

Spatiotemporal Variability of Chemistry and Biota in Boreal Surface Waters

A Multiscale Analysis of Patterns and Processes

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**Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2005**

Acta Universitatis Agriculturae Sueciae

2005: 95

ISSN 1652-6880

ISBN 91-576-6994-5

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Tryck: SLU Service/Repro, Uppsala 2005

Abstract

Stendera, S. 2005. *Spatiotemporal Variability of Chemistry and Biota in Boreal Surface Waters. A Multiscale Analysis of Patterns and Processes*.
Doctoral Dissertation.
ISSN 1652-6880, ISBN 91-576-6994-5.

This thesis focuses on the assessment of spatial and temporal patterns of freshwater communities in relation to spatial variability and changes of the abiotic environment (i.e. water chemistry). The importance of geographic position, regional- and local-scale factors as drivers of the natural variability of lake and stream water chemistry was quantified and compared by variance partitioning using partial redundancy analysis. A major part of surface water chemistry was explained by interactions between geographic, regional and local factors. Streams and lakes were similar in their response, indicating that idiosyncrasies of both systems might be suppressed by effects of large-scale factors, in particular, if human-induced catchment variation generates a high amount of environmental noise.

Regional processes are also important in structuring the composition of local communities. The relationship between local and regional diversity across three spatial scales and the importance of regional and local factors on macroinvertebrate diversity patterns was determined using the additive partitioning concept. Local processes (i.e. habitat heterogeneity) were an important factor contributing to species coexistence resulting in saturating patterns of the communities. On the other hand, local variability may confound the ability to detect perturbation or recovery. A multihabitat analysis of the rates and trajectories of recovery of acidified lakes as well as persistence of pelagic and benthic communities of acidified and reference lakes showed that recovery is a complex and challenging process, influenced by multiple spatial and temporal factors. For instance, climate-induced changes in surface runoff patterns may introduce significant variability in surface water chemistry confounding recovery and influencing the persistence and stability of freshwater communities. As focus is shifting from single-site to regional management of freshwater ecosystems, it is important that policy makers and managers are aware of which factors on which scale are most influencing water quality and biodiversity. The results of this thesis show that a holistic, multiscale analysis, involving several habitats and biotic indicators, is needed to understand ecosystem response to large-scale, regional stressors so as to best protect the world's most precious and vital resource - freshwater.

Keywords: spatiotemporal variability, streams, lakes, water chemistry, benthic macroinvertebrates, phytoplankton, multiple scales, multihabitat, acidification, recovery, persistence.

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'A lake is the landscape's most beautiful and expressive feature. It is earth's eye; looking into which the beholder measures the depth of his own nature.'

- Henry D. Thoreau

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Stendera, S. & Johnson, R. K. Multi-scale drivers of water chemistry of boreal lakes and streams. (Accepted in *Environmental Management*).
- II. Stendera, S. & Johnson, R. K. 2005. Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. *Freshwater Biology* 50, 1360-1375.
- III. Stendera, S. & Johnson, R.K. Recovery trends of phytoplankton and benthic macroinvertebrate communities in acidified and reference boreal lakes – a multihabitat assessment. (Submitted).
- IV. Stendera, S. & Johnson, R.K. Stability and persistence of phytoplankton and benthic macroinvertebrate communities in acidified and reference boreal lakes. (Manuscript).

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Introduction

Imagine any ecosystem of the world as a theatre: there is a script, which together with the stage, the scenery, and the actors consolidates to an entire play. The script determines how the stage and scenery look and these components build a frame determining if and how the actors will interact on the stage. In a freshwater ecosystem, the physico-chemical factors of a specific lake or stream constitute the stage/scenery, i.e. the abiotic frame within the *Romeos and Juliets* - the organisms - live, interact and die. Some organisms possess the adaptations to fit very well within this frame, others not so well and still other organisms not at all. Human-induced disturbances such as eutrophication and acidification often alter the abiotic environment, with the result that some organisms fall outside the frame, i.e. they disappear. To fully understand the causes of species disappearances it is necessary to understand the underlying patterns and processes determining the setting of the abiotic frame.

Aquatic ecologists began early to include a landscape perspective in theories about lakes and rivers, and since the beginning of the 20th century, there has been a continued interest in understanding individual features and spatial patterns of aquatic ecosystems. Many of these ideas have resulted in concepts describing the importance of interactions between terrestrial and aquatic systems (e.g. Thienemann, 1925; Naumann, 1932; Vannote *et al.*, 1980), thereby abandoning the obsolete view of Forbes (1887), who perceived lakes as isolated entities, independent of the surrounding landscape. Position in the landscape and underlying geology provided essential insights into different lake types leading to the formation of lake trophic classification (Wetzel, 2001). Comparative studies of multiple lakes within a single region have advanced the development of limnology (e.g. Pearsall, 1920) and this approach is still considered as a useful method to better understand the processes and mechanisms affecting aquatic ecosystems (e.g. Schindler *et al.*, 1990).

The recognition of the continuous change of a river's physico-chemical and biological attributes depending on the surrounding landscape type resulted in the formation of the River Continuum Concept (RCC; Vannote *et al.*, 1980) and subsequent refinements and modifications (Bruns *et al.*, 1984; Minshall *et al.*, 1985). The RCC describes the river as a continuous gradient, with headwater systems being mainly influenced by shading and detritus from riparian vegetation, whereas larger streams and rivers are more influenced by autochthonous primary production and organic transport from upstream areas. Analogous to the RCC, lakes may also be viewed as situated or connected along longitudinal gradients (e.g. Soranno *et al.*, 1999; Riera *et al.*, 2000). For instance, spatial patterns in lake-water chemistry have been shown to be correlated with landscape position; location within a lake-chain or longitudinal connectivity as defined by gradients of geomorphology and hydrology (Soranno *et al.*, 1999). More recently, Riera *et al.* (2000) have evaluated the importance of lake order on physical and chemical variables. Lake order, analogous to stream order, is based on the type and strength of connections between a lake and its drainage network. Riera *et al.* (2000) found

that lake order is correlated with variables related to lake size and shape, concentrations of major ions, biological and human-use variables. The RCC and lake connectivity/order concepts both focus on the importance of regional-scale factors such as climate, geology and geomorphology in determining the spatial and to some extent even temporal constraints of the ecosystem. Although Hynes (1975) emphasized early that 'in every respect, the valley rules the stream', a large number of studies on river ecosystems have focused solely on the functional role of the riparian zone thereby largely ignoring the importance of the entire catchment (Naiman & Decamps, 1997; Quinn *et al.*, 2001).

It is now widely accepted by freshwater ecologists that the physico-chemical factors of a specific water body are a product of the surrounding landscape (catchment) with its distinct geology, hydrology and climate (e.g. Omernik, Abernathy & Male, 1981; Osborne & Wiley, 1988; Allan, 1995; Kratz *et al.*, 1997; Soranno *et al.*, 1999; Riera *et al.*, 2000). Geographic position of the water body determines regional or catchment characteristics, which in turn are considered to determine the chemical composition of a surface water body. Several studies have highlighted the links between surface water chemistry and catchment characteristics, particularly in relation to sensitivity to nutrient enrichment and acidification (Vollenweider, 1975; Sverdrup *et al.*, 1992; Hornung *et al.*, 1995). Surface water chemistry is regulated by a complex suite of processes and mechanisms operating at several spatial scales (i.e. geographic, regional and local); all of which singly or in concert result in the spatial and temporal variability that can be observed both within and among aquatic ecosystems. Hence, a deeper understanding of the contemporary relationships between landscape characteristics and surface water quality (and indirectly effects on biota) provides a fundamental basis for assessing the impact of future changes in land use or climate and an ideal framework for ecosystem management. Moreover, an understanding of spatial and temporal scales may improve our ability to predict the way in which systems are likely to respond to environmental change.

Changes in land cover/use can have significant impacts on freshwaters (Omernik *et al.*, 1981; Osborne & Wiley, 1988; Soranno *et al.*, 1999). The proportion of a particular type of land cover or use within a catchment has been used to explain, and predict surface water chemistry (e.g. Hunsaker & Levine, 1995; Johnson *et al.*, 1997; Soranno *et al.*, 1999), aquatic invertebrate community composition (e.g. Barton, 1996), and fish communities (e.g. Allan, Erickson & Fay, 1997). However, the spatial scale at which landscape features exert a detectable influence on aquatic systems is not well understood. Recent interest in water quality management has begun addressing the spatially heterogeneous nature of the environment and, in particular, its effect on water quality (Omernik *et al.*, 1991; Lovejoy *et al.*, 1997). It has been recognized, for instance, that the environmental variables affecting water quality are not uniformly distributed across the landscape and do not necessarily change at catchment boundaries (Omernik & Griffith, 1991). The spatial patterns of the driving variables often do not conform to catchment boundaries, and they frequently occur at scales different than catchments.

The use of “relatively homogeneous” ecological regions as opposed to catchment boundaries is a technique being increasingly used to partition natural variability (e.g., Bailey, 1983; Omernik & Bailey, 1997). The European Water Framework Directive proposes the use of ecoregions for classifying river and lake typologies (European Commission, 2000). Although ecoregion-level classifications are considered to be able to partition the physico-chemical and biological variance of lakes and streams (Hawkins *et al.*, 2000), inter-lake and -stream variability might be often the result of intertwined factors acting on geographic, regional and local scales. Thus, the effects of anthropogenic impact (e.g. land use/cover) on ecosystems might be difficult to tease apart from natural factors influencing surface water chemistry (e.g. geography/geology). Classifications used in bioassessment are typically derived from reference or least-impaired sites within a region of interest (e.g. Bailey *et al.*, 1998; Reynoldson & Wright, 2000). Ecoregion delineations are used in several countries as a basic classification unit for aquatic bioassessment programs (Marchant, Wells & Newall, 2000; European Commission, 2000). The potential of ecoregions as an appropriate classification tool is that they offer a starting point for water quality managers to consider to partition natural variation in the aquatic biota, and also how between-region differences may influence how stressors affect biota.

As focus is shifting from single-site to regional management of aquatic integrity and biodiversity (e.g. European Commission, 2000), insight into the diversity patterns of lake and stream macroinvertebrate communities across multiple spatial scales is important for both environmental management and species conservation. Moreover, it is important not only to identify specific patterns of species diversity, but also to improve our understanding of the underlying processes that generate the patterns, if conservation and restoration endeavours are to be successful. Focus on the processes that control biodiversity over a range of spatial and temporal scales helps to understand the importance or interplay between the patterns and processes in assessing disturbed systems and their recovery. Along with the idea of the importance of large-scale, regional processes in determining water chemistry, it has recently been recognized that not only local, but also regional, biogeographical processes are important in structuring the composition of local communities (Ricklefs, 1987; Ricklefs & Schluter, 1993).

Aquatic macroinvertebrate communities are responding to multiple environmental gradients, many of which are scale related (e.g. catchment- vs. habitat-level characteristics) (Minshall, 1988; Poff, 1997). Both lake and stream macroinvertebrate communities experience periodic and unpredictable disturbances (e.g. spring snowmelt discharge) and show high capability of dispersal (Malmqvist *et al.*, 1991). If large-scale patterns in weather (e.g. wave action in lake littoral habitats) or hydrology (e.g. spates) are important predictors, species richness may be considered as being largely influenced by regional-scale patterns (Palmer, Allan & Butman, 1996) and thus the relationship between regional and local diversity would be expected to be linear, i.e. the local species richness is proportional to regional species richness. A linear relation has been shown for some regions and for some aquatic species (e.g. Heino, Muotka & Paavola, 2003; Hugueny & Paugy, 1995). Other studies found that local-scale

environmental factors were important in determining species richness (e.g. Townsend, Hildrew & Francis, 1983; Malmqvist & Maki, 1994; Paavola, Muotka & Tikkanen, 2000) as well as the importance of biotic interactions in structuring community composition (Hart, 1983; Englund, 1991; Kohler & Wiley, 1997; Hildrew *et al.*, 2004). In this case, the relationship between local and regional species richness is considered to show a saturating pattern, i.e. the local species richness becomes independent of the regional species pool. Recently, Johnson, Goedkoop & Sandin (2004) showed, for instance, that local-scale variables were better predictors of lake and stream macroinvertebrate communities than regional-scale variables. If local variables are more important than regional variables in explaining the variability among habitats it might imply that both species interactions and (abiotic) environmental factors are important predictors of community composition. Consequently, assessment of the determinants of community structure must integrate regional factors as well as local environmental factors and, if possible, consider the importance of biological interactions.

A holistic, multiscale analysis of both the abiotic factors determining spatiotemporal patterns and processes of a specific site and its community structure is crucial for determining the causes and consequences of perturbations. For instance, in early phases of acidification, short-term episodic events may result in short-term community responses. However, once pH remains below a biological threshold for a longer period of time the perturbation may result in long-term changes in community composition. The anthropogenic acidification is one of the severest threats to freshwater ecosystems today. Atmospheric deposition of acid components has significantly impacted lakes in North America and Europe (Schindler, Kasian & Hesslein, 1989; Stoddard *et al.*, 1999), resulting in marked decreases in pH, alkalinity/acidity and associated increases in SO₄ concentration and toxic aluminum levels (Gee & Stoner, 1989). These changes in water chemistry resulted in relatively predictable changes in species composition, with the loss of acid sensitive species and increases in the abundance of acid tolerant species. For instance, the number and diversity of pelagic and benthic species have been shown to be strongly related to pH, but also habitat diversity and nutrient level (e.g. Økland & Økland, 1986; Appelberg & Degerman, 1991). At low pH levels (<5.0), phytoplankton communities are often predominated by chlorophytes, chrysophytes (e.g. *Dinobryon*) and pyrrophytes (e.g. *Peridinium* and *Gymnodinium*) (e.g. Almer *et al.*, 1974; Degerman *et al.*, 1995). Likewise, noticeable changes have also been observed for benthic communities, with gastropods, mussels (*Bivalvia*), amphipods and mayflies (Ephemeroptera) often showing decreases in taxon richness and diversity, whilst other groups (e.g. Corixidae and *Notonecta*) often increase in abundance. Although acidification has been shown to affect lake communities in a predictable way (through both abiotic and biotic pathways), the underlying processes and mechanisms are not always clearly understood (e.g. Hildrew & Ormerod, 1995).

As a result of international agreements and actions to protect and restore natural resources threatened by acidification, rates of acid deposition have decreased markedly and widespread increases in surface water pH have been attributed to the improved air quality (e.g. Stoddard *et al.*, 1999; Skjelkvåle *et al.*, 2000; Skjelkvåle

et al., 2003). Because surface water chemistry exerts a major control on aquatic biodiversity (e.g. Resh & Rosenberg, 1993), it is anticipated that improvement in surface water quality (e.g. raised pH) should result in biological recovery, albeit with inherent time lag responses (Evans *et al.*, 2001). However, in contrast to documented raised levels of surface water pH, records of biological recovery are scarce and results are equivocal (Skjelkvåle *et al.*, 2000; Alewell *et al.*, 2001) and thus acidification is still considered as one of the foremost problems affecting the biodiversity of inland surface waters in northern Europe (e.g. Brodin, 1995; Johnson *et al.*, 2003).

A number of factors may confound our ability to detect biological recovery. For instance, inadequate water quality, inadequate or lack of supply of colonists to permit establishment and community-level impediment to recovery dynamics may delay biological recovery (Yan *et al.*, 2003). Moreover, the choice of indicator organism/trophic level as well as habitat may confound assessments of chemical and biological recovery (Wright, 2002). Site-specific factors such as latitude, altitude, catchment characteristics (e.g. soil/bedrock type, land use/cover), ecosystem size, and nutrient status may result in different lag responses. Lag responses may increase with trophic level (e.g. changes or instability at a higher trophic level may affect lower trophic levels), and are generally longer and more variable for systems with long water retention times (e.g. lakes) compared to short retention time systems, like streams (Wright, 2002). Furthermore, a number of climate-related factors such as increased sea-salt episodes, increased droughts, increased turnover of organic carbon in lakes and increased mineralization of nitrogen are considered to confound recovery (Skjelkvåle *et al.*, 2003).

Recovery can be defined as the movement towards a pre-acidified or reference state as stress decreases (Wright, 2002). Accordingly, finding no difference in water chemistry and/or biology (e.g. species composition, diversity and richness) between acidified and reference freshwater ecosystems has been interpreted that these lakes or streams have recovered from acidification. This conjecture recognizes that natural communities are not static but exhibit among-year variability. Knowledge of long-term and year-to-year variability of aquatic communities has clear implications for biological monitoring. The use of reference conditions and predictive modeling are being increasingly used in bioassessment (e.g. Johnson, Wiederholm & Rosenberg, 1993; Hughes, 1995; Wright, Sutcliffe & Furse, 2000). Common to most of the reference condition approaches is the assumption that biological communities display little among-year variability. High natural, interannual variability among reference sites may result in false positive error (the metric/system used indicates perturbation when no perturbation has occurred). Moreover, if variation in reference sites is large it may also confound the detection of true impact (i.e. false negative error) (e.g. Sandin & Johnson, 2000). As species differ in their habitat preferences, different communities might respond differently to environmental variation (both natural and anthropogenic). Multihabitat assessments of community variability or stability and persistence patterns might therefore provide a more holistic view of ecosystem change as well as provide an early indication of environmental change.

Objectives

This thesis focuses on the spatial and temporal patterns of phytoplankton and benthic macroinvertebrate species diversity and community composition in Swedish lakes and streams in relation to the spatial variability and change of their abiotic environment. In particular, the main objectives were to:

- determine which environmental factors and which spatial scale are most important in determining the surface water chemistry of boreal streams and lakes, and to determine possible similarities/differences in the factors driving stream/lake water chemistry (paper I).
- examine the importance of local and regional diversity of aquatic macroinvertebrate communities of lakes and streams for three hierarchical spatial scales (sites, ecoregions and biogeographic regions). Here, the concept of additive partitioning of species diversity was used to quantify the relative contributions of alpha and beta diversity to regional diversity and their possible changes with spatial scale (paper II).
- test the effects that selection of organism group/trophic level and habitat might have on detecting recovery of lake ecosystems from acidification. The recovery rates of different indicators (water chemistry, biota), organism groups/trophic levels (phytoplankton producers, macroinvertebrate consumers), and habitats (pelagic, benthic) were assessed and compared (paper III).
- quantify persistence and stability of phytoplankton and benthic macroinvertebrate communities of non-disturbed (reference) and disturbed (acidified) lakes to gain insight into similarities and differences in persistence and stability across different organism groups/trophic level (producers, consumers) and different habitats (pelagic, benthic). Measures of persistence were correlated to environmental variables (i.e. water chemistry) to determine possible drivers of year-to-year variability of the communities. Additionally, community persistence was related to the North Atlantic Oscillation winter index (NAO_{winter} , Dec-Mar) to determine the importance of large-scale (regional), short-term (decadal) climatic variation on lentic communities (paper IV).

Methods

Three different data sets and various univariate and multivariate statistical procedures were used in this thesis: one spatial data set consisting of water chemistry variables and habitat descriptors, catchment land use/cover and ecoregion delineations of lakes and streams (paper I), one spatial data set consisting of lake and stream macroinvertebrate taxon richness and abundance data (paper II), and a spatiotemporal data set consisting of water chemistry, phytoplankton and benthic macroinvertebrate taxon richness and abundance data from a 16 year sampling period of 13 boreal non-acidified and acidified lakes (papers III and IV). Statistical analyses ranged from simple (linear, polynomial) regressions (papers I, III and IV) and correlations (parametric, non-parametric, papers III and IV), stepwise multiple regressions (papers I-IV) to more advanced multivariate gradient analysis methods as partial redundancy analysis (a direct linear (constrained) ordination, paper I) and correspondence analysis (indirect unimodal ordination method, paper III).

Multi-scale drivers of surface water chemistry (paper I)

In autumn 2000, mid-stream and mid-lake samples of 390 streams and 361 lakes were collected as part of the Swedish national stream and lake survey (Johnson & Goedkoop, 2000; Wilander, Johnson & Goedkoop, 2003), and analyzed for acid neutralizing capacity (ANC), the total phosphorous concentration (TP) and total organic carbon (TOC) according to international (ISO) or European (EN) standards (Wilander *et al.*, 1998). This dataset was considered to be sufficiently robust for examining among-site similarities/dissimilarities in surface water chemistry of boreal streams and lakes, since sites were selected randomly and thus represent an unbiased selection of the lake and stream population. In selecting lakes, only sites with surface areas > 4 ha were included and two size classes were used for stratifying stream sites (catchment area classes of 15 to 50 and 50 to 250 km²). A more detailed description of stream and lake selection is given in Wilander *et al.* (2003). Sites deemed to be affected by liming, acidification (lakes critical load exceedence of S and N > 0; Rapp, Wilander & Bertills (2002)), and agriculture/silviculture (catchments with more than 25% defined as arable and affected by clear-cutting, respectively) were not included in this dataset, since this study attempted to understand the effects of local and regional-scale variables on the expected natural variability of selected water chemistry variables.

The streams and lakes of this dataset can be classified as relatively small, nutrient poor, ranging from clear to brownwater ecosystems, and were distributed fairly evenly across the country (Fig. 1). Streams were generally situated at a somewhat lower altitude than lakes, and stream catchments were smaller than lake catchments since streams with catchments > 250 km² were not included in the national stream survey. During sampling, sites were classified according to (aquatic) substratum particle size and vegetation; six substrate classes (ranging from silt/clay to block), two classes of detritus (coarse and fine) and ten classes of

riparian land use and vegetation cover (shoreline stretches, 50 m long and 5 m wide, adjacent to the sampling quadrats) were classified using four categories as: 0%, < 5%, 5 to 50%, > 50% coverage. Catchments were classified as percentage land use/vegetation cover according to the same land use categories used for riparian zones. Ecoregion delineation of Sweden was obtained from the Nordic Council of Ministers (1984). The ecoregions range from the nemoral region in the south to the arctic/alpine complex in the north. Geographic position descriptors (longitude, latitude, and altitude), ecoregion delineation, discharge, deposition variables, land use/vegetation cover descriptors, physical properties (stream width, lake area) as well as aquatic substrate descriptors resulted into a dataset of 60 environmental variables.

Redundancy analysis (RDA) was used to study the effects of environmental variables representing geographic position and regional-scale and local-scale factors on stream and lake water chemistry. Explanatory variables, which were not significantly correlated with ANC, TP and TOC (Monte Carlo permutation test and Bonferroni corrections), and variables showing covariation with other environmental variables (i.e. variance inflation factors > 100) were removed (n = 22) from the data set. The remaining 38 explanatory variables were grouped into three subsets to yield ecologically interpretable variance components as follows: (1) variables describing the geographic position (G) of the water body, (2) regional scale (R) and (3) local scale (L) variables. The variation partitioning technique (e.g. Borcard, Legendre & Drapeau, 1992) was applied to the three subsets and the entire set of 38 variables to obtain the total variance explained and the unique contributions of each subset and their joint effects. With three subsets of environmental data, the total variation of water chemistry was partitioned into seven components including covariance terms (i.e. the combination of the subsets: GRL, G, R, L, GL, GR, RL, eigenvalues obtained through 13 runs of RDA). The variation explained by these subsets was subtracted from the total variation (1.0 in case of RDA) to obtain the unexplained variation (UX).



Fig. 1: Map of Sweden showing six ecoregions and the locations of lakes (to the left) and streams (to the right) used in paper I and II. 1 = arctic/alpine ecoregion; 2 = northern boreal; 3 = middle boreal; 4 = southern boreal; 5 = boreonemoral, and 6 = nemoral ecoregion.

Additive partitioning of species diversity (paper II)

Macroinvertebrate assemblages of stony bottoms (classified as habitats with > 50% cobble, 5 to 50% block and > 50% boulder/bedrock) of 407 lakes and 446 streams were sampled in 2000 as part of the Swedish national lake and stream survey (Wilander *et al.*, 1998a; Johnson & Goedkoop, 2000). This dataset set was sufficiently robust for examining local-regional relationships of species diversity of lake-littoral and stream-riffle macroinvertebrate assemblages, since, in addition to random selection and classification of sites, a number of measures were taken to reduce natural or operator-induced variability. To reduce within-site variability, sample collection was stratified both temporally (autumn) and spatially (stony habitats), and samples were collected using standardised kick-sampling (European Committee for Standardization, 1994) with a handnet (0.5 mm mesh size). A

composite sample consisting of five kick-samples (each 20 sec x 1 m for lakes and 60 sec x 1 m for streams) was taken from each site (one site per lake or stream) and pooled. Sampling area size varied between lakes and streams; in lakes, sampling sites consisted of a 10 m shoreline to a depth of ca 1 m, in streams, the upstream/downstream length was the same (i.e. 10 m), whereas the sampling sites covered half of the stream width (stream edges were not sampled). Since intercalibration of selected metrics of the 20 s and 60 s standardised kick-sample sampling methods showed no significant difference (Johnson *et al.*, 2001), these two slightly different sampling methods are considered to be comparable. Macroinvertebrate sorting and taxonomic identification was done to a predetermined list of some 500 “operable” taxonomic units (Wilander *et al.*, 1998) at the Department of Environmental Assessment of the Swedish University of Agriculture according to quality control and assurance protocol.

In addition to collecting macroinvertebrate samples, water samples were taken for physical and chemical analyses (following international (ISO) or European (EN) standards), habitats were classified according to type of the substratum and the riparian zone and catchments were classified according to vegetation cover and land use as described above for paper I. The lakes and streams were divided among the major ecoregions of Sweden (Nordic Council of Ministers, 1984)

Local species richness (LSR) was calculated as the number of taxa found at a single lake or stream site. Regional species richness (RSR) was defined as the cumulative number of species across all sites within an ecoregion and across all ecoregions nested within biogeographic regions. In order to determine whether the LSR-RSR relationship was linear (indicating proportional sampling) or curvilinear (indicating local saturation), the decision tree approach of Griffiths (1999) was used as a guideline. Second-order polynomial regressions were fitted to the data using an unconstrained model, since constrained models are considered to involve extrapolation beyond the range of the data and to inflate R^2 values (Griffiths, 1999; Srivastava, 1999).

Regressions of RSR vs. minimum LSR (i.e. the lowest number of species present at a site); RSR vs. mean LSR (i.e. the average number of species present); RSR vs. maximum LSR (i.e. the highest number of species present) were conducted to test the influence of *regional species richness*, and regressions of RSR on LSR ($n = 446$ for streams, $n = 407$ for lakes) were done to test the influence of *region* on local species richness. Stepwise multiple regressions with water chemistry, substratum type, and riparian vegetation representing local environmental conditions, and RSR as independent variables was used to determine potential drivers of local diversity. Further regressions without RSR were performed to test whether this variable masked the influence of any of the environmental variables.

The concept of additive partitioning of species diversity (Allan, 1975; Lande, 1996) can be expressed as $\gamma = (\text{mean})\alpha + \beta$, where regional (γ) diversity is the sum of α (defined as the average within-sample diversity) and β (defined as the average between-site diversity) diversity. The concept was applied to the concave metrics species richness, Simpson diversity D and Shannon index H to examine

the relative contribution of α and β diversity to regional diversity of lake and stream macroinvertebrates on three nested (spatial) scales. At the lowest spatial scale (i.e. the sampling site), the between-site diversity (β_1) is determined by subtracting the within-site diversity (α_1) from the α diversity at the next highest scale (i.e. the within-ecoregion diversity, α_2). Similarly, the between-ecoregion diversity (β_2) is determined by subtracting the within-ecoregion diversity (α_2) from the α diversity at the next highest spatial scale (i.e. the within-biogeoregion diversity, α_3). The between-biogeoregion diversity is calculated by subtracting the within-biogeoregion diversity (α_3) from the total γ diversity.

Assessing recovery of reference and acidified lakes (paper III)

In the late 1980s, Sweden initiated a long-term monitoring program of multiple habitats and trophic levels to follow the effects of acidification and recovery of regionally representative lake ecosystems (Wiederholm & Johnson, 1997; Johnson, 1999). Two lake categories were selected: (i) non-acidified 'reference' lakes to monitor natural, among-year changes and (ii) acidified lakes (> 0 exceedence of critical load of S) to monitor natural recovery from acid stress following implementation of international agreements to reduce acidic emissions.

Water chemistry, phytoplankton and macroinvertebrate communities were sampled from ten lakes distributed across Sweden (Fig. 2). The dataset analyzed here consists of 16 consecutive years (1988 until 2003). Six lakes with a mean pH > 6 are used here as minimally disturbed reference lakes and four lakes with a mean pH < 6 are considered as anthropogenically acidified. All ten lakes are relatively small, shallow, nutrient-poor, and clear-water lakes situated in forested catchments. Reference and acidified lakes differed in pH, alkalinity/acidity, amount of total nitrogen and water colour. Surface water samples (0 - 2 m) were collected six to eight times a year and analyzed for variables indicative of acidity (e.g. pH and alkalinity/acidity), nutrients (e.g. total phosphorus and nitrogen), conductivity and water colour (absorbance of filtered water) at the Department of Environmental Assessment following international (ISO) or European (EN) standards when available (Wilander *et al.*, 2003). For statistical analyses, annual mean values were taken to down-weight seasonal differences.

Phytoplankton was sampled in August of each year by taking a water sample from the epilimnion (0-4 m) using a Plexiglas tube sampler (diameter = 3 cm). In lakes with a surface area $> 1 \text{ km}^2$ a single mid-lake site was used for sampling. In lakes with a surface area $< 1 \text{ km}^2$, five random epilimnion water samples were taken and mixed to a composite sample from which a subsample was taken and preserved with JJK-solution supplemented with acetic acid. Phytoplankton (biovolume) counts were made using an inverted light microscope and the Utermöhl technique modified and commonly used in the Nordic countries (Olrik *et al.*, 1989). Taxonomic resolution was done to the family level resulting in seven groups (Cyanophyceae, Cryptophyceae, Dinophyceae, Chrysophyceae, Bacillariophyceae, Chlorophyceae, miscellaneous species (i.e. low abundant species with low

biovolume not belonging to these groups)), which were used to calculate taxon richness and Simpson diversity.

Benthic macroinvertebrates of three habitats were collected in late autumn (October – November) each year. Littoral samples taken from hard bottom, vegetation-free sites of each lake were collected using standardized kick-sampling (European Committee for Standardization, 1994). Sublittoral samples consisted of five replicate Ekman samples taken within a 50 x 100 m rectangular at 4 - 6 m depth. Sublittoral regions were defined as areas lying above the late-summer thermocline in stratified lakes. Profundal samples consisted of five replicate Ekman samples taken within a 150 x 150 m quadrat within the deepest area of the lake. Macroinvertebrate were identified to the lowest taxonomic unit possible, generally to species level.

Three metrics were used to analyse for changes in phytoplankton and benthic macroinvertebrate communities. Taxon richness was selected as a qualitative measure of changes in community composition. Community diversity was calculated as Simpson's diversity. The first axis scores of correspondence analysis (CA axis 1 scores) were used to represent community composition (i.e. the relative abundance of taxonomic composition).

Space for time comparisons of reference and acidified lakes in water chemistry, phytoplankton and benthic macroinvertebrate richness and diversity (each of the three habitats) were made to test for differences: i) between these two lake types over all years (grand mean of the chemical and biological variables), ii) in chemical and biological variables between these two lake types for the first (1988) and last (2003) years of the study, and iii) in chemical and biological variables between the first (1988) and the last (2003) years of the study within the reference and within the acidified lakes (ANOVA and *t*-test). Separate linear regressions with the biological metrics (CA axis 1 scores, taxon richness and Simpson diversity) were run for water chemistry, phytoplankton and benthic macroinvertebrates (each of the three habitats) for each lake to determine if communities are showing signs of recovery. Analysis of variance (ANOVA) of metric regression slopes (raw and normalized) and coefficients of determination (R^2) was used test for differences in trends between lake type (reference and acidified), organism group (phytoplankton and benthic macroinvertebrates) and habitats (pelagic, littoral, sublittoral and profundal). Stepwise multiple regressions, with forward selection, of phytoplankton and macroinvertebrate CA axis 1 scores, taxon richness and Simpson diversity as dependent and surface water chemistry (pH, alkalinity/acidity, conductivity, TP, TN, water colour, water temperature) and the North Atlantic Oscillation winter index (NAO_{winter}) were conducted to determine the best predictors of changes in community composition. The number of significant relations within each lake group and habitat were combined resulting in a total number of times the specific variable was selected.

Spearman's rank coefficients between species abundance of the two communities was determined to reflect patterns in relative abundance (i.e. stability) between year-pairs. Jaccard's coefficient of similarity was used to assess persistence in species composition. Both metrics were determined for the entire communities (i.e. all taxa) of phytoplankton and for the littoral, sublittoral and profundal communities of both lake types. Stability (z-transformed Spearman's coefficients) and persistence metrics were related to seven water chemistry variables (the same as used in paper III) and the NAO_{winter} index using Pearson product-moment correlations.

Results and Discussion

Multi-scale drivers of surface water chemistry (paper I)

This study showed the importance of interactions between variables acting on multiple spatial scales on among-lake and -stream water chemistry. The major part of the variation in water chemistry in both streams and lakes was explained by all components (i.e. geographic position as well as regional- and local-scale variables) (Fig. 3). The GRL interaction component explained 39.9% of the variance in stream ANC, TP and TOC, somewhat higher than for lakes (30.3%). The importance of interactions between geographic position and regional- and local-scale variables for explaining among-stream and among-lake differences in water chemistry were clearly revealed by variance partitioning. The strongest interaction was found between geographic position and regional-scale variables (G&R), explaining 15.3% of the variance in stream and 10.6% of the variance in lake chemistry. These interactions were better predictors of surface water chemistry than regional and local (R&L) or geographic position and local (G&L) factors. The intertwinement of these factors in predicting surface water chemistry was mirrored by the outcome of the multiple regression analyses, where catchment land use/cover variables together with altitude explained most of the variation in stream and lake water chemistry.

Regional factors alone were also found to account for a large part of the variation in ANC, TP and TOC, explaining 9.9% of the variation in stream and 7.8% of the variation in lake chemistry. The finding that the surface water chemistry of streams and lakes could be partly predicted by regional-scale variables, in particular catchment land use (e.g. arable), agrees with the findings of several earlier studies (e.g. Schonter & Novotny, 1993; Allan *et al.*, 1997; Johnson *et al.*, 1997). These studies showed, for instance, that urban land use and rowcrop agriculture were important factors in explaining variability in-stream water chemistry. Similarly, Hunsaker & Levine (1995) were able to explain more than 40% of the variance in total nitrogen using landscape metrics. Omernik *et al.* (1981) suggested that the total amount of agriculture and forest in a catchment are more important predictors of water chemistry than the vegetation composition of the riparian zone. Likewise, in the present study, local factors (e.g. riparian

vegetation, substrata) were less important than regional factors in explaining surface water chemistry patterns.

Surprisingly, the major drivers were similar between lakes and streams, despite obvious differences in ecosystem types. Lakes and streams are often perceived as structurally and functionally different ecosystems, and indeed major dissimilarities do exist regarding differences in water movement (e.g. unidirectional, turbulent flow vs. mixing regimes) and in the relative importance of benthic vs. pelagic productivity (Essington & Carpenter, 2000). The surface water chemistry of streams is considered to be tightly linked to catchment characteristics, with geomorphology determining soil type and availability of ions through weathering (e.g. Allan, 1995). Lakes, on the other hand, have until recently been perceived as separate entities, more isolated than streams from the surrounding landscape (e.g. Kratz *et al.*, 1997; Soranno *et al.*, 1999; Riera *et al.*, 2000; Quinlan *et al.*, 2003). Clearly, terrestrial – aquatic linkages are important predictors of surface water chemistry for both streams and lakes, but the strength of this interaction should vary with geologic and hydrologic settings. Thus, the major difference between the River Continuum Concept (Vannote *et al.*, 1980) and the concept of lake landscape position (Kratz *et al.*, 1997) probably lies in large differences in water residence times between streams and lakes.

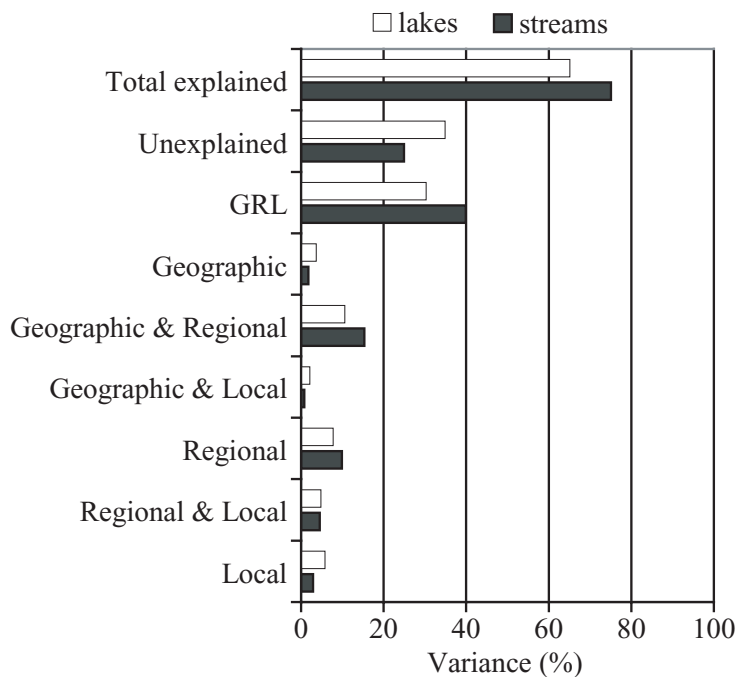


Fig. 3: Sources of variation in lake and stream ANC, total phosphorous and TOC. Column labels indicate the variation (%) accounted for by each subset and their combinations.

Obviously, the chemical composition of a surface water body is a product of a series of mechanisms and processes acting along a scale continuum, i.e. from broad (geographic) to small (local) scales. Surface water chemistry of a particular site is constrained to some extent by macro-scale geomorphic patterns. Small-scale systems develop within the constraints set by broad-scale systems of which they are part and likewise local-scale processes and conditions are generated by broad-scale, geographic patterns and conditions. The idiosyncrasies of both ecosystems might be suppressed by the effects of large-scale factors. Geographic position functions as a template determining both regional and local factors. At the catchment level, geology controls soil type, weathering determines ion concentrations (and buffering capacity) and climate determines vegetation type (and land use). However, changes in land use or cover (e.g. afforestation, deforestation, change of arable to urban) are sources of catchment variation that might generate high amounts of variability or noise making it difficult to tease apart components of natural variation from the effects of anthropogenic impact on surface water chemistry. This inherent catchment variation is probably responsible for the large amount of variation explained by regional factors, which may hide the effects of individual features of lakes and streams appearing similar in their response to environmental factors and influences.

Additive partitioning of species diversity (paper II)

Only few significant relationships between local (LSR) and regional (RSR) species richness were found in both ecosystem types. For streams, RSR versus minimum LSR and RSR versus all estimates of LSR showed curvilinear relationships. For lakes, LSR versus RSR was the only (curvilinear) relationship found to be significant. Total diversity (i.e. regional or γ) consists of both α and β diversity components. One problem of interpreting the 'classical' saturating LSR-RSR curve is that the underlying processes generating the ceiling pattern are not revealed as only the α component (LSR) is known, but the β component is hidden (i.e. under the area of the line). Knowing how much the β diversity component contributes to the total diversity is crucial for interpretation of LSR-RSR relationships and for understanding the underlying processes. For instance, β -diversity will increase with habitat or environmental heterogeneity, and saturation will occur at successively smaller proportions of the regional pool (Cornell & Lawton, 1992).

Using the method of additive partitioning, the contribution of both α and β diversity to total diversity was calculated. At the ecoregion scale, both lake and stream species richness consisted of a small α and a large β component, ranging from 6% to 16% for lakes and from 8% to 22% for streams. Consequently, the β diversity component ranged from 78% (streams) to 94% (lakes). The low α to high β ratio (ca. 25:75% for all ecoregions) indicates that among-site factors are important in describing the variability among the lakes and streams studied here. In stream riffles and wind-exposed lake littorals, flow-related movements of the substratum strongly regulate the structure of biotic communities (e.g. Resh *et al.*, 1988; Lake, 2000), and, in particular, water movement is considered as a strong

determinant of community composition (Allan, 1995; Johnson Goedkoop & Wilander, 2004). A number of studies have shown the importance of other habitat descriptors, such as substratum, water chemistry and riparian vegetation as predictors of macroinvertebrate community composition (e.g. Ormerod *et al.*, 1993; Richards *et al.*, 1997). Here, only local factors such as water chemistry (e.g. TOC, pH), substratum characteristics (e.g. coarse detritus, pebble) and riparian zone vegetation were selected as significant predictors in stepwise multiple regression analysis (both with and without RSR), explaining 3.5% of the variation in stream LSR and 15.9% of the variation in lake LSR.

Certainly, biotic interactions might also be important in structuring communities at both small (e.g. Hart, 1983; Englund, 1991) and large (e.g. Kohler & Wiley, 1997; Hildrew *et al.*, 2004) spatial scales. However, as environmental conditions become harsh and variable, competitive interactions are likely to become less important (Peckarsky, 1983). The ceiling pattern between regional and local richness noted in this study might be more likely due to the physical limitations of the environments studied here and less to biotic interactions. However, clearly the scale of the study will influence the outcome (e.g. Wiley, Kohler & Seelbach, 1997). For instance, small-scale studies (e.g. habitats within a riffle) are more likely to emphasize small-scale processes, whereas large-scale studies like this one (e.g. among-stream comparisons) are more likely to show the importance of large-scale factors. If the sample unit is small in relation to the region size, α diversity is low, but will increase with increasing sampling sizes and the RSR–LSR relationship can shift from a curvilinear to a linear pattern (Caley & Schluter, 1997).

Applying the concept of additive partitioning on three different metrics and three spatial scales, ranging from sites to ecoregions to biogeographic regions, showed that lake and stream species richness were similar to within-site (α_1) and between-site (β_2) diversity at the ecoregion scale (i.e. a significant percentage of species richness was generated by diversity between sampling units at relatively broad scales). For lakes, the percentages of the total species richness (S_T , $n = 207$ species) attributed to within-site diversity (α_1), between-site diversity (β_1), between-ecoregion diversity (β_2), and between-biogeoregion (β_3) diversity were 5:46:16:33 for the whole country. For streams, the percentages of within-site diversity (α_1), between-site diversity (β_1), between-ecoregion diversity (β_2), and between-biogeoregion (β_3) diversity were 7:44:16:32 for the whole country. More than 70% of lake and 80% of stream Simpson diversity could be attributed to the smallest scale (i.e. the ratios were $\alpha_1 : \beta_1 : \beta_2 : \beta_3 = 76:21:2:1$ for lakes and $91:1:5:3$ for streams) indicating that small scales are dominated by common species. This pattern was mirrored by Shannon diversity, albeit to a lesser extent, probably because it gives equal weight to rare and common species. Here, the percentages of the total Shannon diversity attributed to within-site diversity (α_1), between-site diversity (β_1), between-ecoregion diversity (β_2), and between-biogeoregion (β_3) diversity were 46:47:4:3 for lakes for the whole country, whereas streams had percentages of 57:28:6:9 ($\alpha_1, \beta_1, \beta_2, \beta_3$).

These results highlight the importance of using different diversity indices to gain better insight into how rare and common species contribute to total (regional) diversity. For instance, Gering, Crist & Veech (2003) showed that rare species represent a critical component of the community of arboreal beetles and contribute to among-ecoregion differences in community composition, whereas richness of common species was best explained by α diversity at the smallest spatial scale (sampling site was one tree). In this study, β diversity was inversely related to spatial scale. For instance, the difference of between-ecoregion diversity (β_2) was smaller than the between-site diversity (β_1) for lakes (Simpson diversity) and streams (Simpson and Shannon diversity). However, a large between-ecoregion Simpson diversity (β_2) component in the arctic/alpine biogeoregion indicated marked differences in stream macroinvertebrate diversity with arctic/alpine streams having lower diversity than streams in the northern coniferous ecoregion. This was not unexpected, since the arctic/alpine macroinvertebrate communities were strongly dominated by plecopteran taxa occurring in high abundances. This pattern is consistent with the findings of two other studies where freshwater invertebrates revealed generally a north to south gradient in both species richness (Heino, 2002) and community structure (Heino, 2001). However, these studies showed that stoneflies were positively related to latitude, with higher species richness occurring in the northern regions.

Assessing recovery of reference and acidified lakes (paper III)

Positive trends of pH in both reference and acidified lake types occurred during the 16 year study period; median pH increased by 0.008 units year⁻¹ in the reference and by 0.027 units year⁻¹ in the acidified lakes. However, an increase in pH alone does not necessarily imply adequate water quality, as many other factors either alone or combined may restrict biological recovery. For instance, although pH increased in the acidified lakes during the time period, it was still below the biological threshold of many organisms (grand mean = 5.22 ± 0.42 for four acidified lakes). Nutrient levels also changed over the study period (Table 1). Total phosphorous, although relatively low in both reference and acidified lakes (< 10 $\mu\text{g/L}$) at the beginning of the study (1988), decreased significantly in both reference and acidified lakes. In contrast, nitrogen levels increased in three reference lakes, and water colour increased in five reference and three acidified lakes, but changes were more pronounced in acidified than in reference lakes (i.e. higher slopes). Likewise, a decrease in conductivity was more pronounced in acidified than in reference lakes.

Phytoplankton communities recovered quickly in response to raised pH, and temporal trends in phytoplankton taxon richness and diversity were strongly correlated to changes in pH in both lake types. The number of phytoplankton taxa increased in three reference and all acidified lakes and diversity increased in five reference and three acidified lakes during the 16 year study period. Changes in community composition were also noted, with increases in biovolume of, for instance, Crysophyceae and Chlorophyceae in some reference lakes, and Cyanophyceae and Cryptophyceae in others. In acidified lakes, Chlorophyceae

increased in biovolume in only one, while Cryptophyceae increased in three lakes. These positive trends of phytoplankton taxa and diversity and community composition and their relation to raised pH support earlier work that has shown that biological recovery may lag behind chemical recovery. It has been noted that recovery of phytoplankton communities will occur approximately 1 – 4 years following chemical recovery (e.g. Wright, 2002; Findlay, 2003). However, although phytoplankton due to their rapid turnover times, dispersion to new habitats and large seed banks are expected to recover quickly following improvements in water quality, there might be several factors such as regional-level impoverished diversity, inputs of toxic metals and inter-specific interactions delaying or confounding recovery. Findlay (2003) showed, for instance, that natural chrysophyte species became dominant only after a decline of acid tolerant species.

Table 1: Trends in water chemistry of reference (r; n = 9) and acidified (a; n = 4) lakes used in papers III and IV, calculated as Spearman's Rho correlation coefficients. ⁺ = lakes not included in paper III. TN = total nitrogen, TP = total phosphorous. * = p < 0.05; ** = p < 0.01; *** p < 0.001.

Lake	pH	water colour [450 5cm ⁻¹]	Conductivity [ms m ⁻¹]	TN [µg L ⁻¹]	TP [µg L ⁻¹]
Abiskojaure (r) ⁺	0.15	0.03	0.11	0.50	-0.76***
Allgjuttern (r)	0.68**	0.7**	-0.63**	0.31	-0.62**
Fiolen (r)	0.92***	0.63**	-0.67**	0.09	0.08
Fräcksjön (r)	0.75**	0.83***	-0.7**	0.53*	-0.7**
Jutsajaure (r) ⁺	0.29	0.38	0.14	0.15	-0.69**
Remmarsjön (r) ⁺	0.51*	0.46	-0.1	0.06	-0.71**
Stora Envättern (r)	0.16	0.69**	-0.39	0.65**	-0.74**
Stora Skarsjön (r)	0.29	0.7**	-0.67**	0.55*	-0.44
Stensjön (r)	0.58*	0.47	-0.62*	0.29	-0.8***
Brunnsjön (a)	0.40	0.44	-0.65**	0.18	-0.69**
Härsvatten (a)	0.95***	0.67**	-0.82***	0.00	-0.70**
Övre Skärssjön (a)	0.70**	0.70**	-0.77**	-0.41	-0.06
Rotehogstjärnen (a)	0.74**	0.72**	-0.63**	-0.34	-0.35

Similar to pelagic phytoplankton communities, a number of internal and external processes may affect the establishment of benthic species and subsequently the shift from acid-tolerant to pre-disturbance acid-sensitive communities (Legder & Hildrew, 2005). Littoral macroinvertebrate taxon richness and diversity increased in reference and acidified lakes during the study period, indicating biological recovery and thus supporting the trends noted for phytoplankton assemblages. On average, littoral communities of acidified lakes gained nearly one taxon year⁻¹. Two lakes, in particular, had slopes > 1 taxon year⁻¹. By contrast, taxon richness and diversity of both sublittoral and profundal habitats showed strong, negative trends. Sublittoral macroinvertebrate richness decreased markedly in four reference lakes; two lakes had regression slopes indicating a loss of > one taxon

year⁻¹. Taxon loss was also mirrored in decreased diversity in reference lakes. Taxon richness of profundal habitats decreased significantly in five reference lakes, but these changes were not noted in diversity. One lake (L. Fiolen) showed positive trends in taxon richness (slope = 0.44 taxon year⁻¹, p < 0.01). In contrast to reference lakes, negative trends in taxon richness and diversity for sublittoral or profundal communities were not evident.

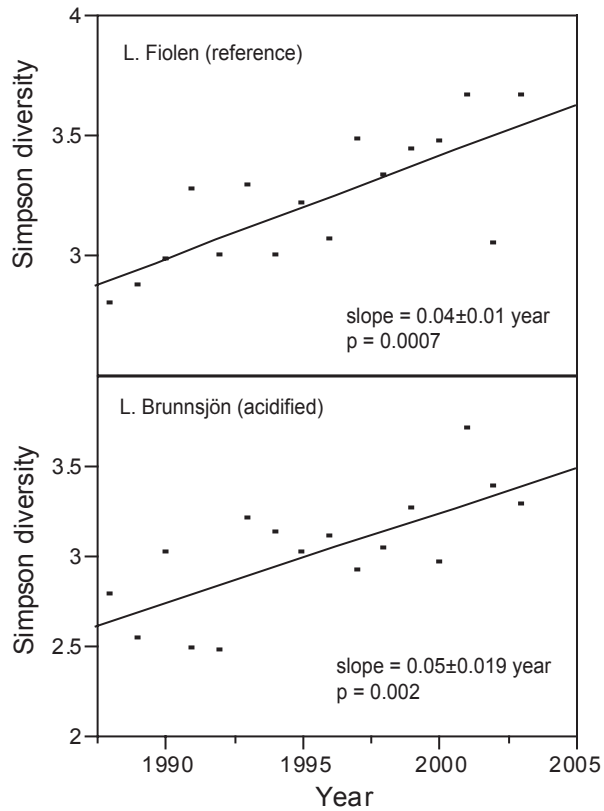


Fig. 4: Example of positive trends in phytoplankton diversity in one reference (L. Fiolen) and one acidified (L. Härsvatten) lake from 1988 until 2003.

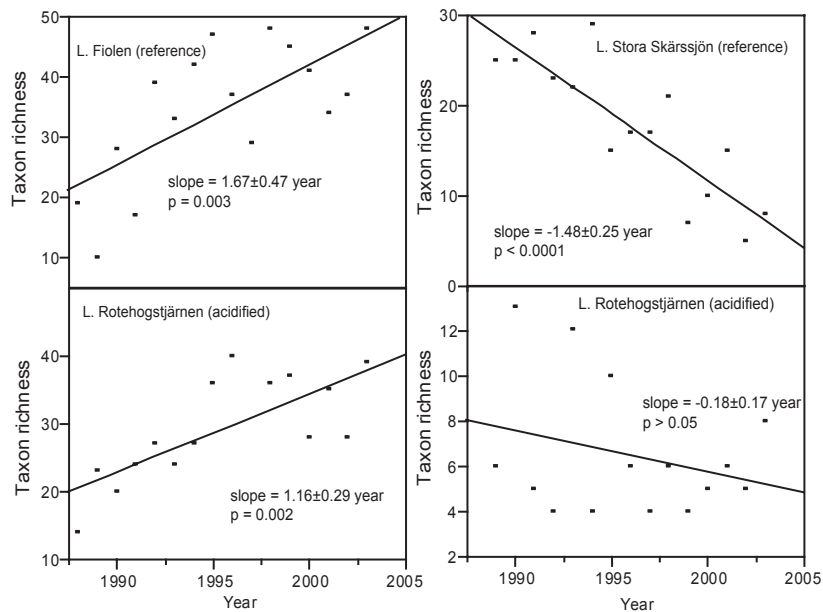


Fig. 5: Example of trends in littoral (left) and in sublittoral (right) macroinvertebrate taxon richness of two reference and one acidified lakes from 1988 until 2003).

Recent studies of recovery of lake-littoral and stream-riffle macroinvertebrate communities in acidified surface waters in Scandinavia have shown similar trends (e.g. Raddum, Fjelheim & Skjelkvåle, 2001; Halvorsen, Heegaard & Raddum, 2002). For instance, Raddum *et al.* (2001) noted an increased distribution of acid-sensitive invertebrates across some Norwegian rivers. In contrast, the clear negative trends of sublittoral and profundal macroinvertebrate communities of both lake types as noted here, were somewhat disconcerting but support recent work on trends in boreal lakes (e.g. Johnson, 2005). The finding that reference communities are not fluctuating around a long-term mean as anticipated, but showing signs of degradation that is not coupled to site-specific stressors, implies the influence of large-scale, regional effects such as climate. Negative trends in sublittoral and profundal communities were correlated with increasing water colour, TN, and decreasing conductivity. Trends of these water chemistry variables might be related to changes in climate such as the unusual warmer and wetter winters during the early 1990s, as indicated by high NAO_{winter} indices. During wet periods, increased surface runoff and higher inputs of dissolved organic matter (water colour), might negatively affect primary productivity and food availability due to shading. A recent study by Weyhenmeyer *et al.* (2005) has suggested that phytoplankton of boreal lakes might be N limited. Hence, increased N inputs may result in increased primary productivity (and may possibly explain the observed phytoplankton community composition shifts), and subsequently negatively affect sublittoral and profundal communities due to oxygen regime

shifts and thus loss of oxygen-sensitive taxa. This conjecture is supported by the fact that TN was the best predictor for profundal community changes, and that temperature, water colour and NAO were also important. Alternatively, changes in oxygen concentration might be indirectly an effect of temperature. Shifts in spring temperature due to warmer winters in the early years of the study (high positive NAO_{winter} indices in 1988-1995) may have resulted in changes of the timing and prolongation of summer stratification. An earlier onset of the spring stratification, due to faster temperature rise in spring temperature, has been found to influence the nutrient cycling (Schindler *et al.*, 1990; Agbeti & Smol, 1995). Moreover, prolonged summer stratification periods caused by climate warming are predicted to result in increased hypolimnetic anoxia (Magnuson *et al.*, 1997). If the sublittoral habitat is periodically situated under the summer thermocline, lower oxygen concentrations and/or lower ambient temperatures may negatively affect sublittoral communities.

Persistence of reference and acidified lakes (paper IV)

Both reference and acidified lakes showed more or less synchronous fluctuations in persistence and stability during the 16 year study. Acidified communities showed significantly higher mean persistence and stability in the pelagic and littoral habitats, and generally slightly higher mean persistence and stability in the sublittoral and profundal habitats. For instance, mean Jaccard's similarity coefficients were higher for acidified lakes for all habitats, indicating a more similar taxonomic composition of acid-stressed communities. Mean community stability, taking relative taxa abundance into account, ranged from 0.44 ± 0.09 for littoral macroinvertebrate communities of reference lakes to 0.66 ± 0.11 for phytoplankton communities of acidified lakes, and was higher in the pelagic, littoral and profundal habitat of acidified compared to reference lakes.

These results were not unexpected and indicate that even 'disturbed' systems are able to maintain their species composition and community structure. As shown in paper III, acidified communities had lower taxon richness and diversity. Winterbourn (1997) showed that unstable and strongly disturbed environments may support some low diverse, but highly persistent macroinvertebrate communities. Since acidified systems are generally species poor, consisting of acid-tolerating specialists, the community structure of these systems may change little over time and hence show low year-to-year variation and consequently high persistence and stability. Persistence has been found to be high where environmental conditions are relatively stable (Robinson, Minshall & Royer, 2000) and where species are adapted to the environmental background conditions (Miller & Golladay, 1996). The finding that low pH regimes are able to promote community persistence has been proposed by Townsend, Hildrew & Schofield (1987), where macroinvertebrate persistence was highest in streams with low discharge, low summer temperatures and acid and stable pH levels.

Acidified communities might also be less complex than reference communities due to fewer or less strong interspecific interactions. The viewpoint that less complex communities are more stable than complex ones has been a long-established paradigm (e.g. May, 1974), but recent studies suggested the opposite (e.g. Lehman & Tilman, 2000; McGrady-Steed, Harris & Morin, 1997). However, although communities of reference lakes had higher taxon richness and diversity and hence may be more complex, they seemed to be more vulnerable to changes of the abiotic environment as indicated by more pronounced negative changes in richness and diversity. By contrast, no trends, either of decreasing or increasing richness or diversity were noted for acidified lakes. As discussed in paper III, taxon and diversity loss in both lake types was related to changes in water chemistry. Likewise, persistence and stability of sublittoral and profundal communities of reference lakes was related to (changes of) TN, conductivity and water colour, indicating that the observed variability in persistence and stability of these communities might be not stochastic in nature or primarily driven by biotic interactions, but can rather be attributed to changes in water chemistry.

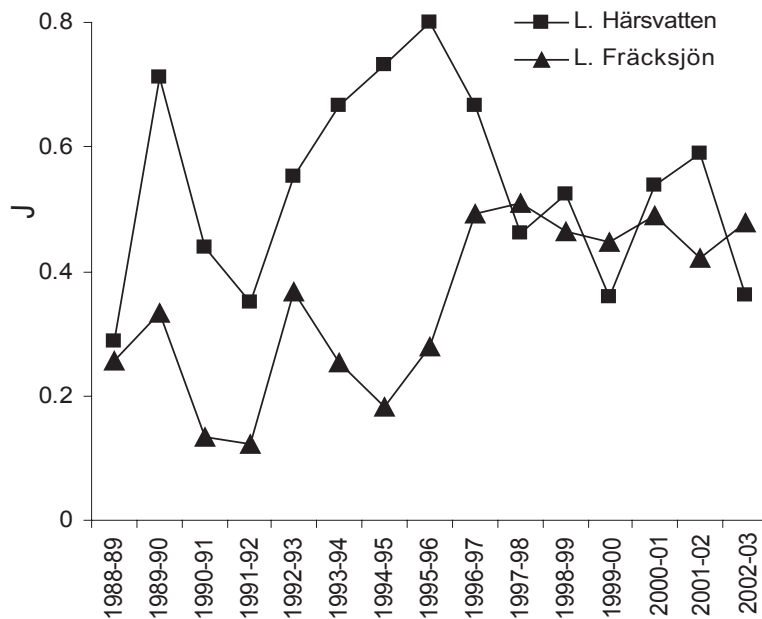


Fig. 6: Example of persistence patterns (Jaccard's similarity index) of littoral macroinvertebrate communities of one acidified (L. Härsvatten) and one reference (L. Fräcksjön) lake located in the western part of southern Sweden (see Figure 2).

Within lake types, significant differences in both persistence and stability patterns were found between the different habitats, emphasizing the importance of habitat partitioning/stratification in monitoring and bioassessment. Differences in community similarity (i.e. persistence) were more pronounced in reference lakes, with littoral communities showing lowest persistence and stability (i.e. highest year-to-year variability). Littoral zones are ecotones between the terrestrial and aquatic zones and are structurally complex habitats experiencing higher environmental background variability compared to more 'simpler' (e.g. sublittoral, profundal, pelagic) habitats studied here. Habitat complexity and the inherent environmental background variability may result in lower persistence as shown by Weatherly & Ormerod (1990) and Bradley & Ormerod (2001), where stream edge or marginal macroinvertebrate communities generally showed lower persistence than communities of the more 'simple' structured riffles. If 'simple' habitats have lower structural or background variability, they may have higher predictability and, consequently, changes in community composition due to environmental changes might be more easily detected making them suitable habitats for biomonitoring (e.g. Weatherley & Ormerod, 1990). However, if complex habitats having inherent high background variability support complex, but instable communities, which are more prone to environmental change, they should be carefully monitored in order to insure the detection of a true impact.

Concluding remarks

Freshwater is our most vital resource and although access to water of high quality is of greatest importance to humankind, we have misused it for a long time. Water has not only the power to give life; it has also the power to take life as recent examples clearly elucidated. In order to protect freshwater as a resource, but also to protect us from its destructive power, the understanding of aquatic-human interactions and thus of aquatic-terrestrial linkages is crucial for future sustainable management of freshwater ecosystems and survival of mankind. This thesis attempts to gain insight into these relationships through the multiscale investigation of the abiotic and biotic patterns determining processes of lakes and streams.

In contrast to traditional belief, a lake is *not* a microcosm; both lakes and running waters are strongly linked to their surrounding landscape and the idiosyncrasy of a particular site is a product of a series of mechanisms and processes acting along a scale continuum, from broad to small scales. Geographic position functions as a template determining regional factors such as geology, land use and cover, which in turn determine the chemical composition and the biota of the surface water body. Understanding the aquatic-terrestrial linkages is important, since many of the threats to the sustainability of lakes and streams can be traced to anthropogenic activities in their catchments, especially agriculture and urbanization. Implementation of this knowledge in regional-based monitoring programs,

restoration action plans and water management is not solely a challenge confronting applied ecologists, but it is also crucial in meeting the socioeconomic needs in attaining high quality and fair distribution of the resource water.

The spatial scale of environmental threats to freshwaters have increased, and today, scientists are more aware that anthropogenic acidification affects are not caused by factors acting on regional or country scales, but by large-scale factors (e.g. emissions and acid depositions), thus making it difficult to mitigate the effects without international agreements. Impacts of climate change may affect the recovery potential of acidified freshwater ecosystems through multiple pathways. For instance, as shown in the present study, the already significant influence of catchment agricultural land use on surface water quality will be reinforced by warmer climate through increased runoff of nitrogen and stored sulphur. Globally acting environmental threats such as acid deposition and climate change will have a considerable effect on local water conditions and regional management and their interaction may lead to unexpected responses of (perturbed) lakes and streams delaying or even confounding recovery and restoration actions. Extreme climate events are predicted to be more common in the future and large-scale acidification of surface waters is still one of the major environmental problems. Both stressors have been assessed separately, therefore, future research should focus on disentangling their interactions and on considering the effects each has on any other as well as on perturbation and recovery across both multiple spatial and temporal scales.

To summarize, some words of Michael E. Soulé (1987) emphasizing the importance of spatial and temporal scales:

‘What are the minimum conditions for the long-term persistence and adaptation of a species or populations in a given place? This is one of the most difficult and challenging intellectual problems in conservation biology. Arguably, it is the quintessential issue [...], because it requires a prediction based on a synthesis of all the biotic and abiotic factors within the spatial-temporal continuum.’

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Acknowledgements

The realization of this thesis had not been possible without the invaluable help and support of the following persons, I would like to thank to:

My particularly gratitude is addressed to **Richard Johnson**, who has guided me through theoretical and practical hurdles throughout the studies, supported and encouraged all my ideas, sent me to conferences, read, discussed and rewrote papers and gave me opportunity to improve my English. I really admire his balanced and calm way to handle simultaneously several EU-projects, being the head of the section, having PhD students, two teenage girls, three smaller kids, two houses, one boat (and several to guard), three lawns (in three cities) to cut during summer, and one dog destroying the house rather than turning it into gold ('wrong name!').

Further thanks go to my assistant supervisors **Anders Wilander** for helping me understanding such tricky things as ANC calculation, catchment liming etc., **Ulf Grandin** for introducing me to multivariate statistics through a great and highly appreciated course, and **Ewa Bringmark** for introducing me to geostatistics and its inherent possibilities.

Thank you, **Leonard Sandin** and **Thorsten Blenckner** for reading manuscripts, giving helpful advice and encouragement at the half-way check. Furthermore, Leonard, thanks for some help with multivariate stats and CANOCO problems and for interrupting tiresome data processing routines through nice chats on the phone ('tja, har du Jenny där?').

By the way, **Jenny Bergfur** and **Daniel Larson**, thanks to you for being great roommates! Work is funnier and problems (e.g. graph troubles) become smaller or are easier solved if there's somebody to discuss, chat or laugh with. Thanks for always putting post-it notes for me on the door!

To you, **Joakim Dahl** I have to return the compliment: you were a great roommate for a long time and I could not think of a nicer person to share a room with, especially in the morning between 7.30 and 10.00 a.m. ('smile!')! We had great discussions and talks about everything, and I wish you all the best for your future. Thanks to all other **PhD students** at the department, gone or still struggling, for nice meetings and coffee breaks, funny BBQ's, bowling, billiards, 'spex', and other social events.

Britta Lidström, thank you for your untiring help filling in travel account forms ('jag fattar det väl aldrig') and for other administrative questions and problems. Furthermore, thanks to **Jacob Nisell**, **Mikael Östlund** for processing figures, **Herman Paz** for helping with the computer, and **Bert Karlsson** for providing data in proper tables. Also, thanks to **Lars Eriksson** and **Björn Wiklund** for sorting and identifying macroinvertebrates. Thanks to **Stellan Sjödahl** for the best parcel delivery one can think about! And thanks to all the **people at the department** for

providing a pleasant working atmosphere, cakes, Christmas lunches etc. Definitely a place worth to leave home for in the morning!

Thanks to all my friends in Germany, and especially to you, **Steph** and **Toddy** for a great friendship in light (summer) and dark (often winter) times, for support and encouragement and comfort in lonely hours ('may you became as bright and perfect as your parents, little 'Stoddy sweetheart!').

Thanks to **db** having such a tremendous catalogue of awesome songs making it difficult to choose from, but easy to discover something new every day ('we can be heroes, just for one day'). And thanks to you, my cute **Zowie** ('you little wonder you') for waking me up every morning before the alarm clock even think about ringing, and for awaiting me (almost) every evening at the mailbox ('finally home, can-opener!').

Last, but not least, I like to thank my husband **Wolfgang Levanti** for his love and support through these four years ('if the sun refused to shine, I would still be loving you. When mountains crumble to the see, there will still be you and me.').