Limnol. Oceanogr., 52(4), 2007, 1346–1353
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Nitrate-depleted conditions on the increase in shallow northern European lakes

Gesa A. Weyhenmeyer[1]
Department of Environmental Assessment, Swedish University of Agricultural Sciences (SLU), Box 7050, SE-750 07 Uppsala, Sweden

Erik Jeppesen
Department of Freshwater Ecology, National Environmental Research Institute, Aarhus University, Silkeborg, Denmark

Rita Adrian
Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, D-12587 Berlin, Germany

Lauri Arvola
University of Helsinki, Lammi Biological Station, Pääjärventie 320, FI-16900 Lammi, Finland

Thorsten Blenckner[2]
Aquatic Environmental Analysis, Department of Earth Sciences, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden

Thomas Jankowski
Water Resources Department, Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

Eleanor Jennings
Center for the Environment, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland

Peeter Nõges
Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 61101 Rannu, Tartumaa, Estonia; European Commission—DG Joint Research Centre, Institute for Environment and Sustainability, I-21020 Ispra (VA), Italy

Tiina Nõges
Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 61101 Rannu, Tartumaa, Estonia

Dietmar Straile
Limnological Institute, University of Konstanz, D-78457 Konstanz, Germany

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[1] Corresponding author (Gesa.Weyhenmeyer@ma.slu.se).

[2] Present address: Erken Laboratory, Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norr Malma 4200, SE-761 73 Norrtälje, Sweden.

Acknowledgments

This work was funded by the European Union within the framework of the European Commission projects CLIME ("Climate and Lake Impacts in Europe," EVK1-CT-2002-00121) and Euro-limpacs ("Integrated Project to Evaluate the Impacts of Global Change on European Freshwater Ecosystems," GOCE-CT-2003-505540). Additional funding was received by the Danish Natural Science Research Council within the projects CONWOY ("Consequences of weather and climate changes for marine and freshwater ecosystems, conceptual and operational forecasting of the aquatic environment," SWF: 2052-01-0034), and CLEAR (Villum Kann Rasmussen Foundation), the Swedish Royal Academy of Sciences, the Swedish Research Council (621-2005-4335), and the Swiss Federal Office of Education and Science. We thank the Swedish Environmental Protection Agency and all laboratories, too many to mention individually, for financing, sampling, and analyzing numerous water samples. We also thank two anonymous reviewers and the editor for their constructive comments.

Abstract

We determined relative nitrate–nitrogen (NO_3-N) loss rates in 100 north–mid-European lakes from late spring to summer by using the exponential function $N_2 = N_1 e^{-k(t_2 - t_2)}$, where N_1 and N_2 are NO_3-N concentrations at the beginning (t_1) and the end (t_2) of the time interval, respectively, and k is the specific NO_3-N loss rate. We found that k decreased with increasing lake depth. Adjusting k to the lake depth (k_{adj}), we observed that k_{adj} was positively related to spring NO_3-N concentrations, but this relationship became insignificant at mean lake depths exceeding 12.5 m. A relationship between k_{adj} and spring NO_3-N concentrations in lakes shallower than 12.5 m implies that changes in spring NO_3-N concentrations influence the NO_3-N loss rate and thereby summer NO_3-N concentrations. Time series from one Estonian, one German, and 14 Swedish lakes shallower than 12.5 m since 1988 revealed that May to August NO_3-N concentrations have decreased over time everywhere, and the number of time periods exhibiting a NO_3-N depleted condition, i.e., NO_3-N levels below 10 μg L^{-1}, in these lakes has tripled since 1988. We explained the decreasing NO_3-N concentrations by a reduction in external nitrogen loading including atmospheric deposition, and by changes in climate. The observed prolongation of NO_3-N depleted conditions might be one possible explanation for the increasing occurrence of nitrogen-fixing cyanobacteria in a variety of lake ecosystems.

Nitrogen plays an important role for the primary productivity of aquatic systems and the microbial recycling of organic matter (Kalff 2002). In its dissolved form it is subject to a series of loss processes as it travels through the landscape. Within aquatic systems and their catchments these include denitrification, releasing gaseous nitrogen into the atmosphere, and biological uptake, followed by immobilization and accumulation of organic nitrogen in soils and sediments (e.g., van Breemen et al. 2002). High loss rates of nitrate–nitrogen (NO_3-N), the main form of dissolved nitrogen in most lakes, might result in very low NO_3-N concentrations in aquatic systems, a condition that has been associated with blooms of nitrogen-fixing cyanobacteria (Smith 1983; Ferber et al. 2004; Köhler et al. 2005). Nitrogen-fixing cyanobacteria can increase their toxicity when NO_3-N concentrations become depleted (Velzeboer et al. 2001), explaining why an understanding of NO_3-N loss rates is important for water management. In this study we examined NO_3-N loss rates within and among 100 North–mid-European lakes. Additionally we analyzed temporal changes in NO_3-N concentrations in a subset of 16 northern shallow lakes with complete time series between 1988 and 2003 and related them to changes in climate and atmospheric deposition. The results might help to gain further insight into changes in algal blooms in lakes, including recently observed increases in harmful algal blooms as reported by, e.g., Charmichael (2001), Huisman et al. (2004), and Peperzak (2005).

Methods

We used lake morphometric, surface water temperature, and nutrient data from 51 Swedish, 40 Danish, four Swiss, one Swiss/German/Austrian, one German, one Estonian, one Finnish, and one Irish lake. The lakes differed substantially in their morphometry (range of mean lake depth, 1–105 m; range of lake area, 0.1–5,550 km^2) and their nutrient status (range of average May to September total phosphorus concentrations, 4–1,111 μg L^{-1}; range of average May to September NO_3-N concentrations, 8–4786 μg L^{-1}; Web Appendix 1, http://www.aslo.org/lo/toc/vol_52/issue_4/1346al.pdf). Water temperature and nutrient data from surface waters (0.5 m) were available for all lakes on a monthly basis (at least from May to September) for a 6- to 25-yr period. In our study nitrate–nitrogen (NO_3-N) was considered to be the sum of NO_3-N and nitrite–nitrogen (NO_2-N), since exclusive NO_3-N measurements were not available for all lakes. To describe changes in surface NO_3-N concentrations from spring to summer, we assumed a first-order decay (Løvstad and Bjørndalen 1990) and fitted an exponential function to all 748 available May to August measurements from 100 lakes, giving us the relative NO_3-N loss rate k,

$$N_2 = N_1 e^{-k(t_2 - t_1)} \tag{1}$$

where N_1 and N_2 are NO_3-N concentrations at time 1 and time 2, t_1 is the beginning of the time interval, t_2 is the end of the time interval, and k is the specific NO_3-N loss rate in months. To model the NO_3-N loss rate k in surface waters, we used a regression tree analysis (de'Ath and Fabricius 2000) with mean lake depth, May total phosphorus, and May NO_3-N concentrations as input variables. Based on the results of the regression tree analysis, we further evaluated long-term NO_3-N data of lakes shallower than 12.5 m. Complete 16-yr data series (1988–2003) for lakes shallower than 12.5 m, including phytoplankton biomass data, were available for 14 Swedish lakes, the German lake, and the Estonian lake. To identify the influence of different variables on long-term surface NO_3-N concentrations in these lakes, we used a generalized linear mixed model (GLMM). This method allows analysis of linear and nonlinear effects of continuous and categorical predictor variables on a discrete or continuous dependent variable for nonnormally distributed data (Littell et al. 1996). All statistical tests in this study were performed using the JMP program, version 5.0.1.2. (SAS Institute 2002), with the exception of the GLMM where we used SAS statistical software (Littell et al. 1996) and the regression tree analysis where we used the open-source statistical software R (R Development Core Team 2005). Data on yearly mean wet nitrate–nitrogen deposition were taken from 11 sites with complete time series and distributed all over Sweden at http://www.ivl.se/miljo/db/statkart.asp.

Results and discussion

In 100 north–mid-European lakes we observed a general exponential decrease in surface nitrate–nitrogen (NO_3-N) concentrations between spring and summer. Fitting an exponential function (Eq. 1) to all available May to August NO_3-N measurements from 100 lakes during different years, we obtained 748 exponential functions. R^2 values for these functions were generally very high, with a median value for all 748 functions of 0.72. However, since only four measurements (May, June, July, and August NO_3-N concentrations) were available to determine one exponential function, R^2 values only became significant when they exceeded 0.89 ($p < 0.05$, $n = 4$). R^2 values greater than 0.89 were found in 64 out of 100 lakes during at least one year. In general, R^2 values were related to spring NO_3-N concentrations ($R^2 = 0.16$, $p < 0.0001$, $n = 748$), with the lowest R^2 values at spring NO_3-N concentrations below 30 μg L^{-1}. We conclude that an exponential function (Eq. 1) is suitable to describe the NO_3-N loss from spring to summer whenever spring NO_3-N concentrations exceed 30 μg L^{-1}, which is the case for the majority of our measurements.

In accordance with studies dealing with NO_3-N budgets in lakes (e.g., Dudel and Kohl 1992; Windolf et al. 1996), we consider the relative NO_3-N loss rate k (Eq. 1) to be a function of lake internal processes such as denitrification, biological uptake, and net sedimentation as well as external loading. We found that our 748 k values varied among and within the 100 lakes. Both between-lake and within-lake variations in k were highest in the shallowest lakes (Fig. 1A,B). We observed a significant logarithmic relationship between k and mean lake depth ($R^2 = 0.18$, $p < 0.0001$, $n = 748$ and, taking the mean k values of each lake, $R^2 = 0.19$, $p < 0.0001$, $n = 100$). Additionally, we observed that k was positively related to NO_3-N concentrations in May ($R^2 = 0.12$, $p < 0.0001$, $n = 748$) and to total phosphorus (TP) concentrations in May ($R^2 = 0.12$, $p < 0.0001$, $n = 748$). To rank the importance of mean lake depth, NO_3-N, and TP concentrations for variations in k, we used a regression tree analysis and found that a mean lake depth of 3.5 m was most decisive for variations in k. The second most important factor for variations in k was a mean lake depth of 12.5 m. An effect of lake depth on k is expected, considering that denitrification is generally seen as the most important process affecting k values, not least in very shallow lakes (e.g., Jensen et al. 1990). Denitrification is strongly influenced by NO_3-N concentrations and typically described as a first-order reaction to NO_3-N concentrations (e.g., Laursen and Seitzinger 2002; Hasegawa and Okino 2004). The process takes place under anaerobic conditions, and thus usually only in the sediments or in the overlying anoxic hypolimnetic waters, resulting in a declining effect of denitrification on k with increasing lake depth.

We accounted for lake depth by using the residuals of the relationship between k and the logarithmic mean lake depth for further analyses:

$$k = -0.44 \log(\text{mean lake depth}) + 0.85 \qquad (2)$$

The slope of the relationship was 0.44 ± 0.03, and the residuals were not skewed with lake depth and evenly distributed around zero along a lake depth gradient. For the whole dataset, the adjusted k values (k_{adj} = residuals of Eq. 2) showed a relationship to NO_3-N concentrations in May ($R^2 = 0.29$, $p < 0.0001$, $n = 748$) and to TP concentrations in May ($R^2 = 0.05$, $p < 0.0001$, $n = 748$). Applying the lake depth division of the regression tree analysis, we found differences in the relationship between k_{adj} and nutrient concentrations in very shallow (mean depth <3.5 m), moderately shallow (mean depth ≥3.5 m and <12.5 m), and deep (mean depth ≥12.5 m) lakes. In very shallow lakes, k_{adj} was strongly dependent on NO_3-N concentrations in May ($R^2 = 0.69$, $p < 0.0001$, $n = 178$; Fig. 1C and D) and weakly positively related to TP concentrations in May ($R^2 = 0.04$, $p < 0.01$, $n = 178$). In moderately shallow lakes, k_{adj} still showed a positive relationship to NO_3-N concentrations in May ($R^2 = 0.17$, $p < 0.0001$, $n = 333$; Fig. 1D and E) and a very weak relationship to TP concentrations in May ($R^2 = 0.01$, $p < 0.05$, $n = 333$). Finally, in deep lakes k_{adj} was no longer positively related to NO_3-N concentrations in May but was positively related to TP concentrations in May ($R^2 = 0.10$, $p < 0.0001$, $n = 237$).

If denitrification was the only process affecting NO_3-N concentrations in our lakes and if the water column had been perfectly mixed, we would have expected a slope in Eq. 2 close to 1. Considering that deeper lakes are not well mixed during May to August, we would even have expected a slope larger than 1. The water exchange between bottom and surface waters is likely to be reduced by thermal stratification already in moderate shallow lakes with a mean lake depth between 3.5 m and 12.5 m, but since a considerable part of the sediment surface where denitrification takes place is still above the thermocline, denitrification is still important for NO_3-N loss rates in surface waters though less so than in the very shallow lakes. In deep lakes with a mean lake depth exceeding 12.5 m, almost the entire sediment surface is located below the thermocline, and the influence of denitrification on the relative NO_3-N loss rate in surface waters is expected to be low. We expect even lower relative NO_3-N loss rates in deep lakes, since processes like resuspension and eddy diffusion at the sediment surface that can enhance denitrification remain unimportant. Consequently, other processes than denitrification need to be considered to explain a slope less than 1 in Eq. 2. These include biological uptake and sedimentation (e.g., Schelske 1975;Løvstad and Bjørndalen 1990). Net sedimentation is likely higher in deeper lakes during summer, where the settled nitrogen is trapped in the hypolimnion, while it may return to the surface water again in shallow lakes after mineralization and nitrification in the surface sediments. Additionally, in especially shallow lakes that typically have a shorter retention time, the input from the catchment during summer may lead to reduced NO_3-N loss rates (Jensen et al. 1990), resulting in a slope less than 1 in Eq. 2. Unfortunately, data for retention time and loading were not available for the dataset used.

Values of k_{adj} influenced by biological uptake and sedimentation processes, indicated by a positive relationship

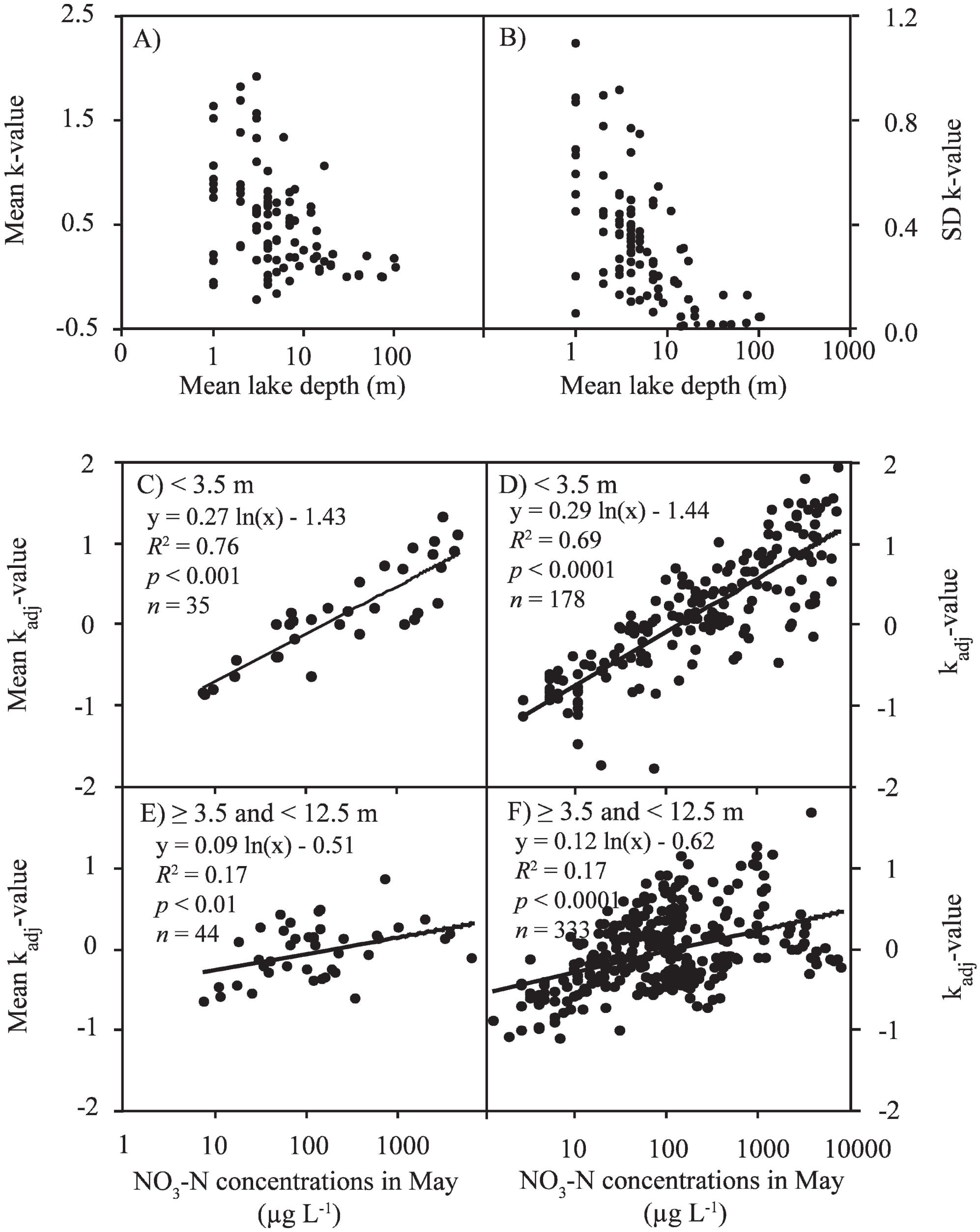

Fig. 1. (A and B) The nitrate–nitrogen (NO_3-N) loss rate k (*see Eq. 1*) and its standard deviation (SD) along a lake depth gradient. Adjusting k to the lake depth by taking the residuals of the relationship between k and the mean lake depth (k_{adj}, $n = 748$) gives a relation to NO_3-N concentrations in May for (C and D) lakes with a mean lake depth <3.5 m, and for (E and F) lakes with a mean lake depth ≥3.5 m and <12.5 m. Panels A, C, and E show mean values for each lake, panels D and F show all available k values for the lakes considered. The lake depth divisions in the figure are based on a regression tree analysis.

between TP concentrations, were mainly found in lakes deeper than 12.5 m ($R^2 = 0.10$, $p < 0.0001$, $n = 237$). For these lakes, we suggest that variations in the relative NO_3-N loss rate, estimated on NO_3-N concentrations in surface waters from May to August when our lakes typically are stratified, are small (Fig. 1B) and mainly influenced by processes related to biological uptake and sedimentation (Fig. 2). The influences of these processes recede in shallow lakes (<12.5 m), where the influence of denitrification becomes dominant (Jensen et al. 1990; Fig. 2). In the shallow lakes, especially in our very shallow lakes, variations in the relative NO_3-N loss rate were large and related to NO_3-N concentrations in May (Fig. 1B–F). Whether this is a consequence of fast reduction in hydraulic and thus NO_3-N loading during late spring in these systems cannot be evaluated because of lack of external loading data, but the consequence is that the relative NO_3-N loss rate in lakes shallower than 12.5 m is sensitive to NO_3-N concentrations in May.

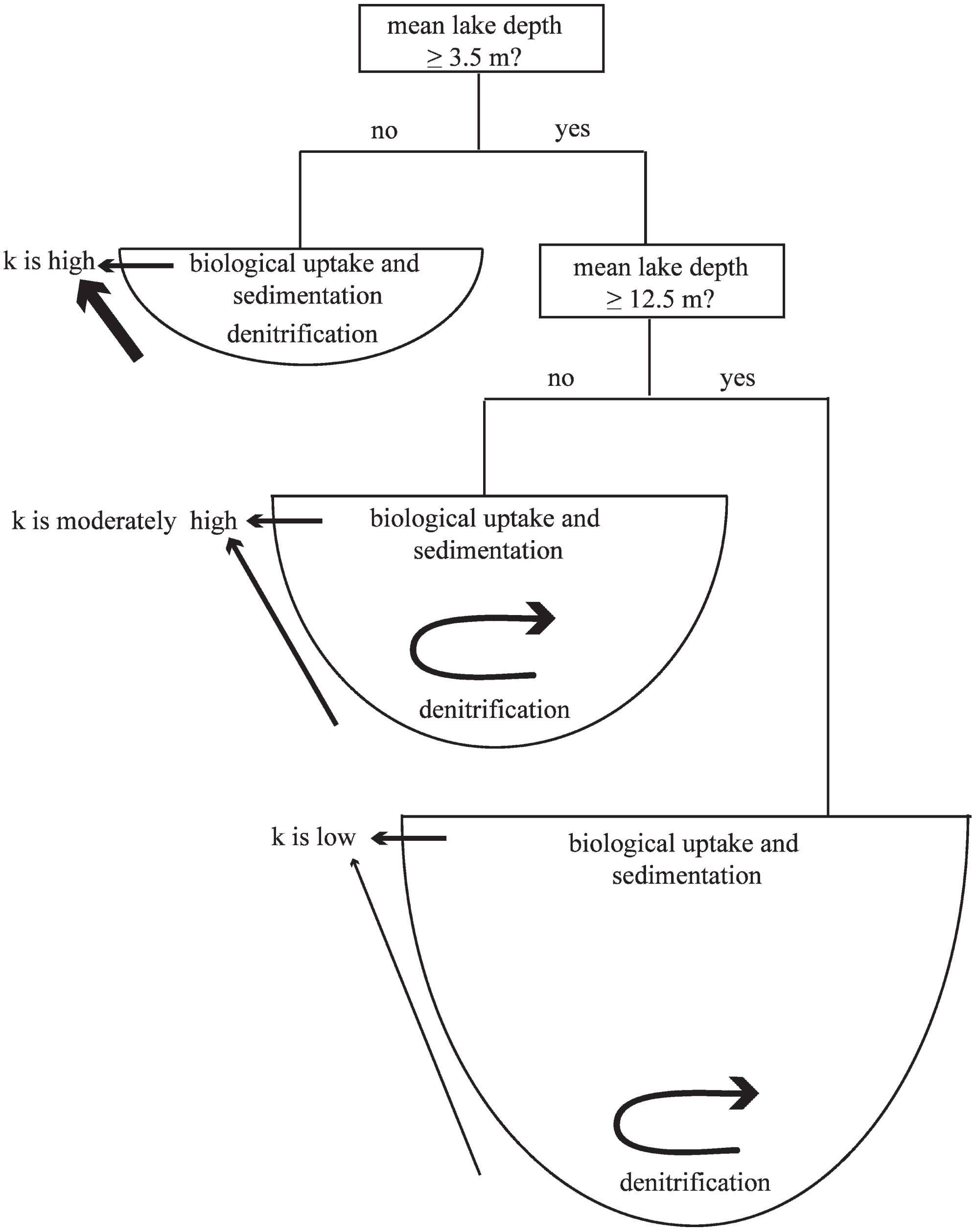

Fig. 2. Conceptual model showing how the nitrate–nitrogen (NO_3-N) relative loss rate k in lakes changes with increasing mean lake depth. The mean lake depth categories have been determined by a regression tree analysis. Arrows indicate the importance of different processes for k in surface waters.

Based on our results, we hypothesize that a decrease in spring NO_3-N concentrations can cause a decrease in NO_3-N summer concentrations with a possible occurrence of NO_3-N depleted conditions, not least in the shallow lakes (mean depth <12.5 m). To test the hypothesis, we focused on temporal variations in spring to summer NO_3-N concentrations in 16 lakes with a mean depth <12.5 m and with continuous data series from 1988 to 2003. Here, we had a bias toward northern Europe, since 14 lakes were located in Sweden, covering latitudes between 55°N and 68°N, one lake was located in Estonia and one lake in Germany, implying that the temporal aspect reflects a northern European perspective rather than a European one.

We found a general decrease in May to August NO_3-N concentrations in all 16 lakes. However, nutrient reduction measures, such as improved sewage treatment and/or changes in agricultural practices, have been implemented in the catchments of some of these lakes (e.g., Köhler et al. 2005; Nõges et al. 2005). Nutrient reduction measures make NO_3-N dynamics in lakes complex and lake specific. We therefore focused initially on Swedish nutrient-poor reference lakes that have experienced no catchment changes other than changes in the climate and nitrogen deposition.

In these 11 lakes, a decrease in May NO_3-N concentrations over time could be explained both by a decrease in the wet NO_3-N deposition and by an increase in the May phytoplankton biomass (generalized linear mixed model where the yearly mean wet NO_3-N deposition and the phytoplankton biomass in May were fixed and the lake was random, $p < 0.05$, $n = 169$, df = 10; both the yearly mean wet NO_3-N deposition and the phytoplankton biomass in May were significant contributors to the model). NO_3-N deposition and the phytoplankton biomass together accounted for between 11% and 82% of the NO_3-N variation in May among the 11 reference lakes (average of 11 lakes, 44%, analyzed with a multivariate regression model with year as independent variable). The influence of atmospheric NO_3-N deposition on nutrient limitation in Swedish lakes has already been discussed by Bergström et al. (2005). Looking at spatial patterns they argued that during the past decades unproductive Swedish lakes have possibly shifted from natural nitrogen limitation to phosphorus limitation because of increased atmospheric nitrogen deposition. Here we show that during the past two decades the yearly mean NO_3-N wet deposition over Sweden has steadily decreased again by about 40% during the period 1988 to 2003 (Fig. 3A). This decrease has probably contributed to the decline in May to August NO_3-N concentrations that we observed in the Swedish reference lakes since 1988. A decrease in atmospheric NO_3-N deposition is not detectable everywhere in the Northern Hemisphere, the Alp region in Central Europe being an example (Rogora et al. 2006). Lack of significant trends in atmospheric NO_3-N deposition might be one of many explanations why, for instance, Evans et al. (2001) and Skjelkvale et al. (2005) found a variety of surface waters across the Northern Hemisphere without significant trends in NO_3-N concentrations.

In addition to atmospheric nitrogen deposition effects, we suggest that climatic factors have had an impact on decreasing May NO_3-N concentrations in our lakes. An earlier uptake of NO_3-N by phytoplankton as the phytoplankton spring bloom shifts toward an earlier time period of the year in a warmer climate can, for instance, also lower May NO_3-N concentrations. This mechanism has earlier been described for Sweden's largest lakes (Weyhenmeyer 2004) and is supported here by our observed negative relationship between spring NO_3-N concentrations and the spring phytoplankton biomass. Other possible climate driven changes in lake ecosystems leading to decreased spring NO_3-N concentrations in lakes might be changes in the amount of water loading per unit surface area of a lake, which has a strong impact on NO_3-N concentrations in lakes (e.g., Höhener and Gächter 1993). Additionally, as pointed out by Windolf et al. (1996), enhanced denitrification processes due to warmer water temperatures, here indicated by a surface water temperature increase in the reference lakes of up to 3.7°C in May during 1988 to 2003, can decrease spring NO_3-N concentrations. Climate driven processes in the catchment can also lead to decreased spring NO_3-N concentrations in lakes, examples being a decreased NO_3-N delivery from the catchment due to changed runoff processes and an enhanced biological uptake in the catchment as a result of warmer temperatures (e.g., George et al. 2004).

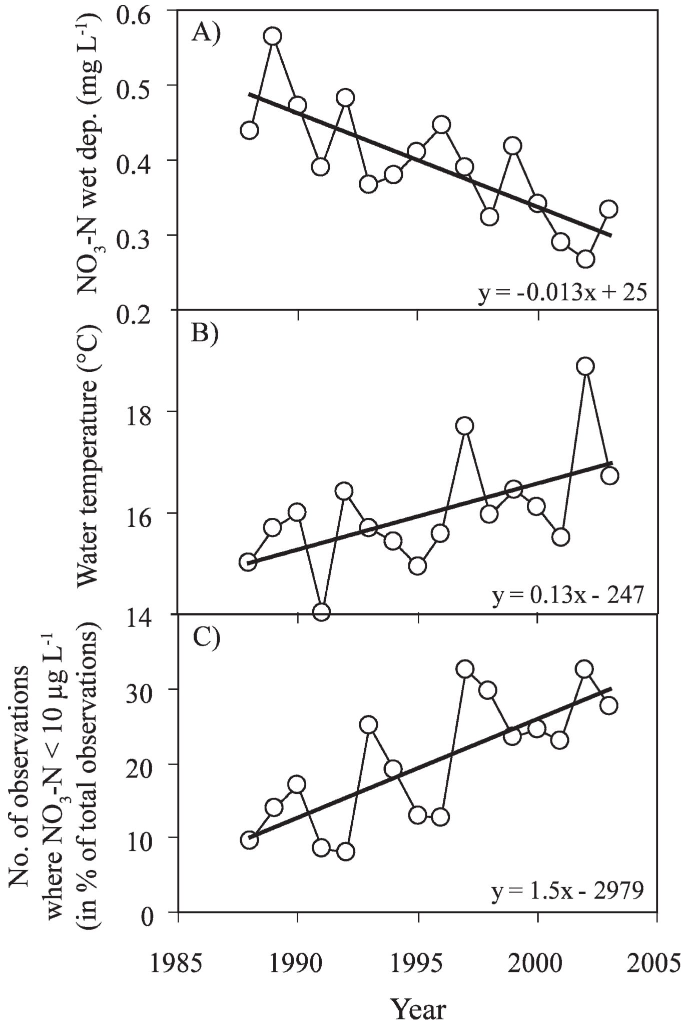

Fig. 3. Changes in surface water temperatures and in the NO_3-N wet deposition across northern Europe since 1988, and their consequences. (A) Decrease in the yearly mean NO_3-N wet deposition over Sweden and (B) increase in the yearly mean (based on available monthly May to October values) median surface water temperatures of 16 European lakes in the period 1988 to 2003. (C) Increase in the number of occasions when nitrate–nitrogen (NO_3-N) concentrations have decreased below 10 μg L^{-1} in 16 European lakes shallower than 12.5 m during the period 1988 to 2003.

We conclude that decreasing NO_3-N concentrations in our 11 northern reference lakes are a result of decreases in atmospheric wet deposition as well as changes in the climate. In our remaining five nonreference lakes with available complete time series, nutrient decreasing measures in the catchment might additionally be responsible for observed decreasing May to August NO_3-N concentrations in the water column. If NO_3-N concentrations decrease below a certain threshold value, NO_3-N can become limiting for a variety of phytoplankton species. However, since this limitation also depends on the fraction of the TP pool that is bioavailable, NO_3-N limitation, as indicated by low NO_3-N : TP ratios, can be reached for various NO_3-N concentrations. We term NO_3-N concentrations below 10 μg L^{-1} as a nitrate-depleted condition, since this value is so low that it might result in NO_3-N limitation for various TP concentrations. Of the 16 study lakes with continuous time series, we found 13 lakes in which NO_3-N concentrations occasionally declined below 10 μg L^{-1}. These were 11 Swedish lakes, the Estonian lake, and the German lake. One Swedish lake, the Estonian and the German lake were eutrophic, while all other 10 lakes were nutrient-poor Swedish reference lakes. All 13 lakes showed an increase in the occurrence of NO_3-N depleted conditions within a year, with the number of occasions when these conditions were observed increasing by a factor of three during the period 1988 to 2003 (Fig. 3C). This increase coincided with an average 40% decrease in the yearly mean atmospheric wet nitrogen deposition over Sweden ($R^2 = 0.46, p < 0.01, n = 16$; Fig. 3A). However, the increase also coincided with an increase in the yearly mean (based on available May to October values) median surface water temperature of our 16 lakes ($R^2 = 0.52, p < 0.01, n = 16$; Fig. 3B), indicating that it is due in part to the climate-induced processes described above. With a standard least squares model, the median surface water temperature of our 16 lakes and the atmospheric wet nitrogen deposition over Sweden together explained 74% of the year-to-year variations in the occasions of NO_3-N depleted conditions in the northern lakes from 1988 to 2003 ($p < 0.001, n = 16$; both the atmospheric deposition and the water temperatures were significant contributors to the model). The model remained significant when all data series were detrended against time ($R^2 = 0.44, p < 0.05, n = 16$).

From our study, we conclude that a decrease in spring NO_3-N concentrations induced by changes in atmospheric deposition and the climate can lead to NO_3-N depleted conditions during summer, both in eutrophic and oligotrophic lake ecosystems with a mean lake depth between 3.5 and 12.5 m. Over northern Europe we observed a strong increase in the occurrence of NO_3-N depleted conditions in a variety of shallow lake ecosystems. Decreasing nutrient concentrations are usually desired to decrease the degree of eutrophication, but if phosphorus and NO_3-N concentrations are not balanced there might be a risk of NO_3-N limitation that can favor the occurrence of potentially toxic nitrogen-fixing cyanobacteria (Hyenstrand et al. 1998; Ferber et al. 2004). Whether NO_3-N depleted conditions are, however, an important concern for very shallow lakes needs further discussion, since low nitrogen loading might shift turbid algal dominated lakes to clearwater macrophyte dominated lakes at intermediate high phosphorus concentrations (González Sagrario et al. 2005; James et al. 2005). We recommend further studies on the environmental consequences of the present upward trend in NO_3-N depleted conditions in lake ecosystems, in particular studies that focus on the occurrence of harmful algal blooms.

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Received: 26 September 2006
Accepted: 25 January 2007
Amended: 12 February 2007