Swedish University of Agricultural Sciences
Department of Forest Ecology
Graduate Thesis in Soil Science 2004

The effects of water chemistry on fish species distribution

-

a comparison between isolated and connected lakes in northern Sweden

Johanna Öhman

Supervisors: Ishi Buffam and Hjalmar Laudon

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Forest Ecology
SE-901 83 UMEÅ

Stencilserie No. 103

ISSN 1104-1870
ISRN SLU-SEKOL-STL-103-SE

Sammanfattning

Den här studien behandlar sambandet mellan vattenkemi och fiskarters spridning i fyrtio små kustnära sjöar i Västerbotten. Sjöarna provfiskades sommartid och vattenproverna togs främst under vintern. Tjugo av sjöarna var isolerade och saknade därmed till- och frånflöden medan de andra tjugo hade ett vattendrag som ledde direkt till havet. Den centrala frågan för studien var ifall kemiska variabler bidrar starkare till fiskarters utbredning i isolerade sjöar eftersom de inte kan återkoloniseras när en art har dött ut. Så mycket som 48 % av variationen i fiskarternas utbredning i isolerade sjöar kunde förklaras av metanförekomst och aciditet. Metan är inte toxiskt i sig utan indikerar syrefri miljö. I sjöar med länk till havet var sjöarea den enda faktor som bidrog signifikant till fiskarternas utbredning och förklarade där 12 % av variationen. Vilka faktorer som styr utbredningen varierar med fiskart. Metan indikerade att utbredningen av gädda och abborre i isolerade sjöar styrs av syrebrist. Utbredningen av ruda och spigg styrs i stället av predation och aciditet. I sjöar som kunde återkoloniseras var effekten av syrebrist inte lika stor. Gädda och abborre var vanliga även i sjöar som var syrefattiga under vintern och som en följd var utbredningen av ruda och spigg lägre i återkoloniserbara sjöar. Mört, gärs, braxen, löja och id förekom endast sparsamt i isolerade sjöar och det gick inte att hitta någon gemensam faktor som styrde utbredningen.

Abstract

The correlation between water chemistry and fish species distribution was examined in forty small, coastal lakes in northern Sweden. Lakes were fished in summer and water chemistry sampled mainly in late winter. Twenty out of the forty lakes were isolated from other water bodies and twenty had a direct connection to the sea. The central question of the study was whether water chemical variables play a greater role in isolated lakes, since these cannot be recolonized if a species once has become extinct. As much as 48 % of the variation in fish species distribution in isolated lakes was explained by methane and acidity. Methane is an indicator of anoxia and not a controlling factor in itself. In connected lakes, lake area was the only significantly contributing factor, explaining 12 % of the variation. Different fish species were controlled in their distribution by different chemical variables. Methane indicated that the distribution of pike and perch was controlled by anoxia in isolated lakes. The distribution of the anoxia-tolerant crucian carp and sticklebacks was instead controlled by predation and acidity. In connected lakes, the possibility of migration decreased the effect of anoxia radically making pike and perch common, depressing the distribution of crucian carp. A third group of fish containing roach, ruffe, bream, bleak and ide was rarely found in isolated lakes and no clear distribution pattern of that group was seen.

Contents

SAMMANFATTNING **1**

ABSTRACT **2**

CONTENTS **3**

INTRODUCTION **4**

MATERIALS & METHODS **6**

- STUDY LAKES 6
- FIELD MEASUREMENTS AND WATER SAMPLING 6
  - *Gradient lake* *7*
- WATER ANALYSIS 7
- FISHING 8
- STATISTICAL ANALYSES 9

RESULTS **10**

- ENVIRONMENTAL VARIABLES 10
  - *Vertical gradients of chemical variables* *11*
  - *Water chemistry in relation to the Swedish Environmental Quality Criteria* *12*
- GRADIENT LAKE 13
- DISTRIBUTION OF FISH SPECIES 14
- DISTRIBUTION OF FISH IN RELATION TO ENVIRONMENTAL VARIABLES 14
- DISTRIBUTION OF FISH IN RELATION TO ENVIRONMENTAL VARIABLES 15
  - *All lakes* *15*
  - *Connected lakes* *15*
  - *Isolated lakes* *16*
  - *Comparison between different measurements* *17*
  - *Grouping fish* *17*
  - *Fish groups in relation to chemical variables* *18*

DISCUSSION & CONCLUSIONS **20**

- ENVIRONMENTAL FACTORS CONTRIBUTING TO FISH SPECIES COMPOSITION 20
  - *Chemical factors* *20*
  - *Physical factors* *22*
- FISH ASSEMBLAGES IN CONNECTED AND ISOLATED LAKES 22
  - *Fish group 1 – crucian carp, three-spined and nine-spined stickleback* *23*
  - *Fish group 2 – pike and perch* *24*
  - *Fish group 3 – roach, ruffe, bream, bleak and ide* *24*
- CONCLUSIONS 25

ACKNOWLEDGEMENTS **25**

REFERENCES **26**

Introduction

Isolation of lakes due to land upheaval is an ongoing process in northern Sweden. It takes about 100 years for a bay to close and turn into a lake (Salonsaari 2002). Lakes formed can either be connected to other water bodies, or be totally isolated, thus not having the possibility of being recolonized by fish naturally. If a species is extinguished from an isolated lake, it might be extinct for all time, why fish assemblages of isolated lakes are results of a long history of factors effecting fish survival (Andersson 2001, Tonn & Magnuson 1982). Therefore, harsh environmental conditions ought to have larger impacts on fish species distributions in isolated than in connected lakes.

Freshwater fish communities are structured by biological, physical and chemical factors. Predation is perhaps the most important biological factor, while competition seems to be of less importance (Jackson *et al* 2001). Lake area and the length and gradient of connecting streams have been shown by Blom (2003) to be significantly important factors structuring fish species distribution in coastal lakes in northern Sweden. Blom also found isolated lakes to have fewer and different species than connected lakes. He found Crucian carp *Carassius carassius* to be the only species clearly more common in isolated lakes and suggested this could be explained by the species being susceptible to predation but tolerant to low concentrations of dissolved oxygen.

Reduction of dissolved oxygen (DO) in lakes was in 1970 considered the most severe anthropogenic impact on freshwater fishes (Doudoroff & Shumway 1970). Today, acidity is considered the single most predominant chemical factor. Concentrations of DO vary greatly between lakes and between seasons, especially in lakes of northern Sweden, which are covered with ice half the year. Winter depletion of oxygen is there due to oxidization of organic substances in combination, an input of oxygen-depleted ground water and no reaeration due to ice cover. Late winter is therefore the period when critical levels for fish survival might be reached (Chambers *et al* 2000). The demand for oxygen varies between species, but also between individuals and over time. Perch *Perca fluviatilis* has been shown not to survive DO concentrations under 0.2-1.4 mg/l while crucian carp only needs 0.0-0.1 mg DO/l (Doudoroff & Shumway 1970).

pH is also affected by the ice cover. An over-pressure of carbon dioxide (pCO_2) can build up during winter and as a result carbonic acid (H_2CO_3) is formed. The acidity of a lake in northern Sweden is however more a result of the input of organic substances and the ability to buffer (Laudon *et al* 2001). Acidity affects fish negatively in several different ways. Two of the most important effects are structural harm caused to the gills, which in turn causes salt loss, and reduced hatching due to inactivation of an hatching enzyme (Degerman & Lingdell 1993). Many chemical variables also interact, causing more harm together than separately. Precipitation of metals on the gills cause suffocation, and the lower the DO concentration the more the fish has to breathe and the more metals precipitate (Stenson *et al* 1993). Also, the solubility of metals depends on pH and since pH often is slightly higher in the vicinity of gills, at certain pH levels metals can dissolve in lake water and precipitate on gills (Stenson *et al* 1993). Organic matter can make condition both better and worse. It brings more organic acids into the water, but on the other hand it binds metals and organic toxicants (Andersson 2001).

Northern pike *Esox lucius* and perch *Perca fluviatilis* are probably the two species in Sweden most tolerable to acidity. Degerman and Lingdell (1993) found pike and perch to be able to reproduce down to pH 4.4-4.9, while the reproduction of the anoxia-tolerant crucian carp was disturbed at pH 5.5. They further found roach *Rutilus rutilus*, nine-spined stickleback *Pungitius pungitius* and three-spined stickleback *Gasterosteus aculeatus* to need pH over 5.5 to reproduce while ruffe *Gymnosephalus cernuus* could survive as long as pH was over 5.0.

The purpose of this study was to investigate what chemical factors play the greatest roll in controlling the distribution of different fish species in northern Sweden, 40 lakes were studied. Half of the lakes had no inlets or outlets, and half of them were linked directly to the sea by streams that fish could use for recolonization. Choosing lakes within a small size range and on a low altitude minimized the effects of physical parameters. Water chemistry samples were collected in late winter and in late summer to include both a period of extreme oxygen deficiency and a period when young fish are exposed to the water chemistry. Fish communities were surveyed in summer using three different methods designed to catch as many species as possible.

The central questions of the study were:

- What chemical factors are the most important for structuring fish communities in small coastal lakes of Northern Sweden?
- At what threshold values of these chemical factors are different fish species missing?
- Is there a difference in the strength of the relationship between different environmental factors and fish populations between connected and isolated lakes?
- How important are chemical factors in relation to physical factors?

Materials & methods

Study lakes

All of the forty lakes studied are situated near the coast of Västerbotten, Sweden, at 70° to 71.5° north. Coordinates are given in RAK: Rikets allmänna koordinatsystem, the coordinate system commonly used in Sweden (appendix 1). The lakes are found in a boreal landscape where the terrain is rather flat. Many lakes are surrounded by mires. All lakes are small with a maximum area of 30 ha and a maximum depth of 5.5 m. Twenty lakes are connected by streams directly to the sea with no other lakes in between. The other twenty are not connected to any other water body and therefore fish can normally not colonize these lakes. The two types of lakes will be referred to as connected and isolated, respectively. The lakes were chosen and studied by Blom (2003) and all fulfil the following criteria:

- Altitude does not exceed 35.2 m.
- Maximum depth is not under 0.9 m.
- Introductions of species by man have not been made as far as known.
- Migration from the Gulf of Bothnia to the connected lakes should be possible (i.e. no migration barriers)
- Migration to isolated lakes should, under normal conditions, not be possible from any other water body.

Land upheaval, due to isostatic rebound, is in Västerbotten up to 0.8-0.9 cm per year (Blom 1993), resulting in the lakes studied being 200-3500 years old. Since the degree of isolation was studied at one occasion one summer, it cannot be excluded that extreme weather can have made recolonization possible on occasions in the past. Birds and humans might also have helped fish recolonize isolated lakes. Apart from the criteria above, the lakes were chosen to make the two groups as similar as possible. Small, connected lakes being too shallow to survey and large isolated lakes not existing in the region complicated this. The average depth was 2.3±1.1 m and 1.7±0.7 m, and the average area 13±7 ha and 6±4 ha for connected and isolated lakes, respectively (appendix 2).

Field measurements and water sampling

The lakes were sampled for water chemistry twice. The first sampling occasion was March 24 to April 14 of 2004 when the lakes were still covered with ice. Water samples were taken from the deepest area of the lake and field measurements performed in the same location. The deepest area was located by studying the surrounding topography. A hole was drilled and the depth measured from the top of the ice. The water level was in most cases on the same level as the ice surface. If the depth was more than 75 % of the maximum depth measured by Blom (2003), that hole was used for the measurements. Otherwise the procedure was repeated until the deepest area was found. In a few lakes, the depth found by Blom (2003) was not managed to be located and therefore the largest difference between maximum depths was 50 %. In two lakes the ice was partly melted in the deepest area, why the hole used for samling was drilled closer to shore. The first sample to be collected was for meassuring over pressure of carbon dioxide (pCO_2) and for measuring methane (CH_4). An air-bubble free water sample was taken approximately 0.4 m from the water surface using a 20 ml syringe. The sample (15 ml) was then squirted into a sealed 60 ml glass serum bottle containing N_2 gas at atmospheric pressure.

Dissolved oxygen concentration, pH, conductivity and temperature were then measured in the field in a gradient every 0.5 m from the top of the ice to the bottom of the lake. All instruments used were from WTW (Wissenschaftlich-Technische Werkstätten); for pH a TA-197 sond and instrument was used and for conductivity and dissolved oxygen a Multi 340i instrument was used with the sonds TA 197-LF and TA 197-Oxi respectively. All instruments were calibrated daily. Water samples were collected using a Ruttner water sampler and then transferred with multiple rinses to an acid-washed 250 ml HDPE plastic bottle. In lakes with an established thermocline, samples were collected above and below that layer. The shallow sample was in most cases taken at 1 m depth and the deep sample was taken 0.2-0.5 m from the bottom, with even 0.5 m-intervals between the samples. In very shallow lakes only one sample was taken, when needed on 0.7 m depth.

The second sampling period was in the late summer of 2004. Samples were collected using a 7 m pole from the shore. An acid-washed 250 ml HDPE plastic sampling bottle was attached to one end of the pole and the bottle was filled close to the bottom of the lake. Water field pH was measured within approximately 2 m of the shore, using a portable pH meter from Mettler Toledo; pH 1120.

Figure 1. Gradient lake with sampling locations marked.

Gradient lake

To study spatial variance in winter chemistry within a single lake, lake Degersjön was chosen. Lake Degersjön is heterogeneous, surrounded by small hills, mire and has both inlets and an outlet. Eight holes were drilled to form a gradient along the lake, each hole in an area with a different environment. (Figure 1)

1. Close to the outlet, which was without ice cover
2. Between the inlet and the outlet
3. Close to a hill on the eastern shore
4. The deepest spot in the lake
5. By the inlet from the mire
6. Close to a hill
7. Very shallow, protected from inlets and mixing of water
8. Very shallow, surrounded by a mire that had a small inlet

Water analysis

Upon returning from the field, water samples were subsampled for analysis of various solutes. pH was measured immediately at the Swedish University of Agricultural Sciences Department of Forest Ecology in Umeå using a Ross 8102 combination electrode (ThermoOrion). Samples for aired pH were stored cool until analysis at the accredited laboratory at the Department of Environmental Assessment, Swedish University of Agricultural Sciences in September 2004. The water samples were first aired for two minutes with a N_2/O_2 gas mix correspondent to that of the atmosphere, with an addition of 330 ppm CO_2. pH was then measured, the method following the Swedish standard SS 028122-2.

Samples for absorbance and dissolved organic carbon (DOC) analyses were filtered at 0.45 μm (mixed cellulose ester single use syringe-driven membrane filter). Samples for DOC were frozen until analysis, while absorbance samples were kept cool. Absorbance was measured at Örebro University on 0.45 μm membrane-filtered samples at 254 and 420 nm in a 1 cm quartz cuvette using an Agilent UV-VIS spectrophotometer equipped with diode array detector. DOC was analyzed at Örebro University using a Shimadzu TOC-V_{PCH} analyzer. Samples were acidified with ultrapure 2 N HCl (1 % v/v) and sparged to remove inorganic carbon, followed by combustion/catalytic oxidation and analysis as CO_2 by NDIR. Replicate injections (2-4) ensured a coefficient of variation <5 % or standard deviation <2 mg/l for all samples.

Samples for dissolved elemental analysis (Al, Fe, P, K, Mg, Na, Ca) were preserved with ultrapure HNO_3 (1 % v/v) and stored cool until analysis using ICP-OES (inductively-coupled plasma optical emission spectroscopy) at Stockholm University Department of Geology and Geochemistry. Base Cation (BC) concentration was calculated as the sum of K, Mg, Na and Ca expressed as μeq/l of charge.

Dissolved gases (CO_2 and CH_4) were analyzed at the University of Gothenburg using a Varian 3800 Gas Chromatograph equipped with flame ionization detector (FID) after the method of Klemedtsson *et al* (1997). Prior to headspace analysis, the water samples were acidified to pH 2-3 with ultrapure 30 % HCl (0.2 % v/v) and allowed to equilibrate at 20 ºC. Total Inorganic Carbon (Tot-IC) was calculated from measured headspace CO_2 of the acidified samples. Bicarbonate (HCO_3^-) for the lake water samples was calculated from Tot-IC and measured pH using standard carbonate equilibria equations (Stumm & Morgan 1996). The partial pressure of CO_2 (pCO_2) in the original sample was calculated using Henry's law for gas/liquid equilibria (Stumm & Morgan 1996).

Fishing

Three different methods were used for fishing in order to catch as many fish species as possible. In the summer and early fall of either 1999 or 2002, each lake was fished with multi mesh size gill nets. The two nets used were made up of twelve sections with mesh sizes ranging from 5 to 55 mm. One was placed near the deepest part of the lake and the other in the littoral zone to cover both habitats. Both nets were set at the bottom and were 1.5 m deep. In very small, isolated lakes only one net was used. The nets were left over night (Blom 2003, Lindgren 2001).

Northern pike *Esox lucius* is difficult to catch using gill nets (Ericson *et al* 1996). In order to determine the presence or absence of pike, complementary spinning rod fishing was performed. Two persons fished for one hour in all connected lakes in August-September of 2002 (Blom 2003) and in all isolated lakes in July-August of 2004.

Many small, littoral fish species as well as fry do not easily get caught in gill nets. Therefore, in July-August of 2004, all lakes were fished again using small detonations. The detonations affect individuals smaller than 10-15 cm within a radius of two meters. They either die or become unconscious and often float to the surface. The fishes affected by the explosion were then collected using a landing net. Ten explosions were set off in each lake and the detonation spots chosen to cover as many different habitats as possible. Detonation depth varied with the depth of the lake, from approximately 0.1 m to 2.5 m. All shots were detonated from shore, using a 7 m fishing rod to reach out. The detonation caps used were 7.8 m long Nonel®LP, lit using Nonel DynoStart 2, both products from Dyno Nobel Sweden AB.

Statistical analyses

18 different variables were measured in the lakes, including 5 physical and 13 chemical variables (table 1). In lakes deep enough, all variables apart from CO_2, CH_4 and total inorganic carbon (IC) were measured at two depths in winter. pH was also measured in summer. This resulted in up to 32 physical and environmental variables being included. Prior to analysis, all variables, except pH, were log 10-tranformed to meet the assumption of normality.

The data was analyzed using several different methods. First of all, multivariate analysis was used to correlate presence or absence of each fish species to environmental variables. For this, the Canoco for Windows 4.5 was used. Within the Canoco program, Canonical Correspondence Analysis (CCA) was used since the species data was unimodally distributed. Running the CCA, downweighting of rare species was used for all analysis since some species were rare and others common among the lakes. First, all 32 variables were used as potential predictors for fish distribution and forward selection was used to choose which variables should be included in the analysis. All variables that contributed significantly to the ordination were included, after the significance level had been Bonferroni-corrected. Apart from the significant factors, remaining variables explaining more than 4% of the variation in fish distribution were included. However, only one measurement of each variable was used. pH was measured at four occasions and most variables at two depths. Different measurements of the same variable were highly co-correlated in all cases and therefore only the first measurement of each variable to be included according to the forward selection in the Canoco program was included in the analysis. Remaining measurements of the same variables were excluded even though some of them did explain over 4 % of the variation. The test was run for all lakes together, as well as for connected and isolated lakes separately. After that a second series if CCA analysis was run, following the same procedure, but only including chemical variables.

In order to be able to study the demands and preferences of species rarely found in the lakes of this study, all fish species were divided into groups of fish (FG). Correspondence analysis (CA) was used to show the distribution of fish species between the lakes and groups were formed based on that distribution. Canoco for Windows 4.5 with downweighting of rare species was used for this test as well. Binary logistic regressions were then used to study the relationship between each fish group and different environmental variables. The regressions were run on significant variables from the CCA, and on additional variables indicative of anoxia or acidity level. JMP 4.0 by SAS Institute was used for the binary logistic regressions. The binary logistic equation takes the form (Andersson 2001):

$$P = \frac{e^z}{1+e^z} \qquad \text{where } z = B_0 + B_1x_1 + B_2x_2 ... + B_nx_n$$

P = predicted probability for binary response variable = 1
X_n = value of respective predictor variable
B_n = a constant scaling factor for each respective predictor variable

Results

Environmental variables

Some of the chemical variables were found in different concentrations in connected compared to isolated lakes. Conductivity, base cations (BC), bicarbonate (HCO_3^-), total aluminum and phosphor (P) all occurred in higher average concentrations in connected lakes than in isolated. Connected lakes were also richer in DO, which apart from DO is shown by a lower concentration of methane (CH_4). The average DO concentration was low in both connected and isolated lakes, but among the connected lakes many also had comparably high concentrations. Average dissolved organic carbon (DOC) concentrations were higher in isolated lakes. Average pH was similar between the two lake groups, but the interval of pH values measured was larger for isolated lakes (figure 2). The difference between aired pH and regular pH measured on the same sample was on average 0.96±0.44 for the winter samples and slightly smaller, 0.54±0.34 for summer samples. Average values and standard deviation of each environmental variable is presented in table 1.

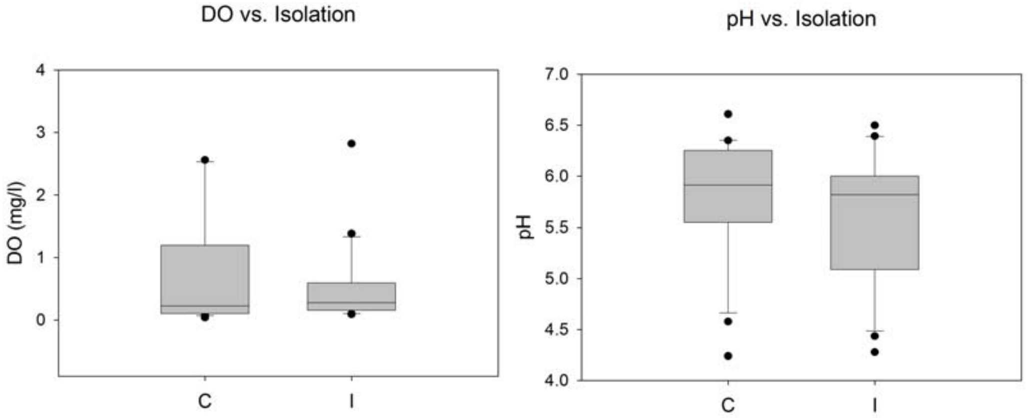


Figure 2. Box plots of the deep winter measurements of dissolved oxygen concentration and pH in connected vs isolated lakes. Average DO concentration is very low in both connected and isolated lakes, but many connected lakes also have comparably high concentrations. The range of pH is larger in connected lakes.

Variable	Summer /winter	All lakes		Connected lakes		Isolated lakes	
		Average	Standard deviation	Average	Standard deviation	Average	Standard deviation
Chemical parameters							
Absorbance 254 nm	W	1.028	0.794	0.909	0.654	1.146	0.915
Conductivity (µS/cm)	W	154	108	168	125	141	89
DOC (mg/l)	W	25.1	17.9	21.9	12.9	28.3	21.6
Tot-IC (uM/l)	W	874	526	865	548	883	519
HCO3- (uM/l)	W	165	215	175	232	155	203
CH4 (uM/l)	W	66	111	63	132	68	90
Al tot ug/l (ppb)	W	616	651	765	783	474	473
Fe tot ug/l (ppb)	W	3610	2544	3531	2730	3684	2424
P tot ug/l (ppb)	W	39.6	35.6	48.2	42.7	25.4	11.2
BC ueq/l	W	1039	633	1212	691	875	540
Oxygen (mg/l)	W	1.23	2.53	1.68	3.40	0.77	1.09
Temperature	W	2.21	0.80	2.29	0.82	2.13	0.80
pH field	W	5.94	0.58	5.97	0.54	5.91	0.64
pH lab	W	5.69	0.64	5.79	0.61	5.58	0.67
pH aired	W	6.69	0.89	6.76	0.91	6.62	0.89
pH field	S	6.21	0.68	6.20	0.65	6.22	0.73
pH lab	S	6.08	0.55	6.21	0.53	5.96	0.56
pH aired	S	6.62	0.71	6.77	0.72	6.48	0.68
Physical parameters							
Altitude (masl)		9.0	9.4	6.6	5.2	11.3	11.9
Distance to sea (m)		2473	3463	1700	1597	3245	4562
Lake depth (m)		2.0	0.9	2.3	1.1	1.7	0.7
Lake area (ha)		9.3	6.9	13	7.3	5.8	4.4

Table 1. Averages values of the variables were fist calculated for each lake, then for all the lakes. Values of pH were calculated without first transforming to H^+.

Vertical gradients of chemical variables

There was a clear vertical gradient in DO concentration in most lakes (figure 3). The concentration measured in the water column in the ice could be as high as 15 mg/l while close to the lake bottom the average was 0.68 and the maximum concentration 3 mg/l. Temperature increased with depth from an average of 0.7 to 3.9 °C. The pH gradient was not as clear but in shallow lakes a slight increase was observed from the shallowest to the deepest measurement. In deep lakes, the measurements taken at intermediate depths had a smaller range of pH than the shallow and bottom measurements. Both average and extreme values of conductivity increased with depth.

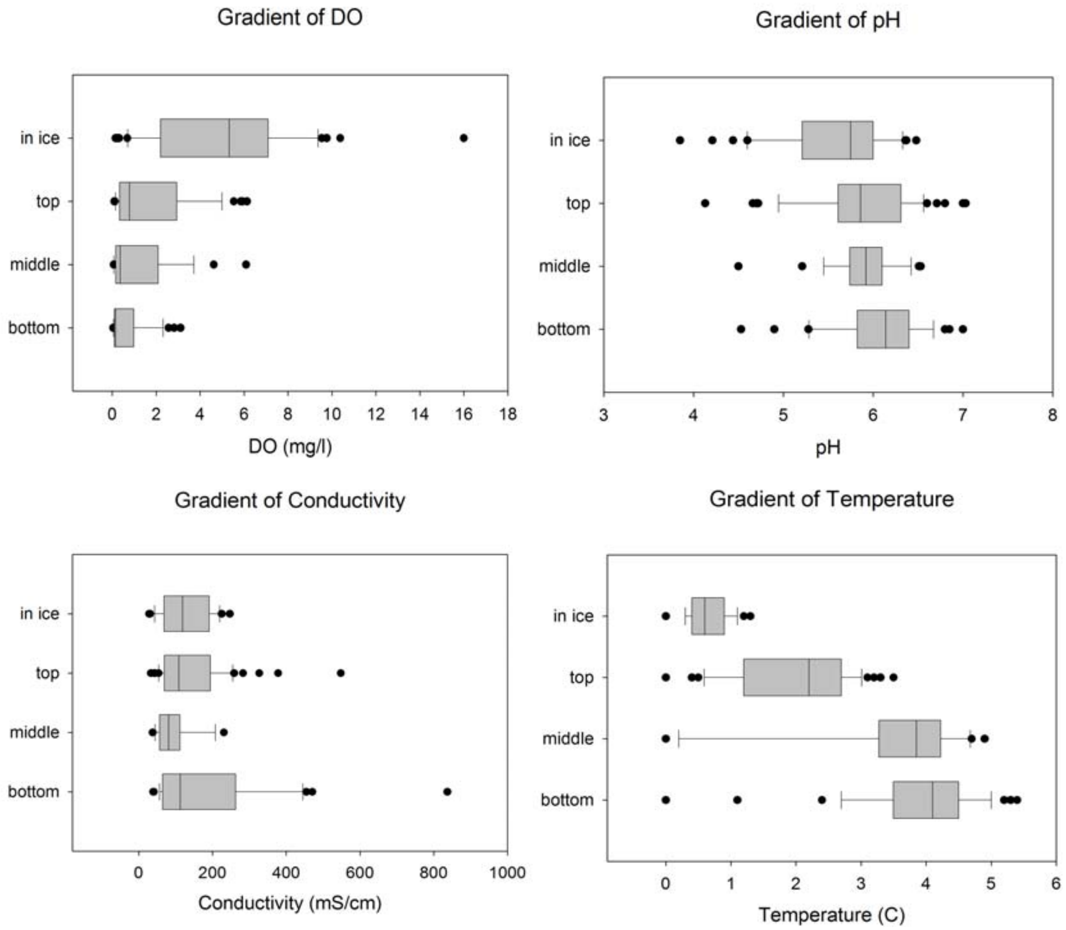


Figure 3. Gradients of dissolved oxygen, pH, conductivity and temperature in all lakes combined. The top measurements were taken 50 cm from the ice surface, in the water column in the ice formed after drilling. The second sampling depth was 0-50 cm from the ice bottom. The bottom measurement was 0-50 cm from the lake bottom and the middle measurement was taken between the top and the bottom samples. The group of top measurements includes all samples taken in depths fulfilling the criteria for both the top- and the bottom measurement, thus containing more samples than the bottom group. The middle measurement contains less data because not all lakes were deep enough for this measurement.

Water chemistry in relation to the Swedish Environmental Quality Criteria

The Swedish Environmental Quality Criteria (SEQC) are based on measurements in lakes throughout Sweden and the purpose is to provide a reference with which measured levels of water chemical parameters can be compared (Wiederholm 2000). The classification system consists of 5 classes where Class 1 represents the highest water quality and Class 5 the lowest. Dissolved oxygen is low in the lakes of the study according to SEQC (table 2). In isolated lakes, 18 out of the 20 lakes classify as anoxic or nearly anoxic. For connected lakes conditions are slightly better, but 14 lakes still belong to Class 5. Five lake would be classified as Class 5 no matter which measurement is used; DO or summer or winter measurements of pH. Twelve lakes would be classified as Class 5 by at least one of the three measurements. Out of those, three and seven lakes, respectively, are isolated. Absorbance values of the lakes are moderate according to SEQC and should not affect fish distribution negatively.

Classification system for the Swedish Environmental Quality Criteria		**pH**			**Dissolved oxygen**			**Absorbance**		
		All	C	I	All	C	I	All	C	I
Very good water quality	**1**	0 - 5	0 - 2	0 - 3	1	1	0	3 - 5	1 - 2	2 - 3
	2	1 - 5	1 - 2	0 - 3	0	0	0	9 - 10	5	4 - 5
Moderate water quality	**3**	9 - 10	5 - 8	2 - 4	0	0	0	12 - 16	9 - 10	3 - 6
	4	10 - 15	4 - 8	6 - 7	7	5	2	7 - 12	1 - 3	6 - 9
Very poor water quality	**5**	10 - 15	4 - 6	6 - 9	32	14	18	3	2	1

Table 2. Number of lakes categorized into the five classes of the Swedish Environmental Quality Criteria. The two numbers given for pH refer to a summer and a shallow winter measurement. The two numbers given for absorbance refer to a deep and a shallow measurement.

Gradient lake

There was little difference in pH level (5.83±0.06 for field measurements) between the eight sampling locations in lake Degersjön (figure 3). That indicates that the spatial variation in pH is small during winter and that the pH measurements probably are valid for each lake as a whole, even though pH was measured only in the middle of the lakes. Concentrations of dissolved oxygen varied more between the sampling locations, due to running water. This problem ought to be minimal in isolated lakes since they by definition do not have running water entering or exiting the lake. Connected lakes with inlets and outlets without ice cover ought to have varying oxygen conditions. The deepest part, where samples were collected, was in most cases located in the middle of the lake. In lakes that were clearly affected by incoming and outgoing streams, the area in the middle was usually affected and measurements were taken between that area and the shore. The measured DO concentrations in affected lakes should thereby be an intermediate value, somewhere between the extremes expected for other parts of the connected lakes. Conductivity was low throughout the lake except for the deep measurements of hole no 6 and 7 (figure 4).

Distribution of fish species

Ten fish species were caught in the lakes studied (table 3). In connected lakes, the most common ones were perch *Perca fluviatilis*, pike *Esox lucius* and roach *Rutilus rutilus*. In isolated lakes, the most common species were crucian carp *Carassius carassius*, pike and perch. Bream *Abramis brama*, bleak *Alburnus alburnus* and ide *Leuciscus idus* were found in few lakes, all of them connected, while three-spined stickleback *Gasterosteus aculeatus* was caught only in an isolated lake. Presence of fish species in each lake is presented in appendix 3.

Fish species	**% of connected lakes with each fish species**	**% of isolated lakes with each fish species**	**% of all lakes with each fish species**
Perch *Perca fluviatilis*	90	35	62.5
Northern Pike *Esox lucius*	85	40	62.5
Roach *Rutilus rutilus*	60	10	35
Crucian Carp *Carassius carassius*	25	50	37.5
Nine-spined Stickleback *Pungitius pungitius*	15	15	15
Ruffe *Gymnosephalus cernuus*	30	0	15
Bream *Abramis brama*	15	0	7.5
Bleak *Alburnus alburnus*	10	0	5
Three-spined Stickleback *Gasterosteus aculeatus*	0	5	2.5
Ide *Leuciscus idus*	5	0	2.5

Table 3. Percentage of lakes in which each species was caught, including all three fishing methods.

Distribution of fish in relation to environmental variables

All lakes

Lake area was the single factor explaining the most variation (16 %, $p<0.05$) in fish species distribution when all lakes and variables were included. The most important chemical variable was pH (14 %, $p<0.025$). When including only chemical variables, CH_4 was instead the factor explaining the most variation; 22 % ($p<0.025$) compared to 16 % ($p<0.025$) for pH. Inorganic carbon (IC), CH_4, absorbance and isolation all explained 4-6% of the variation when including all environmental factors. Together lake area and pH explained 28 % of the variation while all included factors together explained 45 %. (Figure 6, table 4)

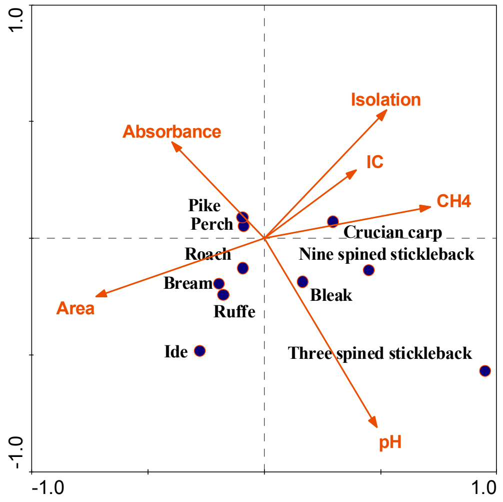


Figure 6. CCA of all 40 lakes, showing the distribution of species in relation to environmental variables. Variables included each explain >5% of the fish species distribution. In total 45% of the variation is explained by the 6 variables included.

Axis 1 explained 58 % of the species-environment correlation (eigenvalue 0.485) and axis 2 explained 21 % (eigenvalue 0.148). The remaining axis explained < 15 % each for all three CCA analysis and were therefore not considered further in the discussion. All variables included in the analysis clearly contributed to axis 1, while only pH, absorbance and isolation contributed strongly to axis 2.

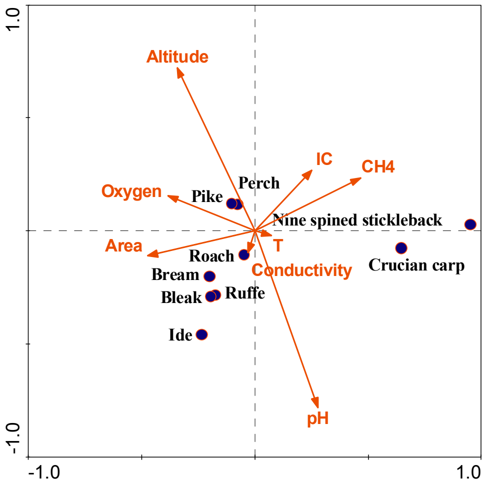


Figure 7. CCA of connected lakes, showing the distribution of species in relation to environmental variables. Variables included each explained >4% of the fish species distribution. In total 65 % of the variation was explained by the 8 variables included.

Connected lakes

In connected lakes, area and pH explained most of the variation (12 % and 11 % respectively). Area was however the only significantly contributing factor ($p<0.05$), leading to no significant correlation being found when only chemical variables were included. DO, CH_4, inorganic carbon (IC), temperature, conductivity and altitude all explained 6-8% of the variation and the 8 variables together explained 65%. (Figure 7, table 4)

Axis 1 explained 38 % of the environment-species correlation (eigenvalue 0.485) while axis 2 explained 11 % (eigenvalue 0.135). Methane, DO, area and altitude all loaded heavily on axis 1 while only pH and altitude loaded heavily on axis 2. (Figure 7, table 4)

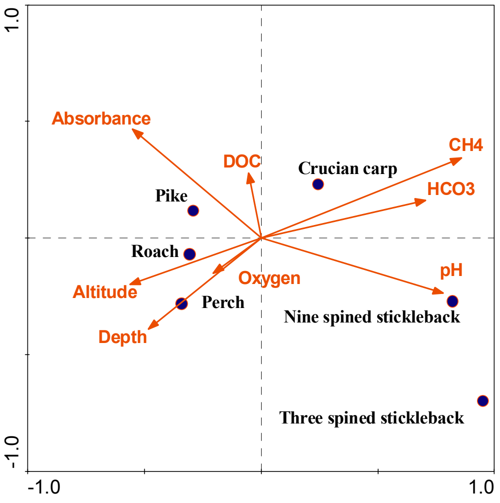


Figure 8. CCA of isolated lakes, showing the distribution of species in relation to environmental variables. Variables included each explain >4% of the fish species distribution. In total 86% of the variation is explained by all 8 variables combined.

Isolated lakes

In isolated lakes, methane explained most of the variation in fish species distribution, both out of the chemical variables and when physical variables were included (34 %, $p<0.05$). pH was also significant in both tests, explaining 14 % ($p<0.025$). The remaining variables explaining more than 4 % when all environmental variables are included were DOC (10 %), altitude (9 %), absorbance, DO, HCO_3 and depth. Together methane and pH explained 48 % of the variation while all included factors together explained 86 %. (Figure 8, table 4)

Axis 1 explained 50 % of the environment-species correlation (eigenvalue 0.643) and axis 2 explained 18 % (eigenvalue 0.227). All variables except DO and DOC loaded heavily on axis 1 while only CH_4, absorbance and depth loaded heavily on axis 2. (Table 4)

Environmental variable	**Level of Explanation in %**			**Loadings on Axis 1**			**Loadings on Axis 2**		
	All lakes	C lakes	I lakes	All lakes	C lakes	I lakes	All lakes	C lakes	I lakes
All chem. var.	**37**	**65**	**90**						
All sign. chem. var.	**24**	**0**	**48**						
Total inertia/eigenvalue	**1.585**	**1.288**	**1.484**	**0.417**	**0.485**	**0.643**	**0.148**	**0.135**	**0.277**
All variables	**45**	**65**	**86**						
All significant var.	**28**	**12**	**48**						
pH	14*	11	14*	**0.3813**	**0.2432**	**0.7547**	**-0.6793**	**-0.7085**	-0.2229
DO		8	5		**-0.3355**	**-0.1978**		0.1407	-0.1414
CH4	4**	7	34*	**0.5618**	**0.407**	**0.8281**	0.1127	0.2121	**0.3216**
IC	6	7		**0.3116**	**0.2198**		0.2442	0.2421	
HCO_3			5			**0.6814**			0.1519
Conductivity		6			-0.0254			-0.0884	
Absorbance	5		6	**-0.3118**		**-0.5313**	**0.3439**		**0.437**
DOC			10			-0.0514			0.2618
Temperature		7			0.0635			-0.0183	
Area	16*	12*		**-0.5698**	**-0.4135**		-0.2103	-0.1007	
Altitude		6	9		**-0.3005**	**-0.5434**		**0.6538**	-0.1867
Depth			4			**-0.4677**			**-0.366**
Isolation	4			**0.4143**			**0.4584**		

Table 4. The first rows of the table show total level of explanation for chemical variables when running CCA on only those. Variable significant only in that test is marked with **. Below that, levels of explanation of for all environmental variables together as well as for each variable separately, when physical parameters were included. For the same test; total inertia and eigenvalues as well as loadings on axis 1 and axis 2. Variables contributing significantly are marked with *.

Comparison between different measurements

When running CCA, the measurement of each variable that explained the most variation, and only one measurement of each variable, was included. For pH, the summer measurement had a slightly stronger correlation than any of the winter measurements. In winter, the deep measurements gave the best correlation for pH, DO, DOC and temperature. For conductivity the shallow measurement explained the most variation and for absorbance it differed between the CCA tests.

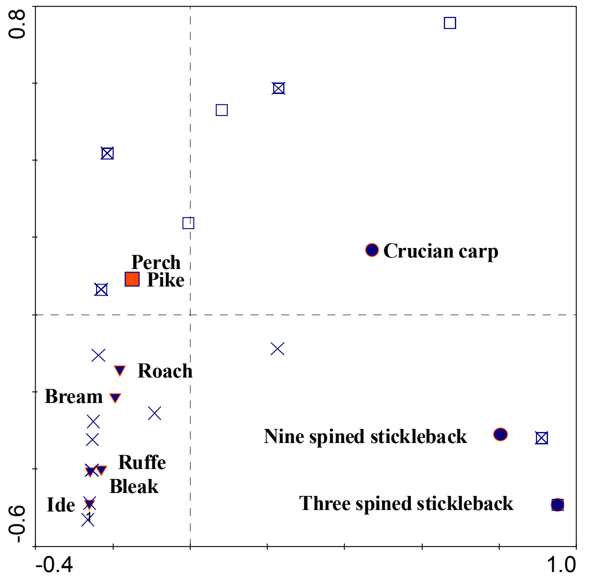


Figure 4. CA of all lakes, showing the distribution of species in relation to which lakes they were caught in. Connected lakes – crosses. Isolated lakes - empty squares. Fishless lakes are not included. Lakes with the same fish assemblage are placed on top of each other. Fish group 1 - filled circle. Fish group 2 - filled square. Fish group 3 - filled triangles.

Grouping fish

Using CA (correspondence analysis), fish species were grouped according to their distribution (figure 4). Axis 1 explained as much as 70% of the variation in fish species distribution between the lakes and the species were clearly divided into two groups on that axis; crucian carp and the sticklebacks in one group (Fish Group 1) and the rest of the fish species in the other. Pike and perch have the same distribution in the CA diagram and they also appear in almost all connected and many isolated lakes. They stand out from the rest and thereby constitute their own group (Fish Group 2). Fish Group 3 includes the rest of the fish species; roach, bream, ruffe, bleak and ide.

The groups of fish formed using CA show differences in distribution partially due to isolation and lake area (figure 5). Group 1 was commonly found in isolated lakes. Group 2 was found in both connected and isolated lakes and in all lake sizes. Group 3 was more common in connected lakes, and preferred large lakes to small ones.

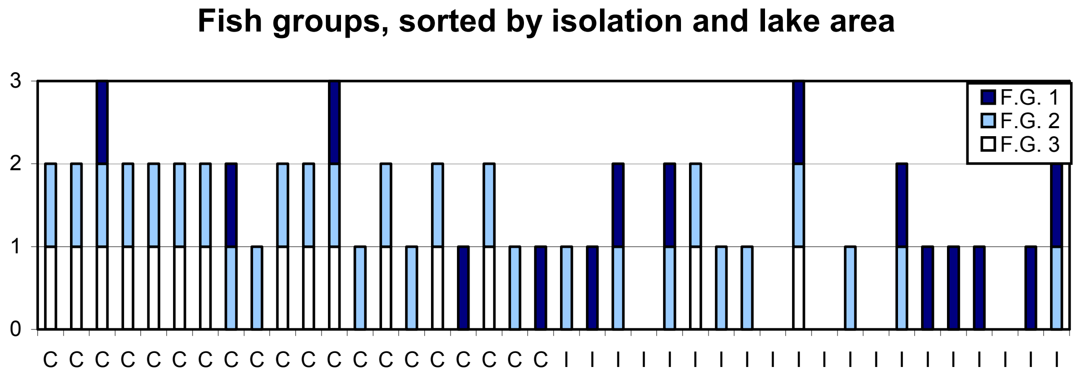


Figure 5. Presence of the different fish groups in isolated and connected lakes. The lakes are sorted by isolation and area, with the largest connected lake furthest to the left and the largest isolated lake next to the smallest connected lake.

Fish groups in relation to chemical variables

Binary logistic regressions were used to relate the presence/absence of different fish groups to six chemical variables. From the CCA analysis, pH and methane were the only significantly contributing variables. As they indicate acidity and anoxia, respectively, all variables included in the binary logistic regression analysis are closely related to those. Variables selected were pH winter and summer, methane, dissolved oxygen, conductivity and alkalinity (table 5). When running binary logistic regressions on chemical variables against presence of fish for the three fish groups, eight tests showed a trend, having a significance level of $p<0.1$. Out of those eight, four were significant using a level of $p<0.05$. Six out of the eight trends were associated with Fish Group 1 (FG 1).

Fish group 1, containing crucian carp, nine-spined stickleback and three-spined stickleback, was more abundant in less acidic lakes (figure 9, table 5). In connected lakes the probability of finding a member of fish group 1 was 0.5 at pH 6.3 and in isolated lakes 0.5 at winter pH 5.7 and summer pH 6.0. The probability of making a correct estimation of presence/absence of FG 1 based on pH was rather high, 80 %, for isolated lakes. For connected lakes, the probability of estimating absence correctly (PC-0, table 5) was still high, 87 %, but the probability of estimating presence (PC-1, table 5) was much weaker, only 40 %. Alkalinity was also important for FG1, and the association was rather strong for isolated lakes with a probability of 80 % to estimate absence or presence correctly.

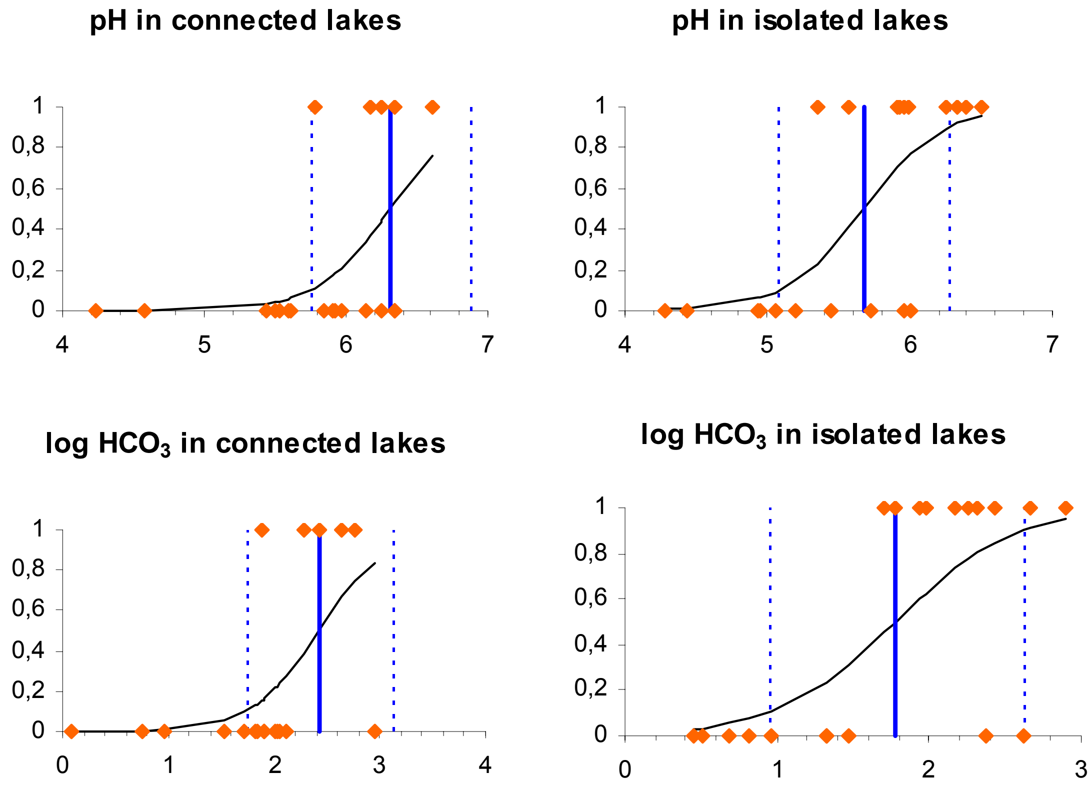


Figure 9. pH and bicarbonate concentration significantly contributed to species distribution of FG 1.

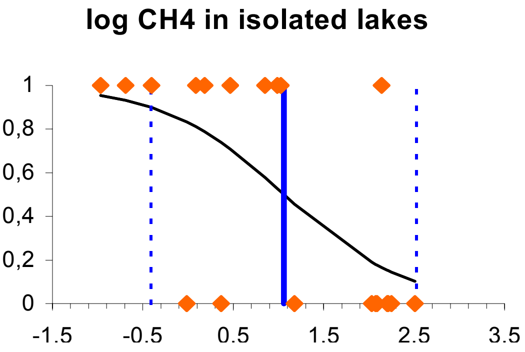


Figure 10. Methane was the only chemical variable the distribution of Fish group 2 was significantly correlated with.

For fish group 2, methane concentration in isolated lakes was the only correlating factor (table 5). The probability of estimating presence and absence correctly was high, about 90 %. However, the regression slope was rather flat and while the cut-off value was 11.5 uM CH_4/l for a probability of 0.5, it was 337 for a probability of 0.1.

Fish group	**Variable**	**C / I**	**Trend**	**Variable P**	**R^2**	**Model P**	**Slope**	**Intercept**	**Cut-off values** (only pH as logged)			**% estimated right**		
			+ / - / 0						**0.1**	**0.5**	**0.9**	**PC-0**	**PC-1**	**PC-tot**
1	pH W	C	+	0.08	0.25	0.02	3.88	-24.51	5.75	6.31	6.88	87	40	75
		I	+	0.02	0.40	0.00	3.68	-20.89	5.08	5.67	6.27	70	80	75
	pH S	C	+	0.11	0.21									
		I	+	0.03	0.23	0.01	2.45	-14.64	5.07	5.97	6.86	80	80	80
	log CH4	C	+	0.17	0.11									
		I	+	0.18	0.07									
	log DO	C	-	0.10	0.40	0.00	-5.26	-5.28	0.26	0.10	0.04	100	60	90
		I	0	0.88	0.00									
	log Cond	C	0	0.96	0.00									
		I	+	0.17	0.08									
	log HCO3	C	+	0.06	0.28	0.01	3.14	-7.64	53.6	268.2	1336.2	93	60	85
		I	+	0.02	0.36	0.00	2.63	-4.68	8.9	60.6	415.3	80	80	80
2	pH W	C	-	0.16	0.37									
		I	-	0.82	0.00									
	pH S	C	-	0.41	0.08									
		I	-	0.24	0.05									
	log CH4	C	-	0.37	0.08									
		I	-	0.02	0.31	0.00	-1.50	1.58	337.22	11.45	0.39	80	100	89
	log DO	C	+	0.40	0.07									
		I	+	0.42	0.02									
	log Cond	C	0	0.84	0.00									
		I	-	0.62	0.01									
	log HCO3	C	0	0.11	0.32									
		I	-	0.44	0.22									
3	pH W	C	+	0.10	0.15	0.05	1.85	-10.09	4.27	5.45	6.64	43	100	80
		I	+	0.21	0.07									
	pH S	C	0	0.97	0.00									
		I	+	0.63	0.02									
	log CH4	C	-	0.16	0.09									
		I	-	0.15	0.27									
	log DO	C	0	0.91	0.00									
		I	+	0.48	0.04									
	log Cond	C	+	0.83	0.00									
		I	0	0.87	0.00									
	log HCO3	C	+	0.38	0.03									
		I	0	0.77	0.00									

Table 5. Table of results from binary logistic regression. For significant correlations, cut-off values and percentage estimated right have been given. Variables with significance level P<0.05 marked as dark gray.

Fish group 3 constitutes of roach, ruffe, bream, bleak and ide, but out of those only roach is found in the isolated lakes, and only in two of those. The probability of finding a fish species belonging to group 3 in connected lakes increased with pH, having the 0.5 probability cut-off value at pH 5.5. The probability of estimating presence of FG 2 in connected lakes was 100 %, but the probability of estimating absence correctly was only 43 %. (Table 5)

Discussion & conclusions

Environmental factors contributing to fish species composition

Chemical factors

The major chemical factors affecting fish species distribution are acidity and dissolved oxygen concentration, which is the same conclusion Jackson *et al* (2001) came to. Dissolved oxygen was not a significant variable in itself in any of the CCA analysis, but methane was significant and explained as much as 34 % of the variation in isolated lakes. Methane is a gas produced in the sediments under anoxic conditions. It diffuses from the sediment into the water column where it can oxidize under oxic conditions (Bastviken *et al* 2002). The methane concentration measured in the samples taken 0.4 m below the surface therefore reflects the anoxic conditions at the bottom. It is probably also affected by ice porosity, lake depth, how much the drill stirred the water and time elapsed from the hole was drilled until the sample was taken. Methane did give a strong correlation with fish species distribution but methane itself has no toxic effect on fish. Because of the strong correlation with DO (Bastviken *et al* 2002), methane is used as an indicator of anoxic conditions in these lakes. The reason the measurement of dissolved oxygen did not give such a strong correlation could be that the differences in DO concentrations were too small in relation to the sensitivity of the oxygen-probe. The stirring of water caused by drilling could also have affected the oxygen concentration more than it affected the methane concentration. This corresponds with DO explaining more of the variation in connected lakes, since they are deeper and the bottom measurement thus less affected. One of the reasons for finding such strong correlations with methane is that water chemistry was measured in late winter when DO concentrations are at minimum. Another reason is that the DO levels found in most lakes are at critical level for survival of many fish species (table 2, Doudoroff & Shumway 1970). That CH_4 only contributed significantly in all lakes combined when physical parameters were excluded could be explained by CH_4 being negatively co-correlated with lake area and altitude, which depreciates the importance of CH_4.

Acidity is important in all lake groups, showing a trend in connected lakes that becomes significant when isolated lakes are included. Water chemistry was however not measured during a period of extreme acidic conditions, which normally occur during episodes such as spring flood (Laudon *et al* 2001). The correlation between fish species distribution and pH was therefore probably underestimated in connected lakes. The average catchment area of isolated lakes is much smaller than that of connected (table 1), resulting in a longer residence time in isolated lakes. In lakes with a long residence time, a temporary change in water chemistry of incoming water causes little change in water chemistry of the lake. In lakes with a short residence time, temporary changes in incoming water such as a drop in pH during spring flood can on the other hand have drastic effects on lake water chemistry. Therefore, the difference in catchment size between connected and isolated lakes probably partly explains why pH only was found to contribute significantly to fish species distribution in the isolated lakes.

The strength of the effect of acidity and anoxia on freshwater fishes depends on concentrations of many other chemical variables. Aluminum is a naturally occurring metal in lakes (Wiederholm 1999). In combination with low pH, aluminum concentrations occurring in Swedish freshwater can be toxic to fish (Carlsson & Johansson 1988, Laudon 2001) by accumulation on gills. It is the inorganic, monomeric form of aluminum (Al_i) that is toxic (Laudon 2001, Wilander *et al* 2003) and the reason no correlation was found with aluminum in the present study could be that only total aluminum concentration was measured. Another reason is that the concentration of Al_i is strongly pH dependant (Wilander 2003) and therefore co-correlated with pH. The highest Al_i concentrations are reached during episodes when pH reaches its minimum values (Laudon 2001) and have not been measured in this study.

Absorbance, the colour of the water, explained a small part of the variation in isolated and all lakes combined, while DOC only was included in the CCA for isolated lakes. This could be due to more humus in isolated lakes, which is confirmed by higher average DOC concentrations (table 1). However, the difference could also be due to differences in catchment size and turnover time since the humus content of freshwater increases during episodes such as spring flood. The CCA:s also show that absorbance is highly co-correlated with pH, which is due to the negatively charged humus attracting hydrogen ions (H^+) that dissolve in the lake water (Andersson 2001). The correlation between humus and fish species distribution is complicated by humus also contributing positively by intoxifying organic toxicants and metals such as aluminum (Andersson 2001), thus raising the critical limit for such substances. The critical pH limit for acid sensitive fish can also be changed due to humus; Andersson (2001) showed that an increase of TOC from 3 to 20 mg/l resulted in a drop in pH sensitivity from 6.0 to 5.5. Humus should to a certain extent increase survival (Kullberg *et al* 1993), but in too high concentrations the negative effects override the positive (Degerman 1987). The concentrations of dissolved organic matter in the lakes studied are not abnormally high and do not have a large affect on species composition.

All pH measurements gave similar correlation results. Summer pH explained slightly more of the variation when running CCA, but the deep winter measurement was instead stronger when running binary logistic regressions. However, winter pH was lower than summer pH, a period when oxygen deficiency and low temperature causes additional stress on the fish (Jackson *et al* 2001). On the other hand, this seems to be compensated by young fish being more sensitive to low pH than adult fish and hatching often being the most sensitive period of the life of a fish (Degerman & Lingdell 1993). The difference in correlation strength between measurements on different depths is small. Most variables had slightly stronger correlations for the deep measurements, indicating fish spend more time deep down in lakes in the winter. Oxygen was found to have a strong, descending, vertical gradient. Crucian carp, the most common species of FG 1, is known to lie still close to the bottom during winter months (Holopainen *et al* 1997). The difference between regular pH and aired pH is due to an over pressure of carbon dioxide (pCO_2) building up in the water, reacting to form carbonic acid (H_2CO_3). Carbonic acid is a weak acid and its influence on pH is small when pH is under 5.

The total level of explanation given when all factors explaining >4 % are included are not comparable between lake groups, partly due to the 4 % cut-off including different amounts of variables in different tests. However, the total proportions explained by significant factors do tell us that chemical variables are much more important in isolated lakes than in connected.

Lakes that can be recolonized do not need to have sufficient amounts of oxygen in winter or spring pH high enough for eggs to hatch. Many of them will have fish in summer as long as summer pH is high enough for adult fish to survive.

Physical factors

Lake surface area was the only physical factor contributing significantly to species composition. Area has also been shown to be strongly related to species diversity (Blom 2003, Jackson *et al* 2001) and the correlation can be explained by larger lakes having a more diverse habitat, thus giving the possibility of co-existence of both prey- and predator species (Jackson *et al* 2001). Also, larger lakes should have more species because populations are larger, which deceases the risk of extinctions due to environmental and demographic stochasticity (Tonn & Magnuson 1982). In the present study, predator species are uncommon in lakes with an area under 3 ha, while prey species are common. The reason lake area is not important among isolated lakes is probably that the fish species have adapted to live in small lakes. Also, the size range of isolated lakes, as well as the average size, is smaller for isolated lakes, making a potential trend less visible.

Apart from lake area, Blom (2003) also found stream gradient and length of stream to be significantly related to species richness in these lakes. Both factors control the rate of recolonization and affect the selection of species that do recolonize (Magnuson *et al* 1998). Lake depth and elevation was neither correlated with species richness (Blom 2003) nor species distribution, but did explain > 4 % of the variation in the isolated lakes.
Elevation is a way to measure the age of land upheaval lakes, in this study ranging from 200 to 3500 years. The reason for elevation not contributing more to species composition is probably due to the altitude being low for all lakes. In studies including a wider range of elevation, elevation has been found to significantly contribute to species composition (Holmgren & Appelberg 2000, Degerman & Nyberg 1987). Depth ought to be of importance in the shallowest lakes of the study since shallow lakes in the area can bottom freeze. Even though the shallowest lake of the study still had a little unfrozen water under the ice during the winter water sampling, shallow lakes may very well freeze solid during colder winters. Few species survive such conditions and species composition is thereby affected directly (Jackson *et al* 2001). Temperature can also effect species composition indirectly, e.g. smallmouth bass *Micropterus dolomieu*, a perchlike fish, has been shown not to develop enough during summer to survive the winter if average July temperature is below 15° C (Jackson *et al* 2001). The average July temperature in Umeå is 15° C (SMHI 2004) and some of the species found in lakes of northern Sweden may be affected negatively by temperature, reducing survival by adding to the environmental stress.

Fish assemblages in connected and isolated lakes

Fish assemblages of lakes are not solely due to differences in the capability of handling harsh environmental conditions. Biological factors such as predation, competition and colonization rate also largely affect species composition (Tonn & Magnuson 1982). Jackson et al (2001) suggested habitat-related differences in combination with predation effects, rather than competition, structure lake fish communities. Tonn & Magnuson (1982) pointed out the differences between the *Umbra*-cyprinid fish group and the centrarchid-*Esox* fish group in lakes, explaining the maintenance of the two groups by biotic and abiotic disturbances and refuges from these disturbances. Tonn & Magnuson's discussion on the relationship and differences between the two fish assemblages found by them and the relationship and differences found between FG 1 and FG 2 in this study are similar.

Fish group 1 – crucian carp, three-spined and nine-spined stickleback

Crucian carp

Crucian carp and the sticklebacks clearly have other needs than the rest of the fish species. On axis 1 of the CCA:s, which explains most of the variation, FG 1 was drawn towards high pH and alkalinity (HCO_3), as well as high concentrations of CH_4 and inorganic carbon. The inorganic carbon is not an affecting variable in itself; it is co-correlated with the presence of methane. FG 1 was also drawn to small, shallow, young, isolated lakes. Tonn & Magnuson (1982) found the *Umbra*-cyprinid group to inhabit isolated lakes with little winter oxygen. The high abundance of FG 1 in isolated lakes with little dissolved oxygen is, I believe, not due to a preference for those conditions, but rather due to lack of predation. Tonn & Magnuson (1982) came to the conclusion the distribution of the *Umbra*-cyprinid group is controlled by predation and competition rather than by chemical variables. The species of FG 1 have adapted well to DO concentrations less than 1 mg/l, but are easily extinguished in the presence of predator species such as pike, perch and roach (Rask *et al* 2000). Both nine-spined stickleback and crucian carp have been known to explode in numbers after rotenone treatment, which kills most fish in a lake (Svärdson 1976). Lindgren (2001) found roach to be a great competitor to or predator of Crucian carp since the latter was absent in lakes containing roach but present in more harsh environments where roach was absent.

Nine-spined stickleback

In the lakes of the present study, FG 1 and FG 2 were both caught in eight lakes out of the 40. FG1 was the only group caught in four out of the nine lakes FG 2 was absent from (figure 5). The reason the segregation was not larger in isolated lakes could perhaps be explained spatial segregation within the lake. Fish have been seen to aggregate around inlets and outlets of low DO lakes (Tonn & Magnuson 1982) and if differences in DO concentrations are found within a low DO lake, FG 2 could be restricted to that area. Crucian carp on the other hand, the most common species of FG 1, can alter its metabolism, be inactive and starve for several months during anoxic, dark and cold conditions (Holopainen *et al* 1997).

Looking at the relationship between fish groups and environmental gradients (table 5), FG 1 was much stronger correlated with acidity than with oxygen. Varying critical levels of pH have been reported for crucian carp; Holopainen & Oikari (1992) found a high mortality of crucian carp four months after a temporary exposure to pH 4 and increased aluminium levels in a natural pond, but crucian carp has earlier been reported to survive pH 4 (Svärdson 1976). Degerman & Lingdell (1982) found problems with reproduction at pH 5-5.5, which better corresponds with this study were crucian carp was absent from lakes with a pH under 5 and the cut-off values of 5.7-6.3.

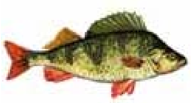
Three-spined stickleback

Few papers discuss critical chemical levels for sticklebacks in Sweden, since they are rarely seen or caught. Degerman & Lingdell (1993) did not determine all sticklebacks down to species, but all individuals caught inhabited lakes with pH within 6.2 to 8.9. Their presumably high sensitivity to acidity corresponds well with the results of the present study where pH is the major factor determining species distribution of sticklebacks.

Fish group 2 – pike and perch

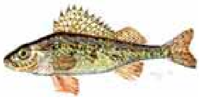

Northern Pike

The species of FG 2 are in many respects the opposite of those of FG 1. Pike and perch are the two most common species in Sweden (Rask *et al* 2000), as well as in the connected as in all lakes combined in this study. They are predators with a demand for high DO concentrations or lake connectedness (Tonn & Magnuson 1982), but instead tolerate low pH (Degerman & Lingdell 1987, Rask *et al* 1998). According to Degerman & Lingdell (1987), reproduction of pike and perch does not occur under a pH of 4.4-4.9, while older pike have been reported down to pH 4.2 and perch to pH 4.4. The most acidic lake in this study had both pike and perch and a pH of 4 in winter and 5.5 in summer. As it was connected, pike and perch could very well have recolonized the lake the summer of the water chemistry measurements, after having fled or died from the low pH in the winter. The isolated lakes with the lowest pH values had no fish at all. Pike and perch were only found in isolated lakes with a pH of at least 5, which supports the theory discussed by Tonn & Magnuson (1982) that pike and perch flea connected lakes with harsh conditions if they can, and recolonize when conditions have improved.


Perch

Drawing conclusions from the CCA:s for connected lakes and all lakes together (figure 6-7, table 4), the distribution of perch and pike is not affected by environmental variables. But looking at the isolated lakes (figure 8, 10, table 4), oxygen (CH_4) is an important factor regulating the distribution of FG 2. According to Doudoroff & Shumway (1970), perch cannot survive DO concentrations lower than 0.2-1.4 mg/l. However, in this study, perch was found in isolated lakes with DO levels down to 0.15 mg/l, and pike was found in the isolated lake with the least oxygen; 0.09 mg/l. Even though pike and perch apparently can survive low DO levels, they are probably severely affected by anoxia, thus being less effective predators on FG 1 in low DO lakes.

Fish group 3 – roach, ruffe, bream, bleak and ide


Ruffe

Fish group 3 constitutes the largest group of fish and also mostly species that are rarely found in this study. They were mostly found in lakes with generally high water quality, suggesting it is a group with high environmental demands. However, it also makes it difficult to see any patterns as to what is the strongest controlling environmental variable. Another problem is that the species within the group might have different tolerance levels. The species were spread out on axis 2 on the CCA:s (figure 6, 7), where pH was the dominating variable. Altitude was also important, indicating that ide, bleak, ruffe and bream all are poor migrators that need high pH. These species are however all rare in this study and if a pH tolerant species happens to be present in one high pH lake and only that lake, it will be marked as pH sensitive. Since down-weighting of rare species was used running CCA, this was compensated for to some extent. FG 3 only showed a trend of higher abundance with an increase in pH, using binary logistic regression. If instead minimum values of pH had been used, the relationship would probably have been stronger. Since the probability of estimating absence of FG 3 was so much lower than the probability of estimating presence, the presence will be underestimated using the cut-off value given at 5.5.


Roach

Roach is a species known to need high pH to survive. It is classified as an indicator of non-acidified lakes (Andersson 2001) and Degerman & Lingdell (1987) found roach to be missing from lakes with pH under 5.5-5.9. This corresponds well with the cut-off value for FG 3 in connected lakes of this study being 5.5. Roach was found only in the two isolated lakes with the highest pH, the most acidic of them having a winter pH of 5.5. The reason for roach not being found in any other isolated lakes is probably due to its sensitivity to acidity.

Bream, just as roach, indicates non-acidified lakes and is missing under pH 5-5.4 (Andersson 2001). Tamii *et al* (2003) found bream to be uncommon in Sweden, but the species was found in 20 % of the lakes studied by Degerman & Lingdell (1987). The latter found latitude, altitude and water temperature to be the most important factors controlling the presence and absence of bream.


Bream


Ide

Both ruffe and bleak are quite rare in northern Sweden, explaining the low occurrence of the two species. Ide needs running water to spawn, why it is excluded from isolated lakes. Ruffe is an indicator of unacidified lakes, missing under a pH of 5-5.4 (Andersson 2001). Degerman & Nyberg (1987) found ide in only one lake, and that lake was species rich.


Bleak

Conclusions

Acidity and anoxia are the two main chemical factors structuring fish communities in small coastal lakes of northern Sweden. Different fish species are restricted in their distribution by different chemical, physical or biological variables, and therefore inhabit lakes with different environmental conditions. A much larger proportion of the differences in fish species distribution can be explained by environmental factors in isolated lakes than in connected. In connected lakes, the size of the lake is instead important. In isolated lakes, methane, an indicator of anoxia, is the environmental variable with the strongest correlation, controlling the dispersal of e.g. pike and perch. Acidity is important especially for controlling the occurrence of crucian carp and sticklebacks in isolated lakes, but its importance in connected lakes might have been underestimated in this study.

Acknowledgements

First and foremost I would like to thank my supervisors; Ishi Buffam for your support and for putting all that time and energy into my project, Hjalmar Laudon for your guidance and encouragement and Göran Englund at the Department of Ecology and Geological science at the University of Umeå for supplying me with fish- and physical data. Thank you Henrik Larsson for lending me the field equipment and Patrik Olofsson and Juha Salonsaari for doing all the fishing. I would also like to thank Kevin Bishop for giving me a room at the department and Andreas Barth for the housing in Umeå. Many others at the Department of Environmental Assessment and at the Department of Forest Ecology at SLU have helped me with various parts of the project and I wish to thank you all. Last, I want to direct my thanks to Gustav Karlsson for your love and support, as well as for watching over me when the ice was getting weak.

References

Andersson, H. C. 2001. Är nuvarande kritiskt kemiska värden relevanta för att bedöma försurningspåverkan på fisk i svenska sjöar? Intern publikation 2001:5, Institutionen för miljöanalys, SLU.

Bastviken, D., J. Ejlertsson and L. Tranvik. 2002. Measurement of methane oxidation in lakes: a comparison of methods. Environmental science and technology. 36: 3354-3361.

Blom, A. 2003. Effect of spatial isolation on fish species richness in small coastal lakes in Northern Sweden. Degree thesis. Dept. of Biology and Environmental Science, Umeå University. Sweden.

Carlsson, U. & T. Johansson. 1988. Effekter av aluminium och kalcium på överlevnad och reproduktion av öring (Salmo trutta L.) i två försurade vattendrag. Information från sötvattenslaboratoriet, Drottningholm, nr 11.

Chambers, P.A., S. Brown, J.M. Culp, R.B. Lowell and A. Pietroniro. 2000. Dissolved oxygen decline in ice-covered rivers of northern Alberta and its effects on aquatic biota. Journal of aquatic ecosystem stress and recovery. 8:27-38.

Degerman, E. 1987. Humösa sjöar – en littersturssammanställning med inriktning på fisk och försurning. Naturvårdsverkets reprocentral, Solna.

Degerman, E. & P.-E. Lingdell. 1993. pHisces – fisk som indikator på lågt pH. Information från Sötvattenslaboratoriet, Drottningholm 3:37-54.

Degerman, E. & P. Nyberg, 1987. Fiskfaunans sammansättning och täthet i försurade och kalkade sjöar – en arbetsrapport. Infortmation från Sötvattenslaboratoriet, Drottningholm, nr 7.

Doudoroff, P. & D.L. Shumway. 1970. Dissolved oxygen requirements of freshwater fishes. Food and agricultural organization of the united nations. FAO Fisheries Technical paper no 86.

Ericson, G., E. Lindesjö., B. Sundelin, A.-K. Eriksson, E. Håkansson, B. Liewenborg, I. Pettersson & L. Balk. 1996. Biologiska effekter i en gradient utanför Sundsvall – studier på abborre, gädda och vitmärla. Statens naturvårdsverk, rapport 4628.

Holmgren, K. & M. Appelberg. 2000. Size structure of benthic freshwater fish communities in relation to environmental gradients. Journal of fish biology. 57: 1312-1330.

Holopainen, I. J. & A. Oikari. 1992. Ecophysiological effects of temporary acidification on crucian carp, Carassius carassius (L.): a case history of a forest pond in eastern Finland. Annales zoologici Fennici. 29:29-38.

Holopainen, I.J., W.M. Tonn & C.A. Paszkowski. 1997. Tales of two fish: the dichtomous biology of crucian carp (Carassius carassius(L.)) in northern Europe. Finnish Zoological and Botanical Publishing Board. Helsinki.

Jackson, D.A., P.R. Peres-Neto & J.D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic and spatial factors. Canadian journal of fisheries and aquatic sciences. 58:157-170.

Klemedtsson, L., Å. Kasimir-Klemedtsson, F. Moldan and P. Weslien. 1997. Nitrous oxide emission from Swedish forest soils in relation to liming and simulated increased N-deposition. Biology and Fertility of Soils. 25: 290-295.

Kullberg, A., K.H. Bishop, A. Hargeby, M. Jansson and R.C. Petersen Jr. The ecoligical significance of dissolved organic carbon in acidified waters. AMBIO. XXII(5):331-336.

Laudon, H., O. Westling, A. Poléo, L.A. Völlestad. 2001. Naturligt sura och försurade vatten i Norrland. Naturvårdsverket, Rapport 5144. Berling skogs, Trelleborg.

Lindgren, E. 2001. When land upheaval turns seas into lakes – patterns of fish diversity. Masters degree thesis. Umeå University, Umeå.

Magnuson, J.J., W.M. Tonn, A. Banerjree, J. Toivonen, O. Sanchez & M. Rask. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology 79(8): 2941-2956.

Rask, M., K. Nyberg, S.-L. Markkanen, & A. Ojala. 1998. Forestry in catchments: Effects on water quality, plankton, zoobenthos and fish in small lakes. Boreal environment research 3: 75-86.

Rask, M., M. Appelberg, U. Beijer, T. Hesthagen, J. Tammi, A. Lappalainen. 2000. Fish Status Survey of Nordic Lakes. Species composition, distribution, effects of environmental changes. Nordic Council of Ministers. TemaNord 2000:508.

Salonsaari, J. 2002. Fish community structure in enclosing bays - effects of habitat use and seasonal patterns of migration and isolation. Masters degree thesis. Umeå University, Umeå.

SMHI. 2004-11-08. The home page of SMHI - the Swedish Meteorological and Hydrological Institute. www.SMHI.se

Stenson, J.A.E., J.-E. Svensson, & G. Cronberg. 1993. Changes and interactions in the pelagic community in acidified lakes in Sweden. AMBIO XXII(5):277-282

Stumm, W., J. J. Morgan. 1996. Aquatic Chemistry. Third edition. John Wiley and sons, Inc. New York.

Tammi, J.,M. Appeleberg, U. Beier, T. Hesthagen, A. Lappalainen & M. Rask. 2003. Fish status survey of Nordic lakes: effects of acidification, eutrophication and stocking activity om present fish species composition. Ambio. 32:2, 98-105.

Tonn, W. M. & J.J. Magnuson. 1982. Patterns of species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology, 63 (4): 1149-1166.

Wiederholm, T. 1999. Bedömningsgrunder för miljökvalitet – sjöar och vattendrag. Bakgrundsrapport 1 – kemiska och fysikaliska parametrar. Naturvårdsverket, rapport 4920.

Wiederholm, T. 2000. Bedömningsgrunder för miljökvalitet – sjöar och vattendrag. Naturvårdsverket, rapport 4913.

Wilander, A., R. Johnson, & W. Goedkoop, 2003. Riksinventering 2000. Institutionen för miljöanalys, SLU, Uppsala. Rapport 2003:1.

Appendix 1 – Physical parameters

Lake name	Connected /isolated	Location ° N	Location ° E	Altitude (masl)	Depth (m)	Area (ha)	Distance to sea* (m)	Catchment area (ha)
Stor-Tannörsavan	C	7043000	1691900	4,0	2,4	16,2	740	56
Hemavan	C	7043000	1682400	3,0	2,6	18,0	250	64
Bredvikssjön	C	7045250	1681400	2,0	1,7	15,0	150	210
Strandsjön	C	7049000	1693000	4,0	1,9	15,0	5510	594
Smörbysjön	C	7051300	1691350	8,0	2,9	30,0	4420	802
Kroken	C	7052250	1694650	2,0	1,6	12,0	490	300
Lillträsket	C	7055600	1696950	4,0	1,9	6,5	1000	688
Svartsjön	C	7059800	1698500	17,0	2,5	11,3	3400	258
Ängerfjärden	C	7060100	1699900	4,0	1,9	8,0	1560	725888
Kroktjärn	C	7071900	1726800	4,0	4,3	2,0	390	36
Bolkarhamn	C	7077200	1728000	2,0	1,4	5,0	340	56
Kasaviken	C	7077500	1727250	2,0	5,5	22,5	330	195
Häbbersvarpet	C	7082750	1733750	2,5	1,1	6,0	1470	72
Degersjön	C	7084500	1729400	10,5	3,6	25,0	3070	134
Baggösundet	C	7085100	1730550	2,0	1,9	10,0	330	90
Bussjön	C	7092000	1735950	12,0	1,1	5,0	3900	395
Lill-Kvasjön	C	7100000	1743650	8,8	2,0	13,8	1120	412
Hartsjön	C	7102700	1743700	9,0	2,8	18,0	840	529
Kråktjärnen	C	7111100	1748650	12,0	1,6	8,0	1980	192
Nördsjön	C	7119000	1748650	19,0	2,1	8,0	2710	97
Boggviksjön (A)	I	7045500	1695950	2,3	1,7	1,0	150	17
Kråksundet	I	7047800	1695900	2,0	2,2	14,0	1500	74
Boggviksjön (B)	I	7048000	1695100	13,0	0,9	12,0	3000	86
Tjärnmyrtjärnen	I	7051000	1693450	12,0	1,3	4,5	3000	22
Öviken	I	7054000	1695800	2,0	1,6	9,0	150	20
Vitskär	I	7069100	1722300	4,0	1,2	2,0	350	27
Harpsjön	I	7074000	1722200	10,0	3,8	8,8	2500	80
Kubbvikssjön	I	7080150	1728200	3,0	1,6	5,0	200	87
Finkarstjärnen	I	7080550	1726850	12,0	1,7	3,0	5000	26
Öster-Skivsjön	I	7093500	1731150	27,0	2,0	6,0	9000	304
Tjärrotessjön	I	7095000	1730100	35,0	1,5	7,0	13500	212
Svarttjärnen (A)	I	7095400	1730750	35,0	2,0	7,5	11000	104
Segasjön	I	7099000	1731950	35,2	2,5	15,0	13000	387
Östra fjärden	I	7107200	1748450	2,0	1,1	9,0	500	28
Klubbsundstjärnen	I	7124350	1750550	2,0	1,3	2,0	100	32
Rudtjärnen (A)	I	7137700	1759850	5,0	1,7	2,0	200	20
Holmtjärnen	I	7142750	1764750	3,0	0,9	1,5	250	8
Rudtjärnen (B)	I	7143100	1764750	3,0	1,1	2,0	600	16
Svarttjärnen (B)	I	7143900	1764800	12,0	2,2	3,0	500	44
Klöstjärnen	I	7144150	1765000	7,0	2,3	1,5	400	30

*Distance to sea was for connected lakes measured along most likely recolonization route.

Appendix 2 – Chemical variables

Lake name	Meas. depth (cm)	Abs. 254 nm	Abs. 420 nm	Cond. µS/cm	DOC (mg/l)	Tot-IC (uM/l)	HCO3- (uM/l)	pCO2 (u-atm)	CH4 (uM/l)
Stor-Tannörsavan	100	0,243	0,011	77	12,8				
Stor-Tannörsavan	150	0,254	0,012	80	11,2				
Hemavan	100	0,476	0,043	230	14,4	615,50	68,74	7048	0,15
Hemavan	150	0,509	0,045	231	15,1				
Bredvikssjön	100	1,766	0,169	139	33,9	1549,16	189,60	17525	192,22
Strandsjön	100	0,501	0,055	283	12,6	1146,06	114,77	13293	54,92
Strandsjön	150	0,620	0,055	455	14,6				
Smörbysjön	100	0,536	0,046	59	14,4	577,73	81,65	6394	0,31
Kroken	100	0,537	0,042	548	14,3	735,17	130,09	7799	19,25
Lillträsket	100	0,858	0,071	149	23,2	354,26	9,13	4449	1,03
Lillträsket	150	0,937	0,087	135	20,0				
Svartsjön	150	1,191	0,114	67	25,2	496,96	33,39	5976	0,12
Svartsjön	200	1,258	0,137	109	24,9				
Ängerfjärden	100	0,585	0,051	63	17,8	310,71	106,20	2636	0,19
Kroktjärn	100	0,681	0,058	82	19,1	891,03	274,87	7942	7,31
Kroktjärn	250	0,970	0,092	106	23,1				
Bolkarhamn	90	0,956	0,089	327	17,2	2648,02	895,53	22589	94,30
Kasaviken	100	0,488	0,033	109	14,4	540,86	77,66	5971	0,10
Kasaviken	500	0,638	0,055	116	15,3				
Häbbersvarpet	100	1,168	0,119	158	25,3	1224,63	593,57	8134	170,24
Degersjön	100	0,848	0,073	55	20,8	519,84	74,64	5739	0,12
Degersjön	250	0,908	0,083	57	23,3				
Baggösundet	100	0,563	0,046	184	16,5	1301,94	445,01	11046	556,35
Baggösundet	150	0,000	-0,001	193	17,8				
Bussjön	100	2,028	0,206	102	42,2	882,87	52,45	10704	26,01
Lill-Kvasjön	100	0,250	0,016	259	8,6	641,49	5,60	8197	25,70
Lill-Kvasjön	150	0,265	0,014	271	9,3				
Hartsjön	100	0,597	0,053	78	15,2	558,00	104,09	5851	3,34
Hartsjön	200	0,740	0,067	109	17,7				
Kråktjärnen	100	0,799	0,074	128	19,4	914,21	66,34	10929	44,08
Nördsjön	100	3,222	0,313	105	69,5	540,10	1,20	6946	0,13
Nördsjön	200	2,513	0,252	101	62,3				
Boggviksjön (A)	100	0,136	0,007	66	6,6	638,59	50,99	7574	7,08
Kråksundet	150	0,902	0,080	279	22,5	1875,89	790,60	13989	123,12
Boggviksjön (B)	90	2,309	0,207	74	54,1	1222,23	60,21	14978	137,65
Tjärnmyrtjärnen	50	1,156	0,113	118	23,9	2252,99	425,01	23562	322,02
Öviken	50	0,461	0,047	113	8,6	1330,45	233,65	14138	176,92
Vitskär	70	0,000	-0,001	190	17,4	911,78	150,05	9819	118,81
Harpsjön	100	1,329	0,119	70	31,1	206,97	21,42	2392	0,11
Harpsjön	250	1,408	0,132	68	33,8				
Kubbvikssjön	100	1,451	0,126	176	36,3	738,03	268,95	6046	2,93
Finkarstjärnen	100	0,541	0,047	69	15,4	643,69	2,81	8261	107,11
Öster-Skivsjön	100	3,928	0,095	127	104,8	776,76	4,88	9950	14,99
Tjärrotessjön	100	1,336	0,136	200	23,3	589,14	20,85	7325	1,21
Svarttjärnen (A)	100	1,012	0,099	236	21,8	538,46	6,51	6857	9,68
Svarttjärnen (A)	150	1,046	0,107	471	22,8				
Segasjön	100	1,194	0,118	44	29,3	472,34	9,23	5969	0,20
Segasjön	150	1,278	0,127	39	29,1				
Östra fjärden	100	0,460	0,042	234	8,7	625,27	182,90	5702	1,53
Klubbsundstjärnen	100	0,000	-0,002	182	17,4	1291,60	207,29	13977	163,31
Rudtjärnen (A)	100	1,158	0,122	98	30,5	547,88	94,94	5838	10,58
Holmtjärnen	80	1,709	0,177	250	31,2	1367,73	457,63	11731	158,92
Rudtjärnen (B)	50	1,523	0,166	92	26,2	466,67	86,73	4897	2,31
Svarttjärnen (B)	100	0,378	0,028	33	14,3	499,08	30,04	6046	0,40
Svarttjärnen (B)	150	0,346	0,031	49	10,6				
Klöstjärnen	100	2,145	0,186	42	59,5	658,58	3,18	8448	0,96
Klöstjärnen	200	1,576	0,172	41	28,1				

Appendix 2 – Chemical variables

Lake name	Meas. depth (cm)	Al tot ug/l	Fe tot ug/l	P tot ug/l	K ueq/l	Mg ueq/l	Na ueq/l	Ca ueq/l	BC ueq/l	DO (mg/l)
Stor-Tannörsavan	100	162	180	<16	38	132	524	224	918	3,55
Stor-Tannörsavan	150	169	203	<16	35	139	268	233	675	1,00
Hemavan	100	491	1262	27	98	392	1040	292	1823	1,70
Hemavan	150	638	3307	60	98	405	1038	303	1844	0,65
Bredvikssjön	100	1138	9055	<16	45	164	334	286	829	0,10
Strandsjön	100	2761	11756	36	100	587	435	1072	2194	0,18
Strandsjön	150	1848	7221	<16	90	503	374	983	1949	0,13
Smörbysjön	100	404	1080	<16	19	83	164	193	460	1,26
Kroken	100	1017	2904	57	113	442	805	723	2083	0,43
Lillträsket	100	771	789	<16	19	58	447	152	676	1,24
Lillträsket	150	813	2214	<16	23	73	597	204	896	0,15
Svartsjön	150	401	2509	<16	16	84	241	176	516	0,14
Svartsjön	200	434	3939	<16	15	92	251	194	551	0,12
Ängerfjärden	100	438	1425	<16	22	84	225	230	561	15,32
Kroktjärn	100	156	960	20	64	175	302	229	769	0,62
Kroktjärn	250	196	4261	<16	68	215	338	372	993	0,08
Bolkarhamn	90	488	8612	43	173	568	1227	1033	3001	0,10
Kasaviken	100	185	1118	19	74	189	295	350	908	1,23
Kasaviken	500	224	6083	39	74	191	292	406	963	0,04
Häbbersvarpet	100	170	5299	17	128	327	527	396	1378	0,26
Degersjön	100	446	1176	<16	33	90	204	210	537	4,64
Degersjön	250	472	1462	<16	30	93	203	224	549	2,21
Baggösundet	100	196	3049	40	110	323	530	559	1523	0,11
Baggösundet	150	208	3302	40	115	343	547	594	1600	0,07
Bussjön	100									0,68
Lill-Kvasjön	100	2662	1914	<16	71	338	568	493	1469	2,83
Lill-Kvasjön	150	3377	2136	<16	74	361	613	511	1559	1,65
Hartsjön	100	231	1615	<16	23	104	184	274	586	0,69
Hartsjön	200	285	3002	<16	28	129	217	371	746	0,11
Kråktjärnen	100	634	2554	<16	45	189	236	281	751	0,19
Nördsjön	100	1991	4833	37	162	509	713	655	2039	6,13
Nördsjön	200	1372	4041	25	110	366	489	487	1452	2,26
Boggviksjön (A)	100	176	670	<16	22	79	96	134	330	0,80
Kråksundet	150	208	4750	24	127	357	882	724	2090	0,12
Boggviksjön (B)	90	1604	3381	<16	20	141	220	338	720	0,86
Tjärnmyrtjärnen	50	219	4862	<16	53	188	225	430	896	0,34
Öviken	50	271	5273	<16	53	192	161	323	729	0,19
Vitskär	70	209	4080	<16	57	138	232	205	632	0,18
Harpsjön	100	494	1224	16	26	101	271	236	634	5,92
Harpsjön	250	533	1744	<16	26	91	276	227	620	0,55
Kubbvikssjön	100	215	3142	19	193	423	528	740	1885	0,43
Finkarstjärnen	100	296	661	<16	19	37	78	59	194	0,25
Öster-Skivsjön	100	1873	5714	19	40	165	425	251	880	0,30
Tjärrotessjön	100	320	2192	<16	21	101	712	231	1066	0,42
Svarttjärnen (A)	100	629	2106	<16	41	123	1242	226	1632	0,59
Svarttjärnen (A)	150	622	3195	<16	41	125	1340	234	1740	0,09
Segasjön	100	348	1483	<16	11	56	137	109	313	5,85
Segasjön	150	377	1767	<16	10	57	115	118	301	2,82
Östra fjärden	100	144	3545	46	119	408	503	366	1396	0,15
Klubbsundstjärnen	100	244	4202	<16	57	184	272	239	751	0,16
Rudtjärnen (A)	100	371	2836	<16	26	135	229	189	579	0,10
Holmtjärnen	80	314	9667	<16	86	352	303	436	1177	1,38
Rudtjärnen (B)	50	347	8647	29	73	224	293	320	909	0,61
Svarttjärnen (B)	100	223	384	<16	15	62	105	63	245	0,84
Svarttjärnen (B)	150	197	684	<16	13	60	95	55	223	0,19
Klöstjärnen	100	1176	3295	<16	25	123	266	148	561	1,39
Klöstjärnen	200	754	4243	<16	12	64	86	84	245	0,13

Appendix 2 – Chemical variables

Lake name	Meas. depth (cm)	Temp. (°C)	pH field winter	pH lab winter	pH aired winter	pH field summer	pH lab summer	pH aired summer
Stor-Tannörsavan	100	2,1	6,31	6,27	7,05	7,00	6,88	7,65
Stor-Tannörsavan	150	3,2	6,30	6,25	7,20			
Hemavan	100	2,6	5,61	5,73	6,80	6,70	6,66	7,19
Hemavan	150	3,6	5,80	5,92	6,78			
Bredvikssjön	100	1,8	5,70	5,78	7,16	6,40	6,45	6,62
Strandsjön	100	2,4	5,46	5,68	6,95	6,00	6,31	7,65
Strandsjön	150	3,7	6,50	5,60	6,91			
Smörbysjön	100	2,7	5,35	5,85	7,13	6,80	6,37	7,79
Kroken	100	2,1	6,22	5,97	7,05	6,80	6,47	6,99
Lillträsket	100	1,5	5,77	5,06	5,58	5,70	5,78	5,96
Lillträsket	150	2,7	6,44	5,50	6,49			
Svartsjön	150	3,2	5,70	5,49	6,68	6,40	5,65	6,07
Svartsjön	200	4,3	6,10	5,62	6,64			
Ängerfjärden	100	0,5	6,37	6,35	6,73	6,75	6,03	6,65
Kroktjärn	100	1,4	6,23	6,28	7,38	7,00	6,54	7,59
Kroktjärn	250	4,2	6,32	6,18	7,62			
Bolkarhamn	90	1,5	7,03	6,34	7,80	6,45	6,87	7,30
Kasaviken	100	1,4	5,90	5,86	6,80	5,30	6,48	6,77
Kasaviken	500	5,0	6,66	6,25	7,28			
Häbbersvarpet	100	1,6	6,32	6,61	7,56		6,47	7,29
Degersjön	100	1,8	5,93	5,86	7,01		6,31	6,68
Degersjön	250	4,1	5,80	5,94	6,69			
Baggösundet	100	1,8	6,53	6,35	7,60		6,89	7,21
Baggösundet	150	2,9	6,51	6,35	7,29			
Bussjön	100	1,4	5,85	5,44	6,51	6,43	5,68	6,26
Lill-Kvasjön	100	1,8	4,66	4,58	4,58	5,00	4,96	5,04
Lill-Kvasjön	150	2,5	4,53	4,58	4,51			
Hartsjön	100	2,5	6,00	6,00	7,09	6,00	6,29	6,79
Hartsjön	200	4,4	6,53	6,14	7,34			
Kråktjärnen	100	1,7	5,77	5,53	6,81	5,15	5,46	6,00
Nördsjön	100	0,4	4,13	3,98	4,05	5,60	5,56	5,98
Nördsjön	200	2,4	5,87	4,24	4,32			
Boggviksjön (A)	100	2,4	6,16	5,57	7,14	5,40	5,44	5,91
Kråksundet	150	3,0	6,80	6,50	7,53	7,40	6,82	7,63
Boggviksjön (B)	90	1,7	5,10	5,35	6,34	5,50	5,68	6,25
Tjärnmyrtjärnen	50	0,7	5,70	6,00	7,54	6,85	6,63	7,12
Öviken	50	1,2	5,70	5,96	7,29	5,55	5,60	6,58
Vitskär	70	2,5	6,32	5,93	7,04	7,70	6,53	6,83
Harpsjön	100	1,4	5,59	5,70			6,26	6,48
Harpsjön	250	3,8	5,51	5,72	6,80			
Kubbvikssjön	100	2,6	6,37	6,39	7,18	5,55	6,02	6,59
Finkarstjärnen	100	2,6	5,71	4,28	6,80	6,50	5,94	7,02
Öster-Skivsjön	100	2,5	5,18	4,44	4,55		4,90	5,03
Tjärrotessjön	100	1,3	5,44	5,20	5,39		5,60	6,09
Svarttjärnen (A)	100	1,5	5,97	4,72	5,23		5,11	5,30
Svarttjärnen (A)	150	3,3	5,72	4,93	5,42			
Segasjön	100	2,1	4,70	4,93	6,07		5,33	6,09
Segasjön	150	3,1	4,90	4,94	5,40			
Östra fjärden	100	2,6	7,00	6,25	6,66	6,15	6,63	7,12
Klubbsundstjärnen	100	2,2	6,71	5,92	7,26	6,60	6,35	6,37
Rudtjärnen (A)	100	2,6	6,19	5,96	7,01	6,10	6,18	7,40
Holmtjärnen	80	1,3	6,80	6,34	7,45	6,70	6,71	7,02
Rudtjärnen (B)	50	0,1	5,96	5,99	7,28	6,10	6,18	6,83
Svarttjärnen (B)	100	2,4	5,46	5,44	6,87	5,80	5,88	5,98
Svarttjärnen (B)	150	3,5	6,10	5,45	6,68			
Klöstjärnen	100	1,6	4,72	4,32	4,61	5,40	5,41	5,86
Klöstjärnen	200	4,0	5,29	5,05	5,86			

Appendix 3 – Fish species

Lake name	**Fish Group 1**			**Fish Group 2**		**Fish Group 3**				
	Crucian carp	**Three spined s.b.**	**Nine spined s.b.**	**Pike**	**Perch**	**Roach**	**Ruffe**	**Bleak**	**Ide**	**Bream**
Stor-Tannörsavan	0	0	0	1	1	1	1	0	1	0
Hemavan	0	0	0	1	1	1	1	0	0	0
Bredvikssjön	1	0	0	0	1	0	0	0	0	0
Strandsjön	0	0	0	1	1	1	0	0	0	0
Smörbysjön	0	0	0	1	1	1	0	0	0	1
Kroken	0	0	0	1	1	1	0	1	0	1
Lillträsket	0	0	0	1	1	1	0	0	0	0
Svartsjön	0	0	0	1	1	0	1	0	0	0
Ängerfjärden	0	0	0	1	1	1	1	0	0	0
Kroktjärn	1	0	1	0	0	0	0	0	0	0
Bolkarhamn	0	0	0	1	1	1	1	1	0	0
Kasaviken	1	0	0	1	1	1	1	0	0	1
Häbbersvarpet	1	0	1	0	0	0	0	0	0	0
Degersjön	0	0	0	1	1	1	0	0	0	0
Baggösundet	1	0	1	1	1	1	0	0	0	0
Bussjön	0	0	0	1	1	0	0	0	0	0
Lill-Kvasjön	0	0	0	1	1	0	0	0	0	0
Hartsjön	0	0	0	1	1	1	0	0	0	0
Kråktjärnen	0	0	0	1	1	0	0	0	0	0
Nördsjön	0	0	0	1	1	0	0	0	0	0
Boggviksjön (A)	1	0	0	0	1	0	0	0	0	0
Kråksundet	1	0	1	0	0	0	0	0	0	0
Boggviksjön (B)	1	0	0	1	0	0	0	0	0	0
Tjärnmyrtjärnen	0	0	0	0	0	0	0	0	0	0
Öviken	0	0	0	0	0	0	0	0	0	0
Vitskär	1	1	1	0	0	0	0	0	0	0
Harpsjön	0	0	0	1	1	1	0	0	0	0
Kubbvikssjön	1	0	0	1	1	1	0	0	0	0
Finkarstjärnen	0	0	0	0	0	0	0	0	0	0
Öster-Skivsjön	0	0	0	0	0	0	0	0	0	0
Tjärrotessjön	0	0	0	1	1	0	0	0	0	0
Svarttjärnen (A)	0	0	0	1	0	0	0	0	0	0
Segasjön	0	0	0	1	1	0	0	0	0	0
Östra fjärden	1	0	0	1	1	0	0	0	0	0
Klubbsundstjärnen	1	0	0	0	0	0	0	0	0	0
Rudtjärnen (A)	1	0	0	1	0	0	0	0	0	0
Holmtjärnen	1	0	1	0	0	0	0	0	0	0
Rudtjärnen (B)	1	0	0	0	0	0	0	0	0	0
Svarttjärnen (B)	0	0	0	0	1	0	0	0	0	0
Klöstjärnen	0	0	0	0	0	0	0	0	0	0

Appendix 3 – Fish species

Lake name	Species richness	FG 1	FG 2	FG 3
Stor-Tannörsavan	5	0	1	1
Hemavan	4	0	1	1
Bredvikssjön	2	1	1	0
Strandsjön	3	0	1	1
Smörbysjön	4	0	1	1
Kroken	5	0	1	1
Lillträsket	3	0	1	1
Svartsjön	3	0	1	1
Ängerfjärden	4	0	1	1
Kroktjärn	2	1	0	0
Bolkarhamn	5	0	1	1
Kasaviken	6	1	1	1
Häbbersvarpet	2	1	0	0
Degersjön	3	0	1	1
Baggösundet	5	1	1	1
Bussjön	2	0	1	0
Lill-Kvasjön	2	0	1	0
Hartsjön	3	0	1	1
Kråktjärnen	2	0	1	0
Nördsjön	2	0	1	0
Boggviksjön (A)	2	1	1	0
Kråksundet	2	1	0	0
Boggviksjön (B)	2	1	1	0
Tjärnmyrtjärnen	0	0	0	0
Öviken	0	0	0	0
Vitskär	3	1	0	0
Harpsjön	3	0	1	1
Kubbvikssjön	4	1	1	1
Finkarstjärnen	0	0	0	0
Öster-Skivsjön	0	0	0	0
Tjärrotessjön	2	0	1	0
Svarttjärnen (A)	1	0	1	0
Segasjön	2	0	1	0
Östra fjärden	3	1	1	0
Klubbsundstjärnen	1	1	0	0
Rudtjärnen (A)	2	1	1	0
Holmtjärnen	2	1	0	0
Rudtjärnen (B)	1	1	0	0
Svarttjärnen (B)	1	0	1	0
Klöstjärnen	0	0	0	0