



## **Understanding the role of lake history in liming management: a structural and functional comparison of multiple communities**

*David G. Angeler, Richard K. Johnson, and Willem Goedkoop*

*Swedish University of Agricultural Sciences*

*Department of Aquatic Sciences and Assessment*

*PO Box 70 50*

*115 35 Uppsala*

*SWEDEN*

*Report to IKEU Focusproject Programme 2010*

*Department of Aquatic Sciences and Assessment Report 2010:18*

---

**Understanding the role of lake history in liming management:  
a structural and functional comparison of multiple  
communities**

**Sjöns historia och kalkningseffekter: en strukturell och funktionell  
jämförelse av organismsamhällen i kalkade och okalkade sjöar**

---

Uppsala, December 2010

## Table of Contents

<b>1. Summaries in Swedish and English .....</b>	<b>4</b>
<b>2. Introduction.....</b>	<b>6</b>
<b>3. Material and methods.....</b>	<b>7</b>
3.1. <i>Data assembly</i> .....	7
3.2. <i>Sampling procedures</i> .....	8
3.3. <i>Structural community metrics and functional groups</i> .....	9
3.4. <i>Statistical analyses</i> .....	10
<b>4. Results.....</b>	<b>14</b>
4.1. <i>Lake characteristics and water quality</i> .....	14
4.2. <i>Univariate analyses of community metrics</i> .....	15
4.2.1. Structural community metrics.....	15
4.2.2. Functional community metrics.....	18
4.3. <i>Multivariate analyses of community similarity</i> .....	20
4.3.1. MDS ordinations and ANOSIM analyses.....	20
4.3.2. Taxonomic contributions to community similarity.....	22
4.3.2.1. PHYTOPLANKTON.....	22
4.3.2.2. ZOOPLANKTON.....	22
4.3.2.3. LITTORAL MACROINVERTEBRATES.....	23
4.3.2.4. SUBLITTORAL MACROINVERTEBRATES.....	23
4.3.2.5. PROFUNDAL MACROINVERTEBRATES.....	23
4.3.2.6. FISH.....	23
4.4. <i>Trophic associations in foodwebs</i> .....	27
<b>5. Discussion.....</b>	<b>28</b>
5.1. <i>Communities in limed, acidified and circumneutral lakes</i> .....	29
5.2. <i>Trophic associations in foodwebs</i> .....	30
5.3. <i>Management implications</i> .....	30
<b>6. References.....</b>	<b>31</b>

## 1. Sammanfattning

I denna studie har vi analyserat samhällsstruktur och trofisk struktur hos växtplankton, djurplankton, bottenfauna (littoral, sublittoral, profundal) och fisk mellan 2000 och 2004 i fyra typer av sjöar. Sjötyperna är försurade och circumneutrala okalkade sjöar samt naturligt sura och försurade kalkade sjöar. Kalkade sjöar klassificerades som naturligt sura eller antropogent försurade baserat på de paleoekologiska undersökningar som gjorts i dem. Detta gör det möjligt för oss att undersöka hur sjöns historia kan påverka det biologiska svaret på kalkning.

Univariata ANOVA-analyser kunde inte urskilja några skillnader i samhällsstruktur och funktion mellan de olika sjötyperna, vilket tyder på att effekten av kalkning inte påverkats av sjöns historia eller om sjön för tillfället är sur eller neutral. Däremot visade multivariata analyser (Non-metric Multidimensional Scaling [MDS] och Analysis of Similarity [ANOSIM]) på signifikanta skillnader i artsammansättning mellan alla typer av sjöar. Även om många arter finns i flera typer av sjöar varierar deras proportioner i antal eller biomassa, vilket resulterar i dessa skillnader. När det gäller näringsvävarna fanns det mindre kopplingar (och komplexitet) mellan funktionella grupper i circumneutrala sjöar jämfört med de andra sjötyperna.

Även om sjötyper skiljer sig i proportioner i antal eller biomassa av arter tyder likheterna i deras samhällsstruktur på att kalkning inte minskar den övergripande strukturen och funktionen som resulterar i liknande totala biologiska mångfald och bred funktionella samhällestrukturer mellan sjötyper. Det tyder på att kalkning inte påverka på ett negativt ekologiskt sätt naturligt sura sjöar. Dessutom tyder resultaten på att kalkning av antropogent försurade sjöar inte leder till märkbart förbättrade ekologiska förhållanden jämfört med försurade sjöar som genomgår naturlig återhämtning. Samhällsstrukturen avviker inte väsentligt från varandra i dessa två sjötyper. Med andra ord, våra resultat tyder på att den sjötyp som genomgått en naturlig återhämtning från försurning (försurade okalkade sjötypen) har en liknande samhällsstruktur som den i de två typerna med kalkade sjöar och att kalkning av dessa sjöar kanske inte behövs längre.

Analyserna är baserade på tre sjöar per sjötyp. Den låga urvalsstorleken begränsar en generalisering av våra resultat. De intressanta och trots allt likartade mönster som framkommit i alla de sex studerade organismgrupperna ger oss förhoppning om att ytterligare forskning om de ekologiska effekterna av ekosystems olika historia kan öka vår förståelse av kalkningseffekter i sjöekosystem i stort.

## Summary

Biological responses of acidified surface waters to liming are sometimes equivocal and limit the overall assessment of food web responses because the ecological consequences of ecosystem history is often not explicitly accounted for. In this study we analysed community structure and trophic associations in the foodwebs in two types of limed lakes (anthropogenically acidified and naturally acidic), acidified and circumneutral lakes, based on the analyses of phytoplankton, zooplankton, macroinvertebrates (littoral, sublittoral, profundal), and fish between 2000 and 2004. We discerned between limed lakes in the IKEU program that were naturally acidic or anthropogenically acidified, based on recent paleoecological evidence highlighting these differences. This allowed us to assess the degree by which historical contingency of lake ecosystems mediate liming outcomes.

Most univariate metrics of structure and function revealed similar community attributes among lake types, suggesting that historical contingency had little influences on liming outcomes. Differences between lake types were clearer in the multivariate analyses. Even though the communities in the different lake types shared many species, their abundance patterns differed, resulting in the observed differences. Regarding foodweb structure, the associations between functional feeding groups indicated less connectivity and food web complexity in circumneutral lakes relative to the other lake types. This contrasts with the findings of a previous study, which speculated that repeated lime applications comprise frequent pulse disturbances, which offset the establishment of stable trophic relationships in the food webs of limed lakes. These differences between studies may arise because of the different ways ecosystems were pooled for the analysis, highlighting the need to study lake food webs using different methods. Analyses of fatty acids and stable isotopes and comparing patterns across lakes could be promising for such a task.

The similarities in univariate community metrics among lake types suggest that liming does not diminish the overall structure and function of naturally acidic lakes when they are limed. Although the set of species are different in this lake type, overall biodiversity and broad functional community aspects are similar to those observed in other lake types. On the contrary, the results also suggest that liming of acidified lakes does not result in improved ecological conditions because the community metrics in this lake type did not deviate significantly from those of acidified lakes that undergo natural recovery. In other words, our results suggest that natural recovery from acidification results in similar community attributes that are otherwise achieved through more costly liming management.

We acknowledge that our analyses are based on three lakes per lake group (circumneutral, acidified, acidified – limed, naturally acidic-limed). While this low sample size limits generalization of our results, interesting patterns were revealed that were consistently observed across the six communities studied here. These results suggest that further research into the ecological effects of ecosystem history is warranted to improve our understanding of liming effects in lake ecosystems.

## 2. Introduction

Anthropogenic acidification of surface waters has been a major environmental problem in northern Europe and eastern North America during the epoch of flourishing industrial activity. Acid rain impacted aquatic ecosystems by lowering pH and increasing aluminium concentrations beyond lethal toxic thresholds for organisms, leading to a loss of biodiversity and profound alteration of community structure and ecosystem processes (Schindler 1988). Although aquatic ecosystems show signs of recovery due to reduced emissions of acidifying compounds (Ormerod & Durance 2009), many countries continue to implement large-scale mitigation programmes based on lime application to surface waters and catchments (Henriksson & Brodin 1995; Sandoy & Romunstad 1995). For example, in Sweden, some 5000 lakes and 9000 km of watercourses are limed at a yearly cost of c. 1.8 million €, in order to restore biodiversity (i.e. facilitate the recovery of acid-sensitive biota) and create conditions for recreational and commercial fishing and aquaculture (i.e. protect and enhance existing fish populations; Appelberg & Svensson 2001; SEPA 2007). Liming has increased pH and alkalinity in many acidified waters resulting in improved conditions for aquatic biota.

However, studies from Europe and North America have reported mixed results considering the biological responses to liming (Clair & Hindar 2005). In lakes, liming has often, but not always, induced improvements in fish (Appelberg & Degerman 1991), phytoplankton (Renberg & Hultberg 1992), zooplankton (Stenson & Svensson 1995) and benthic macroinvertebrates (Persson & Appelberg 2001). Inconsistencies of results among studies may not be surprising, however, given that abiotic and biotic constraints affect biological recovery in context-dependent ways (Yan et al. 1996, 2003; Binks et al. 2005). These include fluctuations in water chemistry caused by repeated liming and re-acidification events, dispersal capacities of organisms, the characteristics of their habitats and taxon-specific time lags.

Research has demonstrated that historical effects can also mediate the outcome of management practices and disturbance impacts (Fischer et al. 2001). To assess the degree by which liming can adversely affect ecosystems and their component communities, it is necessary to take the ecological history of ecosystems explicitly into account. That is, no clear distinctions of ecosystem history have been made in previous studies on liming outcomes in lakes of the IKEU ("*Integrerad Kalknings Effekt Uppföljning*") program (e.g., Goedkoop & Angeler 2010; Angeler & Goedkoop 2010). This was due to the lack of paleoecological data that can document the history of lake ecosystems prior to the onset of the anthropogenic acidification. During times when the acidification problem peaked, managers were forced to take management action without having the necessary information about whether lakes were anthropogenically acidified or naturally acidic, and distinctions could be hardly made between these otherwise ecologically distinct ecosystem types. Thus, while liming may be beneficial for mitigating the negative effects of acidification on communities and ecological integrity in anthropogenically acidified lakes, it can be assumed that liming effects are detrimental in naturally acidic ecosystems (Bishop et al. 2001; McKie et al. 2006). A recent paleolimnological study has shown that such distinctions in acidification history can be made in the limed lakes of the IKEU program (Norberg et al. 2008). This provides the opportunity to assess historical contingency effects on the outcomes of liming (in terms of current abiotic and biotic structure of lakes).

In this report we re-analyze the data that have been used in our previous studies (Goedkoop & Angeler 2009; Angeler & Goedkoop 2010). We studied biological responses to repeated liming across trophic levels (i.e. phytoplankton, zooplankton, invertebrate consumers, fish) and habitats (i.e. pelagic, benthic) using univariate and multivariate statistics. We use data from the Swedish Integrated Liming Effect Studies (IKEU) programme to assess congruencies in community recovery patterns in two types of limed lakes relative to acidified and circumneutral lakes over a 5-year period (2000–2004) using structural metrics, functional feeding categories and multivariate ordinations. In a next step, we determine how individual patterns of community dynamics collectively affect the direct and indirect trophic associations between functional feeding groups within the food webs of limed lakes with different ecological history (anthropogenically acidified vs. naturally acidic), and in acidified and circumneutral lakes.

### **3. Material and methods**

#### *3.1. Data assembly*

We evaluated data of phytoplankton, zooplankton and fish in the pelagic and macroinvertebrate communities in three benthic habitat types (littoral, sublittoral, and profundal) of selected lakes available in the IKEU and national lake monitoring databases. Data have been collected since 1986, but the databases were highly heterogeneous with regard to temporal sampling resolution of communities in acidified, circumneutral and limed lakes. This was primarily due to repeated adjustments of the sampling frequencies and differences in sampling methods. For example, phytoplankton communities were sampled between 2 and 7 times per year while macroinvertebrates were sampled only once a year during most of the program. In order to be able to make standardized comparisons between communities, all analyses for the present report are based on a single yearly sampling occasion (August for phyto- and zooplankton communities, October for macroinvertebrates). Extracting a single yearly value from the databases also helped to avoid potential problems, which would arise from the calculation of annual means based on irregular intra-annual sample sizes among lakes and communities. Our final analysis is restricted to the 5-year period between 2000 and 2004 ultimately constrained by methodological differences in the sampling of littoral macroinvertebrate communities in IKEU (limed lakes) and monitoring programs of acid and circumneutral lakes.

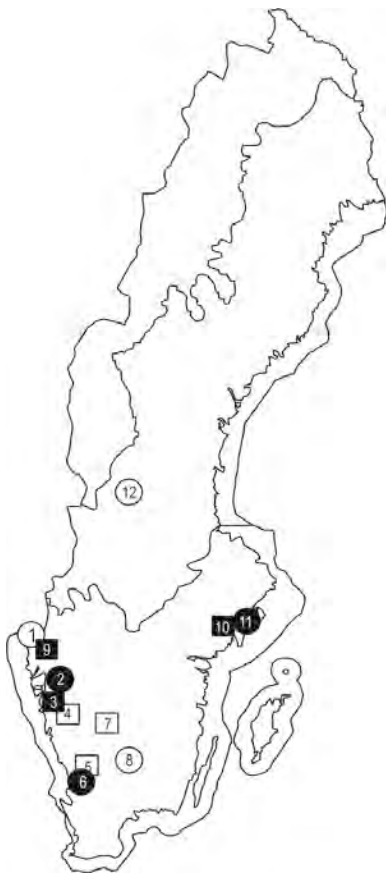
The lakes summarized in Table 1 and Figure 1 met our final selection criteria for standardized comparisons. Three of these lakes are anthropogenically acidified, three are circumneutral, three are naturally acidic and which have been limed (Norberg et al. 2008), and three lakes are anthropogenically acidified which have been limed (Norberg et al., 2008). Almost all lakes are situated in the mixed forest ecoregion of southern Sweden. Some of their water quality variables are shown in Table 1. These lakes represent a subset of lakes, which have been used in our previous report (Goedkoop & Angeler, 2009) and the subsequent scientific publication (Angeler & Goedkoop, 2010). Using this subset of lakes allows for comparisons of results between studies, and hold potential to reveal the outcomes of liming when lake history is explicitly taken into account.

We acknowledge that also the inclusion of overlimed lakes was considered in this study. However, overlimed lakes were sampled during a different period (2006-2010). One of our main aims of this study was to compare the results of the present study with those of our previous work to assess the magnitude of bias when lake history is not explicitly taken into account in assessments of liming effects in lakes. Carrying out this study on a different period would not have allowed for this comparison. Thus, after consultation with IKEU programme leader, Tobias Vrede, we agreed on not including overlimed lakes in the present report.

For the present study all analyses except littoral macroinvertebrates are based on biomass data ( $\text{mm}^3 \text{L}^{-1}$  for phytoplankton,  $\text{mm}^3 \text{m}^{-3}$  for zooplankton,  $\text{g m}^{-2}$  for sublittoral and profundal macroinvertebrates). Littoral macroinvertebrate samples were collected by standardized kick samples, thus resulting in semi-quantitative abundance data.

### 3.2. Sampling procedures

For water quality analysis we used August values of surface-water samples (0–2 m), which were collected with a Ruttner sampler at 0.5m depth in the open-water mid-lake station in each lake. Water was collected with a Plexiglas sampler and kept cool during transport to the laboratory. Samples were analyzed for Alkalinity, and concentrations of Ca, Mg, Na, K,  $\text{SO}_4$ , Cl, F,  $\text{NH}_4\text{-N}$ ,  $\text{NO}_2\text{-N}+\text{NO}_3\text{-N}$ , total N,  $\text{PO}_4\text{-P}$ , total P, Si, total organic carbon (TOC) and Chlorophyll *a*.



**Figure 1:** Localization of study lakes. Lake categories: acidified lakes (A; black squares), circumneutral lakes (N; black circles), naturally acidic, limed lakes (NAL; white circles), anthropogenically acidified, limed lakes (AAL; white squares). 1 = Ejdeshjön (NAL), 2 = Fräcksjön (N), 3 = Härsvatten (A), 4 = Stora Härsjön (AAL), 5 = Gyltigesjön (AAL), 6 = Stora Skärsjön (N), 7 = Stengårdshultasjön (AAL), 8 = Gylättasjön (NAL), 9 = Rotehogstjärnen (A), 10 = Brunnsjön (A), 11 = Allgjuttern (N), 12 = Västra Skälsjön (NAL).



Secchi depth, water temperature, dissolved oxygen concentration, conductivity, and pH were measured in the lakes. Remaining P was calculated by subtracting PO<sub>4</sub>-P from total P. These water quality variables helped to delineate lake types, i.e., while limed lakes clearly comprised two treatment groups, we discerned between acidified and circumneutral lakes, chiefly on the basis of their pH, ANC and alkalinity values (Table 1).

All physicochemical analyses were done at the Department of Aquatic Sciences and Assessment following international (ISO) or European (EN) standards when available (Wilander et al. 2003). Littoral macroinvertebrate samples were collected once in autumn (between September and November) from stony habitats (wind exposed littoral regions) using standardized kick sampling and a handnet (European Committee for Standardisation, 1994) with a 0.5-mm mesh size, and preserved in 70% ethanol. Samples of sublittoral and profundal invertebrates were sampled using an Ekman grab (surface area 0.025 m<sup>2</sup>), screened in a 0.5 mm sieve and preserved in 70% ethanol. Five replicate samples were collected and biomasses were determined by weighing (ethanol weight); the average of the five replicates is used for analyses. In the laboratory, samples were sorted under 10x magnification, identified using dissecting and light microscopy. Organisms were identified to the lowest taxonomic unit possible, generally to the species level, although exceptions occurred with some chironomid larvae and immature oligochaetes.

Zooplankton was sampled quantitatively in August using a 55-cm Plexiglas tube (i.d. 10 cm) equipped with a closing mechanism triggered by a messenger. Samples were generally collected at 2-m intervals from the surface down to 8-m depth. Samples were pooled, screened (40 µm), and preserved in acid Lugol's solution. Taxonomic analyses, enumeration, and length measurements were done using an inverted microscope. Biovolumes were calculated from length measurements and known relationships for different taxa, life stages and/or size classes.

Epilimnetic, integrated samples (0–4 m) of phytoplankton samples were also collected in August were collected with a tube sampler, usually from 5 sites per lake, pooled and preserved in Lugol's solution. Taxonomic analyses and species enumeration was done under an inverted microscope using the Utermöhl technique (Ollrik et al. 1989). Biovolumes were calculated from geometric shapes following Blomqvist & Herlitz (1998).

### 3.3. Structural community metrics and functional groups

For all communities we used structural metrics that are routinely used in the analysis of ecological communities (i.e., total biomass/abundance, species/taxon richness, Pielou's evenness index and Shannon-Wiener index). Regarding the functional classification, we followed to a great extent the schemes used by Sundbom (2009). For example, phytoplankton was divided into autotrophic, mixotrophic and heterotrophic biomass groups following the classification scheme of Jansson et al. (1996). Briefly, Bacillariophyceae, Conjugatophyceae, Cryptophyceae, Cyanophyceae, Loxophyceae, Prasinophyceae, Xanthophyceae and Chlorophyceae were considered to be functionally autotrophic, except the green algae *Polytoma* och *Polytomella* (mixotrophic taxa). Many groups that are known to have many mixotrophic species are Chrysophyceae, Craspedophyceae, Dinophyceae, Euglenophyceae, Haptophyceae and

Raphidophyceae. Taxa were considered heterotrophic when they contained no photosynthetic apparatus (e.g., euglenozoan flagellates).

Zooplankton was divided into the functional groups predators and filter-feeders (Gliwicz 1969ab). The latter group not necessarily ingests only bacterioplankton and phytoplankton, but also preys on small animals. However, as filter feeders “passively prey” on animals with a smaller body size, they are not dealt with as predators in the strict sense. We considered as predators all cyclopoid copepods, the calanoid copepods *Heterocope* and *Eurytemora*, the cladocerans *Bythotrephes*, *Polyphemus* and *Leptodora*, and the rotifer *Asplanchna*. The remaining taxa were assigned as filter-feeders.

Functional guilds of macroinvertebrates were according to the descriptions by Moog (1995). Although Moog’s scheme differentiates between 10 groups we focused on the broader categories detritivores, predators, filterfeeders, and grazers. Many species could sometimes be assigned simultaneously to several guilds, i.e. due to ontogenetic feeding shifts. When this occurred we used the dominant functional category to characterize a species functional role.

It was not possible to unambiguously determine ontogenetic feeding modes for fish (planktivory, benthivory, piscivory), and therefore no analyses of trophic guilds were carried out.

#### 3.4. Statistical analyses

Repeated measures analysis of variance (rm-ANOVA) was carried out in Statistica v.5 (Statsoft Inc, Tulsa, Oklahoma, USA) to test for differences in community metrics (total biomass/abundance, species richness and Shannon-Wiener biodiversity) and functional groups for each of the studied communities between lake type (acid lakes, circumneutral lakes and limed lakes) and over the study years. When significant treatment effects were found, the Tukey HSD test was used to determine pairwise differences in treatment means. All dependent variables were  $\log(x+1)$ -transformed when necessary to fulfill the requirements of parametric tests. Significant effects were inferred at  $P \leq 0.05$ .

Non-metric multidimensional scaling (NMDS) was done in Primer v.6 (Primer-E Ltd, Plymouth, UK) to explore the similarity of community trends over the study period across lake types. As a nonlinear technique, NMDS ranks points in ordination space in a way that the distance between sampling points (in this study aquatic communities) reflects community similarity (ter Braak, 1995). The ordination is based on a Bray-Curtis dissimilarity matrix derived from average values of all replicate lakes and  $\log(x+1)$ -transformation of the sample by species matrix. In addition, a NMDS analysis was carried out for water quality; in this case the ordination is based on a Euclidean distance matrix derived from standardized and  $\log(x+1)$ -transformed water chemistry data, including Secchi depth, water temperature, dissolved oxygen concentration, conductivity, pH, alkalinity, and concentrations of Ca, Mg, Na, K, SO<sub>4</sub>, Cl, F, NH<sub>4</sub>-N, NO<sub>2</sub>-N+NO<sub>3</sub>-N, total N, PO<sub>4</sub>-P, total P, remaining P (total P – PO<sub>4</sub>-P), Si, total organic carbon (TOC) and Chlorophyll *a*. The final solutions for each community and the water quality analysis are based on 999 permutations.

Analysis of Similarity (ANOSIM; 999 permutations) was also run in Primer to test if significant differences in biomass/abundance of communities occurred among lake types. This analysis is an approximate non-parametric analogue of the standard

univariate analysis of variance ANOVA, and it uses the R statistic to test differences between groups (R=0, no differences; R=1, all dissimilarities between groups are larger than all dissimilarities within groups). In the present study, the ANOSIM analysis was used to complement the NMDS analyses. As such it was of prime interest to use the same samples as those used for the ordination. This means that we first calculated the yearly average for each lake type. This resulted in 5 replicates (5 study years) x 4 lake types (acidified lakes, circumneutral lakes, acidified-limed lakes, naturally acidic – limed lakes) = 20 samples for the analysis. Similarity Percentage routine (SIMPER; also included in Primer v.6) was used to reveal which taxa contributed to dissimilarity between lake types.

Spearman rank correlation analyses between biomass data of functional groups were carried out in Statistica to reveal trends in trophic associations in acidified, circumneutral, and the two types of limed lakes as a function of habitat type and trophic position of communities in the food webs. This analysis provides insight into how liming directly or indirectly affects the trophic associations between food web components relative to acidified and circumneutral lakes. To facilitate interpretation of the results, we focused on correlations between trophic levels and habitat types. Food web associations were quantified through the number and strength of significant correlations from the possible number of all correlations, which was identical across lake types.

**Table 1: Morphological and selected water chemistry characteristics of lakes included in the study. Values represent the interannual mean values (bold font) based on summer values (August)  $\pm$  1 standard error (italic fonts; n = 5) for the time period 2000–2004.**

SMHI X SMHI Y	Lake area (km <sup>2</sup> )	Max. Depth (m)	pH	Alkalinity meq L <sup>-1</sup>	Ca meq L <sup>-1</sup>	Mg meq L <sup>-1</sup>	Na meq L <sup>-1</sup>	K meq L <sup>-1</sup>	SO <sub>4</sub> meq L <sup>-1</sup>	Cl meq L <sup>-1</sup>	F mg L <sup>-1</sup>	TOC mg L <sup>-1</sup>	PO <sub>4</sub> -P μg L <sup>-1</sup>	NO <sub>2</sub> +NO <sub>3</sub> -N μg L <sup>-1</sup>	
<b>ACIDIFIED LAKES</b>															
<b>Brunnsjön</b>	627443	0.11	10.60	<b>5.71</b>	< <b>0.01</b>	<b>0.20</b>	<b>0.12</b>	<b>0.21</b>	<b>0.02</b>	<b>0.20</b>	<b>0.17</b>	<b>0.13</b>	<b>20.42</b>	<b>4.20</b>	<b>53.40</b>
	149526		<i>±0.10</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±4.51</i>	<i>±0.86</i>	<i>±11.13</i>
<b>Härsvatten</b>	643914	0.19	26.20	<b>4.84</b>	<b>-0.02</b>	<b>0.03</b>	<b>0.06</b>	<b>0.24</b>	<b>0.01</b>	<b>0.09</b>	<b>0.26</b>	<b>0.03</b>	<b>2.38</b>	<b>1.40</b>	<b>55.00</b>
	127698		<i>±0.07</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.23</i>	<i>±0.24</i>	<i>±8.22</i>
<b>Rotehogstjärnen</b>	652902	0.17	9.40	<b>5.88</b>	<b>0.02</b>	<b>0.07</b>	<b>0.21</b>	<b>0.01</b>	<b>0.01</b>	<b>0.07</b>	<b>0.18</b>	<b>0.05</b>	<b>13.26</b>	<b>2.60</b>	<b>4.60</b>
	125783		<i>±0.03</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±1.65</i>	<i>±0.68</i>	<i>±1.33</i>
<b>CIRCUMNEUTRAL LAKES</b>															
<b>Allgjuttern</b>	642489	0.19	40.70	<b>6.79</b>	<b>0.07</b>	<b>0.17</b>	<b>0.10</b>	<b>0.13</b>	<b>0.01</b>	<b>0.17</b>	<b>0.09</b>	<b>0.22</b>	<b>7.08</b>	<b>1.80</b>	<b>4.00</b>
	151724		<i>±0.15</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±0.01</i>	<i>±0.23</i>	<i>±0.37</i>	<i>±1.05</i>
<b>Fräcksjön</b>	645289	0.28	14.50	<b>6.68</b>	<b>0.08</b>	<b>0.17</b>	<b>0.09</b>	<b>0.26</b>	<b>0.02</b>	<b>0.10</b>	<b>0.26</b>	<b>0.07</b>	<b>9.42</b>	<b>2.40</b>	<b>7.60</b>
	128665		<i>±0.07</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.42</i>	<i>±0.40</i>	<i>±2.73</i>
<b>St Skårsjön</b>	628606	0.31	11.50	<b>6.99</b>	<b>0.13</b>	<b>0.18</b>	<b>0.16</b>	<b>0.32</b>	<b>0.01</b>	<b>0.17</b>	<b>0.31</b>	<b>0.07</b>	<b>5.10</b>	<b>1.80</b>	<b>4.20</b>
	133205		<i>±0.08</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±0.01</i>	<i>±0.01</i>	<i>±&lt;0.01</i>	<i>±&lt;0.01</i>	<i>±0.99</i>	<i>±0.37</i>	<i>±1.59</i>

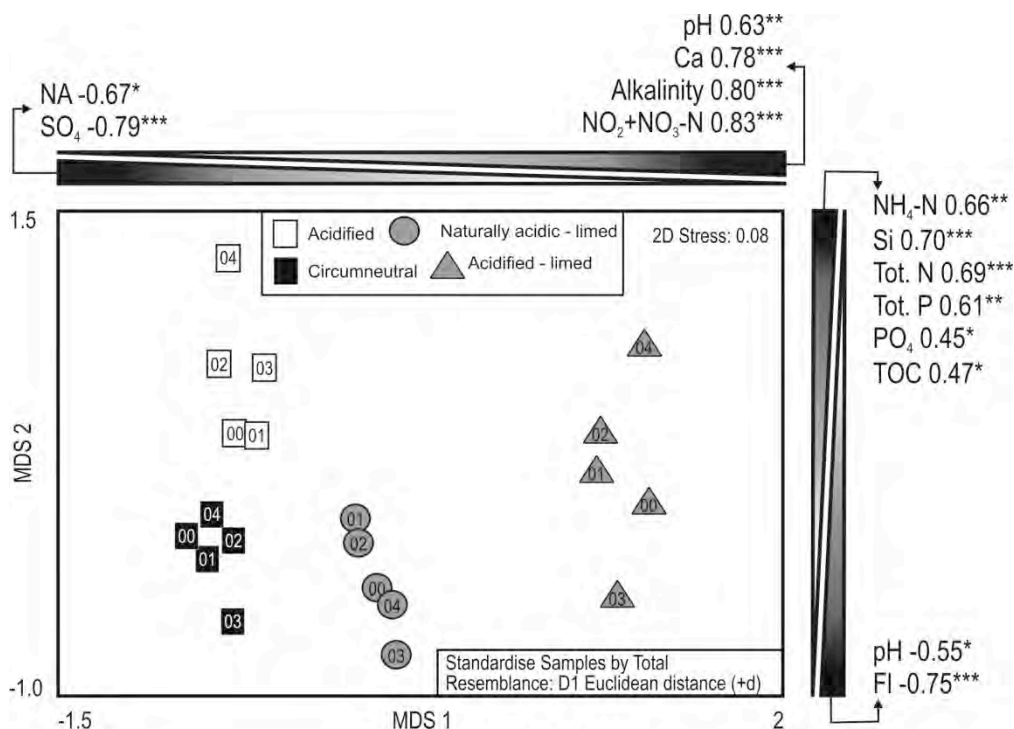
Table 1 continued

SMHI X SMHI Y	Lake area (km <sup>2</sup> )	Max. Depth (m)	pH	Alkalinity meq L <sup>-1</sup>	Ca meq L <sup>-1</sup>	Mg meq L <sup>-1</sup>	Na meq L <sup>-1</sup>	K meq L <sup>-1</sup>	SO <sub>4</sub> meq L <sup>-1</sup>	Cl meq L <sup>-1</sup>	F mg L <sup>-1</sup>	TOC mg L <sup>-1</sup>	PO <sub>4</sub> -P µg L <sup>-1</sup>	NO <sub>2</sub> +NO <sub>3</sub> -N µg L <sup>-1</sup>	
<b>NATURALLY ACIDIC, LIMED LAKES</b>															
<b>Ejdesjön</b>	653737 125017	28.60	7.49 ±0.12	0.25 ±0.03	0.33 ±0.02	0.06 ±<0.01	0.28 ±<0.01	0.01 ±<0.01	0.08 ±<0.01	0.28 ±0.01	0.09 ±<0.01	0.09 ±0.01	5.78 ±0.75	1.80 ±0.58	116.00 ±14.52
<b>V. Skälsjön</b>	664620 148590	18.70	7.00 ±0.15	0.14 ±0.02	0.20 ±0.01	0.03 ±<0.01	0.06 ±<0.01	0.01 ±<0.01	0.09 ±<0.01	0.04 ±<0.01	0.08 ±<0.01	12.58 ±2.37	1.60 ±0.40	3.40 ±0.51	
<b>Gyslättasjön</b>	633209 141991	9.80	6.87 ±0.06	0.12 ±0.01	0.29 ±0.01	0.06 ±<0.01	0.15 ±0.01	0.01 ±<0.01	0.13 ±0.01	0.13 ±0.01	0.08 ±<0.01	12.90 ±1.01	1.60 ±0.24	4.20 ±0.92	
<b>ACIDIFIED, LIMED LAKES</b>															
<b>Gyltigesjön</b>	629489 133906	20.00	7.04 ±0.10	0.26 ±0.03	0.39 ±0.03	0.11 ±0.01	0.21 ±0.01	0.01 ±<0.01	0.10 ±0.01	0.21 ±0.01	0.09 ±<0.01	15.68 ±1.85	5.00 ±1.26	154.20 ±14.96	
<b>Stengårdshultasjön</b>	638317 138010	26.80	7.07 ±0.04	0.18 ±0.01	0.29 ±0.01	0.08 ±<0.01	0.15 ±<0.01	0.02 ±<0.01	0.09 ±<0.01	0.16 ±<0.01	0.07 ±<0.01	10.14 ±0.43	2.40 ±0.75	53.80 ±14.37	
<b>Stora Härsjön</b>	640364 129240	42.00	7.36 ±0.12	0.28 ±0.01	0.39 ±0.01	0.08 ±<0.01	0.30 ±0.01	0.02 ±<0.01	0.12 ±<0.01	0.33 ±0.01	0.07 ±<0.01	4.80 ±0.19	1.20 ±0.20	133.40 ±15.53	

## 4. Results

### 4.1. Lake characteristics and water quality

Most of the lakes had a surface area  $<1 \text{ km}^2$ , but some lakes were up to 5-times larger. Brunnsjön was the smallest lake ( $0.11 \text{ km}^2$ ) while Stengårdshultasjön was the largest ( $4.98 \text{ km}^2$ ) (Table 1). The lakes also showed a depth gradient, with the acidified lake Rotehogstjärnen being the shallowest ( $Z_{\text{max}} = 9.4 \text{ m}$ ) and the acidified, limed Stora Härsjön being the deepest ( $Z_{\text{max}} = 42 \text{ m}$ ). With regard to trophic state characteristics acidified, circumneutral, acidified - limed and naturally acidic - limed lakes showed average total P concentrations of  $8.13$ ,  $11.20$ ,  $10.80$  and  $7.56 \mu\text{g L}^{-1}$ , respectively, and average total N concentrations of  $386.07$ ,  $451.93$ ,  $464.60$  and  $380.81 \mu\text{g L}^{-1}$ , respectively. Differences in water quality were observed among lake types with regard to water quality variables that are most affected by acidification and liming treatments. For example, the mean pH of acidified lakes was always below 6, while circumneutral lakes showed an average pH value of 6.82. The two types of limed lakes showed a  $\text{pH} > 7.0$ . The integral analysis of water quality using multivariate statistics showed that water chemistry in the different lake types clusters distinctly in ordination space (Figure 2), and an analysis of similarity showed significant differences in water quality between lake categories (ANOSIM: global  $R = 0.903$ ,  $P < 0.001$ ).



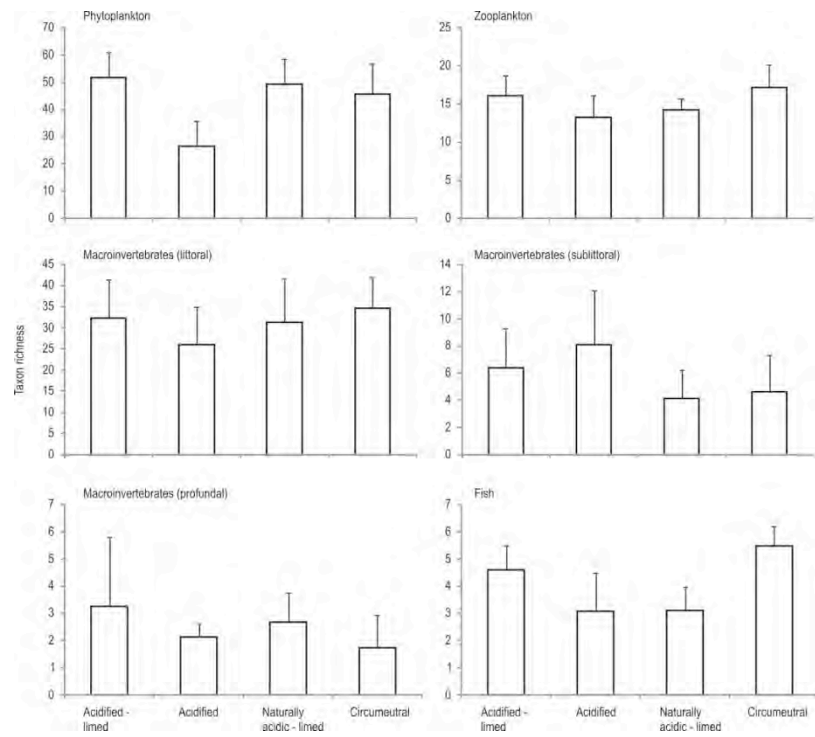
**Figure 2:** Nonmetric multidimensional scaling (MDS) ordinations showing similarities in water quality characteristics between lake types. Shown are also the variables that correlated with the MDS dimensions 1 and 2, and which explained gradients in water quality characteristics in the ordination. The strength of correlation is indicated by the Spearman rank correlation coefficient ( $\rho$ ) and the significance level (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

Relating water chemistry variables to the MDS dimension through Spearman rank correlation analyses revealed gradients in the abiotic environment that help understand the organization of lake types in multivariate ordination space. Lake groups were separated along MDS 1 as a function of variables that clearly captured the management (liming) intervention on one hand, but also nutrient conditions on the other hand. Both types of limed lakes were characterised by higher concentrations of Ca and  $\text{NO}_2+\text{NO}_3\text{-N}$ , a higher alkalinity and pH, and lower concentrations of Na and  $\text{SO}_4$  relative to acidified and circumneutral lakes (Figure 2). Along MDS 2, gradients in the acidity and nutrient status helped explain the observed patterns. Anthropogenically acidified-limed lakes showed lower pH values relative to the other lake groups. Acidified-limed lakes showed a wider spread of sampling dates along MDS 2. Similar trends were observed regarding nutrient conditions ( $\text{NH}_4$ , total P, total N,  $\text{PO}_4$ ) and water colour (TOC), with acidified lakes clearly deviating from circumneutral and anthropogenically acidified-limed lakes, and with naturally acidic-limed lakes occupying intermediate positions.

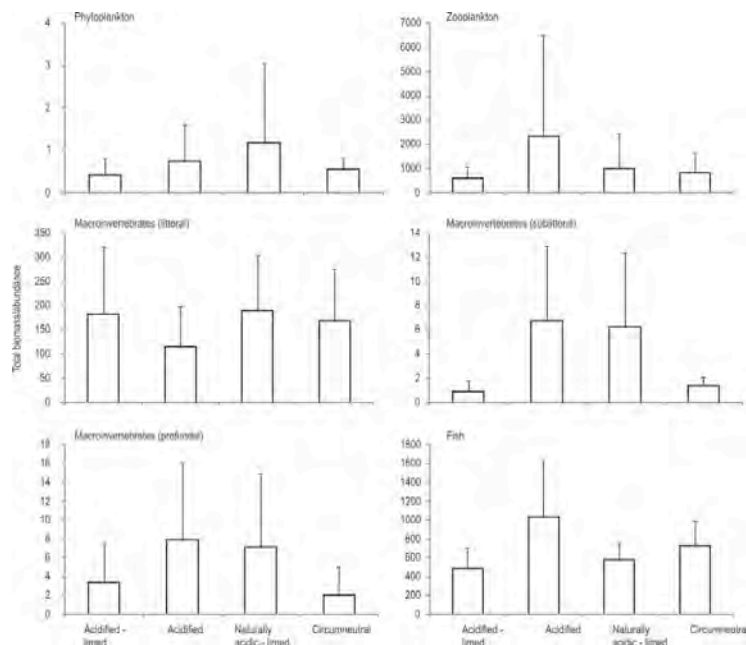
## ***4.2. Univariate analyses of community metrics***

### **4.2.1. Structural community metrics**

Analysing univariate metrics of community structure of phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral and profundal) and fish revealed that circumneutral, acidified and the two types of limed lakes are very similar from a structural perspective (Figure 3-6; Table 2). Only one metric (phytoplankton taxon richness) showed a significant treatment effect in the ANOVA model (Table 2). Phytoplankton taxon richness in acidified lakes was significantly lower compared with the other lake types (Figure 3). The total biomass of profundal macroinvertebrates showed a significant treatment x time interactions in the ANOVA models (Table 2). This means that total biomass was not different between lake types, but these lakes differed in the temporal biomass patterns, resulting in the observed significant interaction term. Significant time effects were found for fish taxon richness and the total biomass of zooplankton and profundal macroinvertebrates (Table 2). This means that all metrics showed temporal variability between years over the study period. Because the study of temporal trajectories was not of primary interest in the present study, only mean values over the study period are shown in the figures.

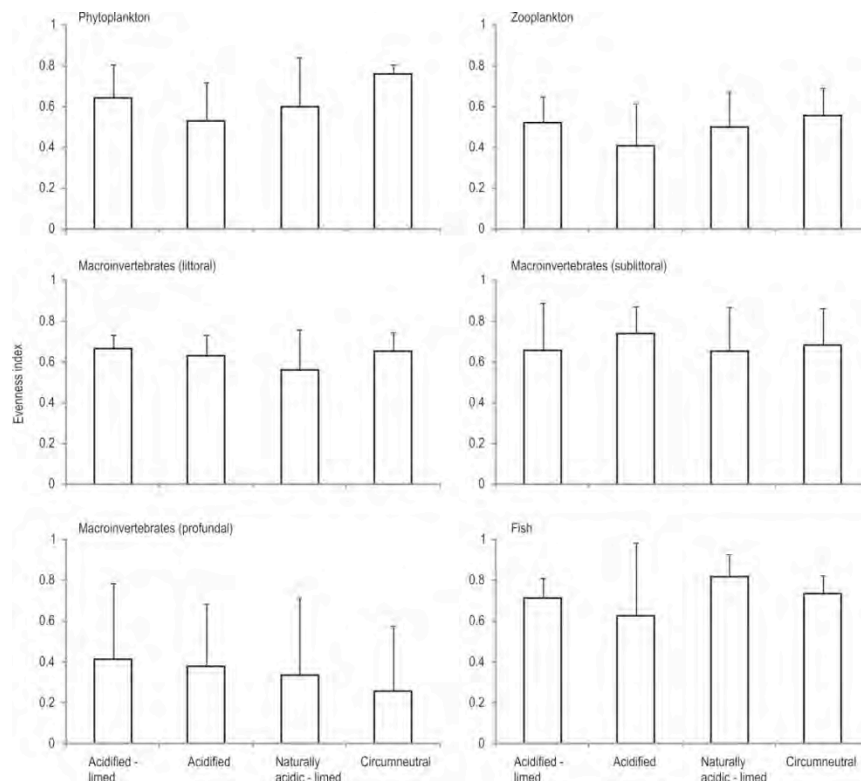


**Figure 3:** Taxon richness of phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral, sublittoral) and fish in circumneutral, acidified, anthropogenically acidified – limed, and naturally acidic – limed lakes. Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar).

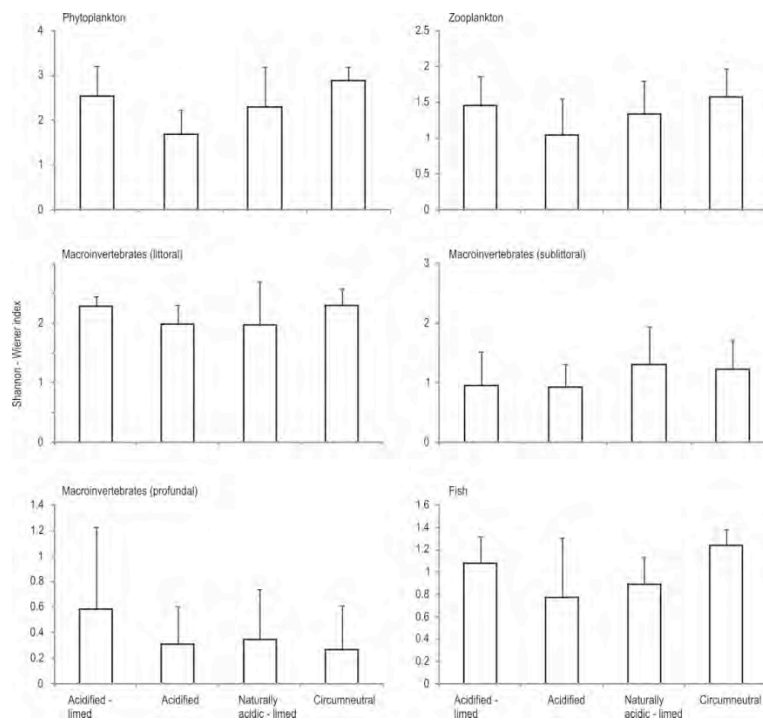


**Figure 4:** Total abundance/biomass of phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral, sublittoral) and fish in circumneutral, acidified, anthropogenically acidified – limed, and naturally acidic – limed lakes. Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar).





**Figure 5:** Evenness index calculated for phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral, sublittoral) and fish in circumneutral, acidified, anthropogenically acidified – limed, and naturally acidic – limed lakes. Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar).



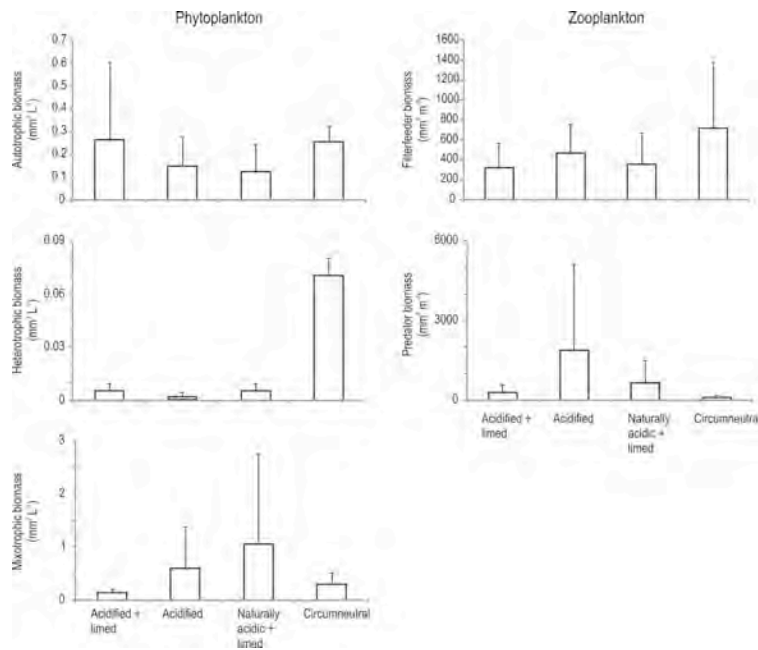
**Figure 6:** Shannon-Wiener biodiversity index calculated for phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral, sublittoral) and fish in circumneutral, acidified, anthropogenically acidified – limed, and naturally acidic – limed lakes. Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar).

**Table 2:** Results of repeated measures ANOVA contrasting structural community metrics between lake types (circumneutral, acidified, anthropogenically acidified – limed, naturally acidic – limed). Shown are the degrees of freedom (df), mean squares (MS), F ratios (F) and significance levels (P). Significant terms are highlighted in bold.

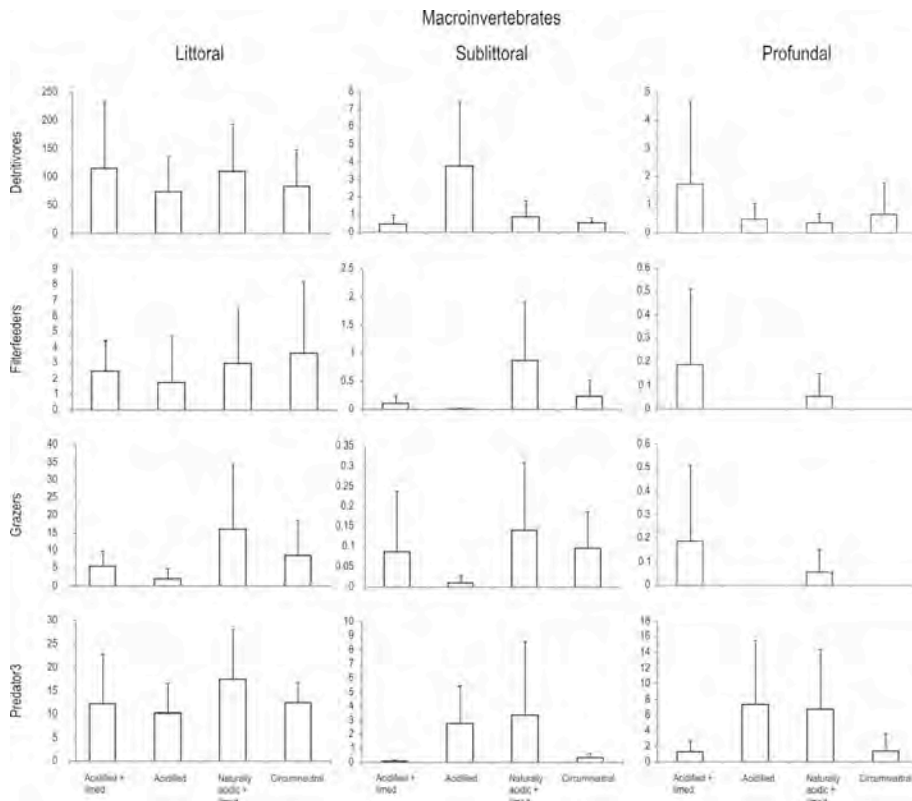
	Treatment (df 3,8)			Time (df 4,32)			Treatment x Time (df 12,32)		
	MS	F	P	MS	F	P	MS	F	P
<b>Phytoplankton</b>									
Taxon Richness	<b>0.297</b>	<b>5.521</b>	<b>0.024</b>	0.012	2.236	0.087	0.004	0.801	0.647
Total biomass	0.023	0.118	0.947	0.009	1.253	0.309	0.006	0.847	0.604
Evenness index	0.011	1.130	0.393	0.001	0.931	0.458	0.002	1.178	0.339
Shannon-Wiener index	0.078	2.291	0.155	0.007	1.505	0.224	0.006	1.231	0.306
<b>Zooplankton</b>									
Taxon Richness	0.034	1.983	0.195	0.003	0.873	0.491	0.003	0.924	0.535
Total biomass	0.156	0.167	0.916	<b>0.537</b>	<b>2.755</b>	<b>0.045</b>	0.128	0.657	0.778
Evenness index	0.006	1.201	0.370	0.002	0.822	0.521	0.001	0.345	0.973
Shannon-Wiener index	0.034	2.120	0.176	0.008	0.951	0.447	0.004	0.444	0.932
<b>Macroinvertebrates (littoral)</b>									
Taxon Richness	0.063	0.493	0.679	0.044	0.999	0.422	0.039	0.891	0.565
Total abundance	0.204	0.294	0.829	0.097	0.660	0.624	0.187	1.268	0.284
Evenness index	0.003	0.862	0.499	<0.01	0.384	0.819	0.001	0.880	0.574
Shannon-Wiener index	0.014	0.931	0.469	0.003	0.532	0.713	0.004	0.702	0.738
<b>Macroinvertebrates (sublittoral)</b>									
Taxon Richness	0.188	0.859	0.500	0.012	0.829	0.517	0.016	1.607	0.418
Total biomass	1.073	3.886	0.055	0.039	1.254	0.308	0.043	1.392	0.220
Evenness index	0.002	0.266	0.848	0.002	0.748	0.567	0.003	1.384	0.224
Shannon-Wiener index	0.022	0.336	0.800	0.002	0.466	0.760	0.007	1.500	0.175
<b>Macroinvertebrates (profundal)</b>									
Taxon Richness	0.085	0.487	0.701	0.012	0.876	0.489	0.010	0.760	0.684
Total biomass	0.690	0.588	0.640	<b>0.101</b>	<b>5.291</b>	<b>0.002</b>	<b>0.048</b>	<b>2.516</b>	<b>0.019</b>
Evenness index	0.007	0.168	0.915	0.005	0.644	0.635	0.004	0.007	0.868
Shannon-Wiener index	0.018	0.220	0.880	0.002	0.327	0.858	0.003	0.592	0.832
<b>Fish</b>									
Taxon Richness	0.110	0.282	0.837	<b>0.010</b>	<b>3.253</b>	<b>0.026</b>	0.002	0.674	0.761
Total biomass	1.756	0.351	0.790	0.008	0.708	0.593	0.008	0.756	0.688
Evenness index	3.450	0.717	0.572	<0.01	0.129	0.971	0.001	0.805	0.643
Shannon-Wiener index	0.259	2.661	0.129	<0.01	0.383	0.129	0.001	1.116	0.386

#### 4.2.2. Functional community metrics

Analysing autotrophic, heterotrophic and mixotrophic biomass of phytoplankton, filterfeeder and predator biomass of zooplankton, and predator, detritivore, grazer and filterfeeder biomass/abundance of macroinvertebrates in three habitat types (littoral, sublittoral and profundal) revealed that circumneutral, acidified and the two types of limed lakes are very similar from a functional perspective. Although variability existed between lake types (Figs. 7 and 8), the differences were never sufficiently strong to result in significant treatment effects in the rm-ANOVAs (Table 3). Only in the case of heterotrophic phytoplankton was a marginally significant treatment effect detected (Table 3), showing that circumneutral lakes have a slightly higher biomass fraction of this functional group compared to the other lake types. A significant time effect was found for zooplankton filterfeeders and profundal macroinvertebrate predators, which indicates that their biomass fractions can vary



**Figure 7:** Functional community metrics of phytoplankton and zooplankton between lake types (circumneutral, acidified, anthropogenically acidified – limed, naturally acidic – limed). Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar).



**Figure 8:** Functional community metrics of macroinvertebrates in three habitats between lake types (circumneutral, acidified, anthropogenically acidified – limed, naturally acidic – limed). Shown are the means and standard deviations from 5 sampling dates per lake ( $N = 5$  sample years  $\times$  3 lakes = 15 for each bar). Functional feeding groups are expressed as semiquantitative abundance data (littoral macroinvertebrates) and biomass ( $g/m^2$ ; sublittoral and profundal macroinvertebrates).

over the study period (not shown). A significant interaction term was found only for sublittoral macroinvertebrate filterfeeders, which indicates that the temporal patterns of this feeding group differ between lake types (not shown).

**Table 3:** Results of repeated measures ANOVA contrasting functional community metrics between lake types (circumneutral, acidified, anthropogenically acidified – limed, naturally acidic – limed). Shown are the degrees of freedom (df), mean squares (MS), F ratios (F) and significance levels (P). Significant terms are highlighted in bold.

	Treatment (df 3,8)			Time (df 4,32)			Treatment x Time (df 12,32)		
	MS	F	P	MS	F	P	MS	F	P
<b>Phytoplankton</b>									
Autotrophs	0.008	0.434	0.735	0.001	0.866	0.495	0.002	1.501	0.175
Heterotrophs	<0.001	3.598	0.066	<0.001	1.162	0.346	<0.001	0.650	0.784
Mixotrophs	0.059	0.360	0.784	0.009	1.218	0.323	0.006	0.870	0.584
<b>Zooplankton</b>									
Filterfeeders	0.241	1.116	0.398	<b>0.494</b>	<b>3.018</b>	<b>0.032</b>	0.128	0.783	0.663
Predators	1.632	0.539	0.669	0.540	0.821	0.521	0.217	0.329	0.978
<b>Macroinvertebrates (littoral)</b>									
Predators	0.049	0.227	0.875	0.192	2.148	0.098	0.133	1.489	0.179
Filterfeeders	0.174	0.365	0.780	0.084	1.383	0.262	0.052	0.861	0.592
Grazer	1.190	1.808	0.224	0.104	0.770	0.553	0.078	0.578	0.843
Detritivores	0.042	0.044	0.987	0.096	0.534	0.677	0.236	1.439	0.200
<b>Macroinvertebrates (sublittoral)</b>									
Predators	0.661	1.950	0.200	0.023	0.909	0.471	0.025	0.973	0.493
Filterfeeders	0.096	1.508	0.285	0.013	1.696	0.175	<b>0.019</b>	<b>2.410</b>	<b>0.023</b>
Grazer	0.006	0.703	0.576	<0.001	0.553	0.699	<0.001	0.358	0.969
Detritivores	0.511	2.129	0.175	0.015	1.074	0.385	0.009	0.600	0.825
<b>Macroinvertebrates (profundal)</b>									
Predators	0.786	0.829	0.514	<b>0.077</b>	<b>2.747</b>	<b>0.045</b>	0.031	1.114	0.383
Filterfeeders	0.013	0.819	0.519	0.002	1.591	0.201	0.001	0.803	0.645
Grazer	0.013	0.819	0.519	0.002	1.591	0.201	0.001	0.803	0.645
Detritivores	0.076	0.223	0.878	0.013	1.198	0.331	0.012	1.120	0.379

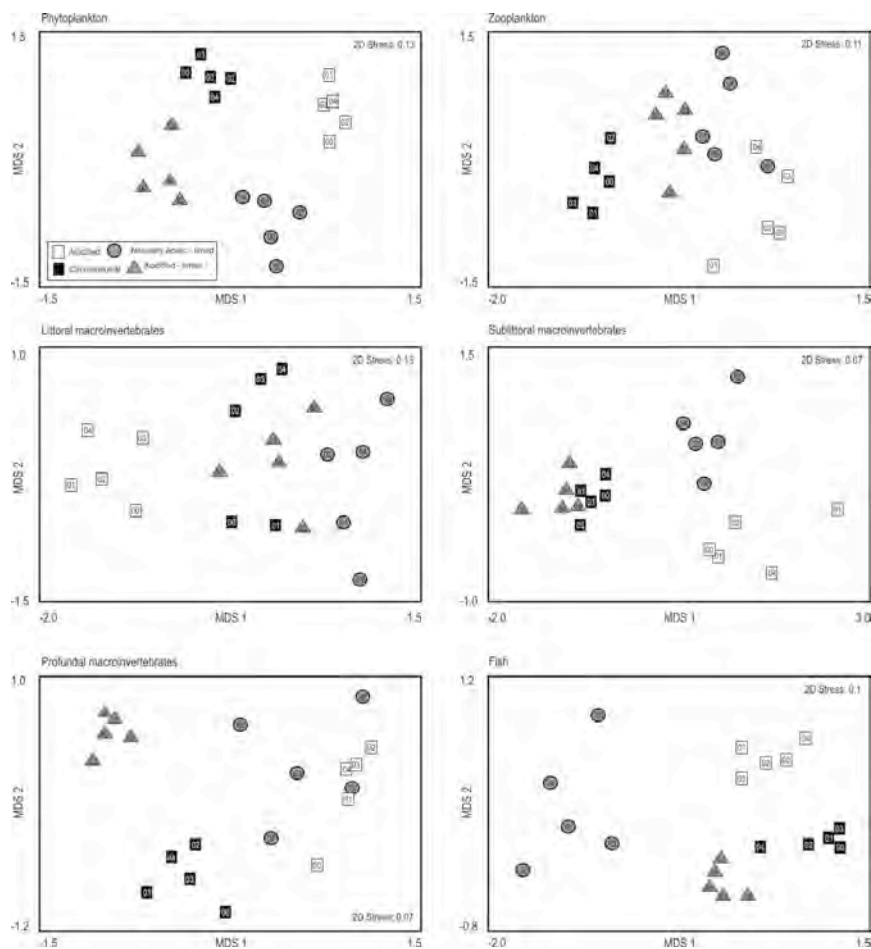
### 4.3. Multivariate analyses of community similarity

#### 4.3.1. MDS ordinations and ANOSIM analyses

Nonmetric multidimensional scaling analyses showed that the phytoplankton, zooplankton, macroinvertebrate (in three habitat types; littoral, sublittoral, profundal) and fish communities formed distinct clusters in ordination space, reflecting circumneutral, acidified, acidified – limed and naturally acidic-limed conditions (Figure 9). The ANOSIM analyses showed that community structure was significantly different between these lake types independent of which community has been analysed (R statistic ranges: 0.308 - 0.969; P level ranges: 0.032 - 0.008); the only exceptions were profundal macroinvertebrate communities which were

similar between acidified and naturally acidic – limed lakes (R statistic: 0.144; P level: 0.135). These results highlight that historical contingency effects can be discerned in liming management of lakes.

Discerning between lake history in liming outcomes helps assessing to what degree liming of anthropogenically acidified lakes results in desired management goals of achieving communities similar to circumneutral lakes. Our results show that despite decades of liming acidified lakes, none of the communities studied converged with those of circumneutral lakes. Considering a linear recovery trajectory, intermediate positions of limed lakes between acidified and circumneutral lakes in ordination space could indicate recovery success (and management efficiency of liming), based on the position of limed lakes along this gradient. Our results indicate such approximations in the case of littoral and sublittoral macroinvertebrate communities. In the case of phytoplankton, fish, profundal macroinvertebrates and partly zooplankton, the communities of anthropogenically acidified lakes that were limed were positioned far off this hypothetical linear recovery path (Figure 9). Interestingly, profundal macroinvertebrate communities in naturally acidic lakes that were limed resembled those of acidified lakes, while liming of acidified lakes lead to the formation of communities that were also positioned off this hypothetical linear recovery path (Figure 9). These “off-track positions” in ordination space suggests that the set of species (and their abundance patterns) that compose the communities in both types of limed lakes differ from those in circumneutral and acidified lakes.



**Figure 9:** Nonmetric multidimensional scaling (MDS) ordinations showing similarities in community structure of phytoplankton, zooplankton, macroinvertebrates in three habitat types (littoral, sublittoral, profundal) and fish between lake types. Stress values < 0.15 means reliable ordination solutions.

#### 4.3.2. Taxonomic contributions to community similarity

Results from the Similarity Percentage (SIMPER) analyses, which allow identifying species contributions to the observed multivariate patterns in the MDS and ANOSIM analyses, are summarised in Table 4. The results will be presented separately for each community studied. Overall, the SIMPER analyses revealed that the different lake types differed in terms of species occurrences and their numerical dominance within the communities.

##### 4.3.2.1. PHYTOPLANKTON

35, 19, 37 and 36 taxa contributed to explain 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic–limed lakes, respectively. *Cryptomonas* spp. (Cryptophyta) (size fraction 20 – 40 µm) were the taxa with highest percentage contribution in circumneutral lakes, even though this contribution to community similarity was low (ca. 7%). The contribution of the remaining species was < 5%, highlighting an even distribution of taxa within the phytoplankton communities of circumneutral lakes (Table 4). In acidified lakes, the raphidophycean flagellate, *Gonyostomum semen*, dominated the phytoplankton community (ca. 25%), followed by *Cryptomonas* sp. (size fraction 20 – 40 µm). The remaining species contributed with < 6% to community structure in acidified lakes (Table 4). In acidified lakes that were limed, an even phytoplankton community was observed with *Aulacoseira alpigena* (Bacillariophyceae) (ca. 5%), *Cryptomonas* sp. (size fraction < 20 µm) (ca. 5%), *Rhodomonas lacustris* (Cryptophyceae) (ca. 6%) and *Tabellaria flocculosa* var. *asterionelloides* (Bacillariophyceae) (ca. 5%) being those with highest percentage contribution to community structure. In naturally acidic lakes which received liming treatment, *G. semen* was dominant (ca. 25%), while the remaining species contributed on average less than 3.5%.

##### 4.3.2.2. ZOOPLANKTON

13, 11, 12 and 9 taxa explained 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic – limed lakes, respectively. In circumneutral lakes, the crustaceans *Eubosmina coregoni* (ca. 21%), *Daphnia* sp. (ca. 18%) and *Daphnia cristata* (ca. 14%) dominated the zooplankton communities. The remaining species contributed with less than 7% to community structure (Table 4). In acidified lakes, the rotifer *Asplanchna priodonta* contributed most to community similarity (ca. 33%), followed by *Eubosmina coregoni* (ca. 15 %) and *Ceriodaphnia quadrangula* (ca. 10%). The remaining species contributed <9% to zooplankton community structure in these lakes (Table 4). In acidified lakes that were limed *Asplanchna priodonta* (ca. 22%), *Daphnia* sp. and *Eubosmina coregoni* (both ca. 15%) were the most abundant species, with the others contributing less than 6% to community structure in this lake type (Table 4). In naturally acidic lakes that were limed, *Asplanchna priodonta* (ca. 28%), *Ceriodaphnia quadrangula* (ca. 15%) and *Eubosmina coregoni* (ca. 10%) dominated the zooplankton communities, with the remaining species explaining on average below 10% of community structure in these lakes (Table 4).

#### 4.3.2.3. LITTORAL MACROINVERTEBRATES

34, 27, 28 and 31 taxa explained 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic – limed lakes, respectively. *Asellus aquaticus* (Crustacea) was numerically dominant in all lake types (ca. 10-13%; Table 4). *Leptophlebia vespertina* (Ephemeroptera) was also dominant in acidified and acidified-limed lakes (ca. 16-18%), while in naturally acidic – limed lakes *Caenis luctuosa* (Ephemeroptera) (<10%) was important (Table 4). The remaining species differed in their incidence patterns and abundance patterns between lake types. Although their percentage contribution to community structure was generally not high, the subtle differences observed at the individual taxon level (Table 4), result in significantly different community structures between lake types when aggregate analysis on all taxa are carried out.

#### 4.3.2.4. SUBLITTORAL MACROINVERTEBRATES

7, 4, 6 and 9 taxa explained 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic–limed lakes, respectively. *Valvata piscinata* (> 30%) and *Chaoborus flavicans* (Diptera) (14-31%) dominated in all lake types (Table 4). Ceratopogonidae (Diptera) were also abundant in acidified lakes and naturally acidic – limed lakes (18 and 14%, respectively). *Physa fontinalis* (Mollusca), *Athripsodes* sp. (Trichoptera) and Anisoptera were also important in acidified lakes (< 10%) (Table 4).

#### 4.3.2.5. PROFUNDAL MACROINVERTEBRATES

3, 2, 5 and 2 taxa explained 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic–limed lakes, respectively. Dominance was reached by the phantom midge, *Chaoborus flavicans*, in circumneutral, acidified and naturally acidic – limed lakes (62-81%) (Table 4). In these lakes Chironomidae and Oligochaeta were the only broad taxonomic group that explained some additional structure of the profundal macroinvertebrate communities in these lake types (Table 4). Only, in acidified-limed lakes were more even communities observed with *Bivalvia* contributing to community structure in addition to Chironomidae, Oligochaeta and *Chaoborus flavicans* (Table 4).

#### 4.3.2.6. FISH

6, 4, 5, 3 taxa explained 90% of community structure in circumneutral, acidified, acidified-limed, and naturally acidic – limed lakes, respectively. All lakes were dominated by *Perca fluviatilis* (>30%) and *Leuciscus rutilus* (>21%). *Salvelinus alpinus* occurred only in naturally acidic, limed lakes. *Abramis brama* and *Esox lucius* contributed to different degrees to community structure in circumneutral, acidified and anthropogenically acidified-limed lakes, while these species were absent in naturally acidic-limed lakes (Table 4).

**Table 4:** Results from Similarity Percentages (SIMPER) Analyses showing percentage contributions of phytoplankton, zooplankton, macroinvertebrate (in three habitat types; littoral, sublittoral, profundal) and fish to community composition in four different lake types (naturally acidic with liming, anthropogenically acidified with liming, acidified lakes without liming, and circumneutral). – means that the taxa were not contributing to community structure considering a 90% cut-off level in the analyses (i.e. only taxa are shown that explained 90% of community structure). Taxa that dominate in each lake type are highlighted in bold.

Species	Lake types			
	Naturally acidic - limed	Acidified – limed	Acidified	Circumneutral
<b>Phytoplankton</b>				
<i>Anabaena planctonica</i>	-	0.67	-	-
<i>Asterionella formosa</i>	0.83	1.76	-	-
<i>Aulacoseira alpigena</i>	-	5.19	-	3.83
<i>Aulacoseira distans</i>	-	3.64	-	-
<i>Aulacoseira distans</i> var. <i>tenella</i>	-	1.41	<b>3.68</b>	-
<i>Bicosoeca</i> sp.	-	-	1.05	-
<i>Botryococcus terribilis</i>	-	-	5.32	4.84
<i>Botryococcus</i> spp.	2.5	1.32	-	-
<i>Ceratium furcoides</i>	2.29	3.74	-	-
<i>Ceratium hirundinella</i>	1.94	-	-	2.63
<i>Chlamydomonas</i> spp. 5-10 µm	0.83	-	-	-
Other unidentified Chlorococcales	1.83	2.17	3.54	2.79
<i>Chroococcus minutus</i>	0.8	-	-	1.24
<i>Chrysidiastrum catenatum</i>	1.52	1.53	-	-
<i>Chrysochromulina parva</i>	2.06	3.74	-	2.84
<i>Chrysococcus</i> sp.	1.02	0.8	-	-
<i>Cosmarium</i> spp. <10 µm	-	-	-	1.38
<i>Cryptomonas marssonii</i> <20 µm	1.42	1.39	-	-
<i>Cryptomonas</i> spp. <20 µm	2.41	<b>5.32</b>	2.53	<b>4.60</b>
<i>Cryptomonas</i> spp. 20-40 µm	2.6	3.19	<b>9.14</b>	<b>7.73</b>
<i>Cyclotella</i> spp. 10-15 µm	1.51	1.66	-	1.74
<i>Cyclotella</i> spp. 15-20 µm	-	1.28	-	-
<i>Dinobryon bavaricum</i>	0.78	-	-	1.07
<i>Dinobryon divergens</i>	-	1.07	-	-
<i>Dinobryon</i> sp.	0.83	-	-	-
<i>Gloeotila pulchra</i>	-	-	-	0.74
<i>Gonyostomum semen</i>	<b>26.78</b>	3.33	<b>25.25</b>	0.86
<i>Gymnodinium</i> spp. >30 µm	1.73	-	-	-
<i>Gymnodinium uberrimum</i>	-	-	4.13	2.95
<i>Katablepharis ovalis</i>	2.58	3.5	-	2.89
<i>Mallomonas allorgei</i>	-	-	-	1.49
<i>Mallomonas</i> sp.	1.05	-	-	-
<i>Mallomonas caudata</i>	-	1.47	-	1.59
<i>Merismopedia tenuissima</i>	-	-	3.16	3.9
Unidentified monads <3 µm	-	-	-	1.54
Unidentified monads >10 µm	1.69	1.22	-	-
Unidentified monads 3-5 µm	3.33	2.96	5.84	-



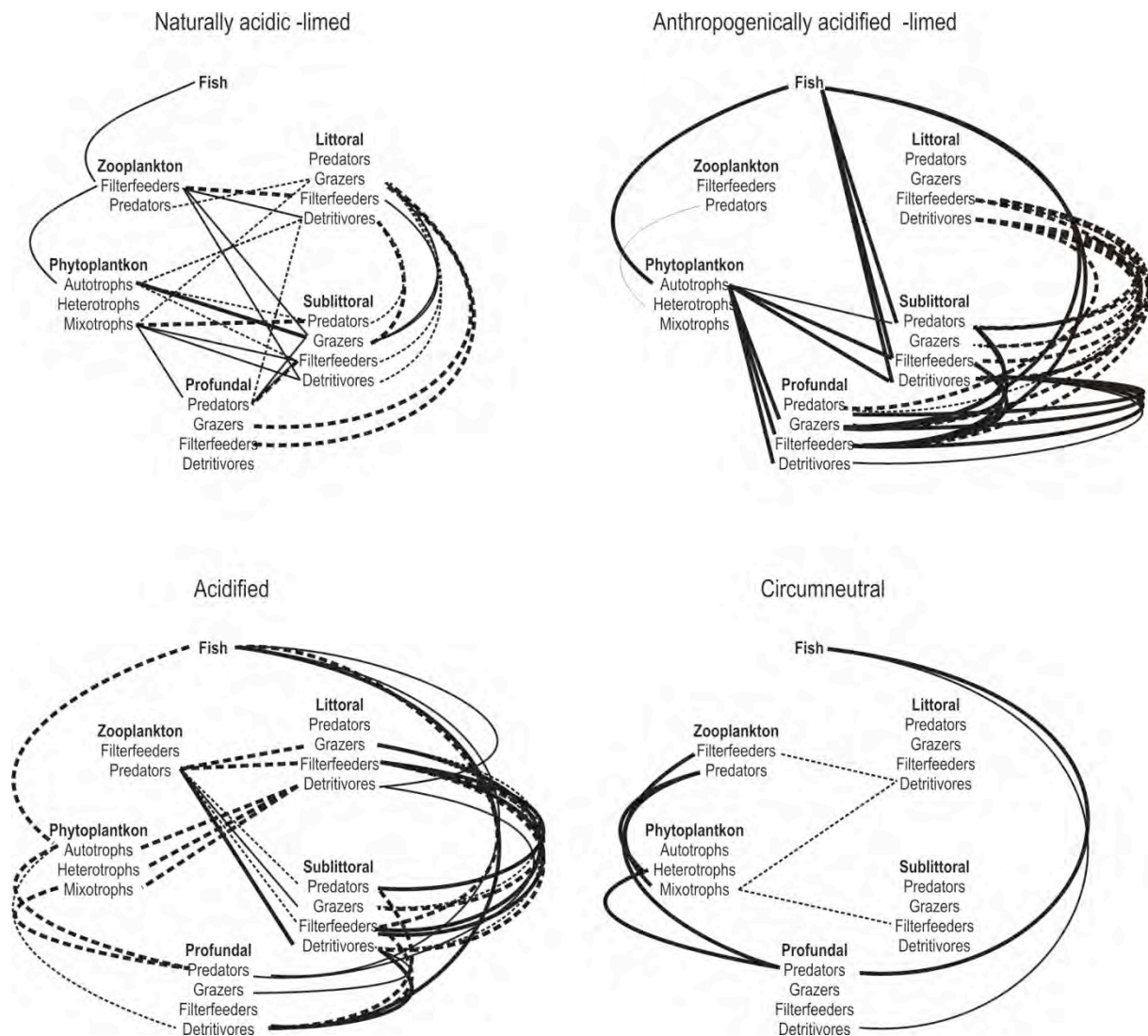
Unidentified monads 5-7 µm	3.34	4.41	3.78	-
Unidentified monads 7-10 µm	3	3.06	-	2.79
<i>Monoraphidium dybowskii</i>	3.21	1.11	4.63	3.47
<i>Monoraphidium griffithii</i>	-	-	-	1.11
<i>Monosigales</i> spp	0.94	-	2.55	1.24
<i>Oocystis</i> sp.	-	1.91	1.45	1.39
<i>Pediastrum privum</i>	1	-	-	0.91
<i>Peridinium inconspicuum</i>	1.54	2.56	3.49	1.94
<i>Peridinium</i> sp.	-	1.29	-	-
<i>Peridinium willei</i>	-	-	3.66	-
Picoplankton cyanobacteria.	-	-	-	1.07
<i>Planktothrix mougeotii</i>	-	1.76	-	-
<i>Pseudopedinella</i> sp.	3.61	4.18	3.03	2.44
<i>Rhizosolenia longiseta</i>	-	1.01	3.11	0.82
<i>Rhodomonas lacustris</i>	2.34	<b>6.03</b>	-	<b>5.51</b>
<i>Snowella atomus</i>	0.8	-	-	-
<i>Spiniferomonas</i> sp.	1.4	1.02	1.6	1.65
<i>Stichogloea doederleinii</i>	-	-	-	1.51
<i>Synura</i> sp.	-	1.09	-	-
<i>Tabellaria flocculosa</i> var. <i>asterionelloides</i>	-	<b>5.08</b>	-	2.48
<i>Tetraedron caudatum</i>	1.59	-	-	-
<i>Tetrastrum triangulare</i>	0.71	-	-	-
<i>Trachelomonas</i> sp.	1.38	-	-	-
<i>Uroglena</i> sp.	3.18	1.54	-	1.83
<i>Woronichinia naegeliana</i>	-	2.21	-	0.73
<b>Zooplankton</b>				
<i>Asplanchna priodonta</i>	<b>27.6</b>	<b>21.68</b>	<b>33.16</b>	2.41
<i>Ceriodaphnia quadrangula</i>	<b>15.14</b>	4.23	<b>10.42</b>	-
<i>Conochilus unicornis</i>	-	-	1.85	-
Cyclopidae	5.22	6.45	5.89	5.05
Cyclopidae nauplius stages	6.74	6.53	4.58	5.91
<i>Daphnia cristata</i>	-	<b>8.61</b>	-	<b>13.87</b>
<i>Daphnia cucullata</i>	-	-	-	2.32
<i>Daphnia galeata</i>	7.55	6.04	-	-
<i>Daphnia</i> sp.	8.11	<b>13.27</b>	6.64	<b>18.4</b>
<i>Diaphanosoma brachyurum</i>	-	3.75	4.18	6.48
<i>Eubosmina coregoni</i>	<b>9.99</b>	<b>13.36</b>	<b>14.81</b>	<b>20.63</b>
<i>Holopedium gibberum</i>	6.93	3.61	-	6.09
<i>Kellicottia bostoniensis</i>	-	-	4.21	-
<i>Keratella cochlearis</i> f. <i>typica</i>	-	-	-	1.66
<i>Limnosida frontosa</i>	-	-	-	2.44
<i>Ploesoma hudsoni</i>	-	2.24	-	-
<i>Polyarthra remata</i>	-	-	2.57	1.68
<i>Polyarthra vulgaris</i>	3.33	1.97	-	4.36
<i>Trichocerca capucina</i>	-	-	1.73	-
<b>Littoral macroinvertebrates</b>				
<i>Ablabesmyia longistyla</i>	2.13	-	-	-

<i>Agrypnia obsoleta</i>	-	-	1.05	-
<i>Argyroneta aquatica</i>	0.61	-	1.24	1.3
<i>Asellus aquaticus</i>	<b>10.67</b>	<b>10.47</b>	<b>12.89</b>	<b>13.47</b>
<i>Athripsodes</i> sp.	-	0.63	-	-
Bivalvia (total)	3.42	2.93	3.08	2.98
<i>Caenis horaria</i>	5.59	4.66	-	4.08
<i>Caenis luctuosa</i>	<b>13.02</b>	<b>6.79</b>	-	<b>7.51</b>
<i>Centroptilum luteolum</i>	1.53	2.84	-	1.1
Ceratopogonidae	3.32	2.96	2.74	2.42
<i>Heterotanytarsus apicalis</i>	0.84	-	-	-
<i>Holocentropus</i> sp.	-	-	0.98	-
Hydracarina	2.29	2.19	2.83	2.58
<i>Hydroptila</i> sp.	-	0.84	-	-
<i>Kageronia fuscogrisea</i>	4.15	3.89	2.83	1.63
<i>Lauterborniella agrayloides</i>	-	-	2.28	1.8
<i>Lepidostoma hirtum</i>	-	0.68	-	1.08
<i>Leptophlebia marginata</i>	3.32	4.9	1.35	2.24
<i>Leptophlebia vespertina</i>	<b>5.63</b>	<b>15.91</b>	<b>17.96</b>	<b>9.57</b>
Libellulidae	-	-	0.87	-
<i>Limnephilus</i> sp.	-	-	1.58	-
<i>Marstoniopsis scholtzi</i>	-	-	-	0.85
<i>Micronecta</i> sp.	-	-	-	1.96
<i>Microtendipes</i> sp.	1.03	-	-	-
<i>Molannodes tinctus</i>	-	-	1.02	-
<i>Molanna angustata</i>	-	-	-	0.75
<i>Mystacides azurea</i>	1.56	0.82	-	1.87
<i>Mystacides longicornis/nigra</i>	1.6	1.28	1.37	2.02
<i>Nebrioporus depressus</i>	0.63	-	-	-
<i>Nemoura avicularis</i>	-	1.63	-	2.12
<i>Oecetis testacea</i>	2.26	0.99	-	-
<i>Oulimnius</i> sp.	0.8	-	-	-
<i>Oulimnius troglodytes-tuberculatus</i>	1.75	1.18	-	1.18
<i>Oxyethira</i> sp.	-	-	1.44	2.32
<i>Pagastiella orophila</i>	2.3	3.98	-	1.14
<i>Paramerina</i> sp.	-	-	2.89	1.12
<i>Phaenopsectra</i> sp.	-	2.45	1.12	-
<i>Pisidium</i> sp.	3.42	1.82	3.08	2.92
<i>Platycnemis penn.-Pyrrhosoma</i> nymph.		2.41	-	1.82
<i>Polycentropus flavomaculatus</i>	1	-	-	-
<i>Polypedilum brevia antennatum</i> group	1.8	-	0.99	-
<i>Procladius</i> sp.	3.8	3.43	4.16	1.25
<i>Psectrocladius</i> sp.	2.01	0.92	8.45	3.47
<i>Pseudochironomus prasinatus</i>	-	1.17	2	1.77
<i>Sialis lutaria</i>	0.93	0.78	2.28	0.78
<i>Stenochironomus</i> sp.	-	-	1.44	-
<i>Tanytarsus</i> sp.	5.52	0.9	3.7	4.26

<i>Thienemannimyia</i> group	1.66	0.63	1.61	0.74
<i>Tinodes waeneri</i>	0.85	-	-	1.28
Turbellaria	-	-	-	1.41
Zygoptera	0.72	-	-	2.41
<b>Sublittoral macroinvertebrates</b>				
Anisoptera	5.43	<b>12.61</b>	-	-
<i>Athripsodes</i> sp.	5.49	<b>10.65</b>	-	8.05
Ceratopogonidae	<b>18.31</b>	5.83	<b>14.02</b>	8.55
<i>Chaoborus flavicans</i>	<b>13.66</b>	<b>22.58</b>	<b>30.56</b>	<b>20.84</b>
<i>Coenagrion</i> sp.	3.53	-	-	-
<i>Ephemera</i> sp.	4.91	-	-	5.3
<i>Molanna albicans</i>	2.99	-	-	-
<i>Physa fontinalis</i>	5.49	<b>10.65</b>	-	8.05
<i>Sialis fuliginosa</i>	-	-	6.86	8.8
<i>Valvata piscinalis</i>	<b>33.09</b>	<b>33.22</b>	<b>39.45</b>	<b>31.7</b>
<b>Profundal macroinvertebrates</b>				
Bivalvia (total)	-	10.24	-	-
<i>Chaoborus flavicans</i>	<b>80.52</b>	<b>30.45</b>	<b>78.6</b>	<b>61.76</b>
Chironomidae (total)	<b>14.61</b>	<b>28.55</b>	<b>20.9</b>	<b>14.72</b>
Oligochaeta (total)	-	14.49	-	<b>23.52</b>
<i>Pisidium</i> sp.	-	10.24	-	-
<b>Fish</b>				
<i>Perca fluviatilis</i>	<b>36.61</b>	<b>38.13</b>	<b>44.77</b>	<b>30.3</b>
<i>Leuciscus rutilus</i>	<b>31.4</b>	<b>26.54</b>	<b>29.53</b>	<b>21.03</b>
<i>Salvelinus alpinus</i>	<b>22.22</b>	-	-	-
<i>Esox lucius</i>	-	11.87	14.94	15.22
<i>Abramis brama</i>	-	9.41	6.84	11.68
<i>Tinca tinca</i>	-	-	-	6.84
<i>Coregonus lavaretus</i>	-	7	-	5.63

#### 4.4. Trophic associations in lake food webs

The patterns of associations between functional groups were lake specific, in terms of numbers, strengths and signs of correlations (Fig. 10). Most notably, circumneutral lakes had fewer connections between functional groups compared to the other lake groups (acidified, acidified-limed, naturally acidic-limed). Only a few associations between components in the pelagic habitat (fish – zooplankton – phytoplankton) were generally found across all lake types. Anthropogenically acidified, limed lakes and acidified lakes that received no liming treatment shared a high number of connections between functional feeding groups of macroinvertebrates across habitat types, and connections between fish and benthic invertebrates. Fish had no associations with benthic invertebrates in the case of naturally acidic – limed lakes. Different degrees of coupling between planktonic and benthic communities were found in all lake types, except circumneutral lakes. In the latter lake type, no correlations between macroinvertebrate feeding groups were found.



**Figure 10:** Associations between functional feeding groups in foodwebs of circumneutral, acidified, acidified – limed, and naturally acidic – limed lakes. Full and dashed lines represent positive and negative correlations, respectively, revealed through Spearman rank correlation analysis. The strength of correlations is indicated by the thickness of the lines (thin lines,  $P < 0.05$ ; thick lines  $P < 0.01$ ).

## 5. Discussion

Our comparative study of multiple communities in two types of limed lakes (naturally acidic and anthropogenically acidified), acidified lakes undergoing natural recovery and circumneutral lakes facilitated an important assessment of ecological responses of boreal lakes to management practices relative to previous studies (Goedkoop & Angeler 2009; Angeler & Goedkoop 2010). While these previous studies could not discern between ecosystem history, the publication of recent paleolimnological research (Norberg et al. 2008) allowed for a reanalysis of the previously used data sets taking historical contingency explicitly into account. Ideally, additional data on the ecological history of the lakes to complement the paleolimnological-inferred conclusions would have been required to

strengthen the inference of this study. However, while we could verify that the acidified lakes used in this study have been anthropogenically acidified according to biogeochemical modelling criteria (Fölster et al. 2007), no similar data was available for the limed lakes studied here. Notwithstanding, we believe that some important insight has been gained regarding the “true” restoration potential when liming is applied to anthropogenically acidified lakes, and the potential negative ecological consequences that can arise when managers are forced to take management action without having the necessary information on the natural history of ecosystems.

### *5.1. Communities in limed, acidified and circumneutral lakes*

Regarding univariate tests, only a few significant differences were found in the comparisons of different communities across different lake types. This suggests that limed lakes with different ecological history, and acidified and circumneutral lakes share to a great extent similar community attributes across different trophic levels and habitat types, which may be due to an ecological compensation within trophic levels (Klug et al. 2000). This ecological compensation can be understood as a replacement of species with similar functional roles in the communities; that is, although the set of species differed between lake types, they carry out similar functional roles in the ecosystem. This finding can be discussed both from the viewpoints of natural recovery of acidified lakes and liming of naturally acidic lakes.

First, regarding liming of lakes that have been affected by anthropogenic acidification, the results of our study contributes to the debate about whether liming is required when acidified systems show signs of natural recovery. Natural recovery from acidification has been documented for European and North American waters (Stoddard et al. 1999; Davies et al. 2005; Skjelvåle et al. 2007), and the success of liming or natural recovery is often evaluated on the basis of the establishment and persistence of acid-sensitive taxa (e.g., charr, salmon, roach, freshwater pearl mussel). While a focus on specific taxa has clear importance regarding their conservation, integral system responses can hardly be determined on the basis of such population-based approaches and a community-based approach may be better suitable for assessing such integral ecological responses. Stendera & Johnson (2008) have analyzed decadal trends in community structure of the acidified lakes we have studied here, and for most communities found clear signs of recovery. Our rm-ANOVA results suggest that natural recovery largely fulfils the desired goals of achieving communities present in circumneutral reference conditions without any need for management intervention. Thus our study, based on an analysis that assured that only acidified lakes with liming treatment were considered, does largely support our previous study where ecological history was not explicitly taken into account (Angeler & Goedkoop 2010).

Second, regarding liming of naturally acidic lakes, the lack of significant differences in structural and functional community metrics revealed by our analyses has important implications regarding the alterations of natural lake disturbance regimes through liming. Liming of naturally acidic ecosystems can be interpreted as an ecosystem-level disturbance (Bishop et al. 2001; McKie et al. 2006). Alterations of natural disturbance regimes often result in catastrophic regime shifts (Scheffer & Carpenter 2003), with a consequent loss of biodiversity and functional characteristics that are important for ecosystem service provision to humans (Folke et al. 2004; Angeler & Sánchez-Carrillo 2010). Our results revealed that despite altering the natural disturbance regimes of acidic lakes through liming, structural and functional community metrics are in the range of those observed in other lake types. This

finding is encouraging, because liming of naturally acidic lakes may not lead to a substantial loss of biodiversity and functional characteristics observed in other ecosystems.

However, it must be highlighted that the multivariate analyses showed significant differences in community compositions between the lake types studied. These differences were found consistently for all communities. Thus, univariate and multivariate analyses provide complementary results. The multivariate statistics allow for an integral analysis of community composition that integrates species distribution patterns and their relative biomass, while the univariate tests permit a comparison of measures that emphasize different aspects of community structure. We acknowledge that the multivariate analyses techniques used here are distance-based approaches; that is, the original data matrices are converted into distance matrices whereby the taxonomic identity of the species is lost. While other techniques, such as e.g. canonical ordination, would have been available for maintaining the taxonomic information (i.e., species contributions to the observed ecological patterns), we could not apply this method because of the low number lakes in this study. However, through the application of the SIMPER routine, we could indirectly also assess the percentage contribution of the most important taxa in the communities of each lake type. By most important we mean that the analysis selects all taxa that contribute with 90% to community composition. This 90% threshold is set by default by the analysis and is routinely applied in this type of statistical procedure. Thus, when a species was not present in our SIMPER table this does not necessarily mean that the species was absent from the community, or that they have been lost from the systems. These species may have simply had a very low abundance, thus being so rare that they were excluded by the analysis.

### *5.2. Trophic associations in the food webs*

The results from this study are in stark contrast to the findings of our previous study (Angeler & Goedkoop 2010) where limed lakes were characterised by fewer associations between functional feeding groups in their food webs relative to acidified and circumneutral lakes. These previous findings were attributed to the ecological impact associated with recurrent liming applications, resulting in the disruption of trophic linkages in food webs. In the present study, circumneutral lakes rather than limed lakes showed the lowest food web complexity, in terms of connections (significant correlations) between functional feeding groups. These differences between studies may be due to how lakes were pooled for carrying out the correlation analyses between feeding groups. Our previous study was based on 11 limed lakes (not discerning between ecological history), 7 circumneutral lakes and 4 acidified lakes, while in the present study only 3 lakes were used for each lake type (acidified, circumneutral, acidified – limed, naturally acidic – limed). We conclude that alternative approaches based on for example stable isotopes (e.g. Goedkoop & Angeler 2009) or fatty acids may be better suitable for characterising structural and functional foodweb properties. Studies in individual lakes can then be carried out to determine lake specific patterns and/or how general the results of a single lake are for other lakes within the same group.

### *5.3. Management implications*

Two main management conclusions derive from this study. The first emphasizes the ecological consequences when naturally acidic lakes are limed. Despite “accidental” restoration and management of “undisturbed” ecosystems having frequently dramatic

negative consequences on biodiversity and resulting ecological functioning, the results of our study suggest that liming does not diminish the overall structure and function of naturally acidic lakes. Biodiversity and broad functional community aspects in naturally-acidic-limed lakes are similar to those observed in other lake types (circumneutral, acidified, acidified – limed), although the set of species and their abundance patterns differed.

The second management implication emphasizes the efficiency of liming of anthropogenically acidified lakes. While the results regarding liming impacts in naturally acidic lakes are encouraging, the results regarding liming of anthropogenically acidified lakes are not. Culturally acidified lakes that are limed are characterised by community attributes that are also found in acidified lakes that are undergoing natural recovery. The lack of important structural and functional community differences between acidified lakes that undergo natural recovery and acidified lakes that are limed suggests that the management costs can outweigh benefits in terms of restoration/management success (i.e. from an exclusively long-term perspective our results suggest that nature can “do the job” without the need of human interventions).

We acknowledge that our analyses are based on three lakes per lake, and we highlight also that a recent study revealed that the limed lakes used in the IKEU program deviate in their morphometric and biological settings from a large number of Swedish lakes that undergo liming treatment (Holmgren & Fölster, 2010). While this low sample size and limited representativeness does not allow for generalization of our results regarding liming management at the nation-wide scale, interesting and promising patterns were revealed that suggest that further research on the effects of ecological contingency of liming outcomes is warranted.

## Acknowledgements

We thank Stina Drakare and Tobias Vrede for helpful comments on a previous version of this report.

## 6. References

- Angeler, D.G. and Goedkoop, W. (2010). Biological responses to liming in boreal lakes: an assessment using plankton, macroinvertebrate and fish communities. *J. Appl. Ecol.* **47**: 478-486.
- Angeler, D.G. & Sánchez-Carrillo, S. (2010). *Synthesis: the past, present and future of Las Tablas de Daimiel*. In: Ecology of Threatened Semi-Arid Wetlands: Long-Term Research in Las Tablas de Daimiel (Sánchez-Carrillo, S. & Angeler, DG. eds.). Series: Wetlands: Ecology, Conservation and Management, Vol. 2, Springer.
- Appelberg, M. & Degerman, E. (1991). Development and stability of fish assemblages after lime treatment. *Can. J. Fish. Aquat. Sci.* **48**: 546–554.
- Appelberg, M. & Svensson, T. (2001). Long-term ecological effects of liming – The ISELAW programme. *Water, Air, Soil Poll.* **130**: 1745–1750.
- Binks, J.A., Arnott, S.E. & Sprules, W.G. (2005). Local factors and colonist dispersal influence crustacean zooplankton recovery from cultural acidification. *Ecol. Appl.* **15**: 2025–2036.

- Bishop, K., Laudon, H., Hruska, J., Kram, P., Köhler, S. & Löfgren, S. (2001). Does acidification policy follow research in northern Sweden? The case of natural acidity during the 1990s. *Water, Air, Soil Poll.* **130**: 1415–1420.
- Blomqvist, P. and Herlitz, E. (1998). Methods for quantitative assessment of phytoplankton in freshwaters, part 2. Naturvårdsverket, Rapport 4861.
- Clair, T.A. & Hindar, A. (2005) Liming for the mitigation of acid rain effects in freshwaters: a review of recent results. *Environ. Rev.* **13**: 91–128.
- Davies, J.J.L., Jenkins, A., Monteith, D.T., Evans, C.D. & Cooper, D.M. (2005). Trends in surface water chemistry of acidified UK freshwaters, 1988–2002. *Environ. Poll.* **137**: 27–39.
- European Committee for Standardization (1994) *Water quality—methods for biological sampling and guidance on handnet sampling of aquatic benthic macroinvertebrates*. European Committee for Standardization, Brussels, Belgium.
- Fischer, J.M., Klug, J.L., Ives, A.R. et al. (2001). Ecological history affects zooplankton community responses to acidification. *Ecology* **82**: 2984–3000.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004). Regime shifts, resilience and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* **35**: 557–581.
- Fölster, J., Andrén, C., Bishop, K., Buffam, I., Cory, N., Goedkoop, W., Holmgren, K., Johnson, R., Laudon, H. & Wilander, A. (2007). A novel environmental quality criterion for acidification in Swedish lakes – an application of studies on the relationship between biota and water chemistry. *Wat. Air Soil Poll.: Focus* **7**: 331–338.
- Gliwicz, Z. M. (1969a) Studies on the feeding of pelagic zooplankton in lakes of varying trophy. *Ekologia Polska A*, **17**, 663–707.
- Gliwicz, Z. M. (1969b) The share of algae, bacteria and trypton in the food of the pelagic zooplankton of lakes with various trophic characteristics. *Bulletin de L'Academie Polonaise des Sciences*, **17**, 159–165.
- Goedkoop, W. and Angeler, D. (2009). *Liming effects on ecosystem structure, function, and trophic relationships in lakes (kapitel 2a:11 i Utvärdering av IKEU 1990-2006 – Syntes och förslag)*. Naturvårdsverket, Stockholm, Rapport 6302:392–422.
- Henriksson, L. & Brodin, Y.-N. (1995). *Liming of Acidified Surface Waters: A Swedish Synthesis*. Springer, Berlin.
- Holmgren, K. & Fölster, J. (2010) *Biologisk och vattenkemisk variation i kalkningsverksamhetens målsjöar – ett förbättrat underlag för bedömning av IKEU-sjöarnas representativitet*. Inst. för vatten och miljö, SLU, Uppsala, Rapport 2010:11.
- Jansson, M., Blomqvist, P., Jonsson, A. & Bergström, A. K. (1996). Nutrient limitation of bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Ötrasket. *Limnol. Oceanogr.* **41**: 1552–1559.
- Klug, J.L., Fischer, J.M., Ivers, A.R., & Dennis, B. (2000). Compensatory dynamics in plankton community responses to pH perturbations. *Ecology* **81**: 387–398.
- McKie, B., Petrin, Z. & Malmqvist, B. (2006). Mitigation or disturbance? Effects of liming on macroinvertebrate assemblage structure and leaf-litter decomposition in the humic streams of northern Sweden. *J. Appl. Ecol.* **43**: 780–791.



- Moog, O. (1995) Fauna Aquatica Austriaca. *Wasserwirtschaftskataster, Bundesministerium für Land- und Fortwirtschaft. Wien, Loseblattsammlung.*
- Norberg, M., Bigler, C., and Renberg, I. 2008. Monitoring compared with paleolimnology: implications for the definition of reference condition in limed lakes in Sweden. *Environ. Monitor. Assess.* **146**: 295–308.
- Olrik, K. P., Blomqvist, P., Brettum, P., Cronberg, G., and Eloranta, P. (1989). *Methods for quantitative assessment of phytoplankton in freshwaters. Part I.* Swedish Environmental Protection Agency, Stockholm, Sweden.
- Ormerod, S.J. & Durance, I. (2009). Restoration and recovery from acidification in upland Welsh streams over 25 years. *J. Appl. Ecol.* **46**, 164–174.
- Persson, G. & Appelberg, M. (2001). Evidence of lower productivity in long term limed lakes as compared to unlimed lakes of similar pH. *Water, Air, Soil Poll.* **130**: 1769–1774.
- Renberg, I. & Hultberg, H. (1992). A paleolimnological assessment of acidification and liming effects on diatom assemblages in a Swedish lake. *Can. J. Fish. Aquat. Sci.* **49**: 65–72.
- Sandoy, S. & Romunstad, A.J. (1995). Liming of acidified lakes and rivers in Norway. An attempt to preserve and restore biological diversity in the acidified regions. *Water, Air, Soil Poll.* **85**: 997–1002.
- Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**:648–656.
- Schindler, D.W. (1988). Effects of acid rain on freshwater ecosystems. *Science* **239**: 149–157.
- Stenson, J.A.E. & Svensson, J.-E. (1995). Changes of planktivore fauna and development of zooplankton after liming of the acidified Lake Gårdsjön. *Water, Air, Soil Poll.* **85**: 979–984.
- Schindler, D.W. (1997). Liming to restore acidified lakes and streams: a typical approach to restoring damaged ecosystems? *Restor. Ecol.* **5**: 1–6.
- Skjelkvåle, B.-L., H. Borg, A. Hindar, & A. Wilander (2007). Large scale patterns of chemical recovery in lakes in Norway and Sweden: Importance of seasalt episodes and changes in dissolved organic carbon. *Applied Geochemistry* **22**: 1174-1180.
- Stendera, S. & Johnson, R.K. (2008). Tracking recovery trends of boreal lakes: use of multiple indicators and habitats. *J. N. Am. Benthol. Soc.* **27**: 529–540.
- Stoddard, J.L., Jeffries, D.S., Lukewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T., Forsius, M., *et al.* (1999). Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **401**: 575–578.
- Sundbom, M. (2009) *Kalkningseffekter på ekosystemstruktur i sjöar (kapitel 2a:10 i Utvärdering av IKEU 1990-2006 – Syntes och förslag).* Naturvårdsverket, Stockholm, Rapport 6302:372-390.
- Swedish Environmental Protection Agency (SEPA) (2007). *Economic Instruments in Environmental Policy.* Report 5678. SEPA (Naturvårdsverket), Stockholm, Sweden. Available at: <http://www.naturvardsverket.se/Documents/publikationer/620-5678-6.pdf>.
- ter Braak, C.J.F. (1995). *Ordination.* In: Jongman R, ter Braak C J F, Van Tongeren O F R (eds) *Analysis in Community and Landscape Ecology.* Cambridge University Press, Cambridge, pp 91-173.
- Wilander, A., Johnson, R.K. and Goedkoop, W. (2003). *Riksinventering 2000. En synoptisk studie av vattenkemi och bottenfauna i svenska sjöar och vattendrag.* Institutionen för miljöanalys, SLU, Uppsala, Sweden.
- Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W. & Girard, R.E. (1996). Recovery of crustacean zooplankton from acid and metal contamination: comparing manipulated and reference lakes. *Can. J. Fish. Aquat. Sci.* **53**: 1301–1327.

Yan, N.D., Leung, B., Keller, B., Arnott, S.E., Gunn, J.M. & Raddum, G.G. (2003). Developing conceptual frameworks for the recovery of aquatic biota from acidification. *Ambio* **32**: 165–169.