

# Large-scale climatic signatures in lakes across Europe: a meta-analysis

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## Abstract

Recent studies have highlighted the impact of the winter North Atlantic Oscillation (NAO) on water temperature, ice conditions, and spring plankton phenology in specific lakes and regions in Europe. Here, we use meta-analysis techniques to test whether 18 lakes in northern, western, and central Europe respond coherently to winter climate forcing, and to assess the persistence of the winter climate signal in physical, chemical, and biological variables during the year. A meta-analysis approach was chosen because we wished to emphasize the overall coherence pattern rather than individual lake responses. A particular strength of our approach is that time-series from each of the 18 lakes were subjected to the same robust statistical analysis covering the same 23-year period. Although the strongest overall coherence in response to the winter NAO was exhibited by lake water temperatures, a strong, coherent response was also exhibited by concentrations of soluble reactive phosphorus and soluble reactive silicate, most likely as a result of the coherent response exhibited by the spring phytoplankton bloom. Lake nitrate concentrations showed significant coherence in winter. With the exception of the cyanobacterial biomass in summer, phytoplankton biomass in all seasons was unrelated to the winter NAO. A strong coherence in the abundance of daphnids during spring can most likely be attributed to coherence in daphnid phenology. A strong coherence in the summer abundance of the cyclopoid copepods may have been related to a coherent change in their emergence from resting stages. We discuss the complex nature of the potential mechanisms that drive the observed changes.

*Keywords:* climate variability, coherence, European lakes, meta-analysis, nutrients, phytoplankton, water temperature, zooplankton

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## Introduction

Lake ecosystems are strongly influenced by many stressors (e.g. eutrophication, climate change, acidification, and pollution). Physically, the most important drivers are the local meteorological variables air temperature,

wind speed, cloud cover, and relative humidity (Edinger *et al.*, 1968). However, it is now clear that large-scale coherence in some of these forcing variables, especially air temperature, can result in a similar coherence also being exhibited by many internal lake variables (e.g. Magnuson *et al.*, 1990). In North America, much research has been conducted recently into the effects of the El-Niño/Southern Oscillation (ENSO) climate phenomenon, which is known to have a strong effect on the climate from the Americas through south-east Asia to east Africa (Wang & Fiedler, 2006 and references therein). The North Atlantic Oscillation (NAO) determines the winter climate variability of much of Europe and large areas of northern Asia (Walker & Bliss, 1932; Hurrell, 1995). It describes the atmospheric mass balance between the Azores High and the Iceland Low. Highly positive winter NAO indices indicate steep surface pressure gradients and strong zonal circulation over the North Atlantic, leading to mild and rainy winters in the western and northern parts of Europe. The reverse situation is associated with low surface pressure gradients and weaker zonal circulation over the North Atlantic, usually bringing cold winters to much of Europe (Hurrell, 1995).

Climatic forcing governs many of the physical aspects of lake ecosystems – including water temperatures and the formation and thawing of lake ice – which, directly or indirectly, affect the physiology, life history, and development of plankton and fish communities. Climate may also affect the dispersal of species (Thomas *et al.*, 2004). Thus, climate warming is very likely to have a pronounced effect on lake ecosystems (Walther *et al.*, 2002). The NAO winter index has been confirmed to be a valuable tool in the investigation of climate-induced changes in aquatic and terrestrial ecosystems (Ottersen *et al.*, 2001; Blenckner & Hillebrand, 2002). Variations in the winter NAO are known to be reflected in the temperatures of lake epilimnia and hypolimnia and in the timing of ice cover (Livingstone, 2000; Gerten & Adrian, 2001; Livingstone & Dokulil, 2001; Straile *et al.*, 2003a, b). However, the nature of the response of lakes to climatic forcing is not necessarily geographically uniform: it can be influenced by latitude and longitude (Blenckner & Hillebrand, 2002) and altitude (Livingstone *et al.*, 2005). The timing of lake ice break-up, for example, which strongly influences the timing of spring algal blooms (Gerten & Adrian, 2000), appears to respond to changes in air temperature in a nonlinear fashion, with the strength of the response depending on mean ambient air temperature, and hence on latitude (Weyhenmeyer *et al.*, 2004). Daphnid populations in lakes several hundred kilometres apart appear to respond coherently to the NAO, specifically with regard to the timing of their population maximum,

and consequently to the timing of the clear-water phase (Straile & Adrian, 2000; Straile, 2002). These synchronous changes in phenology in lake ecosystems are consistent with the clear pattern of advances in plant flowering dates and in animal breeding dates found in terrestrial ecosystems (Walther *et al.*, 2002) and in marine ecosystems (Edwards & Richardson, 2004) that are associated with the NAO or ENSO (for reviews see Gerten & Adrian, 2002a; Stenseth *et al.*, 2002).

Climate-driven changes in the nutrient dynamics of lakes are less apparent. This is because such changes are difficult to distinguish from the effects of local reductions in nutrient loading (Anneville *et al.*, 2004; Köhler *et al.*, 2005; Nöges *et al.*, 2005) and because of the complex way in which catchment characteristics – (e.g. land use, the timing of run-off and the severity of frost) – can modify the effect of climate on nutrient loading (Blenckner, 2005). In a comparative investigation of the chemistry of lakes in Sweden, Weyhenmeyer (2004) found the highest degree of coherence among lakes to exist for variables which were closely linked to water temperature, and thus, to the NAO. In deep lakes and in marine systems, nutrient dynamics have been found to be affected by changing mixing/upwelling or runoff processes related to the NAO (Hagberg & Tunberg, 2000; Oschlies, 2001; Straile *et al.*, 2003a).

Although recent studies have highlighted the impacts of the NAO on lake plankton for specific sites and regions (for reviews see Gerten & Adrian, 2002a; Straile *et al.*, 2003b), here we provide for the first time a systematic, multi-country comparison of climate-induced changes in lakes using an ecosystem-level approach, in order to test whether the lakes respond coherently to large-scale winter climatic forcing, and to assess the persistence of the winter climate signal during the following year. We apply meta-analysis techniques to analyse patterns of coherence. A meta-analysis permits the statistical synthesis of research results from numerous individual studies that need not be related (Gurevitch *et al.*, 1992), making possible the employment of an aggregate statistical test that is more powerful than statistical tests performed on the studies taken individually (Osenberg *et al.*, 1999). It can give information on the overall magnitude of an effect, on whether that effect differs among contrasting categories of studies, and on how the variation is distributed within and among categories (similar to an analysis of variance). Moreover, a meta-analysis allows the factors (categories) that influence the overall pattern of coherence to be determined, and offers the additional advantage of allowing each individual study to be weighted by the number of samples included in the study.

An earlier meta-analysis of NAO effects based on published work provided a quantitative synthesis of the

influence of the NAO on the timing of life history events, on the biomass of organisms, and on biomass on different trophic levels, and clearly demonstrated the presence of an NAO signature in freshwater, marine, and terrestrial ecosystems (Blenckner & Hillebrand, 2002). Our study goes beyond the previous study of Blenckner & Hillebrand (2002) by narrowing and deepening its focus to encompass multiple aspects of lake ecosystems, including water temperature, chemical variables, and phytoplankton and zooplankton communities at high taxonomic resolution. The lakes included in the current analysis represent a much broader range of lacustrine ecosystems than those included in the previous analysis. Moreover, in this study the meta-analysis was performed directly on one large, internally consistent dataset rather than on the results of previously published individual case studies. This provides a more statistically powerful test of the impacts of climatic forcing on lakes, while simultaneously avoiding the problems that are associated with publication bias and with discrepancies in the statistical protocols upon which the published data are based (Blenckner & Hillebrand, 2002). In the current study, we test for climate-induced changes in 18 lakes located in three disparate geographical regions by studying the degree and extent to which interannual variations in the winter NAO influence physical, chemical, and biological variables. A particular strength of our approach is that for each of the 18 lakes, we conducted the same robust statistical analysis of time-series covering the same 23-year period. We chose the meta-analysis approach because we were interested not in the responses of individual lakes to the NAO, but in the overall pattern of coherence in physical, chemical, and biological variables existing among the lakes. In addition to investigating patterns of coherence, we also investigated the persistence exhibited by the NAO signal during the year. We discuss where and when we detect coherence in the response to the NAO, and use our detailed knowledge of the lakes under investigation to discuss some of the underlying mechanisms involved.

## Methods

### *Data and study sites*

The target variables upon which this study is based are: winter air temperature (no. of lakes =  $n = 10$ ; for some lakes situated close to one another, air temperature data from the same meteorological station were employed); surface water temperature ( $n = 18$ ); near-bottom water temperature ( $n = 9$ ); soluble reactive phosphorus (SRP,  $n = 12$ ); total phosphorus (TP,  $n = 9$ ); nitrate ( $\text{NO}_3^-$ ,  $n = 9$ ); soluble reactive silicate (SRSi,  $n = 11$ ); the bio-

masses of diatoms ( $n = 12$ ), cyanobacteria ( $n = 12$ ) and dinoflagellates ( $n = 9$ ); the abundances of daphnids ( $n = 9$ ), calanoid copepods ( $n = 6$ ), cyclopoid copepods ( $n = 6$ ), and total copepods ( $n = 4$ ). All original data were sampled at intervals of between 1 week and 1 month. The data on the target variables were obtained from 18 limnologically diverse lakes (Table 1 and Fig. 1) located in three climatically distinct regions of Europe, here designated the Northern Region (Fennoscandia and Estonia), the Western Region (the United Kingdom and Ireland) and the Central Region (Germany, Switzerland, and Austria). The target variables were chosen *a priori*; these are the most important and the most common variables that are included in the long-term research programmes being conducted on the 18 lakes. Air and water temperatures were available for all lakes ( $n = 18$ ), whereas this was not the case for nutrients, phytoplankton, and zooplankton (see Table 1). Thus, one needs to keep in mind that the results of this study do not necessarily hold for all of the lakes included in the study. It must also be kept in mind that our sample is biased towards large lakes, and therefore, the results will not necessarily hold for small lakes. With respect to the biological variables, we focused on the most common phytoplankton and zooplankton groups found in the lakes studied, except in the case of the cladocerans, for which we decided to focus on daphnids because they are often key species in lake plankton communities (Sommer *et al.*, 1986). Phenological events, such as the timing of ice break-up and the timing of the spring phytoplankton and zooplankton maxima, have been analysed for some individual lakes (reviewed by Blenckner & Hillebrand, 2002; Gerten & Adrian, 2002a; Straile *et al.*, 2003b). As the results of the meta-analysis of phenological events were essentially the same as those known already from the individual lake studies (earlier occurrence of cardinal events in positive NAO years and later occurrence in negative NAO years), we do not include these results here.

For each lake, the correlation coefficient ( $r$ ) of each of the target variables with the winter NAO index was computed for the 23-year period 1980–2002. Before computing  $r$ , all target variables and the NAO index were detrended to remove the effects of very low-frequency variability. The detrending performed was either linear or, in the case of some nutrient time-series, logarithmic. The long-term changes in physical, chemical, and biological variables that occurred in some of the lakes during the study period, therefore, play only a minor role in this analysis. The NAO index used in this analysis was based on the principal component time series of the leading empirical orthogonal function of seasonal (December through March) sea level pressure anomalies over the Atlantic sector ( $20^\circ$ – $80^\circ\text{N}$ ,

**Table 1** The lakes studied, the eight characteristics employed in the meta-analysis, and the data available for each lake

Lake	Climate region	Mean		Critical depth (m)	Dynamic ratio	Residence time (year)	Ice cover	Trophic status	Available data
		depth (m)	Maximum depth (m)						
Pääjärvi, Finland (PA)	Northern	15.3	85	6.7	0.2	3.5	Yes	Oligo-mesotrophic	A, W, N, P
Erken, Sweden (ER)	Northern	9	21	8.5	0.5	7	Yes	Mesotrophic	A, W, N, P
Galten, Mälaren, Sweden (GA)	Northern	3.4	19	12.2	2.3	0.07	Yes	Hypereutrophic	A, W, N, P
Ekoln, Mälaren, Sweden (EK)	Northern	11.5	50	14.2	0.8	1.2	YES	Eutrophic	A, W, N, P, Z
Vättern, Sweden (VT)	Northern	40	128	30.6	1.1	58	No	Oligotrophic	A, W, N, P
Vänern, Sweden (VA)	Northern	27	106	35.6	2.8	9	No	Oligotrophic	A, W, N, P, Z
Võrtsjärv, Estonia (VO)	Northern	2.8	6	19.8	5.9	1.0	Yes	Eutrophic	A, W, N, P
Müggelsee, Germany (MU)	Central	4.9	8	5.1	0.6	0.17	Yes	Eutrophic	A, W, N, P, Z
Lake Constance, Germany (LC)	Central	101	254	23.7	0.2	4.2	No	Oligo-mesotrophic	A, W, N, P, Z
Greifensee, Switzerland (GR)	Central	17.7	34	5.5	0.2	1.1	No	Eutrophic	A, W, N, P, Z
Walensee, Switzerland (WA)	Central	103	145	8.5	0.1	1.4	No	Oligotrophic	A, W, N, P, Z
Upper Lake Zurich, Switzerland (ZU)	Central	23	48	7.9	0.2	0.16	No	Oligotrophic	A, W, N, P, Z
Lower Lake Zurich, Switzerland (ZL)	Central	51	136	12.5	0.2	1.1	No	Mesotrophic	A, W, N, P, Z
Mondsee, Austria (MO)	Central	36	68	6.8	0.1	1.7	Yes	Oligo-mesotrophic	A, W, N
Lough Feeagh, Ireland (LF)	Western	14.5	45	3.9	0.1	0.47	No	Oligotrophic	A, W
Lough Leane, Ireland (LL)	Western	13.4	60	7.9	0.3	0.57	No	Mesotrophic	A, W, N
Windermere, England (WI)	Western	25.1	64	5.3	0.1	0.8	No	Mesotrophic	A, W, Z
Esthwaite Water, England (ES)	Western	6.4	15	2.1	0.1	0.26	No	Eutrophic	A, W, N, Z

A, air temperature; W, water temperature; N, nutrients (TP, SRP,  $\text{NO}_3^-$  and SRSi); P, phytoplankton (diatoms, cyanobacteria and dinoflagellates); Z, zooplankton (daphnids, calanoid copepods and cyclopoid copepods).

90°W–40°E) from 1980 to 2002 (see also <http://www.cgd.ucar.edu/cas/jhurrell/indices.info.html#naopcdjfm>) (Fig. 2). The values of  $r$  between the NAO winter index and each of the target variables, computed for each month from January to December, formed the basis for the meta-analysis. In the following, 'NAO' always refers to the winter NAO, a 'positive NAO year' means the year following a winter during which the NAO index was positive, and a 'negative NAO year' means the year following a winter during which the NAO index was negative. 'Significant' means statistically significant at the  $P < 0.05$  level.

#### Meta-analysis

The effects of the winter NAO on monthly values of all target variables at the time of occurrence of specific

cardinal events of the plankton succession were tested. We defined five cardinal events (1) winter; (2) the spring phytoplankton bloom; (3) the clear-water phase; (4) the summer phytoplankton bloom; and (5) the summer zooplankton abundance maximum. The respective months of occurrence of these events were defined as: (1) January and February; (2) the lake-specific month in spring with maximum phytoplankton biomass; (3) the lake-specific month in early summer with maximum daphnid abundance (because the clear-water phase is related to maximum daphnid abundance: Straile, 2000); (4) the lake-specific month with the maximum summer phytoplankton biomass and (5) the lake-specific month in summer with maximum zooplankton abundance. Winter, in contrast to the other periods, was defined as 2 months because the extremely low values of the different variables in winter can easily cause spurious

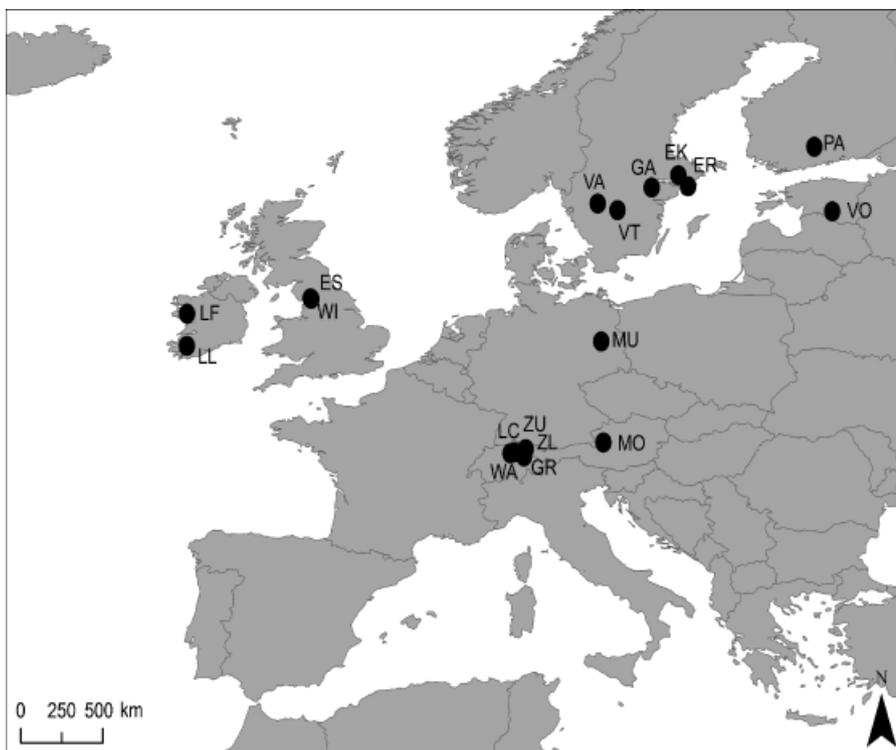


Fig. 1 The geographical locations of the lakes studied. For an explanation of the abbreviations see Table 1.

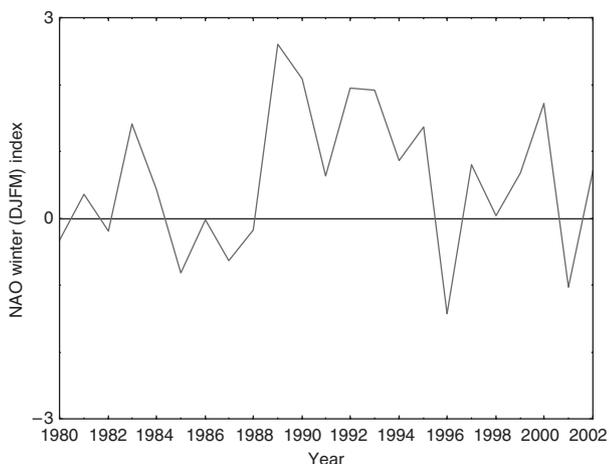


Fig. 2 The time-series of the winter (DJFM) NAO index from 1980 to 2002. Source: <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>.

correlations, and because winter sampling in some lakes was very sparse. Henceforth, for simplicity, the above-mentioned periods will be referred to merely as winter, spring, and summer. The times of occurrence of the cardinal events were defined for each lake separately, as a mean over the 23-year period, to account for the average lake-specific seasonal succession pattern of the plankton. The autumn period was excluded from the analysis as the relationship between the winter

NAO and water temperature overall was not significant after the summer months.

To establish a normalized and variance-stabilized effect size, all correlation coefficients (Pearson's  $r$ ) were converted to a normal distribution ( $r_z$ ) using Fischer's  $z$  transform as follows:

$$r_z = \frac{1}{2} \ln \left( \frac{1+r}{1-r} \right),$$

$r_z$  was then used to calculate the effect size. This allows a weighted analysis to be performed, where the effect size is weighted ( $w_i$ ) for the  $i$ th study by the reciprocal of its sampling variance ( $v_z$ ). The sampling variance of  $r_z$  was calculated from the number of observations ( $n$ ) as follows:

$$v_z = \frac{1}{n-3}.$$

We first calculated the overall effect size ( $E^{++}$ ) of the NAO on air and water temperature and on the lake-specific concentrations of the target chemical and biological lake variables during the five cardinal events mentioned above. We then tested whether the magnitude of the response to the NAO was influenced by eight different characteristics (see also Table 1) that are known to influence the structure and functioning of lake ecosystems. The range of characteristics reflects the type of lakes included in our study. These eight characteristics were: (1) climatic region (Northern, Western,

and Central Regions); (2) mean lake depth; (3) maximum lake depth; (4) critical depth (the water depth separating bottom areas where mixed deposits and transportation processes dominate from areas of sediment accumulation: see Håkanson *et al.*, 2004); (5) dynamic ratio (ratio of lake surface area to mean lake depth); (6) water residence time; (7) the presence or absence of ice cover; (8) trophic status (oligotrophic,  $<10 \mu\text{g TPL}^{-1}$ ; oligo-mesotrophic, ranging from  $<10$  to  $25 \mu\text{g TPL}^{-1}$ ; mesotrophic, ranging from  $10$  to  $25 \mu\text{g TPL}^{-1}$ ; eutrophic,  $>25 \mu\text{g TPL}^{-1}$ ). The meta-analysis was not flawed with respect to outliers, and thus, possible impacts on effect sizes were not due to outliers from one site.

The total overall effect size ( $E^{++}$ ) and the corresponding 95% confidence intervals (CI) were calculated for all target variables as outlined by Rosenberg *et al.* (2000)

$$E^{++} = \frac{\sum_{i=1}^n w_i \times E_i}{\sum_{i=1}^n w_i},$$

where  $E_i$  is the calculated effect size for the  $i$ th study. The variance of  $E^{++}$  is the reciprocal of the sum of the weights given to each of the  $n$  studies:

$$S_{E^{++}}^2 = \frac{1}{\sum_{i=1}^n w_i}.$$

The confidence interval (CI) of  $E^{++}$  is then given by

$$\text{CI} = E^{++} \pm t_{\alpha/2[n-1]} \times S_{E^{++}},$$

where  $t_{\alpha/2[n-1]}$  is the two-tailed value of Student's  $t$ -distribution at the critical level  $\alpha$ , and  $n$  is the number of individual studies.

An overall effect is considered to be significant if the CI does not include zero (Gurevitch *et al.*, 2000). In our study, a positive or negative effect size for a particular variable implies a positive or negative response, respectively, of that variable to the winter NAO. Thus, a significant positive effect size for the water temperature, for example, would imply that overall, a positive winter NAO will result in a significantly higher water temperature and a negative winter NAO in a significantly lower water temperature.

The group effect size ( $E^+$ ) and the CI were calculated for each of the eight above-mentioned characteristics ( $j$ ) as follows:

$$E_j^+ = \frac{\sum_{i=1}^{k_j} w_{ij} \times r_{z_{ij}}}{\sum_{i=1}^{k_j} w_{ij}},$$

where  $k_j$  is the number of studies involving characteristic  $j$ , and  $w_{ij}$  and  $E_{ij}$  are the weight and effect size for study  $i$  and characteristic  $j$ . For each group effect size, the 95% CIs were calculated by bootstrapping 999

randomizations. This nonparametric method creates a distribution of effect sizes based on the actual data set without making any assumptions about the form of the underlying distributions. Nonoverlapping CIs indicate significantly different group effect sizes. We tested for differences in effect sizes between characteristics by computing heterogeneity (heterogeneity test, henceforth HT), within groups ( $Q_{wj}$ ) and between groups ( $Q_M$ ), an approach analogous to analysis of variance. The heterogeneity of the  $j$ th group is

$$Q_{wj} = \sum_{i=1}^{k_j} w_{ij} (E_{ij} - E^+)^2.$$

The heterogeneity between groups is calculated as

$$Q_M = \sum_{j=1}^m \sum_{i=1}^{k_j} w_{ij} (E^+ - E^{++})^2,$$

where  $m = 8$  is the number of characteristics. All calculations were performed using MetaWin 2.0 (Rosenberg *et al.*, 2000).

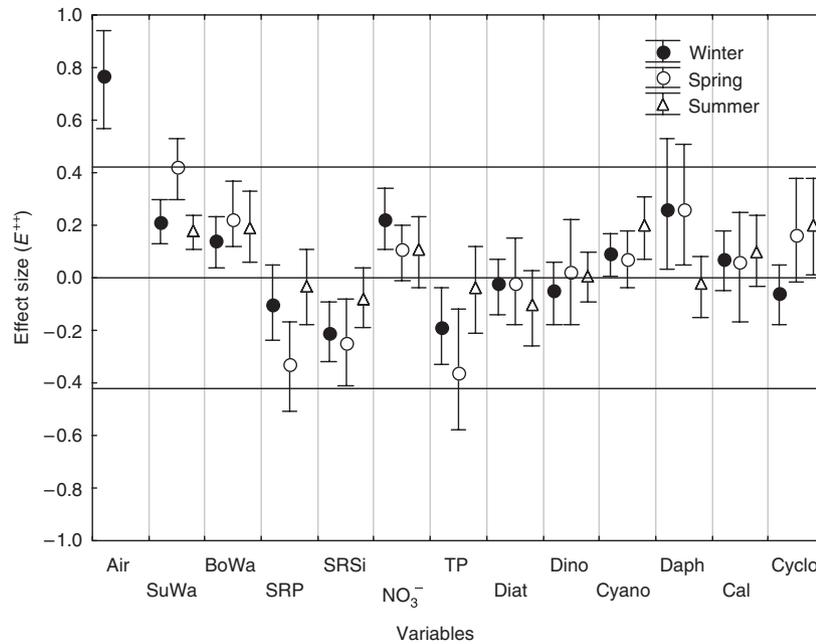
## Results

### Temperature

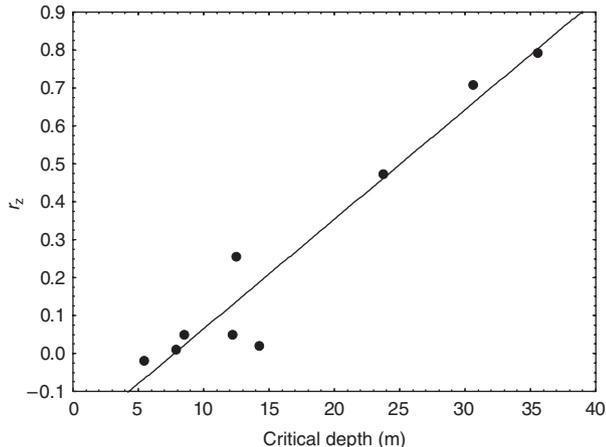
The effect size for winter air temperature was significant and very large (Fig. 3), showing that this variable is highly correlated with the NAO index and, thus, confirming the suitability of the latter for our purpose. Effect sizes for surface water temperature in winter, spring, and summer were all significant (Fig. 3), implying that high surface temperatures tend to occur in positive NAO years and low surface temperatures in negative NAO years. The strongest signal of the winter NAO in surface temperature was detected in spring. The situation for near-bottom water temperatures was similar (Fig. 3), with correlations being particularly high for lakes with long water residence times (HT,  $P < 0.001$ ) and large critical depths (HT,  $P < 0.001$ ; see also Fig. 4).

### Nutrients

SRP and SRSi showed a similar response to the NAO, with effect sizes being of greatest magnitude in spring, when the concentrations of these nutrients tended to be low in positive NAO years and high in negative NAO years (Fig. 3). In winter and summer, variability was much higher than in spring. In positive NAO years, SRSi concentrations in winter were significantly lower in lakes which were not ice-covered than in lakes which were ice-covered (HT,  $P < 0.05$ ).



**Fig. 3** Overall effect size ( $E^{++}$ ) and confidence intervals (95%) for the influence of the winter NAO on the target variables during winter (●) and during the following spring (○) and summer (△). Air, air temperature; SuWa, surface water temperature; BoWa, near-bottom water temperature; SRP, soluble reactive phosphorus; SRSi, soluble reactive silicate;  $\text{NO}_3^-$ , nitrate; TP, total phosphorus; Diat, diatom biomass; Dino, dinoflagellate biomass; Cyano, cyanobacteria biomass; Daph, *Daphnia* abundance; Cal, abundance of calanoid copepods; Cyclo, abundance of cyclopoid copepods. The effect size is considered to be significant ( $P < 0.05$ ) if the standard error does not cross the zero line. The horizontal lines above and below the zero line indicate very strong and significant effects ( $P < 0.01$ ).



**Fig. 4** Relationship between the  $z$ -transformed correlation coefficient of the winter NAO and the near-bottom water temperature from nine lakes in summer ( $r_z$ ) and the critical depth as defined by Håkanson *et al.* (2004).

In contrast to SRP and SRSi, winter  $\text{NO}_3^-$  concentrations tended to be high in positive NAO years and low in negative NAO years, especially in lakes with a high dynamic ratio (HT,  $P < 0.05$ ). In spring and summer, variability for  $\text{NO}_3^-$  was high and the effect size was not significant.

Winter and spring TP concentrations tended to be low in positive NAO years and high in negative NAO years (Fig. 3). In general, spring TP concentrations tended to be higher in lakes with a high dynamic ratio than in lakes with a low dynamic ratio (HT,  $P < 0.05$ ). However, variability was high, presumably because of lake-specific differences. For example, the correlation coefficients were significantly negative in only five lakes, (i.e. in oligotrophic Walensee, in mesotrophic Lake Erken, and in the eutrophic lakes Greifensee, Upper Lake Zurich and Lower Lake Zurich). No other lakes showed a significant response. The response of TP to the NAO was not significantly related to the trophic status of the lake (HT,  $P = 0.65$ ).

#### Plankton

In none of the seasons studied did the diatom biomass show any relationship to the winter NAO (Fig. 3). This also holds for the dinoflagellate and cyanobacterial biomass in winter and spring. Interestingly, we found a significant positive relationship between the summer cyanobacterial biomass and the NAO [i.e. the cyanobacterial biomass was higher in positive than in negative NAO years (Fig. 3)], with no significant differences in the effect based on the categories chosen in the HT.

The maximum abundance of daphnids in winter and spring showed a significant positive relationship with the NAO, although lake-to-lake variability was high, especially during winter. Calanoid copepods, which are usually present throughout the year, showed no overall relationship to the NAO in any season. The abundance of cyclopoid copepods in summer was significantly higher in positive NAO years than in negative NAO years. During spring the same tendency was observed, but this tendency was not strong enough to be statistically significant (Fig. 3).

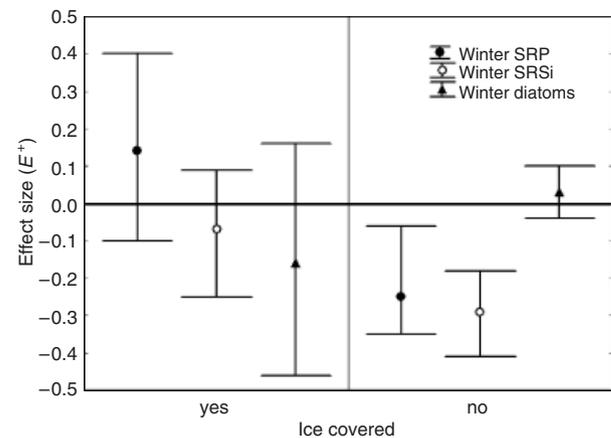
## Discussion

### *Climate-induced variability in air and water temperatures*

Overall, we found the strongest coherent response to the winter NAO in the temperature variables (air temperature, surface temperature, and near-bottom temperature). The effect of the winter NAO on near-bottom temperatures was strongest in the case of lakes with long water residence times and large critical depths (Fig. 4). This is to be expected, as deep-water temperatures during summer stratification, especially in deep lakes, are generally determined by the mean lake temperature attained during spring turnover (Livingstone, 1993; Gerten & Adrian, 2001; Straile *et al.*, 2003a). Overall, the strength of the relationship between water temperature and NAO found in all lakes included in the study confirms the importance of the NAO as a climatic driver across all three climate regions.

### *Climate-induced variability in nutrient concentrations*

The underlying mechanisms driving nutrient concentrations are complex, as they are influenced by catchment-related processes, nutrient uptake by the phytoplankton, shifts in phytoplankton phenology, water level, and interactions with the lake sediment. Thus, nutrient responses might be expected to be strongly site-specific. However, both SRP and SRSi concentrations in spring were found to exhibit a strongly coherent response to the previous winter's NAO, with both being negatively correlated with the winter NAO index. This was probably because an advance in spring phytoplankton phenology in positive NAO years, which has been observed in several lakes (Weyhenmeyer *et al.*, 1999; Gerten & Adrian, 2000; Winder & Schindler, 2004), would result in earlier nutrient uptake (Sommer *et al.*, 1986), while a retardation of spring phytoplankton phenology in negative NAO years would result in later nutrient uptake (Pettersson *et al.*, 2003). The finding that the overall response to the NAO was independent of the trophic



**Fig. 5** Group effect size ( $E^+$ ) and confidence intervals (95%) for winter SRP and SRSi concentrations and winter diatom biomass in lakes with and without ice cover.

status of the lake is consistent with the fact that most lakes are nutrient limited by the time algal biomass peaks in spring. The low SRP and SRSi concentrations in positive NAO years were not reflected in an overall early increase in winter diatom biomass. However, the occurrence of higher biomass could have been missed because of the overrepresentation of lakes with a relatively low (monthly) sampling frequency. Phytoplankton spring blooms are naturally short lived because nutrient depletion and losses through grazing and sedimentation occur rapidly and act on short temporal scales (Sommer *et al.*, 1986).

Moreover, the overall significance of the SRP and SRSi signals during winter might have been negatively affected by the presence of signals of opposite sign in lakes with and without ice cover (Fig. 5). The heterogeneity test, however, yielded a significant result only for SRSi. In lakes with no ice cover and a high degree of turbulence in the water column, diatoms may grow all winter, especially in positive NAO years, and could, therefore, cause a decrease in SRSi and SRP concentrations. The development of an especially high winter diatom biomass in ice-free winters in Müggelsee supports such a hypothesis (Adrian *et al.*, 1999). In ice-covered lakes, inverse thermal stratification and low light intensities, partly due to snow cover on the ice, are likely to reduce diatom growth under the ice (Weyhenmeyer *et al.*, 1999), resulting in a winter diatom biomass that is lower than that found in lakes with no ice cover. We see a tendency for this effect to occur (Fig. 5) but the effect remains statistically insignificant. In the meta-analysis, the two opposing mechanisms in ice-covered and ice-free lakes will, to a large extent, cancel each other out, resulting in the winter diatom biomass exhibiting no overall change. Furthermore, in

deep lakes in which the NAO affects deep-water mixing, warm winters (positive NAO years) may prevent the complete upward mixing of nutrients (Verburg *et al.*, 2003), resulting in a negative correlation between nutrient concentrations and the NAO index (Straile *et al.*, 2003a).

In contrast to SRP and SRSi, winter  $\text{NO}_3^-$  concentrations were generally positively correlated with the NAO (Fig. 3). The underlying processes are rather unclear, as all lake characteristics used in the heterogeneity tests were found to be insignificant. George *et al.* (2004a) explained the positive relationship between  $\text{NO}_3^-$  concentrations in late winter and the NAO in terms of the flushing of  $\text{NO}_3^-$  from the catchment into the lakes by melt water, which occurred earlier in positive NAO years than in negative NAO years. Moreover, mild winters may lead to increased nutrient leaching from catchment soils that have not yet frozen. While we found a positive relationship between  $\text{NO}_3^-$  concentrations and the NAO overall, in the United Kingdom the relationship was negative, probably because of the enhanced terrestrial uptake of  $\text{NO}_3^-$  during very mild winters (Straile *et al.*, 2003b; George *et al.*, 2004b; Blenckner, 2005). It is possible that the positive correlation between the NAO and  $\text{NO}_3^-$  in the Northern and Central Regions, and the negative correlation in the Western Region, reflect the temperature gradient that exists in Europe between the continental and maritime climate regions. During winters in which the NAO index is low, air temperatures in the Western Region are still generally much higher (mostly above freezing) than in the Northern and Central Regions. In addition, during winters in which the NAO index is high, the Northern and Central Regions will normally have above-average amounts of snow, which in the Western Region is generally not the case. Earlier and deeper snow cover in negative NAO years insulates the soil from the low air temperatures and reduces the effects of freezing on soil processes (Brooks *et al.*, 1999; Schimel *et al.*, 2004). In contrast, more frost days would be expected in negative NAO years in the Western Region. A three-way relationship between the number of days with soil temperatures below  $-4^\circ\text{C}$ , peak winter  $\text{NO}_3^-$  concentrations in a stream, and the NAO has been reported for an upland catchment in the United Kingdom, with both the number of frost days and nitrate concentrations being higher than average in negative NAO years (Monteith *et al.*, 2000). We hypothesize that the effect of the number of frost days, together with earlier flushing by melt water (George *et al.*, 2004a) and a higher total nitrogen deposition (due to more precipitation in positive NAO years), may result in a higher  $\text{NO}_3^-$  transport from the catchments into the lakes. That would mean that the direction of the  $\text{NO}_3^-$ -NAO

relationship is opposite to that of the soil temperature-NAO relationship in both cases.

#### *Climate-induced variability in plankton*

The higher abundances of daphnids during spring in positive NAO years can be attributed to the observed advance in the timing of the daphnid abundance maximum in many European lakes rather than to an overall increase in abundance (Straile & Adrian, 2000; Straile, 2002). This emphasizes the need to correct for known phenological shifts when defining the seasons (which was done in this study). The positive signal for daphnids in winter has to be regarded with caution. There may be an increasing tendency towards over-wintering for individuals in the pelagic zone related to an increase in water temperature in winter (George & Hewitt, 1999), but this is very difficult to detect, as winter abundances in almost all years were at the limit of detection.

During summer, however, we found a strong NAO signal, implying enhanced biomass for cyanobacteria and cyclopoid copepods in positive NAO years (Fig. 3). Cyanobacteria may have profited from direct temperature effects (Robarts & Zohary, 1987) and the extension of the period of stratification. Early summer stratification may enable earlier cyanobacterial growth (Weyhenmeyer, 2001; Järvinen *et al.*, 2006). Enhanced predation pressure on edible algal prey by omnivorous summer cyclopoid copepods could have additionally favoured the development of cyanobacteria (Gerten & Adrian, 2002b; Blenckner, 2005).

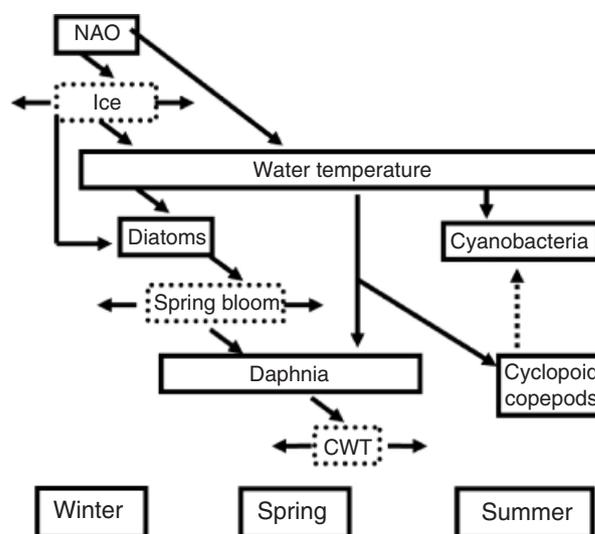
Although previous studies have found the abundance of calanoid copepods to be related to the NAO in both freshwater habitats (George, 2000) and marine habitats (Fromentin & Planque, 1996), we were not able to confirm this in the present study (Fig. 3). The abundance of cyclopoid copepods, however, did respond to NAO variability. In a study on Müggelsee, Gerten & Adrian (2002b) assumed that high spring water temperatures led to the early emergence of copepodid resting stages, and subsequently to early maturity, as the magnitude of the summer abundance maximum was correlated with water temperature in spring. This suggests that the appearance of copepodid resting stages in the pelagic zone more than 1 month earlier than usual allows the development of an extra generation (three instead of two), which may have contributed to the enhanced peak abundances during summer (Gerten & Adrian, 2002b). For *Thermocyclops oithonoides* it has been shown that higher water temperatures do indeed allow the completion of a further generation (Naess *et al.*, 1993). As the other lakes included in this study experienced similar warming trends to those observed in Müggelsee, a similar mechanism may hold

for the general increase in summer cyclopoid copepods in European lakes. We do, however, also know that the type of response of summer cyclopoid species to warming is very much species-specific (Gerten & Adrian, 2002b; Adrian *et al.*, 2006).

### Synthesis

Within the past decade, substantial progress has been made in identifying the direct and indirect effects of climatic forcing on lake ecosystems (Schindler, 2001; Gerten & Adrian, 2002a; Straile *et al.*, 2003b; Blenckner, 2005) and in confirming the existence of a large-scale coherent response (Kratz *et al.*, 1997; George *et al.*, 2000; Livingstone & Dokulil, 2001; Straile, 2002). Integrated responses, in the sense of several overlapping driving mechanisms, are probably the most common responses of all, and, given their complex nature, the most difficult to detect (Blenckner, 2005). For example, the effects of the interaction between a warming trend and a reduction in nutrient loading resulting from anthropogenic and/or climate-induced changes in lake catchments are as yet poorly understood, and thus difficult to predict within the context of future climate change scenarios. The emphasis in this study is on climatic effects. We would, however, like to point out that co-variation with other ecosystem drivers – such as reductions in nutrient loading, recovery from acidification, changes in the stratification pattern and other, still unknown, processes – cannot be excluded. We suggest that climatic factors modify the responses of ecosystems to anthropogenically induced changes, such as nutrient reduction (Schindler *et al.*, 1996). We also need to keep in mind the fact that our study focuses mainly on linear relationships between the target variables and the winter NAO, even though some of the interactions involved – in particular the indirect and integrated responses – may in fact be nonlinear (May, 1986). Moreover, the response lag looked at in this study extended up to a maximum of five months (from the winter NAO to the summer maximum zooplankton biomass). In some cases, however, the response can lag the forcing by over a year (Ottersen *et al.*, 2001; Straile *et al.*, 2003b, 2007), depending on the water residence time of the lake and the life-cycles of the organisms concerned.

In conclusion, this quantitative synthesis, based on 23 years of physical, chemical, and biological data from 18 lakes located in three disparate geographical regions in Europe, shows the existence of a high degree of coherence in the behaviour of water temperature from winter to summer, nutrient concentrations in spring, and the biomass of cyanobacteria and cyclopoid copepods in summer. This coherent behaviour is related to the interannual variability of the winter NAO, which



**Fig. 6** Schematic overview of the effects of the winter NAO on lake ecosystems. The overview is an extension of the concept developed by Straile (2002). The time periods covered by the boxes indicate the periods of the year during which causal links exist between the winter NAO and lake water temperatures, and during which subsequent cascading effects can be detected along different trophic levels. Boxes bordered by dotted lines indicate phenological events. Horizontal arrows denote the advance or retardation of phenological events in time. The winter NAO has a strong effect on the timing of ice break-up and on water temperature in winter, spring and summer. The timing of ice break-up influences the initial growth conditions for diatoms, and thereby the timing of the spring phytoplankton bloom. The water temperature in spring directly influences the growth of *Daphnia*, and thereby the timing of the clear-water phase. Water temperatures in spring and summer influence the biomass of cyanobacteria and cyclopoid copepods in summer both directly and indirectly (e.g. via the duration of the summer stratification period). A high abundance of cyclopoid copepods during years with high spring water temperatures may enhance the predation pressure on edible algal prey, which could additionally favour cyanobacteria biomass in summer (indicated by a dashed line).

appears to induce a strong climatic signal across all three climatic regions included in this study. Given the strong response to the winter NAO exhibited by spring plankton phenology (not shown here), the coherent nutrient depletion in spring in positive NAO years was partly driven by the advance in spring phytoplankton phenology in those years (see Fig. 6). However, the high variability reflects the complex, system-specific conditions existing in the catchments of the lakes. Cyanobacteria obviously profit both from direct temperature effects and from indirect temperature effects acting through the extension of the period of thermal stratification in positive NAO years, while copepods are likely to profit from enhanced temperatures. Overall,

our meta-analysis confirms the existence of climatic signatures detected in individual lake studies that result from processes driven both directly by temperature and indirectly by biotic interactions. Straile (2002) summarized climate-induced changes along pelagic food webs for the winter/spring situation in a schematic figure. Figure 6 represents an extension of this schematic figure to include the summer situation. The interplay between responses driven directly and indirectly by temperature may turn out to be more complex during summer, given the higher proportion of inedible algal prey such as cyanobacteria and slowly growing zooplankton species which exhibit complex life cycles. Moreover, changes in summer cyanobacteria biomass and cyclopoid copepod abundances are likely to be related to changes in spring water temperature (Fig. 6).

### Outlook

A challenge for future climate impact studies is to estimate how lake ecosystems will respond to further climate warming, as projected for instance by Räisänen *et al.* (2004). Based on such climate scenarios, which predict further winter and spring warming, the period of ice cover for lakes in southern Sweden and Finland is likely to be interrupted by periods of open water (Elo *et al.*, 1998), or the lakes may experience years with no ice cover at all (the current situation in many lakes in the Western and Central Regions; e.g. Adrian & Hintze, 2000). Day-length-specific water temperatures appear to be crucial for setting thresholds in spring, as they are important drivers of phytoplankton development (Reynolds, 1984), but are also important cues for emerging zooplankton resting stages (Cáceres, 1998; Vandekerckhove *et al.*, 2005). Enhanced remineralization of nutrients and higher diffusion rates at higher temperatures, combined with a longer ice-free period, will enhance the availability of nutrients to algae, especially in lakes with a long water residence time (Blenckner *et al.*, 2002). During summer, the extension of the stratified period, or more stable stratification and higher water temperatures, may set the boundaries for the structure of future summer plankton communities and the likelihood of species invasion. The bloom-forming cyanobacterium *Cylindrospermopsis raciborskii*, a primarily tropical and sub-tropical species, is, for example, currently invading Europe and North America (Briand *et al.*, 2004). Although our study provides little evidence for a decoupling of currently established food web interactions from one another, further changes in phenology, or the invasion or loss of species under future climate scenarios, may indeed increase the likelihood of a mismatch of interactions within plankton communities.

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