

Phytoplankton response to climate warming modified by trophic state

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Abstract

We investigated the combined effect of reduced phosphorus supply and warmer winter and spring conditions on the diatom spring bloom of a shallow lake. Simulations with a simple dynamic model indicated that reduced ice cover and increasing water temperatures resulted in a more intense and earlier bloom independently of phosphorus concentrations. However, whereas the collapse of the bloom was caused by silicate limitation under high phosphorus supply, it was caused by *Daphnia* grazing under reduced phosphorus supply. This switch from a bottom-up to a top-down driven collapse of the diatom spring bloom explains why, despite similarly mild winters, the bloom was observed earlier under high than under reduced phosphorus supply in the lake studied. Thus, an assessment of possible changes in nutrient loading is crucial when anticipating how phytoplankton could evolve under future climate warming.

Increasing anthropogenic pressure requires a better understanding of how ecosystems react to multiple environmental stressors. During the last decades many freshwater systems were subject to both a changing climate and changes in trophic state due to reduced nutrient supply (Jeppesen et al. 2005). Yet, most analyses of long-term data of these systems focused either on the effect of climate change or on the effect of changes in trophic state. Few studies have tried to disentangle the combined effect of rising temperatures and changing nutrient supply on freshwater ecosystems (e.g., Horn 2003; Elliott et al. 2006).

Abiotic factors, influenced by climatic conditions and trophic state, are the primary drivers of phytoplankton succession in spring (Sommer et al. 1986). In lakes of the temperate zone, the phytoplankton spring bloom is pre-

dominantly initiated by increasing light availability (Sommer 1994), which is directly determined by solar radiation and day length and also indirectly depends on specific lake features such as water transparency and depth. In deep lakes, phytoplankton starts growing once strong mixing ceases and phytoplankton is no longer constantly transported out of the euphotic zone (Peeters et al. 2007). In many shallow lakes, the phytoplankton spring bloom is initiated once the ice cover melts, inducing a change in the underwater regime of light and turbulence (Adrian et al. 1999; Weyhenmeyer et al. 1999). With the exception of very nutrient-rich lakes where grazer-resistant algae dominate early in the year, the phytoplankton spring bloom then collapses leading to a biomass minimum in late spring/early summer called the clear water phase (Sommer et al. 1986). The collapse of the phytoplankton spring bloom is attributed to different environmental factors. First, many studies have shown that zooplankton grazing rates (mainly by *Daphnia*) often exceed algal production rates in early summer, thus producing the clear water phase (Lampert et al. 1986). Second, nutrient limitation (potentially combined with increasing sinking losses) can induce a collapse of the phytoplankton bloom before grazing becomes important (Lund 1950; Smayda 1971). And third, a sharp increase in sinking losses due to the onset of stratification can also cause the collapse of the algal bloom if stable summer stratification develops in moderately deep lakes (Winder and Schindler 2004b).

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In lakes across the northern hemisphere, climate warming has induced forward shifts in the timing of the phytoplankton spring maximum and the clear water phase (Gerten and Adrian 2000; Straile 2002). On the one hand, these phenology shifts have been attributed to a direct effect of increased water temperatures on zooplankton grazers (Straile and Adrian 2000) and to a lesser extent to a direct effect of increased water temperatures on phytoplankton growth (Adrian et al. 1999). On the other hand, warming more indirectly affects the phytoplankton spring bloom through its effect on ice cover and the lake mixing regime (Adrian et al. 1999; Winder and Schindler 2004b; Peeters et al. 2007). Furthermore, it is a classical result from eutrophication studies that in many lakes annual (or seasonal) phytoplankton biomass is correlated to annual (seasonal) phosphorus loading (Vollenweider and Kerekes 1982; Jeppesen et al. 2005). In addition to the effect of nutrient availability on phytoplankton productivity, trophic state is also known to affect the phytoplankton succession patterns, including the timing of the phytoplankton spring bloom (Sommer 1994).

Disentangling the effect of climate and nutrients on phytoplankton growth has proved challenging in the past. In a study of the effect of re-oligotrophication on the phytoplankton growth in a drinking water reservoir, Horn (2003) found that phytoplankton biomass did not decrease despite falling nutrient concentrations and hypothesized that this was because of a change in spring overturn duration dependent on weather conditions. In a modeling study, Elliott et al. (2006) showed that the phytoplankton spring peak always occurred earlier under higher temperatures, but it was species-specific as to whether increasing nutrient concentrations delayed the peak or advanced it further. When Scheffer et al. (2001) stated that the probability of a clear water phase increases with the temperature of a lake, a controversy arose as to whether they had sufficiently accounted for changes in the trophic state (and management regimes) of the lakes studied (Jeppesen et al. 2003; Scheffer et al. 2003; Van Donk et al. 2003).

The shallow lake studied here, Müggelsee, provides an opportunity to gain a better understanding of the combined effect of climate warming and changes in trophic state on the phytoplankton spring development. The lake experienced a reduction of more than 50% in both total phosphorus and total nitrogen loading from a hypertrophic period, 1979–1990, to a eutrophic period, 1997–2003 (Köhler et al. 2005). In spring, phytoplankton is dominated by diatoms in this lake, and phosphorus and silicate are the potentially limiting factors, whereas nitrogen limitation most likely only plays a role in the summer (Köhler et al. 2000; Köhler et al. 2005). Climate-induced changes of physical lake features and resulting phenology shifts in the plankton community are well documented for this lake (Adrian et al. 1999; Straile and Adrian 2000). In particular, a forward shift of the phytoplankton spring bloom of about 1 month was found concurrently with earlier ice break-up dates from 1979–1987 to 1988–2003 (Gerten and Adrian 2000; Adrian et al. 2006). However, although ice break-up dates were generally a good predictor of the timing of the

phytoplankton spring bloom, the bloom occurred relatively late in recent mild years with early ice-out.

In this study, we asked whether the climate signal detected in the phytoplankton time series was altered by decreasing phosphorus loading to the lake. Specifically, we investigated whether the relative delay of the phytoplankton spring bloom in recent years could be attributed to the observed change in trophic state. Based on long-term data (1979–2005) of physical, chemical, and biological variables, we constructed a deterministic model that simulates the dynamics of diatom biovolume, the potentially limiting nutrients (silicate and phosphorus), and *Daphnia* grazing in winter and spring. Using this model, we performed simulation experiments to explore how increased water temperatures and reduced ice cover affected the timing and intensity of the diatom spring bloom under conditions of high and reduced phosphorus loading (hypertrophic and eutrophic phase). These model simulations suggested a switch in bloom collapse mechanisms, rendering the phytoplankton response to climate warming strongly dependent on trophic state.

Methods

Study site—Müggelsee is a shallow, polymictic lake situated in the southeast of Berlin (52°26'N, 13°39'E). It spans an area of 7.3 km² with a mean depth of 4.9 m and a maximum depth of 7.9 m. The lake is moderately flushed by the river Spree with a retention time of approximately 6–8 weeks (Köhler et al. 2005). The climate at this lake is governed by maritime and continental influences. Winter climate shows a high degree of inter-annual variability, with the monthly mean air temperature in January, the coldest month, varying within the approximate range of –7°C to +5°C (Adrian and Hintze 2000). Ice-cover duration varied between 0 days and 125 days in 1979–2005 with an average ice cover of 43 ± 33 SD days. Additional information on physical and limnological characteristics of Müggelsee is documented in Driescher et al. (1993).

Data basis—From 1979 to 2005, water samples for nutrient and plankton analysis were taken weekly during the growing season and biweekly during winter. A detailed description of the sampling methodologies and sample processing is given in Gerten and Adrian (2000). Time series of the aggregated biovolume of total phytoplankton and aggregated biovolume of diatoms (Bacillariophyceae) were used in this study. For model development, we focused on diatoms because these comprised about 81% of the total phytoplankton biovolume in Müggelsee during the spring peak (Fig. 1A). As grazers, only daphnids (mainly *Daphnia galeata*, *Daphnia hyalina*, *Daphnia cucullata*, and their hybrids) were considered in the model; however, other zooplankton groups (ciliates, cyclopoid, and calanoid copepods) were accounted for in a supplementary screening of factors that potentially influence the phenology of diatoms. Long-term records of physical factors (water temperature, ice cover, global radiation, and light extinction) and weekly measurements of nutrients

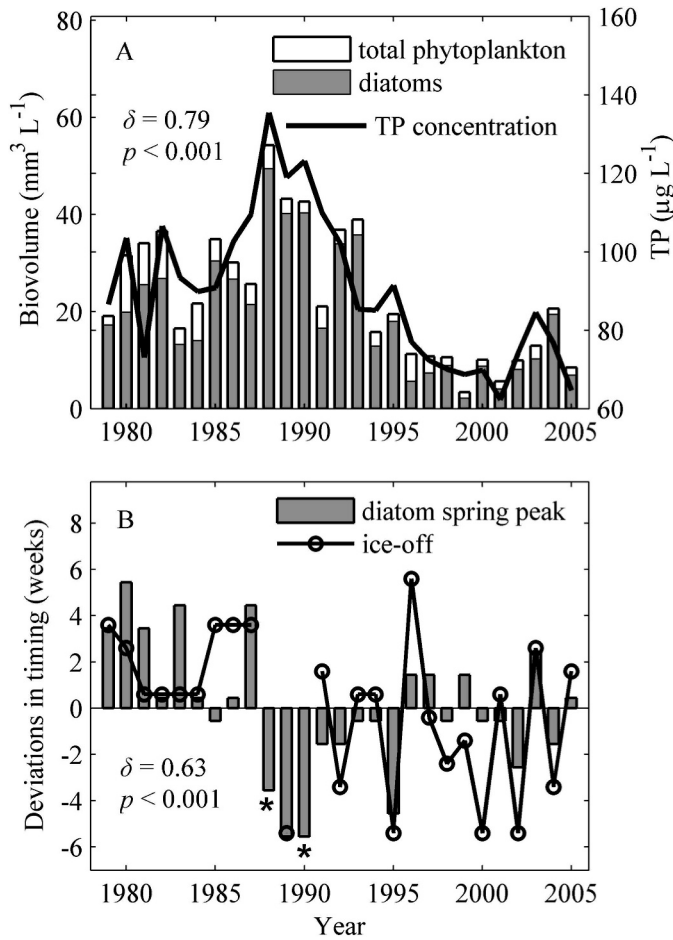


Fig. 1. Inter-annual variability of the (A) magnitude and (B) timing of the diatom spring peak in Müggelsee. (A) Biovolumes ($\text{mm}^3 \text{L}^{-1}$) of diatoms (grey bars) and total phytoplankton (open bars) in the week of the spring peak and mean total phosphorus concentrations ($\mu\text{g L}^{-1}$) until the end of the bloom (solid line). (B) Timing (week) of the diatom spring peak (grey bars) and ice-out dates (open circles) shown as departures from the long-term mean (1979–2005). Asterisks mark years with missing ice cover. Spearman's δ is given for the correlations between the magnitude of the diatom spring peak and mean total phosphorus concentrations (A) and the timing of the diatom spring peak and the timing of ice-out (B).

(total phosphorus concentration [TP] and dissolved silicate concentration [DSi]) were used as forcing variables in the model or for the purpose of parameter estimation (cf. Table 1). Water temperatures were hourly means (8–9 h) recorded daily near the lake surface at 0.3 m depth (from September 2002 onward at 1–2 m depth during winter and at 0.5 m during spring and summer). Ice cover was assessed daily, categorizing whether the lake was fully (>80% of lake surface) or partially covered with ice. Long-term records of mean daily global radiation were provided by Deutscher Wetterdienst for the station in Potsdam ($52^\circ 04' \text{N}$, $13^\circ 06' \text{E}$) for 1979–2002; records from a measurement station at the shore of Müggelsee were used for 2003–2005. Incident photosynthetically available radiation was considered to be 43% of global radiation. This was based on the assumption that, on average, 7% of global radiation

is reflected at the water surface (estimated from measurements at Müggelsee in spring 2002, 2004, 2005, $n = 262$) and that 46% of global radiation is photosynthetically available (Köhler et al. 2000). Light extinction coefficients were estimated based on light measurement in the water column (0–5 m) during 1993–2003, and transmittance through ice was assessed using measurements in the winter of 1995/1996.

Definition of phenology events—Ice-out date was defined as the week (or day of the year for model analysis) when the lake was free of all ice in spring. The timing of the diatom spring bloom was defined as the week (day of the year) when maximal biovolume of diatoms was observed after ice-out in spring. In years when several local maxima were observed (occurring in 6 out of 27 years) the timing of the highest peak was considered. The maximal biovolume was considered as the magnitude of the bloom. Also, we defined the end of the bloom as the week (day of the year) when minimal diatom biovolume was observed after the spring peak. This coincided with the clear water phase (defined as the time of the highest Secchi depth in late spring) during most years. We defined the intensity of the bloom as the mean biovolume from the beginning of the year until the end of the bloom. The timing of the *Daphnia* spring peak was defined as the first clearly distinguishable maximum in spring (with densities $\geq 68 \text{ ind L}^{-1}$).

Model core—The spring diatom phenology model used here builds upon a phytoplankton growth model for a closed system proposed by Diehl et al. (2005) and modified according to an approach used by Klausmeier et al. (2004). It is a pointlike model based on the assumption that the whole water column is well mixed and phytoplankton is homogeneously distributed in the water column, which is realistic for shallow, polymictic Müggelsee in spring. Our model is constructed to simulate diatom dynamics in winter and spring only (January–mid-June). The core of the model consists of four differential equations (Eqs. 1–4) describing changes in diatom biovolume and the dynamics of the potentially limiting nutrients phosphorus and silicate (definitions and units of state variables, parameters, and forcing variables are summarized in Table 1).

$$\frac{dA}{dt} = \left(\mu(T, I, Q, Si) - \left(\frac{v}{z} + F_D(T) c_D D \right) \right) A \quad (1)$$

$$\frac{dQ}{dt} = \rho_{\max} F_A(T) \frac{P}{H_P + P} - \mu(T, I, Q, Si) Q \quad (2)$$

$$\frac{dP}{dt} = r_P (P_{tot} - P - QA) - \rho_{\max} F_A(T) \frac{P}{H_P + P} A \quad (3)$$

$$\frac{dSi}{dt} = r_{Si} (Si_{tot} - Si - Q_{Si} A) - A Q_{Si} \mu(T, I, Q, Si) \quad (4)$$

Table 1. State variables, parameters, and forcing variables for the diatom phenology model. Values in brackets are parameter intervals used during calibration (if available from the literature as indicated); the conversion factor for carbon content of algal biovolume used was $0.12 \text{ mg C mm}^{-3}$ (Rocha and Duncan 1985).

Symbol	Definition	Unit	Default value	Source
A	Diatom biovolume	$\text{mm}^3 \text{ L}^{-1}$	—	—
μ_{max}	Maximum per capita growth rate	day^{-1}	$0.94^\dagger (0.7-2.4)$	calibrated (Andersen 1997)
z	Mixing depth = mean lake depth	m	4.9	Driescher et al. 1993
I_{ce}^*	Ice cover	dimensionless	—	—
P	Concentration of dissolved phosphorus available to diatoms	$\mu\text{g L}^{-1}$	—	—
H_P	Half-saturation constant of phosphorus uptake	$\mu\text{g L}^{-1}$	$60^\dagger (5-60)$	calibrated (Bowie et al. 1985)
Q	Phosphorus cell quota (P : biovolume)	$\mu\text{g P mm}^{-3}$	—	—
Q_{max}	Maximum phosphorus cell quota	$\mu\text{g P mm}^{-3}$	$6.7^\dagger (1-7.5)$	calibrated (Sommer 1994; Diehl et al. 2005; Andersen 1997)
Q_{min}	Minimum phosphorus cell quota	$\mu\text{g P mm}^{-3}$	0.5	Köhler et al. 2000; Diehl et al. 2005
P_{max}	Maximum phosphorus uptake rate	$\mu\text{g P mm}^{-3} \text{ day}^{-1}$	$4.9^\dagger (0.2-12)$	calibrated (Arhonditsis and Brett 2005; Bowie et al. 1985)
r_P	Recycling rate of detrital phosphorus	day^{-1}	$0.38^\dagger (0.05-0.5)$	calibrated
P_{tot}	Maximal concentration of phosphorus	$\mu\text{g L}^{-1}$	—	independent estimation (cf. Methods)
Si	Concentration of dissolved silicate	mg L^{-1}	—	—
H_{Si}	Half-saturation constant of silicate limited algal growth	mg L^{-1}	$0.035^\dagger (0.03-0.5)$	calibrated (Sommer 1994)
Q_{Si}	Silicate cell quota (Si : biovolume)	mg Si mm^{-3}	$0.047^\dagger (0.03-0.1)$	calibrated (Arhonditsis and Brett 2005; Sommer 1989)
r_{Si}	Recycling rate of sedimented silicate	day^{-1}	0.01	Lampert and Sommer 1999
Si_{tot}	Maximal concentration of silicate	mg L^{-1}	—	independent estimation (cf. Methods)
I_0^*	Incident light intensity : 43% of daily global radiation	W m^{-2}	—	—
k_{ice}	Transmittance through ice	dimensionless	0.2	independent estimation (data of 1996)
H_I	Half-saturation constant of light limited algal growth	W m^{-2}	$3.2^\dagger (0.2-8)$	calibrated (Bowie et al. 1985)
K_{bg}	Background light extinction coefficient in the water column	m^{-1}	0.89	independent estimation (cf. Methods)
k_A	Biomass specific light extinction coefficient	$\text{L mm}^{-3} \text{ m}^{-1}$	0.07	independent estimation (cf. Methods)
v	Sinking velocity of diatoms	m day^{-1}	0.65	Schellenberger et al. 1983
T^*	Water surface temperature	$^\circ\text{C}$	20	—
T_{ref}	Reference temperature	$^\circ\text{C}$	20	—
T_{opt}	Optimal temperature for diatom growth kinetics	$^\circ\text{C}$	20	Arhonditsis and Brett 2005
kTA	Temperature constant for diatom growth kinetics	$^\circ\text{C}^{-2}$	0.004	Arhonditsis and Brett 2005
D	Density of <i>Daphnia</i>	ind L^{-1}	—	—
M	Density-dependent mortality of <i>Daphnia</i>	day^{-1}	—	—
c_D	Clearance rate of <i>Daphnia</i>	$\text{L ind}^{-1} \text{ day}^{-1}$	0.005	Wetzel 2001 and references cited therein
f	Fecundity parameter of <i>Daphnia</i> (surviving eggs/fertile individuals)	dimensionless	$4.6 (0.1-9)$	calibrated
τ	Relaxation time of density-dependent mortality of <i>Daphnia</i>	day	$1 (1-45)$	calibrated
m_D	Mortality parameter of <i>Daphnia</i>	$(\text{ind L}^{-1})^{-dd} \text{ day}^{-1}$	$0.52 (0.1-1)$	calibrated
dd	Exponent for density-dependent mortality of <i>Daphnia</i>	dimensionless	$0.23 (0.1-1)$	calibrated

* Forcing variables.

† Parameters varied in the robustness test (cf. Methods).

The biovolume concentration of diatoms A ($\text{mm}^3 \text{L}^{-1}$) increases through temperature, light, and nutrient-dependent growth (integrating all internal processes such as primary production, respiration, exudation, and lysis) and decreases through sedimentation and temperature-dependent *Daphnia* grazing. Sedimentation loss rate was calculated as the ratio of sinking velocity v (m day^{-1}) to mixing depth z (m). For simplicity, we assumed that filtration rates are independent of prey density (type I functional response) so that *Daphnia* grazing loss rate is the product of clearance rate c_D ($\text{L ind}^{-1} \text{day}^{-1}$) and *Daphnia* density D (ind L^{-1}). The temperature dependence of grazing and other *Daphnia*-related process rates (*see below*) was described by the Q_{10} -rule

$$F_D(T) = 2^{\left(\frac{T - T_{ref}}{10 \cdot C}\right)} \quad (5)$$

where T ($^{\circ}\text{C}$) is the seasonally changing water temperature, and T_{ref} ($^{\circ}\text{C}$) is the reference temperature. This is an experimentally backed approach (Norberg and DeAngelis 1997) commonly used in minimal models of phytoplankton–zooplankton interaction (Scheffer et al. 2001; Peters et al. 2007). The algal growth rate, which is dependent on water temperature, light intensity I (W m^{-2}), silicate concentration Si (mg L^{-1}), and phosphorus cell quota Q ($\mu\text{g P mm}^{-3}$), was calculated as

$$\mu(T, I, Q, Si) = \mu_{max} F_A(T) L_1(T, I) \min(L_2(Si), L_3(Q)) \quad (6)$$

where μ_{max} (day^{-1}) is the maximum specific growth rate; L_1 , L_2 , and L_3 are limitation functions described below; and $F_A(T)$ is the temperature function used for diatom growth constants and process rates. For the latter we adopted the optimum curve suggested by Arhonditsis and Brett (2005)

$$F_A(T) = \exp\left(-kT_A(T - T_{opt})^2\right) \quad (7)$$

where kT_A ($^{\circ}\text{C}^{-2}$) describes the strength of the temperature effect, and T_{opt} ($^{\circ}\text{C}$) is the optimal temperature for diatom growth processes. Co-limitation of several resources was accounted for by using Liebig's minimum function for phosphorus and silicate that are considered strictly essential resources (Tilman 1982). Light was assumed to be an interactive essential resource (Rhee and Gotham 1981; Post et al. 1985), and therefore, a multiplicative approach was adopted. Extinction was calculated according to the Lambert–Beer law including self-shading of algae. Based on this, mean underwater light intensity I (W m^{-2}) was determined by integrating over mixing depth

$$\begin{aligned} I &= \frac{1}{z} \int_0^z I_0 \exp\left(- (K_{bg} + k_A A) s\right) ds \\ &= \frac{I_0 (1 - \exp\left(- (K_{bg} + k_A A) z\right))}{(K_{bg} + k_A A) z} \end{aligned} \quad (8)$$

where K_{bg} (m^{-1}) is the background extinction coefficient, and k_A ($\text{L mm}^{-3} \text{m}^{-1}$) is the diatom biovolume specific extinction coefficient. The incident light I_0 (W m^{-2}) was reduced to $k_{ice} I_0$ when the lake was at least partially ice-

covered. Light limitation of diatom growth was modeled using a Monod approach

$$L_1(T, I) = \frac{I}{F_A(T) H_I + I} \quad (9)$$

where H_I (W m^{-2}) is the half-saturation constant for light-limited growth, which is assumed to change with temperature. This temperature dependency of H_I assures that strongly light-limited growth is temperature independent (the initial slope of the hyperbolic curve is constant), as suggested by empirical studies of the interaction of light and temperature on algal growth (Post et al. 1985). We checked that this affected the growth in colder and warmer years similarly and, thus, was not an important control for the differences between colder and warmer years. Because silicate is not stored by phytoplankton, we assumed a constant silicate cell quota Q_{Si} (mg Si mm^{-3}) and also modeled the diatom growth dependency on silicate availability with a Monod equation (Sommer 1994)

$$L_2(Si) = \frac{Si}{H_{Si} + Si} \quad (10)$$

where H_{Si} (mg L^{-1}) is the half-saturation constant for silicate-limited growth. In contrast, growth dependency on a variable phosphorus cell quota (Q) was accounted for by using a Droop-model approach (Droop 1983), modified as suggested by Wernicke and Nicklisch (1986):

$$L_3(Q) = \left(1 - \exp\left(-(\ln 2) \left(\frac{Q}{Q_{min}} - 1\right)\right)\right) \quad (11)$$

Here, growth is increasingly limited by phosphorus shortage [$L_3(Q)$ approaches 0] when the cell quota Q approaches the minimum cell quota Q_{min} , whereas phosphorus limitation decreases as Q increases [$L_3(Q)$ approaches 1]. The phosphorus cell quota increases through phosphorus uptake and decreases through algal growth (Eq. 2). To model the relationship between dissolved phosphorus available to diatoms P ($\mu\text{g L}^{-1}$) and uptake rate, we applied Michaelis–Menten kinetics, where ρ_{max} ($\mu\text{g P mm}^{-3} \text{day}^{-1}$) is the maximal phosphorus uptake rate, and H_P ($\mu\text{g L}^{-1}$) is the half-saturation constant for phosphorus uptake (Eqs. 2 and 3).

Phenomenological approach to nutrient dynamics—The concentration of dissolved phosphorus available to diatoms increases through recycling of detrital phosphorus with a recycling rate of r_P (day^{-1}) and decreases through phosphorus uptake (Eq. 3). Instead of explicitly considering the processes that lead to the recycling of nutrients, such as the remineralization of phosphorus trapped in sedimented algae and the cycling of phosphorus through grazing, we chose a phenomenological approach and considered a closed system with a maximal phosphorus concentration of P_{tot} ($\mu\text{g L}^{-1}$). We neglected all phosphorus potentially stored in grazers, so that the pool of recyclable phosphorus could be calculated as the phosphorus, which was neither dissolved in the water column nor included in algae ($P_{tot} - P - QA$). To estimate the

maximal phosphorus concentration potentially available to diatoms (P_{tot}), we used an empirical relationship based on diatom and phosphorus data measured during winter and spring 1979–2005. In fact, the annual mean diatom biovolume between the beginning of the year and the end of the bloom (A_{bloom}) and the annual mean total phosphorus concentration during the same period (TP_{bloom}) showed a significant linear relationship:

$$A_{bloom} = 0.14 TP_{bloom} - 7.37 \quad (12)$$

$$(n=27, R^2=0.64, p < 0.001)$$

We then assumed that a fixed amount of phosphorus (given by the interception of the regression line with x-axis $TP^* = 52 \mu\text{g L}^{-1}$) was locked in other compartments (such as bacteria, other phytoplankton species, zooplankton, and phosphorus bound to iron or calcite) and not available to diatoms. Thus, we calculated the maximal phosphorus concentration (P_{tot}) available to diatoms each year as the difference between TP_{bloom} and TP^* .

In a similar approach, dissolved silicate was assumed to increase through the recycling of sedimented silicate with a recycling rate of r_{Si} (day^{-1}) and to decrease through growth of diatoms with a fixed silicate cell quota Q_{Si} (Eq. 4). The pool of recyclable silicate was calculated analogous to the pool of recyclable phosphate ($Si_{tot} - Si - Q_{Si}A$), with the difference that the maximal silicate concentration (Si_{tot}) in the model was estimated as the maximal concentration of DSi observed in Müggelsee for each year.

The Daphnia sub-model—Several studies have found that the development of the *Daphnia* biomass in spring is driven primarily by temperature and relatively independent of food availability (Gerten and Adrian 2000; Straile and Adrian 2000; Benndorf et al. 2001). When food becomes limiting in late spring and early summer other algal groups besides diatoms (mainly Cryptophyceae and Chlorophyceae) contribute to *Daphnia* food in Müggelsee. We, therefore, did not couple *Daphnia* to simulated diatom biovolume and included possible food limitation of *Daphnia* later in the season only implicitly through density-dependent mortality. (In fact, the phenomenological approach presented here resulted in a better model performance than a classical predator–prey approach, with *Daphnia* coupled to diatoms.) Density-dependent mortality M (day^{-1}) was simulated using a general formulation adopted from Tirok and Gaedke (2007)

$$\frac{dM}{dt} = \frac{1}{\tau} (m_D D^{dd} - M) \quad (13)$$

where m_D ($(\text{ind L}^{-1})^{-dd} \text{day}^{-1}$) and dd (dimensionless) modulate the strength of the density-dependent mortality and τ (day) corresponds to a relaxation time. Reproduction was calculated as a function of temperature-dependent egg development time $dev(T)$ (day) based on the empirical relationship given by Bottrell et al. (1976):

$$dev(T) = \exp\left(3.3956 + 0.2193 \ln(T) - 0.3414(\ln(T))^2\right) \quad (14)$$

Using a fecundity parameter f (dimensionless), which roughly combines the proportion of reproductively active individuals in the population with the number of eggs per individual, the rate of change in the *Daphnia* population density D (ind L^{-1}) was then calculated following Eq. 15

$$\frac{dD}{dt} = \left(\frac{f}{dev(T)} - F_D(T)M\right)D \quad (15)$$

where $F_D(T)$ corresponds to the Q_{10} rule (see Eq. 5).

Model initialization—Because our model did not enable simulation of the whole annual cycle, it had to be initiated each year. Initial values for diatom biovolume concentration A_0 were the mean of the last observation in the previous year and the first observation in the current year. The phosphorus cell quota Q was initially set to the maximal cell quota Q_{max} . The initial concentration of dissolved phosphorus available to diatoms P_0 (dissolved silicate Si_0) was calculated as the difference between the maximal phosphorus (silicate) concentration P_{tot} (Si_{tot}) and phosphorus (silicate) initially stored in diatoms $A_0 Q_{max}$ ($A_0 Q_{Si}$). Initial values for *Daphnia* densities D_0 corresponded to the first observations of each year, and density-dependent mortality M was set to the steady-state condition $m_D D_0^{dd}$.

Parameter calibration, model validation, and robustness against changes in parameters—Part of the parameter values were independently estimated from the data or directly taken from the literature (as indicated in Table 1). The other parameters (four parameters of the *Daphnia* sub-model and eight parameters of the core model describing the algal–nutrient dynamics) were calibrated, if possible based on biologically plausible intervals as documented in the literature (cf. Table 1). For this purpose, we split the data set into two sub-periods: 1979–1992 for calibration and 1993–2005 for validation. We used a genetic algorithm (adopted from Tietjen and Huth 2006) to efficiently search the parameter space and to find the parameter set that optimizes the fit between the model and the data (for details on the calibration procedure see Web Appendix 1: http://www.aslo.org/lo/toc/vol_53/issue_1/0001a1.pdf).

For model validation we assessed model performance as measured by Willmott's (1982) index of agreement (IoA). It describes the modeling quality with respect to the variance and the mean (\bar{O}) of the observations. $IoA = 0$ indicates complete disagreement between predicted (P_i) and observed values (O_i), whereas $IoA = 1$ indicates complete agreement:

$$IoA = 1 - \frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (|P_i - \bar{O}| + |O_i - \bar{O}|)^2} \quad (16)$$

The index was calculated for the calibration (1979–1992) period and the validation (1993–2005) period separately. The data used were (1) the observed and predicted diatom biovolume and *Daphnia* abundance (IoA_b) and (2) the observed and predicted timing of the diatom and *Daphnia*

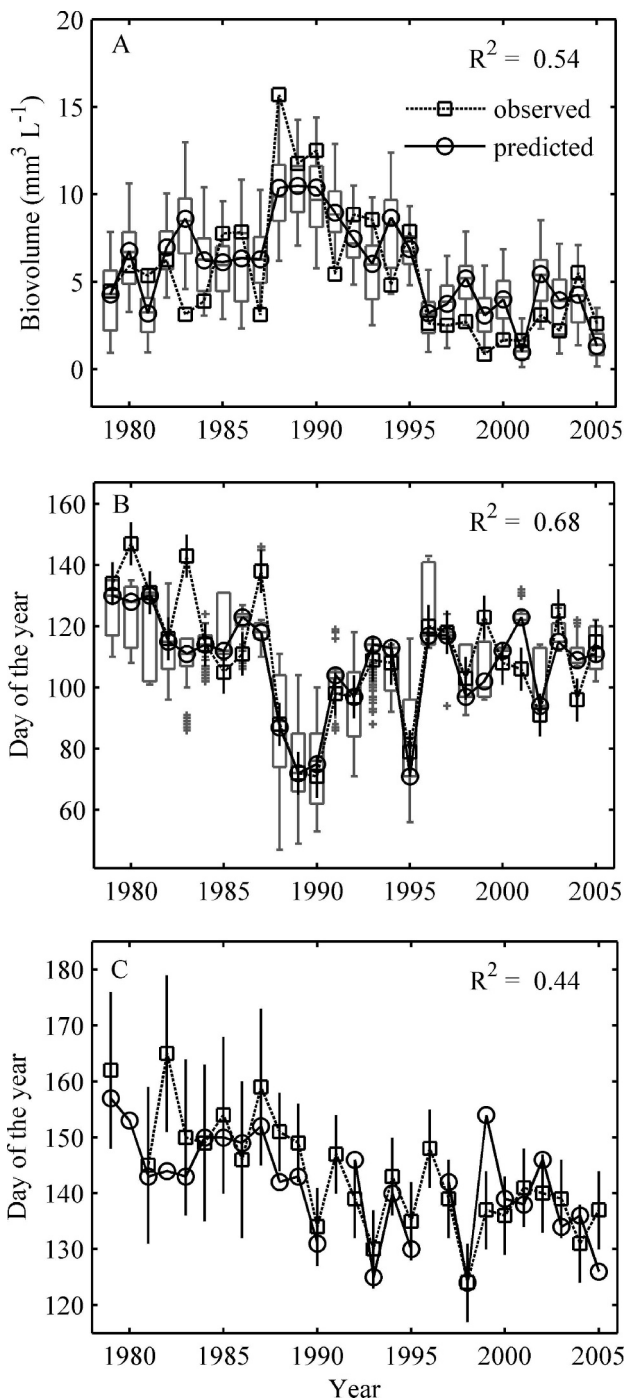


Fig. 2. Model performance and robustness against changes in parameters. Observed (squares) and predicted (circles) (A) intensity of the diatom spring bloom, (B) timing of the diatom spring peak, and (C) timing of the *Daphnia* spring peak. Intensity of the diatom spring bloom is calculated as the mean annual biovolume until the end of the bloom. Vertical black lines (B and C) show ± 7 days (± 14 days), i.e., the uncertainty due to sampling frequencies of 1 week (2 weeks for *Daphnia* until 1987). Missing data points (C) correspond to years when no *Daphnia* peak was observed/predicted until the end of the simulation period. Boxplots (A and B) depict the effect of varying the eight calibrated parameters by $\pm 20\%$ ($n = 1,944$, cf. Methods). The horizontal lines show the median, lower, and

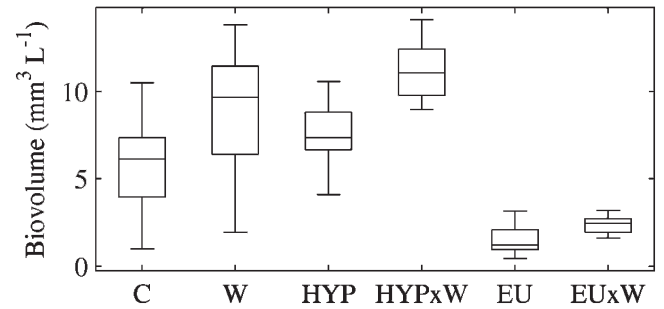


Fig. 3. The effect of warming on the intensity of the diatom spring bloom under different trophic states. Boxplots depict inter-annual variability of the intensity of the diatom spring bloom (1979–2005, $n = 27$) under different scenarios (cf. Methods): A control (C) run using environmental forcing factors as observed (corresponding to predicted values in Fig. 2), simulated warm conditions with increased water temperatures and no ice cover (W), simulated hypertrophic conditions (HYP), hypertrophic conditions combined with warming (HYPxW), eutrophic conditions (EU), and eutrophic conditions combined with warming (EUxW). Boxplot details are as in Fig. 2.

spring peak (IoA_t). In the former case, we used all weekly measurements until the end of the simulation period (mid-June) summing over all years considered (\bar{O} is not the seasonal but the long-term mean). We thereby assessed the ability of the model to reproduce the observed seasonal dynamics during winter and spring. In the latter case, calculations were based on yearly estimations of the timing of the peak.

The robustness of the model was tested by varying the calibrated parameters of the diatom model (Table 1) by $\pm 20\%$ as suggested by Omlin et al. (2001) for moderately inaccurate parameters. Timing and intensity of the simulated diatom blooms were then calculated for all of these parameter combinations ($n = 1944$; three parameter values were excluded that lay outside the biologically plausible interval) and the resulting distributions depicted with boxplots (Fig. 2 A,B).

Control run and simulation experiments—We ran a number of simulation experiments to assess how climate warming affected diatom spring phenology under different trophic states. The validated model, which was forced by current environmental factors (ice cover, water temperature, global radiation, maximal phosphorus, and silicate availability) served as a control (C). Scenarios consisted of setting one or several of these environmental forcing factors to data of extreme years while using current data for the remaining factors. Thus, the effect of missing ice cover and increased water temperatures (warming scenario [W]) was assessed by running the model for every year on climate data from 1990, but keeping current data of global radiation and nutrient availability. The winter and spring (January–May) of 1990 was exceptionally warm, with

←

upper quartile, the whisker extends at most to 1.5 times the interquartile range, and the crosses point to outliers.

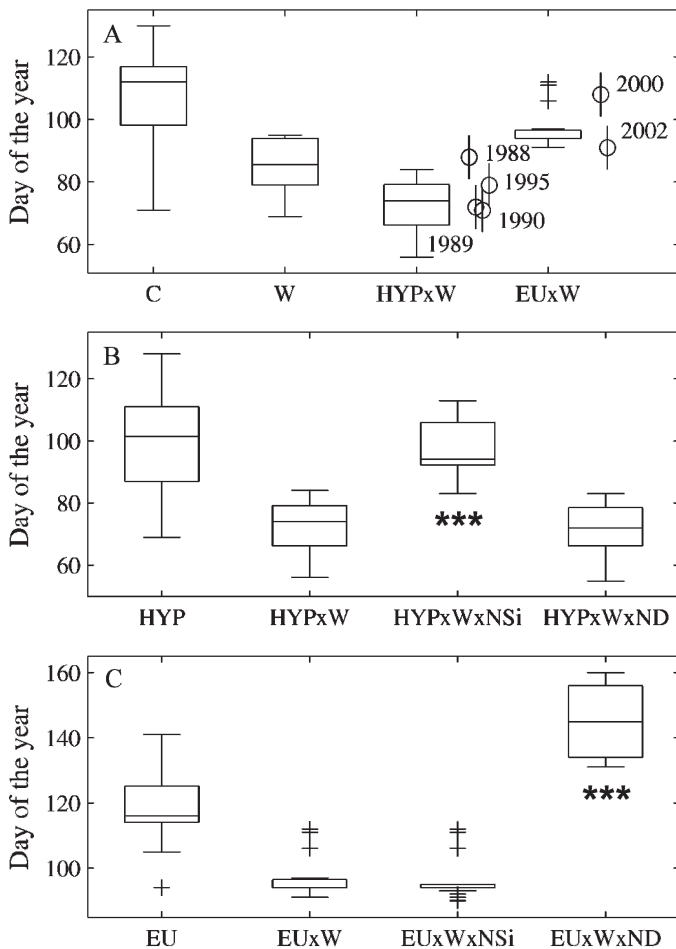


Fig. 4. (A–C) The effect of warming on the timing of the diatom spring peak under different trophic states. Boxplots depict inter-annual variability of the timing of the diatom spring peak (1979–2005, $n = 27$) under different scenarios: Abbreviations are NSi for simulations without silicate limitation and ND for simulations without *Daphnia* grazing. Other abbreviations are as in Fig. 3. Circles (A) mark the observed timing of the diatom spring peak during years of early ice-out (cf. Fig. 1B) with vertical lines depicting ± 7 days, i.e., the uncertainty due to the sampling frequency of 1 week. Asterisks (B and C) mark the results of simulations that differ significantly from warming scenarios (HYPxW and EUxW), as determined by Wilcoxon rank tests ($p < 0.001$). Boxplot details are as in Fig. 2.

average water temperatures 1.6°C higher than the long-term mean of 1979–2005. Hypertrophic conditions (HYP) were simulated by calculating the upper limit of phosphorus concentrations available (P_{tot}) based on the maximum of the observed mean total phosphorus concentrations in spring ($TP_{bloom} = 135 \mu\text{g L}^{-1}$ in 1988, see Fig. 1A). Likewise, eutrophic conditions (EU) were simulated based on the minimum of observed mean total phosphorus concentrations in spring ($TP_{bloom} = 62 \mu\text{g L}^{-1}$ in 2001, see Fig. 1A). Maximum and minimum mean total phosphorus concentrations observed in the time series were assumed to represent two different trophic states according to Köhler et al. (2005). These authors classified a hypertrophic (1979–1990), transient (1991–1996), and eutrophic

phase (1997–2003) at Müggelsee based on data of external and internal nutrient loading. We also investigated the effect of silicate and the effect of *Daphnia* grazing on diatom spring phenology. Silicate limitation was turned off (NSi) by fixing the silicate limitation factor at one. *Daphnia* grazing was turned off (ND) by setting the *Daphnia* grazing constant to zero. Results of simulation experiments were depicted with boxplots showing the inter-annual variability (1979–2005) of the intensity (Fig. 3) and timing (Fig. 4) of the diatom spring bloom under different scenarios. All model simulations and statistical tests were performed using Matlab 6.5 and 7.0 (MathWorks).

Results

Diatom spring phenology—The magnitude and the timing of the diatom spring peak in Müggelsee showed a strong inter-annual variability during 1979–2005 (Fig. 1). Whereas high diatom biovolumes were reached in the spring of the late 1980s and early 1990s, biovolumes have decreased strongly in the last decade. These changes in diatom biovolume were correlated with changes in mean TP concentrations measured in spring (Spearman's $\delta = 0.79$, $p < 0.001$, Fig. 1A). Moreover, the timing of the diatom spring peak showed a positive correlation with the timing of ice-out during the entire study period ($\delta = 0.63$, $p < 0.001$, Fig. 1B). However, whereas years with early ice-out or missing ice cover led to early diatom spring peaks in the late 1980s and 1990s (years 1988, 1989, 1990, 1995), diatom spring peaks occurred relatively late despite early ice-out in recent years (2000 and 2002). Correlation analysis did not reveal any significant relationship between the timing of ice-out and the magnitude of the diatom spring peak ($\delta = 0.05$, $p > 0.1$) nor between the mean total phosphorus concentrations in spring and the timing of the diatom spring peak ($\delta = -0.22$, $p > 0.1$). We applied the diatom phenology model to investigate these relationships further.

Model performance and robustness against changes in parameters—The model predicts very well the intensity and timing of the diatom spring bloom in Müggelsee for the time span considered (with 54% and 68%, respectively, of the observed inter-annual variability explained [Fig. 2A,B]). The index of agreement indicated that the model succeeded in reproducing the timing of the diatom spring peak during years used for calibration (1979–1992, $IoA_t = 0.92$) and during years used for validation (1993–2005, $IoA_t = 0.85$). The same was true for the ability of the model to predict the overall dynamics of diatom biovolume in spring ($IoA_b = 0.81$ for calibration years, $IoA_b = 0.66$ for validation years). With the exception of a few years, the model performance was relatively robust against changes in calibrated parameter values with the highest uncertainty (boxplots in Fig. 2A,B). The large variability in the predicted timing of the diatom spring peak during some years (Fig. 2B) occurred when multiple peaks developed; thus, they result from the phenology definition applied. Also, the sub-model well predicted *Daphnia* spring dynamics. Model performance in years that were used for validation (1993–2005, $IoA_t = 0.69$, $IoA_b = 0.74$) was

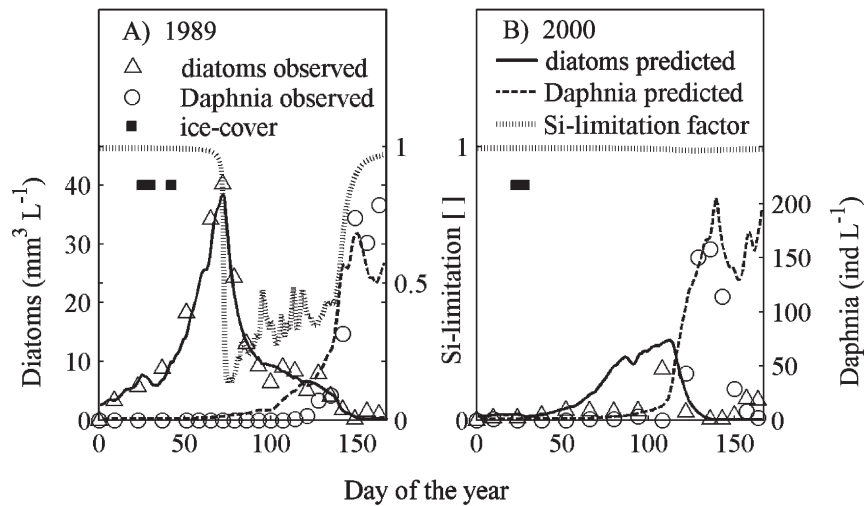


Fig. 5. Observed and predicted spring dynamics of diatom biovolume and *Daphnia* density during 2 years of early ice-out: (A) 1989 (hypertrophic phase) and (B) 2000 (eutrophic phase). The thick shaded line shows silicate limitation as indicated by the model, with a value of one corresponding to no limitation.

about the same as model performance in years that were used for calibration (1979–1992, $IoA_t = 0.73$, $IoA_b = 0.79$). The timing of the *Daphnia* spring peak and, therefore, also the onset of the grazing impact on diatoms were sufficiently well reproduced by the model (with 44% of the observed inter-annual variability explained [Fig. 2C]).

Simulation experiments and the intensity of the diatom spring bloom—Simulation experiments indicated that the strength of the warming effect on the intensity of the diatom spring bloom was dependent on trophic state (Fig. 3). Simulating warm conditions, with missing ice cover and higher water temperatures in all years (W in Fig. 3), significantly increased the mean biovolume of the diatom spring bloom compared to the control (C) run (Wilcoxon rank test, $p < 0.001$). We separated hypertrophic from eutrophic conditions by simulating very high (HYP) and reduced (EU) phosphorus supply, respectively, in all years. Additionally, simulating warm conditions provoked a significant increase ($p < 0.001$) of the bloom intensity under both trophic states (compare HYP with HYPxW and EU with EUxW in Fig. 3). Still, the increase in the mean biovolume due to warming was smaller under eutrophic than under hypertrophic conditions. Thus, in our simulations a reduction in nutrient supply attenuated the effect of climate warming on the intensity of the phytoplankton spring bloom.

Simulation experiments and the timing of the diatom spring peak—Trophic state also influenced the effect of climate warming on the timing of the diatom spring peak (Fig. 4). Simulating warm conditions (W in Fig. 4A) resulted in an earlier peak when compared to the control (C) run (Wilcoxon rank test, $p < 0.001$). These changes were reinforced by additionally simulating the increased availability of phosphorus, i.e., hypertrophic conditions (HYPxW in Fig. 4A). In contrast, decreased availability of

phosphorus, i.e., eutrophic conditions, counteracted the effect of climate warming on the timing of the diatom spring peak (EUxW in Fig. 4A). Comparing our simulations with the observed timing of the peak during years with mild winter conditions and early ice-out (circles in Fig. 4A) suggests that the relative delay of the diatom spring peak in recent mild years (Fig. 1B) can be attributed to the observed shift in trophic state. We explored this further by analyzing the mechanisms that induce the collapse of the spring bloom and thereby determine the timing of the peak.

Bloom collapse mechanisms under different trophic states—Analyzing the role of silicate limitation and *Daphnia* grazing showed that the mechanisms that underlie diatom spring phenology differ under hypertrophic and eutrophic conditions (Fig. 4B,C). Whereas neglecting silicate limitation under hypertrophic conditions (Fig. 4B) strongly decelerated the warming-induced forward shift of the peak (HYPxW vs. HYPxWxNSi, $p < 0.001$), the effect of warming persisted when silicate limitation was neglected under eutrophic conditions (Fig. 4C, EUxW vs. EUxWxNSi, $p > 0.1$). By contrast, neglecting *Daphnia* grazing had hardly any effect on the timing of the peak under simulated hypertrophic conditions (Fig. 4B, HYPxW vs. HYPxWxND, $p > 0.1$), whereas the effect of warming was annulled and the peak delayed significantly under eutrophic conditions (Fig. 4C, EUxW vs. EUxWxND, $p < 0.001$). Hence, whereas the collapse of the bloom was caused by silicate limitation under very high phosphorus supply (hypertrophic conditions), it was caused by *Daphnia* grazing under reduced phosphorus supply (eutrophic conditions).

Two example years, which both experienced relatively warm conditions in winter, illustrate that the collapse of the diatom spring bloom can, as found above, be induced by different environmental factors depending on the trophic state (Fig. 5). The model indicates that the diatom spring bloom was terminated through silicate limitation in 1989

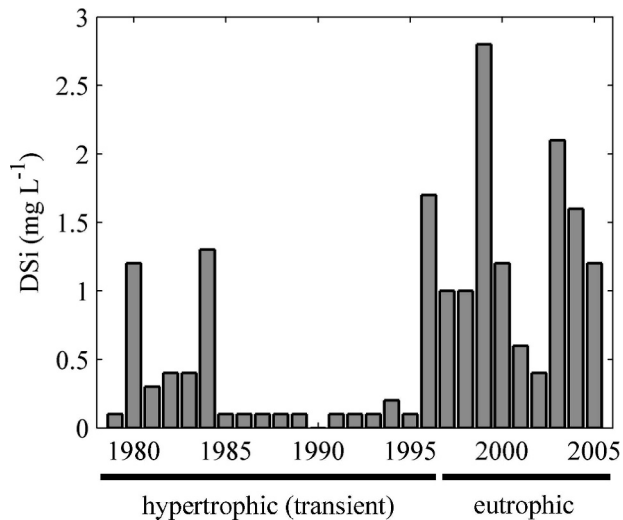


Fig. 6. Minimal concentrations of dissolved silicate (mg L^{-1}) during the diatom spring bloom in Müggelsee, measured during phases of high (hypertrophic and transient 1979–1996) and reduced (eutrophic 1997–2005) phosphorus supply.

(i.e., in the hypertrophic phase) as suggested by our simulation experiments (Fig. 4B). In contrast, the diatom spring bloom in 2000 (i.e., in the eutrophic phase) did not collapse until *Daphnia* densities became important, again in accordance with our simulation results (Fig. 4C). Correspondingly, minimal dissolved silicate concentrations measured in Müggelsee until the end of the diatom spring bloom differed between the phases of very high (1979–1996) and reduced (1997–2005) phosphorus supply (Fig. 6). Whereas during the hypertrophic (and transient) phase they often reached the detection limit of 0.1 mg L^{-1} , below which diatom growth is likely to be silicate limited, during the eutrophic phase they always remained on a level where silicate limitation is unlikely.

Discussion

Our model well reproduced observed spring dynamics of diatoms (and *Daphnia*) in Müggelsee during 1979–2005. Simulation experiments indicated that the effect of climate warming on both the timing and intensity of the diatom spring bloom was reinforced through high phosphorus availability (hypertrophic conditions), whereas decreasing phosphorus availability (eutrophic conditions), as prevailing in the last decade, counteracted the warming effect. Further analysis suggested that the collapse of the bloom was caused by silicate limitation during hypertrophic conditions. In contrast, silicate concentrations did not reach the limitation threshold during eutrophic conditions such that the bloom was terminated by *Daphnia* grazing. This switch in bloom collapse mechanisms explains why the phytoplankton response to mild winter and spring conditions differed between the periods of very high and reduced phosphorus loading in the lake studied here.

Plausibility of bloom collapse mechanisms—Diatom biovolume in Müggelsee is dominated by small centric

species in spring ($<30 \mu\text{m}$), which belong to the preferred food size range of *Daphnia*. In fact, the mean yearly contribution of centric diatom species to total diatom biovolume until the clear water phase was $65\% \pm 18\% \text{ SD}$ ($n = 27$) in our study period. In addition, larger diatoms such as *Asterionella formosa* and *Fragilaria crotonensis*, also present in Müggelsee, were found to be suppressed by *Daphnia* in other freshwater lakes (Vanni and Temte 1990). The role of silicate limitation during the diatom spring bloom is well documented in marine systems (Allen et al. 1998), but is also important in freshwater systems (Lund 1950). Thus, both of our explanations for the collapse of the diatom bloom are plausible.

The bloom collapse mechanisms proposed here might also contribute to a better understanding of the effects of climate warming on phytoplankton phenology described in other studies. Interestingly, in a simulation study by Elliott et al. (2006), increasing the nutrient (phosphorus and nitrogen) load enhanced the warming-induced forward shift of the spring peak of the diatom species *Asterionella* sp., whereas the timing of the spring peak of the two non-diatom species *Chlorella* sp. and *Plagioselmis* sp. was delayed under increased nutrient load. This finding is in accordance with our results assuming that in the simulations of Elliott et al. (2006) increasing phosphorus and nitrogen availability resulted in higher growth rates of *Asterionella* sp. and subsequently in an earlier collapse of the peak caused by silicate limitation. In contrast, *Chlorella* sp. and *Plagioselmis* sp., which were not limited by an additional nutrient, peaked later in that study because they could fully exploit the larger resource base.

Potential food web consequences of a switch in bloom collapse mechanisms—A bloom collapse induced by silicate limitation, as suggested for mild years during the hypertrophic phase of Müggelsee (Fig. 4B), decouples diatoms from *Daphnia* (Fig. 5). We wondered whether this decoupling of predator and prey had any consequences for the growth success of *Daphnia*. In fact, Winder and Schindler (2004a) showed that a climate-induced decoupling of the phytoplankton bloom from the onset of *Daphnia* growth in spring can produce a mismatch situation causing a decline in *Daphnia* abundance. However, in a supplementary analysis, we did not find any relationship between the number of weeks elapsed between the phytoplankton peak and the *Daphnia* maximum in spring (as an indicator of the potential mismatch) and *Daphnia* densities in late spring and summer (not shown). Moreover, when *Daphnia* started growing in spring, the diatom biovolume always stayed above 0.2 mg C L^{-1} (approximately $1.7 \text{ mm}^3 \text{ L}^{-1}$), which is regarded as the food limitation threshold for *Daphnia* (Lampert 1978). Considering that other phytoplankton species besides diatoms contribute to *Daphnia* food, it is not surprising that although the phytoplankton spring peak is decoupled from *Daphnia* growth in some years, we do not find any evidence for a mismatch situation between phytoplankton and *Daphnia* in this nutrient-rich lake.

Phenomenological approach to phosphorus limitation—A strong correlation between phytoplankton biomass and total

phosphorus concentrations as found in spring for Müggelsee (Eq. 12) does not necessarily indicate that algal growth rates are indeed limited by phosphorus (Sommer 1994). Still, we chose the phenomenological approach presented here, based on the assumption that decreasing concentrations of total phosphorus reflect decreasing concentrations of phosphorus available for algal growth. In fact, previous studies have pointed to increasingly phosphorus-limited phytoplankton spring growth in Müggelsee (Köhler et al. 2000; Köhler et al. 2005). Such a limitation is plausible, as concentrations of soluble reactive phosphorus fell below the limitation threshold of $10 \mu\text{g L}^{-1}$ during the phytoplankton spring bloom in all years (Köhler et al. 2005).

When estimating the maximal phosphorus available for diatom growth, we assumed that a constant amount ($TP^* = 52 \mu\text{g L}^{-1}$) is locked in other compartments (such as bacteria, other phytoplankton species, zooplankton, and phosphorus bound to iron or calcite) each year (cf. Methods). This is a strong assumption because, intuitively, the amount of phosphorus locked in other compartments should decrease as total phosphorus concentrations decrease in the lake. We, therefore, performed two additional regressions (cf. Eq. 12) of mean spring diatom biovolume (A_{bloom}) on mean spring total phosphorus concentrations (TP_{bloom}) for the periods 1979–1993 (high TP concentrations) and 1994–2005 (reduced TP concentrations). The estimation of the phosphorus locked in other compartments was clearly not lower under reduced total phosphorus concentrations ($TP^* = 56 \mu\text{g L}^{-1}$, $p < 0.001$, $R^2 = 0.54$) than under high total phosphorus concentrations ($TP^* = 47 \mu\text{g L}^{-1}$, $p < 0.01$, $R^2 = 0.41$). This supports our assumption that, during the study period, a relatively equal amount of phosphorus was not available to diatoms independently of trophic state. Interestingly, a large amount of particulate phosphorus in Müggelsee and its inflow is bound to iron and not available to phytoplankton growth (Kirchner 1997). Better understanding the phosphorus limitation of phytoplankton in Müggelsee definitively requires further research; however, the main conclusions of this study are independent of the exact mechanisms that determine the intensity of algal biovolume under different trophic states.

Other model simplifications—Model development poses the challenge to find a balance between including the key processes while keeping the model as simple as possible. This process necessarily leads to the exclusion of mechanisms that are known to be important in other systems. For instance, we are aware of the fact that grazing by copepods and ciliates can be an important loss factor for phytoplankton early in the year (Huber and Gaedke 2006; Tirok and Gaedke 2006; Peeters et al. 2007). But, a model that included the effect of winter grazers (based on observed densities and clearance rates from the literature) as additional forcing factors negligibly improved the fit of the model (not shown). We also ignored that the maximal uptake rate of phosphorus ρ_{max} can be dependent on cell quota (Morel 1987). The reason for this was that the regulation of nutrient uptake rates is poorly understood yet (Klausmeier et al. 2004), and modeling the negative feedback of internal nutrient stores on uptake rates has hardly affected the system behavior in

similar models (Klausmeier et al. 2004; Diehl unpubl. data). Also, studies of phytoplankton physiology have clearly demonstrated that it is not only the average light availability but day length that influences phytoplankton growth rates (Nicklisch and Kohl 1989). Accounting for the latter mechanism would certainly be one of the many steps to render the model more realistic.

The importance of considering changes in trophic state besides climate warming—Previous studies on the phytoplankton response to climate warming in Müggelsee did not find any effect of nutrients (Adrian et al. 1999; Gerten and Adrian 2000). This might be explained by the shorter time series used in these studies ending in the late 1990s, when the nutrient effect might not have been apparent yet. Another explanation could be that, as found here, simple correlation analysis is not the right tool to detect more subtle relationships as those between the trophic state and the timing of the phytoplankton spring bloom. Our results are clearly in accordance with other observational and modeling studies, showing that the effect of climate warming on the phytoplankton spring bloom can be counteracted by decreasing nutrient concentrations (Jeppesen et al. 2005; Elliott et al. 2006). These authors explain their findings by the well-known positive effect of increasing temperatures and the negative effect of decreasing nutrient concentrations on phytoplankton growth (Wernicke and Nicklisch 1986). Here, we show that decreasing phosphorus concentrations do not only imply a gradual shift of increasingly phosphorus-limited algal growth, but a qualitative switch from a bottom-up driven (by silicate limitation) to a top-down controlled (by *Daphnia* grazing) collapse of the phytoplankton spring bloom.

The interaction between climate warming and a change in nutrient loading can be expected to occur in other aquatic ecosystems of different trophic state (such as meso- or oligotrophic lakes) and of different types (such as deep lakes or marine systems). The mechanisms underlying this interaction might differ between the ecosystems. However, there are some indications that the switch in bloom collapse mechanisms that we propose here for the shallow, heavily loaded lake might also be relevant for other systems. Schelske and Stoermer (1971) first postulated a relationship between eutrophication and the increasing occurrence of silicate limitation of diatom growth for the deep, oligotrophic Lake Michigan. This relationship has also been described for marine systems, such as the heavily loaded, mesohaline part of Chesapeake Bay and for coastal waters of the North Sea (Conley et al. 1993). Thus, it is conceivable that a switch from an algal bloom collapse induced or at least accelerated by silicate limitation to a collapse induced by some other factor (such as grazing or sedimentation) takes place in the course of a load reduction in these systems as well. Simultaneous climate warming should then amplify the changes brought about by a shift in trophic state just as it has been found in this study.

In conclusion, other studies have pointed to the risk of falsely attributing observed changes in aquatic ecosystems to climate warming (Jeppesen et al. 2003; Van Donk et al. 2003; Jeppesen et al. 2005). Here, we emphasize the

necessity of gaining a better understanding of the mechanisms that underlie phenology shifts and other climate-induced changes in aquatic ecosystems. For instance, it has become increasingly clear that the mechanisms determining the phytoplankton response to climate warming differ strongly between shallow and deep lakes (Adrian et al. 1999; Peeters et al. 2007). Our results show that it is equally important to consider the trophic state of a lake when investigating the mechanisms underlying the effect of global warming on phytoplankton bloom formation. In view of future climate warming, further studies are needed to determine how climatic conditions influence the external and internal nutrient loading of lakes (e.g., Malmaeus et al. 2006). Moreover, other anthropogenic interventions (such as land use and management changes), which influence the nutrient supply to lakes and rivers, must be taken into account to establish more realistic scenarios of freshwater ecosystems under anticipated climate change.

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