

Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton

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Abstract In many lakes, the most conspicuous seasonal events are the phytoplankton spring bloom and the subsequent clear-water phase, a period of low-phytoplankton biomass that is frequently caused by mesozooplankton (*Daphnia*) grazing. In Central European lakes, the timing of the clear-water phase is linked to large-scale climatic forcing, with warmer winters being followed by an earlier onset of the clear-water phase. Mild winters may favour an early build-up of *Daphnia* populations, both directly through increased surface temperatures and indirectly by reducing light limitation and enhancing algal production, all being a consequence of earlier thermal stratification. We conducted a field experiment to disentangle the separate impacts of stratification depth (affecting light supply) and temperature on the magnitude and timing of successional events in the plankton. We followed the dynamics of the phytoplankton spring bloom, the clear-water phase and the spring peak in *Daphnia* abundance in response to our experimental manipulations. Deeper

mixing delayed the timing of all spring seasonal events and reduced the magnitudes of the phytoplankton bloom and the subsequent *Daphnia* peak. Colder temperatures retarded the timing of the clear-water phase and the subsequent *Daphnia* peak, whereas the timing of the phytoplankton peak was unrelated to temperature. Most effects of mixing depth (light) and temperature manipulations were independent, effects of mixing depth being more prevalent than effects of temperature. Because mixing depth governs both the light climate and the temperature regime in the mixed surface layer, we propose that climate-driven changes in the timing and depth of water column stratification may have far-reaching consequences for plankton dynamics and should receive increased attention.

Keywords Algal spring bloom · Clear-water phase · *Daphnia hyalina* · Enclosure experiment · Phytoplankton · Zooplankton

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Introduction

The impacts of global climate change on earth's ecosystems are the subject of an increasing number of studies in terrestrial and aquatic habitats (reviewed in Hays et al. 2005; Harrington et al. 1999). Global warming has been found to correlate with changes in organisms' distributions and in the timing of seasonal events (Hughes 2000; Parmesan and Yohe 2003; Root et al. 2003). For example, the onset of spring is advancing in many terrestrial ecosystems (Parmesan and Yohe 2003). Similarly, seasonal abundance shifts of short-lived organisms such as marine copepods occur earlier during warm years and are tightly coupled

with sea surface temperatures (Mackas et al. 1998; Greve et al. 2001). While there are many examples of strong statistical relationships between climate variability and ecological patterns, the nature of the underlying mechanisms is often uncertain (Stenseth and Mysterud 2002). Climate impacts on the distribution and phenology of biota may not only act directly through individual physiology, but also indirectly through species interactions. Disentangling the interplay of climatic drivers with density-dependent processes is therefore a major challenge, which calls for the increased use of proper experimental approaches (Stenseth and Mysterud 2002).

In many temperate lakes, the most conspicuous events during seasonal succession of the plankton community are the phytoplankton spring bloom and the subsequent clear-water phase, a period of low phytoplankton biomass. Although the decline of a phytoplankton spring bloom can sometimes be explained by the exhaustion of a pool of limiting nutrients (O'Brien 1974; Huppert et al. 2002), the clear-water phase is usually attributed to intense grazing from a growing population of crustacean zooplankton (Lampert et al. 1986; Sarnelle 1993; Winder and Schindler 2004a). In Central European lakes, the timing of the clear-water phase is empirically linked to large-scale climatic forcing, with warmer winters being followed by an earlier onset of the clear-water phase (Straile 2000, 2002; Scheffer et al. 2001). This synchronising effect of large-scale climate patterns on the timing of the clear-water phase has been observed across lakes varying in morphometry and nutrient state (Straile and Adrian 2000; Straile 2002). In the particularly well-researched case of Lake Constance, Straile (2000) documented a cascade of meteorological, hydrological and ecological processes linking the winter index of the North Atlantic Oscillation (NAO) to events in the seasonal succession of the plankton occurring up to almost 6 months later. Based on a time series spanning 16 years of data, the temporal sequence of events was as follows. Mild (=high NAO) winters were followed by high-water temperatures and high-population growth of rates of *Daphnia* (the major grazing zooplankton) in April and May. Thus, a critical daphnid biomass necessary to suppress phytoplankton was reached earlier during high NAO years, resulting in an earlier and longer-lasting clear-water phase, but also in an earlier summer decline of *Daphnia*.

Because algal biomass in Lake Constance during early spring (prior to the seasonal increase in *Daphnia*) was, at best, only weakly related to the NAO winter index, Straile (2000) suggested that the influence of

winter climate on *Daphnia* dynamics in April/May was most likely a direct effect of water temperature on *Daphnia* growth and was not mediated through changes in algal food abundance. Individual metabolism and growth of *Daphnia* are indeed highly dependent on temperature (Lampert 1977; Orcutt and Porter 1983; Dawidowicz and Loose 1992; Reichwaldt et al. 2005). Still, a lack of a relationship between winter climate and algal density does not rule out the possibility that a significant part of the effects of winter climate on *Daphnia* population growth in spring is mediated through food supply. Sustained growth of a consumer requires sustained *production* of food, but food production is not necessarily correlated with food *abundance* if, e.g., the additional production is harvested by a simultaneously growing grazer population.

It seems plausible that in deep lakes such as Lake Constance specific algal production is positively affected by mild winters and early warming in spring, as has been reported from other temperate lakes and oceans (Weyhenmeyer et al. 1999; Richardson and Schoeman 2004; Winder and Schindler 2004a). In most deep, temperate lakes, phytoplankton production in late winter and early spring is limited by light availability, because under the prevailing non-stratified conditions individual algal cells spend most of the time below the euphotic zone (Reynolds 1984; Huisman and Weissing 1999; Diehl 2002). It is therefore commonly assumed that the timing of the spring phytoplankton bloom in deep lakes depends on the onset of water column stratification (Sommer et al. 1986; Reynolds 1989). In a detailed time series analysis of data from Lake Constance, Gaedke et al. (1998a, b) did indeed find that substantial algal development in spring only occurred when algae were largely safe from being mixed below a depth of 20 m. Similarly, Winder and Schindler (2004b) found that the timing of the phytoplankton spring bloom in Lake Washington correlated with the onset of stratification. This is consistent with data showing a strong negative dependence of specific algal production on depth of the mixed water column (Diehl et al. 2002, 2005; Ptacnik et al. 2003). The onset of water column stratification in spring in turn depends on regional weather conditions such as air temperature and wind speed. Relatively high temperatures and low wind speeds during winter and early spring promote an early onset of stratification (Gaedke et al. 1998a, b; Winder and Schindler 2004a) thus alleviating light limitation and boosting phytoplankton production.

In summary, there are two non-exclusive mechanisms by which mild winters might favour an early

build-up of *Daphnia* biomass in deep lakes: (1) enhanced algal production, and (2) increased metabolic rate. Ultimately, both are consequences of an earlier stratification of the water column alleviating light limitation and preventing heat loss to deeper strata. Thus, successful prediction of climate effects on seasonal succession in the plankton requires a detailed understanding of the separate contributions of mixing depth-dependent light climate and temperature to the production and loss rates of phytoplankton and zooplankton.

Because increased light supply and increased water temperature inevitably co-vary with reduced mixing depth, their separate contributions to the spring dynamics of the plankton cannot be assessed without experimentation. We therefore conducted a field enclosure experiment in which we manipulated mixing depth and water temperature largely independently and investigated their effects on the magnitude and timing of three major events during spring succession of the plankton: (1) the peak of the phytoplankton spring bloom, (2) the beginning of the clear-water phase, and (3) the spring peak of the *Daphnia* population. We hypothesised that mixing depth should have strong direct effects on algae (by mediating light-dependent production) but not on *Daphnia*. In contrast, we expected *Daphnia* grazing and growth rates to depend strongly on temperature, but phytoplankton production only weakly so. These direct effects of light and temperature should propagate across the plant-herbivore interface. We therefore expected the peak densities of both phytoplankton and *Daphnia* to correlate negatively with mixing depth (because of reduced algal production at lower light levels), but increased temperature should shift the timing of these peaks and the beginning of the clear-water phase forwards (because increased *Daphnia* grazing should deplete algae earlier).

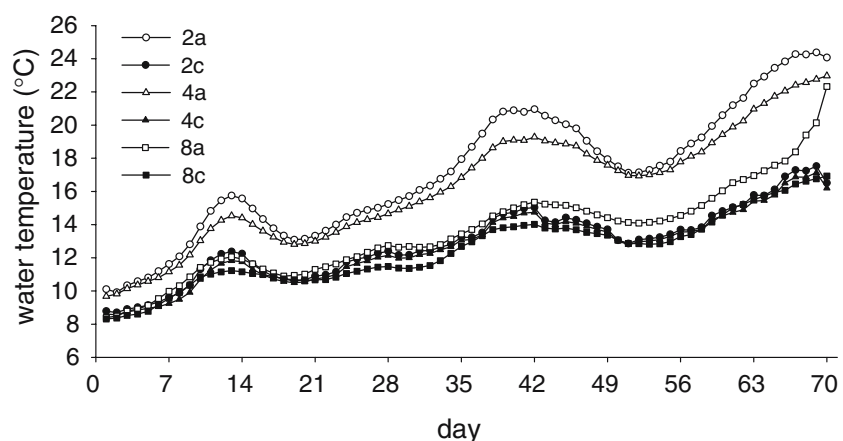
Materials and methods

Study site and experimental design

The enclosure experiment was run in a 3×2 factorial design: three enclosure depths (2, 4 and 8 m) were cross-classified with two temperature treatments ('ambient' and 'cold'), with two replicates per treatment. Enclosures (cylindrical bags of transparent Tricoron; RKW Wasserburg, Germany) had a diameter of 0.95 m, were heat-sealed at the bottom and open to the atmosphere. We suspended them from a raft anchored at a water depth of 16 m in Lake Brunnsee (47°56'N, 12°26'E), close to the University of Munich's Limnological Research Station at Seeon. Lake Brunnsee (area 5.8 ha, max. depth 19 m) is fed by silica- and nitrate-rich groundwater with a low-total phosphorus content (usually below 10 µg P l⁻¹).

We maintained well-mixed conditions inside the enclosures by intermittently (5 min on, 35 min off) blowing compressed air through tubing to the bottom of each enclosure. The mixing was highly effective, i.e. vertical temperature gradients *within* enclosures were negligible. However, because the lake usually stratifies in late spring at a depth of 3–4 m, temperature differences *between* enclosures developed over time in the 'ambient' treatments: temperatures there were highest in the 2 m enclosures and lowest in the 8 m enclosures (Fig. 1), mimicking a natural situation where depth and temperature of the mixed layer are inversely related. We surrounded all enclosures of the 'cold' treatment by a large, 12-m-deep bag. The water inside this bag was kept well-mixed, creating a water bath of homogeneous, reduced temperature for the 'cold' enclosures. The procedure was highly effective, i.e. temperatures in the 'cold' enclosures were independent of mixing depth and were considerably lower than in the 2 and 4 m 'ambient' treatments (Fig. 1).

Fig. 1 Average daily water temperature (°C) of the two replicates of each enclosure treatment versus time (day 1=21 April, day 70=28 June). 2, 4, 8=mixing depth (in metres), *a* ambient temperatures (*open symbols*), *c* cold temperatures (*filled symbols*). Data points are running means of three consecutive measurements



We surrounded each enclosure with black silage film in order to enhance background light extinction, making the enclosures optically deeper (see Diehl et al. 2002). Depth-averaged light attenuation coefficients were 0.65, 0.73 and 0.83 m^{-1} in the 2, 4 and 8 m enclosures, respectively, compared to 0.28 m^{-1} (calculated from 0–8 m) in the lake. The vertical light gradients in the 2, 4 and 8 m enclosures therefore corresponded to light gradients down to approximate depths of 4.6, 10.3 and 23.6 m, respectively, in natural lake water, thus mimicking a much wider range of stratification depths characteristic of larger and deeper lakes.

We ran the experiment for 10 weeks from 21 April to 28 June 2005. On 20 April, we filled all enclosures with lake water sieved through a 50- μm gauze, which excluded crustacean zooplankton, but preserved the natural phytoplankton spring community consisting mostly of small diatoms and cryptomonads (*Cyclotella* spp. and *Rhodomonas minuta*, with 60 and 13%, respectively, of total algal biovolume). We enriched all enclosures with 14.3 $\mu\text{g l}^{-1}$ phosphorus (as KH_2PO_4) to an initial total phosphorus content of about 25 $\mu\text{g l}^{-1}$ in order to stimulate a more pronounced algal spring bloom. To simulate spring recruitment from an egg bank in the sediment, we added small inocula of *Daphnia hyalina* (which is the naturally occurring *Daphnia* species in the lake) to all enclosures weekly over the first 4 weeks of the experiment. The *Daphnia* were descendants of three clones that had been isolated from the lake and been cultured separately at 20°C on a diet of *Scenedesmus*. Prior to stocking, the *Daphnia* were acclimated to 13°C for one night in a climate chamber. After transport to the lake, we mixed the clonal populations carefully in a 200-l tub and added appropriate aliquots to each treatment. Approximate stocking densities were 1.2 individuals l^{-1} on 21 April, 0.6 individuals l^{-1} on 26 April, 0.15 individuals l^{-1} on 3 May and 0.3 individuals l^{-1} on 11 May. Subsequent density counts suggest that initial mortality was ~90% leading to an emergence rate between 0.002 and 0.017 individuals l^{-1} per day, which is close to observations by Càceres (1998).

Sampling programme

In all enclosures, water temperature was recorded every 30 min by a sensor located 15 cm below the water surface and connected to a data logger (SE-309; Conrad Elektronik, Germany) on the raft. Additionally, we recorded vertical temperature profiles with a multi-probe (LT1/T; WTW-Weilheim, Germany) in 1-m steps several times a week in the outer water bath

and once weekly in each enclosure to monitor the mixing regime. At bi-weekly intervals, we measured vertical profiles of photosynthetically active radiation (PAR) in 1 m steps with a spherical quantum sensor (LI-139SA; Licor, Lincoln, Neb., USA). Parallel to each underwater reading we took a reading of incident PAR (flat quantum sensor LI-190SA) just above the water surface. For each enclosure, we then calculated the depth-averaged intensity of PAR as a percentage of incident PAR (as described in Diehl et al. 2005) and the depth-averaged light attenuation coefficient (as described in Diehl et al. 2002).

Once per week, we took a 2-l water sample from just below the water surface in each enclosure. Measurements of vertical chlorophyll *a* (Chl *a*) profiles with a fluorescence probe confirmed that the samples were representative of the perfectly mixed water columns. The samples were filtered through a 250- μm mesh to remove mesozooplankton and were immediately analysed for alkalinity. To determine particulate organic carbon (POC) and Chl *a* concentrations, we filtered aliquots of 100–300 ml onto glass fibre filters (Whatman GFF, precombusted for POC). Chl *a* was determined in a fluorometer (TD 700; Turner Design, Sunnyvale, Calif., USA) after extraction in acetone. Seston POC content was determined by infrared-spectroscopy (C-Mat; Ströhlein, Korschbroich, Germany).

Once per week, we sampled zooplankton by means of vertical hauls with a 55- μm mesh net, taken from the bottom to the surface in each enclosure. Zooplankton samples were immediately fixed with cold sugar formalin (250 g sugar in 1 l formalin) to a final concentration of 4%. To estimate the abundances of *D. hyalina*, all individuals of a haul were counted under a dissecting microscope at 25 \times magnification.

Data processing and statistics

In all enclosures, we observed similar temporal dynamics of the plankton. Phytoplankton densities increased from a starting value of 2 ($\mu\text{g Chl } a \text{ l}^{-1}$) to a peak several weeks into the experiment and subsequently declined to densities below the starting value. *Daphnia* densities showed the same 'boom and bust' pattern, but with a time delay of several weeks compared to phytoplankton. Thus, we observed three distinct successional events: a phytoplankton peak, a phytoplankton decline (=clear-water phase), and a *Daphnia* peak. We characterised these events by their magnitude (=peak height) and their timing (=date when a peak was reached or the clear-water phase started). We defined a peak as the highest density observed in a given enclosure during the experiment.

The beginning of the clear-water phase was defined as the first sampling date (following a peak) when the Chl *a* concentration had declined below 2 ($\mu\text{g l}^{-1}$).

Our ability to characterise the timing and magnitude of successional events was limited by our weekly sampling resolution. To obtain a continuous temporal resolution, we fitted the following Weibull function to the dynamics of Chl *a* and *D. hyalina* in each enclosure.

$$N(t) = c + m \left(\frac{b}{a} \right) \left(\frac{t}{a} \right)^{b-1} e^{-(t/a)^b}, \quad (1)$$

where $N(t)$ is either Chl *a* concentration ($\mu\text{g l}^{-1}$) or *Daphnia* density (individual l^{-1}), a , b , c and m are fitted constants, and t is the time (in days) since the start of the experiment. We used Eq. 1 because it can describe unimodal distributions with both symmetric and asymmetric peaks (see examples in Supplementary electronic material Fig. 1). Because *Daphnia* densities were zero at the start and approached very low values at the end of the experiment, c was dropped from the model for *Daphnia* dynamics. The maxima of the fitted Weibull functions yielded estimates of the timing and height of density peaks. The beginning of the clear-water phase was estimated as the time when the fitted Chl *a* function dropped below 2 $\mu\text{g l}^{-1}$.

To statistically test for effects of mixing depth and temperature on the magnitude and timing of successional events, we performed two-way ANOVA with enclosure depth and temperature treatment ('ambient' versus 'cold') as fixed factors. As response variables we used both the directly measured values (with weekly temporal resolution) and the values derived from the fitted Weibull functions (with daily temporal resolution). All statistical analyses were performed with SPSS 13.0. If necessary, data were ln transformed to stabilise variances.

Results

The temperature treatment was successful. Water temperatures in the 'ambient' 2 and 4 m treatments differed on average by less than 1°C from each other and were considerably higher than in the 'cold' treatments; all 'cold' treatments were, in turn, very similar to one another, the 'ambient' 8 m treatment being on most days only slightly warmer (Fig. 1). As the lake warmed up during the course of the experiment, water temperatures increased over time in all enclosures, starting at 8.3°C (2–8 m 'cold' and 8 m 'ambient') and 10.1°C (2–4 m 'ambient') on 21 April and reaching 16.5±0.2°C (2–8 m 'cold'), 22.3°C (8 m 'ambient'), 23.0°C (4 m 'ambient') and 24.1°C (2 m 'ambient') on 28 June (Fig. 1).

The mixing depth treatments were similarly successful. Average light intensity in the water column was strongly negatively related to enclosure depth throughout the experiment but was independent of temperature treatment (Fig. 2a; ANOVA, effects of mixing depth: $P < 0.001$, effects of temperature treatment and depth × temperature interaction: $P > 0.77$; $R^2 = 0.98$). Alkalinity measurements indicate that lower light availability led to decreased algal production in deeper enclosures. In hard-water lakes such as Lake Brunsee (alkalinity $\approx 3.5 \text{ mmol l}^{-1}$), primary production causes precipitation of dissolved calcium carbonate at a rate roughly proportionate to carbon fixation (Wetzel 1983). This decalcification is reflected in a proportionate loss of alkalinity. Although this balance calculation ignores heterotrophic processes and fluxes of inorganic carbon among water and air, primary production over a certain period can be roughly approximated from the loss of alkalinity over that period (see Diehl et al. 2002). The average loss of alkalinity per day (calculated as the slope of a linear

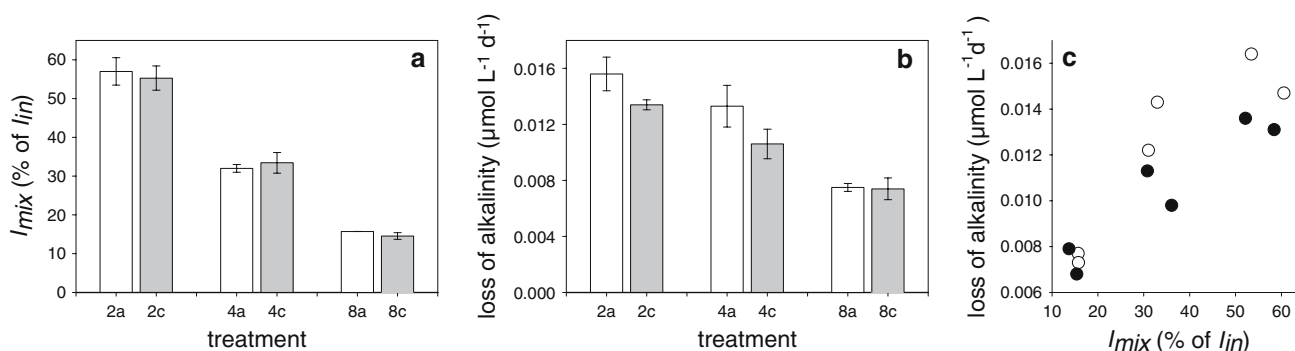


Fig. 2 **a** Average light intensity of PAR (I_{mix} in % of incident PAR, I_{in}), and **b** loss of alkalinity ($\text{mmol l}^{-1} \text{day}^{-1}$) versus experimental treatment. *Open bars* indicate 'ambient' temperature treatments, *filled bars* 'cold' temperature treatments and 2,

4, 8 represent the mixing depths (in metres). *Error bars* represent SE. **c** Average light intensity versus loss of alkalinity, *open circles* indicate 'ambient' and *filled circles* 'cold' temperature treatments

regression of alkalinity versus time) was negatively affected by mixing depth and was lower in ‘cold’ than in ‘ambient’ treatments (Fig. 2b; ANOVA, effects of mixing depth: $P < 0.001$; effects of temperature treatment: $P = 0.023$; depth \times temperature interaction: $P = 0.22$; $R^2 = 0.95$). Alkalinity losses were strongly positively related to average light intensity (Pearson Correlation 0.87, $P < 0.001$), suggesting that algal production was light limited (Fig. 2c). Moreover, temperature treatment affected alkalinity losses only in the 2 and 4 m enclosures but not in the 8 m enclosures (Fig. 2b,c), probably because actual water temperatures hardly differed among the 8 m ‘cold’ and 8 m ‘ambient’ treatments (Fig. 1). A stepwise multiple regressions indicated indeed that light and temperature had additive effects on algal production. The relationship of alkalinity losses (AL , in $\text{mmol l}^{-1} \text{ day}^{-1}$) to average light intensity (I_{mix} , in % of incident PAR) and mean temperature during the experiment (T , in $^{\circ}\text{C}$) was best described by the equation $AL = -0.003 + 0.00013 I_{\text{mix}} + 0.00067 T$ ($R^2 = 0.89$), the term $I_{\text{mix}} \times T$ being excluded from the model.

We analysed treatment responses of both Chl a and POC as proxies of phytoplankton biomass. The concentrations of Chl a and POC were highly correlated throughout the experiment (Pearson $r = 0.75$, $P < 0.001$, $n = 108$) and responded very similarly to the treatments.

We therefore only show and discuss the Chl a results below.

In all treatments, we observed the same progression of seasonal events: a phytoplankton bloom was followed by a clear-water phase, a peak in *Daphnia* density and, finally, a decline of the *Daphnia* population to low densities (Fig. 3). To statistically analyse treatment effects on the magnitude and timing of these events, we used both the directly measured values (Fig. 3) and the values derived from the fitted Weibull functions, which allowed a finer temporal resolution (Figs. 4, 5). Because the results and statistical outcomes were very similar for both types of response variables, we do not refer to them separately in the following.

As expected, peak densities of phytoplankton and *Daphnia* were strongly negatively affected by mixing depth (Figs. 3, 4, Table 1), suggesting that *Daphnia* population growth depended strongly on the availability of light for phytoplankton production. In line with this, *Daphnia* peak densities were positively correlated with the average loss of alkalinity (Pearson $r = 0.80$ and $r = 0.85$ for measured and Weibull fitted peak densities, respectively, $P < 0.002$, $n = 12$) and with peak concentrations of Chl a (Pearson $r = 0.81$ and $r = 0.85$ for measured and Weibull fitted peak densities, respectively, $P < 0.002$, $n = 12$). In contrast, temperature

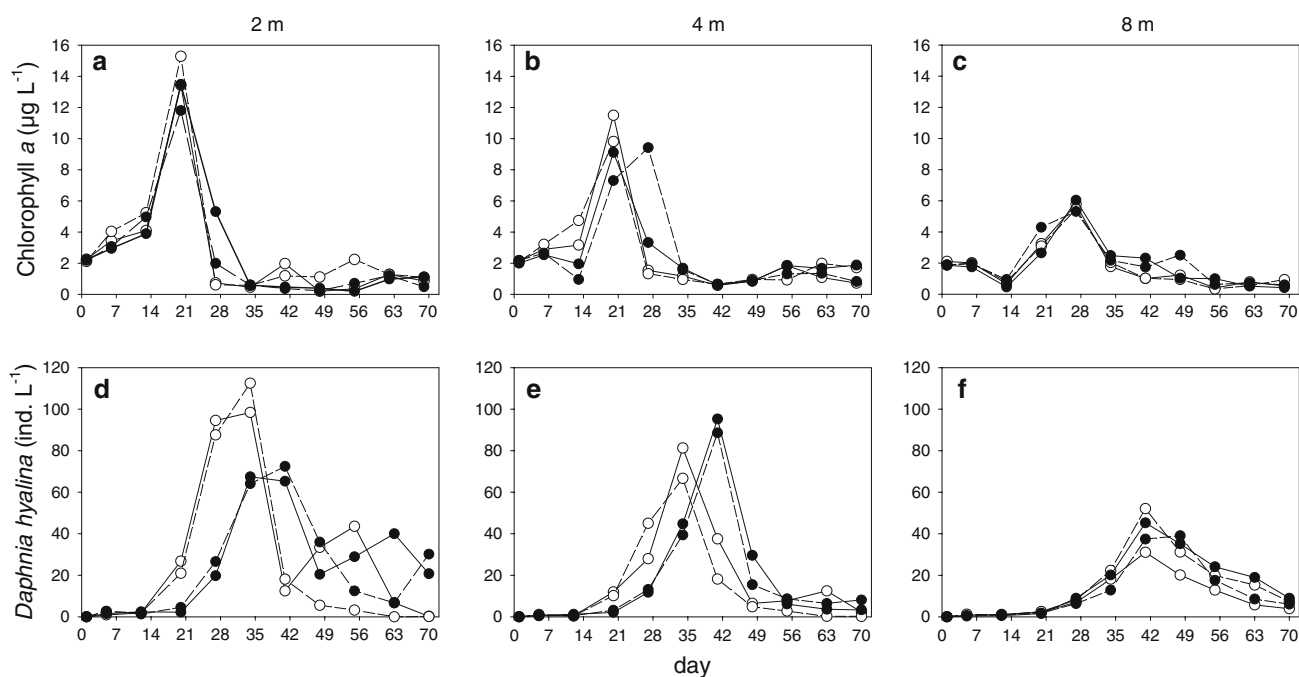


Fig. 3 a–c Phytoplankton biomass concentration (chlorophyll a , $\mu\text{g l}^{-1}$) and d–f, *Daphnia hyalina* abundance (individual l^{-1}) versus time (day 1 = 21 April, day 70 = 28 June). Open circles indicate ‘ambient’ temperature treatments, filled circles ‘cold’

temperature treatments. 2, 4 and 8 m mixing depths are shown in the left, middle and right panels, respectively. Dashed and solid lines distinguish the two replicates of each treatment

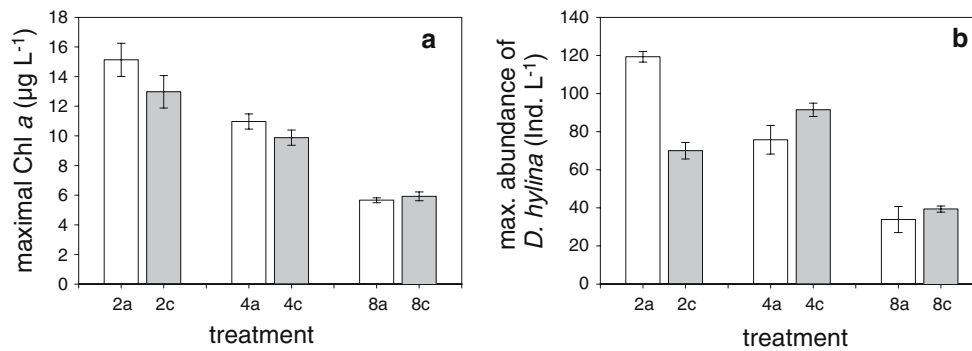


Fig. 4 Peak densities of **a** phytoplankton peak (chlorophyll *a* maximum, µg l⁻¹), and **b** *Daphnia hyalina* (individual l⁻¹) versus experimental treatment. Peak densities were estimated from Weibull functions fitted to the data (see [Materials and methods](#)).

Open bars indicate ‘ambient’ temperature treatments, *filled bars* ‘cold’ temperature treatments and 2, 4, 8 represent the mixing depths (in metres). *Error bars* represent SE

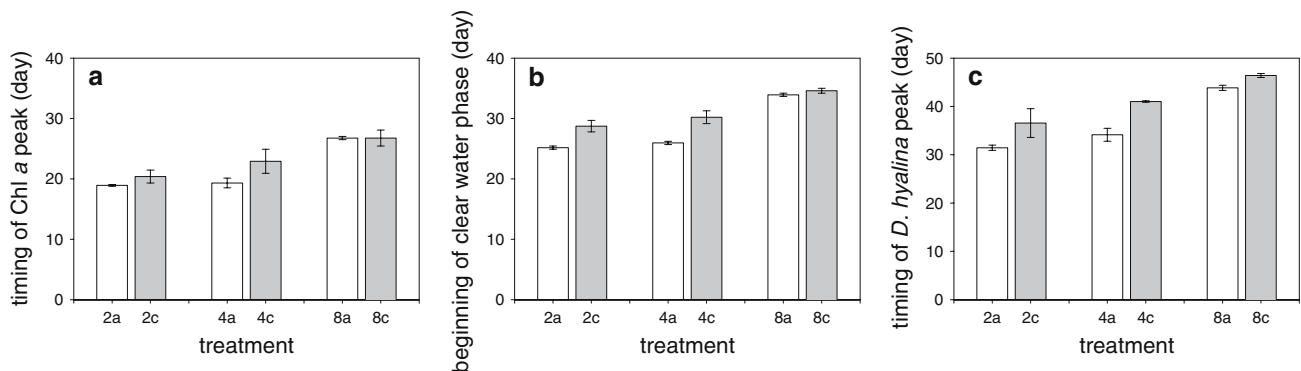


Fig. 5 a Timing of the phytoplankton peak (chlorophyll *a* maximum), **b** beginning of the clear-water phase (chlorophyll *a* < 2 µg l⁻¹) and **c** timing of the *Daphnia hyalina* peak (abundance maximum) versus treatment. The timing of events was estimated

from Weibull functions fitted to the data (see [Materials and methods](#)). *Open bars* indicate ‘ambient’ temperature treatments, *filled bars* ‘cold’ temperature treatments and 2, 4, 8 represent the mixing depths (in metres). *Error bars* represent SE

treatment had no consistent effects on peak densities. While the heights of the Chl *a* peaks were independent of temperature treatment, *Daphnia* peak densities were considerably lower in ‘cold’ than in ‘ambient’ enclosures at a mixing depth of 2 m, but not at 4 and 8 m (Figs. 3, 4, Table 1).

In accordance with expectations, both the clear-water phase and the *Daphnia* population peak occurred earlier in ‘ambient’ than in ‘cold’ enclosures (Figs. 3, 5b,c, Table 1), suggesting that increased temperature speeded up the timing of these successional events. In contrast to expectations, the timing of the first successional event, i.e. the peak of the phytoplankton bloom, was independent of temperature treatment (Figs. 3, 5a, Table 1). Most strikingly, however, the timing of all three successional events was negatively affected by mixing depth. The peak of the phytoplankton bloom, the beginning of the clear-water phase and the peak of the *Daphnia* population all occurred earlier in shallow than in deep enclosures

(Figs. 3, 5, Table 1). This strongly suggests that higher light availability speeded up the progression of successional events.

Discussion

Our enclosure experiment corroborates several of our previously stated hypotheses: (1) deeper mixing reduced the intensities of the phytoplankton bloom and the subsequent *Daphnia* peak; and (2) colder temperatures retarded the timing of the clear-water phase and the subsequent *Daphnia* peak. Our first hypothesis is based on the consideration that sustained population growth rate of *Daphnia* requires sustained algal production. Algal production, in turn, depends on light supply, which is inversely related to mixing depth (Fig. 2a). Previous enclosure experiments have indeed revealed a strong negative influence of mixed water column depth on the specific production of

Table 1 Summary of ANOVAs of the effects of mixing depth and temperature treatment on the intensity and timing of phytoplankton and *Daphnia* density peaks (maximal Chl *a* in $\mu\text{g l}^{-1}$ and maximal abundance in individual l^{-1}), and the beginning of the clear-water phase (day)

Dependent variable	Treatment effects (<i>P</i> values)			Overall model <i>R</i> ²
	Depth	Temperature	Depth × temperature	
Phytoplankton peak				
Measured	<0.001	0.122	0.424	0.98
Fitted	<0.001	0.188	0.287	0.98
<i>Daphnia hyalina</i> peak				
Measured	0.002	0.647	0.096	0.90
Fitted	<0.001	0.506	0.017	0.95
Timing of phytoplankton peak				
Measured	0.007	0.356	0.422	0.83
Fitted	0.002	0.117	0.343	0.89
Timing of clear-water phase				
Measured	0.001	0.001	0.216	0.94
Fitted	<0.001	0.002	0.062	0.97
Timing of <i>Daphnia hyalina</i> peak				
Measured	0.031	0.030	0.630	0.79
Fitted	0.001	0.005	0.354	0.94
Difference in timing of phytoplankton and <i>Daphnia hyalina</i> peak				
Measured	0.196	0.091	0.959	0.58
Fitted	0.027	0.007	0.178	0.85

Peaks and timing were estimated from weekly measurements ('measured') or fitted with a Weibull function ('fitted') (see [Materials and methods](#)). Significant *P* values are indicated in bold

phytoplankton (Diehl et al. 2002, 2005; Ptacnik et al. 2003). To our knowledge, there are so far no published experimental studies relating the production and biomass of zooplankton to mixing depth. In addition to the experiment reported here, we have conducted similar experiments in Lake Brunnsee in different seasons (Haas 2002; Haupt 2004) and in a North Atlantic marine system (Kunz 2005), all of which revealed strong negative effects of mixing depth on the biomass of crustacean zooplankton. Moreover, we found a strong negative relationship of crustacean biomass to mixed layer depth in a comparative study of thermally stratified North German lakes (Berger et al. 2006). Together, these studies suggest that mixing depth is an important, so far overlooked, environmental factor determining the abundance of zooplankton in deep lakes.

Our second hypothesis is based on the well-established, positive influence of water temperature on individual growth rate of *Daphnia* (Lampert 1977; Ocrutt and Porter 1983; Dawidowicz and Loose 1992; Reichwaldt et al. 2005). Because the spring clear-water phase usually coincides with intense grazing from a growing *Daphnia* population (Lampert et al. 1986; Sarnelle 1993), high temperatures would be expected to foster an earlier onset of the clear-water phase via the faster build-up of significant grazer densities. Observational data have indeed reported an earlier build-up of *Daphnia* densities and an earlier onset of

the clear-water phase following warmer winters (Straile 2000, 2002; Scheffer et al. 2001). Interestingly, we did not find a relationship of crustacean biomass to water temperature in our comparative lake study, which analysed this relationship across seasonally averaged summer data (Berger et al. 2006). The latter suggests that temperature may affect the dynamics of crustacean zooplankton more strongly in spring (when the water is still relatively cold and high-quality food is temporally abundant) than in summer (when growth rates are often limited by the availability of high-quality algal food and by predation from planktivorous fish) (Sommer et al. 1986).

In our comparative lake survey, the epilimnetic concentration of algal biomass during summer was negatively related to mixing depth and weakly positively related to water temperature (Berger et al. 2006). We therefore asked whether the plankton communities in our enclosures settled to such a pattern towards the end of spring succession, when phytoplankton densities had stabilised. Early summer phytoplankton biomass (averaged over the last 3 weeks of the experiment) was indeed negatively related to mixing depth, but was unrelated to temperature (Fig. 3; ANOVA, effects of mixing depth: $P < 0.007$; effects of temperature treatment: $P = 0.59$; depth × temperature interaction: $P = 0.343$, $R^2 = 0.83$). We did not perform a similar analysis on the *Daphnia* data, because *Daphnia* populations in several enclosures

were still in transient dynamics towards the end of the experiment.

Notably, the timing of successional events was not only affected by temperature but also by mixing depth, with shallower mixing fostering an earlier onset of the spring phytoplankton bloom, an earlier onset of the clear-water phase, and an earlier occurrence of the *Daphnia* peak. These effects of mixing depth on successional events could be plausibly explained by the following scenario: (1) higher algal growth led to initially higher algal biomass in shallower enclosures; (2) higher food densities fostered faster *Daphnia* population growth in shallower enclosures; (3) the resultant higher *Daphnia* densities and grazing rates led to an earlier depletion of algal biomass (i.e. an earlier clear-water phase) in shallower enclosures; and (4) as a consequence, *Daphnia* populations eventually experienced severe food limitation and started to decline earlier (= earlier *Daphnia* peak) in shallower enclosures.

This scenario is consistent with the data from the ‘cold’ enclosures, where temperature differences among depth treatments were negligible. Accordingly, any differences in the timing of successional events in the ‘cold’ enclosures are most plausibly attributed to mixing depth-mediated differences in algal production. Consistent with step 1, phytoplankton biomass increased initially faster in shallower ‘cold’ enclosures (day 21: ~12, 8 and 4 $\mu\text{g Chl } a \text{ l}^{-1}$ in the 2, 4 and 8 m enclosures, respectively; Fig. 3a–c). Consistent with step 2, *Daphnia* biomass subsequently followed this pattern (day 28: ~20, 10 and 5 *Daphnia* l^{-1} ; day 35: ~60, 40 and 15 *Daphnia* l^{-1} in the 2, 4 and 8 m enclosures, respectively; Fig. 3d–f). Consistent with steps 3 and 4, shallower ‘cold’ enclosures entered the clear-water phase and reached the *Daphnia* peak earlier (Fig. 5b,c). Step 2 requires that algal biomass was not in the fully saturating range of *Daphnia*’s functional response, because otherwise *Daphnia* populations should have increased at identical rates in all depth treatments. Peak densities of seston biomass were around 0.8, 0.5 and 0.3 mg C l^{-1} in the 2, 4 and 8 m enclosures, respectively (data not shown). At these food densities, the ingestion rate of *Daphnia galeata* (a similar sized species as *D. hyalina*) is at 85, 75 and 65%, respectively, of its maximum following data of Muck and Lampert (1984) and at 45, 35 and 25% of its maximum following data of Lynch et al. (1986) and Urabe and Watanabe (1991) (see McCauley et al. 1996; Rinke and Vijverberg 2005), suggesting that even peak algal densities did not saturate *Daphnia*’s functional response during our experiment.

In retrospect, effects of mixing depth on the timing of successional events are not surprising. Increased

growth rates usually speed up population dynamics in simple resource-consumer models. Specifically, algal biomass in a dynamic light–nutrient–phytoplankton model approaches equilibrium much faster in shallow than in deep mixed water columns owing to higher transient growth rates at higher light supply (see Fig. 5 in Diehl et al. 2005). We were surprised, however, that the effects of mixing depth on the timing of successional events were more prevalent than effects of temperature, despite the rather strong temperature differences among treatments. Again, this suggests that climate-driven changes in the timing and depth of stratification may have at least as far-reaching consequences for plankton dynamics as have changes in temperature.

It should be noted, however, that treatment effects on the timing of successional events were relatively small in absolute terms, given the rather large treatment ranges especially with respect to mixing depth (recall that the black enclosures mimicked a much larger range of optical than physical depths). The timing of the clear-water phase in the shallowest, warmest enclosures differed by no more than 9 days from the deepest and coldest enclosures (treatments ‘2a’ and ‘8c’ in Fig. 5b), which is a relatively minor difference compared to the year-to-year variability observed in natural lakes. For example, the difference between the earliest and latest occurrence of the clear-water phase in Lake Constance was 45 days in the periods 1979 and 1994 (Straile 2000). This discrepancy may in part be explained by the relatively late start of our experiment and the relatively high initial water temperatures (both being consequences of a late ice-out followed by a period of rapid warming of Lake Brunnsee in 2005), leaving a limited scope for the development of treatment differences. In particular, one might expect larger temperature effects on the growth of *Daphnia* in the range 5–10°C (Orcutt and Porter 1983), which was only marginally covered in our experiment. Furthermore, although the temperature differences between ‘ambient’ and ‘cold’ treatments were large compared to current climate change scenarios (IPCC 2001), they were only moderate compared to the observed year-to-year temperature variation in temperate lakes. Moreover, the timing of seasonal events in most real lakes should be influenced by more complex biotic interactions than were possible in our experimental plankton communities. For example, Lampert and Schober (1978) observed that the *Daphnia* population in Lake Constance remained low in early spring in spite of high fecundity and suggested that *Daphnia* population growth and, consequently, the onset of the clear-water phase were

retarded by predation from *Cyclops vicinus* until the latter diapaused in May.

Shifts in phenology and the timing of seasonal events in response to global climate change have been described from a multitude of terrestrial, marine and freshwater habitats (see [Introduction](#)). Because different species may show independent responses to climate variability, there is growing concern that climate change may de-synchronise the life cycles of resources and their consumers, disrupting the flow of energy through food webs (Thomas et al. 2001; Visser and Holleman 2001; Edwards and Richardson 2004). The importance of a seasonal match between food availability and nutritional demands of developing consumers has long been recognised in fisheries biology (Cushing 1974). Recently, this ‘match–mismatch’ concept has been applied to the plankton dynamics of Lake Washington under global warming, where increased temperatures coincided with decreased synchrony in the seasonal development of phytoplankton and *Daphnia*, and thus possibly with a decreased transfer efficiency of primary production to higher trophic levels (Winder and Schindler 2004b). We caution, however, that the ‘match–mismatch’ concept may be most applicable to strictly donor-controlled systems. It is well documented that *Daphnia* populations can control phytoplankton biomass (Sarnelle 1992, 2003; Murdoch et al. 1998). It therefore, seems plausible to assume that the spring dynamics of phytoplankton and *Daphnia*, and thus the timing of their respective peak densities, are mutually interdependent. Our data support this view. Decreasing mixing depth (= increasing average light supply) and increasing temperature both decreased the time difference between the successive peaks in phytoplankton and *Daphnia* densities (Fig. 6, Table 1), which is in line with the observation that increased (light-dependent) algal production and increased (temperature-dependent) *Daphnia* growth both speed up successional dynamics in coupled *Daphnia*-phytoplankton models (S. Diehl, unpublished results).

In summary, our experiment revealed strong effects of mixing depth-dependent light supply, but not of temperature, on an algal spring bloom and a subsequent *Daphnia* population peak, and that temperature and mixing depth had separate and largely independent effects on the timing of these successional events including the onset of the clear-water phase. Mixing depth and temperature are highly correlated in real lakes (Mazumder and Taylor 1994; Berger et al. 2006). We therefore emphasise that these patterns could only be detected through experimentation. Furthermore, because mixing depth governs both the light

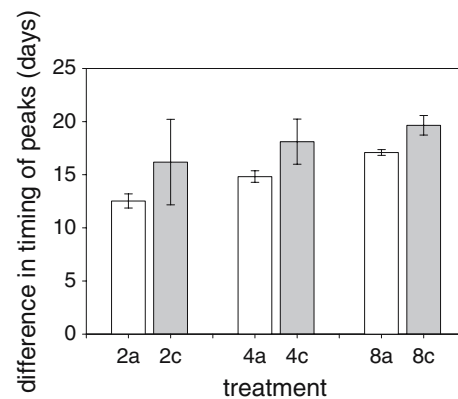


Fig. 6 Difference in timing of the peak densities of phytoplankton and *Daphnia hyalina* versus treatment. The timing of events was estimated from Weibull functions fitted to the data (see [Materials and methods](#)). *Open bars* indicate ‘ambient’ temperature treatments, *filled bars* ‘cold’ temperature treatments, and 2, 4, 8 represent the mixing depths (in metres). *Error bars* represent SE

climate and the temperature regime in the mixed surface layer, we propose that climate-driven changes in the timing and depth of water column stratification may have particularly far-reaching consequences for plankton dynamics and should receive increased attention.

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