

# Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability

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## Abstract

The assessment of possible implications of anthropogenic climate change requires the evaluation of results obtained with complex climate models. Here we considered the problem of assessing the impact of climate variability on successional events in a lake (Plußsee) of the temperate region between January and May. We first established a statistical link between large-scale air temperature, at about 1500 m height, and the local temperature, in order to bridge the spatial gap of information obtained from global climate models and local climate which forces processes in the lake. Secondly, the local temperatures were statistically related to biologically induced dynamic features in the lake, derived from Secchi depths readings (as integrated measures). The observed relationships were compared with results from a phyto- and zooplankton population-dynamic model run under different temperature regimes. The local temperatures approximated closely the large-scale temperature. The timing of phyto- and zooplankton maxima (clearwater phase) were negatively related to the temperature. Thus, with a temperature increase both occurred earlier. The intensity of the spring algal maximum was negatively related to its timing, whereas no clear relation between the timing and intensity of the clearwater phase (zooplankton maximum) could be obtained.

*Keywords:* climate change, downscaling, seasonal succession

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## Introduction

General circulation models (GCMs) predict a global mean atmospheric temperature increase during the next few centuries with increased CO<sub>2</sub> emission scenarios (Cubasch *et al.* 1992). This is known as anthropogenic global warming. GCMs are designed to simulate the large scale of the climate (von Storch 1995a). Thus, the climate model output generates usable information only on the large scales of hundreds of kilometres at best. On the other hand, the impact of climate occurs on smaller scales. Ecosystems are linked to the local climate, and ecosystem models need climate information with high spatial and temporal resolution as forcing variables. Since GCMs fail to predict the details of climate on the local scale, GCMs output cannot be directly used for climate impact studies on ecosystems. In order to bridge the gap in spatial resolution, statistical downscaling can be used (von Storch 1995a). However, statistical downscaling requires long-term homogeneous data sets to reveal

statistical relationships with a certain skill, between the variability of large scale atmospheric data and the variability of local observed phenomena.

Variability within an ecosystem can have two different reasons: variability caused by the abiotic environment (allogenic), or by dynamic processes within the biotic system (autogenic, Reynolds 1984). For phytoplankton, besides chemical factors (mostly nutrients), physical allogenic factors (light, temperature) are of major importance for conditioning the structure of phytoplankton assemblages (Reynolds 1989). For zooplankton, temperature acts as the primary climate factor which can affect the timing of their occurrence (Kratz *et al.* 1987) and abundance (Sandercock 1967; van den Bosch & Ringelberg 1985).

Most lakes in temperate regions exhibit a characteristic seasonal succession as a result of species replacements. The succession of seasonal events within the pelagial was generalized by the Plankton Ecology Group (Sommer *et al.* 1986), who described the dependence of these events on the physical environment and biotic interactions. Here we analyse the influence of interannual variability in

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temperature on the variation in succession. Typical events within the succession are the spring algal maximum and, thereafter, the clearwater phase. The present study concentrates on the variability of both succession events, which happen in the first half of the year. To reveal the successional pattern, Secchi depth readings were chosen. They can be taken as an integrated parameter which is methodologically relatively easy to determine and homogeneous records of a certain length exist. We address three major questions:

1 Can we detect temperature-influenced differences in seasonal succession of plankton with an overall measure like Secchi disc transparencies?

2 Can a phytoplankton–zooplankton model help to understand the mechanisms of plankton dynamics behind the successional pattern, which are affected by inter-annual temperature variability?

3 Can a connection be found between locally observed temperature data (air and lake temperatures) and observed large-scale meteorological data, which have a similar spatial resolution to the GCMs?

We analysed long-term meteorological data (large scale and local scale) and long-term data for one lake (Plußsee). Observational data were compared to model results from a numerical ecosystem model which was forced with different temperature regimes.

## Material and Methods

### *Climatic data*

Large-scale atmospheric data were obtained from the US National Meteorological Centre. Data of the area between 25° W to 20° E and 40° N to 65° were considered. The data represent weekly temperatures at the height at which the pressure is 850 mbar (around 1500 m altitude). Spatial resolution of these data is a grid of 5° longitude × 5° latitude (around 320 km × 550 km). For each year ( $t$ ) between 1978 and 1989 and each gridpoint ( $x$ ), the temperatures were averaged over the period from January until April (2nd–18th week) giving a spatial–temporal temperature field ( $T(x,t)$ ). From this field, an average field over all years ( $T(x)$ ) was calculated. Anomalies  $T_{\text{ano}}(x,t)$  for each year were obtained by subtracting  $T(x)$  from  $T(x,t)$ .

As an indicator for large-scale interannual variability, spatially averaged anomalies ( $T_{\text{ano}}(x,t)$ ) over all field points ( $x$ ) cannot be taken, because spatial variability is not uniform. Thus we used the time coefficients ( $a_i(t)$ ) of the 'Empirical Orthogonal Functions' (EOFs, von Storch 1995b) as indicators. The technique separates the variability of the anomalies in space from that in time by characteristic orthogonal spatial patterns  $e_i(x)$ , EOFs, and their pairwise uncorrelated coefficients  $a_i(t)$ .

$K$  is the number of EOFs and coefficients which are

used for the approximation. The first pair ( $K = 1$ ),  $e_1(x)$  and  $a_1(t)$ , is determined from the data, such that its product represents a maximum of variance of the anomalies. The second pair explains the maximum of the remaining variance, its pattern is orthogonal to the former one and its coefficient is uncorrelated with the coefficient of the former pair. If more pairs ( $e_i, a_i, K = 2,3,7$ ) are consecutively derived, the product approximation gets closer to the original data.

Local climate data were obtained from the Deutscher Wetter Dienst. The records of daily air temperatures were taken in Plön at the Max-Planck-Institut für Limnologie, 5 km from Plußsee. Mean air-temperature values from January until March (1<sup>st</sup>–13th week) for each year were calculated as by Adrian *et al.* (1995) for better comparison with their study.

### *Observational lake data*

The Plußsee (North Germany) is a eutrophic lake which was formed during the last glaciation. It has a surface area of 0.14 km<sup>2</sup>, a maximal depth of 29 m and a mean depth of 9.4 m and is situated in a valley surrounded by woodland. It has been a subject of investigation by the Max-Planck-Institut für Limnologie for several years (for a review see Overbeck & Chrost 1989).

Weekly data from the Plußsee were obtained from the Max-Planck-Institut für Limnologie. Vertical temperature readings were taken with a WTW-probe, Secchi depth readings were determined with a Secchi disc. Although Plußsee data are available since 1970, we concentrated on the period from 1978 until 1992, excluding the data from 1986 because of the installation of a circulation pump in the lake. In 1977 a major change within the phytoplankton community occurred for unknown reasons (Hickel 1988) and only three years prior to 1977 were sampled in weekly intervals and thus useful for our statistical analyses. However, even in those years a clearwater phase could not be determined from the Secchi transparency readings and therefore only a comparison was made in respect to the phytoplankton maxima.

Mean lake temperatures in Plußsee were calculated as a vertical average of temperatures weighted by the depth-dependent area of the lake. Before ice break-up no temperature readings were available. Thus the temperatures during winter were specified as follows. During ice coverage, a temperature of 2.8 °C was assumed, according to measurements during ice coverage in 1977. At times when no ice cover was reported, a linearly interpolated value between 2.8 °C and the value of the first reading was assumed.

First we related large-scale variability to local-scale variability of mean air (January–March) and lake (January–April) temperatures. Then we compared local tem-

perature data (air, lake) and related lake temperatures to dynamic processes in the lake observed as Secchi transparency differences and model results. Lake temperatures from January to April (2nd–15th week) were compared with minimal Secchi readings (phytoplankton maximum), and temperatures between January and May (2nd–21st week) used for comparison to maximal Secchi depth readings (zooplankton maximum).

### Dynamic model

A simple numerical population model was created. The mathematical description is presented in Appendix 1. Here we present a verbal description of the model and the underlying assumptions.

The temporal evolution of the depth and temperature of the mixed layer (maximal 29 m and minimal 10 m) and the light at the lake surface are parameters to be specified. In the present study, we used hyperbolic tangent functions but the model could also be driven with temperatures as an output from atmospheric or hydrological models. The temporal evolution of light at the lake surface is specified by global radiation at  $f = 53^\circ\text{N}$ . Underwater light is then assumed to decay exponentially in the mixed layer. The biological processes are influenced by these abiotic parameters of the mixed layer.

The biomass of phytoplankton ( $N_a$ ) and zooplankton ( $N_z$ ) were modelled as basic functional units. Phytoplankton growth ( $\mu$ ) was assumed to be light-limited in winter and spring (Sommer *et al.* 1986; Jassby *et al.* 1990), and the growth rates were calculated by Monod kinetics (Reynolds 1989), with a half-saturation constant assumed to be temperature dependent. When calculating the phytoplankton biomass an upper carrying capacity ( $K$ ) was introduced into the equation. Loss processes for phytoplankton are grazing by zooplankton ( $r$ ) and sinking out of the mixing layer ( $\epsilon$ ). Phytoplankton biomass is determined as follows:

$$dN_a/dt = \mu (K - N_a/K) N_a - r N_z - \epsilon.$$

Zooplankton growth rates ( $\eta$ ) depend on temperature and food. A logistic zooplankton growth function in relation to food is obtained from *Daphnia* growth rate measurements with seston (Müller-Navarra 1993). An exponential temperature dependence was included, assuming a doubling of the growth rate with a  $10^\circ\text{C}$  increase. Zooplankton biomass is calculated as follows:

$$dN_z/dt = \eta N_z.$$

The model was run for the first 155 days of the year with a time step of one day. Different temperature regimes were calculated with initial values at the beginning of the year varying between  $3^\circ\text{C}$  and  $7^\circ\text{C}$ . Initial plankton

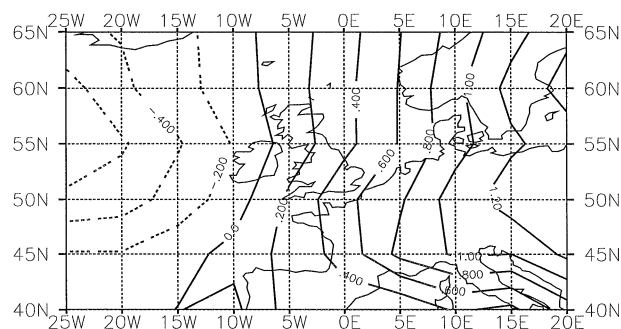


Fig. 1 First Empirical Orthogonal Function (EOF) of the large scale temperature anomalies at the 850mbar level, calculated from January to April averages between 1978 and 1989. The spacing of isolines is  $0.025^\circ\text{C}$ .

concentrations were  $0.02\text{ mg C L}^{-1}$  for phytoplankton and  $0.001\text{ mg C L}^{-1}$  for zooplankton.

## Results

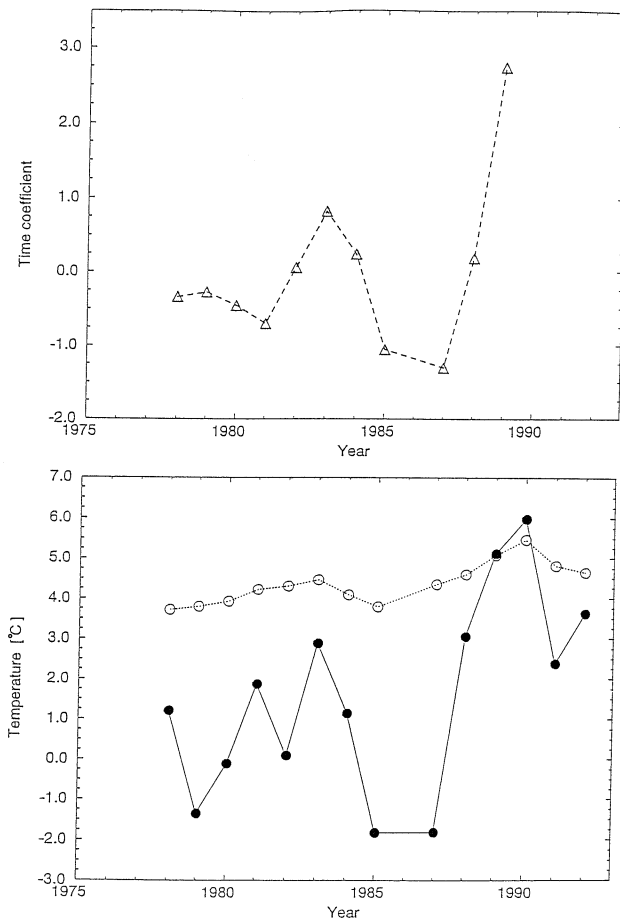
### Climatic data

Figure 1 shows the most important spatial pattern (first EOF) of the large-scale temperature field. The pattern represented 52% of the variability, with large anomalies over central and eastern Europe and smaller anomalies over Great Britain and Spain. The coefficients of the time evolution for each year yielded positive values (warmer years) in 1983 and 1989 and negative values in 1978–81, 1985 and 1987 (Fig. 2a). The local mean air temperatures varied between  $-2^\circ\text{C}$  and highest values in 1990 of  $6^\circ\text{C}$  (Fig. 2). Variation in whole lake temperatures was less pronounced, but followed the air temperatures (Fig. 2).

There is a good correlation between the time coefficients of the EOF analysis from large-scale anomalies and local air temperature ( $r^2 = 0.71$ ) as well as lake temperature of Plußsee ( $r^2 = 0.55$ ). Including more EOF-coefficient time series by multiple regression did not improve the relationship. Correlation of local air and Plußsee temperatures yielded a highly significant regression with  $r^2 = 0.79$  (Fig. 3). In this regression air temperatures between  $0^\circ\text{C}$  and  $4^\circ\text{C}$  seemed to have a pronounced effect on the lake temperature. Overall mean lake temperatures followed longer (more than one year) fluctuations in atmospheric temperatures.

### Model

The prescribed temperature time series used in the model (Fig. 4) were in good qualitative agreement with observed temperatures in Plußsee (Fig. 5). The sharp increase from day 100 onwards in the upper 4 m (Fig. 5a) were well

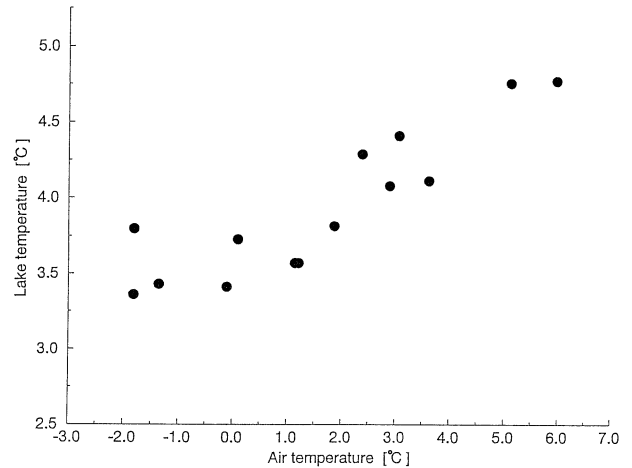


**Fig. 2** (a) Coefficient time series of the first EOF of the large scale temperature anomalies from 1978 to 1989. (b) Mean (January–March) air temperatures (full circles) and mean (January–April) lake Plußsee temperatures (open circles) from 1978 until 1992.

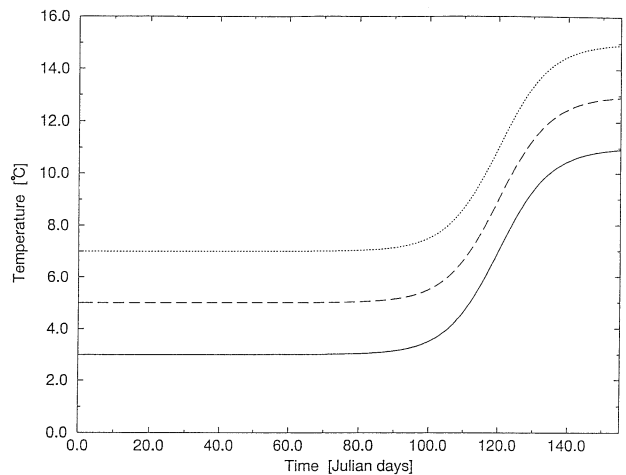
represented in the model, but short-term variability was not considered in the model.

The model reproduced the observations qualitatively with respect to the phytoplankton spring maximum (Secchi depth minimum) and the zooplankton maximum (clearwater phase) (Fig. 6). Differences in minimum phytoplankton abundances corresponding to different maximum zooplankton abundances were not resolved by the model. Phytoplankton were always grazed down to almost zero. Nevertheless, we compared zooplankton peaks in the model data with measured Secchi depths of the clearwater phase in the lake.

Phytoplankton increases at the beginning were slightly enhanced with increasing temperatures. Zooplankton started growing between Days 90 and 110 depending on temperature. The zooplankton maximum occurred earlier with increasing temperature in the model, about 5–6 days for every 1 °C temperature increase. Zooplankton peak abundances decreased with increasing temperatures



**Fig. 3** Regression between mean air and lake temperature.  $Y = 0.01x + 0.209$ ;  $P < 0.0001$ ;  $r^2 = 0.79$ .

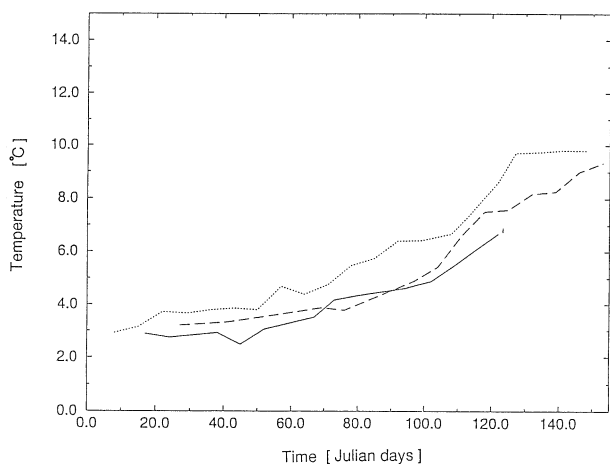
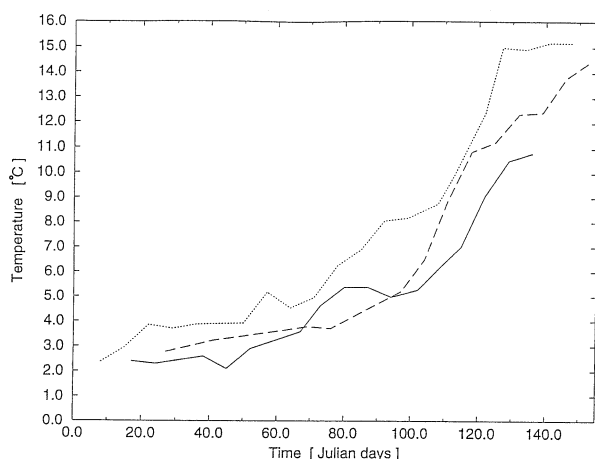


**Fig. 4** Temperature profiles calculated from the ecosystem model.

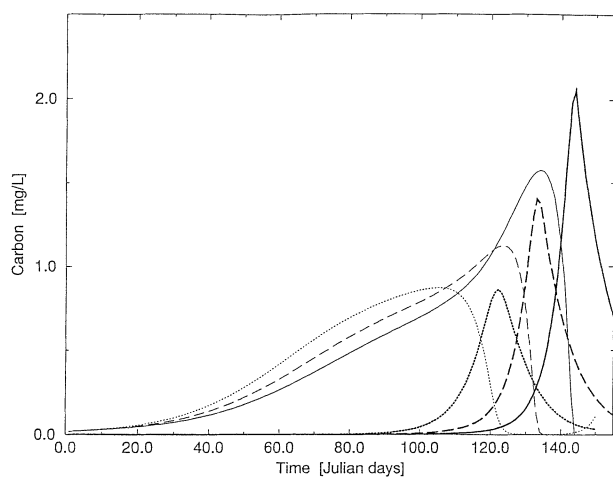
(0.3 mg C L<sup>-1</sup> per 1 °C; Fig. 6). The spring algal maximum decreased (0.1–0.2 mg C L<sup>-1</sup>) with increasing temperature of 1 °C due to earlier zooplankton increase. The sensitivity of the intensity of the spring algal maximum to temperature changes depended also on the temperature itself (0.2 mg C L<sup>-1</sup> between 3 °C and 4 °C and 0.09 mg C L<sup>-1</sup> between 6 °C and 7 °C).

#### Long-term Plußsee data

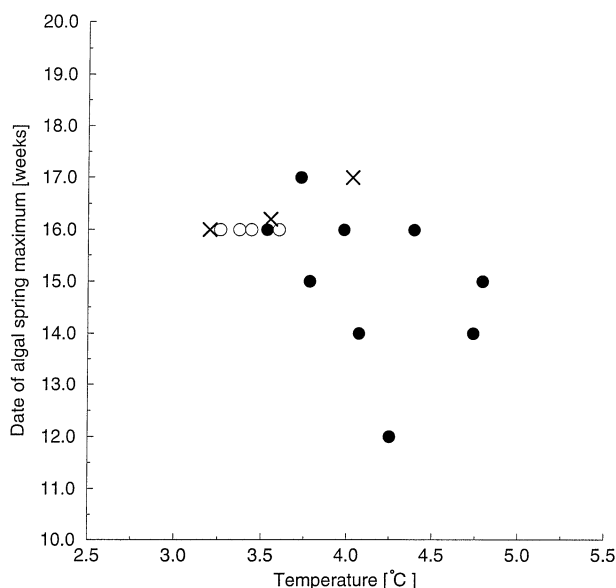
Long-term Plußsee data revealed a negative relationship between temperature and the timing of the spring algal maximum (measured as the Secchi depth minimum,  $P < 0.05$ ;  $r^2 = 0.29$ ; Fig. 7). Hence, the spring algal maximum occurred earlier with increasing temperatures, which is in accordance with the model results. Including the data from the 3 years prior the change in the phytoplankton community decreased the explained variance from 29% to 23% and changed the level of signific-



**Fig. 5** (a) Temperature profiles in Plußsee (average of upper 4 m) for three specific years (1977, 1987, 1990, respectively). (b) Temperature profiles in Plußsee (whole lake) for 3 specific years (1977, 1987, 1990, respectively).



**Fig. 6** Development of phytoplankton (thin lines) and zooplankton (thick lines) over time as model output. Denotation of temperature regimes see Fig. 4.



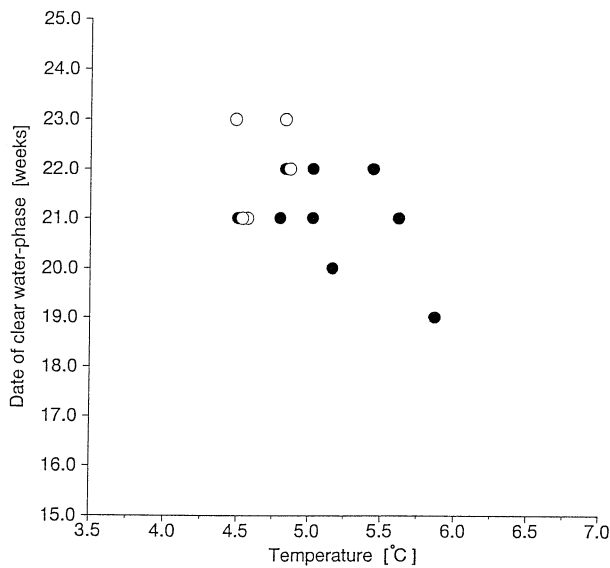
**Fig. 7** Regression between mean lake temperature (2nd–15th week) and date of spring algae maximum in Plußsee. Open circles denote years with ice coverage. Full circles denote years without or only weak ice coverage (less than 3 weeks).  $Y = -1.4x + 20.5$ ;  $P < 0.05$ ;  $r^2 = 0.29$ . Including data from years prior the phytoplankton regime change (crosses) changed the regression towards  $Y = -1.1x + 19.9$ ;  $P = 0.059$ ;  $r^2 = 0.23$ .

ance ( $P = 0.059$ ;  $r^2 = 0.23$ ). In years with intense ice coverage, minimal Secchi depths readings were always recorded in the 16th week.

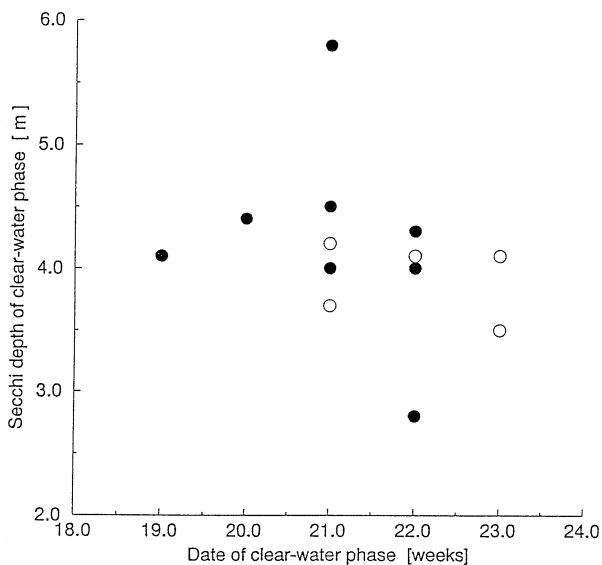
Data confirmed a negative relationship between mean temperature and the timing of the clearwater phase ( $P = 0.07$ ;  $r^2 = 0.25$ ; Fig. 8) as suggested by the model. Overall the clearwater phase happened 1–2 weeks later than the zooplankton maximum in the model. The modelled dependence of the temperature (time shift around 6 days per 1 °C) agreed with observed Plußsee data.

The effect of temperature on maximal zooplankton abundances (intensity of the clearwater phase) is less clear in the observational record. The statistical analysis of the long-term Plußsee data had no significant relationship ( $P = 0.31$ ;  $r^2 = 0.10$ ; Fig. 9).

In contrast, timing and intensity of minimal Secchi disc transparencies had a significant negative regression ( $P < 0.05$ ;  $r^2 = 0.35$ ; Fig. 10). Early spring algal maxima were less pronounced than later ones. The positive relation between temperature and the intensity of the spring algal maximum was even better ( $P = 0.0003$ ;  $r^2 = 0.67$ , not shown). This agrees with our model result, where grazing by zooplankton leads to reduced algal spring maxima with rising temperature regime. However, when including the data from the three years prior to the change in the phytoplankton community, the regression dropped to  $r^2 = 0.15$  ( $P = 0.135$ ).



**Fig. 8** Regression between mean lake temperature (2nd–21st week) and date of clearwater phase in Plußsee. Open circles denote years with ice coverage. Full circles denote years without or only weak ice coverage (less than 3 weeks)  $Y = -1.3x + 27.8$ ;  $P = 0.070$ ;  $r^2 = 0.25$ .

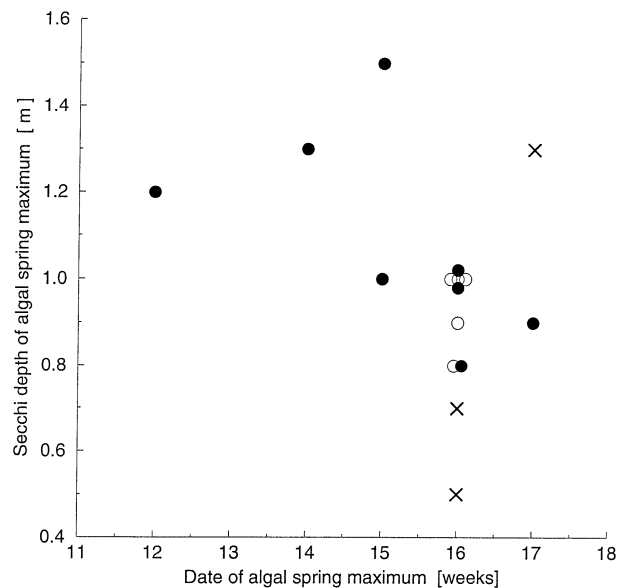


**Fig. 9** Relationship between date of clearwater phase and their intensity. Denotation see Fig. 7.  $Y = 8.1x - 0.18$ ;  $P = 0.307$ ;  $r^2 = 0.10$ .

## Discussion

### *Relations within the climate system*

Strong relations could be demonstrated within the physical environment. Mean air temperatures in Plön were well represented by the large-scale temperature field. They also matched closely with observed temperature means of Adrian *et al.* (1995; 300 km apart). The consist-



**Fig. 10** Regression between date of algal spring maximum and their intensity. Denotation see Fig. 7.  $Y = -0.09x + 2.47$ ;  $P < 0.05$ ;  $r^2 = 0.35$ . Including data from years prior the phytoplankton regime change (crosses) changed the regression towards  $Y = -0.08x + 2.24$ ;  $P = 0.135$ ;  $r^2 = 0.15$ .

ency is probably due to averaging over three to four months which have larger spatial structures in the temperature field (Werner & von Storch 1993). Local mean air and lake temperatures were also linked. Variation in winter and spring air temperatures changed the heat budget of the lake, especially when above 0 °C. Due to greater heat capacity of water, the range of lake temperature changes was much smaller than for the air temperatures. The lake seems to accumulate the atmospheric heat (Adrian *et al.* 1995). Since we calculated the whole lake mean temperature, instead of the upper 4 m as calculated by Adrian *et al.* (1995), we detected variation in lake temperature to a lesser extent depending on air temperature variability. Warmer winter air temperatures above 0 °C affected ice coverage of the lake and thus the mixing regime which then changed from dimictic to warm monomictic. This can have an indirect effect on the relative importance of temperature and wind to determine the date of stratification (Demers & Kalff 1993). A faster temperature rise in spring preceded the beginning of the spring stratification, which can influence the nutrient recycling (Schindler *et al.* 1990; Adrian *et al.* 1995).

### *Spring algal maximum*

The negative relationship of whole lake mean temperature and the timing of spring maxima is in accordance with findings of Adrian *et al.* (1995), who concluded it as a

direct temperature-dependent effect on phytoplankton. However, in years with intense ice cover, minimal Secchi depths in Plußsee were always recorded in the 16th week (with small but detectable differences in temperature among those years). A change of light conditions with the break-up of ice coverage may have triggered the spring algal outburst in those years. The negative relation between the date of the spring algal maximum and its extent represents decreased algae peak abundances with increasing temperature. The model suggests that this might be due to an earlier onset of grazing pressure by zooplankton. However, additional factors which are not considered in the model can have similar influences. The loss of ice coverage during mild winters might have sustained an algal population during winter. Thus, less nutrients might have been available for the actual spring population leading to a decreased algal peak concentration. However, the statistical relationship is weakened from  $r^2 = 0.35$  to  $r^2 = 0.15$  when including the three data points from the years prior the phytoplankton regime change (Hickel 1988) from a subsurface cyanobacterial community towards an epilimnetic spring bloom consisting of diatoms and cryptophytes. In contrast, Jassby *et al.* (1990) found primary production (accompanied with a chlorophyll maximum) diminished after harsh winters (heavy snowfall, late thaw) in Castle Lake. However, several differences exist between the high-mountain Castle Lake and the low-land Plußsee. The algal maximum in Castle Lake is a deep layer maximum (15–25 m depth) which is probably stronger light limited than the epilimnetic spring algal maximum in Plußsee. Flushing out of part of the initial algal community, as proposed for Castle Lake, is probably of no importance in Plußsee due to its different hydrologic condition.

#### Clearwater phase

High Secchi depth readings in spring (clearwater phase) are usually induced by maximal zooplankton abundances in lakes (Lampert & Schober 1978; Lampert *et al.* 1986). Thus, Secchi transparencies at that time are an indirect measure of maximal zooplankton occurrence. The earlier timing of the clearwater phase with increased temperatures is probably due to temperature-controlled zooplankton growth under high algae abundances in spring. This matches well with observations of Kratz *et al.* (1987) who found climate to be a major forcing factor for seasonal timing of several zooplankton species in several lakes in North America. Our empirical evidence of this link is only associated with a statistical significance of  $P = 0.07$ , but we suggest that this level would be increased if sampling would have been done more frequently during that time. In Plußsee the clearwater phase varied by one month contrary to findings of Lampert & Schober

(1978), who found the clearwater phase restricted to a certain week in Lake Constance probably due to the predatory control of daphnids by *Cyclops vicinus* in Lake Constance.

In the model, differences in zooplankton timing under different temperature regimes were roughly correctly determined when comparing to Plußsee data of the clearwater phase, but the overall timing of the modelled zooplankton was earlier. This is probably because the temperature profile used in the model was more similar to that of the epilimnetic temperature than for the whole lake temperature. In addition, features not taken into account in the model, like overwintering of zooplankton and their mortality rate can also affect the timing in the lake and might change with temperature.

Climate (mainly spring environmental temperatures) affect the timing of processes at different trophic levels of the aquatic ecosystem (George & Harris 1985; Durbin & Durbin 1992; White & Roman 1992; Plourde & Runge 1993 for zooplankton; Cushing 1982; Eckmann *et al.* 1988; Hutchings & Myers 1994 for fish recruitment). Relative timings of peak abundances of members of different trophic levels are of importance insofar that they determine the degree of material and energy transfer through the system (match/mismatch of seasonal events). For example, George & Harris (1985) found June temperatures in the North basin of Lake Windermere negatively correlated with the summer zooplankton biomass in the lake. Due to weather conditions which determined the timing of stratification and thus the growth of edible algae, the zooplankton matched or mismatched with its preferred food. In Narraganset Bay, Durbin & Durbin (1992) found a shift in timing of maturation and development of *Acartia hudsonica* in spring in relation to a 2 °C increase in temperature. This three week shifting altered the grazing intensity and therefore the coupling between primary and secondary production in spring. However, our temporal shifts are only half of that observed for these copepods. Distances between phyto- and zooplankton peak abundances did not vary so much, but were more pronounced at higher temperatures (17 instead of 10 days). This might have contributed to lower zooplankton peak abundances with increased temperatures in the model.

Contrary to our findings, Adrian *et al.* (1995) recorded a reduction in maximal Secchi depths in Heiligensee since 1988. The difference could be due to changes in the spring algal composition in favour of cyanobacteria in the hypertrophic Heiligensee. However, a reverse trend of cyanobacteria bloom disappearance happened in 1977 in Plußsee (Hickel 1988), and no clearwater phase could be determined from those years prior to the change in Plußsee. During spring 1988 and 1990 Plußsee was dominated by diatoms and cryptophytes (Makulla &

Sommer 1993; Sommer 1993). Under this high food quality condition an elevated clearwater phase might be attributed to higher zooplankton filtering rates and therefore grazing at increased temperatures. Also the model showed lower zooplankton peak abundances with increasing temperature, but differences in phytoplankton concentrations at that time could not be resolved. For the long-term Plußsee data the dependence of lake temperature and intensity of clearwater phase was only vague. Also Kratz *et al.* (1987) who found abundances and (vertical) distribution of most zooplankton species more dependent on the lake characteristics than on climate. It seems that species specific shifts are more important when considering the extent of seasonal events. Unfortunately, very little is known about the impact of climate or even temperature on processes like competition (Sandercock 1967 for abundances of two copepod species; Van den Bosch & Ringelberg 1985 for birthrates of two rotifer species).

Finally, we combined our various links, as a 'back of an envelope' calculation to roughly estimate possible implications of anthropogenic climate change for succession events in Plußsee. We used monthly mean air surface temperatures from Cubasch *et al.* (1995) who examined the output of numerical experiments conducted with enhanced resolution in a 91 grid point box (each grid point about 250 km apart) covering Northern Europe. We assume that averaging over this area is a reasonable guess for the local air temperature, because our calculated first EOF (Fig. 1) has a uniform structure. Data corresponding to present day CO<sub>2</sub> concentrations, 2 × CO<sub>2</sub> (in 2035) and 3 × CO<sub>2</sub> (in 2085) were analysed for a model run performed with continuously increasing atmospheric CO<sub>2</sub> concentration. The simulated temperature changes in February through April were 0.5°–1.5° in 2035 with doubling CO<sub>2</sub> and 2°–3° with tripling CO<sub>2</sub> concentrations. With these rough estimates we used our regressions from air to lake temperature and from lake temperature to timing of algal spring maximum and clearwater phase. In that manner we estimated that both events might be staged 1–4 days earlier at the time of CO<sub>2</sub> doubling and 2–8 days at the time of tripling CO<sub>2</sub>. Within this range, the temperature sensitivity of the time of the spring-algal maximum is slightly, but not significantly, greater than that of the clearwater phase. Natural variability was too large to detect differences between both timings. These numbers were small when compared to natural variability, for both the temperature increase and consequently the timing of successional events. However, there are a number of caveats, thus the exercise should be considered with reservations. First, our statistical model calculations reveal regression steps such that a considerable uncertainty is associated with the final number. Unfortunately we cannot specify this uncertainty

numerically because of the limited extent of the dataset. Second, there were variances represented by the regressions between lake temperature and the timing of the seasonal events. Third, as revealed by comparison with other lakes (Goldman *et al.* 1989; Jassby *et al.* 1990), even climatic dependence of seasonal events is influenced by the characteristics of the lake. Furthermore, these estimations were based on the assumption that temperature is the only relevant abiotic factor and that no changes (species specific shifts) within the biotic system occur. However, these kind of changes have been observed (Hickel 1988; Adrian *et al.* 1995), and might even be the major effect if the climatic condition changes.

## Conclusions

Local lake and air temperatures could be related to the large-scale temperature field, when considering averaged data over months. This climate information of coarse spatial and temporal resolution could be statistically related to features in the lake. Thus the gap to the spatial resolution of global climate models could be bridged.

Variation in timing of seasonal events in relation to climate variability could be detected with a comprehensive and simple measure like Secchi transparency. The relation is not necessarily established by a direct link. The ecosystem model helped to understand phyto- and zooplankton interactions under different temperature regimes. For the extent of seasonal events, species specific characteristics seemed to be more important and thus cannot be resolved from an overall measure.

Although we concentrated on the beginning of the year when the direct control from abiotic factors is more important than during summer (Sommer *et al.* 1986), events during summer and fall might also vary in relation to climatic events via thermocline alteration (Sommer 1993). This is an area for further investigation.

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**Appendix 1**

Symbols used to denote state variables

<i>Symbol</i>	<i>Variable</i>
$t$	time [day]
$\Theta$	temperature
$Z$	mixing depth
$f$	geographical latitude [°N]
$L$	global radiation
$A$	attenuation of the lake water
$I_a$	ambient light at the algae
$\mu$	phytoplankton growth rate
$k_1$	half saturating concentration for algae growth
$v_s$	sinking velocity of an ideal algae
$\varepsilon$	phytoplankton loss due to sinking
$N_a$	phytoplankton concentration [mg C*L <sup>-1</sup> ]
$\rho$	phytoplankton loss due to zooplankton grazing
$K$	upper carrying capacity for algae
$\eta$	zooplankton growth rate
$\eta_{\max}$	maximal zooplankton growth rates
$q_0$	threshold concentration for zooplankton growth
$N_z$	zooplankton concentration [mg CL <sup>-1</sup> ]

temperature evolution:

$$\Theta = -\Theta_{\max} * \tanh((t-120)/15)(1)$$

mixing-depth evolution:

$$Z = -10 + 10 * (\tanh((t-120)/20)-1) (2)$$

light conditions in the atmosphere determined from global radiation:

$$L = [2 * \cos(-\tan(\delta)*\tan(\phi*2\pi/360))]/7461.6(3)$$

light condition in water:

$$I_a = L * (1 - e^{-AZ}) / -Z$$

Phytoplankton growth rate is determined by a monod kinetic:

$$\mu = (\mu_{\max} * I_a) / (I_a + k_1)(4)$$

Phytoplankton sinking loss:

$$\varepsilon = N_a * (v_s / (-Z))(5)$$

Phytoplankton mortality due to zooplankton grazing:

$$\rho = 1.6 * (r_{\max} * (1 - e^{-2*N_a})) * 0.16 * e^{0.1*\Theta}(6)$$

Phytoplankton concentration:

$$dN_a/dt = \mu * (K - N_a / K) * N_a - \rho * N_z - \varepsilon(7)$$

Zooplankton growth rates were determined with an logistic fit:

$$\eta = (\eta_{\max} * (1 - e^{-2*N_a - q})) * 0.16 * e^{0.1*\Theta}(8)$$

Zooplankton concentration:

$$dN_z/dt = \eta * N_z(9)$$