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North Atlantic Oscillation synchronizes food-web interactions in central European lakes

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A regular and distinct feature of seasonal plankton succession in temperate lakes is the early summer period of algal suppression by herbivores, i.e. the clearwater phase. Within the last 30 years the timing of this food-web interaction between algae and herbivores has advanced on average by approximately two weeks in central European lakes due to faster population growth of herbivores in warmer water. Trend and interannual variability in clearwater timing were strongly related to the climate dynamics of the North Atlantic, i.e. the North Atlantic Oscillation (NAO). Due to its large-scale effects, the NAO synchronized plankton succession in central European lakes, causing a striking temporal coherence of a food-web interaction over several hundreds of kilometres.

Keywords: North Atlantic Oscillation; phenology; plankton succession; *Daphnia*; clearwater timing; coherence

1. INTRODUCTION

Climate warming that has occurred over the past decades (Easterling *et al.* 1997) is already affecting the distribution (Epstein *et al.* 1998; Thomas & Lennon 1999), behaviour (Post *et al.* 1999; Sparks 1999), and phenology (Beebee 1995; Forchhammer *et al.* 1998; Bradley *et al.* 1999) of animal and plant species. Most probably, these changes observed so far for individual species will give rise to further indirect effects of global warming, affecting communities and entire food webs (Harrington *et al.* 1999; Hughes 2000). At present, we do not know much about the strength of indirect effects of global warming and its consequences for animal and plant communities and food webs. Small plankton with a short generation time may be one of the best systems to study such indirect effects as the seasonal plankton development can be divided into a sequence of regular periods differing in community composition, food-web structure, and carbon flow (Sommer *et al.* 1986; Straile 1998).

Seasonal phytoplankton development is controlled by a complex interplay between hydrodynamical and chemical factors, and food-web interactions (Sommer *et al.* 1986; Sommer 1989). One spectacular and even macroscopically observable event in phytoplankton succession is the clearwater phase (figure 1). It is a period of extremely low algal densities in late spring–early summer caused by the grazing activity of herbivores; in particular water-fleas of the genus *Daphnia* (Lampert *et al.* 1986). Recent work has shown that the timing of the clearwater phases in two limnologically distinct central European lakes 700 km apart was influenced by the North Atlantic Oscillation (NAO), that is the dominant mode of winter climate variability in Europe (Hurrell 1995). Over the past three decades the NAO exhibited a trend towards a more positive phase (Hurrell 1995), characterized by low-pressure anomalies over the Icelandic region and high-pressure anomalies across the subtropical Atlantic causing stronger-than-average westerlies across middle latitudes and a trend towards warmer winters in Central and Northern Europe (Hurrell 1995).

The strong association between the NAO and the clearwater phenology in both Lake Constance (which is large, deep and mesotrophic), located close to the European Alps and Müggelsee (which is small, shallow and hypertrophic), near Berlin, was the complex result of meteorological and hydrodynamical forcing of a predator–prey interaction between *Daphnia* and algae (figure 2) (Straile 2000; Straile & Adrian 2000). Given the indirect nature of this relationship, the large distance between Lake Constance and Lake Müggelsee and additionally strong differences between the two lakes regarding their morphology, thermal and flushing regime, trophic state, and food-web structure the observed patterns in the two lakes were surprisingly similar (Straile & Adrian 2000). This observation suggests that the strong influence of the NAO on thermal warming and plankton dynamics might not be specific to these two lakes but could be typical for central European lakes. Here, I test this hypothesis by comparing the clearwater timing (CWT) in central European lakes with regional air temperatures (ATs) and with the winter NAO index of Hurrell (1995) to estimate the degree of spatial coherence in this food-web response and to determine to what extent CWT may have reflected synoptic-scale climatic forcing.

2. MATERIAL AND METHODS

The long-term AT development across the study region was analysed using 18 German stations provided within the world weather records (Deutscher Wetterdienst 2001). These stations cover the temperature development in Germany from 47° 41′ to 54° 32′ and from 4 to 1213 m.a.s.l. Data on CWT were assembled from the time-courses of water transparency for 136 seasons in a total of 28 lakes covering an area of more than 10^5 km^2 and 7° of latitude (figure 3). The data were obtained from the literature and from limnological institutions. Only lakes and seasonal courses that exhibited typical clearwater phases and that were sampled at least twice per month were used. The timing of the clearwater phase was defined as the date of maximum Secchi-disc depth, i.e. water transparency, during late spring–early summer after the spring bloom of algae (figure 1). The

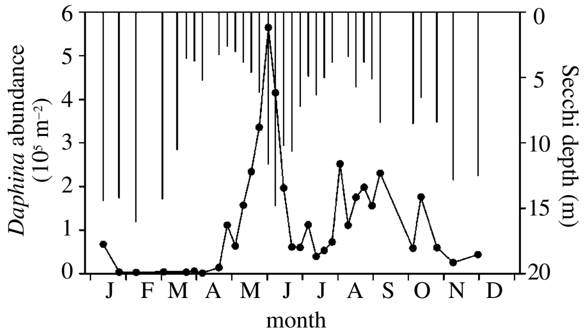

Figure 1. Typical seasonal course of transparency in temperate lakes measured with a Secchi disc in Lake Constance during 1993 (vertical lines). During winter the transparency was high and declined with the spring bloom of algae to a few metres. An increase in *Daphnia* abundance (black dots) during spring and subsequent grazing of algae resulted in the 'clearwater phase' and caused the transparency to increase again to winter values in May–June.

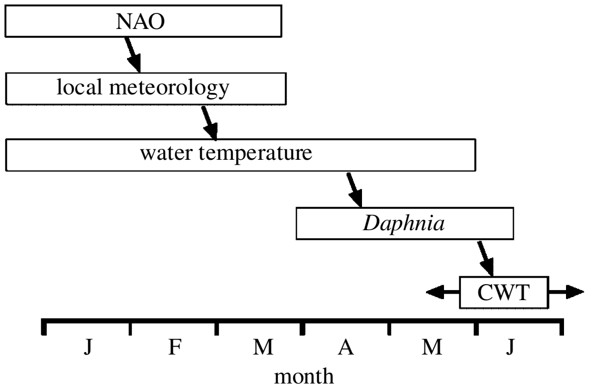

Figure 2. Schematic of the impact of the NAO on CWT based on analyses of physical variables and plankton dynamics in Lake Constance and Müggelsee (Straile 2000; Straile & Adrian 2000). Bars show the seasonal periods of influence of each causal link between the NAO and CWT. The NAO had a strong influence on local meteorological conditions in the form of winter air temperatures. ATs in turn influence the vernal warming of epilimnetic water. Water temperature strongly controls the *Daphnia*-population development, that after attaining maximum biomass initiates the clearwater phase and hence controls its timing. As all links in this chain fit tightly together, the timing of the clearwater phase is significantly related to the NAO.

statistical analysis of the time-series data has to account for unequal spacing of the data and for autocorrelation. This has been done using the spatial covariance structures available in the mixed procedure available in SAS by viewing the unequally spaced longitudinal data as a one-dimensional spatial process (Littell *et al.* 1996).

3. RESULTS AND DISCUSSION

For the winter time period (December–March, DJFM) AT anomalies across Germany, during the last three decades, are very similar (figure 4) and highly correlated to each other (mean correlation coefficient: 0.87 ± 0.09 s.d.). This similarity makes it possible to calculate a composite-series GWWR (German world weather record) representing regional AT by taking the arithmetic mean of the temperature anomalies of the 18 stations that can be compared with the CWT series. In addition to this similarity, the time-series of all meteorological stations were highly correlated to the winter NAO index (mean correlation coefficient: 0.58 ± 0.08 s.d.). Multiple regression models explain 46% of the variability in winter AT using the altitude and latitude of the stations as independent variables as follows:

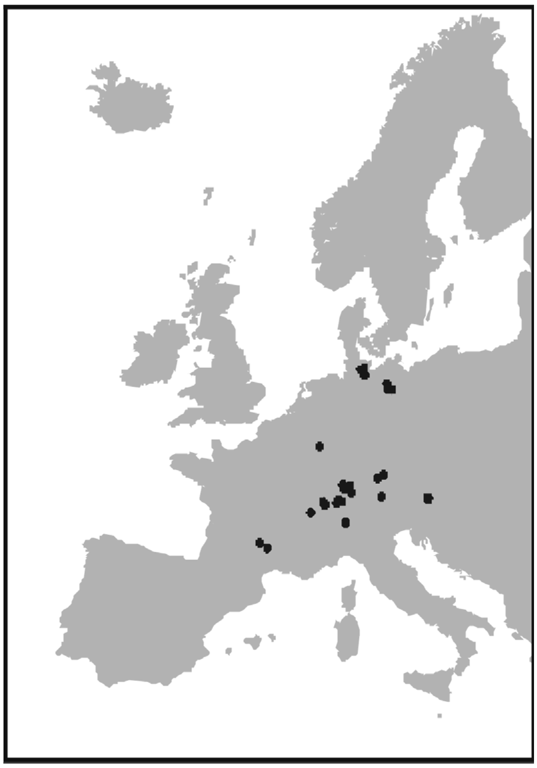

Figure 3. Locations of the 28 lakes in Central Europe from which 136 seasonal courses of water transparency (Secchi-disc depth) data used in this study were collected.

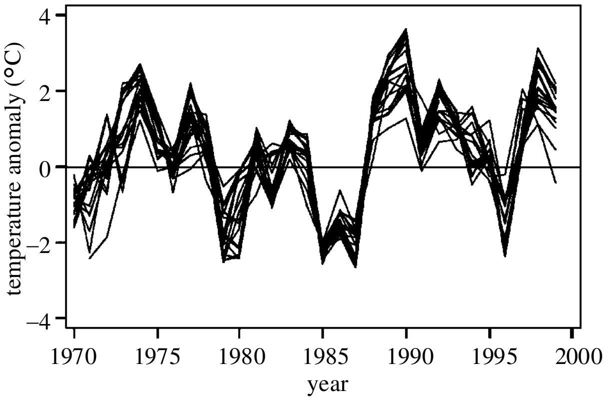

Figure 4. Winter (DJFM) temperature anomalies from 18 weather stations across Germany from 1970 to 1999. Data were obtained from the Deutscher Wetterdienst home page (http://www.dwd.de/research/klis/daten/online/wwr/e _form.htm).

$$AT_{P1} = 24.3 - 0.41 \times \text{latitude} - 0.005 \times \text{altitude}. \quad (3.1)$$

On including the winter NAO index as a third independent variable, 62% of the variability is explained as follows:

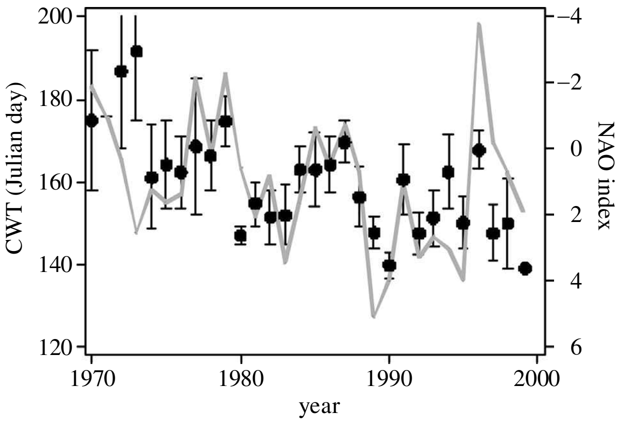

Figure 5. The winter (DJFM) NAO index (grey line) and the timing of the clearwater phases (mean values ± 1 s.e.) in 28 central European lakes are significantly related ($p < 0.01$). Since 1970 the average timing of the clearwater phase advanced significantly ($p < 0.001$). After detrending of both series by linear regression the relationship is significant at $p < 0.05$. A positive NAO index indicates strong westerly winds across the Atlantic Ocean and unusually warm winters over north and central Europe; opposing conditions prevail during negative NAO index years (Hurrell 1995). The NAO index was obtained from the Climate Analysis Section (Colorado, SA) Internet home page (http://www.cgd.ucar.edu:80/cas/climind/). References and data for the timing of the clearwater phase are available from the author upon request.

$$AT_{P2} = 23.8 - 0.41 \times \text{latitude} - 0.005 \times \text{altitude} + 0.42 \times \text{NAOI}, \qquad (3.2)$$

where NAOI is the NAO index.

The timing of the clearwater phase in central European lakes was in phase with the NAO during the last three decades ($r = -0.5$, $p < 0.01$). High NAO years were associated with an early clearwater in central European lakes, while there was a strong tendency for late clearwater phases in low NAO years (figure 5). This association is not only due to a common linear trend in both variables, as the relationship was still significant ($p < 0.05$) after linear detrending of both variables. In addition, the data clearly show that the average earliness of the clearwater phase has increased during the last decades (figure 5, $r = -0.67$, $p < 0.001$) as a result of the trend of the NAO towards a more positive phase (Hurrell 1995). Hence, CWT in central European lakes showed a coherent response to the NAO and recent climate warming during the last 30 years.

Patterns of temporal coherence, i.e. the degree to which different ecosystems within a region behave similarly through time (Magnuson *et al.* 1990), progress from strong coherence for physical variables to moderate coherence for chemical variables, and weak or no coherence for biological responses (Magnuson *et al.* 1990; Kratz *et al.* 1998; Baines *et al.* 2000; George *et al.* 2000). Coherence in lake surface temperature has been shown to extend over several hundred kilometres in the European northern perialpine region (Livingstone & Dokulil 2001) and in Wisconsin, USA (Kratz *et al.* 1998). Regarding ice break-up, the NAO signature is detectable in historical observations ranging from central Europe (Livingstone 2000), to Northern Europe (Weyhenmeyer *et al.* 1999; Livingstone 2000) and even to Lake Baikal, Siberia (Livingstone 1999). Coherence of chemical variables has been observed, e.g. in the English Lake District (George *et al.* 2000) and in neighbouring northern Wisconsin lakes (Baines *et al.* 2000). In the Wisconsin lakes lake temperature was the most synchronous variable, followed by chemical variables (Kratz *et al.* 1998; Baines *et al.* 2000). In the English Lake District phosphorus and nitrate–nitrogen concentrations showed a coherence as high as physical variables. However, this high degree of coherence was to a large extent caused by increasing artificial fertilizer application on adjacent farmlands and only secondly due to climate variability (George *et al.* 2000). In these studies coherence in biological variables such as chlorophyll and zooplankton was lowest (Kratz *et al.* 1998; Baines *et al.* 2000; George *et al.* 2000). In contrast to physical variables, there is no evidence to date for temporal coherence of biological variables in lakes extending a geographical range of more than 50 km^2 (Rusak *et al.* 1999; Baines *et al.* 2000; George *et al.* 2000).

Using a phenological approach to the temporal coherence of lake ecosystems, I found strong evidence for coherence in plankton succession across a geographical area of more than 10^5 km^2 and encompassing an altitude range of almost 1000 m. This underlines the importance of large-scale abiotic parameters in regulating interannual variability in plankton succession and controlling the timing of food-web interactions. Additionally this finding highlights the striking regularity and predictability of plankton succession that in central European lakes proceeded with marked regularity, influenced by interannual differences in vernal warming, that in turn seem to be caused by the climate dynamics of the North Atlantic.

The dataset allows a further test of the importance of vernal warming in determining the timing of the clearwater phase. In addition to interannual climatic variability, vernal warming of lakes is influenced by lake-specific, geomorphological factors such as lake depth and the latitude and altitude of the lakes' setting (Straskraba 1985). On average, shallow lakes located at lower altitude or latitude warm up faster than deep lakes at higher altitude and latitude (Straskraba 1985). Consequently, shallow lakes located at lower altitude or latitude should exhibit an early clearwater phase and vice versa.

Testing the influence of altitude, latitude and lake depth on CWT using mixed models showed that in addition to the NAO, altitude, and to a lesser extent latitude and lake depth, did influence CWT (table 1, model 1). Substituting the NAO with GWWR (model 2) did not change the parameter estimates of altitude, latitude, and lake depth significantly. The same is true when testing for a monotonic trend with time instead of the effect of the NAO (model 3). This model shows that when the effects of altitude, latitude and lake depth were considered, CWT advanced by 0.5 d yr^{-1} during the study period, i.e. approximately two weeks during the last three decades. Model 3 is slightly inferior to models 1 and 2 based on Akaike's information criterion, i.e. its Akaike's information criterion (AIC) is higher. Additionally, no significant linear trend in the data can be detected after the influence of the NAO has been accounted for (model not shown). This again suggests that the correlations observed are not primarily due to a com-

Table 1. Solutions for the fixed effects of mixed models with CWT as a dependent variable and various combinations of the independent variables: NAO index; GWWR; $\mathrm{AT}_{\mathrm{P1}}$; $\mathrm{AT}_{\mathrm{P2}}$; year; lake depth; altitude; and latitude.

(The AIC is given as an overall model fit statistic. Lake depth was logarithmically transformed prior to analysis. GWWR represents the arithmetic mean of the anomalies of average winter (DJFM) temperature from the GWWR stations. $\mathrm{AT}_{\mathrm{P1}}$ and $\mathrm{AT}_{\mathrm{P2}}$ represent predicted winter ATs from equations (3.1) and (3.2). See text for more details.)

model	variable	parameter estimate	*t*-value	*p*
model 1: AIC = 1151.3				
	NAO	−2.95 ± 0.75	−3.9	0.0002
	altitude	0.038 ± 0.007	5.3	0.0001
	latitude	1.65 ± 0.90	1.8	0.09
	log (lake depth)	7.3 ± 4.4	1.6	0.12
model 2: AIC = 1150.5				
	GWWR	−4.2 ± 1.07	−3.9	0.0002
	altitude	0.04 ± 0.007	5.5	0.0001
	latitude	1.85 ± 0.9	2.0	0.06
	log (lake depth)	8.55 ± 4.5	1.9	0.08
model 3: AIC = 1162.6				
	year	−0.51 ± 0.01	−2.4	0.02
	altitude	0.03 ± 0.008	4.1	0.0004
	latitude	1.2 ± 0.9	1.2	0.25
	log (lake depth)	6.6 ± 4.6	1.4	0.2
model 4: AIC = 1145.0				
	NAO	−3.0 ± 0.76	−4.0	0.0001
	$\mathrm{AT}_{\mathrm{P1}}$	−7.0 ± 1.4	−5.2	0.0001
	log (lake depth)	12.9 ± 3.1	4.1	0.0004
model 5: AIC = 1146.7				
	$\mathrm{AT}_{\mathrm{P2}}$	−7.07 ± 1.09	−6.5	0.0001
	log (lake depth)	12.9 ± 3.0	4.2	0.0003

mon long-term trend of the NAO and CWT but rather due to fluctuations on the annual or decadal scale.

To obtain a more direct relationship of CWT with AT, I used the AT predictions from equations (3.1) and (3.2) ($\mathrm{AT}_{\mathrm{P1}}$ and $\mathrm{AT}_{\mathrm{P2}}$, respectively) as independent variables (models 4 and 5). According to these two models, CWT advanced by approximately 1 week $°\mathrm{C}^{-1}$. This parameter estimate fits well with the effect of altitude in models 1–3: on average, an increase in altitude of 100 m resulted in a delay of the clearwater phase of *ca*. 4 days. Surface ATs increase typically linearly with altitude at a rate of *ca*. 0.6 °C per 100 m (Tabony 1985). The shift in CWT of 4 days per 100 m altitude is hence due to a shift of 0.6 °C, i.e. 6.6 d $°\mathrm{C}^{-1}$, which is close to the AT parameter estimates in models 4 and 5 (table 1). Hence, the mixed models provide coherent parameter estimates and support the hypothesis that the shift in CWT is due to a faster increase in vernal water temperatures.

Due to its regularity and strong climate control, the timing of the clearwater phase can be used as a food-web mediated phenological marker for temperate lake ecosystems, integrating information on the vernal warming of the lake and the spring population increase of a key herbivore, i.e. *Daphnia*. Lake transparency is increasingly monitored by volunteering programmes in order to survey the trophic status of lakes. For example, within the Great American Secchi Dip-in (Anon. 2000), coordinated by Kent State University, about 2000 lakes from 41 states have been monitored since 1994. Given that transparency data are sampled with sufficient temporal resolution these data may easily be used to analyse patterns of temporal coherence and the response of lakes to interannual climatic variability on an even larger geographical scale. The most important biotic player in the relationship between the NAO and the clearwater phase is *Daphnia*, which is of central importance within freshwater pelagic food webs (Jürgens 1994; Gaedke & Straile 1998). Hence, the trend in the earliness of the clearwater phase may be regarded as a proxy for *Daphnia*-mediated cascading effects of warming on the composition and structure of pelagic communities in lakes. As it is the population dynamics of a critical species that is strongly influenced by water temperature (Straile & Adrian 2000; Straile 2000; Gillooly & Dodson 2000), freshwater food webs may be especially prone to changes due to climate warming. As the current positive phase of the NAO may be stabilized by increased concentrations of greenhouse gases (Paeth *et al.* 1999), warm winters will probably influence plankton succession in temperate lakes in the future.

To summarize, the observed relationship between the NAO and CWT has at least three important implications for the consequences of climate warming on freshwater ecosystems, as follows.

(i) This relationship shows that climatic impacts on, for example, lake physics, can be mediated, prolonged, and even enhanced by food-web interactions.

(ii) It shows that the prolongation of impacts can cause a temporal shift between the timing of meteorological forcing, that in the case of the NAO is strongest during winter and early spring, and the timing of an ecological impact, e.g. CWT during early summer.

(iii) Finally, it shows, that complex food-web-mediated responses to meteorological forcing may not be specific to individual lakes, but can occur synchronously across large areas.

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