

# Warmer Winters: Are Planktonic Algal Populations in Sweden's Largest Lakes Affected?

Winters in Sweden have become warmer in the 1990s, and as a consequence the timing of ice break-up and the growth and decline of spring phytoplankton has shifted, starting earlier. Even spring temperatures have become warmer, leading to an earlier beginning of the summer phytoplankton growth. The spring-ward shift in phytoplankton population growth has resulted in an extension of the growing season by at least one month. Although mean total phytoplankton biomass from May to October has not increased, the spring and early summer biomass of temperature-sensitive phytoplankton groups, such as cyanobacteria and chlorophytes, has increased in the 1990s. No increase was noted for other phytoplankton groups. Considering that some species of cyanobacteria that commonly occur during a summer bloom, such as *Anabaena*, *Aphanizomenon*, and *Microcystis*, can be toxic, the effect of warmer winters on aquatic ecosystems is potentially far-reaching.

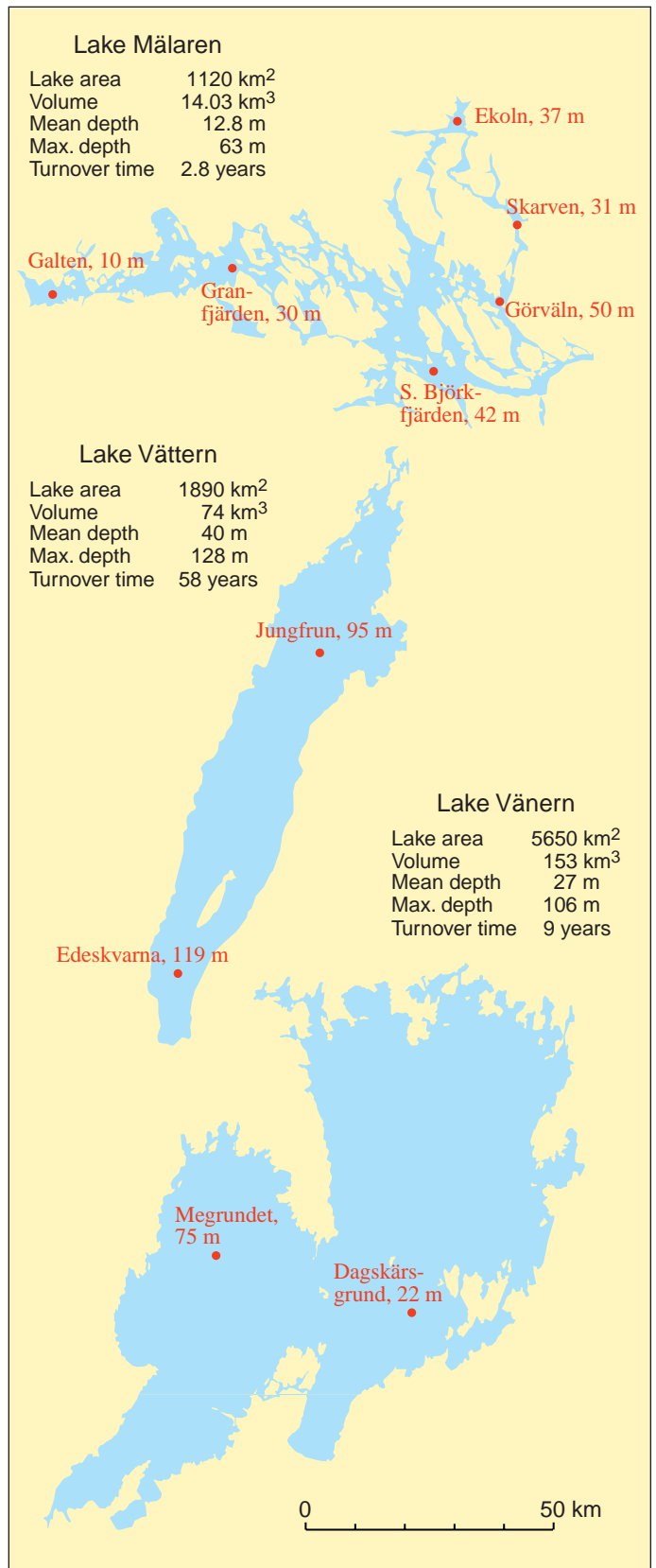
## INTRODUCTION

The debates on climate change have increased in frequency and intensity since reports that global mean surface air temperature has increased (1, 2) and natural catastrophes like hurricanes and floods are devastating the landscape. Although forecasts of climate change are not fully reliable, due to uncertainties in quantifying natural and anthropogenic-induced climate change, Allen et al. (3) contend that global mean temperatures will increase by 1 to 2.5 K between the decade from 2036 to 2046. Similar results are suggested for air temperatures in Sweden. Annual mean air temperature in Sweden is expected to increase by 3 to 4 K in the next 100 years according to climate simulations done by the Swedish Climate Prediction Center (Rossby) (4). Increases in winter (December through February) air temperatures are expected to be even more pronounced in Sweden; about 5 K warmer in the next 100 years.

Increases in air temperatures can affect aquatic ecosystems through multiple pathways and mechanisms. For example, Magnuson et al. (5), analyzing a dataset of 39 lakes and rivers in the Northern Hemisphere, found that an air temperature increase of about 1.2 K during the past 100 years has resulted in an earlier ice break-up by, on average, 6.5 days. Since the timing of ice break-up may affect the timing and development of individual species and communities (e.g. 6–8), increases in air temperature can have profound ecosystem-level effects.

In this study, I have analyzed air temperature and ice break-up data from Sweden's three largest lakes over the past 40 years. In particular, I was interested in determining if and how the winter and spring climate affects the development of spring (e.g. diatom) and summer phytoplankton populations. Phytoplankton was chosen because this group of organisms is dominated by short-lived organisms that respond rapidly to changes in the weather, i.e. they may be considered as an ideal sentinel of a tempera-

Figure 1. Sampling sites in the lakes Mälaren, Vänern and Vättern and some morphometric data.



ture change (9). At the end of this paper I address the question of possible responses of aquatic ecosystems towards the forecasted future global warming

## STUDY SITES AND DATA COLLECTION

Morphological and hydrological characteristics of Sweden's three largest lakes Vänern, Vättern and Mälaren are described in detail by Kvarnäs (10). Data on phytoplankton, zooplankton, phosphate-phosphorus, nitrate- and nitrite-nitrogen, reactive silica, lake water color (measured as the absorbance at 420 nm of 0.45 µm filtered water in a 5 cm cuvette) and water temperature are taken from a national dataset of monthly monitoring which regularly runs from May through October. In order to make among-lake comparisons, analyses were restricted to data collected between 1979 and 1999. Before 1979, sampling was too infrequent, especially in L. Vänern. Descriptions of the monitoring programs and the methods used can be found in Wilander and Willén (11). Seasonal mean values of phytoplankton growth were only calculated for 1979 to 1995, since from 1996 and onwards the monitoring program was reduced to 4 sampling occasions per year. In 1992, the method used for counting phytoplankton was modified (11). This modification might result in higher estimates of especially summer biomass, but here a significant difference of summer (July to September) phytoplankton biomass before and after 1992 was not revealed (Wilcoxon test).

The dataset consisted of 6 sites in L. Mälaren, 2 sites in L. Vänern and 2 sites in L. Vättern (Fig. 1). At the site Görväln in L. Mälaren also ice break-up data, received by the Swedish Meteorological and Hydrological Institute (SMHI), were available. In addition, ice break-up was measured at other sites in Mälaren, Vänern, and Vättern by SMHI. Those sites usually do not show large differences in ice break-up during 1 year (the between-site variations in one lake are much smaller than year-to-year variations, determined by a standard least squares model fitting). Therefore, the sites where ice break-up was measured can be used for interpretation of phytoplankton data. SMHI also delivered air temperature data at meteorological stations close to L. Mälaren, L. Vänern and L. Vättern.

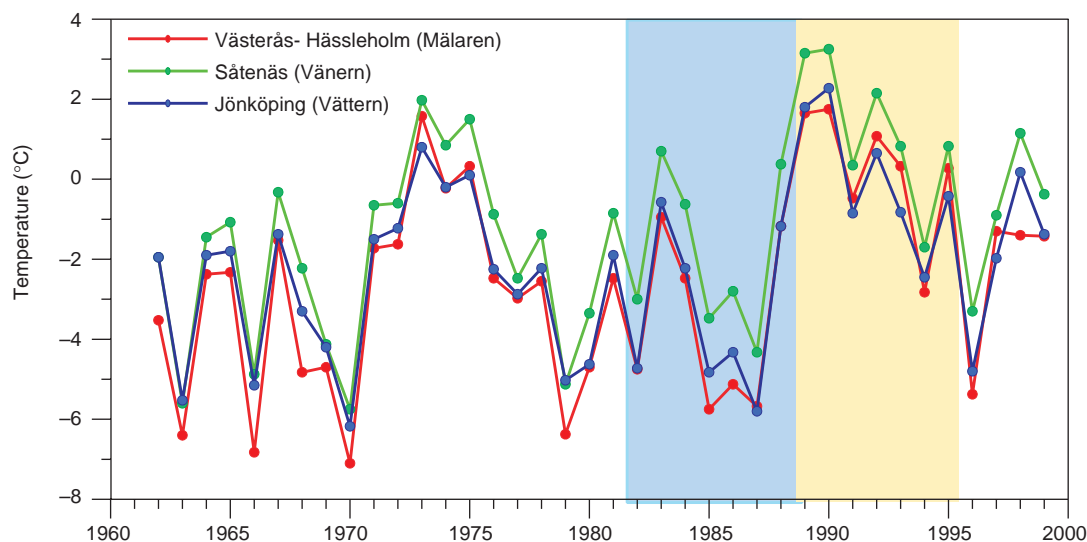
## WARMER WINTERS IN THE 1990s

Year-to-year variations of winter air temperatures at meteorological stations close to Sweden's three largest lakes are strikingly similar (Fig. 2). The highest winter air temperatures are registered close to L. Vänern, but increases in winter air temperatures were noted at all stations. Except for the winter 1995/1996, which was very cold again, all winter air temperatures in the 1990s exceeded the long-term average values (1961–1990) by 0.1 to 4.8 K. In particular, the winters of 1988/1989 and 1989/1990 were exceptionally warm. Comparing a cold period 1982–1988 with a warm period 1989–1995, the mean winter air temperatures differed at all three lakes (*t*-test;  $p < 0.002$  for Västerås-Hässleholm at L. Mälaren,  $p < 0.009$  for Sätenäs at L. Vänern,  $p < 0.005$  for Jönköping at L. Vättern). Also April air temperatures differed significantly between the 2 time periods 1982–1988 and 1989–1995 while May, June, and July air temperatures did not reveal a significant change.

## EARLIER ICE BREAK-UP IN THE 1990s

Weather changes in the late 1980s and in the 1990s have resulted in changes in the timing of ice break-up. Time series data of ice break-up for Mälaren, Vänern, and Vättern show a marked change in the timing of ice break-up since the very warm winter 1988/1989 (Fig. 3). In the basin of Görväln in L. Mälaren, for example, ice break-up had always occurred between March 24 and May 2 from 1964 to 1988. In 1989 and 1990 this basin had no ice-cover at all and quite early ice break-up during the 1990s. Other basins in L. Mälaren as well as sites in Vänern and Vättern show a similar pattern, i.e. no ice or very early ice break-up in 1989 and 1990 and early ice break-up during the 1990s (Fig. 3). Similar to winter air temperatures, the mean in the timing of ice break-up for the period 1982–1988 differed from the mean of the period 1989–1995 (*t*-test;  $p < 0.01$  at Görväln in L. Mälaren,  $p < 0.01$  at Brandsfjorden in L. Vänern,  $p < 0.05$  at Södra in Lake Vättern). Considering global warming, the tendency towards earlier ice break-up in lakes is likely to continue, although individual years might occur with a long-lasting ice-cover.

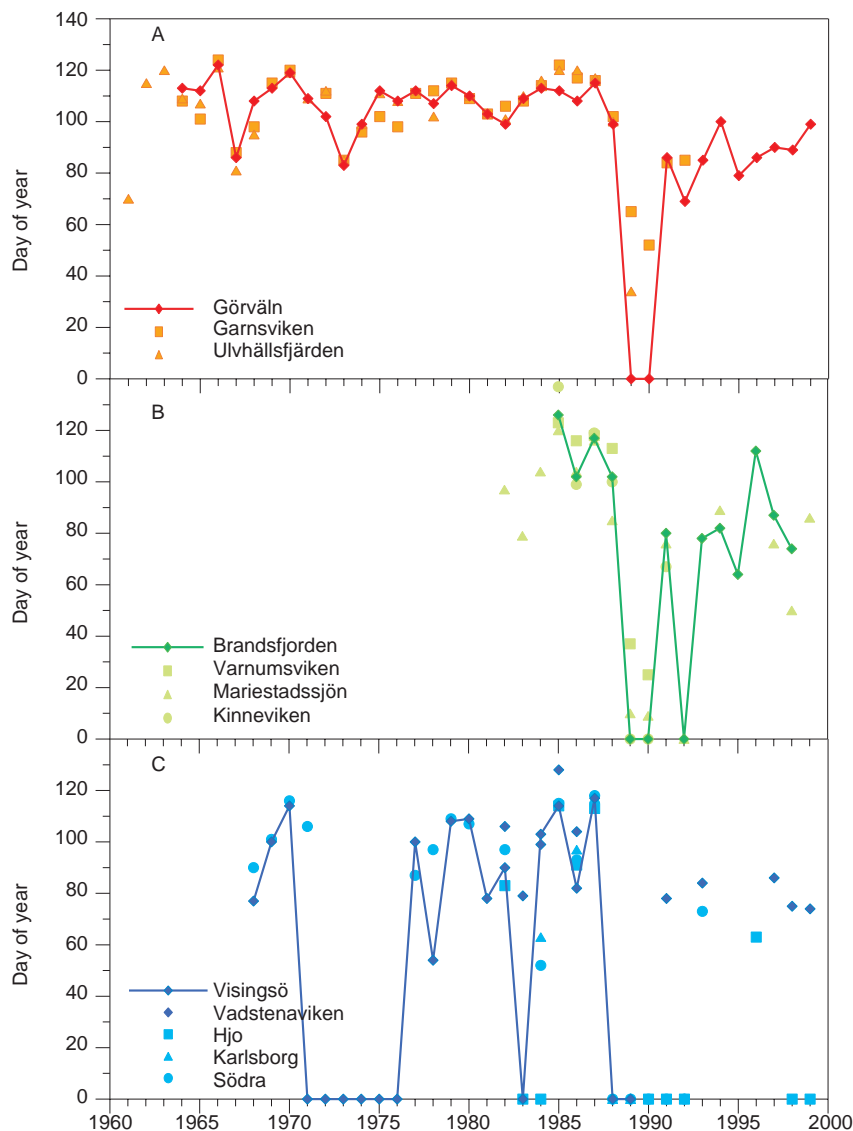
**Figure 2.** Mean winter (December–March) air temperatures at Västerås-Hässleholm (close to L. Mälaren), Sätenäs (close to L. Vänern) and Jönköping (close to L. Vättern) for 1961 to 1999. The shaded areas show the periods 1982–1988 with cold winters and 1989–1995 with warm winters.



## SHIFT OF THE PHYTOPLANKTON SPRING SEASON

Ice-cover on lakes, both thickness and duration, strongly affects phytoplankton development due to reduced light conditions and reduced turbulence (12). A spring (e.g. diatom) phytoplankton peak usually appears around ice break-up when light conditions in the water become nonlimiting. The only exception is a spring phytoplankton bloom dominated by phytoplankton species (e.g. small dinoflagellates) which can develop under ice, at low light intensities, if the ice is clear (13). However, such clear ice conditions are rare in Sweden's three largest lakes. Consequently, it can be expected that in Mälaren, Vänern, and Vättern, an earlier ice break-up generally leads to an earlier spring phytoplankton bloom development. A relationship between ice break-up and the timing of a spring phytoplankton bloom has already been observed in, e.g., L. Erken in central Sweden (13) and in Müggelsee in Germany (14).

The exact timing of the phytoplankton spring peak in Mälaren, Vänern, and Vättern cannot be reliably determined using the long-term datasets, since sampling is only monthly and does not start before May when the spring phytoplankton biomass is already declining during some years. Hence, instead of analyzing the timing of the phytoplankton spring peak, I focused my analyses on the timing of population declines of the spring phytoplankton. The decline of spring phytoplankton is not directly linked to ice break-up, but an early ice break-up and a following early spring phytoplankton bloom is likely to cause an early nutrient depletion and consequently an early spring phytoplankton decline. In addition, the decline of spring phytoplankton is caused by grazing losses, leading to a clear-water phase (15) that has also been found to be strongly dependent on winter climatic conditions (16, 17). Comparing nutrient concentrations of the cold period 1982–1988 with nutrient concentrations of the warm period 1989–1995 it becomes obvious that during the warm period much less bioavailable nutrients were in the water column in May than during the cold period (Table 1), indicating that the depletion of nutrients began earlier during the warm period. In addition to the earlier nutrient depletion after warm winters, zooplankton biomass was higher in May as a result of warmer water temperatures (Table 1). An early nutrient depletion and a higher zooplankton biomass should affect the timing of the spring phytoplankton decline. Here, I use diatoms as a representative of the spring phytoplankton because they are known to be one of the most typical spring phytoplankton groups (15). During the warm period 1989–1995 diatoms at some lake sites obviously declined earlier in the year than during the cold period 1982–1988. The shift in the decline of spring phytoplankton can best be seen in the west-



**Figure 3.** Ice break-up dates at different stations in the lakes **A.** Mälaren (1961–1999); **B.** Vänern (1981–1999); and **C.** Vättern (1968–1999). In each lake the station that has most observations is represented by a solid line.

**Table 1.** Concentrations of phosphate-phosphorus ( $\text{PO}_4\text{-P}$ ), nitrate- and nitrite-nitrogen ( $\text{NO}_3 + \text{NO}_2$ ) and reactive silica (Si), absorbance at 420 nm of 0.45  $\mu\text{m}$  filtered water in a 5-cm cuvette ( $\text{Abs } f_{420/5}$ ), water temperature ( $T_{\text{wat}}$ ) and zooplankton biomass (zoo) in May. The values are mean values of the cold period 1982–1988 and the warm period 1989–1995 at 6 sites in L. Mälaren (A–F), 2 sites in L. Vänern (G–H) and 2 sites in L. Vättern (I–J).

		$\text{PO}_4\text{-P}$ ( $\mu\text{g L}^{-1}$ )	$\text{NO}_3 + \text{NO}_2\text{-N}$ ( $\mu\text{g L}^{-1}$ )	Si ( $\text{mg L}^{-1}$ )	Abs ( $f_{420/5}$ )	$T_{\text{wat}}$ ( $^{\circ}\text{C}$ )	zoo ( $\text{mm}^3 \text{L}^{-1}$ )
A. Galten	Mean 82–88	10.1	460	3.0	0.152	10.3	not available
	Mean 89–95	11.1	364	2.1	0.171	11.5	available
B. Granfjärden	Mean 82–88	9.0	604	2.2	0.114	8.3	169
	Mean 89–95	7.9	519	0.9	0.099	10.0	319
C. Björkfjärden	Mean 82–88	13.6	326	0.6	0.055	4.7	155
	Mean 89–95	4.4	172	0.2	0.040	7.5	250
D. Görväln	Mean 82–88	12.9	405	1.2	0.063	6.4	not available
	Mean 89–95	4.6	187	0.3	0.044	8.6	available
E. Skarven	Mean 82–88	31.7	1223	4.3	0.123	8.3	not available
	Mean 89–95	16.3	1070	3.3	0.098	9.4	available
F. Ekoln	Mean 82–88	37.8	1353	4.3	0.158	7.1	131
	Mean 89–95	23.7	1519	3.8	0.142	7.7	240
G. Megrundet	Mean 82–88	1.3	571	0.3	0.038	3.2	not available
	Mean 89–95	1.9	536	0.2	0.030	6.0	available
H. Dagskärsgrund	Mean 82–88	1.5	592	0.4	0.043	5.6	24
	Mean 89–95	1.9	556	0.3	0.033	8.2	32
I. Jungfrun	Mean 82–88	2.1	449	0.4	0.007	2.9	not available
	Mean 89–95	1.7	507	0.2	0.007	6.3	available
J. Edeskvärna	Mean 82–88	1.2	454	0.4	0.010	2.7	not available
	Mean 89–95	1.4	510	0.2	0.009	7.4	available

Ice-cover of Lake Mälaren. Photo: G. Weyhenmeyer.

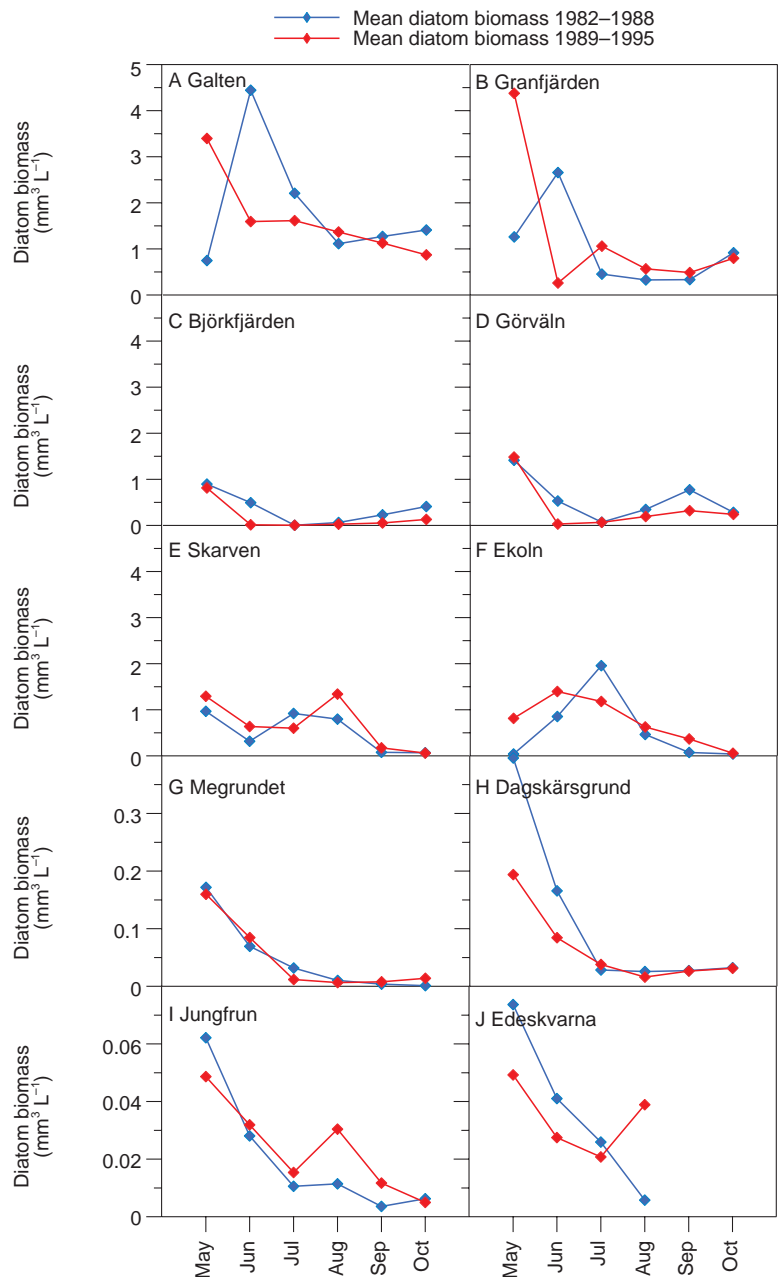


ern part of L. Mälaren at Galten and Granfjärden. At these 2 sites diatoms began to decline in June during the cold period 1982–1988 compared to May or earlier during the warm period 1989–1995 (Fig. 4 A and B). Also in the northern part of L. Mälaren at Ekoln an earlier decline of diatoms could be observed after the warm winters in the early 1990s (Fig. 4 F). In the central part of L. Mälaren, at S. Björkfjärden, and Görväln, it was not possible to determine when diatom declines started since this process fell outside the monitoring program. But it can be seen that the diatom decline had already finished in June after warm winters while it first had finished in July after cold winters (Fig. 4 C and D). The only site in L. Mälaren that did not show a shift in the spring phytoplankton was Skarven. Skarven is somewhat atypical in both morphology and hydrology; this site is located in a deep narrow strait (Fig. 1) that is highly influenced by the surrounding terrestrial and urban landscape. As a consequence, the hydrological flow regime is very unusual, causing a different phytoplankton succession at Skarven compared to the other sites in L. Mälaren.

Shifts in the phytoplankton spring bloom in Vänern and Vättern were not as obvious as in L. Mälaren, presumably because the phytoplankton spring bloom occurs even more outside the monitoring program than in L. Mälaren due to a more southern location of these two lakes. However, since the biomass of diatoms in May during the cold period 1982–1988 was much higher than during the warm period 1989–1995 (Fig. 4 G–J) it can be assumed that the declining of diatoms began earlier in the year after warm winters.

### EXTENDED PHYTOPLANKTON GROWING SEASON

The observed shift of the spring phytoplankton season after warm winters implies that the total growth period was extended by at least one month during the early 1990s. An extended phytoplankton growing season might lead to changes in the annual (January through December) mean total phytoplankton biomass. Studies in a number of European lakes could not support this hypothesis (18) because nutrients and not meteorological factors seem to limit the annual mean phytoplankton biomass. In the lakes Mälaren, Vänern, and Vättern the annual mean



**Figure 4.** Mean diatom biomass for May through October for 2 time periods; 1982–1988 (a cold period) compared to 1989–1995 (a warm period). Diatom biomass values are shown for 6 sites in L. Mälaren (A–F), 2 sites in L. Vänern (G, H), and 2 sites in L. Vättern (I, J). Note the y-axes are scaled differently. At Edeskvärna in L. Vättern phytoplankton data from September and October are missing for some years so no mean was calculated.

phytoplankton biomass cannot be calculated because phytoplankton was only sampled during the main growing season from May to October. The May to October mean phytoplankton biomass did not significantly change from 1982–1988 to 1989–1995 (Wilcoxon test not significant). However, years with very warm winters, such as 1989 and 1990, caused the May–October mean phytoplankton biomass values to become very low, because the phytoplankton spring peak presumably occurred earlier (i.e. prior to sampling), and hence these values are not included in the May–October mean. This example shows that it is important to adjust monitoring programs to new climatic conditions. In Mälaren, Vänern, and Vättern the monitoring programs were adjusted in 1995 when it was decided to start sampling of phytoplankton in April.



Sampling below ice-cover.  
Photo: G. Weyhenmeyer.

## SHIFT OF THE PHYTOPLANKTON SUMMER SEASON

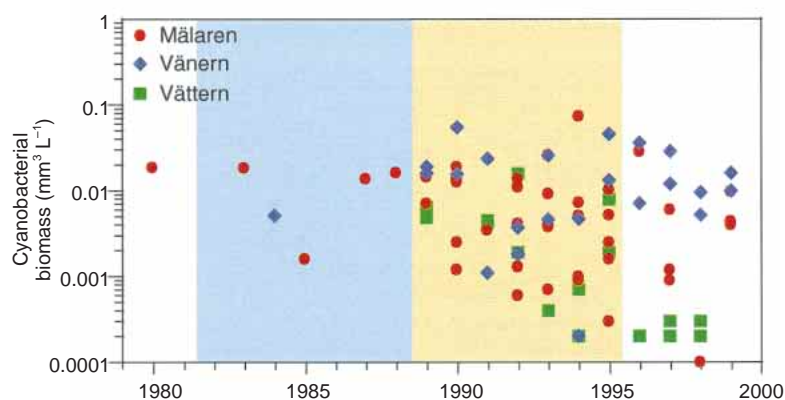
Not only winter temperatures increased in the 1990s but also the temperatures in April which could affect the beginning of the summer phytoplankton development. Here, the beginning of the summer phytoplankton development is defined as the first appearance of cyanobacteria in the water column. Cyanobacteria represent a typical summer phytoplankton group (14). During the 1990s cyanobacteria already occurred in May in the water column, probably due to the warmer water temperatures (Table 1). Before 1989, cyanobacteria had never been recorded in the water column of L. Vättern in May, while they have frequently been observed in that month since 1989 (Fig. 5). Also in L. Vänern, cyanobacteria suddenly appeared in May in 1989 (Fig. 5). In L. Mälaren, cyanobacteria were found in the water column in May on a few occasions before 1989, but biomass was low compared to the 1990s. During the 1990s cyanobacteria in L. Mälaren frequently occurred at all lake sites in May, and the biomass was high (Fig. 5). The occurrence of cyanobacteria already in May during warm springs indicates that the begin-

ning of the phytoplankton summer season shifts towards spring during warm springs. Since warmer springs coincide with warmer winters it is not possible to determine whether this shift in the summer phytoplankton season is only dependent on the spring situation or whether warmer winters and a consequent earlier decline of spring phytoplankton favors an earlier beginning of the summer phytoplankton development.

## EFFECTS OF WARMER WINTERS AND SPRINGS ON DIFFERENT PHYTOPLANKTON GROUPS

Phytoplankton groups differ in their response to changes in the environment. Some groups are most sensitive to changes in nutrient conditions, others to changes in temperatures or to changes in light conditions (19). The effects of warmer winters on diatoms have already been discussed here. It has also been shown here that cyanobacteria respond to warmer temperatures since they started to grow earlier in the year at all lake sites and in all three lakes after warm winters/during warm springs. As a consequence the cyanobacterial biomass in May during the warm period 1989–1995 significantly exceeded the biomass of the cold

**Figure 5.** May cyanobacterial biomass at 10 different stations in Mälaren, Vänern and Vättern for 1979 to 1999. If no data points are visible then no cyanobacteria were recorded in May. The shaded areas show the periods 1982–1988 with cold winters and 1989–1995 with warm winters. After 1995 the monitoring program was changed resulting in missing values for L. Mälaren at Galten and Skarven 1996–1999, at Granfjärden and S. Björkfjärden 1996, 1998, and at Görvåln 1996–1998.



**Table 2. Comparison (Wilcoxon-test) of the mean biomass of different phytoplankton groups between the cold period 1982–1988 and the warm period 1989–1995 at 6 sites in L. Mälaren (A-F), 2 sites in L. Vänern (G-H) and 2 sites in L. Vättern (I-J) during May, June, and July. \* means significant at the  $p < 0.05$  level, \*\* means significant at the  $p < 0.01$  level and n.s. abbreviation for not significant; + indicates a significant increase and – a significant decrease.**

	Total biomass			Cyanobacteria			Diatoms			Dinoflagellates		
	May	June	July	May	June	July	May	June	July	May	June	July
A Galten	+	n.s.	n.s.	+	+	n.s.	+	-	n.s.	n.s.	+	n.s.
B Granfjärden	+	-	n.s.	+	+	n.s.	+	-	n.s.	+	n.s.	n.s.
C Björkfjärden	n.s.	-	-	+	n.s.	n.s.	n.s.	-	n.s.	+	n.s.	n.s.
D Görvåln	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
E Skarven	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+
F Ekoln	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+
G Megrundet	n.s.	n.s.	n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
H Dagskärsgrund	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
I Jungfrun	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
J Edeskvärna	n.s.	n.s.	n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	+	n.s.

	Chrysophytes			Cryptophytes			Chlorophytes		
	May	June	July	May	June	July	May	June	July
A Galten	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	+
B Granfjärden	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	+
C Björkfjärden	+	n.s.	+	+	n.s.	-	+	+	+
D Görvåln	n.s.	n.s.	+	+	n.s.	n.s.	+	+	+
E Skarven	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.
F Ekoln	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
G Megrundet	+	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	+
H Dagskärsgrund	n.s.	n.s.	n.s.	n.s.	n.s.	-	+	n.s.	+
I Jungfrun	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
J Edeskvärna	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

period 1982–1988, except at the sites Ekoln and Skarven in L. Mälaren (Table 2), which are the sites with the least pronounced water temperature increase in May from 1982–1988 to 1989–1995 (Table 1). The increased cyanobacterial biomass in May during the warm winter/spring period 1989–1995 lasted until June at most stations (Table 2), although the June water temperatures remained more or less the same from 1982–1988 to 1989–1995. Not until July, when water temperatures again remained unchanged from 1982–1988 to 1989–1995, did the cyanobacterial biomass during 1989–1995 reach values close to those of 1982–1988 (Table 2). Since the main increase of cyanobacteria occurred in May and not during the summer, cyanobacterial biomass was still low even after the significant increase; cyanobacterial biomass in May in 1989–1995 ranged from  $0.003 \text{ mm}^3 \text{ L}^{-1}$  at Edeskvärna in L. Vättern to  $0.017 \text{ mm}^3 \text{ L}^{-1}$  at Galten in L. Mälaren.

While cyanobacteria showed a response to temperature changes at most sites in May, chlorophytes that are also known to be a temperature sensitive phytoplankton group (19), only significantly increased in May at lake sites which had similar light conditions, expressed as the absorbance of filtered water (Tables 1 and 2). Not until June, when light conditions at other sites reached values close to the ones at the sites where the increase was registered, did chlorophytes also significantly increase at these sites (Table 2). Chlorophytes changed even in July from 1982–1988 to 1989–1995. Changes in July cannot be directly linked to changes in temperature since both air and water temperatures do not show changes in June and July from 1982–1988 to 1989–1995.

Unlike cyanobacteria and chlorophytes, the biomass of other phytoplankton groups such as dinoflagellates, chrysophytes, and cryptophytes, in May and June, did not reveal a consistent response to warmer temperatures. Only at some lake sites was a significant change of one or more (maximum 3) other phytoplankton groups observed, but no clear patterns were evident (Table 2). A combination of factors such as nutrient availability, grazing pressure, turbulence, and light conditions are strong de-

terminants of phytoplankton growth (19), hence these variables may confound a temperature response.

## FUTURE PERSPECTIVES: DIRECT AND INDIRECT CLIMATIC EFFECTS ON PHYTOPLANKTON

Most of recent climate studies point to a continuous temperature increase in the near future. This temperature increase can have direct effects on the phytoplankton biomass. However, also indirect temperature effects have to be taken into account. The most obvious indirect temperature effect on phytoplankton is ice break-up. An increase in temperature leads to an earlier ice break-up which again has a large impact on light conditions, turbulence, and thereby nutrient availability. Increases in temperature should also result in increased mineralization and hence changes in nutrient dynamics and availability. The complex interactions of direct and indirect temperature effects should affect different phytoplankton groups differently, and this may partly explain why the response of biomass was different for various phytoplankton groups and the same groups at different stations in Mälaren, Vänern, and Vättern (Table 2). Better knowledge of the importance of indirect temperature effects is needed, and should be the focus of future studies. In addition, changes in precipitation and wind speed are also expected to occur, hence a better understanding of how these variables affect phytoplankton communities is needed.

## CONCLUSION

There is evidence that warmer winters cause a shift in the phytoplankton spring season. Due to an earlier ice break-up, spring phytoplankton starts to grow earlier in the season; nutrients are depleted earlier and as a consequence, the spring phytoplankton declines earlier. In addition, warmer spring temperatures cause an earlier growth of zooplankton, also leading to an earlier decline of the spring phytoplankton. If the trend of earlier ice break-up or no ice cover at all continues, monitoring



Ice break-up in Sweden's largest lake.  
Photos: G. Weyhenmeyer.



programs should be adjusted to encompass early population growth of spring phytoplankton communities.

Not only the phytoplankton spring season was affected by temperature changes, but also the beginning of the summer phytoplankton season. Summer phytoplankton began to grow earlier, resulting in a higher biomass of cyanobacteria and chlorophytes in spring and early summer. Dinoflagellates, cryptophytes and chrysophytes in spring and early summer did not reveal a consistent response to temperature changes in winter and spring.

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