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Increasing algal biomass in Swedish lakes despite decreasing phosphorus concentration

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Abbreviation list

List of chemical and physical water variables

- Total Phosphorus (Tot-P), measured in µg/l
- Total Nitrogen (Tot-N), measured in µg/l
- Nitrate (NO3), measured in µg/l
- Ammonium nitrogen (NH4-N), measured in µg/l
- Nitrite and Nitrate (NO2+NO3-N), measured in µg/l
- Total Organic Carbon (TOC), measured in mg/l
- Sulphate (SO4_IC), measured in mekv/l
- Temperature (Temp), measured in °C
- Temperature difference (Temp diff), measured in °C
- Absorbance (Abs.), measured in 420nm/5cm
- pH
- Conductivity Kond_25, measured in mS/m25
- Total volume of all the algal groups (Tot.volym)
- Alkalinity (Alk./Acid), measured in mekv/l
- Chloride (Cl), measured in mekv/l
- Calcium (Ca), measured in mekv/l
- Magnesium (Mg), measured in mekv/l
- Sodium (Na), measured in mekv/l
- Potassium (K), measured in mekv/l
- Total organic carbon / Total phosphorus ratio (TOC:TP)
- Total organic carbon / Total nitrogen ratio (TOC:TN)
- Ammonium nitrogen / Total phosphorus ratio (NH4:P)
- Nitrate / total phosphorus ratio (NO3:P)
- Total Nitrogen / Total phosphorus ratio (N:P)

Abstract: Algal growth in freshwaters is usually limited by phosphorus but occasionally even nitrogen and light limitations can occur, particularly in unproductive systems. In order to investigate what kind of variables might affect algal growth in Swedish oligotrophic lakes I used time series of 22 years of physical, chemical and biological lake variables for 13 lakes distributed all over Sweden. The study showed that algal biomass significantly increased at the same time as phosphorus, nitrogen and light conditions significantly decreased. Many variables showed strong significant changes over time and several of the changes occurred coherently among the lakes. I suggest that pH, temperature and to some extent even absorbance are among the variables that most likely stimulated algal growth in the Swedish unproductive lakes. Temperatures increased by about 0.5 - 2 degrees over the time period and pH increased by 0.1-0.3 units. I conclude from this study that algal growth in Swedish unproductive lakes is presently not primarily driven by phosphorus and nitrogen concentrations that both decline but rather by pH and temperature increases. Future studies should have more focus on dominance patterns of certain species that might be responsible for the observed algal biomass increase.

Introduction

Eutrophication of both inland- and marine waters has increased tremendously during the last decades from a global perspective (Savage *et al.* 2010) causing large algal blooms. The main reason for this strong increase is thought to be higher anthropogenic releases of nutrients into nature, primarily in form of phosphorus (Smith & Schindler 2009) but also nitrogen (Elser *et al.* 2009). The increasing release of phosphorus and nitrogen has substantially contributed to elevated levels even in inland waters (Abell *et al.* 2010). In the northern hemisphere increasing precipitation due to climate changes might accelerate the process, resulting in enhanced runoff of phosphorus and nitrogen from land to water, this especially being the case in coastal regions (Jeppesen *et al.* 2009). Nitrogen has an additional source, i.e. atmospheric deposition, which has caused strong nitrogen pollution in nature during the last century. The strong pollution is largely due to an increased production of reactive nitrogen, where global rates have doubled during the last century (Galloway & Cowling 2002). Attempts to counteract eutrophication have primarily been done by decreasing the anthropogenic release of phosphorus, but despite these attempts algal blooms still occur and increase in many areas. Schindler (1977) performed several experimental studies in Canadian lakes during the 1970´s and showed that algal blooms are limited by phosphorus. Consequently, Schindler (1997) concluded that a reduction of phosphorus is the most efficient way to reduce algal blooms in lakes. Due to the results of the Canadian studies phosphorus excess has been seen as the largest problem when inland waters suffer from algal blooms.

But in fact the paradigm of phosphorus as the limiting nutrient for algae can be rooted back as far as Neumann's paper from 1919 (Lewis & Wurtsbaugh 2008). Nutrient reductions have been performed in many lakes around the world and often with a positive result (Sas 1989; Marsden, 1989; Jeppesen *et al.* 2005). Due to the paradigm of phosphorus as the most important limiting nutrient, nutrient reductions have mainly focused on a decrease of anthropogenic phosphorus. Even though water quality, here defined as presence and absence of algal blooms, has in many cases improved by the removal of phosphorous, there are cases where phosphorus removal was not sufficient and water- and environmental goals have not been fulfilled, especially in estuaries and coastal environments (Conley *et al.* 2009).

Recent studies showed deviating conclusions about the causes of eutrophication, some claiming that a decrease of phosphorus is not the only solution due to nitrogen limitation

(Conley *et al*. 2009, Howarth & Pearl 2008) and some others claiming that phosphorus is the most important component to achieve decreasing algal blooms (Smith & Schindler 2009). A debate over the Redfield ratio (N:P) is also currently increasing. Studies showed that the optimal N:P ratio might differ dramatically, all the way from 8,2 to 45,0, depending on lake condition. One of the explanations for this is that the Redfield ratio might be an average on species-specific ratios instead of an optimum (Klausmeier *et al.*2004). N:P ratio might also differ depending on algal species since different algal species have different N:P optima and also their capability of adaptive plasticity may differ considerably (Rhee 1978, Sterner & Elser 2002 and Klausmeier *et al.*. 2004). One of the phytoplankton genera that show plasticity in altered N:P conditions are cyanobacteria. When both pH and N:P ratios are low, cyanobacteria become phosphorus limited and can then have a higher cellular N:P ratio (Sterner 1994). This is why cyanobacterial blooms often can be seen as a key symptom to eutrophication (Conley *et al.* 2009). There is also a risk with altered N:P ratios with nitrogen increase, if the lake already is natural nitrogen-limited, increasing inorganic nitrogen may lead to eutrophication (Bergström *et al.* 2005).

With climate change not only runoff patterns and thereby nutrient loading but also several other aspects will change in the lakes, as for example mixing conditions, trophic structure and water temperature (Jeppesen *et al.* 2009). With new research concerning increases of nutrient loads in nature a debate has erupted about what really is controlling algal blooms and how these blooms can be managed. New studies show that other factors may play an important role for the explanation of increasing algal biomass, such as temperature, light, stratification, and other nutrients than phosphorus and nitrogen (Houser 2006, Karlsson *et al.* 2009 and Evans *et al.* 2005) . One of those studies showed that in nutrient-poor lakes in Sweden algal biomass growth are not limited by nutrient availability, as the usually paradigm (Karlsson *et al.* 2009). In the study it was suggested that nutrient limitation might not be the controlling factor in unproductive lakes and that lakes´ productivity can be limited by light instead of nutrients. Other studies on light limitation have shown the correlation between an increasing water colour and decreasing light penetration (Houser 2006). Water colour is not only affecting the light climate, but also the water temperature and thermocline depth, especially in small lakes (Houser 2006).

The objective of this study was to explore temporal variations of algal biomass in unproductive Swedish lakes and to relate them to temporal variations of physical and chemical lake variables both in surface and bottom waters. Due to Karlsson's *et al.* (2009) observation that nutrients might not limit algal biomass in unproductive lakes, I hypothesized that algal biomass is increasing as a result of warmer water temperatures and stronger thermal stratifications. To test the hypothesize I first analyzed temporal variations of algal biomass where I considered different phytoplankton groups, I also analyzed temporal variations of physical and chemical lake variables in both surface and bottom waters. For the analyses I used a dataset of 13 lakes distributed all over Sweden from the Swedish lake inventory program. As a next step I tried to link physical and chemical variables to algal biomass growth. As a last step I investigated changes in seasonality of algal biomass, water chemical and physical variables in order to evaluate whether changes occurred during a specific season.

Materials and methods

Study lakes

To perform this study I used the Swedish lake inventory database, available at (www.slu.se/vatten-miljö). I selected the 13 lakes that had a monthly monitoring program. The 13 lakes were distributed all over Sweden and monthly data were available during the ice-free season from May to October from 1988 to 2010 (Figure 1).

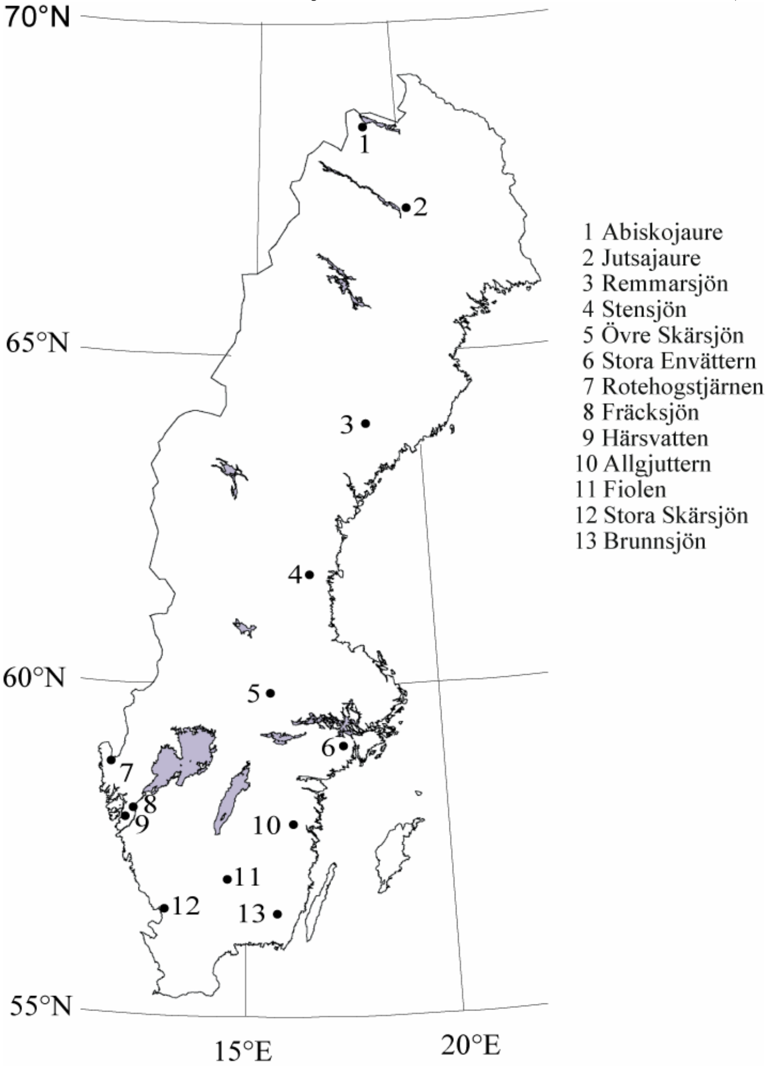

Figure 1. Map over Sweden with the locations of the 13 lakes (figure taken by permission of Gesa Weyhenmeyer)

Lake catchment areas

Depending on their location in Sweden the catchment area for each lake differed, but all lakes were boreal lakes with a natural acidity. The 13 lakes were distributed along a latitudinal gradient, with Abiskojaure as the most northern lake and Brunnsjön as the most southern lake. Abiskojaure was the only lake that was not a boreal but instead an alpine lake. The only lake that has notable agriculture in its catchment area is Lake Fiolen, with 26% agriculture and open terrain area (Table 1).

Table 1. Catchment characteristics of the 13 study lakes.

% Catchment area/lake	Abiskojaure	Jutsajaure	Remmarsjön	Stensjön	Övre Skärsjön	Stora Envättern	Rotehog-stjärnen
Lake	1	6	1	13	18	24	5
Other water	4	1	2	-	-	1	-
Forest	8	62	53	57	54	55	69
Clear cut	0	0	30	11	14	0	5
Bare rock	-	4	-	-	-	-	-
Block and rocky ground	16	-	-	-	-	-	-
Glaciers	3	-	-	-	-	-	-
High and low herb meadows	12	-	-	-	-	-	-
Sticks and grass heath	42	-	-	-	-	-	-
Snow patches	10	-	-	-	-	-	-
Willow	3	-	-	-	-	-	-
Mire, open	1	25	7	19	3	0	18
Mire, covered	0	0	6	0	7	20	0
Agricultural land	0	1	0	0	4	0	1
Open terrain, roads etc.	0	1	1	0	0	0	2

% Catchment area/lake	Fräcksjön	Härsvatten	Allgjuttern	Fiolen	Stora Skärsjön	Brunnsjön
Lake	6	10	16	30	14	4
Other water	-	9	-	-	4	-
Forest	79	68	66	39	54	85
Clear cut	5	0	14	1	12	6
Bare rock	-	-	-	-	-	-
Block and rocky ground	-	-	-	-	-	-
Glaciers	-	-	-	-	-	-
High and low herb meadows	-	-	-	-	-	-
Sticks and grass heath	-	-	-	-	-	-
Snow patches	-	-	-	-	-	-
Willow	-	-	-	-	-	-
Mire, open	1	7	1	1	4	0
Mire, covered	7	6	3	3	10	4
Agricultural land	1	0	0	19	0	0
Open terrain, roads etc.	1	0	0	7	2	1

Data material

Data from each lake were downloaded from two different measured depths, surface - (depth 0.5 m) and bottom water (approximately 1 m above the lake bottom). The dataset consisted of several water chemical variables (List of chemical- and physical water variables, abbreviation list) and also the biomass of the main eight phytoplankton groups.

Statistical analyses
To test variations over time I chose to work with the program MULTMK/PARTMK, which is a program for multivariate and partial Mann-Kendall statistics that runs in excel. The Mann-Kendall test is a non-parametric statistical test, which is used to check for the significance in trends, especially when working with hydrological time-series (Yue *et al.* 2002). The advantage of using a non-parametric test is that the data doesn’t have to by normally distributed. The Mann-Kendall test shows the increase or decrease of a data point as a binary result (P. H. Dimberg 2011). This means that the Mann-Kendall test works well for randomly distributed data. However, the higher variation the data have, the lower is the power of the test (Yue *et al.* 2002).

When using MULTMK/PARTMK I performed three steps. The first step was a combined partial test which shows the general trend over a whole time-series for each variable, giving a Mann-Kendall value (MK-stats) for increasing/decreasing trends. The calculated MK- stats are the standardized test-given statistics (who are standard normal distributed). The p-value is form a two-sided test, which gives twice the probability to receive a MK-stat as low/lower or as high/higher as the computed MK-statistic.
The second step was a univariate test that shows in which month the increase or decrease has occurred and if these changes are significant. This approach gives the opportunity to compare the months against each other to see if a trend is stronger during a particular month, i.e. it is a measure of changes in seasonality for each variable.
The third step was a correlation matrix over all variables, which gives the similarity in the different trends the variables have.

The program was first developed by Anders Grimvall (MULTIMK) and later amended by Claudia Libiseller (MULTIMK/PARTMK) (Libiseller 2004).

Data preparation

a. Interpolation

Although the 13 lakes where chosen for their availability of long-term data, interpolation was still needed on all datasets in order to receive complete data series. The number of missing data differed widely both between the lakes and between the phytoplankton- and water chemistry data (Table 1).

Table 1. Number of missing values for the 13 study lakes, the numbers show how many years there were when at least one data point was missing, the numbers in brackets indicate the maximum number of missing data points within one year. The star marks lakes for which there were no data during the last six years.

LAKE	NUMBER OF MISSING CHEMISTRY DATA		NUMBER OF MISSING PHYTOPLANKTON DATA
	SURFACE	BOTTOM	
Abiskojaure	8	9	10 (6)
Jutsajaure	10 (1)	9 (1)*	10 (6)
Remmarsjön	3	3	10 (4)
Stensjön	3	3	7 (4)

Övre Skärsjön	0	0	4 (4)
Stora Envättern	0	0	4 (4)
Rotehogstjärnen	2	3	8 (4)
Fräcksjön	0	1	3 (1)
Härsvatten	7	6	7 (1)
Allgjuttern	3	2	7 (4)
Fiolen	1	1	5 (4)
St Skärsjön	1	1	6 (4)
Brunnsjön	2	2	8 (4)

All lake datasets needed some interpolation. After year 2000 there are no data for the variables Ca, Mg, Na, K, alkalinity, SO_4 and Cl in the bottom water. Due to the high degree of missing data, these variables were never interpolated between the years 2000-2010.

There were also some algal groups which were almost never found in the lakes, hence pointing to very scare existence. To clarify the presence of the different algal groups I put a criterion for existence, to get an idea of how common the different groups were and to be able to remove the groups which never were present. The requirement for present was that the algal groups should at least have a mean that’s higher than 0.01 mm^3/L during the whole time period. This left me with eight different algal groups, which at least in one lake had a mean that was higher than 0.01 mm^3/L.

The interpolation of the datasets where all done in the same way, with data sets ranging from 1988-2010, from May to October. Except from the two most northern lakes, Abiskojaure and Jutsajaure, where only values from June to August during the same time where used, this due to the longer ice cover over the lakes. The interpolation was done in three steps, were steps 2 and 3 only were used if step 1 didn’t fully interpolate the dataset.

Step 1: In many cases when no data were recorded for one month, there were two measurements in the month before or after. This could look like: no data available for June but two data points available for July. I considered then the first measurement in July as a June value. Most commonly for this step was missing May values where I could use late April values instead.

Step 2: Linear interpolation done by the TREND-function in excel, which returns values along a linear trend. For example; one May value was missing in 2002, then I could calculate that value by using all the other May values during my time period. This was done only on the first and last month, were the formula used in step 3 couldn’t be used.

Corrections after step 2: Sometimes after using the TREND-function corrections were needed. This was the case when I calculated values for the different algal groups. If one algal group was present in the beginning of the time period but no longer later in the year, the TREND function showed negative values after the disappearance. These values were instead corrected to zero.

Step 3: Linear interpolation by using the formula: $Y2 = Y0 + (Y1-Y0)/(X1-X0)*(X2-X0)$, where X corresponds to months and Y to the required variable. The equation is a linear interpolation where extreme values are not considered. This step was important for minimizing the risk of missing a trend that a specific year could have.

The variable total phytoplankton volume was never interpolated, but instead calculated by adding all values from the different phytoplankton groups, this was done so the total volume would always be consistent with the total algal groups and never exceed/fall below them.

To make sure that the interpolation did not affect any trend over time, several graphs were made where I compared unmodified time series with interpolated ones.

Results

Reliability of interpolated data

Comparing interpolated with raw-data showed that there was a good agreement (Fig. 2), making the interpolation method reliable

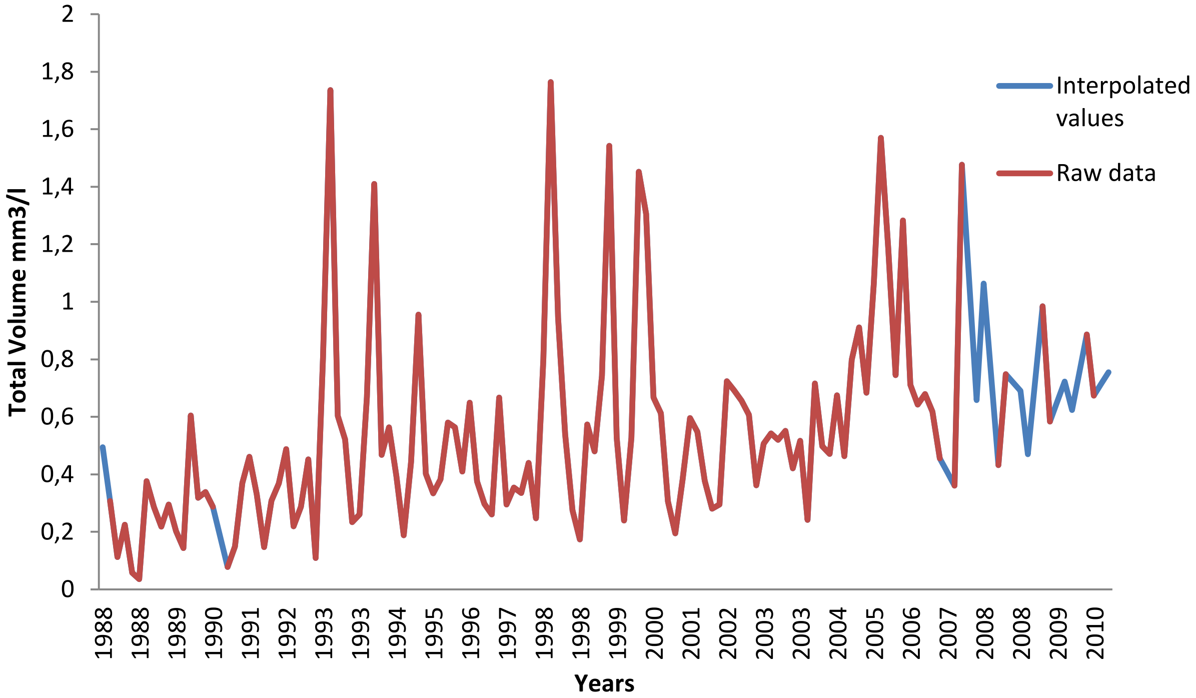

Figure 2. Example of joint interpolated data and raw data: Graph showing algal biomass growth in the lake Stora Skärsjön from 1988 unto 2010, where the raw data is showed in red and the interpolated data in blue.

Trends in algal biomass

The total algal biomass significantly increased in 10 out of 13 lakes and only decreased in one of the lakes, though not significantly (Table 3.) Among different algal groups the most significant and coherent increase was for Cryptophyceae that were increasing in 12 out of 13 lakes during 1988 to 2010. Least changes were observed for Haptophyceae, which only had an increase in six out of 13 lakes. All the other groups had significant increases in between 7 to 11 lakes. The lake that was deviating most from the general trend of increase was Rotehogsstjärnen, where both the total volume and three of the algal groups were decreasing, although the decrease was not significant. Several of the lakes showed an increase in all of the algal groups and in total volume, where the lake with most significant increases was Stora Envättern (Table 3).

Table 3: MK-stats for growth of the different algal groups and the total volume, where a positive MK-value stands for an increase and a negative for a decrease. Significant MK-values are shown with; *<0.05, **<0.001, *<0.001. When no MK- value was available it's marked with N/A. Test results that are deviating from the general trend are marked with red. The lakes are arranged in order from north to south, with Abiskojaure as the most northern lake and Brunnsjön as the southernmost lake. The number in brackets after the algal groups name indicates in how many of the lakes the algal group is present in. Where requirement for present is that the algal groups should at least have a mean that's higher then 0.01mm^3/L during the whole time period**

Lakes/ Algae group	Total volym	Cyanophyceae (7)	Cryptophyceae (12)	Dinophyceae (13)	Raphidophyceae (4)
	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat
Abiskojaure	2.8*	N/A	4.2***	2.5*	N/A
Jutsajaure	3.8***	2.3*	3.5***	2.5*	N/A
Remmarsjön	1.3	3.8***	2.1*	1.1	-1.0
Stensjön	0.2	2.3*	3.5***	3.7***	2.5*
Övre Skärsjön	2.7*	2.1*	3.9***	1.8	2.6**
Stora Envättern	4.0***	2.9**	3.5***	3.0**	3.5***
Rotehogstjärnen	-1.3	3.0**	1.8*	-0.6	-1.8
Fräcksjön	3.1*	2.7**	3.3***	3.3**	2.9**
Härsvatten	2.8*	-1.1	4.2***	2.4*	2.0*
Allgjuttern	4.3***	3.4***	4.1***	-1.8	N/A
Fiolen	3.0*	4.2***	2.7**	0.5	3.2**
St Skärsjön	4.2***	2.9**	0.8	3.6***	3.9***
Brunnsjön	2.2*	-1.1	4.0***	1.7	0.9

Lakes/ Algae group	Chrysophyceae (13)	Bacillariophyceae (10)	Chlorophyceae (11)	Haptophyceae (2)
	MK-Stat	MK-Stat	MK-Stat	MK-Stat
Abiskojaure	1.0	2.1*	3.2**	1.9
Jutsajaure	4.0***	1.5	3.3**	2.6**
Remmarsjön	4.2***	-1.8	2.8**	0.1
Stensjön	4.1***	1.4	-2.6**	2.8**
Övre Skärsjön	3.3***	2.0	3.2**	1.3
Stora Envättern	3.4***	3.9***	2.6*	1.9
Rotehogstjärnen	2.6**	4.2***	3.1**	0.0
Fräcksjön	2.7**	1.5	3.0**	4.0***
Härsvatten	3.3**	2.7**	1.8	0.2
Allgjuttern	2.7**	4.0***	4.6***	4.7***
Fiolen	1.6	2.5*	3.5***	3.2**
St Skärsjön	3.7***	0.3	2.5*	4.0***
Brunnsjön	1.0	3.4***	1.0	0.6

Trends in water chemical and physical variables in lake surface waters

Total phosphorus was the variable with most significant coherent changes, where in 12 out of 13 lakes a significant decrease was observed. Other variables with strong coherent changes was the absorbance and the TOC, where they were increasing in all lakes except one, and significantly changing in 12 out of 13 lakes. In contrast total nitrogen was the variable with least changes, with only two lakes that showed significant decrease. The variables that showed most coherencies, though not significant, were the pH and the temperature difference with an increase in all lakes (Table 4). The lake that were deviating the most from the general trend was Lake Abiskojaure, with three out of seven variables deviating. Also lake Fiolen showed deviating trends concerning the variables Tot-P and Tot-N, which where both increasing, though not significantly (Table 4).

Table 4. MK-stats on the chemical and physical variables in the surface waters of the 13 studied lakes. A positive MK-stat stands for an increase and a negative for a decrease. Significant Mann-Kendall values are shown as *<0.05, **<0.001, *<0.001 When no Mann-Kendall value was available it's marked with N/A. Test results that are deviating from the general trend are marked with red.**

Lakes/Water variables	Tot-P	Tot-N	pH	Abs.	TOC	Temp.	Temp. diff.
	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat
Abiskojaure	-3.8***	0.6	3.8***	-2.1*	-2.1*	1.5	0.2
Jutsajaure	-3.6***	-2.6**	3.4***	1.3	0.7	0.3	2.7**
Remmarsjön	-2.4*	-1.0	2.2*	2.3*	2.1*	2.5*	1.7
Stensjön	-3.6***	-1.7	1.5	3.6***	2.4*	1.7	0.5
Övre Skärsjön	-2.8**	-3.1**	4.3***	3.6***	4.1***	2.0*	2.1*
Stora Envättern	-2.5*	-0.1	1.7	3.9***	4.2***	2.6*	3.7***
Rotehogstjärnen	-2.3*	-1.4	1.9	3.1**	3.4***	1.5	0.8
Fräcksjön	-2.3*	-1.3	3.5***	4.1***	4.3***	3.3**	3.2**
Härsvatten	-2.9**	-1.7	5.6***	4.4***	3.8***	2.2	2.5*
Allgjuttern	-3.2**	-1.6	2.7**	3.4***	3.0**	-0.3	0.8
Fiolen	0.7	1.0	4.5***	4.3***	4.1***	2.6**	1.7
St Skärsjön	-2.4*	-1.3	3.6***	4.2***	2.0*	2.5*	2.6**
Brunnsjön	-2.2*	0.0	3.1**	2.2*	2.4*	0.3	1.7

Trends in water chemical and physical variables in lake bottom waters

Bottom waters showed some deviating trends from the surface waters, where the variables with highest differences from the surface water were temperature, Tot-P and Tot-N (Table 4 and 5). For the variables pH, absorbance and TOC, the general trend was similar to the trends in the surface water (Table 4 and 5). The variable that showed most significant coherent trends was the absorbance where it was significant in all the lakes except of Lake Abiskojaure which showed a decrease instead although not significant. The variable that had least significant trends was temperature, were only trends in three lakes were significant (Table 5). The lake that differed mostly from the general trend was Lake Abiskojaure, which had significant decrease in both Abs. and TOC, which no other lake had (Table 5).

Table 5. Mann-Kendall values on the chemical variables in the bottom water in all the lakes, where a positive MK-value stands for an increase and a negative for a decrease. Significant Mann-Kendall values are shown with; *<0.05,

****<0.001, ***<0.001 and when no Mann-Kendall value is available it's marked with N/A. Test results that are deviating from the general trend are marked with red.**

Lakes/Water variables	Tot-P	Tot-N	pH	Abs.	TOC	Temp.
	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat
Abiskojaure	-3.7***	0.3	4.4***	-2.8**	-2.3*	2.4*
Jutsajaure	-3.9***	-0.4	3.0**	2.9**	1.2	-1.2
Stensjön	-3.8***	-1.5	2.1*	2.6**	2.1*	1.8
Remmarsjön	-2.1*	-0.6	1.6	3.7***	2.1*	0.7
Övre Skärsjön	-0.6	-2.7**	3.0**	3.0**	4.0***	-1.3
Stora Envättern	0.0	2.6**	-0.8	3.7***	4.2***	-3.6***
Rotehogstjärnen	2.0	1.8	2.9**	3.7***	3.1**	1.1
Fräcksjön	-0.9	0.1	2.5*	2.9**	3.7***	-0.2
Härsvatten	3.0**	3.0**	5.2***	5.2***	4.3***	-1.6
Allgjuttern	-1.0	-0.7	0.8	3.8***	3.3**	-2.7**
Fiolen	0.6	1.3	4.0***	4.1***	4.3***	0.0
St Skärsjön	-1.3	0.7	2.6**	2.3*	1.4	-1.4
Brunnsjön	0.8	2.1*	3.3***	2.9**	3.0**	-2.9**

Seasonality changes in algal biomass

The month that had the highest increase for all algal groups was June and it was also during this month were the two most significant increasing groups, Cryptophyceae and Chrysophyceae, were increasing in most lakes. May was the month with least significant increases, by nearly half as many increases as compared to other months, were the months July to October all were quite similar (Table 6).

There was no clear seasonality within the algal groups, but two main trends were stronger in the different groups. The first trend had a high increase during the summer months (June to August/September), with lower increases in May and October, as for Cryptophyceae, Chrysophyceae. Whereas the other trend was increasing more and more over the months and had highest values in the last months, as for Dinophyceae, Chlorophyceae (Table 6). The total volume showed no clear sign of seasonality (Table 6).

Table 6. Seasonality patterns of different algal groups and the total algal biomass, A significant increase is shown as 1+ and a significant decrease is shown as 1-. The table shows the results from all 13 lakes which give a maximum/minimum number of 13 for each month, except for May and October were the maximum number is 11 due to missing data in the two most northern lakes.

Algal groups/Months	Total volume	Cyanophyceae	Cryptophyceae	Dinophyceae	Raphidophyceae
May	4+	2+	7+	1+	2+
June	6+	6+	11+	4+	3+
July	6+	4+	9+	3+1-	3+1-
August	6+	5+	11+	4+	1+
September	4+	8+	6+	5+1-	4+1-

October	5+	7+1-	5+	6+1-	6+

Algal groups/Months	Chrysophyceae	Bacillariophyceae	Chlorophyceae	Haptophyceae
May	4+	1+	3+1-	3+
June	9+	7+	6+	6+
July	8+	7+	6+	4+
August	7+	4+	8+1-	5+
September	7+	8+1-	8+1-	5+
October	5+	4+	8+2-	4+

Seasonality changes in water chemical and physical variables of surface waters
The variables with strongest seasonality in the surface water were temperature and the temperature difference, both with high increases under September and none/few increases in the early months. Also pH showed seasonality, with highest increases in the early months towards a declining increase (Table 7). The other variables didn't show any seasonality, with absorbance and Tot-N showing the highest coherency with high increases/low decreases during all months, while the other variables showed a random stochasticity (Table 7).

Table 7. The seasonality of chemical variables in the surface water, A significant increase is shown as 1+ and a significant decrease is shown as 1-. The table shows the results from all 13 lakes which give a maximum/minimum number of 13 for each month, except for May and October were the maximum number is 11 due to missing data in the two most northern lakes.

Water variables/Months	Tot-P	Tot-N	pH	Abs.	TOC	Temp.	Temp. diff.
May	3-	2-	9+	10+	9+	0	0
June	5-	1-	9+	11+	7+	0	1+
July	7-	2-	9+	9+	9+	3+	3+
August	5-	1-	8+	9+	4+	1+	2+
September	8-	2-	6+	10+	8+	7+	6+
October	6-	1-	5+	11+	6+	2+	3+

Seasonality changes in water chemical and physical variables of bottom waters
None of the variables in the bottom water showed any strong seasonality, though some of the variables showed similarity in trends against the surface water. The variables most similar to the surface water were absorbance and TOC, though the absorbance didn't show the same coherency as in the surface water (table 8).

Table 8. The seasonality of chemical variables in the bottom water, A significant increase is shown as 1+ and a significant decrease is shown as 1-. The table shows the results from all 13 lakes which give a maximum/minimum number of 13 for each month, except for May and October were the maximum number is 11 due to missing data in the two most northern lakes.

Water variables/Months	Tot-P	Tot-N	pH	Abs.	TOC	Temp.
May	3-	0	5+	11+	10+	2-
June	3-2+	1+	8+	11+1-	9+	3-
July	2-2+	2+	6+	9+	9+	2-1+
August	3-1+	3+	7+	7+1-	6+	1-1+
September	4-1+	4+	8+	7+	8+1-	3-
October	3-1+	3+1-	3+1-	9+	9+	3-1+

Correlations between algal biomass and water chemical and physical variables in surface waters

The correlation matrix from all 13 lakes showed that pH had the strongest correlation with the algal increase. Least significant correlations to the algal biomass were achieved for Tot-N and the temperature. Tot-P is the only variable that showed a clear negative correlation, were the decrease in Tot-P was correlating with the increase in the different algal groups (Table 9).

The algal groups that showed strongest correlation with the different variables was Cryptophyceae and Chrysophyceae, both with strong correlation to the increase in pH, also a clear correlation to absorbance, TOC and Tot-P. While the groups that had least correlation with the different variables were Dinophyceae and Raphidophyceae (Table 9).

Table 9. Correlation between surface water variables and the different algal groups, where a correlation with similar trend is shown with 1+ and correlation with an opposite trend is shown with 1-. If their only are positive correlations the cell is marked yellow, only negative correlation the cell is marked blue and if there is both the cell is marked green. This is a combined matrix with values from all lakes, which gives a maximum of correlations to 13+/13-.

Water variables/ algal groups	Temp.	Temp. diff.	pH	Tot-N	Tot-P	Abs.	TOC
Tot.volym	1+	1+	10+		1+,4-	6+	4+
Cyanophyceae	2+	2+	4+			3+,1-	3+,1-
Cryptophyceae	2+	3+	9+	1-	5-	7+	5+
Dinophyceae	1+	1+	2+		1-	5+	3+,1-
Raphidophyceae			2+		1+	4+	6+
Chrysophyceae	3+	2+	9+		4-	7+	4+
Haptophyceae	2+	1+	4+	1-	2-	3+	2+
Bacillariophyceae	1+	2+	7+		3-	5+,1-	2+
Chlorophyceae	1+		8+		3-	4+	4+

Correlations between algal biomass and water chemical and physical variables in bottom waters

Compared to the surface waters, the bottom waters showed some difference in character through the correlation matrix. The pH was still the variable that correlated most strongly with algal biomass and the different algal groups, even though it’s a bit weaker here than in the surface water (Table 9 & 10). The largest difference compared to the surface water was the correlation between tot-N and the algal groups were here it were several positive correlations compared to only two and negative correlations in the surface water (Table 9 & 10).

The groups that showed strongest correlation with all the variables were still Cryptophyceae and Chrysophyceae, though not as clearly as in the surface water. The groups with least correlation to the variables were Cyanophyceae and Dinophyceae (Table 10).

Table 10. Correlation between bottom water variables and different algal groups. Numbers indicate significant correlations ($p < 0.05$). The maximum number is 13. + indicates positive correlations, - negative ones. If their only are positive correlations the cell is marked yellow, only negative correlation the cell is marked blue and if there is both the cell is marked green. This is a combined matrix with values from all lakes, which gives a maximum of correlations to 13+/13-.

Water variables/ algal groups	Temp.	pH	Tot-N	Tot-P	Abs.	TOC
Tot.volym	1-	9+	1+	1-	4+	2+
Cyanophyceae		1+			1+	1+
Cryptophyceae	1+,2-	6+	1+	3-	6+	4+
Dinophyceae	1-	1+		1-		2+
Raphidophyceae	1-	2+	1-		2+	5+
Chrysophyceae	2-	9+	3+	2+,2-	6+	3+
Haptophyceae	1-	3+	1+	1-	3+	1+
Bacillariophyceae	2-	4+	2+	1+	4+	6+
Chlorophyceae		5+	3+	1+,2-	3+,1-	1+

Discussion

The present study showed a significant increase in algal biomass in Swedish lakes during 1988 to 2010 (Table 3). This increase is in contrast to significantly decreasing phosphorus trends (Table 4). Thus phosphorus seems not to be a limiting nutrient for the growth of algal in the unproductive study lakes. The same is true for nitrogen as well as nitrite and nitrate (Appendix 2), which also is decreasing in Swedish lakes. These results support the hypothesis that other factors than phosphorus and nitrogen limit algal growth in unproductive Swedish lakes. The only lake that didn't show a decrease in phosphorus, but instead had an increase in both phosphorus and nitrogen though not significant, is Lake Fiolen (Table 3). But this is also the only lake with noteworthy agriculture land and open terrain in its catchment area (Table 1), which may explain the divergent trend. According to the hypothesis temperatures might influence the growth of algae.

This study shows that surface water temperature is increasing in 12 out of 13 lakes, though only six lakes had significant trends (Table 4). The bottom water is going into the opposite direction, i.e. it is getting colder over the years, but here it varies a bit more between the lakes and quite few trends were significant (Table 5). An overall trend in all the lakes is that the difference between surface- and bottom water is increasing, even though it's only significant in six of the lakes (Table 4). This can be interpreted as an increase in thermal stratification in the studied lakes. Even though algal biomass is increasing and temperature seems to have a similar trend, correlation between the two of them are weak and in only one lake they were correlated with each other (Table 9). Consequently there must be additional variables driving algal biomass patterns.

Even though earlier studies have shown clear interspecific differences in the growth rates of algae at various temperatures, there is not much proof for algal species to be stenothermal, with narrow ranges of temperature for growth (Butterwick *et al.* 2005). Although a direct effect as increasing temperature in the epilimnion usually is small in phytoplankton, the more indirect effects can be pronounced. At the highest temperature it's often blue-green algae that are dominating which are then succeeded by green algae. At lower temperature it is primarily Chrysophytes and diatoms which predominate (Magnuson *et al.* 1997). This correlates quite well with my study, though diatoms are present in all lakes without having a strong coherent increase, while Chrysophytes are one of the algal groups with most significant coherent increase (Table 3). But even if some phytoplankton is favoured by low or high temperature, competition usually results in a phytoplankton community that is optimal at any temperature, due to the short life cycle of the phytoplankton (Magnuson *et al.* 1997). What seems to be more important with increasing temperature is the seasonality, where the most enhancement of growth is happening under the spring to summer transit, not during the warmest period (Butterwick *et al.* 2005). This is consistent to some extent with this study, were the most coherent algal groups have highest increase during the month of June (Table 6), while the most evident increase of temperature takes place in September (Table 7). The temperature response might also be affected by modifying factors such as the light flux density and the photoperiod (Butterwick *et al.* 2005). So even if the temperature isn't directly affecting the algal growth, the temperature combined with other factors might. It is also shown that temperature changes affect the pH strongly, where both increasing air- and surface water temperature is correlated with increasing pH (Houle *et al.* 2010).

So instead for temperature, it seems that two other factors are more strongly correlated with algal growth, namely, pH and absorbance. The factor that are strongest correlated with the increase in algal biomass is pH, where in 10 out of 13 lakes a correlation between increasing pH and increasing total algal biomass has been observed (Table 9). The pH is also one of the variables that show the strongest coherent trend of increase, with 10 out of 13 lakes that have significant increase in the surface water and the remaining three have an increase though not significant (Table 4). Even in the bottom water, where trends were more shifting, pH had a clear trend of increase, where only one lake had a decreasing trend, though not significant (Table 5). The increase in pH and the significant coherent decrease in sulphate (Appendix 2), as well as the quite strong correlation between decreasing sulphate and increasing total algal biomass (Appendix 1), is also pointing at that the lakes are recovering from acidification (Findlay *et al.* 2003). Even though it might be hard to distinguish if pH increase is leading to an increase in algae growth, or if an increase in algal biomass is increasing the pH, it's known that different algal groups prefer different pH conditions, which would lead to advantages for some algal groups (Findlay *et al.* 2003).

Earlier studies have shown that lakes recovering from acidification often get a decrease in algal biomass but the species richness increases (Perez *et al.* 1994, Findlay *et al.* 2003, Findlay *et al.* 1996). This study shows that the algal biomass is increasing with increasing pH. Explanations for this might be that dominant species at low pH have found their own niche and are tolerant, which will make them cope with the increasing pH, at least to a certain level (Findlay *et al.* 2003). This is also strengthened by the finding that Dinophyceae, which is a common algal group in acidic fresh water (Findlay *et al.* 1999, Findlay *et al.* 1996), still is present in all the studied lakes, though not increasing in the same amount as some of the other groups (Table 3). The only other group that is present in all of the lakes is Chrysophyceae, which is commonly the group that increases mostly within lakes that are recovering from acidification (Findlay *et al.* 1996). Perez *et al.* (1996) also conclude that in precipitated acidified waters the ability to tolerate fluctuations in pH might be a stronger factor determine which algal species going to dominate, instead of nutrient competition. It is also well known from earlier studies that biological recovery is slower than chemical recovery (Findlay *et al.* 1996 and Havas *et al.* 1989). The biological recovery might even be further delayed with persistent acid-tolerant algal species, which by competition exclude other species (Vinebrook *et al.* 2003).

Apart from temperature and pH influences, several studies have shown the importance of light penetration to the water column, with increasing photoperiod and light flux density as an important factor for increasing phytoplankton growth (Karlsson *et al.* 2009, Findlay *et al.* 2001). This is consistent with one of my lakes, Lake Abiskojaure, but this is also the only lake, in the other lakes my results go into the opposite direction (Table 4). In this study, 11 out of 13 lakes were significantly increasing in absorbance and in six of the lakes absorbance also correlated to the increase in algal biomass (Table 4). With higher absorbance the light penetration will decrease, which is thought to lead to a decrease in primary production (Karlsson *et al.* 2009). Why my result goes against this may have several explanations.

One explanation might be that many of the species present in the lakes are mixotrophic, which will free them some from light limitation as an important factor for photosynthesis, since they might move in the water column and graze on bacteria as a carbon source (Isaksson *et al.* 1999). Mixotrophic phytoplankton is also usually less prone to be grazed on by zooplankton due to their mobility, size and protective plates. Their turnover time is also usually slower, which makes them retain nutrients in the water column for a longer time period (Findlay *et al.* 2001). This could give the mixotrophic species a robust defence against the changes that are occurring in the lakes, which would premit them to survive longer. This while new niches are initiated, which would give new species room for an increase, might partly explain why the algal growth is correlated with absorbance. My results also show that different algal groups with strongest coherent increases are the groups that usually have flagellates, as for Cryptophyceae and Chrysophyceae (Olrik 1998), which provide them with a mechanism to cope with a decreased light climate.

Another explanation is that the absorbance was strongly correlated (in 11 out of 13 lakes) with increasing TOC (appendix 1), which shows that even though light penetration decreases in the lake, the water is getting more nutrient rich. The TOC showed a strong overall coherent increase, i.e. it significantly increased in 11 out of 13 lakes. The only lake without an increase in TOC was also the only lake without an increase in absorbance, Lake Abiskojaure. This is also the only lake without forest as its major habitat in the catchment area, which would give less allochthonous material to the lake and might explain the deviating trend (Table 1). However the correlation between both absorbance and TOC to algal biomass is quite low, with only four/two out of 13 lakes in the surface water (Table 9), which points at a more indirect effect.

From the results I suggest that increases in pH combined with increases in temperature as well as absorbance are the main reasons for an increase in algal biomass despite decreasing phosphorus and nitrogen concentrations.

Conclusion

The results of this study show that pH and temperature increases seem to have a stronger impact on algal growth than phosphorus and nitrogen decreases in oligotrophic boreal lakes. This was unexpected and they raise new questions. Since the results were valid for the majority of the lakes they seem to be robust. However, there were also some limitations. The main limitations of this study were a certain inhomogeneity of the data as well as too infrequent sampling. In addition, zooplankton and fish dynamics have been neglected. For the future, I recommend including food web interactions, to consider species interactions and to analyse nutrient bioavailability to further understand increases in algal biomass in unproductive lakes despite decreasing nutrient concentrations.

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Appendix 1. Correlation between surface water variables. Numbers indicate significant correlations ($p < 0.05$). The maximum number is 13. + indicates positive correlations, - negative ones. If their only are positive correlations the cell is marked yellow, only negative correlation the cell is marked blue and if there is both the cell is marked green. This is a combined matrix with values from all lakes, which gives a maximum of correlations to 13+/13-.

	Tot.volym	Temp. °C	Temp diff	pH	Kond_25	Alk./Acid	SO4_IC	Cl	NH4-N	NO2+NO3-N	Tot-N_ps	Tot-P	Abs._OF	TOC
Tot.volym	13	1+	1+	10+	6-	4+	8-			6-		1+,4-	6+	4+
Temp. °C	1+	13	12+	5+	6-	1+	3-	3-	1+	3-			5+	3+
Temp diff	1+	12+	13	5+	6-	1+	4-	5-	1+,1-	3-		1-	6+	3+
pH	10+	5+	5+	13	4-	11+	1+,6-	3-	2-	6-	1-	5-	4+,1-	4+
Kond_25	6-	6-	6-	1+,4-	13	2+,4-	13+	11+,1-	1+,3-	5+	1+	6+,1-	11-	9-
Alk./Acid	4+	1+	1+	11+	2+,4-	13	1+,4-	1+,4-	1+	3-	1-	2-	2+,2-	2+
SO4_IC	8-	3-	4-	1+,6-	13+	1+,4-	13	7+,1-	1+,3-	8+	2+	9+,1-	12-	10-
Cl		3-	5-	3-	11+,1-	1+,4-	7+,1-	13	1+,2-	1+	2+	2+	7-	6-
NH4-N		1+	1+,1-	2-	1+,3-	1+	1+,3-	1+,2-	13	1+	1+	2+	3+,1-	2+,2-
NO2+NO3	6-	3-	3-	6-	5+	3-	8+	1+	1+	13	2+	7+	1-	4-
Tot-N_ps				1-	1+	1-	2+	2+	1+	2+	13	3+	1+,1-	1+,1-
Tot-P	4-,1+		1-	5-	6+,1-	2-	9+,1-	2+	2+	7+	3+	13	4-	4-
Abs._OF	6+	5+	6+	4+,1-	11-	2+,2-	12-	7-	3+,1-	1-	1+,1-	4-	13	11+
TOC	4+	3+	3+	4+	9-	2+	10-	6-	2+,2-	4-	1+,1-	4-	11+	13

Appendix 2. MK-stats on the chemical and physical variables in the surface waters of the 13 studied lakes. A positive MK-stat stands for an increase and a negative for a decrease. Significant Mann-Kendall values are shown as *<0.05, **<0.001, *<0.001 When no Mann-Kendall value was available it's marked with N/A. Test results that are deviating from the general trend are marked with red.**

	N:P	NH4-N µg/l	NH4:P	NO2+NO3-N	NO3:P	TOC:TN	TOC:TP	Kond_25	Alk./Acid	SO4_IC
	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat	MK-Stat
Abiskojaure	2.8**	1.3	3.6***	-2.3	0.6	-1.1	2.5*	3.5***	-0.3	-1.5
Jutsajaure	2.3*	-0.6	0.8	-1.9	-0.7	1.9	2.9**	-2.4*	0.8	-4.7***
Stensjön	3.0**	-0.5	2.0	-3.3***	-1.6	2.5*	4.3***	-3.4***	1.4	-5.8***
Remmarsjön	1.6	0.9	1.8	-2.6**	-2.9**	2.1*	2.9**	-2.5*	1.0	-4.7***
Övre Skärsjön	1.6	-0.1	1.7	-3.7***	-2.1*	4.3***	3.8***	-5.4***	3.1**	-6.3***
Stora Envättern	2.3*	2.9**	3.1**	-2.9**	-2.0	3.7***	3.4***	-4.7***	0.3	-6.0***
Rotehogstjärnen	1.1	0.6	-0.6	-3.2**	-3.2**	3.9***	3.9***	-3.3***	-0.5	-4.6***
Fräcksjön	1.2	0.1	1.3	-3.6***	-2.6**	3.4***	3.5***	-3.8***	4.2***	-5.8***
Härsvatten	2.2*	-2.5*	0.2	-4.9***	-2.3*	3.7***	3.9***	-4.5***	0.4	-6.1***
Allgjuttern	2.8**	-1.9	1.5	-4.1***	-2.5*	2.5*	3.4***	-5.1***	2.4**	-5.8***
Fiolen	-0.2	3.6***	3.0**	-1.4	-1.3	3.0**	2.9**	-4.7***	5.4***	-5.7***
St Skärsjön	1.5	0.9	2.5*	-2.6**	-1.8	2.3*	2.9**	-4.8***	3.8***	-5.8***
Brunnsjön	2.0*	2.5*	3.5***	-2.2*	-0.3	2.8**	3.1**	-3.9***	1.3	-4.4***