

Changes of the plankton spring outburst related to the North Atlantic Oscillation

Abstract—Changes in the timing, composition, and intensity of freshwater phytoplankton blooms are known to have an impact on water quality and aquatic ecosystem functions. Factors provoking these changes are, therefore, of major importance. In Lake Erken in southeastern Sweden considerable changes in the timing and large variations in the composition of phytoplankton spring peaks have been observed during the past 45 yr. Here we show that long-term changes and variations in Lake Erken are strongly related to a single global parameter—the North Atlantic Oscillation (NAO). Even regional parameters that are known to have most influence on the spring development of phytoplankton such as ice break-up and nutrient concentrations could not provide a more conclusive explanation of the observed changes in spring phytoplankton, making the NAO a very powerful and simple tool in determining the timing and composition of phytoplankton spring peaks in a temperate lake.

Freshwater plankton communities are often used to identify and quantify water quality problems. It is therefore important to understand the dynamics of freshwater plankton and to find explanations for changes in plankton communities. Previous studies have shown that plankton communities are determined by a combination of physical, chemical, and biological factors (Soranno 1997) and quickly respond to changes in the catchment and the weather. Considering a longer time scale, changes in plankton communities can also be linked to global processes, like the position of the Gulf Stream in the Atlantic or global warming (e.g., George and Taylor 1995; Adrian and Deneke 1996). So far, most studies that try to couple global processes to changes in plankton communities are dealing with zooplankton, and the majority of the studies refer to the marine environment. Because zooplankton only accounts for one part of the plankton communities, this paper concentrates on phytoplankton. The development of phytoplankton can be very sensitive to changes in the weather. The development of the spring phytoplankton bloom in lakes that are frequently ice-covered is known to be sensitive especially to changes in the weather, because in these lakes the instigation of the phytoplankton explosion is strictly dependent on the availability of radiant energy (Pechlaner 1970). Assuming that the availability of radiant energy is strongly influenced by global climate processes, we tested whether a global climate process, the North Atlantic Oscillation (NAO), can be used to explain local changes in the occurrence of spring phytoplankton blooms in Lake Erken in southeastern Sweden. The NAO is often defined in terms of differences in sea-level pressure (the barometric pressure adjusted to the mean sea level) measured at stations close to the centers of the Azores High and the Iceland Low (Hurrell 1995). The NAO is an expression for the tendency of the wintertime mean North Atlantic atmospheric circulation to oscillate between a strong and a weak state. The switches in sea-level pressure from one state to another result in changes

in the temperature regime (Plaudt et al. 1995), snow fall (Hartley and Keables 1998), west wind stress (Rogers 1997), and the timing of the lake ice break-up (Livingstone 1999) in countries surrounding the North Atlantic. These results indicate the strong influence of the NAO on all physical parameters that are known to be most important for the occurrence of phytoplankton spring blooms provided that nutrients are available in sufficient concentrations. To test the hypothesis that the NAO has an influence on the occurrence of the spring phytoplankton bloom, long-term data series of the timing, intensity, and the composition of phytoplankton spring blooms from Lake Erken were analyzed and related to the NAO.

Study site and data collection—Lake Erken is a moderately eutrophic lake in southeastern Sweden (59°25'N, 18°15'E) at 11 m above sea level with a surface area of 23.7 km², a maximum depth of 21 m, and a mean depth of 9 m. The lake is always ice-covered during the winter. Ice break-up dates are available for most years since 1954. At a station 700 m offshore from the limnological field laboratory, water samples were taken with a Ruttner sampler at different depths (mostly at 1, 5, and 10 m) above the deepest part of the lake at least on a weekly basis during 21 spring periods since 1954. From these water samples, chlorophyll *a* (Chl *a*) and nutrient concentrations were measured according to Ahlgren and Ahlgren (1975). Most Chl *a* data for this paper were taken from the publications of Pechlaner (1970), Pettersson (1985), and Eriksson and Forsberg (1992). In addition to the Chl *a* and nutrient analyses, water was preserved with Lugol's iodine for the identification and counting of phytoplankton under an inverted microscope. For a detailed description of phytoplankton determination and calculations see Padisák and Dokulil (1994). The phytoplankton biovolume was determined for 16 yr since 1954. For this study, the volume-weighted averages of the measurements in 0–10-m water depths were used. Snow data close to Lake Erken were obtained from the Swedish Meteorological and Hydrological Institute since 1961. Data for the commonly used NAO winter (December through March) index were taken from the homepage of the National Center for Atmospheric Research, U.S. The values of this NAO winter index differ slightly from those of the well-known winter index of Hurrell (1995) because of continual updates to the data and a change in the base period. The sea-level pressure (SLP) anomalies at each station were normalized relative to a 120-yr period 1864–1983 while Hurrell (1995) normalized relative to 1864–1994. Because the NAO winter index is based on the difference of normalized sea-level pressures between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland we chose the NAO March index from the homepage of the Climate Prediction Center in Washington, U.S. that is also based on the difference of normalized SLP between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland. Because

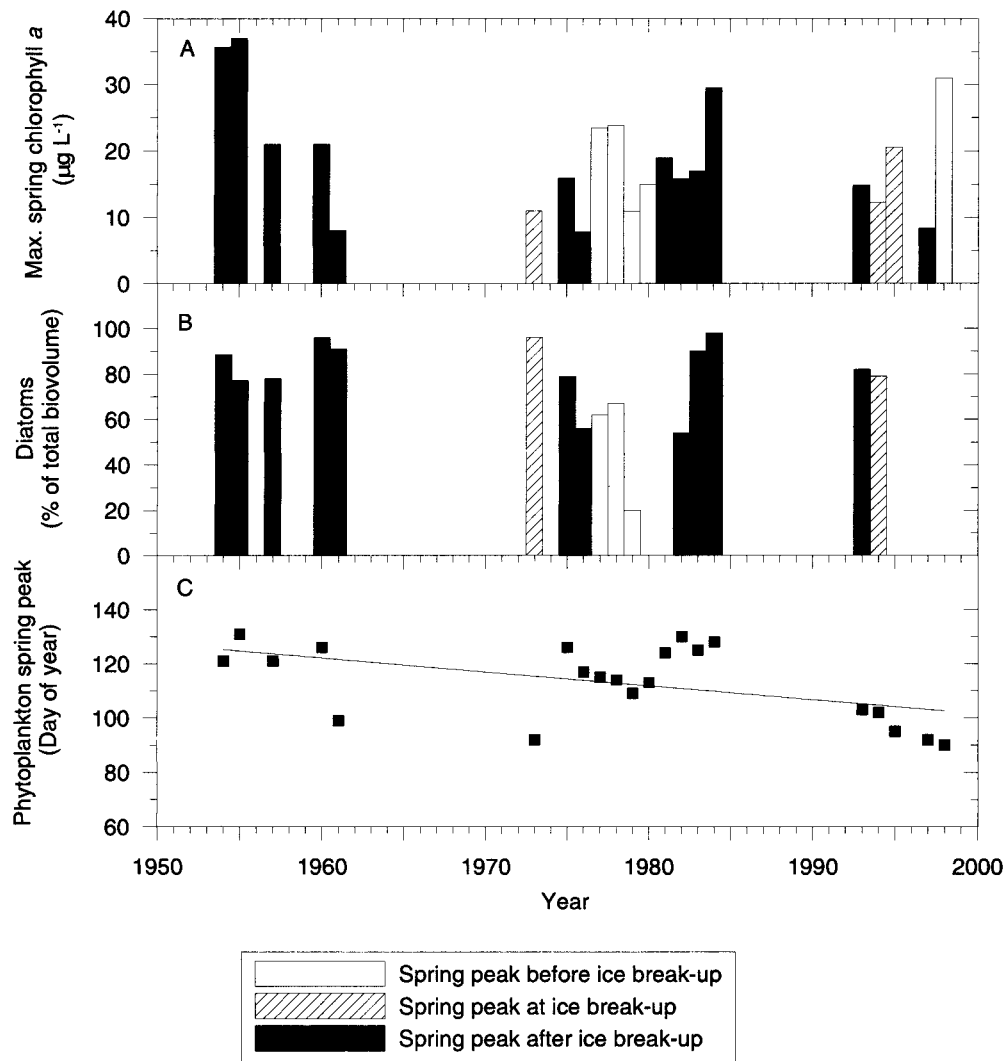


Fig. 1. (A) Maximum measured Chl *a* concentrations, based on at least weekly measurements in Lake Erken during spring periods since 1954. The staples indicate whether the phytoplankton spring peak occurred before, at, or after ice break-up. (B) Diatoms as a percentage of the total biovolume at the time of the phytoplankton spring peak in Lake Erken since 1954. (C) Timing of the phytoplankton spring in Lake Erken since 1954 and its trends.

the Climate Prediction Center in Washington does not present any seasonal index of the NAO we had to take the seasonal (December through February) NAO index of the homepage of the National Center for Atmospheric Research, U.S. This seasonal index is based on the difference of normalized SLP between Ponta Delgada, Azores, and Stykkisholmur/Reykjavik, Iceland. The SLP anomalies at each station were normalized by division of each seasonal pressure by the long-term (1865–1984) standard deviation.

Long-term data series of phytoplankton spring peaks—In Lake Erken, large interannual variations of the maximum phytoplankton spring biomass, expressed as Chl *a* concentrations, have been observed during the past 45 yr (Fig. 1A). During some years Chl *a* concentrations showed two peaks during the spring. In that case the last peak before the clear-water phase was taken. The maximum spring Chl *a* concen-

trations varied from 7.8 to 37 $\mu\text{g liter}^{-1}$. The variations seem to be independent of the ice cover, i.e., a high biomass was observed both when the spring peak occurred below the ice and when it occurred after ice break-up. In contrast, the large variations of the species composition, ranging from 20 to 98% of present diatoms, showed a dependency on the ice cover. A very low relative abundance of diatoms at the time of the peak was observed only when the spring peak occurred below the ice (Fig. 1B). This observation could be verified by a Mann–Whitney test, which showed that the difference between the abundance of diatoms during the periods of presence and of absence of ice cover is significant ($P < 0.05$).

Neither the maximum phytoplankton spring biomass nor the relative abundance of diatoms at the time of the spring peak showed any obvious upward or downward trend over the past 45 yr. In contrast, the timing of the phytoplankton

Table 1. Spearman Rho correlation coefficients between the North Atlantic Oscillation (NAO) and several parameters associated with the phytoplankton spring peak in Lake Erken, 1954–1998. The Spearman Rho correlation coefficient was taken because of the non-normality of the data.

	NAO _{winter}	NAO _M	NAO _{DJF}
Timing ice break-up	-0.43**	-0.39**	-0.43**
Snow _M	-0.54**	NS	-0.49**
Timing phytoplankton spring peak	NS	-0.57**	NS
% diatoms of total biovolume	0.49*	NS	0.70**
Max Chl <i>a</i>	NS	-0.45*	NS

NAO_{winter}, NAO winter index (December through March); NAO_M, NAO index of March; NAO_{DJF}, NAO seasonal index (December through February); Snow_M, snow cover in March; Max Chl *a*, maximum spring Chl *a* concentration; NS, not significant.

* Significant at the $P < 0.05$ level.

** Significant at the $P < 0.01$ level.

spring peaks has changed, now occurring approximately 30 d earlier than 45 yr ago (Fig. 1C). Only during the very warm winter–spring periods in 1961 and 1973 were phytoplankton spring peaks observed as early in the year as during recent years. A Mann–Whitney test revealed that there is a significant difference between the timing of the phytoplankton spring peak at the beginning (1950–1970), the middle (1971–1990), and the end of the series (1991–present) ($P < 0.05$).

Relationships to the NAO—In Lake Erken, the snow cover and the timing of the ice break-up, both physical parameters that are known to be most important for the occurrence of phytoplankton spring blooms, were significantly related to the NAO (Table 1). The snow cover in March was chosen for correlation because it was assumed that the snow cover during the month of March has the most influence on the development of the spring phytoplankton bloom. In addition to the relationships between the NAO and the local physical parameters ice break-up and snow cover, a significant relation between the NAO and the timing of the phytoplankton spring peak in Lake Erken could be achieved (Fig. 2A, Table 1). No significantly better correlation could be obtained by directly relating the timing of the ice break-up to the timing of the phytoplankton spring peak (Fig. 2B, Table 1).

Not only was the timing of the phytoplankton spring peak significantly related to the NAO but so too was the species composition at the time of the phytoplankton spring peak (Fig. 2C, Table 1). Increasing NAO values resulted in an increasing relative abundance of diatoms during the spring peak. Diatoms during the spring peak are dominated by the species *Stephanodiscus hantzschii* var. *pusillus*. When their relative abundance decreases, dinoflagellates, in particular *Peridinium aciculiferum*, become important. The total biomass of all species, expressed as Chl *a* concentrations, during the time of the spring peak could also be linked to the NAO (Table 1). Due to the non-normality of most data, not the Pearson but the Spearman Rho correlation was used, which is more robust to the violation of normality.

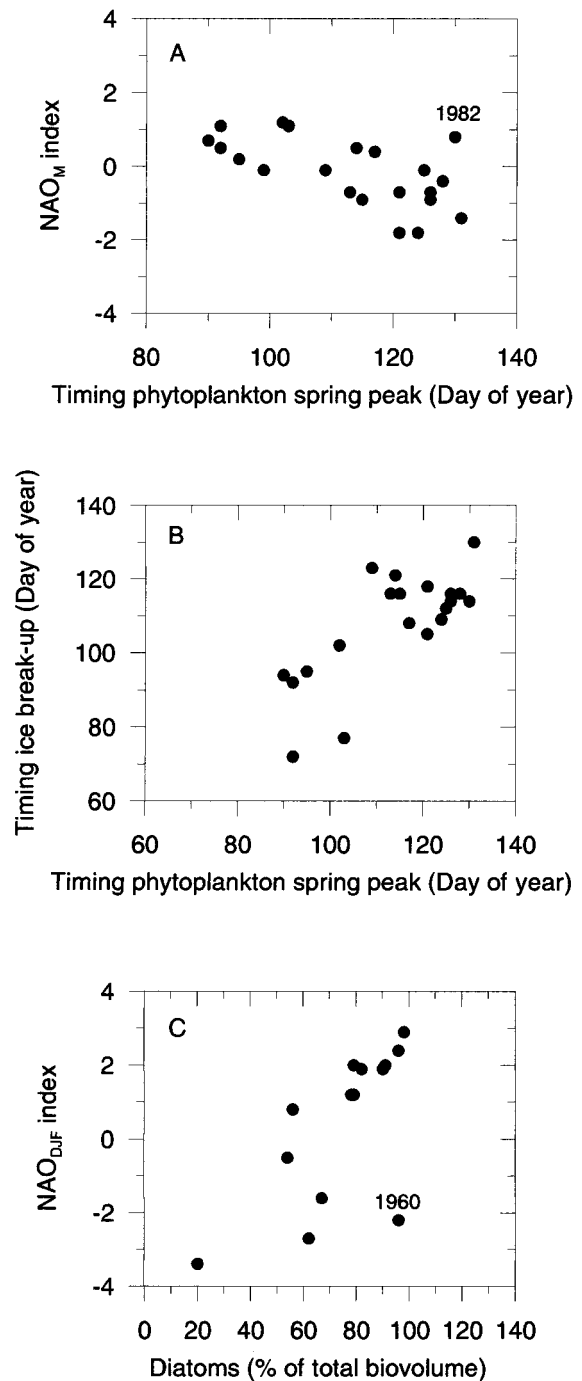


Fig. 2. (A) The relationship between the NAO of March (NAO_M) and the time of the phytoplankton spring peak in Lake Erken since 1954 (for correlation coefficients see Table 1). (B) The relationship between the time of ice break-up and the time of the phytoplankton spring peak in Lake Erken since 1954. (C) The relationship between the NAO of the period December–February (NAO_{DJF}) and the ratio between the biovolume of diatoms and the total biovolume at the time of the maximum spring Chl *a* concentration in Lake Erken since 1954. In the plots unusual years are marked.

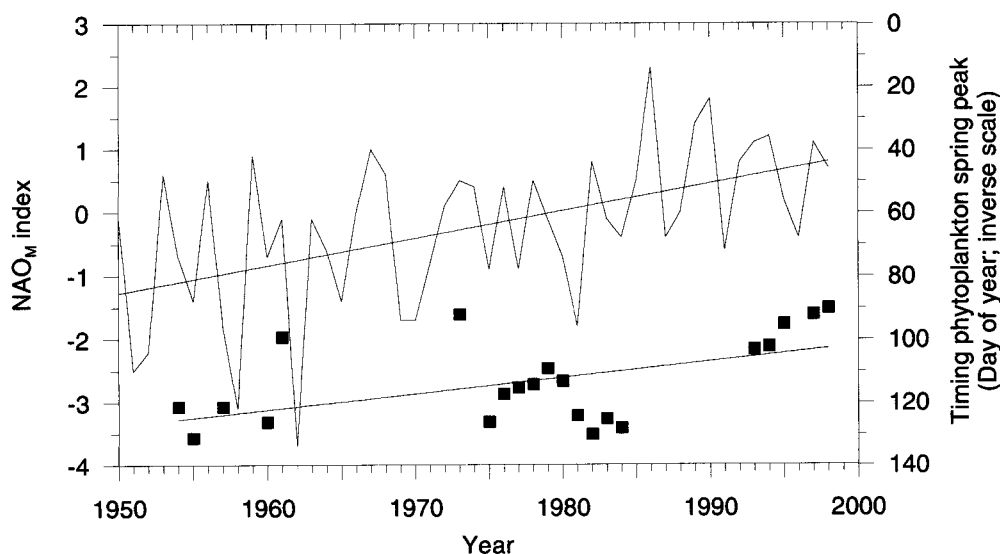


Fig. 3. The upward trendline of the NAO of March (NAO_M) since 1950 and the trendline of the time of the phytoplankton spring peak in Lake Erken.

Variations in species composition and maximum spring biomass—Phytoplankton spring peaks are known to be dependent mainly on light conditions. The key factor for the occurrence of the spring peak is sufficient radiant energy, usually first given directly after ice break-up (Pechlaner 1970). Only under clear ice conditions, is a peak below the ice cover possible. If the spring phytoplankton peak occurs at or after ice break-up, which is the usual case, diatoms are the dominant species during the peak. If the peak is observed below the ice, the percentage of diatoms is significantly decreased and dinoflagellates become important (Fig. 1B). In 1979 cryophilic dinoflagellates were even the dominant species during the spring peak. During that spring, the peak occurred as soon as 14 d before ice break-up. Dinoflagellate-dominated spring peaks are very rare and only possible below the ice when light conditions are sufficient and water mixing is prevented. Water mixing is essential for the development of diatoms because diatoms are not able to resist sedimentation, whereas dinoflagellates are able to swim. Generally, light conditions below the ice do not allow significant development of both dinoflagellates and diatoms, and as soon as the ice cover is gone, the development of diatoms is able to drive out the development of dinoflagellates. Nutrient availability cannot explain the species composition at the time of the phytoplankton spring peak because major nutrients like phosphate, nitrate, and silicate were always present in sufficient concentrations for the development of phytoplankton from the beginning of the ice cover to the beginning of the phytoplankton spring outburst. However, nutrient concentrations seem to be important for the maximum spring biomass. An intensive comparison of two spring peaks in Lake Erken revealed that the maximum spring biomass is dependent on nutrient availability at the time of the peak (Eriksson and Forsberg 1992). Due to the dependency of the maximum spring biomass on nutrient concentrations, the relationships between physical parameters and the maximum spring biomass are weak.

It became obvious that the variations in the timing of the phytoplankton spring peaks and the species composition at the time of the spring peak are strongly dependent on the timing of the ice break-up and the snow cover on the ice. Because the timing of the ice break-up has shifted to an earlier date and the snow cover decreased during the past 45 yr, the timing of the phytoplankton spring peak occurs about 1 month earlier than 45 yr ago. Both the timing of the ice break-up and the snow cover can be determined by one single driver—the NAO. This explains why the global parameter NAO is almost as powerful in determining the timing of the phytoplankton spring peak as the local parameter ice break-up. To avoid getting good correlation only because of similar positive trends in the NAO and the timing of the phytoplankton spring peak (Fig. 3), the series of the NAO and the timing of the spring phytoplankton peak were detrended by a linear function and related to each other. The relationships of the residuals were significant ($r^2 = 0.18$, $P < 0.05$), indicating that not only the trend, but also year-to-year fluctuations, of the NAO are related to the timing of the phytoplankton spring peak.

Memory effects—To consider different NAO indexes—the NAO winter index, the NAO seasonal index, and the NAO March index—has the advantage that meteorological memory effects of different parameters can be identified. For the ice break-up in April–May and for the snow cover in March, the weather conditions from the whole winter period are most relevant (Table 1). Also, the species composition at the time of the phytoplankton spring peak in April–May is determined early in the year when the lake is still ice-covered. The fact that the species composition at the time of the spring peak is better correlated with the NAO seasonal index than the NAO winter index indicates that the species composition at the time of the spring peak in April–May is already determined during the period December–February. It seems that the spring phytoplankton slowly develops below an ice cover just to explode

as soon as light conditions are sufficient. This final outburst is very sudden due to a fast phytoplankton growth rate, which explains why the occurrence of the phytoplankton spring peak was observed to barely depend on weather conditions just before the peak (Table 1).

The effects of global processes on aquatic ecosystem functions—In order to detect future trends in a lake ecosystem it is essential to distinguish NAO variations from NAO trends. For this distinction, accurate NAO indexes have to be chosen. The seasonal NAO index (December–February) varied during the past 45 yr but did not show any upward or downward trend. Consequently, the species composition varied according to the variations in the NAO but did not reveal a consistent long-term change. In contrast, the NAO of March shows a strong upward trend that might be due to global warming (Fig. 3). This upward trend caused a shift in the timing of the phytoplankton spring peak that is likely to continue into the future (Fig. 3). Because ice break-up also follows this trend and because no change in the onset of summer stratification could be observed during the past 45 yr, the period of light limitation below the ice cover decreased at the same time as the period of water-column mixing increased. During this extended isothermal period following ice loss (1 month longer), nutrient deficiency occurred after the spring bloom accompanied by a low phytoplankton biomass. The phytoplankton at this time was found to be dominated by mixotrophic species, defined as organisms that combine photoautotrophic and heterotrophic nutrition (Riemann et al. 1995). These diverse fast-growing organisms increase the trophic efficiency of the ecosystem (Sommer 1996), which demonstrates that the NAO has an impact on ecosystem functions. To use phytoplankton as an indicator for changes in ecosystem functions is practical because the response time of phytoplankton to environmental and climatic changes is within a suitable time scale for a human observer (Reynolds 1998). Conclusively, a relationship between the NAO and phytoplankton is advantageous to quickly detect the effects of global climate changes on ecosystems.

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References

- AHLGREN, I., AND G. AHLGREN. 1975. Methods of water-chemical analyses compiled for instruction in limnology. Institute of Limnology, Uppsala.
- ERIKSSON, C., AND C. FORSBERG. 1992. Nutrient interactions and phytoplankton growth during the spring bloom in Lake Erken, Sweden. *Int. Rev. Gesamten Hydrobiol.* **77**: 517–551.
- GEORGE, D. G., AND A. H. TAYLOR. 1995. UK lake plankton and the Gulf Stream. *Nature* **378**: 139.
- HARTLEY, S., AND M. J. KEABLES. 1998. Synoptic associations of winter climate and snowfall variability in New England, USA, 1950–1992. *Int. J. Climatol.* **18**: 281–198.
- HURRELL, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**: 676–679.
- LIVINGSTONE, D. 1999. Large-scale climatic forcing detected in historical observations of lake ice break-up. *Verh. Int. Verein. Limnol.* In press.
- PADISÁK, J., AND M. DOKULIL. 1994. Meroplankton dynamics in a saline, turbulent, turbid shallow lake (Neusiedlersee, Austria and Hungary). *Hydrobiologia* **289**: 1–20.
- PECHLANER, R. 1970. The phytoplankton spring outburst and its conditions in Lake Erken (Sweden). *Limnol. Oceanogr.* **15**: 113–130.
- PETTERSSON, K. 1985. The availability of phosphorus and the species composition of the spring phytoplankton in Lake Erken. *Int. Rev. Gesamten Hydrobiol.* **70**: 527–546.
- PLAUDT, G., M. GHIL, AND R. VAUTARD. 1995. Interannual and interdecadal variability in 335 years of central England temperatures. *Science* **268**: 710–713.
- REYNOLDS, C. S. 1998. The state of freshwater ecology. *Freshwater Biol.* **39**: 741–753.
- RIEMANN, B., H. HAVSKUM, F. THINGSTAD, AND C. BERNARD. 1995. The role of mixotrophy in pelagic environments, p. 87–114. *In* J. Joint [ed], *Molecular ecology of aquatic microbes*, Springer Verlag.
- ROGERS, J. C. 1997. North Atlantic storm track variability and its association to the North Atlantic Oscillation and climate variability of northern Europe. *J. Climate* **10**: 1635–1647.
- SOMMER, U. 1996. Plankton ecology: The past two decades of progress. *Naturwissenschaften* **83**: 293–301.
- SORANNO, P. A. 1997. Factors affecting the timing of surface scums and epilimnetic blooms of blue-green algae in a eutrophic lake. *Can. J. Fish. Aquat. Sci.* **54**: 1965–1975.

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