

Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation

Dieter Gerten¹ and Rita Adrian

Institut für Gewässerökologie und Binnenfischerei, Müggelseedamm 260, D-12562 Berlin

Abstract

Climate is increasingly recognized as a major factor driving long-term changes in plankton communities in both marine and limnetic ecosystems. In a shallow and polymictic lake, marked changes in the dynamics of phytoplankton and in the timing of distinctive successional events in spring were observed during two recent decades. We studied whether and how these changes were linked to a series of uncommonly warm winter and spring seasons, focusing on the predictive power of a macroscale atmospheric circulation pattern, the North Atlantic Oscillation (NAO). In the warm period 1988–1998, phytoplankton developed about 1 month earlier than in the cool period 1979–1987, and high total phytoplankton biomass was recorded in early spring. These changes were significantly related to the NAO, which explained about 35% of the variance, and can be attributed to a shortening or lack of ice cover periods in winter. Zooplankton (*Keratella*, *Bosmina*, *Daphnia*) developed about 2 weeks earlier in the warm period, consequently leading to an early establishment of the clearwater phase. The shift in the timing of the daphnid peak and of the clearwater phase required an additional warming trend in late April and early May and was not significantly correlated with the winter situation. The memory effect of the NAO was restricted to a rather short postwinter period and was overtaken by the prevailing weather in April. Our results suggest that assessments of potential impacts of climate warming on biological processes in freshwater ecosystems demand basic knowledge about the relationships between global climate indices, local meteorological conditions, and the thermal response of various lake types.

Knowledge about factors that influence interannual and interdecadal variability in plankton dynamics and the phenology of successional events is needed to predict how lake ecosystems will respond to anticipated global change. Climate is a major factor responsible for long-term changes of thermal properties and biological processes in freshwater ecosystems, if anthropogenic influences are absent (Carpenter et al. 1992). Profound impacts of air temperature, and global warming in particular, on water temperature, lake stratification, and the duration of ice cover are documented for a variety of lakes around the world (Schindler et al. 1990; King et al. 1999; Livingstone 1999). As a consequence, climate-driven changes of water temperature have been discussed to provoke alterations of plankton community structure in lakes (George and Harris 1985; Adrian and Denneke 1996; Müller-Navarra et al. 1997).

Macroscale atmospheric and oceanic phenomena responsible for regional or global climatic fluctuations are increasingly recognized to control long-term variations in aquatic ecosystems, such as the El Niño Southern Oscillation (Strub

et al. 1985; Anderson et al. 1996), or the Gulf Stream (George and Taylor 1995). Throughout the northern hemisphere, the North Atlantic Oscillation (NAO) is a major source of interannual and interdecadal weather and climate variability. This large-scale climate phenomenon usually is expressed in terms of the NAO index, a measure of the difference in atmospheric pressure anomalies between the subtropical Azores high and the subpolar Icelandic low (Hurrell and van Loon 1997). Effects of the NAO on weather conditions are most pronounced in winter. Highly positive winter NAO indices indicate zonal circulation over the Atlantic, leading to mild and rainy winters in the western and northern parts of Europe. The reverse situation is associated with low pressure gradients over the Atlantic, usually bringing cold winters over Europe (Hurrell 1995).

Recently, effects of the NAO on population dynamics were documented for terrestrial (Post et al. 1997; Post and Stenseth 1998), coastal (Fromentin et al. 1998; Kröncke et al. 1998), and marine environments (Reid et al. 1998). Moreover, there are indications that the NAO affects biological processes in European inland waters. In large and deep Lake Constance (Germany), population dynamics of *Daphnia* were closely related to the winter NAO signal, which was detectable in plankton time series until July (Straile and Geller 1998; Straile 2000). For Lake Erken (Sweden), Weyhenmeyer et al. (1999) found that the timing, magnitude, and composition of the phytoplankton spring peak were associated with the winter NAO index. Thus, the NAO seems to influence important planktonic successional events from winter to early summer in lakes over a wide geographical range in Europe.

It is doubtful that intraannual effects of the NAO last as long in shallow, polymictic lakes with low heat storage capacity, a lake type we focus on here, as in deep or sheltered

¹ Corresponding author (gerten@igb-berlin.de).

Acknowledgements

We thank the staff of the Institut für Gewässerökologie und Binnenfischerei, especially Rüdiger Biskupek, Marianne Graupe, Thomas Hintze, and Bernd Schütze, without whose commitment in sampling and technical support this study would not have been possible. Sigrid Hoeg and Renate Rusche are acknowledged for phytoplankton and zooplankton analysis. Nutrient analyses were performed by Liselotte Dollan, Hans-Jürgen Exner, Doris Schneider, Monika Spangenberg, and Elke Zwirnmann. The manuscript benefited from critical readings by Stephen Carpenter, Ursula Gaedke, Sarah Poynton, Dietmar Straile, Norbert Walz, and two anonymous reviewers. The study was funded by the Deutsche Forschungsgemeinschaft (AD 91/10-2).

lakes, since the former are likely to be more vulnerable to variations in ambient weather conditions (Shuter et al. 1983). This might be especially true for shallow lakes in the temperate region, where meteorological conditions in spring are highly variable and are mostly independent of conditions during the preceding winter (Rocznik 1995). In fact, there is evidence that in shallow lakes, direct and indirect effects of winter conditions on plankton dynamics are restricted to a relatively short period. In the lake under investigation, plankton groups that appeared first in the seasonal succession (diatoms, rotifers, and daphnids) were found to reach peak abundances early after mild winters, whereas the magnitudes of the zooplankton peaks were independent of winter conditions (Adrian et al. 1999).

Hence, our hypothesis is that in shallow and polymictic lakes of the central European region, the impact of the global winter NAO signal on water temperature, and finally on biological processes, is restricted to a rather short postwinter period. Therefore, we presume that the NAO influence on successional events in late spring is overtaken by local weather conditions.

The present study reports marked long-term (2 decades) changes in the dynamics of dominant phytoplankton and zooplankton groups and in the timing of successional events in spring in shallow, polymictic Müggelsee (northeastern Germany). The purpose was to test whether these changes in the plankton actually were related to temperature conditions and, specifically, to distinguish between changes that were induced by a warming in winter (i.e., by high positive NAO indices) and those related to an additional warming in late spring. Time series of climatic, hydrological, and limnological data from 1979 to 1998, including a period of uncommonly warm winter and spring seasons, were analyzed.

Material and methods

Study site—Müggelsee (area 7.3 km², mean depth 4.9 m, maximum depth 8.0 m) is a shallow, polymictic, and highly eutrophic lake lying to the southeast of Berlin, Germany (52°26'N, 13°39'E). It is situated between maritime and continental climatic zones, characterized by high intraannual and interannual weather variability. The lake is flushed by River Spree and has an average retention time of about 6 weeks. Further physiographical and limnological characteristics are described by Driescher et al. (1993).

Air temperature—Daily mean air temperatures for 1979 to 1998 were provided from the Deutscher Wetterdienst for the nearby airport station of Berlin-Schönefeld (52°23'N, 13°31'E). Recent conditions were rated using historical air temperature data (since 1756) from Berlin-Tempelhof (52°29'N, 13°24'E), which were available at <http://www.wetterzentrale.de/klima/tberlintem.html>.

NAO index—The winter (December through March) index of the NAO was used, as provided by the National Center of Atmospheric Research, Boulder, Colorado (<http://goldhill.cgd.ucar.edu/cas/climind/>). Monthly NAO indices (available at the same site) were used to check for correlations with air and water temperature only. The indices ex-

press the difference of sea level pressures between Lisbon (Portugal) and Stykkishólmur (Iceland), normalized relative to the period 1864–1983.

Water temperature—Water temperature was recorded daily between 0800 and 0900 h at the north shore of the lake at a depth of 0.3 m. From 1979 to 1993, manual measurements were performed using a mercury thermometer; afterward, water temperature was recorded automatically by a temperature transducer. As there were synchronous records for the growing seasons (April–October) 1979–1993, both recording methods could be compared, and no significant differences were found (pairwise Wilcoxon-Mann-Whitney test on biweekly means: $p > 0.05$). For periods when the lake was covered with ice, and temperature was not recorded, we assumed that the surface water temperature was 0°C, according to measurements during the ice cover period of 1996.

Phytoplankton and zooplankton—Plankton samples were taken at weekly or biweekly intervals (sporadically during periods with ice cover) using a 5-liter Friedinger sampler. Between 1979 and 1986, phytoplankton samples were drawn weekly (in winter: biweekly) at the deepest section of the lake (integrated from 0.5, 4, and 7 m) and fixed with Lugol's solution. Since April 1987, integrated volumetrically weighted samples were taken each Monday at 1-m intervals from the surface to the bottom at five different stations across the lake, accounting for possible spatial inhomogeneities (for more detail, see Driescher et al. 1993). Cell number and biovolume were determined using an inverted microscope. Between 1979 and 1986, zooplankton were sampled biweekly at the deepest point of the lake at 1-m intervals from the surface to the bottom. Since 1987, integrated samples were collected weekly (see above). Zooplankton samples were screened through a 50- μ m mesh and fixed with formaldehyde (4% final concentration). We recorded rotifers (as the sum of both the dominant species *Keratella cochlearis* Hauer, and *K. quadrata* O. F. Müller), bosminids (sum of *Bosmina longirostris* O. F. Müller, which is the most dominant species in spring, and *B. coregoni* Baird), and daphnids (sum of *Daphnia cucullata* Sars, *D. galeata* Sars, *D. longispina* O. F. Müller, *D. hyalina* Leydig, and the hybrids: *D. cucullata* \times *D. galeata* Flößner, *D. hyalina* \times *D. galeata* Flößner). We assumed that the change in the sampling strategy did not cause a significant bias in the plankton series, as analysis of synchronous zooplankton counts in 1987 ($n = 15$) revealed no significant differences (Wilcoxon-Mann-Whitney: $p > 0.1$). Moreover, Schellenberger and Stellmacher (1986) found that seston concentrations were quasihomogeneously distributed across the lake.

Net growth rates of phytoplankton and zooplankton were estimated by the quotient of specific biweekly abundances and the abundance of the preceding biweek (\log_{10} -transformed values), divided by the time span (14 d). The timing of spring peaks of phytoplankton and zooplankton was defined by the week when maximal abundances were reached in spring. When two peaks developed, the timing corresponds to the first one. The clearwater phase was defined

herein by the week when lowest total phytoplankton biomass was recorded after the spring bloom.

Statistical analysis—Prior to analysis, each year (January–June) was divided into 13 biweekly periods. The biweekly value of a variable was taken as the arithmetic mean of all measurements within a biweek (usually one or two plankton samples; 14 temperature values). The search for evidence of climate-driven changes in plankton dynamics was structured as follows. First, trends in any climatic and limnological variable were visualized and tested for significance. In a next step, two subsets of the investigation period (1979–1987 and 1988–1998) were defined, which differed significantly in their temperature conditions. This distinction enabled us to analyze the impact of both increased winter and spring temperature on the plankton. We then tested for changes in plankton dynamics (biweekly abundances, net growth rates, timing of peak abundances) by comparing their values of the first and the second subperiod, respectively. To check whether significant changes detected by this procedure actually were related to the observed shift in temperature conditions, the respective series were correlated with the NAO index and with water temperature in spring. All statistical analyses were performed separately on each biweekly time series, i.e., there was one value per year.

Trend detection and elimination—Two complementary techniques were applied to detect trends in the time series: (1) Cumulative z -score plots to visualize the transient behavior (z scores are standardized anomalies, i.e., deviations from the long-term mean of the series under examination divided by the standard deviation, which can be smoothed by calculating their cumulative sums. Plots of these cumulative z scores indicate periods with predominantly positive or negative anomalies, and can be used to determine the date of trend initiation) and (2) the nonparametric, rank-based Mann-Kendall trend test (e.g., Helsel and Hirsch 1992), which tests for significant monotonous trends over time, based on Kendall's correlation coefficient.

Correlating time series afflicted with a trend, or other serial dependencies, may lead to spurious correlations that do not represent actual mechanistic relationships, but occur only due to the presence of these instationarities (Chatfield 1996). Therefore, we detrended those series for which the Mann-Kendall test indicated a significant linear trend by fitting a linear regression versus time and used the residuals for the subsequent correlation analysis. We could not identify AR-IMA_{p,d,q} processes (Box et al. 1994) to eliminate the transient components because they usually were weak and were not obvious in the autocorrelation functions of the series. In particular, we were concerned about a human-induced negative trend in the flushing rate of the lake that began close to the time (1990) when climatic conditions were changing. However, major influences of the flushing rate on the plankton could be excluded, since there actually were no significant correlations between the detrended runoff and plankton series ($p > 0.05$). These findings were confirmed by partial correlation analyses between the flushing rate and plankton abundances, with water temperature as the constant variable ($p > 0.05$).

A few series (without trend) were autocorrelated significantly at time lag 1, i.e., the values depended on the value of the preceding year. This kind of serial correlation was removed by fitting an appropriate model from the ARIMA family, following the methodology of Box et al. (1994). A first-order autoregressive model (AR₁) appeared to be the most suitable process to fit the data. The residuals of the model were independent of each other, and thus could be used for correlation analysis.

Comparison of mean levels—To ensure mean temperature differences between the subperiods 1979–1987 and 1988–1998 were statistically significant, t -tests were applied on each biweekly series of air and water temperature (all data were approximately normally distributed). To test for significant shifts in plankton time series, which often contained outliers and showed skewed frequency distributions, the nonparametric U -test (Wilcoxon-Mann-Whitney test) was used. We note that there were only few values in both subsamples ($n = 9$ in the first, and $n = 11$ in the second period, respectively), but the results of the trend and correlation analyses ($n = 20$) principally confirmed the findings of the t - and U -tests.

Correlation analysis—Plankton time series for which the U -test signaled a significant shift were cross-correlated with the winter NAO index and with water temperature in April and May. All years under investigation were used for correlation analysis, without division into two subperiods. For correlations with the nonnormal plankton series, Spearman's rank correlation coefficient, δ , was used. The correlations allowed corroboration of the presumption that the changes in plankton abundances were linked with meteorological conditions in winter and/or spring.

All statistical analyses were performed using SAS/ETS® 6.12 (SAS Institute 1995) and SPSS® 6.1.3 (SPSS 1993).

Results

Relationships between NAO, air temperature, and water temperature—Monthly means of air temperature from December to March were closely correlated with both the winter (December through March) NAO index and the corresponding monthly NAO indices ($r > 0.5$, $p < 0.01$; Fig. 1). Thus, the winter index can be regarded as a surrogate for the respective monthly NAO indices, which therefore will not be discussed further. No significant correlations existed between the NAO and air temperatures beyond March ($r < 0.3$, $p > 0.1$ for winter index and monthly indices), despite a certain overlap of warm winter and warm spring seasons in the late years.

Biweekly means of water temperature from December to March were significantly correlated with air temperatures during the preceding month ($r > 0.6$, $p < 0.01$). In April and May, however, this correlation was reduced to a period of about 2 weeks, i.e., water temperature in spring was hardly influenced by winter conditions. Accordingly, the NAO signal (winter and monthly indices) was reflected in water temperature from December to March only ($r > 0.55$, $p < 0.01$).

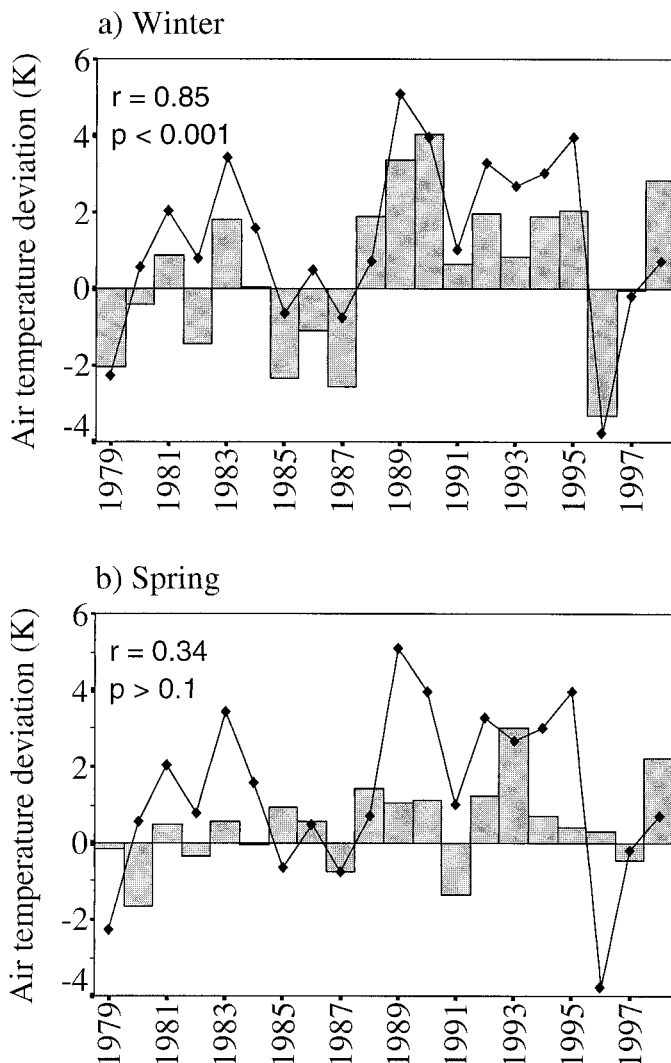


Fig. 1. Departures (K) of mean winter (December–March) and spring (April–May) air temperatures from their long-term mean (climate normal period 1961–1990) at Berlin-Schönefeld 1979–1998 (bars). The solid lines represent the winter NAO index (dimensionless). Values of r and p are given for the Pearson correlation between the NAO index and air temperature deviations.

Changes in air and water temperature—High interannual fluctuations of air temperature particularly in winter were obvious, as well as a warming tendency in winter and in spring since the late 1980s (Fig. 1). Cumulative z -score plots of winter and spring temperatures exhibited a turning point toward warmer conditions in 1988 (Fig. 2a,b). On average, biweekly means of winter and spring air temperature were about 1–5 K higher in the second subperiod, yet not all of these shifts were significant (Table 1). Note, however, that air temperature in late March/early April (biweeks 7, 8) did not show a warming tendency. Not surprisingly, the warming trend in air temperature was also evident in winter and spring water temperatures, which increased by 0.5–2 K beginning in 1988 (Fig. 2a,b; Table 1). We note that the winter of 1995/1996, which was the coldest winter during the investigation period, lies within the warmer period, but found that it did

not considerably affect the general pattern. The increase of the winter NAO index was marginally nonsignificant ($p = 0.12$), but was significant excluding that cold winter ($p = 0.04$).

Rating the recent conditions with historical air temperature recordings, we found that some of the winter and spring seasons in the second half of the investigation period were among the 2% warmest of the last 240 yr. The highest observed NAO winter indices ever (since 1864) appeared in 1989, 1990, and 1995. These findings tally with the increasing trend in winter and spring air temperature observed in central Europe during the last century (Rapp and Schönwiese 1995; Davis et al. 1998). Concomitant with the exceptional increase of air temperature, annual means of Müggelsee water temperature for most years since 1988 were the highest on record (since 1946; Behrendt et al. 1987).

Changes in phytoplankton abundances in relation to the NAO—In the warmer period 1988 to 1998, phytoplankton biomass often remained quite high during winter, whereas in the preceding cooler period, algae usually did not start to grow until March. Thus, in the latter years, phytoplankton biomass in early February was already at concentrations achieved in late March in preceding years (Fig. 3). Accordingly, the integrated sum of phytoplankton biomass from January to April was significantly higher in the warm period ($p < 0.01$). Phytoplankton biomass in March was significantly correlated with the NAO index (Fig. 4). Very high abundances were observed after ice-free winters, which essentially contributed to high variation of phytoplankton biomass during the warm period (Fig. 3). Net growth rates of phytoplankton were lower in the warmer period, significantly so in late March ($p < 0.05$).

The timing of the phytoplankton spring peak was closely correlated with the NAO index and was reached about 1 month early in the warm period (Table 2; Fig. 2c). The height of the peak did not differ significantly between both subperiods and was weakly correlated with the NAO index ($\delta = 0.44$, $p < 0.1$). In May, again a time lag of about 2 weeks appeared, i.e., the clearwater phase established significantly earlier in the warmer period (Table 2; Fig. 2d). The correlation between the timing of the clearwater phase and water temperature in spring (Table 2) most probably was spurious, as mediated by daphnid grazing.

Changes in zooplankton abundances in relation to the NAO—Population development of zooplankton started about 2 weeks earlier in the warm period (Fig. 5). Significant differences in biweekly abundances turned out to be simply the consequence of this temporal shift. Spring peaks of *Keratella*, *Bosmina*, and *Daphnia* were observed earlier in the warmer period, yet significantly so only in the case of *Daphnia* ($p < 0.05$). In contrast to the changes in phytoplankton dynamics, zooplankton dynamics (net growth rates, integrated sum of abundances before spring maximum, height of maximum) did not alter from the cool to the warm period.

The NAO only marginally influenced spring (biweeks 5–11) abundances of rotifers ($-0.15 < \delta < 0.55$, $0.53 > p > 0.01$) and of cladocerans ($0.35 < \delta < 0.5$, $0.12 > p > 0.03$). The timings of peak abundances of both *Keratella* and *Bos-*

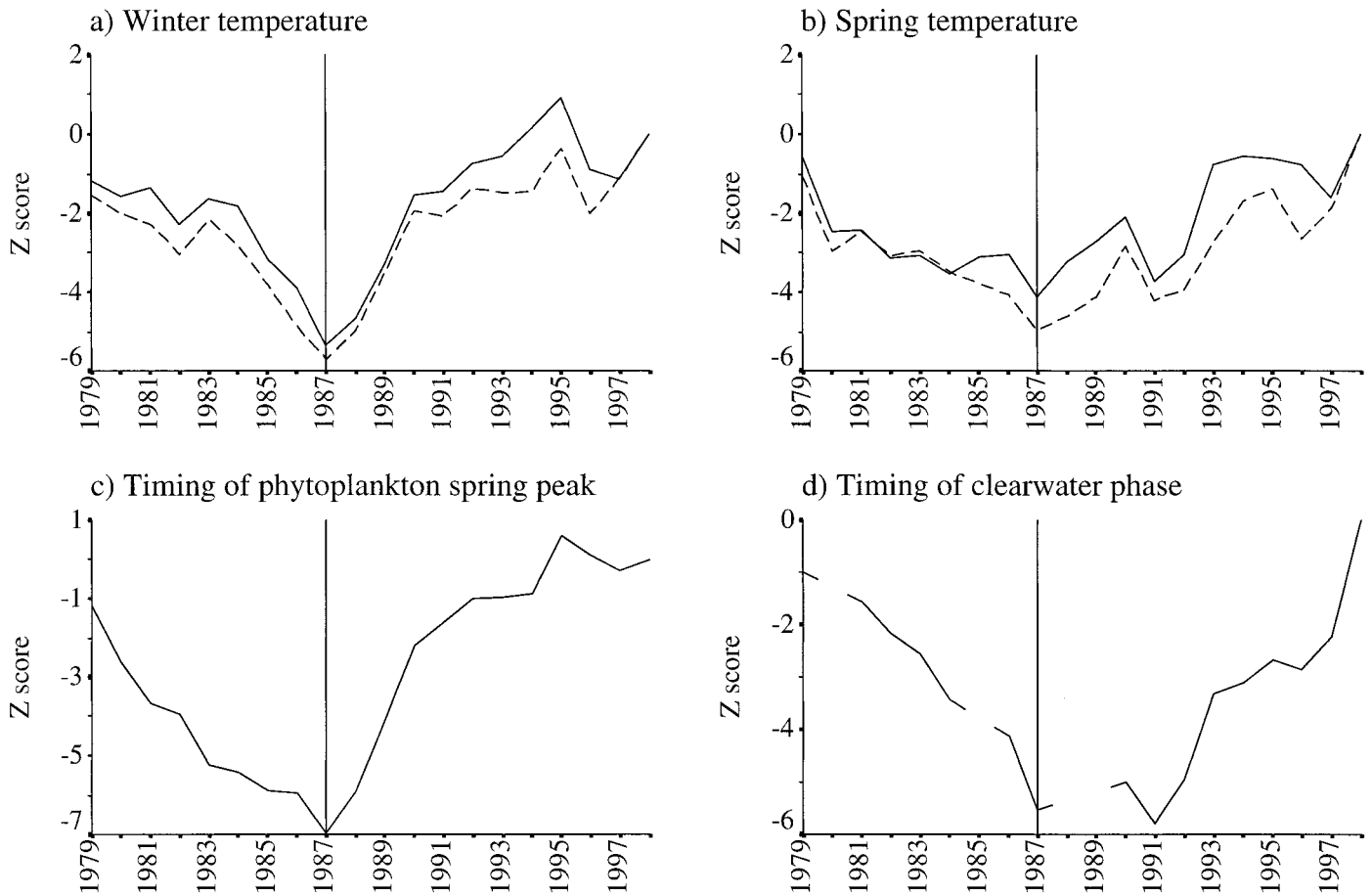


Fig. 2. Cumulative z -score plots for 1979–1998 of (a) mean winter (December–March) air temperature at Berlin-Schönefeld (solid lines) and surface water temperature of Müggelsee (dashed lines); (b) mean spring (April–May) air and water temperature; (c) the timing of the phytoplankton spring maximum; and (d) the timing of the clearwater phase (in 1980, 1985, 1988, and 1989 no clearwater phase was observed). (c) and (d) z scores with opposite sign. Vertical lines indicate the year of trend initiation, 1987/1988.

Table 1. Biweekly arithmetic means of air temperature at Berlin-Schönefeld, and water temperature of Müggelsee ($^{\circ}\text{C}$) for 1979–1987 and 1988–1998. Asterisks denote significant differences in the t -test: $p < 0.01$ (***), $p < 0.05$ (**), $p < 0.1$ (*), not significant (n.s.). Bold numbers indicate significant trends according to the Mann-Kendall test ($p < 0.05$). The assignment of months to biweeks is approximated.

Biweek and month	Air temperature			Water temperature		
	1979–1987	1988–1998	p	1979–1987	1988–1998	p
1 Jan	-2.4	1.2	*	1.0	2.0	n.s.
2 Jan	-3.1	1.4	**	0.7	1.9	**
3 Feb	-0.5	0.7	n.s.	0.8	1.9	**
4 Feb	-2.5	2.7	***	0.8	2.2	***
5 Mar	-0.6	3.5	***	1.0	3.0	***
6 Mar	2.8	4.8	*	2.5	4.5	**
7 Mar/Apr	6.5	5.8	n.s.	4.8	6.0	*
8 Apr	7.4	7.4	n.s.	7.6	8.1	n.s.
9 Apr	8.7	11.8	**	9.8	11.8	**
10 May	12.3	13.2	n.s.	12.9	14.7	**
11 May	15.0	15.0	n.s.	16.8	17.0	n.s.
12 Jun	16.3	16.3	n.s.	18.3	19.0	n.s.
13 Jun	15.8	16.7	n.s.	18.2	19.4	n.s.

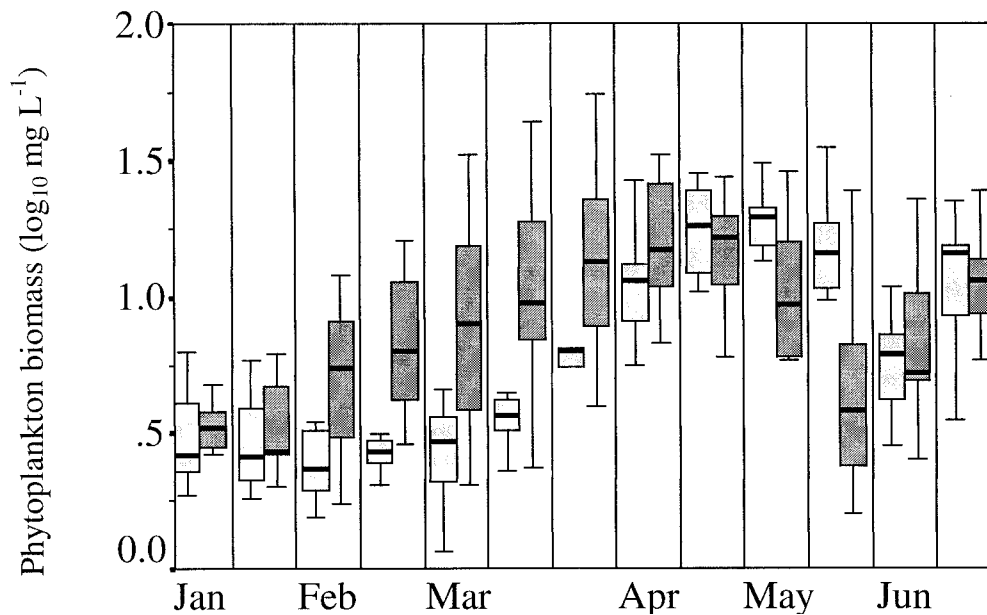


Fig. 3. Biweekly boxplots of total phytoplankton biomass ($\log_{10} \text{ mg L}^{-1}$) in Müggelsee from January to June 1979–1987 (light shading) and 1988–1998 (dark shading). Each box illustrates the approximated 25 and 75% interquartile ranges. The median is represented as a thick horizontal line within a box. Upper and lower whiskers comprise values within an interval ± 1.5 times the box height. Note that March includes three biweeks.

mina were significantly correlated with the NAO index, although they only slightly differed between the two periods (Table 2). Contrarily, the timing of the *Daphnia* peak was largely independent of the NAO, but demonstrated a strong relationship with concurrent water temperature ($p < 0.01$). A partial correlation analysis confirmed that there was no significant overlap between the NAO signal and the late spring temperature signal. Water temperature in late April or early May alone had a high predictive power for the timing of the daphnid peak and of the associated clearwater phase

(partial $r = -0.57$, $p < 0.01$), whereas the NAO only weakly influenced the timing of both events (partial $r = -0.1$, $p > 0.6$). After the clearwater phase, in June, phytoplankton and zooplankton abundances did not differ significantly in the cold and the warm period (Fig. 3, Fig. 5), and no significant correlations with temperature existed.

Discussion

The present paper documents prominent shifts in the successional pattern of phytoplankton and zooplankton in spring observed in a shallow polymictic lake in central Europe from 1979 to 1998. These findings indicate potential effects of anticipated climate warming on freshwater ecosystems, as during this period there was an exceptional increase of both winter and spring temperatures. We were able to distinguish between changes associated with a warming in winter and changes associated with a warming in late spring.

High vernal phytoplankton biomass and early development of phytoplankton in the warm period 1988–1998 (Fig. 3) were linked to the high frequency of positive NAO indices in those years (Fig. 4, Table 2); this relationship is most likely attributable to a shortening of ice cover periods in that period (Adrian and Hintze, in press). In fact, extensive algal blooms developed after winters with short ice cover periods or no ice at all and with turbulent conditions within the entire water column, which favored diatom growth (Adrian et al. 1999). However, diatoms developed even under ice [mean of January–March in winters with ice cover: 0.8 mg L^{-1} ($\pm 0.9 \text{ SD}$)], as was also observed in Lake Erken (Weyhenmeyer et al. 1999) and in Lake Baikal under conditions of convective mixing (Granin et al. in press). In addition, other

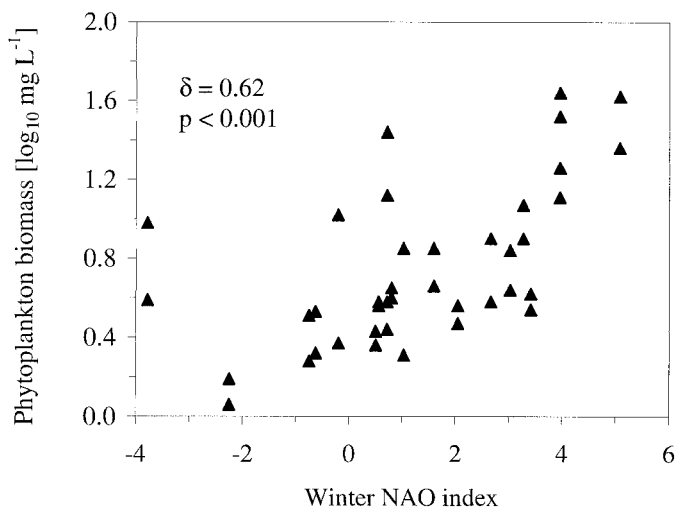


Fig. 4. Scatterplot of total phytoplankton biomass ($\log_{10} \text{ mg L}^{-1}$) in Müggelsee in March (biweeks 5, 6) versus the winter NAO index 1979–1998.

Table 2. Pearson correlation coefficients of the timing of successional events in spring (April and May) versus the winter NAO index and water temperature in late April/early May (biweeks 9, 10). The significance level is indicated by asterisks: $p < 0.01$ (***), $p < 0.05$ (**), $p < 0.1$ (*), not significant (n.s.). The arithmetic means of timing for both the cold and the warm subperiod are also given. Note there were 4 yr without a clearwater phase (see Fig. 2 legend).

Variable	Mean date		Pearson's r	
	1979–1987	1988–1998	Winter NAO index	Spring water temperature
Phytoplankton peak	06 May	07 Apr	−0.61***	—
<i>Keratella</i> peak	12 May	06 May	−0.55***	−0.29 n.s.
<i>Bosmina</i> peak	12 May	06 May	−0.54***	−0.25 n.s.
<i>Daphnia</i> peak	06 Jun	22 May	−0.33 n.s.	−0.66***
Clearwater phase	04 Jun	21 May	−0.43*	−0.67**

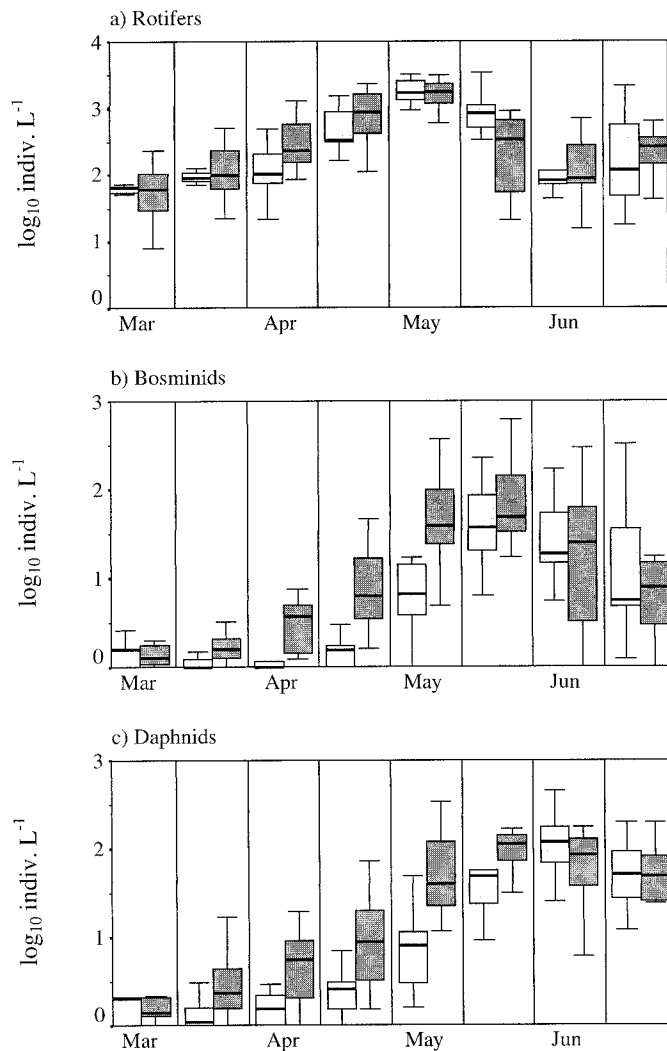


Fig. 5. Biweekly boxplots of (a) *Keratella*, (b) *Bosmina*, and (c) *Daphnia* abundances (\log_{10} indiv. L^{-1}) in Müggelsee from March to June for 1979–1987 (light shading) and 1988–1998 (dark shading). Details as in Fig. 3.

factors probably influenced the timing and intensity of the phytoplankton peak. Light limitation of phytoplankton growth might have been more pronounced in the warmer years with high phytoplankton biomass. Nutrient limitation at times of maximal algal mass cannot be precluded, since in each year concentrations of soluble reactive phosphorus depleted below $10 \mu g L^{-1}$ in April and May. Furthermore, earlier population growth of herbivores in the warmer period (Fig. 5) probably led to earlier predatory losses of the algae. These findings are in accordance with those of Weyhenmeyer et al. (1999), who found that the NAO index was a good predictor for the timing of the phytoplankton spring peak in Lake Erken (southern Sweden). This is probably valid for small eutrophic Plußsee (Germany) also, where an early phytoplankton spring peak occurred after mild winters (Müller-Navarra et al. 1997). In Lake Constance, however, the development of the spring bloom generally is tied to the onset of thermal stratification, and, thus, there is no significant correlation with the NAO index (Gaedke et al. 1998; Straile 2000).

Although phytoplankton dynamics in Müggelsee were closely related to the NAO, winter effects on zooplankton were superimposed by a warming trend in late April/early May (Table 1), which demonstrated no significant relationship with winter conditions or with monthly NAO indices in spring. This warming happened in a biologically relevant range of about 10 – $13^{\circ}C$ (Table 1), when reproduction rates of cladocerans are positively correlated with temperature (Peters and De Bernardi 1987). The earlier daphnid peak and the earlier clearwater phase in the 1990s most probably required that warming trend (Table 2). In fact, positive growth rates of cladocerans were not observed before late April even in the warm period (Fig. 5). In 1991, for example, the clearwater phase occurred quite late (4 June), which was in coherence with low spring temperatures (Fig. 2b,d), despite a relatively mild winter. Moreover, daphnids did not respond to enhanced algal food availability in the latter years, and food was not limited in any year (given a threshold concentration for *Daphnia* egg production of $0.2 mg C L^{-1}$ for edible algae, Lampert 1978). Thus, a strong food effect is not to be expected, and temperature in spring was the major driving force for *Daphnia* development. Unfortunately, the role of fish predation remains unanswered, since no long-term data on fish abundance were available. However—since there was no significant change in population dynamics of

cladocerans in both periods, and since food limitation was unimportant in all years—it is most likely that a climate-driven change in the timing of fish spawning and corresponding predation followed the same time-lagged development as found in the zooplankton (Carpenter et al. 1992). Top-down mechanisms to structure zooplankton communities (Carpenter et al. 1985) obviously did not change, otherwise we would expect to see changes in zooplankton dynamics.

Population development of *Keratella* and *Bosmina* also was about 2 weeks early in the warm period (Fig. 5), but observed differences were less significant. These zooplankton usually peak earlier in the seasonal cycle than daphnids (Sommer et al. 1986), which suggests better adaptation to lower temperatures. This might be the reason that there was a significant correlation between the NAO index and peak abundances of *Keratella* and *Bosmina* (Table 2). Both groups did not respond to the second warming trend, most likely as an indirect effect due to competition with *Daphnia*. The overall early development of several zooplankton groups that differ substantially in their feeding behavior and filtering efficiency supports the hypothesis of temperature-driven changes.

Effects similar to those seen in Müggelsee were observed in Plußsee, where high water temperature in spring led to an early clearwater phase, presumably constrained by early zooplankton growth (Müller-Navarra et al. 1997). In large and deep Lake Constance, daphnid abundances in May and the timing of the clearwater phase were correlated with the winter NAO index, most probably as a consequence of the high heat storage capacity of that lake (Straile 2000). Based on time series from 1979 to 1994, Straile and Adrian (2000) proposed that the winter NAO partly synchronized successional events in late spring in both Lake Constance and Müggelsee, irrespective of differences in their size and trophic state. In the present study, the inclusion of four additional years, 1995–1998, when the course of spring temperatures partly contrasted with that of the NAO index (Fig. 1) revealed that the NAO actually had no significant influence on water temperature of Müggelsee in late spring. Thus, in large water bodies, plankton dynamics even in late spring may still be influenced by meteorological conditions in winter, whereas in shallow and polymictic lakes, the same processes probably are to a high degree related to the prevailing weather.

We conclude that in shallow productive lakes of the temperate region, vernal population development of phytoplankton most likely is dependent on the strength of the preceding winter (namely on ice conditions), and thus is related to the NAO. Hence, given a continuing trend toward mild winters in the future (Giorgi et al. 1998), it can be expected that an early development of phytoplankton spring blooms will become a persistent phenomenon in a variety of lakes in the north temperate region. The timing of the clearwater phase is determined by critical abundances of daphnids in particular, which were tightly associated with water temperature in spring, but not with the NAO. Air temperature, water temperature, and the NAO are not necessarily intercorrelated in spring, depending primarily on the geographic and climatic regime, and on the size, morphometry, and trophy of

a lake. Consequently, beyond phytoplankton, the NAO index has only limited power to make predictions about limnological processes in late spring in shallow polymictic lakes. With respect to anticipated climate warming, not only will the degree of the warming be crucial, but also the time of the year when it will happen. Assessments of potential impacts of climate change on processes in freshwater ecosystems therefore have to consider the sensitivity of thermal parameters of individual lakes to changes in air temperature and possible variations of this sensitivity within the annual cycle. The analysis of long-term observations, ideally in combination with hydrophysical and meteorological modeling studies, would be of great value to help understand relationships between global climate indices (such as the NAO), regional and local meteorological conditions, and the response of different lake types to climate change.

References

- ADRIAN, R., AND R. DENEKE. 1996. Possible impact of warm winters on zooplankton succession in eutrophic lakes of the Atlantic European area. *Freshw. Biol.* **36**: 757–770.
- , AND T. HINTZE. Effects of winter air temperature on the ice phenology of the Müggelsee (Berlin, Germany). *Verh. Int. Ver. Limnol.* **27**. In press.
- , N. WALZ, T. HINTZE, S. HOEG, AND R. RUSCHE. 1999. Effects of ice duration on the plankton succession during spring in a shallow polymictic lake. *Freshw. Biol.* **41**: 621–632.
- ANDERSON, W. L., D. M. ROBERTSON, AND J. J. MAGNUSON. 1996. Evidence of recent warming and El Niño-related variations in ice breakup of Wisconsin lakes. *Limnol. Oceanogr.* **41**: 815–821.
- BEHRENDT, H., R. STELLMACHER, AND M. OLBERG. 1987. Long-term changes in water quality parameters of a shallow eutrophic lake and their relations to meteorologic and hydrologic elements, p. 535–544. *In* S. I. Solomon, M. Beran, and W. Hogg [eds.], *The influence of climate change and climatic variability on the hydrologic regime and water resources*. IAHS Publ. 168.
- BOX, G. E. P., G. M. JENKINS, AND G. C. REINSEL. 1994. *Time series analysis—forecasting and control*. 3rd ed. Prentice Hall.
- CARPENTER, S. R., S. G. FISHER, N. B. GRIMM, AND J. F. KITCHELL. 1992. Global Change and freshwater ecosystems. *Annu. Rev. Ecol. Syst.* **23**: 119–139.
- , J. F. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**: 634–639.
- CHATFIELD, C. 1996. *The analysis of time series—an introduction*. Chapman & Hall.
- DAVIS, T. D., D. VINER, AND P. D. JONES. 1998. Changes in atmospheric circulation and climate over the North Atlantic and Europe, p. 1–14. *In* D. G. George, J. G. Jones, P. Punčochář, C. S. Reynolds, and D. W. Sutcliffe [eds.], *Management of lakes and reservoirs during global climate change*. NATO Adv. Sci. Inst., 2, Vol. 42.
- DRIESCHER, E., H. BEHRENDT, G. SCHELLENBERGER, AND R. STELLMACHER. 1993. Lake Müggelsee and its environment, natural conditions and anthropogenic impacts. *Int. Rev. Gesamten Hydrobiol.* **78**: 327–343.
- FROMENTIN, J.-M., N. C. STENSETH, J. GJØSÆTER, T. JOHANNESSEN, AND B. PLANQUE. 1998. Long-term fluctuations in cod and pollock along the Norwegian Skagerrak coast. *Mar. Ecol. Prog. Ser.* **162**: 265–278.

- GAEDKE, U., D. OLLINGER, P. KIRNER, AND E. BÄUERLE. 1998. The influence of weather conditions on the seasonal plankton development in a large and deep lake (L. Constance)—III. The impact of water column stability on spring algal development, p. 71–84. *In* D. G. George, J. G. Jones, P. Punčochář, C. S. Reynolds, and D. W. Sutcliffe [eds.], *Management of lakes and reservoirs during global climate change*. NATO Adv. Sci. Inst., 2, Vol. 42.
- GEORGE, D. G., AND G. P. HARRIS. 1985. The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. *Nature* **316**: 536–539.
- , AND A. H. TAYLOR. 1995. UK lake plankton and the Gulf Stream. *Nature* **378**: 139.
- GIORGI, F., AND OTHERS. 1998. Simulation of regional climate change with global coupled climate models and regional modeling techniques, p. 429–437. *In* R. T. Watson, M. C. Zinyowera, R. H. Moss, and D. J. Dokken [eds.], *The regional impacts of climate change—an assessment of vulnerability: A special report of IPCC Working Group II*. Cambridge University Press.
- GRANIN, N. G., AND OTHERS. Turbulent mixing under the ice and the growth of diatoms in Lake Baikal. *Verh. Int. Ver. Limnol.* **27**. In press.
- HELSEL, D. R., AND R. M. HIRSCH. 1992. *Statistical methods in water resources*. Elsevier.
- HURRELL, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**: 676–679.
- , AND H. VAN LOON. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. *Clim. Chang.* **36**: 301–326.
- KING, J. R., B. J. SHUTER, AND A. P. ZIMMERMAN. 1999. Signals of climate trends and extreme events in the thermal stratification pattern of multibasin Lake Opeongo, Ontario. *Can. J. Fish. Aquat. Sci.* **56**: 847–852.
- KRÖNCKE, I., J. W. DIPPNER, H. HEYEN, AND B. ZEISS. 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. *Mar. Ecol. Prog. Ser.* **167**: 25–36.
- LAMPERT, W. 1978. A field study on the dependence of the fecundity of *Daphnia* spec. on food concentration. *Oecologia* **36**: 363–369.
- LIVINGSTONE, D. M. 1999. Ice break-up on southern Lake Baikal and its relationship to local and regional air temperatures in Siberia and to the North Atlantic Oscillation. *Limnol. Oceanogr.* **44**: 1486–1497.
- MÜLLER-NAVARRA, D. C., S. GÜSS, AND H. VON STORCH. 1997. Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability. *Glob. Chang. Biol.* **3**: 429–438.
- PETERS, R. H., AND R. DE BERNARDI. [EDS.] 1987. *Daphnia*. *Mem. Ist. Ital. Idrobiol.* **45**: 1–502.
- POST, E., AND N. C. STENSETH. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *J. Anim. Ecol.* **67**: 537–543.
- , ———, R. LANGVATN, AND J.-M. FROMENTIN. 1997. Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond., B* **264**: 1317–1324.
- RAPP, J., AND C.-D. SCHÖNWIESE. 1995. *Atlas der Niederschlags- und Temperaturtrends in Deutschland 1891–1990*. Frankfurter Geowiss. Arb. Ser. B, Bd. 5, Frankfurt.
- REID, P. C., M. EDWARDS, H. G. HUNT, AND A. J. WARNER. 1998. Phytoplankton change in the North Atlantic. *Nature* **391**: 546.
- ROCZNIK, K. 1995. *Wetter und Klima in Deutschland*. 3rd ed. Hirzel Verlag.
- SAS INSTITUTE. 1995. *SAS/ETS® user's guide—Version 6*. 2nd ed. Cary.
- SHELLENBERGER, G., AND R. STELLMACHER. 1986. Zur Frage der Quasihomogenität des Müggelsees. *Acta Hydrophysica* **30**: 161–173.
- SCHINDLER, D. W., AND OTHERS. 1990. Effects of climate warming on lakes of the central boreal forest. *Science* **250**: 967–970.
- SHUTER, B. J., D. A. SCHLESINGER, AND A. P. ZIMMERMAN. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. *Can. J. Fish. Aquat. Sci.* **40**: 1838–1845.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106**: 433–471.
- SPSS. 1993. *SPSS® for Windows™—Base system user's guide, release 6.0*. SPSS.
- STRAILE, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* **122**: 44–50.
- , AND R. ADRIAN. 2000. The North Atlantic Oscillation and plankton dynamics in two European lakes—two variations on a general theme. *Glob. Chang. Biol.* **6**: 1–8.
- , AND W. GELLER. 1998. The response of *Daphnia* to changes in trophic status and weather patterns: A case study from Lake Constance. *ICES J. Mar. Sci.* **55**: 775–782.
- STRUB, P. T., T. POWELL, AND C. R. GOLDMAN. 1985. Climatic forcing: Effects of El Niño on a small, temperate lake. *Science* **227**: 55–57.
- WEYHENMEYER, G., T. BLECKNER, AND K. PETERSSON. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. *Limnol. Oceanogr.* **44**: 1788–1792.

Received: 24 November 1999

Accepted: 3 April 2000

Amended: 19 April 2000