Workshop on Models for Biological Recovery from Acidification in a Changing Climate.

9-11 September 2002 in Grimstad, Norway. Workshop report

Acid Rain Research

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Abstract

An international expert workshop on models for biological recovery from acidification in surface waters was held September 2002 in Grimstad, Norway. Presentations and discussion at the workshop encompassed philosophical considerations, empirical data, the importance of reference conditions, the confounding factors presented by climate change, and possible ways forward to development of dynamic biological response models.
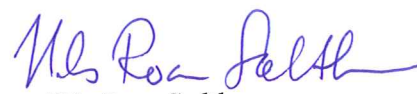
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Workshop on Models for Biological Recovery from Acidification in a Changing Climate

9-11 September 2002 in Grimstad, Norway

Workshop report

Preface

As a step towards development of models for biological recovery in surface waters, an international expert workshop was held September 2002 in Grimstad, Norway.

The workshop came about as result of initiatives from several projects:
- the Canadian-Norwegian joint research project Northern Lakes Recovery Study (NLRS)
- the International Co-operative Programme on Assessment and Monitoring of Acidification of Rivers and Lakes (ICP Waters), an activity under the United Nations Economic Commission for Europe, Convention on Long-range Transboundary Air Pollution (UN-ECE CLTRAP)
- the EU project RECOVER:2010, and
- the project Human Impacts on Lake Ecosystems (LIMPACS), part of the International Geosphere-Biosphere Programme (IGBP) Past Global Changes (PAGES).

The organising committee consisted of the following individuals:

Atle Hindar	NIVA-South
Dick Wright	NIVA
Gunnar Raddum	University of Bergen
Ann Kristin Schartau	NINA
Steinar Sandøy	Directorate for Nature Management
John Gunn	Ontario Ministry of Natural Resources
Norm Yan	York University

The secretariat for the workshop was run by Mette Cecilie Lie, NIVA-South.

The workshop received financial support from:
The Norwegian Directorate for Nature Management (DN)
The Norwegian State Pollution Control Authority (SFT)

Oslo, November 2002

Richard F. Wright

Contents

Summary

Just as there are delays between changes in acid deposition and changes in surface water chemistry, there are delays between changes in chemistry and the biological response. Dynamic models for biological response for surface waters are needed. Active research on the subject is ongoing in several countries in North America and Europe. As a step towards development of models for biological recovery in surface waters, an international expert workshop was held September 2002 in Grimstad, Norway.

Some philosophical considerations were raised related to biological recovery in acidified waters, and empirical data were presented from various areas in Europe and North America. The term recovery implies the knowledge of a pre-acidification target, a reference condition or expectations based on regional distribution. A generalised picture emerged. The time lag to recovery could be divided into two parts. The first is the lag for return of extirpated populations. The second is for sensitive species to achieve densities and distributions typical of undamaged lakes and rivers.

Once the chemical threshold is reached, lag times for common, widely distributed species might be:
- algae: 1-2 years
- macroinvertebrates: 1-3 years in streams (for first appearance of sensitive species; normal populations 5-10 years). 1-10 years in lakes
- zooplankton: 1 year (species with resting stages in the sediments) – >10 years (for whole communities)
- fish: 2-20 years

Finally the way forward with modelling biological recovery was discussed at the workshop.

1. Background, objectives and topics

1.1 Background

Just as there are delays between changes in acid deposition and changes in surface water chemistry, there are delays between changes in chemistry and the biological response. Because the goal in recovery is to restore good or healthy population of key indicator organisms, the time lag in response is the sum of the delays in chemical and biological response. Thus dynamic models for biological response for surface waters are needed. Active research on the subject is ongoing in several countries in North America and Europe. As a step towards development of models for biological recovery in surface waters, an international expert workshop was held September 2002 in Grimstad, Norway.

1.2 Objectives

The workshop had the following objectives:
- examine evidence to date for biological recovery
- identify factors affecting biological recovery
- identify reference conditions and recovery targets
- point to possibilities for predicting future recovery

1.3 Topics

The workshop discussed the following topics:
- empirical data from monitoring
- empirical data from liming
- empirical data from large-scale experiments
- role of episodes
- reference conditions
- climate change and other confounding factors
- modelling biological recovery

2. Results and discussion

From the presentations and ensuing discussion some philosophical considerations were raised related to biological recovery in acidified waters:
- There exists no theoretical basis to predict recovery. Predictions are based on empirical evidence.
- The simplest hypothesis is: recovery is reverse of acidification. More probable is hysteresis (acidification path differs from the recovery path).
- Acidification (and recovery) is likely to be unique (i.e. each stream/lake unique).
- At present there are few if any examples of return to an anticipated pre-acidification community.
- Acidification is ecosystem disturbance, and disturbance generally lowers diversity.
- Biological recovery will occur in irregular steps.
- Biological systems will always change with time; thus the recovered state is not necessarily the same as the pre-acid condition, but functionality should be restored.
- Episodes cause false starts with multiple recolonisations.

Empirical data were presented from various areas in Europe and North America. The examples included:
- Canada, Sudbury lakes: zooplankton, macroinvertebrates, fish
- Finland, lakes: fish
- Sweden, lakes: fish
- Germany, streams: macroinvertebrates
- Norway, lakes: zooplankton, fish
- Norway, streams: macroinvertebrates, fish
- UK, lakes: diatoms

Data from mesocosm and whole-lake experimental manipulations in Canada were also presented.

From these and other data a generalised picture emerged. The time lag to recovery could be divided into two parts. The first is the lag for return of extirpated species. The second is for sensitive species to achieve densities and distributions typical of undamaged lakes and rivers. For some species of macroinvertebrates and fish the second is longer than the first. The lag times for return of fish depend on connections to source populations. If the lake or river is isolated from sources of colonisers, the return of fish will depend on stocking (at least if we want them to return sometime before the next glaciation). Stocking means that the fish can return as soon as chemistry recovers, essentially a lag time of zero. Most of the other taxa (algae, macroinvertebrates, and zooplankton) are more mobile, and many species will return without human intervention.

Once the chemical threshold is reached, lag times for common, widely distributed species might be:
- algae: 1-2 years
- macroinvertebrates: 1-3 years in streams (for first appearance of sensitive species; normal populations 5-10 years). 1-10 years in lakes
- zooplankton: 1 year (species with resting stages in the sediments) – >10 years (for whole communities)
- fish: 2-20 years

Lag time apparently increases with higher trophic level. Changes or instability at the higher trophic level (i.e. in the fish community) may affect lower levels for a longer time period than indicated by the generalised picture. Lag-times are generally longer and more variable for lakes relative to running waters.

Biological recovery is characterised by:
- bottlenecks due to dispersal (=arrival factor)
- bottlenecks (biological resistance) due to interactions with other biological groups (=survival factor)
- dispersal mechanisms affected by stream/lake characteristics (size, morphology, distance from refuge, etc.)
- episodes cause set backs, false starts, multiple recolonisations
- dispersal and recolonisation dependent on life style and cycle (resting eggs, flying, size etc.)

The term recovery implies the knowledge of a pre-acidification target, a reference condition or expectations based on regional distribution. In theory recovery can be measured by the progress towards pre-acidification state or an expected state once the acidification stress is removed. There are several approaches available to estimate the reference condition.
- time: what was pre-acidification condition (historical measurements, paleolimnological evidence from sediments)
- space: otherwise similar sites in low deposition areas
- time-space: use analogue matching of paleo-data to match sites in space

If the defined target is not achieved, this could be due to one or more factors:
- deposition still above critical limits
- irreversibility
- boundary conditions changing (=confounding factors -- land-use, climate change, invasive exotics, other pollutants)
- wrong expectations
- need for triggering step (e.g. restocking fish)

Finally the way forward with modelling biological recovery was discussed at the workshop. Static methods are already in use, such as statistical models (i.e. Raddum's invertebrate index) and probability (risk) models (i.e. trout in Norwegian lakes).

Dynamic models that can predict biologically related lag-times have not yet been developed. A possible way forward would be to use output water chemistry from MAGIC (or similar model) as input for biological models. The various biological models could be constructed for individual groups of organisms and run independently (and concurrently). Sufficient knowledge and data for testing are available for a dynamic model of brown trout in Norwegian lakes, macroinvertebrates in streams and microcrustaceans and diatoms in lakes.

Extensive data are also available for other groups such as pelagic species of zooplankton in lakes, but here the modelling appears to be more complicated due to trophic interactions. Pelagic zooplankton, for example, may be strongly influenced by presence/absence of fish, and thus one may wish to use a fish model first as a pre-requisite for a general zooplankton model. Studies on littoral microcrustaceans show that these communities are highly correlated with pH and other acidification-related variables. The littoral species are to a minor degree influenced by presence/absence of fish, and thus provide a robust tool when evaluating acidification status and recovery of lakes. Environmental authorities, however, may be more interested to know if the water quality is good enough to support an expected zooplankton community rather than "knowing" the exact composition of the whole biological community.

3. Appendices

3.1 Workshop programme

3.2 Abstracts

3.3 Participant list

3.1 Workshop programme

Monday 9 September

1200-1300 Lunch

1300 Opening. Welcome, introductions, and objectives of the workshop. Dick Wright

1315-1700 (with coffee/tea break at 15:00 hrs). FIRST SESSION. Chair: John Gunn
Empirical data for biological response – long-term data from monitoring.

Bill Keller & Norman Yan: Empirical observations on the recovery of crustacean zooplankton in lakes
    near Sudbury, Ontario, Canada
Ed Snucins: Recovery of benthic invertebrates and fish in Killarney lakes
Martti Rask: Recovery processes in acidified Finnish headwater lakes (REPRO)
Kerstin Holmgren: Recovery of fish in acidic lakes?
Johannes Bauer, Reinhold Lehmann & Bruno Kifinger: Biological recovery at ICP Waters sites in
    Germany
Godtfred Anker Halvorsen: Recovery of benthic invertebrates in Norway
Bjørn Rosseland and Trygve Hesthagen: ANC recovery – recovery of trout populations in Norway
Frode Kroglund: Recovery, ANC, and Atlantic salmon in River Otra
Jens Petter Nilsen & Svein Birger Wærvågen: Biotic patterns in recovery of acidified lakes

1900 Dinner at Helmerhus Hotel

Tuesday 10 September

0900-1200 (with coffee/tea break at 10:30 hrs). SECOND SESSION. Chair: Shelley Arnott
Role of episodes in biological recovery
Art Bulger: Blood, Poison and Death: Recovery from aquatic acidification?
Torstein Kristensen: Fish response to episodes of acid water (ANC-recovery)

Empirical data for biological response – liming
Gunnar Raddum: Examples from Rivers Audna and Vikedal in Norway

Empirical data for biological response – large-scale experiments
Rolf D. Vinebrooke, Michael A. Turner, David L.H. Mills & David W. Schindler: Differential
    trajectories of resistance and resilience in an experimentally acidified lake ecosystem

1200-1300 Lunch

1300-1600 (with coffee/tea break at 14:30 hrs). THIRD SESSION. Chair: Art Bulger
Reference conditions
Rick Battarbee: Reference conditions
Gavin Simpson: Defining biological reference conditions for acidified lakes: the modern analogue
    approach

Climate change and other confounding factors
Shelley Arnott: Setbacks in biological recovery: climate change and other confounding factors
Don Monteith: Diatom sensitivity to changing acidity and the potentially confounding influence of
    climate on a signal of biological recovery.

1700-2100 Boat trip with dinner. Departure from Grimstad centre.

Wednesday 11 September

0900-1200 (with coffee/tea break at 10:30 hrs). FOURTH SESSION. Chair: Atle Hindar
Modelling biological recovery: the way forward

Maximilian Posch: Dynamic modelling under the LRTAP convention
Gunnar Raddum & Arne Fjellheim: Modeling Invertebrate Recovery of ACidified Lotic /lentic
    Ecosystems (MIRACLE)
Rachel Helliwell: MAGIC modelling and the biological response in the Galloway area, Scotland
Rick Battarbee: pH, diatoms and dynamic modelling

1200-1300 Lunch

1300 Departures

3.2 Abstracts

Reference Conditions

Rick Battarbee

Environmental Change Research Centre, University College London, London WC1H 0AP, UK

Why are we interested in "Reference Conditions?" In the "acid rain" debate we have moved over the last three decades from issues of detection and diagnosis (i.e. we have a problem and we know the cause) to remediation (how can we remedy the problem?).

One, but not the only, remediation option is ecosystem restoration. It is the most demanding, but probably in terms of sustainability the most desirable option. It assumes (i) we understand how the ecosystem has been changed (damaged?) by the impact in question; and (ii) that changes are reversible;

A central requirement is a target and ideally a time-scale over which the target is to be reached. The ultimate target may be full restoration. Although we can define this, or attempt to define it, it may be unachievable and a compromise target may be selected instead that allows or accepts some of the consequences of the impact into the future. Whether or not policy makers adopt such a compromise does not lessen the importance of defining the ideal target as a means of measuring the gap between the compromise target and the ideal target i.e. as a measure of the progress being made towards the target.

How can we define ecosystem restoration targets? For this we need "reference conditions" that may be defined as the physical, chemical and biological status of the lake/stream in the absence of a specific or specified human impact e.g. acid deposition

There are several complementary approaches or options:

Time – what were the physical, chemical and biological conditions before the impact of acid deposition? There are three possibilities for time travel: (i) the instrumental record – but this is probably not long enough anywhere; (ii) the archive or documentary record of e.g. herbarium specimens, fish catch data. Where records are available this approach has great value; and (iii) the sediment record. This does not exist for streams, but it has, however, great potential for lakes, both through the use of transfer functions to infer past chemical conditions or directly through the microfossil record of diatoms, chrysophytes, cladocera, chironomids etc.

Space – Spatial references are sites that are similar to (or analogous to) the acidified sites in their sensitivity to acidification and in as many other characteristics as possible (e.g. depth, area, altitude, catchment – lake ratio, habitat structure) but are not acidified to any extent. This latter condition can in theory be assessed using a critical loads model. The weakness of this approach is that (i) no two systems are the same so perfect matching is impossible and targets are imprecise; (ii) the space-time assumption weakens as distance increases, due to climate and biogeographic factors; (iii) a large database of potential matching sites is needed for good matches to be selected; and (iv) there is no quantitative measure of the suitability of a spatial reference site as an analogue. However, in contrast to the "time" approach a spatial reference enables full present-day chemical and biological surveys to be carried out at sites in the reference region.

Time-space - Weakness (i) and (iv) above, but not (ii) and (iii) can be tackled using a statistically-based palaeolimnological method to match acidified sites with potential analogue sites. This can be done either chemically or biologically. The chemical approach is a weak one. It uses a transfer function (e.g. with diatoms) to reconstruct past chemistry for a site and then seeks an analogue with

matching chemistry. The problem is that at least pH, DOC and calcium would need to be reconstructed and the reconstructions we have are good for pH, poor for DOC and non-existent for calcium. Moreover target biology requires matching habitat structure and this is not addressed by a purely chemical approach.

Consequently a biological approach, independent of transfer functions is preferred. The methodology was first demonstrated by Flower et al. (1997) and is being further developed by Simpson (2002). This approach uses a large database of lake sites arranged along an acidification gradient to match the pre-acidification microfossil assemblages of a specific acidified site with the equivalent contemporary assemblage (surface sediment) of all sites in the database. Simpson has shown that the best analogues are found when both diatoms and cladocera are used together.

Once the best analogue sites have been identified they can be surveyed to determine the chemical and biological characteristics of the site that might then be expected at the acidified site following recovery. This is a statistically and ecologically rigorous procedure because it is based on comparisons that reflect both chemical and biological conditions, as the fossil assemblages used in the analysis are derived from surface sediments that integrate taxa from the full range of planktonic and benthic environments in the lakes.

Probability of occurrence - Research on acid and acidified surface waters over the last 20 years has led to the generation of large databases on the occurrence and distribution of taxa and groups of taxa in acid waters with respect to chemistry. The taxonomic groups usually include fish, macro-invertebrates, aquatic macrophytes, zooplankton and algae (mainly diatoms). From these datasets the probability of occurrence of taxa that should occur in a restored lake of given chemistry can be calculated. The emphasis is on common species, i.e. those such as the mayfly *Baetis rhodani,* or benthic diatom *Achnanthes minutissima* that would have occurred at all or most sites before acidification.

Confounding issues

Having defined the targets – are they achievable? They are not achievable if:

- acid deposition is not reduced to zero
- the changes are not reversible, chemically (e.g. long-term base cation depletion) or biologically (e.g. site extinction has occurred and there are barriers to re-colonisation)
- boundary conditions in the system have changed i.e. there are confounding processes taking place that drive the system in a different direction.

Confounding factors can include:

- a change in catchment land-use or land management (including hydrology)
- an increase/change in other pollutants, especially toxic metals and organics
- a change in climate

In these cases, targets based on reference conditions, however defined and measured, need to be modified to accommodate these additional influences. How this can be done quantitatively or predictively is not at all clear as complex interactions between the multiple stresses may take place. High quality, long term monitoring of acid water sites will be necessary to observe and understand these interactions and to provide data to calibrate the new generation of models needed to simulate them.

LIMPACS

LIMPACS is an IGBP-PAGES research programme concerned with "Human Impact on Lake Ecosystems". It seeks to bring together palaeolimnologists, limnologists and modellers in understanding lake dynamics on interannual and decadal time-scales. The central theme of LIMPACS is "understanding the past variability of lake ecosystems in order to predict better their future". Future prediction requires process-based dynamic modelling. Such models, however, need to be properly validated against high quality time series that span time-scales from years to centuries, and need information about the past states of lakes in order to run appropriate scenarios. This is a role that only palaeolimnology can play, but palaeolimnology itself is model-based. Consequently palaeolimnological output also needs verification, in this case against instrumental lake records where they are available. On this basis interaction and collaboration between palaeolimnologists and neolimnologists is essential and focuses specifically on the need for linkages between: (i) recent sediment records; (ii) long-term lake records, and (iii) lake models that operate on annual time-steps. Surface water acidification research is central to the LIMPACS agenda and studies of ecosystem recovery from acid stress provide an excellent example of the power of this approach to limnological thinking. More information is available at the LIMPACS website: http://www.geog.ucl.ac.uk/ecrc/limpacs.

Biological recovery at ICP Waters sites in Germany

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Reinhold Lehmann & Bruno Kifinger, *Geo-Ökologie-Consulting (GÖC), D 82362 Weilheim, Germany*

Germany participates in ICP Waters since the beginning in 1986 thereby investigating a total of 34 sites (30 running water and 4 lakes). 33 sites are located in the forested lower mountain ranges of Middle and South Germany. The underground at these sites consists of calcium poor bedrock such as granite, gneiss, sandstone and rarely slate. The regions are characterised by the presence of brooks and small rivers but only a few lakes. As soon as the running waters leave the forested regions they are impacted by nutrients from agricultural land use and sewage treatment plant effluents. As a consequence water is neutralised and acidification is stopped. In Northern Germany some lakes of the lower region of Lauenburg and some brooks are also acidified.

According to deposition data the sulphate content in waters decreased significantly at 27 sites, while pH-values were increasing at 16 sites. At 17 sites either a not significant trend or constant conditions could be observed. The data on nitrate contents did not show such improvements. At 16 sites a significant decrease could be observed. In contrast further 6 sites showed a significant deterioration due to increasing nitrate concentrations. At 11 sites no significant trend was obvious.

The biological effects with regard to macroinvertebrates in running waters are considered to be slight; only in three waters (Elberndorfer Bach and Zinse in Rothaargebirge, Taubenbach in Elbsandsteingebirge) an increase of sensitive species indicates a significant improvement. The situation in these brooks improved by one category of the four-scaled category system used in Germany. In contrast in 16 running waters there is no constant trend, whereas at 10 sites there is a constant trend. At one site deterioration has to be noted. The waters with no significant trend are non-stabile systems. In dry years sensitive species appear, whereas in wet years they disappear (e. g. Waldnaab, Oberpfälzer Wald). However, during the next years, in some brooks in the Bavarian Forest improvements are to be expected. Waters with significant constant trends are often settled by stabile macroinvertebrate communities. There are either strong acid waters tolerating species with low taxa numbers (e.g. in Fichtelgebirge mountains) or weak acid waters with a big number of species (e.g. in Bavarian Forest).

Blood, Poison and Death: Recovery from aquatic acidification?

Art Bulger

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Acidification is a widespread and worsening problem in the eastern U.S. Rainwater is too acidic to support any fish life, and must be buffered. Landscape and surface water responses depend on buffering capacity of local soils and bedrock. Buffering capacity in some areas has been depleted. Acid-sensitive soils release aluminum. Aluminum poisons electrolyte regulation at gills. The cause of death is circulatory collapse secondary to electrolyte imbalance.

The US clean Air Act mandates a 40% reduction in sulfur emissions from power plants nationally, and sulfur in most surface waters has declined. However, modelling studies indicate that this 40% reduction will not produce wide recovery in the northeastern US, and will allow continuing acidification in the southeastern US. These studies show that cuts of at least 80% will be needed to produce recovery in the southeast.

Acidification is a disturbance. Disturbance always lowers species richness. Loss of species usually lowers productivity and stability of ecosystems. Fish biodiversity loss is a predictable consequence of acidification. There are abundant examples of this in North America and Europe. Continued fish biodiversity loss is not sustainable, and carries significant economic costs.

There is no theoretical basis on which to predict the paths of biological recovery, because climatic events during recovery may be unique, and at some scale each lake or river is unique. The null hypothesis of recovery paths is that recovery will be like acidification, only backwards. Thus, for example, the last species lost (the most acid tolerant) would be the first to return. However, time lags are expected because of species recolonization times, which differ widely. Initial recolonization may fail. In acidification, organisms respond immediately to acute stress, and may disappear, but recolonization is dependent on processes occurring outside the ecosystem. In the early stages of recovery, transient communities are expected. The biological response to chemical recovery may appear chaotic.

Measures of recovery can include species counts. In some cases comparative studies may be limited by the confounding affect of lake area on species richness. However, there is a regular relationship between fish species richness and lake area worldwide. This occurs for three reasons: larger areas contain more habitat diversity and more ecological niches, and thus host more species; lakes are like islands, and small islands host small populations which have higher extinction rates; a larger lake is a larger sampling unit for the regional fauna. A log-log plot of species number versus lake area (worldwide) yields an r-squared value of 0.3. Limiting the inclusion of lakes by continent, country, latitude or geology increases the r-squared value. Pre-acidification species counts, or counts from unaffected reference sites, will yield a species-area regression line which is steeper than the slope of species-area relationships based on acidified lakes. Recovery can be measured regionally by the increase in the slope of the species-area regression line over time. Thus reference sites uniquely paired to affected sites need not be found at the regional level.

In northern latitudes the multiple year classes of salmonids may function like a community of several different fish species. A measure of recovery could be simply the count of year classes, or an index based on this. Other variables to measure in recovery are biomass, body size, and density. All may show chaos in transient communities during recovery from acidification.

A number of studies suggest that full recovery of biological function in lakes and streams requires the presence of roughly similar numbers of species (at each trophic level) as in unaffected reference lakes. The same studies suggest that this cannot be achieved until a recovery pH has reached about 6.0.

Modeling studies may be used to estimate the time to chemical recovery, which for aquatic animals, could be set at pH 6.0. Model studies could also be used to determine the time to some desired percentage of lakes reaching this target level of pH 6.0.

There seem to be no cases of limed acid lakes or lakes recovering from experimental acidification in which the exact community of zooplankton and fish were re-established. However, an apparently fully functional lake zooplankton community (with perhaps some different species and /or different proportions of species) is established about 10 years after a pH of 6.0 is achieved. Some species will be present at pH values below 6.0, but with species numbers, biomass, and density at much lower values than above 6.0. Even with very long recovery times, animal communities in lakes or streams with pH values indefinitely below 6.0 are unlikely to reach the diversity and stability characteristic of communities living at pH values above 6.0.

Stream macroinvertebrate communities are often dominated by the immature life stages of flying insects, such as mayflies, dragonflies, and stoneflies. Such species have rather rapid colonization times, such that a functional stream macroinvertebrate community may be present in about 3 years.

Fish community recovery is expected to be quite variable, depending on sources of colonists. In lakes and streams, fish could be introduced as soon as the zooplankton (about ten years in lakes) or macroinvertebrate (about three years in streams) community becomes established. In lakes or streams which had simple fish communities in the past, a fish community might become rapidly established with species introductions, or might take as long as 30 years for complex communities without species introductions.

Recovery of benthic invertebrates in Norway

Godtfred A. Halvorsen

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Recent research has shown that surface water chemistry in Norway and Northern Europe showed significant trends of recovery during the period from 1989 to 1998. Monitoring data of benthic invertebrates from riffle localities in five watersheds in the southernmost and western Norway have been analysed using two approaches, the acidity indices and partial redundancy analysis (partial RDA). The three southernmost watersheds are situated in the region most strongly affected by acid rain, while the two in the northern part of western Norway are in an area with less intensive acidification.

The period analysed with the acidity indices goes from the early 1980ies to the present. The indices, calculated as the average of the scores of all localities in each watershed, show an increase in all of the watersheds during this period. This means that the number of localities with sensitive species present has increased in each watershed. The increase or recovery starts in the late 80's or the early 90's in all of the watersheds.

Three of the watersheds had sufficient data of both biology and water chemistry, so that the 10-years period from 1989 to 1998 could be analysed with a partial RDA. These analyses showed that a linear change, that can be interpreted as a response in the benthic invertebrates to a recovery in the water chemistry, were present in all of the three watersheds. However, the signal was weak in the unlimed part of the Vikedal watershed and in the Gaular watershed, with only one locality in each watershed showing a significant trend. The signal in the Nausta watershed was stronger. Seven out of twenty localities showed a significant signal of recovery. These were mainly situated in the tributaries and in the upper reaches of the main river. The amount of abundance variation explained by the linear trends in water chemistry were, however, quite small and below 10 % of the total variation in all of the localities. Additional RDA analyses showed that seasonal changes in water chemistry explains more of the variation than the linear ones. This means that a signal of recovery may be obscured by seasonal variation in water chemistry due to the snowmelt in spring or to acidic episodes caused by winter storms.

The acidity indices are very sensitive. One specimen of a very sensitive species in a locality will give this locality an index value of 1, and will consequently affect the mean index for the whole watershed. The partial RDA is more conservative. When both approaches are used we may gain valuable information about the development in the benthic community. So far we see evidence of a recovery in the benthic invertebrates in the acidified watersheds in Norway following an amelioration in the water chemistry in the surface waters. The recovery seems to be most pronounced in the northern part of western Norway, where the acidification has been weaker than in the southernmost part of the country.

Recovery of fish in acidic lakes?

Kerstin Holmgren

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Fish are still present in three acidic lakes within the Swedish program of environmental monitoring, i.e. in Lake Brunnsjön (five species), Lake Rotehogstjärnen (three or four species) and Lake Övre Skärsjön (two species). Eurasian perch, *Perca fluviatilis*, has recently been the most abundant species in each of the lakes. The more acid-sensitive roach, *Rutilus rutilus*, disappeared from Lake Övre Skärsjön during the 1970's, while scarce populations survived in the other lakes. Water chemistry has been regularly sampled since 1984. Standardised test-fishing was first applied in 1985, 1987 or 1989, and annual sampling started in 1988, 1990 or 1994.

In 2001, the lakes had mean pH of 5.48-5.56 and minimum pH of 4.89-5.27. Mean annual pH has increased significantly since 1984 in each of the lakes, while annual minimum showed no significant trends. During the same period, mean air temperature in April tended to increase at three selected weather stations (P-values 0.06-0.15), while mean air temperature during the growth season (May-September) varied more erratically between years.

The Swedish criteria for environmental quality were applied to test-fishing data. Final scores, on a five-degree scale, were too rough to reveal any clear-cut trends. Since 1990, the fish community of Lake Rotehogstjärnen showed none or minor deviation (score = 1) from reference values, while small to large deviation (scores = 2-4) appeared in the other lakes. Annual mean scores of nine included metrics, however, revealed some indication of biological recovery in Lake Rotehogstjärnen (P = 0.058) and Lake Övre Skärsjön (P = 0.100).

Age structures revealed considerable between-year variation in recruitment of all perch and roach populations. The recruitment of roach in Lake Rotehogstjärnen showed the most consistent improvement in recent years, and the importance of favourable water temperature conditions will be further evaluated.

Empirical observations on the recovery of crustacean zooplankton in lakes near Sudbury, Ontario, Canada

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Large reductions in emissions of sulphur from the Sudbury, Ontario, area smelters have resulted in water quality improvements in the surrounding lakes. Biological changes have followed the chemical changes. However, biological recovery is still at an early stage in most lakes, and our knowledge of biological recovery processes is very incomplete. Crustacean zooplankton are probably the most widely studied group of organisms in recovering Sudbury lakes, and surveys and long-term monitoring studies of this group reveal some of the major mechanisms important in biological recovery. Influences on recovery include factors related to both habitat quality and to the ability of organisms to colonize. During recovery, existing species and colonists from internal and external sources interact to form new species assemblages. The relative roles of internal and external influences, and abiotic and biotic factors, remain poorly understood. Long-term studies in the Sudbury area have also shown that the recovery of aquatic ecosystems from acidification may be affected by other environmental stressors including climate change, calcium depletion and UV-B irradiance. Future studies of biological recovery need to be conducted in a multiple-stressor context. It will also be important to determine the metrics that best describe biological recovery and to establish acceptable endpoints for the biological recovery process.
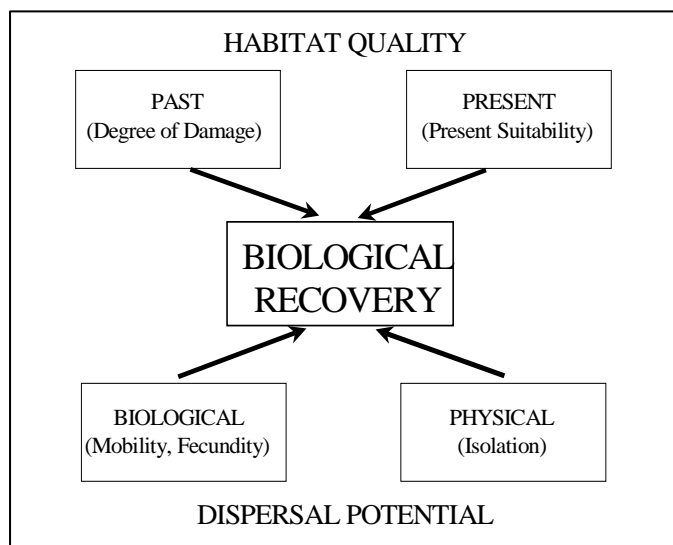
Major Factors Affecting Biological Recovery

ANC-RECOVERY: What is the chemical threshold for natural reproduction of brown trout during recovery from acidification. Part 2: Ecotoxicological experiments.

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Ecotoxicological experiments in inlet and outlet brooks at time of spawning (October) and hatching (April), have been performed in Lake Saudlandsvatn and Lake Tveitvatn (for lake history see Rosseland *et al.* this report). At Lake Saudlandsvatn, local and hatchery reared brown trout of the Byglandsfjord strain were kept in cages (Fig. 1a) at 5 sites and water chemistry, blood physiology and mortality were measured. In October 2001, no mortality occurred but a significant stress was observed in the experimental fish (Fig 1b) whereas the local fish was more tolerant (Fig. 1c). A significant mortality occurred in spring.
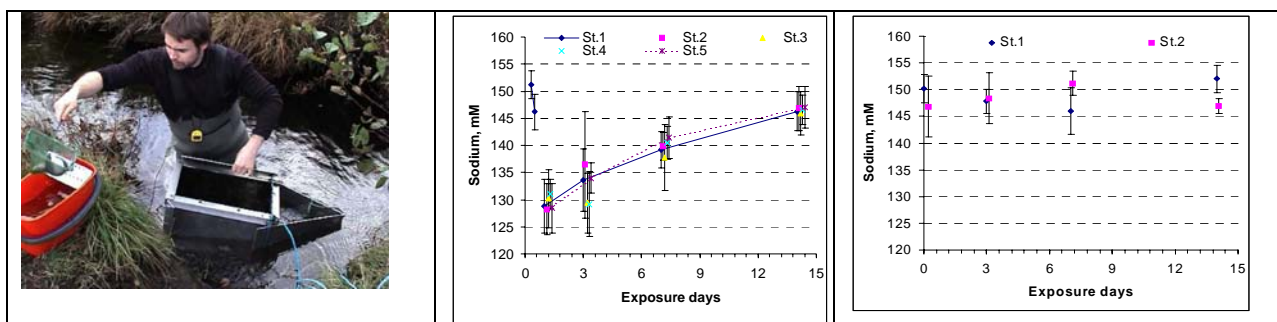

Figure 1. Experiments at Lake Saudlandsvatn: the cages (Fig. 1a), blood sodium levels in the spring (Fig. 1b), and in the autumn (Fig. 1c).

At Lake Tveitvatn, a dosing-rig (Fig. 2a) was used to test toxicity of the natural water (Fig 2b), with Al added (Fig 2c), and with limestone added (2d); the water quality was clearly sub-optimal in October 2001. A slight increase in Al adversely affected the physiology (Fig 2c) and resulted in mortality, while a slight increase in Ca improved the physiology (Fig. 2d).
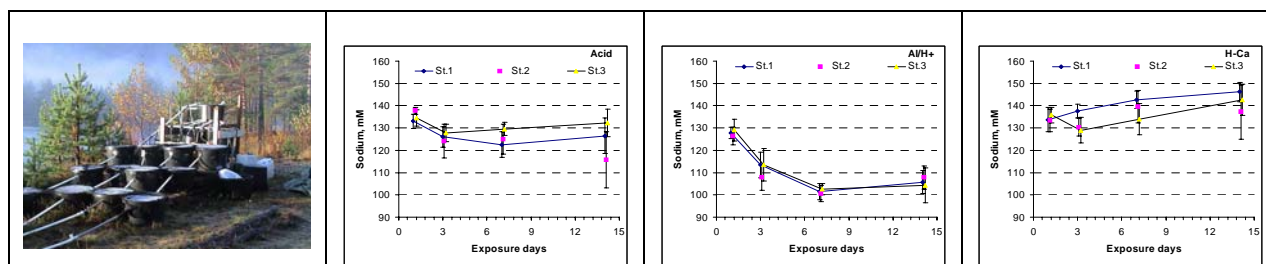

Figure 2. The experiments at Lake Tveitvatn (Fig. 1a), with blood sodium levels in fish exposed to natural water (Fig. 2b), Al-enriched water (Fig. 2c), and Ca-enriched water (Fig. 2d).

A new monitoring technology based on the "passive sampler", DGT (Diffusion Gradient in Thin films), for bio-available metals such as Al and Fe was tested at Lake Tveitvatn. The DGT accumulation of Al was related Al accumulation onto fish gills and changes in physiology and mortality of brown trout. The relation between Al on gill tissue compared well with the DGT.
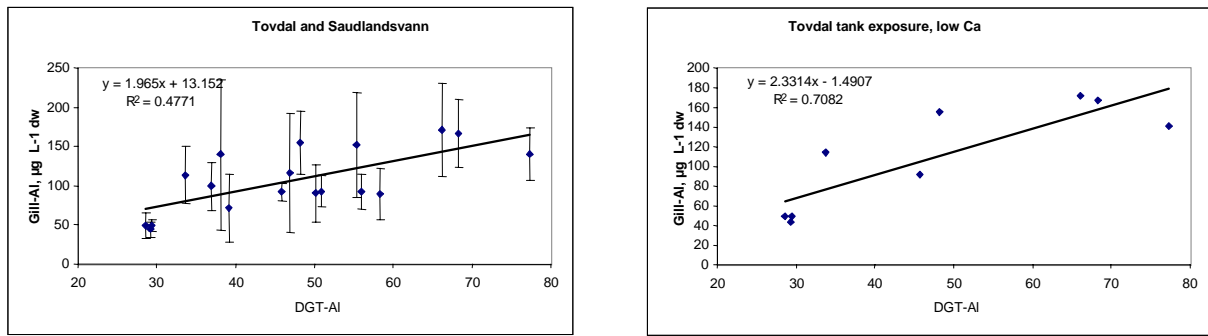
Figure 3. Comparison of Al accumulated on fish gill with that on DGT. The complete data set (Fig 3a) and data for Ca addition experiments only (Fig. 3b).

Recovery, ANC, and Atlantic salmon in River Otra

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The Atlantic salmon population in the River Otra, southern Norway was lost during the 1960's due to acid rain and industrial and municipal pollution. The industrial and municipal pollution sources were sanitized by 1995. A concurrent reduction in acid deposition occurred during the 1990´s, raising ANC from 8 to 20 µeq L^{-1}, pH from 5.2 to 5.7 and reducing inorganic monomeric Al from 71 to 28µg Al L^{-1}. Salmon fry were observed in the watershed for the first time in >40 years in 1993. The annual salmon catches are now at historic high levels. *Baetis rhodani* (the mayfly) has become reestablished.

The density of older (>0+) fry (for the period 1997-2000) is however alarmingly low. This suggests poor survival. A survey of smolt quality performed in 1999 and 2000 concluded that the smolt had normal physiological status and achieved normal hypo-osmotic capacity. It was concluded that the fish appeared to be in good health. This does not suggest any adverse effects of acidification. At the same time, gill samples revealed accumulation of aluminum and major changes in tissue structure. These findings suggested that the fish had experienced acidified water, most likely during winter. The hypothesis is that fish that survived the winter episodes recovered and could smoltify normally. These "toxic" episodes are not apparent in the in the monthly water samples. A further indication of acidification episodes is that despite *B. rhodani* being established, the density is low and the species is not restored at all stations all years. The biological recovery rate differs from the rate described from limed rivers.

To gain a better understanding of factors that could influence the day to day chemistry, water quality of all major tributaries to River Otra between Lake Byglandsfjord and the anadromous stretch of the river were documented during the spring of 2000. Hydrological data from both sites were collected for a 10-year period. Most of the tributaries were acid (pH<5.5). The main river has normally pH-values higher than 5.8. The data suggest that there is a clear negative correlation between water discharge from the tributaries and pH measured close to the river mouth for the winter period (Sep-March). When the tributaries contribute to 60% or more of the total water flow at the river mouth, pH is estimated to fall to 5.4. This is a pH-level where mortality cannot be excluded provided the episodes last for some days. Periods with high discharge from the tributaries are most common during winter, and occur only rarely during spring and summer.

Although the average water chemistry has improved greatly, and to levels that can support salmon, winter episodes caused by high discharge from acidic tributaries can offset the recovery rate. Large lakes that can withhold water following dry periods can enhance the effect of the tributaries. Short episodes are not easily detected in a monthly surveillance programme. There need therefore not be any good correlation between chemical recovery and the restoration of the biological community.

Diatom sensitivity to changing acidity and the potentially confounding influence of climate on a signal of biological recovery.

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Changes in the assemblage of diatoms in sediment cores from upland lakes provided one of the clearest indications of a biological response to acidification in the UK. Now, a reversal in the assemblages of freshly deposited sediment is expected to be one of the first signs of biological recovery as chemical improvement follows a major decline in acid deposition. However, species shifts indicative of recovery have been extremely patchy to date.

Data from the UK Acid Waters Monitoring Network (UKAWMN) suggest that this important group of primary producers are indeed extremely sensitive to changes in acidity but for a relatively short period during spring only, which may represent the main growing season for the benthic taxa dominating these systems.

The primary influence on variance in the acidity of many UKAWMN lakes since the onset of monitoring in 1988 has been the amount of recent precipitation rather than a reduction in deposition and this has therefore had a dominant effect on acidity-related diatom species changes. A rise in the diatom inferred pH of annually collected sediment trap samples over the past 10 years in low deposition areas of central and northern Scotland can almost solely be explained by a reduction in spring precipitation over the same period. At the more heavily impacted Round Loch of Glenhead in southwest Scotland, however, the dual influence of falling sulphate concentration and climatic variation is apparent.

The benthic diatom species composition of these systems should therefore track any change in water chemistry in spring without a significant time lag. However, as spring chemistry is particularly vulnerable to climatic influences including varying precipitation, as well as sea-salt inputs and, possibly, temperature dependent nitrate release, linearity between acid deposition decline and biological recovery is not expected.

Recent climate change scenarios for the UK suggest increased storminess which is likely to increase the frequency and intensity of rainfall and seasalt events and therefore impact on acid-sensitive surface waters. These results highlight the need for a better quantification of climatic influences on the acidity of these systems, and a better understanding of the seasonal sensitivity of target organisms, before biological recovery trends over forthcoming decades can be reliably predicted.

Biotic patterns in recovery of acidified lakes

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Norwegian aquatic ecosystems now experience the first indication of biotic recovery following decades of acidic deposition, mainly from other European sources. Many of the present investigated regions, still suffered serious acidic stress through continuous atmospheric outfall. To facilitate analyses of biotic recovery, lakes were subdivided according to their ability to buffer acidic inputs. Sites outside the bicarbonate buffering system with pH < 4.7 stayed chronically acidic, irrespective of a less acidic atmosphere during recent years. Sites with pH down to 5.3-5.5 during the major acidic period 1970-1990 were recovering through natural watershed and within-lake processes, with a present pH around 5.7-6.0. Some strongly coloured lakes with pH between 4.8-5.3 were able to neutralise and partly detoxify aluminium and heavy metals, whereas most clear-water lakes within this pH interval were up to now unable to recover naturally from long-term acidification. Biotic recovery was studied by monitoring a large number of limed and some naturally recovered lakes, since trajectories of limed and natural recovered sites seemed to follow similar pathways in the same geographical regions. Recovery was most easily identified at low to medium fish predation intensity, with sufficient predation to eliminate or keep in check most invertebrate predators, but with less predation than decisively influencing zooplankton community structure. Fish species producing intensive predation effects, such as Eurasian perch, Arctic charr, whitefish, and planktivorous brown trout, impeded interpretation of biological observations during recovery. Local lake communities influenced trajectories and time scales of the recovery process. Most species possessed sediment egg-bank or internal species refuge, speeding up reappearance of local populations and their build-up to pre-acidic densities. Chronically acidified lakes and lakes totally dependent upon external refuges for species invasions, probably are the last to recovery biologically to pre-acidic ecosystem structures.

Modeling Invertebrate Recovery of ACidified Lotic /lentic Ecosystems (MIRACLE)

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The proposed model will predict the development/composition of invertebrate populations following reduced acid deposition and increased pH and ANC in watersheds. For modeling the recovery, including time lag, we need information about the improvement in water chemistry (starting and endpoint), distance to source localities (refugia) of sensitive species, inter - and intra watershed dispersal, life cycle/fecundity and water chemistry variation in relation to critical limits (responds curves) of the species. Species composition of key invertebrates is available from more than 50 different watersheds in western and southern Norway. The number of sampling sites within each watershed is between five and twenty. Water chemistry exists from one or more sites in most of the watersheds. From this database we can calculate the probability of recording a species/community in relation to water chemistry.

The recovery of sensitive invertebrates will depend on the following main stages:

1. Time needed to achieve the target chemistry after reduction of acid deposition. (The endpoint of water chemistry will either be above, vary around or be below the critical limits, of species).

2. Time needed for dispersal of the species to the watershed (inter watershed dispersal)

3. Time needed for occupation of suitable sites (internal dispersal)

4. Time needed for reaching a stage of natural fluctuations

Stage 1
The initiating parameters are the improvements in water quality, which can be predicted through the MAGIC model. (The chemical starting point is very important, as this will determine the fauna before the recovery starts. Serious damaged ecosystems containing very tolerant species recover more slowly than systems still having some sensitive species). The chemical endpoint will give information about the time needed to achieve the target chemistry and consequently an estimate of the starting time for sensitive fauna to recover. At this point chemistry should be compared with the critical limits of different species. The water quality can be:

      i)   below the critical limits of the species and excluding them,
      ii)   vary around the critical limit, giving an on/off situation of species,
      iii)   or above the critical limit, allowing sensitive species to recover.

Stage 2
Reappearance of sensitive species depends on their dispersal ability, distance to source populations and inter watershed dispersal. Fast dispersal occurs among winged insects. Slow dispersal is among invertebrates with the whole life cycle in water like molluscs, Oligochaeta etc. The lowest dispersal rate is probably among organisms fulfilling their life cycle in deep waters. However, for the different types there are variations. In lotic systems recovery from source localities can occur immediately through drift of organisms.

Stage 3
When the pioneer individuals have been established, the intra watershed dispersal starts. Again winged insects can spread out rapidly, while molluscs etc. have to move or be transported in water or sometimes by birds through air. The drift of invertebrates in running water secures a rapid dispersal

downstream. When all or most of the suitable habitats have been occupied by the species, stage 3 is finished. This stage can be define and is proposed to be the most suitable in a predictive model.

Stage 4 (optional)
Time needed for reaching the stage of natural fluctuations is difficult to predict or measure. However, this is also of interest in the recovery process, but will depend on biological interactions as well as changes in physical and chemical factors independent of recovery from acidification. For the most common and wide spread species in running water the time needed to achieve this stage seem to be close to that of stage 3. For other species this will be difficult to define and measure, especially among species with many generations per year and species vulnerable to predation which is especially pronounced in lakes.

We propose that MIRACLE in the beginning focus on the time needed for achieving stage 3. If good model(s) for evaluations of stage 4 come up, they can easily be added to MIRACLE.

# Recovery processes in acidified Finnish headwater lakes (REPRO)

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The substantial reductions in air pollutant emissions have resulted in clear signs of recovery in sensitive surface water ecosystems in certain parts of Europe and North America. In Finland, recovery from acidification have been recorded in water quality (Mannio 2001) and in fish populations of some acidified lakes (Nyberg et al. 2001, Rask et al. 1995, 2001). Generally, scientific evidence on the recovery of biological systems in Finnish headwater lakes is currently sparse or non-existent. Therefore, the current recovery project (REPRO), 2001-2003, was initiated, by the financial support of the Academy of Finland, in the lead of Finnish Environment Institute (coordinator Martin Forsius, martin.forsius@ymparisto.fi) and in the partnership of the University of Helsinki, University of Jyväskylä, and Finnish Game and Fisheries Research Institute. The main aims of the project are to:

- Identify the character of lakes and processes behind different recovery patterns in lake chemistry
- Quantify the changes in selected biological indicators (fish, macrozoobenthos, littoral periphyton) by re-sampling selected lakes (30 to 60) of HAPRO-project (1985-1990)
- Quantify the dose-response functions and treshold values between lake chemistry and biological changes, in circumstances of decreasing acid deposition and expected recovery
- Examine the relationships between changes in deposition chemistry vs. lake chemistry and biological change, and identify how the biological recovery is connected to chemical recovery
- Extrapolate the results to a large regional scale using lake survey data

The first clear signs of recovery in fish populations of acidified Finnish lakes were recorded in early 1990s (Rask et al. 1995). In the figure below, some examples of the recovery are given, inluding the decrease of mean weight of perch (*Perca fluviatilis*) after appearance of new strong year-classes (A), and the decrease of perch growth due to the same reason (B). Some signs of recovery have been recorded also in roach (*Rutilus rutilus*) populations, given here as mean number of roach in one NORDIC survey net (C). According to mark and recapture monitoring, the perch population of a small lake in Evo recovered in the mid 1990s after appearance of strong year-classes in 1991-1993 (D).
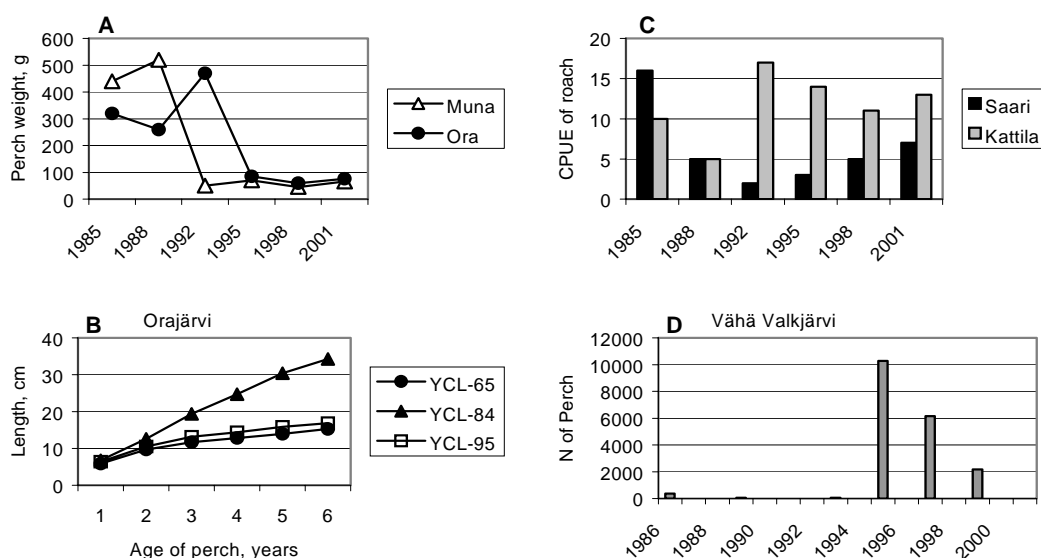
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ANC-RECOVERY: What is the chemical threshold for natural reproduction of brown trout during recovery from acidification. Part 1: Background.

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The main goals of the ANC-RECOVERY project (2001 – 2003) are:
- To find the relation between an increased ANC and time for re-establishment of natural reproduction in brown trout (*Salmo trutta* L.) populations in Norway, i.e. find ANC_{limit}
- To test the new monitoring technology based on the "passive sampler", the DGT-technology (Diffusion Gradient in Thin films) for bio-available metals (aluminium (Al), iron (Fe) etc.), and relate these to metal accumulation onto fish gills and changes in physiology and mortality of brown trout.

The project is focuses on water chemistry and fish populations in three lakes in Norway all of which have a long "acidification history": Lake Saudlandsvatn near Farsund, Lake Tveitvatn in the Tovdal River, both in southernmost Norway, and Lake Langtjern, southeastern Norway. Ecotoxicological experiments in inlet and outlet brooks at time of spawning (October) and hatching (April) are combined with standard testfishing (gillnet series and electro fishing). ANC calculated by MAGIC demonstrates a time lag to population response of 10-15 years (Fig. 1a).

At Lake Saudlandsvatn, the population decline from late 1970's to early 1990's (Fig 1c) was mainly caused by low survival rate of spawned egg and fry at the major spawning and nursery area at the lake inlet, Fig.1b. In March 2002, the egg mortality was 55% in the inlet stream, compared to 5% at the outlet.
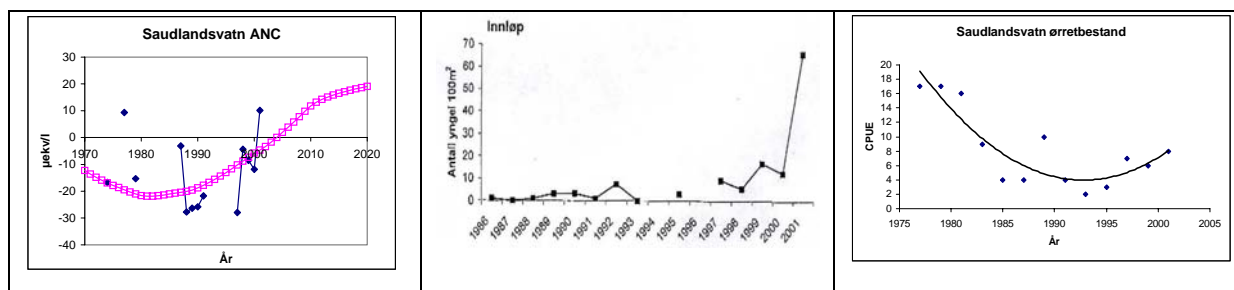

Figure 1. Modelled ANC for Lake Saudlandsvatn 1970-2020 (a), numbers of fry pr. 100m^2 in the inlet brook (b), and catch per unit effort (CPUE) 1977-2001 (c).

The brown trout population in Lake Tveitvatn became barren in the mid 1980s, but started to reappear in the mid 1990s and apparently started to reproduce during the last 3-4 years, Fig 2a.
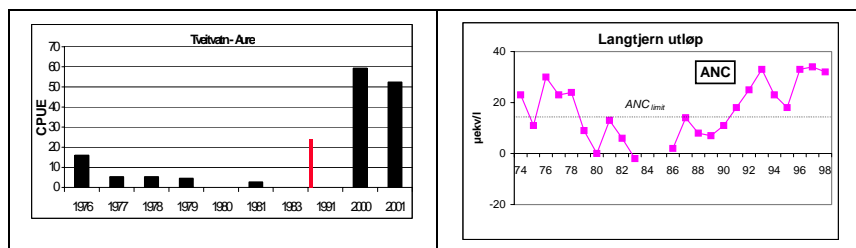

Figure 2. Catch per unit effort of brown trout in Lake Tveitvatn 1976-2001 (a), and measured ANC in runoff from Lake Langtjern 1974 – 1998 (b).

Microcrustaceans (Cladocera and Copepoda) as indicators of acidification and biological recovery of lakes

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The monitoring programme "Monitoring of long-range transported air-pollution" includes studies of pelagic and littoral microcrustaceans from approximately 100 lakes in Norway. The aim of the programme is to evaluate the acidification status and trends following improvements in water quality. In order to assess the acidification status of a lake, knowledge about the expected natural conditions is necessary. Studies of comparable softwater lakes in less acidified areas (reference lakes) and palaeolimnological studies from the acidified lakes show several points of resemblance with acidified lakes concerning the microcrustacean. The fauna of these reference conditions is characterised by low species richness and a low ratio of acid sensitive species.

We identify littoral microcrustacean indicators of acidification in two surveys of Canadian Shield lakes conducted 10 years apart. We found a total of 90 cladoceran and copepod species with richness increasing several fold from acidic to non-acidic lakes. The fauna of the non-acidic lakes differed between the surveys. The 1987 survey employed sediment emergence traps, and caught more littoral taxa, than the more recent, net-haul-based survey. Similar faunas were identified in the acidified lakes in both surveys, and several good indicator species were identified. For example, *Acanthocycops vernalis* was restricted to lakes with pH <6. *Sinobosmina* sp. was very common but only in lakes with pH > 4.8. *Tropocyclops extensus, Mesocyclops edax,* and *Sida crystallina* were commonly found but only at pH > 5, and *Chydorus faviformis* only at pH >5.9. These indicators showed promise in gauging the early stages of recovery from acidification in three lakes that were included in both surveys.

Chemical and biological recovery was studied in 22 acidified lakes in Killarney (NLRS), Canada. The between-lake variation in pH, aluminium and ANC was 4.7 - 7.5, 4 - 462 μg l^{-1} (total Al) and –74 - 442 μeq l^{-1}, respectively. Substantial changes in the water quality have been recorded in these lakes during the last decades, and also during the three years of study there have been small but unambiguous improvements in variables related to acidification. Multivariate methods were used to relate crustacean composition (absence/presence) to water quality and other environmental variables. Of 16 variables tested, pH showed strongest correlation with the main gradient in the crustacean composition and explained about 20% of the variance in the species data (CCA). pH, elevation, lake size, conductivity, DOC, Al and fish species richness together accounted for about 60% of the total variance. Stronger species-environment correlation was obtained in analysis that took into account the between-year differences compared with analysis based on the total species recorded during the study combined with the median values of chemical variables.

Our analyses are based on data of pelagic and littoral crustaceans from 23 lakes in Killarney Provincial Park along a pH-gradient from 4.7 to 7.5. Included in the study are recovering acidified lakes (N=19) and non-acidified reference lakes (N=4).

 Crustaceans: Sampling was conducted between 1997 and 1999. One of the lakes was studied for one year (1997), ten lakes for two years (1998-99) and twelve lakes for three years (1997-99). Each year there have been two sampling periods, May/June and September/October. From the littoral part of the lake there have been taken two samples, one from stony substrata and one from the vegetation. The sampling of pelagic crustaceans is comparable with Sprules (1975), Loche et al. (1994) and Holt & Yan (2001).

Environmental data: Lake water has been sampled as surface grabs or composite tube samples by the Cooperative Freshwater Ecology Unit in Sudbury (CFEU). Analyses for pH and alkalinity were performed at the CFEU. All other analyses were done at the Ministry of Environment and Energy (MOEE) laboratory in Toronto (Snucins & Gunn 1998). For this study, we used data obtained from water samples taken during October/ November, after fall turnover in these lakes. Environmental variables included in the analyses were as follows: pH, ANC, total aluminium, labile aluminium, dissolved organic carbon, calcium, conductivity, total phosphorus, Secchi depth, lake area, average lake depth, maximum lake depth, elevation, fish species richness separated into three groups according to feeding habits (planktivorous, littoral crustaceans, macroinvertebrates).

Analyses: Simple and multiple regression analyses were used to relate the number of microcrustacean species (pelagic and littoral) to environmental variables. In multiple regression, the predictive power of the model parameters is given by the adjusted coefficient of determination (r^2). The correlations between species richness and environmental data were analysed for two separate subsets including all lakes: one subset representing cumulative species records, and one subset representing yearly species records (see Schartau et al. 2001). Microcrustacean species richness (range 13-53 species/lake) was positively correlated with fish species richness, DOC, pH, ANC, tot-P, and lake area and negatively correlated with aluminium, Secchi disk readings, and elevation (Schartau and Walseng, *unpublished*). Fish species richness and average depth explained up to 79% of the variance in species richness. Fish species richness and the acidity related variables were highly correlated.

Direct gradient analyses with forward selections (CCA: Canonical Correspondence Analysis) were used to provide an overview of the relationships between the sample sites, based on records of presence/ absence of microcrustacean species, and environmental variables. The analyses were performed with help of the program CANOCO version 4 (ter Braak & Smilauer 1998). Downweighting was applied to all species with frequency below the median frequency (Eilertsen et al. 1990) to reduce the effect of unusual samples on the ordination (ter Braak & Smilauer 1998). All of the environmental data except pH, lake depth and fish species number were transformed (Ln (x+1)) to improve normality. The correlation between the microcrustacean composition and environmental data were evaluated for different subsets (see Schartau et al. 2001). For subsets where each data entry represents separate years our aim was to control for autocorrelation in time and to use the ordination to focus on effects of acidification and other explanatory variables. The effect of time (sampling year) was first tested and then removed by specifying time as covariable. Each environmental variable was tested by Monte Carlo permutation significance test with 199 unrestricted permutations (ter Braak & Smilauer 1998) before adding it to the model. Sequential Bonferroni adjustments of the significance level were performed for all multiple tests (Rice 1989). In the CCA of the microcrustaceans composition was strongly correlated with pH (13-16 % of the total variance) and other acidity-related parameters like ANC (9-15 %) and aluminium (10-16 %) (Schartau et al. 2001).

Patterns in the distributions of microcrustaceans of the different sites were summarised by Detrended Correspondence Analysis (DCA) using the program CANOCO. The aim of DCA-ordination is to arrange sites in a low dimensional space such that sites which are geographically close correspond to sites which are similar in species composition. Sites that are far apart correspond to sites that are dissimilar in species composition. The correlations between the environmental variables and the species-derived sample scores along axis 1 were tested by Spearman correlation tests. Axis 1 was strongly correlated with pH (r^2=0.89 for the cumulative species records). The species score thus provide information about which species are associated with acidic and neutral lakes respectively. For our purpose we desired to divide the species in five groups of equal size depending on their position along axis 1, starting with group I in the acidic end, ending up with group V in the opposite end of axis 1. The groups are; acidic (I), weakly acidic (II), indifferent (III), weakly sensitive (IV) and sensitive (V). It is important to stress that these groups are not truly ecologically defined. The results are presented in Walseng & Schartau (2001).

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Defining biological reference conditions for acidified lakes: the modern analogue approach

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Evaluating the recovery of presently acidified lakes towards a target based on their pre-acidification status is a difficult task. Few biological records exist that could potentially be used as reference conditions for these remote, upland fresh waters. Analogue matching is a palaeoecological technique used most widely in the field of palynology. In analogue matching the dissimilarity (computed using a suitable dissimilarity coefficient) between a pre-acidification sub-fossil assemblage from an acidified lake and a series of modern assemblages taken from a range of lakes is calculated. The lakes whose sub-fossil species assemblage is most similar to that of the reference assemblage from an acidified lake are known as modern analogues.

Using these modern analogues we may infer from them the hydrochemical conditions likely to have occurred prior to the onset of acidification in the presently acidified lakes. More importantly, the presence or absence of those aspects of the flora and fauna that are not preserved in lake sediments can be inferred for the reference conditions of acidified lakes from the species found in the modern analogue lakes.

A series of 83 upland, acid sensitive fresh waters was identified and the sub-fossil remains of the *Cladocera* were counted in the surface sediment samples of each lake. These were combined with the previously counted diatom samples from the same set of lakes to create a modern species training set. Hydrochemical and physical characteristics of each lake were also compiled.

Samples that represent the pre-acidification period in 10 lakes from the UK Acid Waters Monitoring Network (UKAWMN) were analysed for diatom and cladoceran remains. The dissimilarity between each sample from the UKAWMN lakes and every lake in the training set was calculated using the squared chord distance coefficient. Those lakes in the training set with a squared chord distance to a UKAWMN lake of less than a critical value were chosen as modern analogues for that lake.

Close modern analogues were identified for 7 UKAWMN lakes. The majority of these modern analogues are located in North and Northwest Scotland, areas of low sulphur and nitrogen deposition. Comparison of the hydrochemical characteristics of the UKAWMN lakes to those of the modern analogues showed that the modern analogues had higher lake water pH and alkalinity levels and lower aluminium concentrations. Ionic strength and calcium concentrations in the analogue lakes were similar to observed values in the UKAWMN lakes.

The results of this work indicate that the analogue matching approach using diatom and cladoceran remains is a simple, robust and reliable method of identifying modern analogues for acidified lakes in upland areas of the UK.

Recovery of Benthic Invertebrates and Fish in Killarney Lakes

Ed Snucins

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Between 1997 and 2002 recolonization of two acid-damaged lakes by three species of benthic invertebrates, two mayflies (*Stenonema femoratum, Stenacron interpunctatum)* and an amphipod *(Hyalella azteca*), was monitored at the level of patchy habitats within lakes. This study found that, in cases when timing of the events could be estimated, species re-establishment occurred less than 4-8 years after water quality recovered to species pH thresholds. Dispersal of one mayfly species to all habitat patches was complete three years after colonization of the smallest lake (11 ha) but will take longer in the largest lake (189 ha). The time lag from pH recovery to re-establishment and subsequent dispersal of mayflies to all habitat patches within a lake was estimated to be as much as 11 to 22+ years. Mayfly densities increased after establishment in a lake, but stable endpoints were not yet apparent after six years. In contrast with the rapid between-lake dispersal of invertebrates, the return of fish to isolated lakes has been slow and dependent on stocking. Monitoring during 2001 found that some stocked populations of smallmouth bass (*Micropterus dolomieui*) and lake trout (*Salvelinus namaycush*) are reproducing, but that recovery rates differ between species. Reintroduced smallmouth bass populations achieved abundance similar to undamaged reference lakes 3-5 years after stocking or recovery of water quality to the species pH threshold. On the other hand, reestablishment is a much slower process for lake trout, with evidence of successful reproduction obtained 5-15 years after water quality recovery and very few natural recruits present.
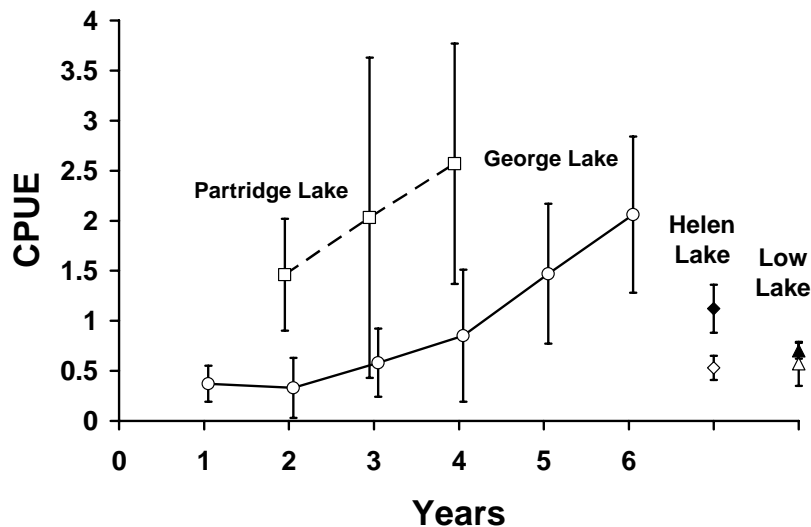
Plot of mean catch-per-unit-effort (CPUE) (number/minute) in May 2002 of *S. interpunctatum* in George Lake and Partridge Lake versus number of years since presence detected at the sites. Reference lake (Helen, Low) values are also presented for *S. interpunctatum* (open symbols) and *S. femoratum* (closed symbols). Bars indicate 2 standard errors.

Differential trajectories of resistance and resilience in an experimentally acidified lake ecosystem

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Ecosystem resistance depends on tolerant species compensating for sensitive competitors, while resilience (i.e., recovery rate) relies on the re-establishment of extirpated and suppressed species and ecological processes. Here we present evidence from a whole-lake acidification experiment (Lake 302S, Experimental Lakes Area, Ontario, Canada) of contrasting trajectories of resistance and resilience across trophic groups. Diverse and fast-growing algal and rotifer assemblages with high dispersal potentials over-compensated for 30 – 80% declines in species richness, resulting in increased total biomass during acidification from pH 6.8 to 4.5 between 1982 and 1990. Further increases in algal and rotifer biomass during early chemical recovery have since declined to near pre-acidification levels within ten years (1990 –2000) of recovery to pH 6.5. In contrast, less diverse crustacean zooplankton and fish assemblages showed significant declines in total biomass in response to changes in species richness during acidification. Thereafter, total cladoceran biomass exceeded pre-acidification levels by ~300% during early recovery to pH 5, but has since shown an equally dramatic decline. Total copepod biomass increased steadily during chemical recovery, and at pH 6.0, exceeded pre-acidification levels by ~100%. Fish species richness and total abundance showed the least resilience, and both remain suppressed despite the reappearance of cyprinids and the reintroduction of whitefish.

Consequently, trophic groups have shown differential recovery rates, resulting in striking differences between biological recovery and acidification trajectories (see figure below). Our findings demonstrate that modelling of recovery trajectories cannot be based on simple reversal of observed patterns of resistance in acidified lake ecosystems. Biotic factors, such as compensatory species dynamics, dispersal/colonization potential, competitive exlusion, founder effects, and trophic interactions must also be considered.
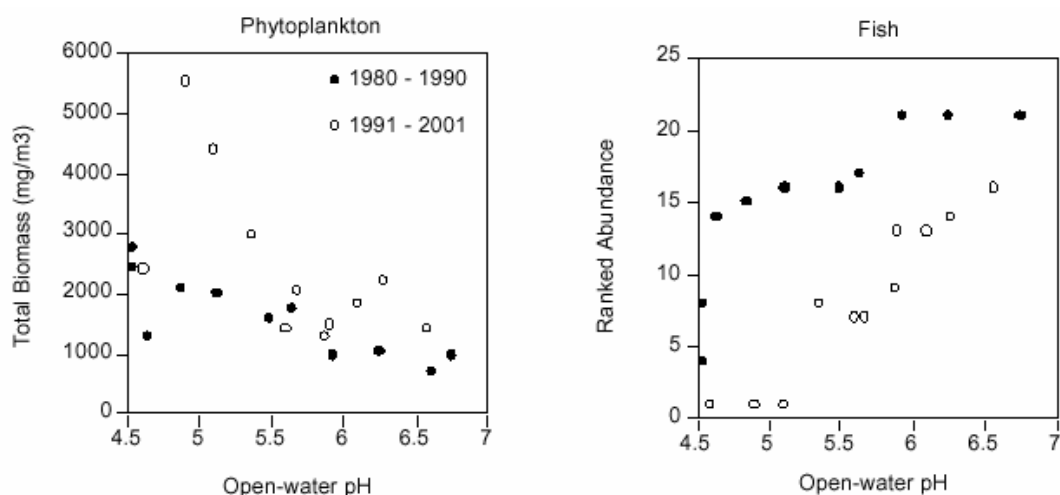
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