strongest drivers for the shift in state were the disappearance of the acid-sensitive species (e.g. *Daphnia mendotae*; Keller *et al.*, 1990; Walseng and Schartau, 2001) and the appearance of the acid-tolerant species (e.g. *D. catawba*; Sprules, 1975). In addition, unlike what was observed for the littoral cladoceran community, although the Lake 302N and Lake 223 pre-manipulation pelagic communities differed slightly (dominant daphniid in Lake 223 - *D. mendotae*; dominant daphniids in Lake 302N - *D. longiremis* and *D. retrocurva*), their respective trajectories of change in response to manipulation were fairly similar.

The trajectory of change: The littoral versus the pelagic cladoceran communities

Overall, the Lake 302N and Lake 223 littoral and pelagic cladoceran communities differed in their strength and trajectories of change in response to the disturbances in each lake. Changes in the pelagic community were stronger and more often consistent between the study lakes and with that observed in the literature. In contrast, changes in the littoral community were weaker, often inconsistent with the literature, and occasionally inconsistent between the study lakes. In addition, for the littoral community, the detectability of the trajectory of change differed, depending on the method used (i.e. species or community level; univariate or multivariate metrics). Muted responses to perturbation in the littoral cladoceran community, as compared to reference lakes and to the pelagic cladoceran community, have previously been noted (Hann and Turner, 2000; Hann *et al.*, 1994). A study on ecosystem resistance and species compensation in the acidified Lake 302S (ELA) found the species-poor pelagic cladoceran community to show weak species compensation (Vinebrooke *et al.*, 2003a). Although the compensatory dynamics of littoral cladocerans have not been characterized, and relatively little is known about their species-specific functional roles, diverse communities, with a high dispersal and reproductive potential, are more likely to exhibit functional compensation (Ives *et al.*, 1999). In addition, communities with larger species pools are more likely to exhibit multiple stable states, as initial invaders are more likely to preclude species occupying a similar niche (Chase, 2003). It is the higher diversity of the littoral cladoceran community that may have increased its stability and resistance to the disturbance, through functional compensation, in comparison to the pelagic cladoceran community.

Community state at recovery

The process of predicting recovery pathways is difficult, at both the species and community level, as even natural communities have high amounts of variability (Palmer, Ambrose and Poff, 1997). However, it is important to define target endpoints. If species habitat has recovered from a perturbation, then the pre-manipulation community may be a feasible recovery state (Niemi *et al.*, 1990). However, the high natural variability in community structure makes it unrealistic to assume a community will recover to its pre-manipulation state (Arnott *et al.*, 2001). An alternative is recovery to a state that is typical of reference, non-perturbed lakes (Keller and Yan, 1998; Keller *et al.*, 2002).

For the reassembly of cladoceran communities, a variety of factors may influence the rate of recovery. Invasion order and dispersal rate have typically been characterized as important factors in driving community assembly (Robinson and Dickerson, 1987; Drake, 1991); therefore, dispersal limitation may drive the community structure (Keller and Yan, 1998). However, as recolonization by the cladoceran community will most likely be from an internal refuge (i.e. the egg bank; Hairston, 1996) or expansion by species that have persisted in the perturbed state, rather than dispersal from the regional species pool, it is likely local processes, such as biological resistance, will shape community structure (Shurin, 2000; Jenkins and Buikema, 1998).

The extent of recovery of community structure can be identified at the species level, by the disappearance of acid-tolerant species and the reappearance of acid-sensitive species (Holt and Yan, 2003; Locke *et al.*, 1994; Gunn and Sandøy, 2003; Walseng, Halvorsen and Sloreid, 2001). However, when shifts in the relative abundance of species, rather than species turnover, appear to be driving the community response to the

disturbance, multivariate metrics are likely more sensitive than univariate metrics (Yan *et al.*, 1996). Both species and community level (both univariate and multivariate) metrics were used to follow the trajectory of recovery and to determine the recovery state of the littoral and pelagic cladoceran communities as the pre-manipulation or an alternative natural state.

Species-level indicators of recovery

In the littoral communities of Lake 302N and Lake 223, chydorid species that had been previously identified as acid-sensitive (i.e. *A. nana*; Walseng and Schartau, 2001) did not return to their pre-manipulation relative abundances. In Lake 302N, *A. nana* remained the dominant species throughout manipulation and recovery; however, in Lake 223, *A. nana* was replaced by *C. brevilabris* as the dominant species. In addition, *C. sphaericus*, characteristic of shallow, acid lakes (Yan *et al.*, 1996; Walseng and Schartau, 2001), remained abundant during recovery. *C. sphaericus* (likely inclusive of *C. brevilabris*, due to their morphological similarity; Frey, 1980) has been characterized as an early opportunist in the recovery process, found in the pelagic zone of lakes when acid-sensitive species are missing and there is a lack of predation (Yan *et al.*, 1996; Keller and Yan, 1998; Malley and Chang, 1994). This agrees with the lack of predation (i.e. *Mysis*, *Chaoborus* and planktivorous fish) observed during early recovery in Lake 223 (Mills, Chalanchuk and Allan, 2000; Malley and Chang, 1994), where *Chydorus* spp. persisted in the pelagic zone until 1993 (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data). However, the continued dominance of *C. brevilabris* and *C. sphaericus* in the sediment core, long after its time of

disappearance in the contemporary record, suggests it was able to maintain its abundance in the littoral zone, potentially aided by its exploitation of the pelagic zone during the early recovery period. Although I hypothesized that the persistence of lake whitefish in Lake 302N with epilimnetic fertilization (Mills *et al.*, 2002) may have maintained *Chaoborus* populations at low densities (Bird, Mills and Schwartz, 1999), the absence of the shift to *C. sphaericus* and *C. brevilabris* in Lake 302N, as in Lake 223, suggests that predation pressures in the pelagic zone may have prevented this from occurring.

In the pelagic communities of Lake 302N and Lake 223, species that had increased in relative abundance during the acidification phase (i.e. *B. (N.) tubicen*, *Daphnia pulex*-type group), as recorded in the fossil record, remained dominant during recovery. Although *Daphnia* spp. provide a variety of acid-tolerant (e.g. *D. catawba*; Sprules, 1975) and acid-sensitive (e.g. *D. mendotae*; Keller *et al.*, 1990; Walseng and Schartau, 2001) indicators in the manipulated lakes, the inability to identify their post-abdominal claws to species from the fossil record limited their use. For example, a shift in *Daphnia* spp. was recorded in the contemporary community from *D. mendotae* to *D. dubia* and *D. catawba* in Lake 223 with acidification (Malley and Chang, 1994). However, because the *D. mendotae*-type group combined all postabdominal claws with spines of medial and distal pecten of similar size, the shift from *D. mendotae* to *D. dubia* could not be detected in the fossil record. Therefore, the use of the pelagic cladoceran fossil record, at the species level, for detecting recovery trajectories and states will depend on more reliable identification to species.

At the species level, for both the littoral and pelagic cladoceran communities, the persistence of species that responded during acidification indicates that recovery to the

pre-manipulation state has not occurred. However, even in communities where acid-sensitive species have returned, the community has not recovered to the pre-manipulation state (Yan *et al.*, 2003). Therefore, further exploration at the community level is needed.

Community-level indicators of recovery: Univariate metrics

An increase in species richness, diversity and evenness is often characteristic of the recovery of acidified communities (Locke *et al.*, 1994; Keller *et al.*, 2002). However, as diversity and evenness had already increased during the period of acidification in the littoral cladoceran community, a decrease, or return with the range of pre-manipulation values was also likely to have suggested recovery. For both Lake 302N and Lake 223, richness, diversity and evenness values during recovery were slightly above what was observed during pre-manipulation; however, similar to acidification, the change in response to chemical recovery was minimal. Similar to the observed response to acidification, littoral cladoceran abundance and accumulation rates also remained within the pre-manipulation range during recovery.

During the recovery period, the pelagic cladoceran community exhibited higher abundance and accumulation rates than seen during the pre-manipulation period. However, Lake 302N remained at similar abundance and accumulation rates as seen during the acidification period, with the exception of the confounded 4 cm sample depth, whereas Lake 223 pelagic cladoceran abundance and accumulation increased in early recovery and then remained stable. Increases in accumulation rate are indicative of increases in productivity (Frey, 1986b). The ecological basis for this strong increase during recovery in Lake 223, which was larger than the increase in abundance and

accumulation rates from pre-manipulation to acidification, is unknown. Although phytoplankton (Findlay and Kasian, 1996) and fish (Mills, Chalanchuk and Allen, 2000) communities have mostly recovered in Lake 223, one major change that has occurred in the ecosystem, in comparison to pre-manipulation, is the inability of *Mysis relicta* to become re-established (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication). Although the food habits of *Mysis relicta* are not well known, it has been considered to be important in structuring zooplankton communities (Grossnickle, 1982). However, as the daphniid community is underrepresented in the fossil record, any species compensation provided to maintain pelagic cladoceran community abundance over time will have been overlooked. As a result, no inferences on the effect of the loss of *Mysis* on the Lake 223 pelagic cladoceran population can be made from the fossil record. In addition, no increase in pelagic cladoceran abundance during recovery, as recorded in the fossil record, was seen in the contemporary data (data not shown; Malley and Chang, 1996; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data).

Univariate metrics of community recovery, for both the littoral and pelagic cladoceran communities, did not strongly depict recovery or assist in defining the recovery state. Those values that remained within the pre-manipulation range of variation (i.e. littoral cladoceran species abundance and accumulation) were ones that did not respond to the initial manipulation. Other univariate indicators (i.e. littoral cladoceran species richness, diversity and evenness; pelagic cladoceran abundance and accumulation) remained above pre-manipulation values. Therefore, it appears that recovery to the pre-manipulation state has not occurred; however, the position along the

trajectory of recovery and the recovery state cannot be inferred from the univariate metrics. Yan *et al.* (1996), in their study of crustacean zooplankton recovery of Sudbury (Ontario) lakes from acid and metal contamination, found abundance to be the poorest indicator of the recovery trajectory and state, while species richness and diversity were more effective univariate metrics in depicting community change. Although species richness and diversity were not calculated from the fossil record for the pelagic community, changes in species richness and diversity inferred from the contemporary record would likely have suggested recovery to have occurred, due to the large amount of species turnover in response to acidification (Malley and Chang, 1994; M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data). In comparison to the pelagic community, the higher diversity of the littoral cladoceran community, suggesting compensatory dynamics, may have obscured the recovery trajectory at the community level, as depicted using species richness, diversity and evenness.

Community-level indicators of recovery: Multivariate metrics

When recovery is associated with change in species abundances, rather than species occurrences, multivariate metrics have been found to more accurately depict the recovery trajectory and state (Yan *et al.*, 1996; Holt and Yan, 2003; Arnott *et al.*, 2001). The constrained cluster analysis, CA, ANOSIM and SIMPER were all more effective at depicting the recovery trajectory and state of the littoral and pelagic cladoceran communities.

Recovery trajectory: Hysteresis

Much of the literature indicates that communities, when recovering, do not recover along the original disturbance trajectory (Holt and Yan, 2003; Locke *et al.*, 1994; Frost *et al.*, 2006; Malley and Chang, 1994). Simply removing the stress does not necessarily produce recovery (O'Neill, 1999). Rather, communities undergo a period of hysteresis, due to variable invasion rates (Locke *et al.*, 1994) and biological resistance (i.e. predation and competition; Holt and Yan, 2003; Frost *et al.*, 2006). In both the littoral and pelagic cladoceran communities of Lake 302N and Lake 223, hysteresis was evident along the recovery trajectory. In the constrained cluster analyses of both the littoral and the pelagic cladocerans, the pre-manipulation phase community clustered more closely than the recovery phase community. Similarly, in the CA for the fossil littoral cladocerans and the CA for the contemporary pelagic cladocerans, the recovery trajectory did not follow that from the pre-manipulation period.

Cladocerans have an internal refuge from which to disperse (i.e. the egg bank; Hairston, 1996); therefore, variable dispersal rates within the community should not be the main factor contributing to the hysteresis. Rather, it is more likely that the recovery trajectory was limited by biological resistance, either at the community or the ecosystem level. In the littoral cladoceran community, little is known about the species' competitive interactions. However, in the case of Lake 223, the increase in *C. brevilabris* and *C. sphaericus*, beginning during the acidification period, seemed to be key in driving the recovery trajectory. Similarly, in the pelagic cladoceran community for both Lake 302N and Lake 223, the increase in *B. (N.) tubicen* abundance, beginning during the acidification period, also strongly influenced the recovery trajectory. Frost *et al.*, (2006)

found that acid-tolerant zooplankton species that persisted during acidification, did not maintain their dominance into recovery. However, the recovery of acid-sensitive species tended to follow the recovery of acid-tolerant species, suggesting shifts in competitive hierarchy with increasing pH. Louette, Vander Elst and De Meester (2006) also found that, following dispersal into newly created experimental pool communities, species sorting of competitive ability was important in determining the overall cladoceran community structure. Therefore, the persistence of the acid-tolerant *C. brevilabris*, *C. sphaericus* and *B. (N.) tubicen* may be due directly to their competitive ability, or a change in environmental factors that has allowed them to persist.

Recovery state: The littoral community

For the littoral cladoceran community, the constrained cluster analysis was able to separate a community state at recovery, which was distinct from the community structure during pre-manipulation and manipulation. Similarly, the ANOSIM detected a significant difference between the pre- and post-manipulation littoral cladoceran communities for Lake 302N and Lake 223. In the CA, the cluster of depths from the recovery periods of each lake did not overlap with depths in the pre-manipulation period, indicating differences in community structure. For Lake 223, approximately fourteen years after the cessation of acid addition, the recovery state was separate from both the pre-manipulation and the acidified state, due to the persistence of *C. brevilabris* and *C. sphaericus*. However, the state appeared to be more constant in recent sediment depths. Therefore, the recovery state of Lake 223 may have been driven by biological resistance, where *C. brevilabris* and *C. sphaericus* have prevented an increase in the relative abundance of

Alonella nana. In the case of Lake 302N, approximately eight years after the cessation of acid addition, the recovery state overlapped with the acidification state, as many of the species that had increased during acidification still persisted. Whether insufficient time has elapsed for recovery to occur, or if the current littoral cladoceran community will persist is unknown. Generally, the more severe the damage from the perturbation, the longer the process of recovery (Yan *et al.*, 2003). Whether an additional two years at a lower pH, as compared to Lake 223, caused Lake 302N to persist at the acidified community structure is unknown. However, what is thought to lengthen the process of recovery following severe stress is a limitation in colonist availability. Due to the cladoceran colonization ability from the egg bank, this should not be an issue. In addition, the effects of the severity of the stressor on the recovery process may not be relevant on the short timescale of experimentally-acidified lakes, as compared to atmospherically-acidified lakes.

Little to no research has been done on the trajectories and states of recovery in littoral cladoceran communities, and the ability of this community to return to a pre-manipulation state. In Lake 302S (ELA), there was little evidence of littoral microcrustacean recovery eight years after the minimum pH of 4.5 had been achieved, following chemical recovery to pH 5.9 (Hann and Turner, 2000). In a study of community reassembly in the partitioned Lake Kraenepoel (Belgium), recovery trajectories for both sections were similar and deterministic (Louette *et al.*, 2008). Yet, in most cases, the metrics used for this experiment did not demonstrate a return to the pre-manipulation (1930) state. Phytoplankton communities are diverse communities that have been demonstrated to exhibit compensatory dynamics in response to acidification

(Vinebrooke *et al.*, 2003a). In the recovery of Lake 302S (ELA) from experimental acidification, fourteen years after the chemical recovery from a minimum pH of 4.5, the phytoplankton community has not recovered to the pre-manipulation state, but to an alternative state (Graham *et al.*, 2007). A similar response was seen in the recovery of the epilithic algal community of Lake 302S, where nearly a decade following the chemical recovery from the minimum pH, recovery was to an alternative state (Vinebrooke *et al.*, 2003b). The duration at which these communities were expected to persist at an alternative state was unknown. Also, a number of lake specific factors exist to potentially explain the cause for recovery to an alternate state in both cases, including hysteresis along the recovery trajectory. However, if such resilient, speciose communities do not always recover to their pre-manipulation state, then a similar recovery pattern may be expected in the diverse littoral cladoceran community.

Recovery state: The pelagic community

From the fossil record, for Lake 302N and Lake 223, the constrained cluster analysis was able to separate a distinct pelagic cladoceran community during the recovery period from that which occurred during acidification. From the CA of the contemporary data, the community structure during the recovery period was distinctly separate from the acidification and pre-manipulation periods for both Lake 302N and Lake 223. Overall, as indicated by the multivariate metrics, recovery to the pre-manipulation state does not appear to have occurred. For Lake 302N, this follows thirteen years since the minimum pH of 5.1 was achieved and nine years since the cessation of acid addition. For Lake 223, this follows twenty-one years since the minimum pH of 5.0 was achieved and a decade

since the cessation of acid addition. From studies of crustacean zooplankton communities, biological recovery has been known to lag behind chemical recovery, by about a decade (Keller and Yan, 1998; Locke *et al.*, 1994; Yan *et al.*, 2003). In the experimental acidification of Little Rock Lake (Wisconsin), the recovery lag, specifically for cladocerans, was four years (Frost *et al.*, 2006). However, in the atmospherically-acidified Middle Lake (near Sudbury, Ontario) local factors have prevented recovery after three decades (Yan *et al.*, 2004). As inferred from the CA of the contemporary pelagic data, all acid-tolerant cladoceran species (with the exception of *B. (N.) tubicen*) had disappeared, and all acid-sensitive species cladocerans had returned. This suggests that the recovery of both the Lake 302N and Lake 223 pelagic cladoceran communities has occurred. However, due to the invasion of *B. (N.) tubicen*, recovery has not occurred to the pre-manipulation state, but to a state that has been potentially dictated by biological resistance.

Littoral and pelagic cladoceran community reassembly

Although some studies state that assembly depends on dispersal (Robinson and Dickerson, 1987; Drake, 1991), at the community level, cladoceran reassembly appeared to be mainly dependent on local factors, including competition and biological resistance. On the other hand, dispersal limitation outside of the cladoceran community (i.e. dispersal limitation of *Mysis relicta* in Lake 223) may have had an indirect effect on community recovery. However, in this study, the indirect effect of dispersal limitation on the cladoceran communities was not able to be inferred from the paleorecord.

Overall, the paleorecord was effective at reconstructing the pattern of reassembly of the littoral cladoceran community, particularly with the use of multivariate metrics. Further research is required into the competitive abilities of species that may influence the reassembly process following a perturbation. Is the recovery structure highly influenced by species that have dominated the perturbed state? O'Neill (1999) stated that "... small alterations in the succession process invariably lead to multiple recovery trajectories and multiple stable states." Even for two similar communities, with fairly similar manipulation histories, this was evident. In the case of the pelagic cladoceran community, because of the existence of indicator species, determining the recovery trajectory and state from the paleorecord was feasible at the species level. However, with the incorporation of contemporary data (including species that preserved poorly in the fossil record) and multivariate metrics, the recovery trajectory was more clearly defined.

Trajectory of recovery, relative to baseline conditions

In addition to the pre-manipulation state, baseline conditions may also be used in defining recovery targets. Baseline conditions act to quantify changing regional variables, that may confound the expected response to a stressor, as well as the recovery trajectory (Battarbee *et al.*, 2005). Although the ELA is well removed from any direct anthropogenic influences, the effects of climate warming have been recorded in the region (Schindler, 1996). It was therefore necessary to estimate if any changing regional variables may have confounded the observed manipulation response in the cladoceran community, due to the duration of the experimental manipulations of Lake 302N and Lake 223 (1972-1997). Reference Lake 377 served as the baseline for the ELA region, to which the trajectory of recovery of the two manipulated lakes could be compared. The littoral and pelagic cladoceran communities were, once again, considered separately.

The littoral community

The overall littoral community structure of Lake 377 was found to differ from that of the pre-manipulation communities of Lake 302N and Lake 223. Lake 302N and Lake 223 possessed a more diverse and even chydorid community structure, whereas Lake 377 was dominated by *C. brevilabris* and *C. sphaericus* throughout most of its fossil record. A CCA was performed to identify environmental and morphological variables that might have driven this overall difference in littoral cladoceran community structure. Key environmental variables that partitioned Lake 377 from Lake 302N and Lake 223 included higher maximum depth, lower annual averages of nitrate, suspended phosphorus

and ammonium, and higher aqueous calcium concentrations. Maximum depth has been found to be an important driver of cladoceran community composition, in that the shallower a lake, the greater abundance and diversity of littoral habitat and the greater the diversity of littoral cladocerans (DeSellas *et al.*, 2008; Lildal Amsinck *et al.*, 2006). In the case of *C. brevilabris* and *C. sphaericus*, which have the ability to exploit the open-water habitat (Fryer, 1968), the greater maximum depth, lesser littoral to planktonic area and lower littoral habitat diversity (L. Frazer, personal observation) may have lead to the dominance by these two species in Lake 377, as compared to Lake 302N and Lake 223. Unusually, *C. sphaericus* (likely inclusive of *C. brevilabris*, due to their morphological similarity; Frey, 1980) has typically been considered characteristic of more nutrient rich waters (Frey, 1986b; Hann *et al.*, 1994). Therefore, its dominance in the more oligotrophic of the three study lakes is curious. Rather, it might be an indirect influence of lower nitrate, suspended phosphorus and ammonium levels on the phytoplankton community, as its food source in Lake 377. In addition, although a recent floater mussel extirpation in Lake 377 has been hypothesized to be caused by declining aqueous calcium concentrations in the ELA region (Turner *et al.*, 2007), it was the higher calcium ion concentrations that separated Lake 377 from the two manipulated communities. Calcium requirements for chydorids are, as of yet, unknown (A. Jeziorski, Queen's University, Kingston, ON, personal communication); therefore, no inferences can be made as to how aqueous calcium concentrations might influence the structure of the littoral cladoceran communities. Other variables that were not considered, including abundance of predators on the littoral cladoceran community, may also be driving this difference in overall littoral cladoceran community structure. However, Fryer (1985) hypothesized that habitat

preference and presence of appropriate food were more important in driving overall community structure than dispersal, competition or predation.

Although a direct comparison was not able to be made between the manipulated lakes and the baseline lake, due to overall differences in littoral cladoceran community structure, the baseline could still be used to infer if response to disturbance in the manipulated lakes was greater than regional change over time. In the ANOSIM, no significant difference was found between pre- and post-1970s littoral community structure in Lake 377. Similarly, pre- and post-1970s depths in the CA overlapped for Lake 377. This suggests that the response observed to manipulation and the recovery trajectories observed in Lake 302N and Lake 223 (see sections on 'Trajectory of change in response to the disturbance, relative to the pre-manipulation state' and 'Community state at recovery') was mainly driven by the perturbations and not regional change. However, caution must be used in extrapolating the Lake 377 baseline to the two manipulated lakes, due to the differences in overall community structure and its potential influence on response.

In addition to quantifying the trajectory of recovery relative to baseline conditions for Lake 302N and Lake 223, Lake 377 may be used as a target for recovery to an alternate natural community (i.e. a chydorid assemblage dominated by *C. sphaericus* and *C. brevilabris*). During the period of recovery in Lake 223 from ca. 1996 to ca. 2007, the trajectory of the littoral cladoceran community, as depicted in the CA, had been moving in a direction towards the community structure of Lake 377, with an increase in *C. brevilabris* and *C. sphaericus*. This direction of change following the cessation of acid addition was not seen in Lake 302N. Although the ANOSIM showed the Lake 302N and

Lake 223 post-manipulation communities to be more similar than the Lake 223 and Lake 377 post-manipulation communities, a shift to this alternative natural community might be a long-term recovery target for Lake 223.

The pelagic community

As the daphniid community was largely underrepresented in the fossil record for Lake 302N, Lake 223 and Lake 377, the contemporary data helped to substantiate the trajectory of recovery observed in Lake 302N and Lake 223, as compared to Lake 377. Although the CA on contemporary zooplankton abundance data showed recovery of the daphniid communities in Lake 302N and Lake 223, the appearance and subsequent increase of *B. (N.) tubicen* in Lake 302N and Lake 223 indicated strong changes in pelagic cladoceran community structure. Although the appearance and increase in *B. (N.) tubicen* coincided with the period of acidification in each of these lakes, the reference Lake 377 also showed a similar appearance, in both the fossil record and contemporary data, of *B. (N.) tubicen* (as confirmed by re-examination of the contemporary samples; see 'Results - Contemporary pelagic cladoceran community'). By having a reference community, this suggests that the trajectory of recovery for the pelagic cladoceran community was driven largely by changing baseline conditions for the region, rather than a response to acidification alone (Malley and Chang, 1994). In addition to its appearance in Lake 377, Lake 302N and Lake 223, *B. (N.) tubicen* was also recorded in four other lakes, both manipulated and reference, in the ELA region over a similar time period (Lake 239 in 1974; Lake 302S in 1987; Lake 377 and Lake 240, at the start of their records, in 1988; Lake 227 in 1988; Lake 223 and Lake 302N in 1989; M. Paterson,

Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication).

Although the appearance and subsequent increase of *B. (N.) tubicen* was seen in both the fossil record and the contemporary data, the timing and strength of the appearance differed between the two records. In the contemporary data, prior to its appearance in Lake 239 in 1974, *B. (N.) tubicen* had not been recorded at ELA (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication). In the fossil record, however, *B. (N.) tubicen* was recorded in each of the lakes prior to 1974, albeit at low relative abundances (less than 10% for Lake 302N; less than 2% for Lake 223; less than 3% for Lake 377). In the contemporary record, *B. (N.) tubicen* often replaced *B. longirostris* as the dominant bosminid in each of the lakes, following its invasion (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, unpublished data). In the fossil record, however, even though a strong increase in *B. (N.) tubicen* was recorded ca. 1989, the species was never observed to become the dominant bosminid within the pelagic cladoceran community. Finally, although the strong increase in *B. (N.) tubicen* coincided in the contemporary data and the fossil record for Lake 302N and Lake 223 (ca. 1989), in Lake 377 the increase, recorded in the contemporary data in 1991, was not seen in the fossil record until ca. 2005.

There could be a variety of causes of the discrepancy between the fossil record and contemporary data, including the reliability of identification, contamination of sediments and detection limits in contemporary samples. The identification of bosminids is notoriously difficult (DeMelo and Hebert, 1994) and several different taxonomic schemes are in use by different taxonomists. Differences in the taxonomic sources used

for identification, morphological structures chosen for identification to species and seasonal cyclomorphosis may have lead to differences in the species identification of the bosminids by different taxonomists. Although different taxonomists identified the contemporary zooplankton samples over time, a single person (L. Frazer) identified *B. (N.) tubicen* fossil fragments in the sediment samples and then confirmed these identifications in the contemporary samples. Therefore, consistency in identification is assumed. The occurrence of *B. (N.) tubicen* in sediment from Lake 302N, Lake 223 and Lake 377 prior to 1989 also could have been due to contamination of sediment samples by more recent depths. Care was taken within the laboratory when handling samples to ensure this would not occur and should not have caused different results between the fossil record and the contemporary data. Finally, the occurrence of *B. (N.) tubicen* prior to 1989 may have been at abundances below detection limit to be recorded in contemporary samples. Sampling error (i.e. the failure to detect a species that was actually present in the community), due to species rarity or patchiness, has been found to strongly influence the apparent rate of zooplankton species turnover (Arnott *et al.*, 1999). Although compared to most sampling programs, the ELA zooplankton sampling program is particularly intensive, this might explain why *B. (N.) tubicen* was present at low relative abundances in the fossil record prior to 1989 yet was absent from an initial survey of the region in 1967 (Patalas, 1971).

Not all invasions are initially successful and several recolonization events are often necessary for a population to become established (Yan *et al.*, 2003). Therefore, a reintroduction may have provided sufficient enough numbers to allow for the success of *B. (N.) tubicen*. When a species occurs at rare numbers in the fossil record, it cannot be

determined whether a species is established in the regional species pool, or is existing on the edge of its range (Hann, 1989). However, *in situ* downward mixing in the sediments, due to bioturbation, may have resulted in the appearance of *B. (N.) tubicen* earlier in the sediment record than when it actually occurred (Davis, 1974). Therefore, confirmation cannot be made of the historical presence of *B. (N.) tubicen* in the ELA lakes (i.e. the low relative abundance in the fossil record), prior to its appearance and increase in the contemporary samples. However, reasons exploring the increase in this species, or its invasibility, are examined below.

Bosmina (Neobosmina) tubicen invasion

Overall, relatively little is known specifically about *B. (N.) tubicen*, including its dispersal or competitive ability, in order to reason why it may have had such a successful invasion into the pelagic cladoceran community of the study lakes. Although discovered at the ELA lakes in 1974 in Lake 239 (M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication), *B. (N.) tubicen* had been found to be entirely absent in surveys of northwestern Ontario lakes (Keller and Pitblado, 1989; Patalas, Patalas and Salki, 1994). Its absence from northwestern Ontario, yet presence in northeastern Ontario lakes, could not be explained by east-west limnological variation (Keller and Pitblado, 1989). Although an exclusion of *B. (N.) tubicen* from northwestern Ontario due to competition with or predation by glacial relict species was hypothesized, this reason alone could not clearly justify absence from an entire region.

A variety of potential passive mechanisms of dispersal exist for *B. (N.) tubicen*, including areal (i.e. wind, waterfowl) dispersal, downstream dispersal, egg bank

emergence and human introduction (Havel and Shurin, 2004). Both areal dispersal and downstream dispersal are potential reasons for the range expansion of *B. (N.) tubicen* and its appearance at ELA. However, long distance dispersal mediated by birds along an east-west direction is unlikely, due to the absence of flyways (Hebert and Hann, 1986). In addition, contrary to previous beliefs, most zooplankton, including cladocerans, do not appear to be readily dispersed by wind (Jenkins and Underwood, 1998). Finally, as multiple, isolated ELA lakes were invaded over a short period of time, successful range expansion by areal or downstream dispersal seems less likely. Although Keller and Pitblado (1989) and Patalas, Patalas and Salki (1994) considered *B. (N.) tubicen* to be absent from northwestern Ontario, there is the potential for this species to have had previous, unsuccessful invasions and have deposited resting eggs in the egg bank. Changing environmental variables in 1989, favoring the emergence of *B. (N.) tubicen* from the egg bank, is a plausible explanation for the appearance of *B. (N.) tubicen* in multiple ELA lakes in a short time frame. At this time, however, there is no known change in environmental conditions that could have made the hatching successful. Finally, human introductions have assisted in the long distance range expansion of many invasive cladocerans and could have allowed for the range expansion of *B. (N.) tubicen* into ELA. The exotic cladoceran, *Daphnia lumholtzi*, has had successful long distance range expansions because of its ability to survive in the live wells of boats (Havel and Stelzleni-Schwent, 2001). The isolated event of long distance range expansion by *Daphnia exilis* was suspected to have been mediated by transport by industrial equipment (Hairston *et al.*, 1999). Transportation by boat or by construction equipment is unlikely in the ELA region, as there is limited public access. However, the use of sampling

equipment from the previous *B. (N.) tubicen* range may be a plausible introduction pathway for this species to multiple ELA lakes within a short time frame.

In addition to the potential methods of dispersal, the cause for the success of *B. (N.) tubicen* in the pelagic cladoceran community is also unknown. Much of the research that has been done on *B. (N.) tubicen* has been restricted to the topic of cyclomorphosis. Post, Frost and Kitchell (1995), for example, found that the body size and mucrone length of *B. (N.) tubicen* allowed it to resist predation by a large predatory copepod and be the dominant bosminid in the Little Rock Lake (Wisconsin) community. However, when the abundance of predatory copepods declined with experimental acidification of Little Rock Lake, most *B. (N.) tubicen* individuals sampled did not respond with a change in morphology and they were replaced as the dominant bosminid by *B. longirostris* (which had shortened its mucrone length in response to reduced predation). Although *B. (N.) tubicen* may have a competitive advantage in the pelagic cladoceran community by resisting predation due to its size, it is unlikely that simultaneous changes in predation occurred in all invaded lakes to allow for its increase.

Overall, the invasion of *B. (N.) tubicen* into ELA lakes presents a unique and intriguing example of the successful, long distance range expansion of and invasion by a native zooplankton species. Species interactions have been found to be important at repelling invaders (Shurin, 2000). In addition, most invasive species have minimal impacts on the invaded community (Williamson and Fitter, 1996; Shurin, 2000). Although the effect of *B. (N.) tubicen* on the lake ecosystem is as yet unknown, its effect on the community structure is evident. Cause for the success of this species should be explored further. However, as it is often unclear whether the geographic ranges of many

cladoceran species are driven by passive dispersal of the species, human-mediated range expansion or taxonomic reassignments (Havel and Shurin, 2004; Frey, 1982; Dumont, 1997), caution must be used in the classification of *B. (N.) tubicen* as an invader.

Degree of change, relative to natural variability

Univariate and multivariate metrics were used to quantify the degree of community change, in comparison to the amount of natural variability that existed in the baseline Lake 377. Chapman (1999) argued that by having a single reference site in a study of community recovery, one is constraining the amount of natural variability that is appropriate. However, the pre-manipulation data for Lake 302N and Lake 223 (essentially, Chapman's 'control') should also aid in quantifying natural variability (see section on 'Trajectory of change in response to the disturbance, relative to the pre-manipulation state').

Univariate metrics

In terms of species richness, diversity and evenness, the natural variability in the Lake 377 chydorid community appeared to be greater than the amount of change during acidification and recovery for Lake 302N and Lake 223. However, the majority of this variability in species richness for Lake 377 can be accounted for by the appearance and disappearance of rare species (less than 2% relative abundance in all sample depths) throughout the sediment core. Although Smol (1981) cautions on the artifact that changing sedimentation rates might have for the analysis of diversity (i.e. particularly at the core surface), the amount of variability in species richness, diversity and evenness in Lake 377 was consistent in the bottom half of core as well, where sedimentation rates were fairly constant over time. Rarefaction curves for each of the lakes confirmed that an optimal number of slides had been counted for each lake (data not shown); therefore, it

was not a sampling bias that led to this variability. Overall, in comparison to Lake 302N and Lake 223, Lake 377 had more rare species. Therefore, the amount of variability, as determined by species richness, may be characteristic of the littoral cladoceran community in Lake 377 (dominated by *C. brevilabris* and *C. sphaericus*) and may not be comparable to the other two lakes. With lower community diversity, the stronger strengths of species interactions, relative to the weak interaction strengths in a diverse community, leads to decreased community stability (McCann, 2000). Although community stability was not able to be quantified from the paleorecord, the differences in community structure between the manipulated lakes (i.e. diverse, even chydorid community) and the reference lake (i.e. *C. brevilabris* and *C. sphaericus* dominated community) may, in the future, shed some light on the diversity-stability debate.

In terms of abundance and accumulation rates, for both the littoral and pelagic cladoceran communities, the degree of change in response to the manipulation appeared to be greater than the natural variability over time in the baseline Lake 377. An exception, however, existed in the top of the Lake 377 core (ca. 1996-2004), where a decrease was observed in both abundance and accumulation rates for the littoral and pelagic cladoceran communities. As such a decrease was not observed in the two manipulated lakes, it is likely that lake specific factors may be the cause (see section below – ‘Exploration of recent change in reference Lake 377’).

Multivariate metrics

Once rare species were removed, the variability in reference Lake 377, as quantified in terms of spread in CA ordination space, appeared to be less than the degree

of change that occurred during acidification in the two manipulated lakes. This was also observed from the constrained cluster analysis, for both the littoral and pelagic communities, where depths clustered more closely than observed for the two manipulated lakes. It also appeared, as inferred from the CA, that there was an increase in natural community variability in recent years (14 cm to 2 cm; ca. 1979-2004) in Lake 377. Most likely it is confounding factors, including decreasing sedimentation rates in recent depths, that may have lead to the appearance of increased variability. However, there is the possibility that lake specific factors or regional occurrences may have lead to this recent increase in variability in Lake 377. If regional evidence existed for this increase in natural variability, it could then be extrapolated as a baseline to the two manipulated lakes. However, even reference basins may exhibit a greater degree of change than expected. In the experimental acidification of Little Rock Lake (Wisconsin), a CA revealed greater variation in the reference basin than expected, although the change was not directional (Frost *et al.*, 2006). Similar to Little Rock Lake (Wisconsin), throughout most of the core, variability observed in Lake 377, through univariate and multivariate metrics, was not directional. However, an exception existed in the most recent years (ca. 1996-2004). Decreasing sedimentation rates, cladoceran abundance and accumulation rates, as well as separation of the top depth from the rest of the core in the littoral and pelagic constrained cluster analysis, suggest there have been recent changes occurring in Lake 377. Overall, decreasing sedimentation rates imply either a decrease in sediment supply, or an alteration in the sediment focusing pattern of a lake (Dearing, 1991). A variety of local (i.e. logging, road construction) and regional (i.e. drought) factors are considered below, in an attempt to infer the cause for a decrease in the sedimentation pattern of Lake 377.

Exploration of recent change in reference Lake 377

Logging has occurred within the catchment of Lake 377 over the last century (K. Beaty, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication; J. Van Walleggem, Ontario Ministry of Natural Resources, Dryden, ON, personal communication). Increases in sedimentation rate typically follow catchment deforestation (Dearing, 1991); however, no increases in sedimentation rate were observed around the time period when the most recent logging had occurred (ca. 1980). Therefore, logging does not appear to have induced the recent changes in Lake 377. A regional drought has also affected the ELA region, from 1970 to 1990 (Schindler, 1996). A recent paleolimnological study in northwestern Ontario, using the remains of scaled chrysophytes, found the effects of the regional drought on community structure to be greater than the effects of logging and forest fires (Paterson *et al.*, 1998). Associated with this drought was a decline in lake sedimentation rates in the region after 1980 (Blais *et al.*, 1998); however, a dramatic decline in sedimentation rate in Lake 377 was not detected until ca. 2000. A stratigraphic profile of the Lake 377 planktonic:littoral ratio was used to detect changes in water level (Alhonen, 1970), which might be indicative of drought; however, a slight increase littoral species (suggesting a decrease in water level) was only detected ca. 2000. As the last decade in the ELA region has been wetter than normal (K. Beaty, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication), it is therefore not likely that this shift towards littoral species was caused by decrease in water level. In addition, the planktonic:littoral stratigraphy for Lake 302N and Lake 223, which indicated a slight increase in pelagic species in recent

years, suggesting that regional drought was not likely the cause for the increase in littoral species in Lake 377. Lake 377 also is located directly adjacent to Pine Road, the main access road to the ELA field camp. This road was built during the logging time period (ca. 1980) and, once again, does not appear to correspond to the recent changes.

However, a split culvert bridge installed ca. 1994 on Pine Road, at the lake inflow, corresponds more closely to the recent changes in Lake 377. The installation of the split bridge culvert is thought to have had no effect on inflow to Lake 377 (K. Beaty and M. Paterson, Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, personal communication); however, there is the potential that it may have altered the pattern of sedimentation. Although only inferences can be made about the cause of the decrease in sedimentation rate in Lake 377, the process has likely confounded the recent cladoceran subfossil record. Apparent changes in the most recent community structure must, therefore, be treated with caution. Overall, Lake 377 provides an example that, even in remote areas, caution must be used when assuming reference lakes will be unchanged over time.

Summary and future directions

The main purpose of this study was to follow the pattern of community reassembly, through the use of cladoceran microfossils. Contribution to the understanding of the process of community assembly was gained by documenting the recovery process of two experimentally-manipulated lakes. Lake 302N and Lake 223 of the Experimental Lakes Area provided excellent study lakes for a preliminary attempt at using cladoceran microfossils to reconstruct community reassembly, due to their known manipulation histories and previous documentation of the ecosystem response to change in the scientific literature. In addition to the reconstruction of community reassembly, cladoceran microfossils were found to be strong biological indicators of recovery. Through the use of the two experimentally-manipulated lakes, the feasibility of the return to the pre-manipulation state, or an alternative stable state (i.e. state limited by dispersal, state limited by biological resistance or an alternative 'natural' state) was described. However, in order to put the recovery process into context, description of the trajectory of change, relative to the pre-manipulation state was necessary. Reference Lake 377 provided a baseline not only to which change in the manipulated lakes could be compared, but also natural cladoceran community variability could be quantified. Overall, this study confirmed the use of cladoceran microfossils in applied paleolimnology. This discussion highlights some of the key findings of this study, as well as future directions that should be considered.

Cladoceran community assembly: The importance of local versus regional factors

Evaluating whether local or regional processes determine community structure can assist in focusing efforts in restoration studies (Chase, 2003). In this study, local (i.e. competition, predation), rather than regional factors, appeared to be most important in driving cladoceran community structure. However, upon closer examination of the littoral and pelagic communities, in comparison to the theoretical literature, it appears that the influence of regional factors should not be completely overlooked. In addition, although previous research has suggested that the presence of the egg bank and species sorting of competitive ability will lead to deterministic recovery trajectories within the cladoceran community (Louette *et al.*, 2008), this study found contrasting results from the reassembly trajectories of the littoral and pelagic cladoceran communities.

Within the pelagic community, acid-sensitive species that had been replaced by acid-tolerant species during acidification were able to return during recovery, suggesting an absence of any limitation to dispersal. Without dispersal limitation, and a high dispersal rate from the egg bank, the community should have been mainly structured by local factors (Jenkins and Buikema, 1998). However, the invasion of *B. (N.). tubicen* into the pelagic community during acidification suggested otherwise. In communities that have not achieved quorum, local processes, including competition, act on only a subset of species from the regional pool (Jenkins and Underwood, 1998). Therefore, these communities are particularly vulnerable to invasion by new species and are more sensitive to the elicited effects of invasions on interspecific interactions. Although previous evidence would suggest that local factors should be most influential in

determining pelagic community structure, the invasion of *B. (N.) tubicen* into the community suggests that regional factors still contribute to guiding community assembly.

Communities with high levels of dispersal are thought to develop to a single stable state, as insufficient time is allowed for priority effects to occur (Chase, 2003).

Although the egg bank should have supported a high internal dispersal rate, the Lake 302N and Lake 223 littoral cladoceran communities followed different recovery

trajectories and ‘recovered’ (whether the Lake 302N littoral cladoceran community has recovered is still to be determined) to different states, rather than a single stable state.

Most littoral cladocerans would have been invading from the egg bank, as it is a stronger source for colonization than the regional species pool (Jenkins and Buikema, 1998).

Although this rate of internal dispersal should be much faster than external dispersal from the regional species pool, relative differences in hatching time from the egg bank may have been influential. Such differences in hatching time among species have previously been hypothesized to be influential in determining community structure (Louette, De Meester and Declerck, 2008). Earlier emergence of *C. brevilabris* from the egg bank, for example, compared to other littoral species, may have played a role in establishing its dominance during acidification and into recovery. Whether this can be deemed as priority effects, however, is uncertain, as *C. brevilabris* and *A. nana* inhabit different habitats (Fryer, 1968) and likely occupy different niches. Therefore, how *C. brevilabris* may have potentially inhibited the increase in relative abundance of *A. nana* during recovery is still unknown. Although communities with high levels of dispersal are thought, hypothetically, to develop to a single stable state, large regional species pools are suspected to lead to multiple equilibria, due to the multiple species combinations that

may be able to coexist (Chase, 2003). High levels of dispersal from the egg bank may limit priority effects from occurring, however the size of the regional species pool may still have been influential in the reassembly pathway. Therefore, it may be the multiple species combinations that can coexist (i.e. functional compensation) that may have lead to multiple equilibria.

Overall, caution must be used in applying observations from this study, particularly with respect to the importance of local versus regional factors in structuring the cladoceran community. Unlike experimentally-acidified lakes, atmospherically-acidified lakes will be exposed to long-term regional disturbance, and are therefore more susceptible to local species extirpation, damage to the egg bank and alteration of the regional species pool, depending on the severity of the stressor (Keller and Yan, 1998). These changes may, therefore, influence the relative importance of regional factors (i.e. rate of dispersal) in structuring the community, as compared to the strength of local factors as observed in these experimentally-acidified lakes.

Biological indicators of recovery: The littoral and pelagic cladoceran communities

Both the littoral and the pelagic cladoceran communities permitted inference of the recovery pathway from the fossil record; however, the level at which recovery could be evaluated differed between the two communities. For littoral cladocerans, because there was no major species turnover or replacement, evaluation at the community level using multivariate metrics was the most effective. However, for pelagic cladocerans, recovery could be evaluated at the species level, with the disappearance of acid-tolerant species and the return of acid-sensitive species. Although the pelagic community does not

preserve as well in the fossil record, as compared to cladocerans in the littoral community, its capacity to reflect change at the species level may allow for the recovery trajectory to be inferred, even with the limited available material. In order to be able to utilize the diversity of littoral cladoceran exuviae preserved in the sediment record, however, an increased knowledge of their habitat specificity and environmental preference is essential. Many studies have explored the habitat preferences of littoral cladoceran species, particularly the chydorids (Paterson, 1993; Tremel *et al.*, 2000), as well as environmental preferences, through regional surveys (DeSellas *et al.*, 2008). An increased knowledge of habitat specificity would illuminate how changes in the relative abundance of individual littoral species reflects specific changes in habitat, as well as environmental variables, in response to perturbations. Techniques are currently being explored in restoration ecology, using habitat preference to predict colonization success (Kadoya *et al.*, 2008), as well as using indicator species to represent the presence of rare and undisturbed habitat (Brewer and Menzel, 2009). Littoral cladoceran microfossils have the potential to apply these new techniques for predicting recovery trajectories. However, further species-specific targeted research of the extant community is required, in order to utilize the diversity of littoral cladoceran microfossils as a model community.

Applying a baseline

The use of a reference lake, in order to evaluate the regional baseline and natural community variability, was an important addition to the study. The appearance of *B. (N.) tubicen* in Lake 302N and Lake 223 was able to be identified as a changing regional baseline, rather than as a consequence of the acidification manipulation. In addition, the

natural variability and recent changes observed in Lake 377 cautions against assuming unchanging conditions in reference lakes. Temporal reference lakes, as used in this study, are effective at evaluating changing baselines and natural variability. However, when few temporal references are used, the amount of natural variability deemed to be acceptable is constrained (Chapman, 1999). In future studies, the use of multiple temporal reference lakes should aid in further characterizing natural variability. In addition to the temporal reference lake, a variety of spatial reference lakes might also be useful in an applied paleolimnology study. Multiple spatial reference lakes may help quantify the community structures of potential stable equilibria that exist in a region, as well as estimate the size of the regional species pool. In restoration ecology, the prevalence of a species within the regional species pool, as well as its habitat preference, has been used to estimate colonization capacity in order to predict community recovery trajectories (Kadoya *et al.*, 2008). Overall, the addition of both temporal and spatial reference lakes will further aid in predicting recovery targets.

The difference in littoral community structure of reference Lake 377 (community dominated by *C. brevilabris* and *C. sphaericus*), as compared to the two manipulated lakes (diverse and even littoral cladoceran community), limited its application as a baseline to estimate recovery targets. In addition, the amount of natural variability observed in the Lake 377 littoral community appeared, at the community level using univariate metrics, to be greater than the manipulated lakes' response to change. Although it was not the intention of this study, the differences in natural variability observed in these two community types lies at the heart of the diversity-stability debate. Not only does increased diversity increase the likelihood that some species will respond

differently to a disturbance, but it also increases the likelihood of functional redundancy and compensation within the community (Naeem and Li, 1997). With decreasing freshwater biodiversity across North America (Ricciardi and Rasmussen, 1999), mean interaction strength between species is likely to increase, precipitating destabilizing dynamics that potentially lead to ecosystem collapse (McCann, 2000). Further understanding of the interspecific interactions within these two community types, as well as their functional redundancy, may, in future, add to the understanding of the relationship between diversity and stability.

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