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The North Atlantic Oscillation and plankton dynamics in two European lakes — two variations on a general theme

DIETMAR STRAILE* and RITA ADRIAN†

**Limnologisches Institut, Universität Konstanz, D–78457 Konstanz, Germany, †Institut für Gewässerökologie und Binnenfischerei im Forschungsverbund Berlin e.V., Müggelseedamm 260, D-12562 Berlin, Germany*

Abstract

Long-term data on water temperature, phytoplankton biovolume, *Bosmina* and *Daphnia* abundance and the timing of the clear-water phase were compared and analysed with respect to the influence of the North Atlantic Oscillation (NAO) in two strongly contrasting lakes in central Europe. In small, shallow, hypertrophic Müggelsee, spring water temperatures and *Daphnia* abundance both increased more rapidly than in large, deep, meso/oligotrophic Lake Constance. Because of this, the clear-water phase commenced approximately three weeks earlier in Müggelsee than in Lake Constance. In Müggelsee, the phytoplankton biovolume during late winter/early spring was related to the NAO index. In Lake Constance, where phytoplankton growth was inhibited by intense downward mixing during all years studied, this was not the case. However, in both lakes, interannual variability in water temperature, in *Daphnia* spring population dynamics and in the timing of the clear-water phase, were all related to the interannual variability of the NAO index. The *Daphnia* spring population dynamics and the timing of the clear-water phase appear to be synchronized by the NAO despite large differences between the lakes in morphometry, trophic status and flushing and mixis regimes, and despite the great distance between the lakes (~700 km). This suggests that a great variety of lakes in central Europe may possibly have exhibited similar interannual variability during the last 20 years.

Keywords: Daphnia, lake trophy, long-term time series, meteorological forcing, North Atlantic Oscillation, Population dynamics, seasonal succession

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Introduction

The North Atlantic Oscillation (NAO) is a major source of interannual variability of weather and climate around the Northern Hemisphere (Hurrell & van Loon 1997). Increased air temperatures during winter over much of Europe in the late 1980s and early 1990s are related to an extreme phase of the NAO with anomalously low pressures near Iceland and anomalously high pressures across the subtropical Atlantic (Hurrell 1995; Hurrell & van Loon 1997). Changes in the abundances of phytoplankton (Reid *et al.* 1998; Belgrano *et al.* 1999), and copepods (Fromentin & Planque 1996) in the Atlantic, and in the abundances of macrofauna off Norderney Island (Kröncke *et al.* 1998) and the Swedish west coast (Tunberg & Nelson 1998) have been linked with changes in the NAO. A strong connection between the NAO and the timing of seasonal succession events in the pelagic food-web of a large continental lake, Lake Constance, was established recently (Straile & Geller 1998a). Higher epilimnetic water temperatures in spring in years with a high NAO index resulted in faster growth and higher spring biomasses of daphnids (Straile & Geller 1998a), which in turn caused an earlier suppression of algae in Lake Constance (Straile 2000). The effects of winter temperatures on plankton dynamics have been studied in small lakes in Berlin (Adrian *et al.* 1995; Adrian & Deneke 1996; Adrian 1997; Adrian *et al.* 1999). Although interannual differences in winter temperatures were not linked directly to the NAO by Adrian and coworkers, the occurrence of warm winters during the late 1980s and

Correspondence: Dietmar Straile, fax +49 7531 88 3533, e-mail dietmar.straile@uni-konstanz.de

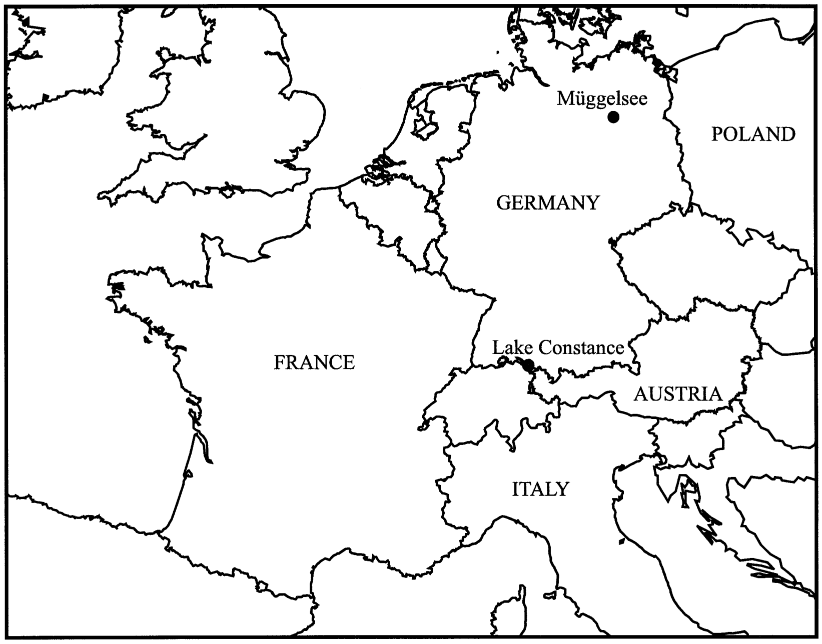

Fig. 1 Map showing the location of Lake Constance and Müggelsee.

early 1990s suggests an influence of the NAO in the Berlin region also. That is, Lake Constance and the small and shallow lakes in Berlin seem to be influenced by the same large-scale meteorological signal.

Here we study the temporal coherence in the timing of seasonal succession events between Lake Constance and Müggelsee, two European lakes, which differ considerably in morphology and trophic status. We analyse the effects of the NAO on air and water temperatures, phytoplankton biovolume, *Bosmina* and *Daphnia* abundance in both lakes and examine to what extent interannual differences during spring in Müggelsee and Lake Constance could have been synchronized by the NAO.

Study sites and methods

Study sites

Müggelsee (52°26′N, 13°39′E) and Lake Constance (47°36′N, 9°25′E) are situated approximately 700 km apart (Fig. 1). Physicochemical aspects and the food webs of both lakes have been studied thoroughly during the last few decades [see the recent monographs on Müggelsee (Driescher *et al.* 1993) and Lake Constance (Bäuerle & Gaedke 1998)]. Lake Constance is 20 times deeper and 60 times larger than Müggelsee, and its residence time is approximately 40 times greater than that of Müggelsee (Table 1). In addition, the lakes differ strongly in trophic status and mixing regime. Data series of air and water temperatures and phytoplankton and zooplankton composition and abundances dating back to 1979 are available for both lakes. For our analysis we use the time span from 1979 to 1994 because plankton dynamics in Lake Constance changed strongly after 1994 due to an ongoing decline in nutrient concentrations (Straile, unpubl. data).

NAO index and measurements of water and air temperatures

In this study we have used the NAO index (Dec. – March mean) provided by the National Center of Atmospheric Research, Boulder, USA (available on-line at http://www.cgd.ucar.edu/cas/climind/nao_winter.html). It is based on the differences in normalized sea-level pressures between Lisbon, Portugal and Stykkisholmur, Iceland (Hurrell 1995). Müggelsee water temperatures were recorded at daily intervals at 0.5 m depth near the northern shore of the lake. Due to the polymictic character of the lake, the temperature at 0.5 m depth is close to the average temperature of the water column. Until 1993 temperature was measured using mercury thermometers; thereafter a temperature transducer was used for *in situ* monitoring. In Lake Constance, water temperatures at various depths were recorded on the plankton sampling dates (see below) in 1979, 1980, 1981 and 1986 and quasi-continuously (every 20 min) during the other years. To allow a meaningful comparison with the shallow Müggelsee, we use the mean water temperature of the uppermost 8 m of the water column. Air temperatures were measured at the nearby meteorological stations of Berlin-Schönefeld and Konstanz and provided by the German weather service.

Table 1 Morphological and limnological characteristics of the study lakes

	Lake Constance	Müggelsee
Mean depth	101 m	4.9 m
Maximum depth	253 m	8 m
Area	473 km^2	7.3 km^2
Residence time	4.2 y	40 d
Trophic state	meso/oligotrophic	hypertrophic
Mixis regime	monomictic	polymictic

Sampling of phytoplankton and zooplankton in Müggelsee

Plankton samples were taken at biweekly (zooplankton from 1979 to 1986) or weekly (zooplankton from 1987 to 1994, phytoplankton from 1979 to 1994) intervals during the vegetation period and at least once per month during winter using a 5-L Friedinger Sampler (Hydro-Bios Apparatebau GmbH, Kiel, Germany). From 1979 to 1987 samples were taken from the deepest point at 1-m depth intervals. From 1988 to 1994 spatial heterogeneity was taken into account by sampling at five different sites (for details see Driescher *et al*. 1993). Phytoplankton samples were fixed with Lugol's solution and cell numbers and volumes were determined using an inverted microscope. Zooplankton samples were screened through a 50-µm mesh and fixed with formaldehyde (4% final concentration).

Sampling of phytoplankton and zooplankton in Lake Constance

Plankton samples were taken weekly during the vegetation period and approximately biweekly during winter at the deepest point ($z = 147$ m) of the north-western fjord-like arm of Upper Lake Constance (Überlinger See) from 1979 to 1994. No zooplankton samples were taken during 1983 and no phytoplankton samples during July – December 1983. Phytoplankton was sampled from the upper 20 m of the water column at 2-m intervals, using a 2-m long tube sampler, and further processed as described above. Zooplankton were collected using a Clarke–Bumpus sampler (mesh size 140 µm) by vertical hauls from 140 m depth.

Statistical analysis

Time-series of phytoplankton biovolume, *Bosmina* and *Daphnia* were logarithmically transformed. All time-series were smoothed by calculating four-week moving averages within each year; for example, average *Daphnia* abundances for week 1–4 in 1979, week 2–5 in 1979 … week 49–52 in 1979, …, week 1–4 in 1994, week 2–5 in 1994, …, week 49–52 in 1994. Then Pearson correlation coefficients were calculated between the NAO index and the respective mean values of each four-week period. The resulting correlograms express the response windows of each parameter to winter and spring conditions as expressed by the NAO index. To account for autocorrelation in the dependent and independent variables, we adjusted degrees of freedom according to the formulation given by Bartlett (1946): $N' = N[(1 - a_1a_2)(1 + a_1a_2)]$, where N is the number of paired observations, a_1 is the degree of first-order autocorrelation in the dependent variable and a_2 is the degree of first-order autocorrelation in the independent variable. If one series is negatively autocorrelated, this correction can lead to an increase of the degrees of freedom. To avoid this, we set $N' \leq N$ (*sensu* Post & Stenseth 1998).

Because interannual variability of phytoplankton biovolume in the Müggelsee is strongly enhanced by the occurrence of massive blooms of cyanobacteria (Nixdorf & Hoeg 1993), phytoplankton biovolume in Müggelsee was analysed both including and excluding cyanobacteria. The timing of the clear-water phase in both lakes was defined as the date of minimum algal biovolume after the spring phytoplankton maximum. Statistical analysis was performed using SAS (SAS Institute 1988).

Results

Seasonal variability

Seasonal variations in monthly air temperatures at Berlin and Konstanz during the study period were roughly similar (Fig. 2a). Only during March were air temperatures at Konstanz significantly higher than at Berlin (Pairwise t-test, $P < 0.005$). Mean water temperatures in Müggelsee were lower in winter and showed a faster spring warming and autumn cooling than water temperatures in Lake Constance (Fig. 2b). Phytoplankton biovolume in Müggelsee exceeded that in Lake Constance by almost one order of magnitude (Fig. 2c) and its spring maximum occurred during April, i.e. one month earlier than in Lake Constance (Fig. 2c). Phytoplankton biovolume showed a higher variability in February and March as compared to Lake Constance. Within both lakes, algal biovolume decreased during early summer and exhibited a summer maximum in July/August. Average *Bosmina* abundance in the two lakes was roughly similar during the winter months (Fig. 2d), but was higher in Müggelsee during summer and autumn. Additionally, the spring increase in *Bosmina* abundance was more pronounced in Müggelsee than in Lake Constance. In contrast, abundances and seasonal

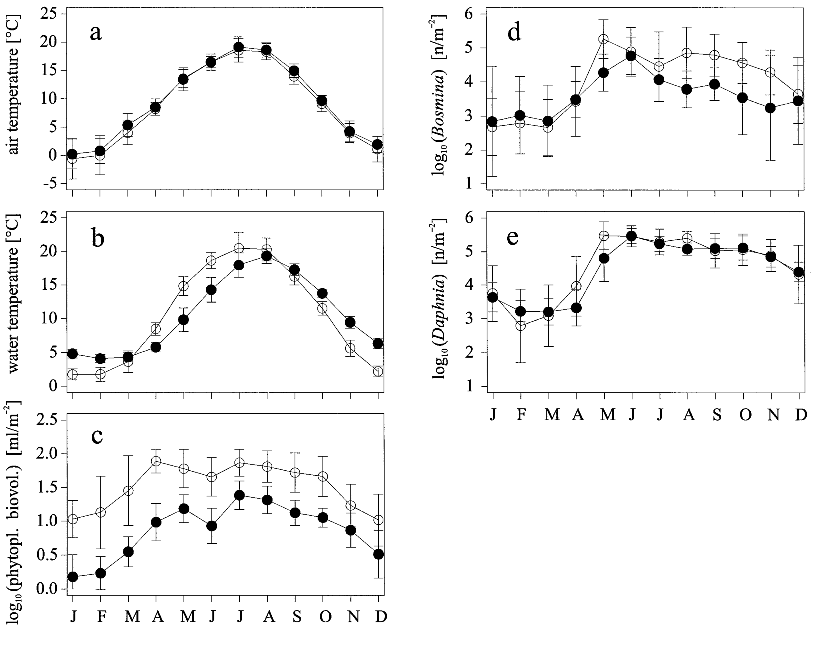

Fig. 2 Mean seasonal variations of (a) air temperature (b) water temperature (c) phytoplankton biovolume (d) *Bosmina* abundance and (e) *Daphnia* abundance in Müggelsee (circles) and Lake Constance (dots) during 1979–94.

variations of *Daphnia* were much the same in both lakes, with the exception of an earlier vernal increase of *Daphnia* numbers in Müggelsee than in Lake Constance (Fig. 2e). Note that algal biovolumes and abundances of *Daphnia* and *Bosmina* in Fig. 2 are expressed per unit area, implying that *Daphnia* abundances per unit volume are higher in Müggelsee than in Lake Constance.

Correlations with the NAO index

Air temperatures in Konstanz in January, March and during a period in July/August were significantly correlated with the NAO index (Fig. 3a). Air temperatures in Berlin were strongly related to the NAO index during the first three months of the year and occasionally also later in the year. At both lakes correlation coefficients declined during April. In contrast, correlation coefficients between average water temperatures and the NAO index remained high until May in both lakes (Fig. 3b). Even though correlation coefficients declined gently in April in both lakes, they stayed > 0.4 and were still significant at $P < 0.1$. In Lake Constance, positive correlation coefficients were also obtained in July/August (Fig. 3b). Total phytoplankton biovolume was positively related to the NAO index in Müggelsee during two periods in February/March and in June/July, but negatively during a period in October/November (Fig. 3c). Considering only eukaryotic phytoplankton, i.e. omitting cyanobacteria, significant negative correlations were also evident in April/May in Müggelsee. In contrast, phytoplankton biovolume in Lake Constance was not significantly related to the NAO index during the first half of the year, and only occasionally thereafter (Fig. 3c). A similar picture emerged for *Bosmina*, whose abundances in spring were significantly related to the NAO in the case of Müggelsee but not in the case of Lake Constance (Fig. 3d). *Bosmina* in Lake Constance was negatively correlated with the NAO index during July and August. In contrast, *Daphnia* abundances in both lakes during April/May were positively related to the NAO index (Fig. 3e).

The seasonal timing of significant correlations differed strongly among the analysed variables (Fig. 4). In Müggelsee, a clear seasonal sequence emerged with positive correlations of the NAO index with phytoplankton in February/March, i.e. during the late winter/early spring phytoplankton bloom, with *Bosmina* in March/April, and with *Daphnia* in April/May, i.e. during the periods of population increase of the two herbivores. In both lakes the response windows of water temperatures and of herbivores overlapped temporally, but those of phytoplankton and herbivores did not.

The start of the clear-water phase differed significantly between the two lakes (*t*-test: $t = 3.9$, $P < 0.001$) and occurred on average in Müggelsee [minimum phytoplankton biovolume on Julian day 147 ± 3.6 d (SE)] two to three weeks earlier than in Lake Constance (minimum phytoplankton biovolume on Julian day 165 ± 3.6 d). The start of the clear-water phase in Lake Constance was significantly related to the start of the clear-water phase in Müggelsee (Fig. 5, $r = 0.63$, $P < 0.05$).

Discussion

Lake size is considered to be an important factor influencing food-web structure and regulation of lakes,

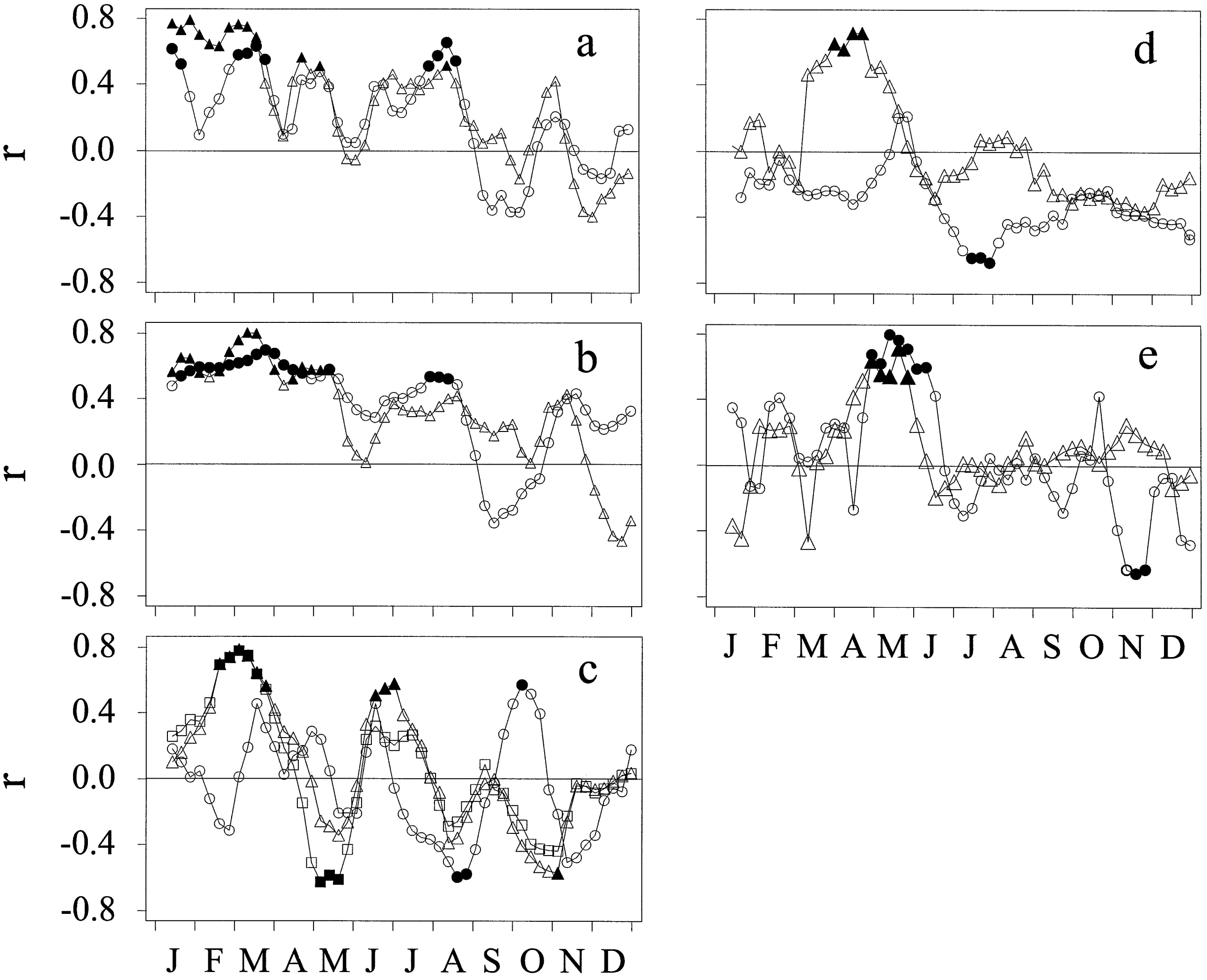

Fig. 3 Correlograms between the NAO index and four-week moving averages of (a) air temperature (b) water temperature (c) phytoplankton biovolume (d) *Bosmina* abundance, and (e) *Daphnia* abundance in Müggelsee (triangles) and Lake Constance (circles). Additionally, correlation coefficients between the NAO and Müggelsee phytoplankton excluding cyanobacteria is shown (Fig. 3c, squares). Solid symbols indicate correlations significant at $P < 0.05$.

and entire monographs (Tilzer & Serruya 1991) and textbooks (Scheffer 1998) have been devoted to the ecology of large vs. small lakes. For example, the higher proportion of littoral habitats compared to total lake area that exists in small lakes provides a larger potential for littoral zone feeding of fishes, resulting in increased fish biomass per unit area and increased predation pressure of fish on zooplankton (Schindler *et al.* 1996). Additionally, there is evidence for an increased ratio of autotrophic to heterotrophic plankton biomass in small as compared to large lakes (Straile 1998), which may provide herbivores in small lakes with an increased abundance of food. Considering these differences, the results obtained for Müggelsee in respect, for instance, to the interannual variability of *Daphnia* abundance, are surprisingly similar to the results obtained for Lake Constance. This exemplifies the important role of meteorological forcing in causing interannual variability in the seasonal succession dynamics of lakes, at least until the start of the clear-water phase.

In addition to the observed significant relationships of various parameters in winter, spring and early summer to the NAO index, we also observed several significant correlations from June onwards in both lakes. The reasons for these correlations are not clear at present. The discussion will hence focus on the effects of the NAO on the plankton dynamics up to the start of the clear-water phase.

For Lake Constance, the analysis of temporal forcing of *Daphnia* abundances largely confirmed former results from an analysis of *Daphnia* biomass (Straile & Geller 1998a; Straile 2000). During late winter and early spring, growth of *Daphnia* is severely restricted by low food concentrations and low temperatures. After the onset of

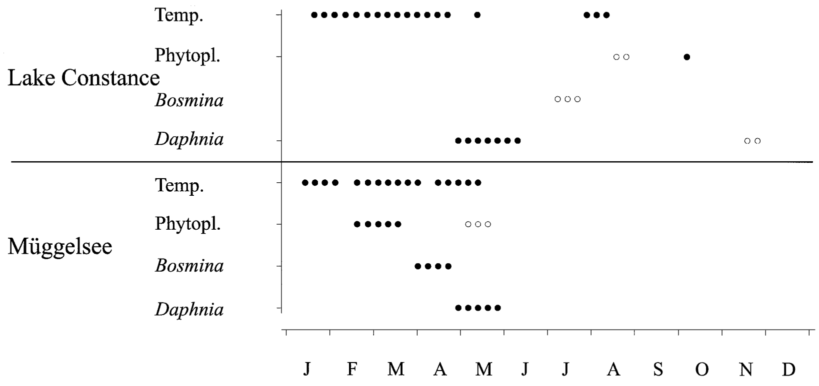

Fig. 4 Seasonal setting of significant correlations ($P < 0.05$) between the NAO index and the analysed time series from both lakes. Dots refer to significant positive correlations; circles indicate significant negative correlations. Seasonal setting of significant correlations with Müggelsee phytoplankton is shown for phytoplankton excluding cyanobacteria.

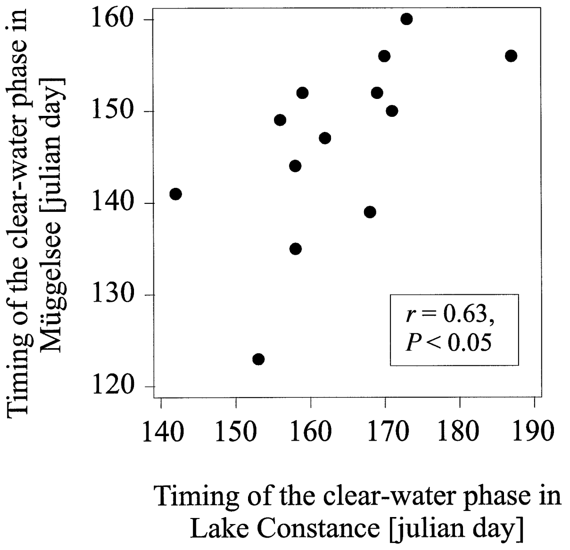

Fig. 5 Relationship between the timing of the clear-water phase in both lakes. Years with no clear-water phase in Müggelsee (1980, 1985, 1986, 1988, 1989) were excluded.

stratification, this 'colimitation' switches to a temperature control of *Daphnia* growth, because water temperature increases more slowly than phytoplankton biovolume (Gaedke *et al.* 1998; Straile 2000). Despite a much higher overall phytoplankton biovolume in Müggelsee and a response of phytoplankton to the NAO as early as February in Müggelsee, the response of *Daphnia* to the NAO was delayed until April/May, when increased temperatures allowed substantial population growth. This resulted in a separation of the response windows, i.e. a decoupling of phytoplankton and *Daphnia*. The faster vernal increase of water temperatures in Müggelsee than in Lake Constance resulted in higher daphnid abundances in spring in Müggelsee (Fig. 2e). Furthermore, using an ANCOVA with *Daphnia* abundances during May as the dependent variable and the NAO as the independent variable revealed significant differences between the lakes, i.e. 'lake' contributes significantly to the model (Fig. 6a). An ancova with May temperature as independent variable yielded no significant 'lake' effect (Fig. 6b), i.e. differences in May *Daphnia* abundances between the lakes can be explained by differences in water temperatures. Hence, the Müggelsee data and the comparison between Lake Constance and Müggelsee support the hypothesis of the regulation of interannual *Daphnia* variability in spring by abiotic factors, e.g. temperature, and not by food concentration.

Owing to the faster growth response of *Daphnia* in Müggelsee, the clear-water phase started on average two to three weeks earlier there than in Lake Constance. Significantly negative correlations between the NAO and phytoplankton biovolume in Müggelsee in April additionally suggest an earlier negative influence of *Daphnia* on phytoplankton in this lake than in Lake Constance. Extensive blooms of cyanobacteria developed in Müggelsee around May in 1980, 1985, 1986, 1988 and 1989 (Nixdorf & Hoeg 1993), i.e. independently of the NAO and *Daphnia* numbers, which, for example, were low in 1985 and high in 1989. Cyanobacteria are known to be less susceptible to zooplankton grazing. Possible mechanisms for this include the release of substances that inhibit the feeding activity of zooplankton (Haney *et al.* 1994) or the formation of colonies that may clog the filtration apparatus of, for example, daphnids (Gliwicz & Lampert 1990). Consequently, the occurrence of cyanobacteria may result in high phytoplankton biovolume despite high *Daphnia* abundance. Hence, only when cyanobacteria were excluded did we find a significant negative relationship between phytoplankton biovolume and the NAO index during late April and early May (Fig. 3c) and a negative relationship between phytoplankton biovolume and *Daphnia* abundance in Müggelsee during May (Fig. 7).

In contrast to the coherent response of water temperatures, daphnids, and the timing of the clear-water phase, there were differences in the response profiles of both lakes for phytoplankton and *Bosmina*. In Müggelsee, both were significantly related to the NAO index, whereas in

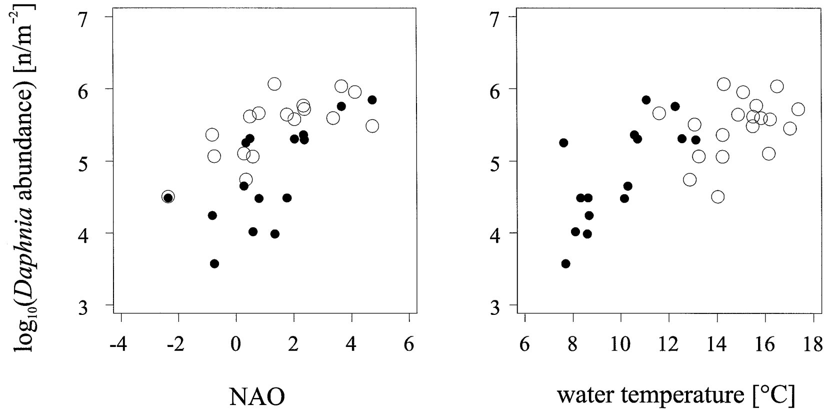

Fig. 6 Scatterplot of mean *Daphnia* abundances in the Müggelsee (open circles) and Lake Constance (filled circles) in May vs. (a) the NAO Index (ANCOVA reveals significant effects of the NAO, $P < 0.0001$ and significant differences between the lakes, $P < 0.0005$) and (b) water temperatures in May (ANCOVA reveals significant effects of water temperature, $P < 0.0005$, but no significant differences between the lakes, $P > 0.1$).

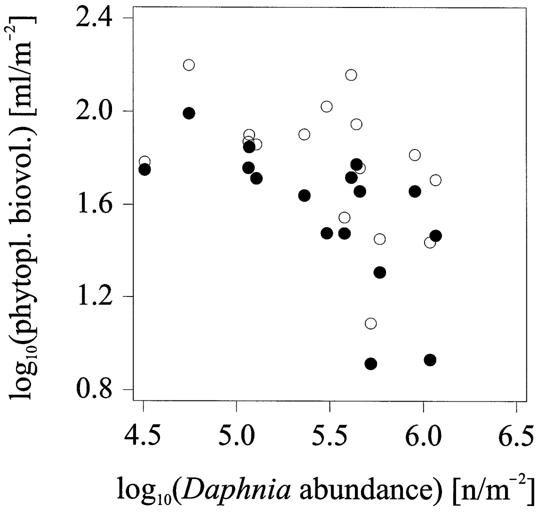

Fig. 7 Scatterplot of average *Daphnia* abundance vs. average total phytoplankton biovolume (circles, $r = -0.45$, $P < 0.1$) and phytoplankton biovolume excluding cyanobacteria (dots, $r = -0.63$, $P < 0.01$) during May in Müggelsee.

Lake Constance this was not the case. The strong positive relationship between the NAO index and phytoplankton biovolume in Müggelsee can be attributed to the lack of ice development in mild winters. Adrian *et al.* (1999) observed pronounced diatom blooms in Müggelsee during late winter/early spring of years with no ice cover, when increased turbulence favoured diatom growth. Lake Constance, however, was not covered by ice during the study period. In contrast, high rates of vertical mixing prevented the occurrence of a late winter/early spring bloom in Lake Constance, because phytoplankton growth in this lake is inhibited by a lack of thermal stratification strong enough to prevent the transport of algae below 20 m depth (Gaedke *et al.* 1998). Hence, the response of phytoplankton to meteorological forcing would seem to depend on lake depth.

In contrast to phytoplankton, the lack of a response of *Bosmina* to meteorological forcing in Lake Constance may reflect the effect of confounding variables. In contrast to *Daphnia*, *Bosmina* decreased strongly during the observation period in this lake, most probably as a result of ongoing re-oligotrophication (Straile & Geller 1998b). This decline most probably outweighed the effects of the *Bosmina* response to meteorological forcing in Lake Constance. In Müggelsee, both *Daphnia* and *Bosmina* abundances during spring were related to the NAO index. However, significant positive relationships were observed as early as March for *Bosmina* and approximately one month later for *Daphnia.* This agrees with the observation that abundance peaks of *Bosmina* occur prior to abundance peaks of *Daphnia* in many lakes (Sommer *et al.* 1986) and may suggest that *Bosmina* is better adapted to lower temperatures.

To conclude, the comparative analysis of meteorological forcing revealed a difference in the responses of phytoplankton biovolume and *Bosmina* numbers to the NAO in Lake Constance and Müggelsee. Despite the difference in the response of primary producers, we found strong evidence for temporal coherence in *Daphnia* development during spring, due to the coherence in the vernal warming. In addition, early clear-water phases in Lake Constance were observed in years that also showed early clear-water phases in Müggelsee, when years with a strong development of cyanobacteria in Müggelsee were excluded. The temporal coherence over a large geographical region, despite large differences between the lakes, suggests that a great variety of lakes in central Europe may possibly have exhibited a similar interannual variability in the timing of successional events during the last 20 years. An additional example of this may be given by the plankton dynamics in Pluss-See, where a relationship between average winter temperatures and the timing of the clear-water phase has also been observed (Müller-Navarra *et al.* 1997).

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