

# Temperature is the key factor explaining interannual variability of *Daphnia* development in spring: a modelling study

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**Abstract** Plankton succession during spring/early summer in temperate lakes is characterised by a highly predictable pattern: a phytoplankton bloom is grazed down by zooplankton (*Daphnia*) inducing a clear-water phase. This sequence of events is commonly understood as a cycle of consumer-resource dynamics, i.e. zooplankton growth is driven by food availability. Here we suggest, using a modelling study based on a size-structured *Daphnia* population model, that temperature and not food is the dominant factor driving interannual variability of *Daphnia* population dynamics during spring. Simply forcing this model with a seasonal temperature regime typical for temperate lakes is sufficient for generating the distinctive seasonal trajectory of *Daphnia* abundances observed in meso-eutrophic temperate lakes. According to a scenario analysis, a forward shift of the vernal temperature increase by 60 days will advance the timing of the *Daphnia* maximum on average by 54 days, while a forward shift in the start of the spring bloom by 60 days will advance the *Daphnia* maximum only by less than a third (17 days). Hence, the timing of temperature increase was more important for the timing of *Daphnia* development than the timing of the onset of algal growth. The effect of

temperature is also large compared to the effect of applying different *Daphnia* mortality rates (0.055 or 0.1 day<sup>-1</sup>, 38 days), an almost tenfold variation in phytoplankton carrying capacity (25 days) and a tenfold variation in *Daphnia* overwintering abundance (3 days). However, the standing stock of *Daphnia* at its peak was almost exclusively controlled by the phytoplankton carrying capacity of the habitat and seems to be essentially independent of temperature. Hence, whereas food availability determines the standing stock of *Daphnia* at its spring maximum, temperature appears to be the most important factor driving the timing of the *Daphnia* maximum and the clear-water phase in spring.

**Keywords** Algae · Structured population model · Clear-water phase · Climate change

## Introduction

The annual succession of plankton organisms in temperate lakes was shown to follow constantly reoccurring patterns (PEG model, Sommer et al. 1986). The classic view of this succession is that primary production during winter is limited by physical factors (temperature, light limitation through mixing) and low winter phytoplankton biomasses are prevalent until mass development of algae starts in spring. High biomass of rapidly growing, small algae leads to increasing growth rates of herbivorous zooplankton. This finally results in a biomass maximum of zooplankton. First, the abundance of small zooplankters with high growth rates (e.g. ciliates, rotifers) increases (Weisse et al. 1990). Afterwards, usually cladocerans, e.g. *Daphnia*, become dominant. The growth of zooplankton and the associated predation pressure ultimately initiates the

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occurrence of a spring clear-water phase with very low concentrations of phytoplankton (Lampert et al. 1986).

Interestingly, the development of zooplankton stocks in this context is classically viewed as a trophic interaction being primarily related to the corresponding dynamics of their food, i.e. of phytoplankton (but see Lampert 1978). Also recent minimal models of zooplankton seasonal dynamics emphasise the predator–prey character of this interaction (Scheffer et al. 1997, 2001). However, zooplankton growth also depends strongly on temperature (Hall 1964; Rinke and Petzoldt 2003) which, besides food availability, increases strongly during spring development. In fact, more recent analyses of long-term data suggest that the spring development of, for example, *Daphnia* may be governed primarily by temperature and not by food availability (Adrian and Deneke 1996; Benndorf et al. 2001; Straile 2000; Straile and Adrian 2000).

Besides temperature development and food availability, *Daphnia* spring dynamics may also be influenced by other factors, for example, the timing of the *Daphnia* spring increase was strongly related to its winter abundance in Lake Washington, USA (Romare et al. 2005), whereas in Bautzen reservoir, Germany, variability in *Daphnia* mortality due to fish predation was suggested to influence *Daphnia* spring dynamics (Benndorf et al. 2001). Hence, interannual variability of *Daphnia* spring dynamics may be the result of several biotic and abiotic factors acting in concert.

An important focus in the analyses of algal–*Daphnia* interactions based on long-term time series (Straile 2002; Winder and Schindler 2004) but also in experiments (Berger et al. 2007) is the timing of cardinal points, i.e. the phenology of this interaction. For example, the timing of the *Daphnia* maximum or the timing of maximum algal suppression due to *Daphnia* herbivory, i.e. the clear-water phase, has been the focus of several studies (Straile 2002; Anneville et al. 2002; Gerten and Adrian 2000). The relative importance of the various factors influencing the timing of these cardinal points is unclear, as in statistical analyses of field data it is often difficult to disentangle the effects of the different factors on plankton phenology as they are often highly interrelated in situ. A thorough understanding of the relative importance of these factors is, however, required to predict the response of the zooplankton dynamics to a change in, for example, the abiotic conditions in lakes that are expected as a consequence of climate warming.

One possible method to investigate the relevance of environmental conditions for the growth of *Daphnia* and algae is to control forcing conditions in mesocosm experiments (e.g. Berger et al. 2007). Alternatively, numerical experiments can be performed to study the impact of forcing conditions and physiological parameters on the *Daphnia*–algae interaction by changing specific factors, e.g.

the water temperature or the mortality rate, in numerical simulations. Such a more theoretical, process-based approach will help to develop a mechanistic understanding of the drivers of spring development and, therefore, of the likely factors producing long-term trends in phenology.

Here, we adopt the latter approach and specifically investigate the relative importance of temperature, food dynamics, overwinter biomass and *Daphnia* mortality for *Daphnia* spring dynamics based on numerical modelling. A modelling study allows varying one environmental factor, e.g. temperature, whilst keeping all other factors constant, but also the study of potential interactions between different forcing factors. We use a physiologically structured population model of *Daphnia* (Rinke and Vijverberg 2005) to simulate *Daphnia* spring dynamics in response to temperature, food dynamics, overwinter biomass and *Daphnia* mortality. A structured population model with a dynamic age- and size-structure (physiologically structured population models, De Roos and Persson 2001) is employed because demographic effects can play a major role in cladoceran population dynamics (Hülsmann and Weiler 2000; Slobodkin 1954).

The focus of this work is an exploration of consumer–resource dynamics in a system consisting of *Daphnia* (consumer) and one resource (algae) by means of a physiologically structured population model. We particularly concentrate on the timing of cardinal events in these dynamics (e.g. *Daphnia* maximum, algal minimum) in a seasonal simulation and the effect of temperature on these dynamics. Although the growth of the consumer necessarily depends on the availability of its resource, the rate of this interaction is mediated by temperature. We therefore hypothesise that the timing of cardinal events under field conditions is predominantly determined by the temperature development and to a much lesser extent by resource levels. Our approach will be an important step towards a mechanistic understanding of the drivers of spring plankton dynamics and, therefore, of the likely factors producing variability and long-term trends in phenology.

## Materials and methods

### Model

In order to study the influence of environmental conditions on zooplankton dynamics in early spring we applied a physiologically structured population model of *Daphnia galeata*, which was introduced and extensively studied in Rinke and Vijverberg (2005). This model consists of an individual level model (Table S1 in Electronic supplementary material), integrated into a structured population model via an escalator boxcar train (see De Roos 1997;

De Roos et al. 1992). The latter represents a numerical method to simulate population dynamics on the basis of age-based cohorts and links individual physiology and life history to population level processes. The application of a structured model is important because daphnid life history leads to delaying effects on the population level, e.g. by egg development or by time needed to reach maturity. A detailed description of the structured population model is given in the Electronic supplementary materials (Table S2).

The individual-level model describes size-dependent metabolic rates and follows the concept of dynamic energy budget models (see Kooijman 2000, 2001). These kind of models simulate the individual life history on the basis of a closed carbon budget and defined rules for resource allocation. Assimilated resources are partitioned between somatic growth, maintenance and reproduction/maturation according to the  $\kappa$ -rule (Kooijman 2001). By following this rule a fixed proportion (given by parameter  $\kappa$ ) of assimilated resources are allocated to somatic growth and maintenance, whereas the remaining assimilate (given by  $1 - \kappa$ ) is allocated to reproduction. For details refer to Table S1 in the Electronic supplementary material.

We slightly changed energy allocation under conditions of starvation in order to simplify the original model of Rinke and Vijverberg (2005) by applying the following rules:

1. If assimilation rate ( $A$ ) is not sufficient to meet maintenance ( $M$ ), mortality increases due to the detrimental effects of starvation and the mortality rate is set to a value of  $0.35 \text{ day}^{-1}$  (Rinke and Vijverberg 2005). At the same time, somatic growth rate and reproductive rate are set to zero.
2. If the assigned energy flow to somatic growth and maintenance ( $\kappa \times A$ ) is not sufficient to meet maintenance, but overall assimilation rate is larger than maintenance requirements, we first subtracted the maintenance from the assimilation rate. The remaining assimilate ( $A - M$ ) is then completely allocated to reproduction, i.e. somatic growth is ceased under this condition.
3. Whenever  $\kappa \times A$  is adequate to meet maintenance, we followed the given energy allocation rule ( $\kappa$ -rule, see Table S1 in the Electronic supplementary material).

The dynamic model of phytoplankton resources consists of a logistic growth model describing the change in phytoplankton density with constant maximal growth rate ( $\alpha$ ) and carrying capacity ( $CC$ ) of phytoplankton ( $P$ ):

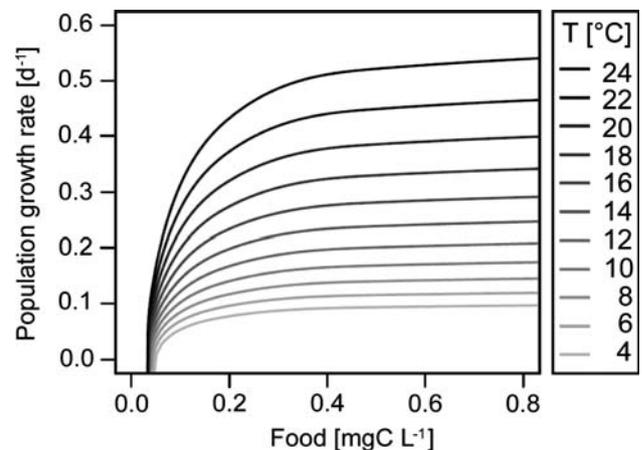
$$\frac{dP}{dt} = P\alpha \frac{CC - P}{CC} - \sum_{i=0}^{i=n} I(T, P, L_i) \cdot N_i. \quad (1)$$

Phytoplankton losses in the model are entirely due to *Daphnia* grazing combined over the different *Daphnia* ages

classes ( $i = 0, \dots, n$ ). Grazing in each age class  $i$  is determined by the dependency of the ingestion rate per individual ( $I$ ) on temperature ( $T$ ), on phytoplankton concentration ( $P$ ) and on *Daphnia* size in the respective age class ( $L_i$ ).  $N_i$  is the number of *Daphnia* in age class  $i$ .

For a basic depiction of model performance and a straightforward interpretation of model outcomes, we calculated the population growth rates of *Daphnia* at equilibrium age structure under different conditions of ambient food concentrations and temperature (Fig. 1). In these calculations the mortality rate was set to zero and we assumed a maximum life span of *Daphnia* of 70 days. Note that these population growth rates emerge from a model formulation purely focused on individual-level processes and are not the result of model parameters describing population growth as in simpler biomass models. Maximum population growth rates of *Daphnia* (calculated at a saturated food concentration of  $1 \text{ mg C l}^{-1}$ ) in the size-structured model are above  $0.5 \text{ day}^{-1}$  at  $24^\circ\text{C}$  and below  $0.1 \text{ day}^{-1}$  at  $4^\circ\text{C}$ . Hence, at low winter temperatures the *Daphnia* population will decline when the mortality rate is e.g.  $0.1 \text{ day}^{-1}$ , even when food concentration is at its maximum. Note also that positive population growth in the physiologically structured population model begins only above a threshold food level (see Fig. 1) required for daphnids to meet basic maintenance requirements and to reach the length at maturity.

To implement the model we used the simulation software MATLAB. A maximal lifespan of daphnids of 70 days (Lynch 1980) was assumed. Our escalator boxcar train formulation is based on age cohorts of individuals



**Fig. 1** Population growth rates of *Daphnia galeata* at equilibrium age structure at different conditions of food and temperature. Mortality rate was set to zero and the maximum life span of daphnids was assumed to be 70 days. Note that the temperature and food dependence of the population growth rates follows from the temperature and food dependence of length growth and egg production in the individual-level model.  $d^{-1} \text{ Day}^{-1}$

born within 0.1 day, i.e. the whole population consists in total of 700 cohorts and the age classes were renumbered at a discrete time step of 0.1 day. During each time interval between the re-numbering of the age classes, we applied a 4th order Runge–Kutta algorithm with variable step size to solve the coupled differential equations for all cohorts.

#### A “naive” simulation

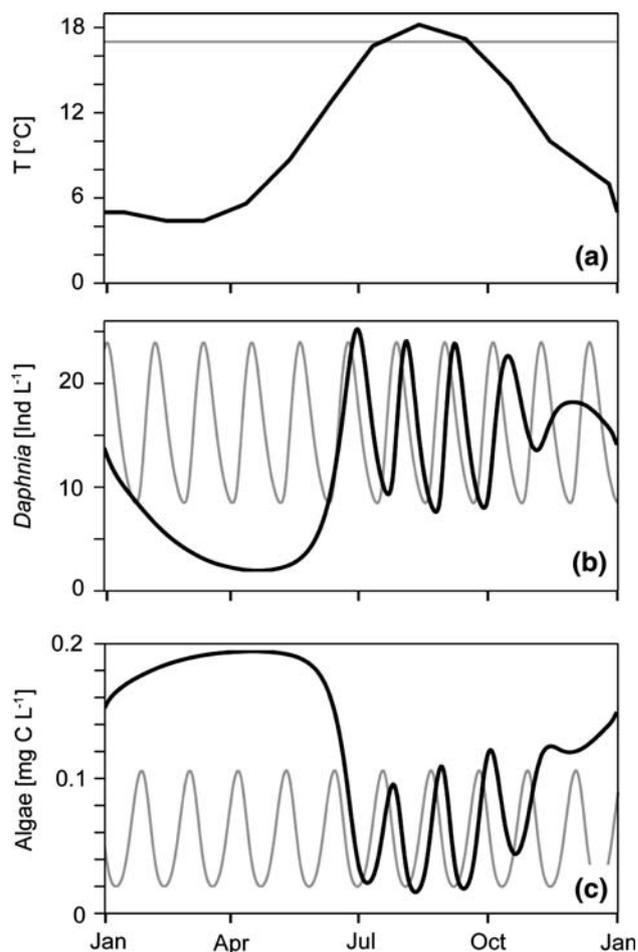
In order to simulate seasonal dynamics of zooplankton we forced the structured population model with the seasonal temperature (average temperature in 0–8 m) development typical for a deep lake, e.g. Lake Constance (Fig. 2a; Straile and Adrian 2000). *Daphnia* mortality rate ( $d_b$ ) was set to  $0.1 \text{ day}^{-1}$  (Hülsmann 2000). Algal dynamics were calculated according to Eq. 1 using a constant carrying capacity of  $0.2 \text{ mg C l}^{-1}$  throughout the season. We consider this simulation “naive” since environmental forcing acts directly only on the physiology of *Daphnia* (via a temperature effect on, e.g. ingestion, maintenance, reproduction, length growth), but not on phytoplankton. Environmental forcing of phytoplankton growth is therefore only indirect, i.e. mediated by *Daphnia*, and potential direct effects of e.g. seasonal changes in light availability and temperature on algal growth are ignored. Nevertheless, this “naive” simulation already captures the main features of the development of phytoplankton and *Daphnia* populations in spring (Fig. 2b, c). However, to disentangle the effects of food versus temperature on *Daphnia* dynamics it is necessary to allow seasonal forcing to also act directly on algal growth. To achieve this we modified the algal model of Eq. 1 and performed a scenario analysis with the modified formulation.

#### Scenario analysis

To include seasonal forcing on phytoplankton growth, we added a seasonal component ( $\sigma_{\text{al}}$  = seasonal cycle of ambient light of the water column) modifying the growth rate and the carrying capacity of phytoplankton in Eq. 1:

$$\frac{dP}{dt} = (\alpha_{\text{min}} + \sigma_{\text{al}}(\alpha_{\text{max}} - \alpha_{\text{min}}))P \times \left(1 - \frac{P}{\text{CC}_{\text{min}} + \sigma_{\text{al}}(\text{CC}_{\text{max}} - \text{CC}_{\text{min}})}\right) - \sum_{i=0}^{i=n} I(P, T, L_i) \cdot N_i. \quad (2)$$

The parameters  $\text{CC}_{\text{max}}$  and  $\text{CC}_{\text{min}}$  describe maximal and minimal phytoplankton carrying capacity,  $\alpha_{\text{max}}$  and  $\alpha_{\text{min}}$  specify the maximal and minimal growth rate of phytoplankton in our scenarios.  $\sigma_{\text{al}}$  is modelled as a hyperbolic tangent function (Fig. 3b; for a detailed description of variables and parameters see Table 1):

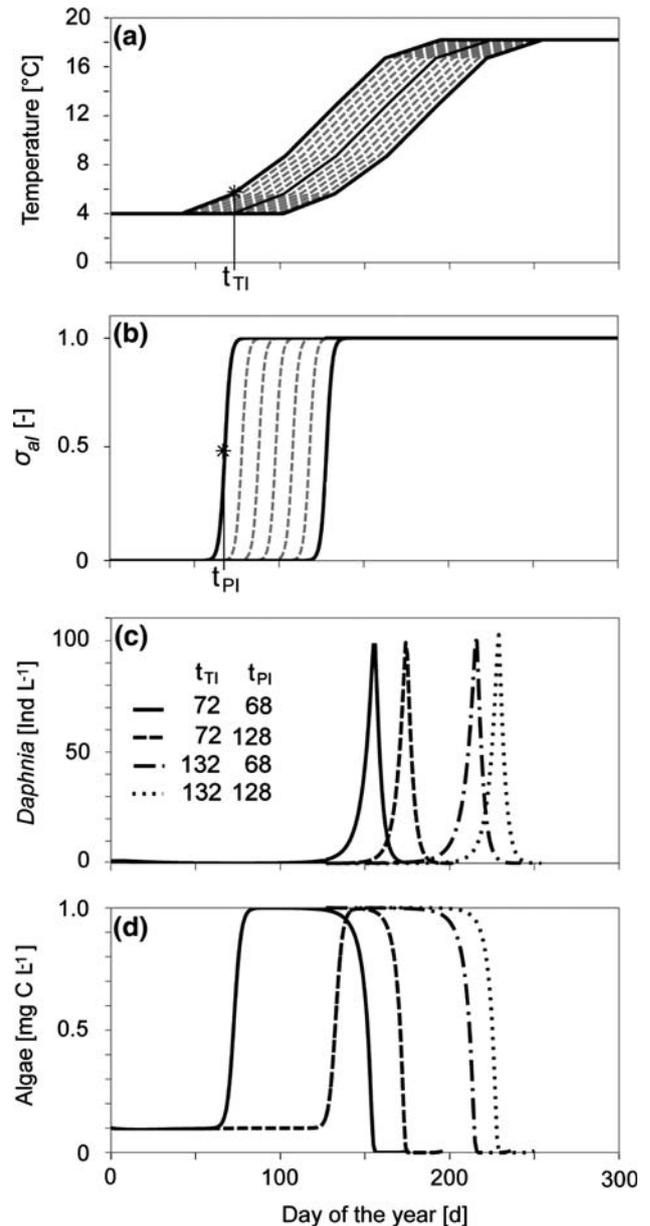


**Fig. 2** Simulation of the physiologically structured population model of *D. galeata* (Rinke and Vijverberg 2005) at a constant temperature of  $17^\circ\text{C}$  (grey lines) and forced with the mean seasonal variation of water temperature in Lake Constance (Straile and Adrian 2000) (black lines), respectively (“naive” simulation). Algal carrying capacity was kept constant at  $0.2 \text{ mg l}^{-1}$ . The mean seasonal variation of water temperature is based on data from 1979 to 1994 in Lake Constance. In both cases we show the model results after the seasonal dynamics were independent of initial conditions. *Ind* Individual, *Jan* January, *Apr* April, *Jul* July, *Oct* October

$$\sigma_{\text{al}} = \frac{1}{2} \cdot (\tan h(0.3(t - t_{PI})) + 1). \quad (3)$$

The parameters  $t_{PI}$  and  $\text{CC}_{\text{max}}$  allowed us to influence two aspects of algal spring dynamics separately: the timing of the phytoplankton bloom and the height of the phytoplankton biomass. The timing of the seasonal transition in the phytoplankton growth parameters can be interpreted as the timing of the release of algal growth from severe light limitation during winter due to, e.g. ice-break up in shallow or moderately deep lakes or stratification in deep lakes. Field studies have shown that the timing of algal growth may vary from year to year by 2 months due to variability in the start of stratification (Peeters et al. 2007b) or the timing of ice break-up (Adrian et al. 1999).

**Fig. 3 a, b** Scenario definitions for the onset of temperature increase ( $t_{TI}$ ) varying from 12 March until 11 May (a), and the timing of release of phytoplankton growth from light limitation ( $t_{PI}$ ) varying from 8 March until 7 May (b). The middle trajectory in a (bold line) closely corresponds to the temperature regime in Fig. 2a (January–August) that was used in the “naive” simulations of Fig. 2b, c. Exemplary model results for *Daphnia* abundance (c) and algae concentration (d) obtained from different scenarios. Trajectories are shown until the *Daphnia* winter abundance after the *Daphnia* spring maximum was reached. The timing of vernal temperature increase ( $t_{TI}$ ) and the timing of the release of phytoplankton growth from light limitation ( $t_{PI}$ ) differs between simulations:  $t_{TI}$  and  $t_{PI}$ , respectively, are the 12 March and 8 March (solid lines); 12 March and 7 May (dashed); 11 May and 8 March (dashed dotted lines); 11 May and 7 May (dotted lines). In these simulations the *Daphnia* winter abundance was 1 ind  $l^{-1}$ , the *Daphnia* mortality rate ( $d_b$ ) was 0.1 day $^{-1}$  and the maximal phytoplankton carrying capacity was 1 mg C  $l^{-1}$ . Note that the trajectories of the *Daphnia* populations coincide until day 100 (c), whereas in the case of phytoplankton the solid and dashed dotted lines as well as the dashed and dotted lines coincide until reaching their maximum (d)



The factor 0.3 in Eq. 3 shapes the slope of the sigmoid curve and results in a seasonal transition of  $\sigma_{al}$  from 0 and 1 within approximately 2 weeks corresponding to a transition from  $\alpha_{min}$  ( $CC_{min}$ ) to  $\alpha_{max}$  ( $CC_{max}$ ) within this time period. The length of this transition period reflects the fast build-up of phytoplankton blooms after the occurrence of suitable conditions (Peeters et al. 2007a).

In all scenarios, the model was run from 1 January until the clear-water phase. All model runs were started with an exponentially declining *Daphnia* age distribution (for further information of the initial conditions see Electronic supplementary material). Altogether we varied five different parameters in our scenarios. Two of them modify the timing of cardinal events and hence are strongly related to meteorological forcing:

1. The timing of vernal temperature increase ( $t_{TI}$ ): varying from 12 March until 11 May in steps of 5 days (Fig. 3a). Note that the middle trajectory in Fig. 3a corresponds to the temperature regime of Fig. 2a (January–August) that was used in the “naive” simulations of Fig. 2b, c.
2. The timing of the release of phytoplankton growth from light limitation ( $t_{PI}$ ), i.e. the timing of the onset of the phytoplankton spring bloom: varying from 8 March until 7 May in steps of 10 days (Fig. 3b).

The impact on the *Daphnia* and algae dynamics of these two meteorologically related parameters representing the timing of forcing conditions is exemplified in Fig. 3c, d, presenting simulations with different combinations of the earliest and the latest  $t_{TI}$  and  $t_{PI}$ .

Variability in the other three parameters of the scenarios is strongly associated with, e.g. the trophic status and/or the

depth of a lake, although it can also be due to meteorological interannual variability (see “Discussion”):

1.  $CC_{max}$ : varying from 0.15 to 1.0 mg C  $l^{-1}$  with values of 0.15, 0.2, 0.3, 0.4, 0.6 and 1 mg C  $l^{-1}$ .
2. *Daphnia* winter abundance ( $D_w$ ): one or ten individuals  $l^{-1}$ .
3.  $d_b$ : 0.055 or 0.1 day $^{-1}$ .

Forcing the model with all possible combinations of these values for the five parameters resulted in 2,184 model runs, i.e. 2,184 different realizations of algae and *Daphnia* spring dynamics. To reduce the complexity of statistical analysis, we extracted the following cardinal events from

**Table 1** Variables and parameter values used in the scenario analysis

Parameter	Value	Unit	Description
$\alpha_{\min}$	0.1	day <sup>-1</sup>	Minimal growth rate of phytoplankton
$\alpha_{\max}$	0.5	day <sup>-1</sup>	Maximal growth rate of phytoplankton
CC <sub>min</sub>	0.1	mg C l <sup>-1</sup>	Minimal phytoplankton carrying capacity
CC <sub>max</sub>	0.15–1.0	mg C l <sup>-1</sup>	Maximal phytoplankton carrying capacity
$t$	–	Julian day	Simulation time
$t_{PI}$	8 March–7 May	Julian day	The timing of release of phytoplankton growth from light limitation
$t_{TI}$	12 March–11 May	Julian day	The onset of temperature increase
$D_w$	1 or 10	Ind l <sup>-1</sup>	<i>Daphnia</i> winter abundance
$D_b$	0.055 or 0.1	day <sup>-1</sup>	<i>Daphnia</i> mortality rate

each model run for analyses of effect sizes and simple and multiple regression analysis:

1. The timing and the height of the *Daphnia* minimum, defined as the global minimum in the *Daphnia* abundance before the *Daphnia* spring maximum ( $t_{D,\min}$ ,  $h_{D,\min}$ , respectively).
2. The timing and the height of the *Daphnia* spring maximum, defined as the maximum in the spring *Daphnia* abundance ( $t_{D,\max}$ ,  $h_{D,\max}$ , respectively).
3. The timing and the height of the spring phytoplankton minimum (clear-water phase), defined as the minimum in the phytoplankton concentration after the *Daphnia* spring maximum.

## Results

### “Naive” simulation

Running the model with a constant temperature of 17°C resulted in regular predator-prey cycles with a period of approximately 35 days. In contrast, forcing the model with the mean seasonal variation of water temperature showed a seasonal cycle of *Daphnia* with low *Daphnia* abundances during winter and high abundances during the vegetation period and the maximum *Daphnia* abundance occurring in July (Fig. 2). As soon as temperature increased sufficiently in late spring, positive population growth rates were realised by the *Daphnia* population. During the cold season, population size was decreasing since population birth rates were low and unable to compensate for mortality. Within this “naive” simulation of *Daphnia* dynamics, water temperatures appear to be the key environmental factor controlling whether population rate of change is positive or negative. However, since the algal dynamics are modelled without considering seasonally varying growth conditions of algae, the model predicts algae to approach their carrying capacity during winter, i.e. during the period of

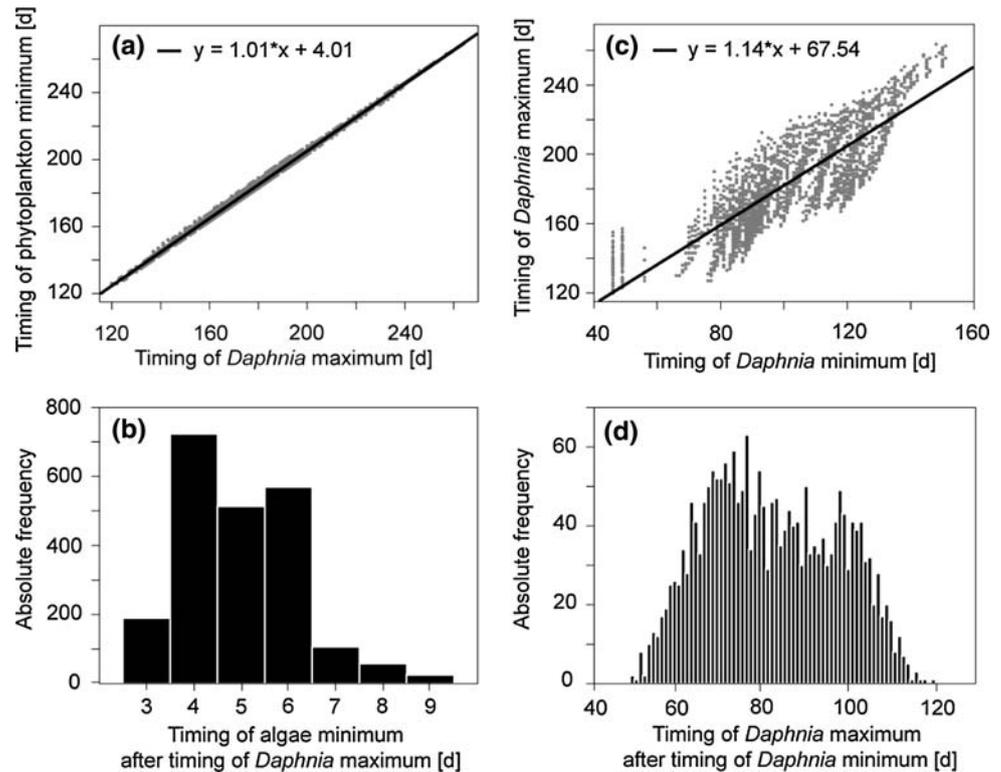
lowest *Daphnia* grazing. Despite this large phytoplankton concentration in winter, the model describes the qualitative development of the *Daphnia* population in deep temperate lakes surprisingly well; i.e. a depressed population in winter and the initiation of growth in spring followed by an early summer decline. This pattern of *Daphnia* population development obtained with the “naive” simulation qualitatively agreed well with empirical observations (see, e.g. Straile 2000, 2002) suggesting that the seasonal temperature variation is an important factor controlling *Daphnia* development.

In particular, the start of the growing season appeared to be predominantly determined by ambient temperature, but since food concentration reached high values during winter and early spring in the simulation, i.e. before *Daphnia* growth starts, these results do not reveal what kind of influence a possible food limitation can exert on the initiation of *Daphnia* population growth. The relative importance of food versus temperature for the spring dynamics of *Daphnia* can, however, be assessed from the outcome of the scenario analysis.

### Scenario analysis

The statistical analysis of the 2,184 model runs indicates that, despite the wide range of parameter sets, the timing of succession events were related to each other. The timing of the *Daphnia* spring maximum was closely related to the timing of the spring phytoplankton minimum ( $R^2 = 0.998$ ,  $P < 0.0001$ ; Fig. 4a), whereas it was less tightly related to the timing of the *Daphnia* winter minimum ( $R^2 = 0.715$ ,  $P < 0.0001$ ; Fig. 4c). The phytoplankton minimum occurred on average 5 days (range 3–9 days; Fig. 4b) after the *Daphnia* maximum, whereas the latter followed the *Daphnia* winter minimum on average after 82 days (range 46–120 days; Fig. 4d). Because of the tight relationship between the timing of *Daphnia* maximum and phytoplankton minimum, we do not explicitly present results regarding timing of phytoplankton minimum in the

**Fig. 4** Linear relationship between the timing of *Daphnia* maximum and (a) the timing of the phytoplankton minimum, and (c) the timing of the *Daphnia* minimum, respectively. The phytoplankton minimum occurred on average 5 days after the *Daphnia* maximum (b). The *Daphnia* maximum followed the *Daphnia* winter minimum on average after 82 days (d)



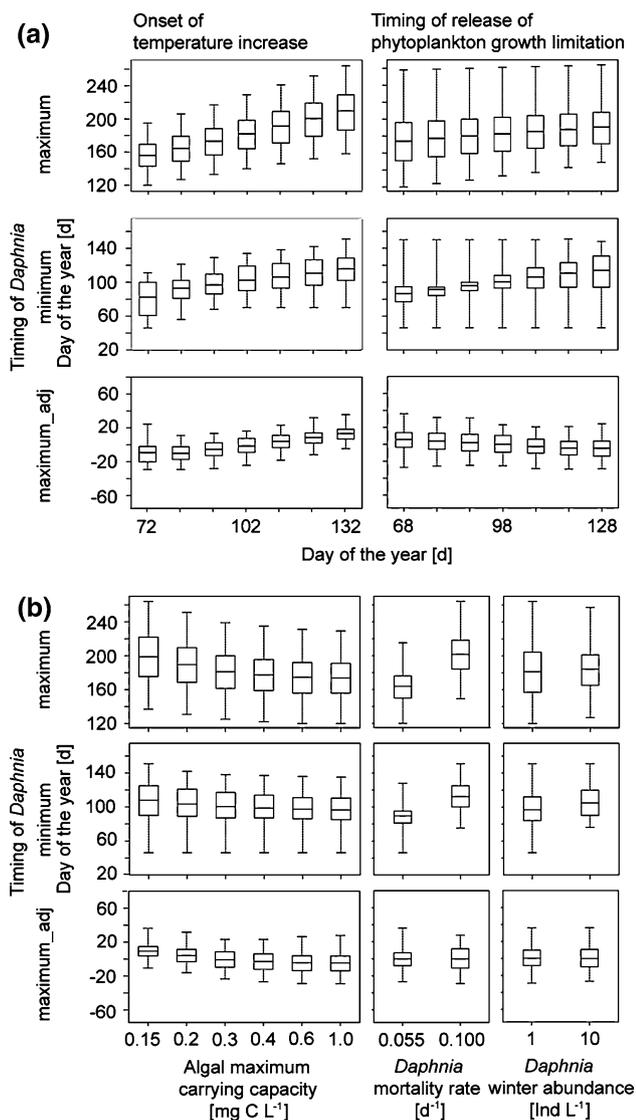
following but focus our analysis only on the timing of the *Daphnia* maximum and minimum. But note that all statements about the timing of the *Daphnia* maximum are also valid for the timing of the phytoplankton minimum, i.e. for the timing of the clear-water phase.

The timing of the *Daphnia* maximum was more strongly affected by the timing of vernal warming than by shifts in the timing of phytoplankton growth release (Fig. 5a). While a 60-day advance in  $t_{PI}$  advanced the *Daphnia* maximum by 17 days, a similar advance in  $t_{TI}$  advanced the *Daphnia* maximum by 54 days (Fig. 5a). The large effect of  $t_{TI}$  relative to  $t_{PI}$  is also reflected by regression analysis: variability in  $t_{TI}$  accounted for 36% of the variability in the timing of *Daphnia* spring maximum ( $t_{D,max}$ ), whereas  $t_{PI}$  could explain only 4% (Table 2). An increase in the  $D_w$  by 1 order of magnitude on average resulted in a 3-day delay of  $t_{D,max}$ , whereas an increase in the maximal phytoplankton carrying capacity by 1 order of magnitude on average advanced  $t_{D,max}$  by 25 days (Fig. 5b). The increase in mortality rate from 0.055 to 0.1 day<sup>-1</sup> resulted in an average delay of  $t_{D,max}$  of 38 days and variability in mortality explained 45% of  $t_{D,max}$  variability (Fig. 5b; Table 2). Due to the strong effect of  $d_b$ , statistical analysis was also performed separately for the two mortality rates:

The timing of temperature increase explained 72 and 60% of  $t_{D,max}$  variability at high and low *Daphnia* mortality, respectively, i.e. the temperature effect increases with mortality rate (Table 2). Accordingly, the influence of

the timing of phytoplankton growth ( $t_{PI}$ ) on  $t_{D,max}$  decreased with increasing  $d_b$  ( $R^2$  decreased from 14 to 3%; see Table 2). In conclusion, temperature development (i.e.  $t_{TI}$ ) did explain a considerably higher percentage of  $t_{D,max}$  variability than food dynamics (i.e.  $t_{PI}$ ) in both mortality regimes. This is also reflected in contour plots showing mean  $t_{D,max}$  as a function of both  $t_{TI}$  and  $t_{PI}$  under the two mortality regimes (Fig. 6a, b; variability in  $x$ -direction is higher than in  $y$ -direction). Although the importance of  $t_{TI}$  and  $t_{PI}$  for explaining variability in  $t_{D,max}$  is very different, both factors appeared to act almost additively as is reflected by the almost linear isolines in Fig. 6a, b.

In contrast to this,  $t_{TI}$  and  $t_{PI}$  were of approximately similar importance for the timing of the *Daphnia* minimum ( $t_{D,min}$ ) when considering both mortality regimes together (Fig. 5a; Table 2). However, the relative importance of  $t_{TI}$  and  $t_{PI}$  reverses at the two different mortality regimes. At low mortality,  $t_{TI}$  (33%) did explain a higher percentage of  $t_{D,min}$  than  $t_{PI}$  (21%), while  $R^2$  was 29 and 38% for  $t_{TI}$  and  $t_{PI}$ , respectively, at high mortality (Table 2). The interaction between  $t_{TI}$  and  $t_{PI}$  with respect to the timing of the *Daphnia* minimum appeared to be clearly non-additive and non-linear since isolines were convex and concave, respectively (Fig. 6c, d). When *Daphnia* mortality was low, early  $t_{TI}$  resulted in early  $t_{D,min}$  irrespective of  $t_{PI}$ , while  $t_{PI}$  was important for  $t_{D,min}$  if mortality was high (compare Fig. 6c, d). When *Daphnia* mortality was high, early  $t_{D,min}$  was only achieved when both  $t_{TI}$  and  $t_{PI}$  were



**Fig. 5** The effect of external (a) and internal (b) factors on the timing of *Daphnia* spring maximum, of late winter minimum and of adjusted spring maximum. Note that the horizontal line within a box represents the mean value, whiskers show the minimum and the maximum values and boxes describe the 25 and 75% percentile, respectively

early, i.e.  $t_{TI}$  and  $t_{PI}$  seemed to have an additive effect on  $t_{D,min}$  if mortality was high (Fig. 6d).

The timing of the *Daphnia* maximum depends not only on the timing of the *Daphnia* minimum (Fig. 4c) but also on the magnitude (not shown) of the *Daphnia* minimum: a late and low *Daphnia* minimum will cause a later occurrence of the *Daphnia* maximum, whereas an early and elevated *Daphnia* minimum will result in an earlier *Daphnia* maximum. The timing of the *Daphnia* minimum and the logarithm of the *Daphnia* minimum biomass together explain 79% of the variability in the timing of the *Daphnia* maximum in our simulations [ $t_{D,min}$ ,  $F = 1,247.1$ ,  $P < 0.0001$ ;  $\log(h_{D,min})$ ,  $F = 714.4$ ,  $P < 0.0001$ ]. That is,

factors influencing early *Daphnia* population dynamics, i.e. before the start of its growing season, strongly influence the timing of the *Daphnia* maximum in the model. To account for this, we used the residuals of this relationship ( $t_{D,max\_adj}$ ) as a measure for the timing of the *Daphnia* maximum adjusted for the early season influences on timing and magnitude of the *Daphnia* minimum. Interestingly,  $t_{D,max\_adj}$  is mostly explained by  $t_{TI}$  ( $R^2 = 0.37$ , Table 2), whereas the  $D_w$  and the  $D_b$  were not any more influential ( $R^2 = 0$  for both, Table 2). Furthermore,  $t_{PI}$  explained only 9% of  $t_{D,max\_adj}$  variability (Table 2), which is less than a quarter of  $t_{TI}$ . An advance in  $t_{TI}$  by 60 days resulted in an advance of  $t_{D,max\_adj}$  by 23 days, whereas a similar advance in  $t_{PI}$  advanced  $t_{D,max\_adj}$  by only 10 days (Fig. 5a). Considering both mortality rates separately, the relative importance of  $t_{TI}$  remained the same (Table 2). Besides  $t_{TI}$  and  $t_{PI}$ , the  $CC_{max}$  also had an influence on  $t_{D,max\_adj}$ , explaining 10% of its variability (Table 2). The response of the adjusted *Daphnia* maximum is similar to the results obtained from the unadjusted cardinal events: a late onset of temperature increase delays the timing of the *Daphnia* maximum, minimum, as well as the adjusted *Daphnia* maximum (indicated by positive residuals). However, this response is reversed for the timing of release of phytoplankton from growth limitation. Whereas later release from algal growth limitation delayed *Daphnia* minimum and maximum, the timing of the adjusted maximum was advanced (indicated by negative residuals). The reason for this advance is given by higher average temperatures during the growth period of *Daphnia* (i.e. time between *Daphnia* minimum and maximum): when release from algal growth limitation was late, the whole growth period of *Daphnia* was shifted to later times in the year and, therefore, averaged over all scenarios, took place at higher temperatures. So, in fact, the intuitively unexpected effect that a delayed timing of algal growth speeds up the development of *Daphnia* (adjusted by early season influences as given by  $t_{D,max\_adj}$ ) is mediated by temperature.

The timing of the *Daphnia* maximum occurred at an average water temperature of 15.0°C ( $\pm 2.4^\circ\text{C}$  SD). Considering the two mortality regimes separately, the corresponding water temperatures at low and high  $d_b$  are 12.9°C ( $\pm 1.7^\circ\text{C}$  SD, range 8.2–16.7°C) and 17.0°C ( $\pm 0.7^\circ\text{C}$  SD, range 15.0–18.2°C), respectively (Fig. S1 in Electronic supplementary material). In the majority of scenarios (97%) the *Daphnia* maximum was reached before temperatures reached the seasonal temperature maximum of 18.2°C (Fig. 3) used in our simulations.

In contrast to  $t_{D,max}$ ,  $h_{D,max}$  (the height of the *Daphnia* spring maximum) was neither affected by *Daphnia* overwintering biomass,  $t_{TI}$  nor  $t_{PI}$  (Fig. S2a in Electronic supplementary material). Instead, phytoplankton carrying capacity was strongly related to  $h_{D,max}$  ( $R^2 = 92\%$ ,

**Table 2** Results of single and multiple regressions (without interaction terms) for timing and height of *Daphnia* spring maximum and late winter minimum as a function of  $t_{TI}$ ,  $t_{PI}$ ,  $d_b$ ,  $D_w$  and  $CC_{max}$ .

Regressions were calculated for all scenarios (A) and for the two mortality regimes separately [ $0.055 \text{ day}^{-1}$  (B) and  $0.1 \text{ day}^{-1}$  (C)]. For abbreviations, see Table 1

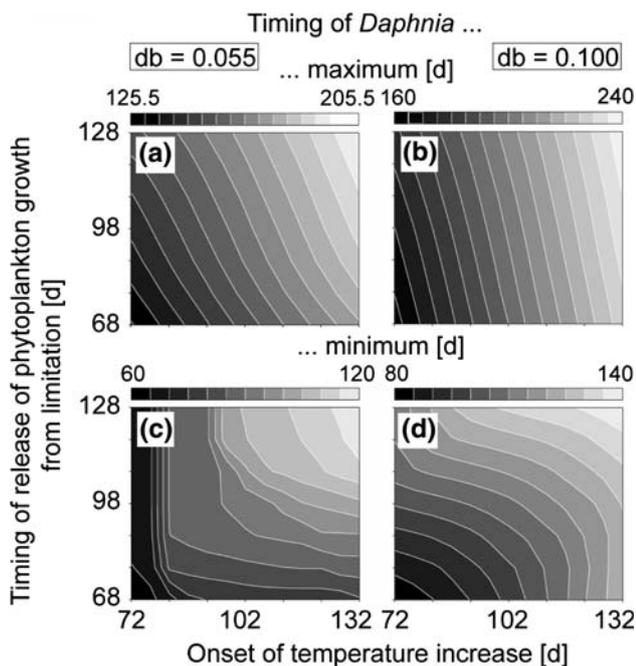
Dependent		Independent variables					Total	
Variable	Treatment	$t_{TI}$	$t_{PI}$	$D_w$	$CC_{max}$	$d_b$	$R^2$	
Timing of the <i>Daphnia</i> maximum ( $t_{D,max}$ )	A	$F^a$	8,859.10***	945.50***	67.30***	1,534.70***	11,134.00***	0.91
		Slope <sup>b</sup>	+	+	+	–	+	
		$R^2$ <sup>c</sup>	0.36	0.04	0.00	0.06	<b>0.45</b>	
	B	$F^a$	8,800.40***	2,058.90***	1,571.20***	1,242.10***		0.93
		Slope <sup>b</sup>	+	+	+	–		
		$R^2$ <sup>c</sup>	<b>0.60</b>	0.14	0.11	0.08		
	C	$F^a$	8,368.40***	385.90***	193.40***	1,658.00***		0.91
		Slope <sup>b</sup>	+	+	–	–		
		$R^2$ <sup>c</sup>	<b>0.72</b>	0.03	0.02	0.14		
Timing of <i>Daphnia</i> minimum ( $t_{D,min}$ )	A	$F^a$	2,153.80***	1,975.00***	363.90***	234.80***	2,940.10***	0.78
		Slope <sup>b</sup>	+	+	+	–	+	
		$R^2$ <sup>c</sup>	0.22	0.20	0.04	0.02	<b>0.30</b>	
	B	$F^a$	1,358.60***	854.20***	752.50***	11.20***		0.73
		Slope <sup>b</sup>	+	+	+	–		
		$R^2$ <sup>c</sup>	<b>0.33</b>	0.21	0.19	0.00		
	C	$F^a$	1,447.80***	1,921.60***	0.40 ns	543.60***		0.78
		Slope <sup>b</sup>	+	+	+	–		
		$R^2$ <sup>c</sup>	0.29	<b>0.38</b>	0.00	0.11		
Timing of the adjusted <i>Daphnia</i> maximum ( $t_{D,max\_adj}$ )	A	$F^a$	1,774.10***	425.10***	1.00 ns	474.90***	0.00 ns	0.55
		Slope <sup>b</sup>	+	–	–	–	–	
		$R^2$ <sup>c</sup>	<b>0.37</b>	0.09	0.00	0.10	0.00	
	B	$F^a$	580.60***	2.10 ns	14.90***	320.20***		0.46
		Slope <sup>b</sup>	+	+	–	–		
		$R^2$ <sup>c</sup>	<b>0.29</b>	0.00	0.01	0.16		
	C	$F^a$	2,807.90***	2,074.20***	12.70***	375.80***		0.83
		Slope <sup>b</sup>	+	–	+	–		
		$R^2$ <sup>c</sup>	<b>0.44</b>	0.33	0.00	0.06		
Height of <i>Daphnia</i> maximum ( $h_{D,max}$ )	A	$F^a$	18.00***	49.00***	16.90***	142,110.00***	10,297.00**	0.99
		Slope <sup>b</sup>	+	–	–	+	–	
		$R^2$ <sup>c</sup>	0.00	0.00	0.00	<b>0.92</b>	0.07	
	B	$F^a$	44.70***	93.60***	50.40***	97,647.00***		0.99
		Slope <sup>b</sup>	+	–	–	+		
		$R^2$ <sup>c</sup>	0.00	0.00	0.00	<b>0.99</b>		
	C	$F^a$	0.00 ns	2.50 ns	1.00 ns	135,090.00***		0.99
		Slope <sup>b</sup>	+	–	+	+		
		$R^2$ <sup>c</sup>	0.00	0.00	0.00	<b>0.99</b>		
Height of <i>Daphnia</i> minimum ( $h_{D,min}$ )	A	$F^a$	84.70***	96.20***	1,589.90***	2.30 ns	4,383.10***	0.74
		Slope <sup>b</sup>	–	–	–	+	–	
		$R^2$ <sup>c</sup>	0.01	0.01	0.19	0.00	<b>0.53</b>	
	B	$F^a$	827.40***	877.40***	24,982.00***	14.20***		0.96
		Slope <sup>b</sup>	–	–	–	+		
		$R^2$ <sup>c</sup>	0.03	0.03	<b>0.90</b>	0.00		
	C	$F^a$	666.90***	1,029.00***	1,218.60***	76.00***		0.73
		Slope <sup>b</sup>	–	–	+	+		
		$R^2$ <sup>c</sup>	0.16	0.25	<b>0.30</b>	0.02		

\*\*\*  $P < 0.0001$ , ns =  $P > 0.05$  [note that even a small  $R^2$  close to 0 (rounded down to 0.00 in the table) was significant in the regression analysis as most independent variables will have a significant effect in this data set generated by a deterministic model]

<sup>a</sup> The F-Values and  $R^2$ s (last column) for the multiple regression models including all five (A), respectively 4 (B, C) independent variables.

<sup>b</sup> The slope shows whether the relationship between dependent or independent variable is positive (+) or negative (–)

<sup>c</sup> Values for the single regressions between the respective dependent and each separate independent variable



**Fig. 6** Contour plots of the average timing of *Daphnia* maximum (a, b) and minimum (b, c) as a function of the onset of temperature increase and the timing of release of phytoplankton growth from limitation. Simulations were performed with mortality rates ( $db$ ) of  $0.055 \text{ day}^{-1}$  (a, c) and  $0.1 \text{ day}^{-1}$  (b, d), respectively

Table 2).  $h_{D,\min}$  (the height of *Daphnia* minimum) was strongly related to  $d_b$  ( $R^2 = 53\%$ ) when considering the total data set (Table 2). For both *Daphnia* mortalities, *Daphnia* overwintering biomass was the most important predictor of  $h_{D,\min}$  ( $R^2 = 90\%$  and  $R^2 = 30\%$  for the low and high mortality rate, respectively, Table 2).

## Discussion

The results of the “naive” simulation indicated the steering role of ambient temperature on the population dynamics of *Daphnia* in temperate lakes. We used time series of temperature development typical for a rather large and deep lake in order to simulate *Daphnia* population dynamics by means of a structured population model (Rinke and Vijverberg 2005). Just by applying this simple setting we were able to simulate a seasonal development of *Daphnia* abundance with a sequence of cardinal events that qualitatively complies with observations in temperate lakes (PEG model, Sommer et al. 1986). This outcome of the naive model is surprising as a number of mechanisms possibly influencing the timing of *Daphnia* maximum, e.g. a seasonal increase in *Daphnia* mortality due to young-of-the-year fish or hatching of *Daphnia* from resting eggs, were not included in the model. Additionally the simplified phytoplankton model did not consider ecological processes

associated with, e.g. nutrient limitation, light availability or phytoplankton succession. For example, in our “naive” simulation phytoplankton grew up to carrying capacity during winter, whereas in situ phytoplankton growth is limited by reduced temperature and low light availability due to intense vertical mixing or ice cover (Reynolds 1992; Sommer et al. 1986, Peeters et al. 2007a). Hence, when *Daphnia* begins to grow in spring, food concentrations are high in our “naive” simulation, whereas in reality a food dependency may not be excluded. Therefore, we performed a scenario analysis to elucidate which of the environmental factors—food concentration or temperature—are most crucial for the phenomenology of *Daphnia* population dynamics in spring.

In our model, *Daphnia* growth ultimately depends on the availability of its algal resource. However, despite this intrinsic resource-dependent growth, our results suggest that temperature, which modifies the rate of the consumer-resource interaction, has a stronger effect on the phenology of the resulting consumer-resource dynamics than food availability itself. The strong effect of temperature suggested by our model results is supported by analyses of mesocosm studies (Berger et al. 2007) and field data. For example, differences in average *Daphnia* abundances in May between two lakes in Germany, Lake Constance and Müggelsee, as well as the interannual variability in average *Daphnia* abundances within both lakes were found to be strongly related to differences in May water temperatures between the lakes and between years, respectively (Straile and Adrian 2000). Also, comparative studies of the timing of the spring *Daphnia* maximum or the clear-water phase in lakes support the dominant role of temperature as a regulating factor. For example, clear-water timing in Central European lakes was found to be related to factors associated with the temperature development of lakes, e.g. altitude and depth of the lake, as well as interannual climatic variability (Straile 2002). These relationships were evident although the trophic status of the lakes in this data set varied from hypertrophic to oligo/mesotrophic. Likewise, Gilloly and Dodson (2000) showed in a study of latitudinal differences that the timing of the *Daphnia* maximum occurred later at increasing latitude. The water temperature at the time of the *Daphnia* maximum in their study was  $18.5^\circ\text{C}$  ( $\pm 3.1 \text{ SD}$ ,  $n = 27$ ). The temperature range ( $14\text{--}25^\circ\text{C}$ ) was considered by Gilloly and Dodson (2000) as narrow, resulting in their suggestion that it “may be more appropriate to speak of *Daphnia* thermal dynamics instead of seasonal dynamics”. The mean water temperatures at the *Daphnia* maximum in our simulations (Fig S1 in the Electronic supplementary material) were lower than the corresponding temperatures reported by Gilloly and Dodson (2000) as the latter did consider surface temperature, whereas our model is based on average temperatures

within the mixed layer. However, despite the large range of environmental conditions considered in our scenarios, the temperature at the *Daphnia* maximum was as constrained in our simulations as in the data set of Gilloly and Dodson (2000). Hence, both the analyses of interannual variability of *Daphnia* phenology in time-series within individual lakes as well as the comparative analysis of *Daphnia* phenology across different latitudes strongly support the important role of temperature as a key driver of algal-*Daphnia* dynamics.

Clearly, *Daphnia* population growth requires availability of food and is limited at low food concentrations in our simulations (see Fig. 1). Depending on the scenario, *Daphnia* may be strongly food limited during a significant part of the simulated time period. The effect of food on the phenology can be clearly seen in our statistical analyses. However, the scenario analysis indicates that, on average, the effect of temperature on phenology is of higher importance than that of food because temperature determines the rates of the consumer-resource interactions between *Daphnia* and its algal food. Nevertheless, our simulations allow a detailed investigation of the influence of food availability on spring *Daphnia* phenology. First, food availability limits *Daphnia* growth during winter, i.e. before the onset of phytoplankton growth. In fact the onset of algal growth is still an important predictor of the timing of the *Daphnia* minimum. Second, after the onset of algal growth, a low carrying capacity results in slower *Daphnia* growth when temperatures have increased. Slow population growth rates of *Daphnia* resulting from the low carrying capacity on average delay the *Daphnia* maximum (Fig. 5b). Third, algal carrying capacity affects the height of the *Daphnia* spring maximum. In all scenarios, we obtain a maximum in the *Daphnia* population in spring/early summer. This maximum is the result of the rapid *Daphnia* population growth during the spring period followed by a decline in the *Daphnia* population caused by grazing-induced food limitation. Both the *Daphnia* growth rate during the spring period and the onset of food limitation leading to the decline in the *Daphnia* abundance are influenced by the algal carrying capacity. An increase in the algal carrying capacity might either advance (due to its effect on *Daphnia* growth rate) or delay (due to its effect on maximum algal concentration that is available for *Daphnia* grazing) the timing of the *Daphnia* maximum. Over the range of carrying capacities considered in the scenario analysis the first process was dominant. This finding supports results from mesocosm experiments showing that an increase in carrying capacity both increases maximum *Daphnia* abundances and shifts the *Daphnia* maximum to earlier in the year (Berger et al. 2007). At very large carrying capacities, however, the second process becomes

dominant leading to a delayed timing of the *Daphnia* maximum. For example, a very high carrying capacity of  $4 \text{ mg C l}^{-1}$  delays the timing of the *Daphnia* maximum on average by 2 days as compared to the scenarios with  $1 \text{ mg C l}^{-1}$  (data not shown).

The timing of temperature increase ( $t_{TI}$ ) and the start of phytoplankton growth ( $t_{PI}$ ) are often tightly coupled in the field, suggesting that some of our scenarios are not likely to occur in nature. Especially, it seems unlikely that  $t_{PI}$  lags considerably behind  $t_{TI}$  as vernal warming will immediately improve light conditions for phytoplankton by establishing stratification in deep lakes (Peeters et al. 2007a) or by eliminating ice-cover in lakes, which are frozen during winter (Adrian et al. 1999). In contrast, an increase in algae before temperature increase is much more common: in many moderately deep lakes the spring bloom starts during the spring mixing period, i.e. before warming results in stratification (Horn and Paul 1984). Even in deep lakes algal blooms can develop at low temperatures during periods of low wind and/or inverse stratification (Bleiker and Schanz 1997). This suggests that in contrast to our scenarios, which consider all possible combinations of the onset of temperature and algal growth, it will be much more likely in situ that the temperature increase is delayed with respect to the start of algal growth than vice versa. In these situations, *Daphnia* growth will be strongly affected by low temperatures, whereas food availability is already sufficient to sustain maximum temperature-dependent *Daphnia* growth rates. Restricting the statistical analysis to those scenarios that are in a realistic range did not change the outcome of our study.

The timing of temperature increase was more important than the timing of the onset of algal growth at both mortality regimes, even though the food effect increased at low mortality. The different role of food at the two mortality regimes can be easily understood when examining the temperature and food dependency of *Daphnia* population growth rate in the size-structured model (Fig. 1). At the lower mortality rates ( $d_b = 0.055 \text{ day}^{-1}$ ) positive net growth in our simulations can already be realised at temperatures of  $4^\circ\text{C}$  if food concentration is sufficiently high (above  $0.104 \text{ mg C l}^{-1}$ ), which leads to an increased importance of food at this mortality level. In contrast to this, at the higher mortality ( $d_b = 0.1 \text{ day}^{-1}$ ), positive population growth cannot be achieved at a temperature of  $4^\circ\text{C}$  irrespective of food concentration, i.e. no positive population growth can be realised unless temperature has increased sufficiently (e.g. at food concentrations  $> 0.2 \text{ mg C l}^{-1}$  a temperature of  $6^\circ\text{C}$  is adequate to enable population growth rate compensating mortality). Hence, the relative importance of food will decrease with increasing mortality rates. In a more generalised view one can state that our models show that mortality of the consumer is a key factor

mediating the relative importance of food and temperature on the cardinal dates in spring dynamics. Since food-dependent population growth rates are described by a hyperbolic function and temperature determines the maximum growth rates at saturating food (Fig. 1), the consumer mortality level determines whether increasing food alone will lead to positive growth (if mortality is low) or not (if mortality is high). There is empirical evidence that winter mortality of *Daphnia* can be considerably lower than in our simulations, for example, in oligotrophic high-mountain lakes (Gliwicz et al. 2001). At such low mortality rates (e.g.  $0.02 \text{ day}^{-1}$ ) the model predicts *Daphnia* to immediately grow from January onwards, invoking consumer-resource cycles. However, since population growth of *Daphnia* during the winter is uncommon in field observations (even in the studied lakes in Gliwicz et al. 2001) we have not considered mortality rates below  $0.055 \text{ day}^{-1}$  in the scenarios employed in the statistical analysis. Obviously, in systems with extremely low mortality rate of *Daphnia* during winter, positive population growth is prohibited by other factors such as very low food availability and/or temperatures close to  $0^\circ\text{C}$  (compare Gliwicz et al. 2001).

$d_b$  and overwintering biomass affect the timing and the magnitude of the *Daphnia* minimum and thus also influence the timing of the *Daphnia* maximum in our model. However, if the consequences of the timing and magnitude of the *Daphnia* minimum is removed in the statistical analysis (see  $t_{D,\text{max\_adj}}$  in Table 2), overwintering biomass and mortality rate have no significant effect on the timing of the *Daphnia* maximum. Furthermore, the importance of these factors will be reduced in situ since the spring *Daphnia* development originates not only from overwintering animals but often from *Daphnia* hatching from resting eggs (De Senerpont Domis et al. 2007). In other words, the dependence of early spring dynamics of *Daphnia* on winter conditions will be reduced with increasing importance of resting eggs for *Daphnia* recruitment in early spring. As an increase in temperature is an important cue for hatching (Vandekerkhove et al. 2005), this process will also contribute to the importance of temperature and will further modify spring *Daphnia* population dynamics.

The relative importance of temperature versus food in controlling *Daphnia* spring dynamics in lakes depends also on the scale of the study. For example, a study comparing *Daphnia* dynamics in lakes of different trophic status will likely find that food availability is an important factor (Sommer et al. 1986). Hence, the use of different algal carrying capacities in our scenarios is more relevant for between-lake comparisons of *Daphnia* phenology. In principle, interannual differences in algal carrying capacity might also result from climate variability via indirect

climate effect on, e.g. nutrient (George et al. 2004; IPCC 2001; Straile et al. 2003) and/or light availability (Berger et al. 2006; Peeters et al. 2007a). The statistical analysis of our simulations suggests that the algal carrying capacity strongly affects maximum *Daphnia* abundances but only slightly influences *Daphnia* phenology. In contrast, our model predicts that a change in the timing of temperature increase will strongly affect *Daphnia* phenology but not *Daphnia* peak abundances. There are several studies investigating long-term field data showing that climate variability has a strong impact on *Daphnia* phenology (e.g. Gerten and Adrian 2000; Benndorf et al. 2001; Straile 2000, 2002; Anneville et al. 2002), but there is no evidence that climate variability also affected *Daphnia* peak abundances in these studies. Hence, the results from long-term field data combined with the predictions from our model suggest that the inter-annual variability in *Daphnia* phenology observed in situ is most likely a consequence of variability in temperature rather than in phytoplankton abundance.

In summary, temperature appears to be the most crucial factor for the interannual variability in spring development of *Daphnia*. Based on a statistical analysis of 2,184 scenarios we found cardinal points in *Daphnia* spring dynamics to be predominantly driven by the temperature development in spring and to a lesser extent by food dynamics. This is surprising since *Daphnia* growth, of course, depends on the availability of its algal resource. However, the strong effect of temperature on the rates of the consumer-resource interactions results in a strong influence of temperature on the timing of cardinal events in the emerging algal-herbivore dynamics. Our simulations further revealed that the relative importance of food and temperature scales with the  $d_b$ . The higher the mortality rate the more important becomes temperature over food for spring *Daphnia* development since temperature accelerates growth over the whole range of possible temperatures whereas food accelerates growth only if it is below saturating concentrations (compare Fig. 1). However, the standing stock of *Daphnia* at its peak emerges as almost exclusively controlled by the phytoplankton carrying capacity of the habitat and seems to be essentially independent of temperature. Hence, whereas food availability determines the standing stock of *Daphnia* at its spring maximum, temperature appears to be the most important single factor driving the timing of *Daphnia* population development during spring.

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# Electronic Supplementary Material

## Initial conditions for model runs of scenario analysis

### 1. *Daphnia* population:

- Initial population size was set to 1 or 10 Ind. L<sup>-1</sup> with an exponentially declining age-distribution as determined by the prevalent winter mortality.
- Length (L(t)) and egg clutches (E(L)) were calculated following von Bertalanffy growth according to Rinke and Vijverberg (2005):

$$L(t) = L_{\max} - (L_{\max} - L_0)e^{-k \cdot t} \quad (\text{S1})$$

with

$$L_{\max} = \left( \frac{\kappa(P/(P + k_P))p_{\text{ing}} [E_{A,\max} - (E_{A,\max} - E_{A,\min})(P/(P + k_P))]}{m_{f,\min} + (m_{f,\max} - m_{f,\min})(P/(P + k_P))} \right) a^{-1/3} \quad (\text{S2})$$

and

$$k = \frac{\left[ \kappa(P/(P + k_P))p_{\text{ing}} \{E_{A,\max} - (E_{A,\max} - E_{A,\min})(P/(P + k_P))\} a^{2/3} L_{\text{SON}}^2 - \frac{T_A - T_A}{T_{\text{ref}} - T} \right]}{3aL_{\text{SON}}^2 (L_{\max} - L_{\text{SON}})} \quad (\text{S3})$$

$$E(L) = (P/(P + k_P))p_{\text{ing}} e^{\frac{T_A - T_A}{T_{\text{ref}} - T}} \{E_{A,\max} - (E_{A,\max} - E_{A,\min})(P/(P + k_P))\} a^{2/3} L(t)^2 (1 - \kappa) \frac{1}{c_E} D \quad (\text{S4})$$

whereas  $P = 0.2$  [mg C L<sup>-1</sup>] and  $T = (281.15)$  [K] as an assumption of growth conditions during the previous autumn. All other parameters are listed in Tab. S2 and S3.

### 2. Phytoplankton population:

- Initial algal concentration was set to 0.1 mg C L<sup>-1</sup>

Table S1: Equations of the individual level model from Rinke and Vijverberg (2005) describing the physiological rates of *Daphnia galeata* (detailed record of variables and parameters see electronic supplementary materials Table S2).

Description	Formula
Length-weight relationship	$W = a \cdot L^3$
Ingestion rate	$I = p_{ing} \cdot W^{2/3} \cdot f_P(P) \cdot f_T(T)$
Functional response	$f_P(P) = \frac{P}{P + k_P}$
Temperature scaling	$f_T(T) = e^{\left(\frac{T_A - T_A}{T_{ref} - T}\right)}$
Assimilation rate	$A = I \cdot E_A$
Assimilation efficiency	$E_A = E_{A,max} - (E_{A,max} - E_{A,min}) \cdot f_P(P)$
Maintenance coefficient	$m_f = (m_{f,min} + (m_{f,max} - m_{f,min}) \cdot f_P(P)) \cdot f_T(T)$
Maintenance	$M = m_f \cdot W$
Somatic growth rate	$g(T, P, L) = \begin{cases} \frac{1}{3} \cdot \left( a^{-\frac{1}{3}} \cdot \kappa \cdot E_A \cdot p_{ing} \cdot f_P(P) \cdot f_T(T) - m_f \cdot L \right) & \text{for } \kappa \cdot A \geq M \\ 0 & \text{otherwise} \end{cases}$

Reproductive rate		$p_E(T, P, L) = \begin{cases} 0 & \text{for } A < M \\ \frac{A - M}{c_E} & \text{for } \kappa \cdot A < M \leq A \text{ and } L \geq L_{SAM} \\ \frac{c_E}{(1 - \kappa) \cdot A} & \text{for } \kappa \cdot A \geq M \text{ and } L \geq L_{SAM} \end{cases}$
Mortality rate		$q(T, P, L) = \begin{cases} d_s & \text{for } A < M \\ d_b & \text{otherwise} \end{cases}$

For the somatic growth rate we followed Rinke and Vijverberg ( 2005):

somatic growth rate: 
$$\frac{dW}{dt} = \kappa \cdot A - M$$

$$= \kappa \cdot E_A \cdot p_{ing} \cdot f_P(P) \cdot f_T(T) \cdot W^{2/3} - m_f \cdot W \quad (S2)$$

length–weight relationship: 
$$W = a \cdot L^3 \quad (S3)$$

transformation of (S3): 
$$L = \left( \frac{W}{a} \right)^{1/3} \quad (S4)$$

differentiate (S4): 
$$\frac{dL}{dt} = \frac{1}{3} \cdot a^{-1/3} \cdot W^{-2/3} \cdot \frac{dW}{dt} \quad (S5)$$

using (S2) and (S3) in (S5): 
$$\frac{dL}{dt} = \frac{1}{3} \left( \kappa \cdot E_A \cdot p_{ing} \cdot f_P(P) \cdot f_T(T) \cdot a^{-1/3} - m_f \cdot L \right) \quad (S6)$$

Table S2: Escalator boxcar train (EBT) formulation for the individual level model.

Parameter	Unit	Description
$T$	[K]	Temperature
$P$	[mg C l <sup>-1</sup> ]	Phytoplankton concentration
$D$	[d <sup>-1</sup> ]	Egg development time
$N_i$	[Ind l <sup>-1</sup> ]	Number of individuals in the $i$ th cohort
$L_i$	[mm]	Mean length of individuals in the $i$ th cohort
$W_i$	[μg C]	Mean size of individuals in the $i$ th cohort
$E_i$	[egg d <sup>-1</sup> ]	Mean clutch size in the $i$ th cohort
$L_0$	[mm]	Total length, relative to $L_{SON}$ , of the individuals in the cohort in creation
$L_{SON}$	[mm]	Body length of a newborn
$n$	[0.1 d]	Number of cohorts
$q$	[d <sup>-1</sup> ]	Mortality rate
$g(T,P,L_i)$	[mm d <sup>-1</sup> ]	Somatic growth rate (depends on food concentration, temperature, and individual body length)
$p_E(T,P,L_i)$	[Egg d <sup>-1</sup> ]	Reproductive rate expressed as produced eggs per time (depends on food concentration, temperature, and individual body length)
$I(T,P,L_i)$	[μg C d <sup>-1</sup> ]	Ingestion rate (depends on food concentration, temperature, and individual body length)
$g_L$	[d <sup>-1</sup> ]	Derivative of $g$ with respect to body length
$\alpha$	[d <sup>-1</sup> ]	Maximal growth rate of phytoplankton
$CC$	[mg C l <sup>-1</sup> ]	Carrying capacity of phytoplankton

$g_L$	<b>Fehler! Textmarke nicht definiert.</b> $-\frac{1}{3} \cdot m_f$
$D$	$e^{bottrell.a+bottrell.b \cdot \ln(T[^\circ C])+bottrell.c \cdot \ln(T[^\circ C])^2}$

Dynamics of the cohort in creation (until first renumbering operation)	$\left. \begin{array}{l} \frac{dN_0}{dt} = -qN_0 + \sum_{i=1}^{i=n} \frac{1}{D} E_i N_i \\ \frac{dL_0}{dt} = g(T, P, L_{SON})N_0 + g_L(T, P, L_{SON})L_0 - qL_0 \end{array} \right\}$
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Dynamics of all other cohorts, in between two renumbering operations	$\left. \begin{array}{l} \frac{dN_i}{dt} = -q \cdot N_i \\ \frac{dL_i}{dt} = g(T, P, L_i) \\ \frac{dE_i}{dt} = p_E(T, P, L_i) - \frac{1}{D} E_i \end{array} \right\}$
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Renumbering operation and initial values for the cohort with newborns (first cohort)	$\left. \begin{array}{l} N_1(t + \Delta^+) \leftarrow N_0(t + \Delta^-) \\ L_1(t + \Delta^+) \leftarrow L_{SON} + \frac{L_0(t + \Delta^-)}{N_0(t + \Delta^-)} \\ E_1 \leftarrow 0 \\ N_0(t + \Delta^+) \leftarrow 0, L_0(t + \Delta^+) \leftarrow 0, E_0(t + \Delta^+) \leftarrow 0 \end{array} \right\}$
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Renumbering operations for all other cohorts	$\left. \begin{array}{l} N_{i+1}(t + \Delta^+) \leftarrow N_i(t + \Delta^-) \\ L_{i+1}(t + \Delta^+) \leftarrow L_i(t + \Delta^-) \\ E_{i+1}(t + \Delta^+) \leftarrow E_i(t + \Delta^-) \end{array} \right\}$
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Dynamics of the food concentration	$\left. \begin{array}{l} \frac{dP}{dt} = P\alpha \frac{CC - P}{CC} - \sum_{i=0}^{i=n} I(T, P, L_i) \cdot N_i^* \end{array} \right\}$
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The presentation of the EBT follows De Roos et al. (1992). All included rates, e.g. somatic growth rate, reproductive rate, mortality rate, are declared in the individual level model including the assumptions about starvation. Parameter values are the same as for the individual level model (see Table S3); further explanations see Rinke and Vijverberg (2005). Index  $i$  indicates the cohorts each representing an age group that was born within 0.1 day. Body size is expressed as weight and length. At renumbering operations we used “ $\leftarrow$ ” as assignment operator and  $(t + \Delta^-)$  and  $(t + \Delta^+)$  denote state variables immediately before and after the renumbering operation, respectively. The quantity  $\pi_0$  is a length measure in the cohort in creation and expresses the total length (i.e. the summed length of all individuals) relative to length of neonates  $L_{SON}$ .

\*Include the zeroth cohort if  $N_0 \neq 0$

Table S3: List of parameters for *Daphnia galeata* used in the physiologically structured population model of Rinke and Vijverberg ( 2005).

Parameter	Description	Value	Unit	References
$a$	length-weight relationship	1.6	$\mu\text{g C mm}^{-3}$	a, b
$\kappa$	energy allocation factor	0.35	dimensionless	c
$T_A$	Arrhenius temperature	6400	K	c
$T_{ref}$	reference temperature	293	K	k
$p_{ing}$	ingestion factor	5.02	$\mu\text{g C}^{1/3} \text{ d}^{-1}$	a
$k_P$	half saturation coefficient	0.164	$\text{mg C l}^{-1}$	d
$m_{f,max}$	max. respiration rate	0.3	$\text{d}^{-1}$	b, f
$m_{f,min}$	min. respiration rate	0.15	$\text{d}^{-1}$	e, f
$E_{A,max}$	max. assimilation efficiency	0.9	dimensionless	a, g
$E_{A,min}$	min. assimilation	0.5	dimensionless	a, g
$c_E$	carbon investment per egg	1.3	$\mu\text{g C egg}^{-1}$	k
$L_{SAM}$	length at maturity	1.2	mm	k
$L_{SON}$	length of neonates	0.65	mm	k
$bottrell.a$	egg development time	3.3956	dimensionless	h
$bottrell.b$	egg development time	0.2193	dimensionless	h
$bottrell.c$	egg development time	-0.3414	dimensionless	h
$d_b$	background mortality rate	0,1; 0.055	$\text{d}^{-1}$	l, i
$d_s$	mortality at strong starvation	0.35	$\text{d}^{-1}$	j
$n$	Number of cohorts	700	0.1 d	m

References are: (a) Urabe and Watanabe ( 1991); (b) Lynch et al. ( 1986); (c) Kooijman (2000); (d) Muck and Lampert ( 1984); (e) Bohrer and Lampert ( 1988); (f) Urabe and

Watanabe (1990); (g) Porter et al. ( 1982); (h) Bottrell et al. ( 1976); (i) Hülsmann and Voigt (2002); (j) Rohrlack et al. ( 1999); (k) Rinke and Vijverberg ( 2005), (l) Hülsmann (2000); (m) Lynch (1980).

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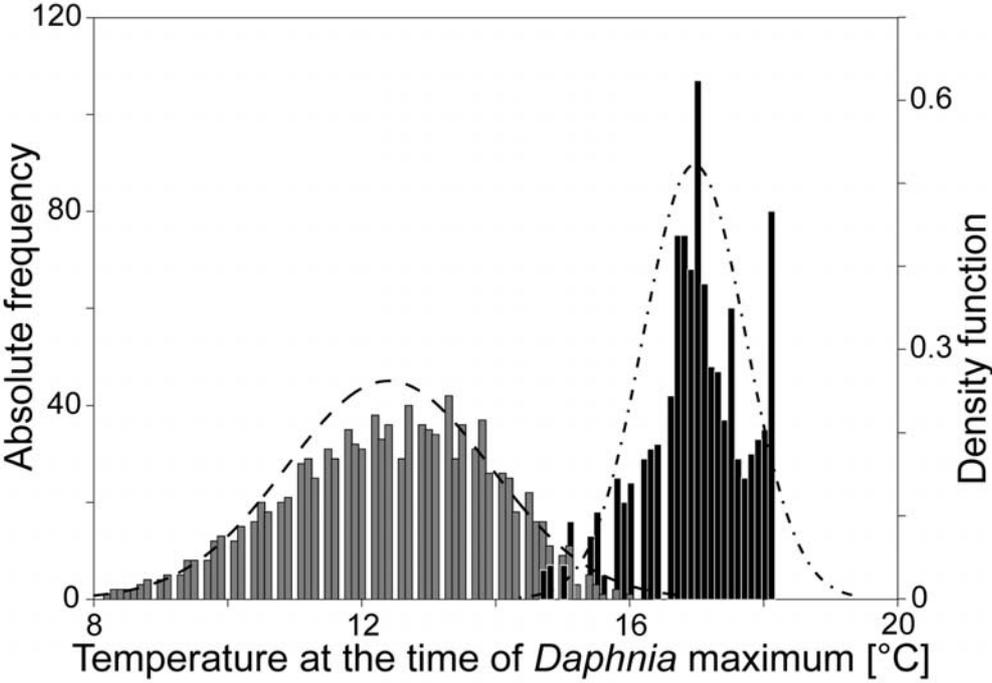


Fig.S1. Histogram (absolute frequency) of the actual water temperature at the timing of *Daphnia* maximum for both mortality rates (0.055 d<sup>-1</sup> grey bars and 0.1 d<sup>-1</sup> black bars).

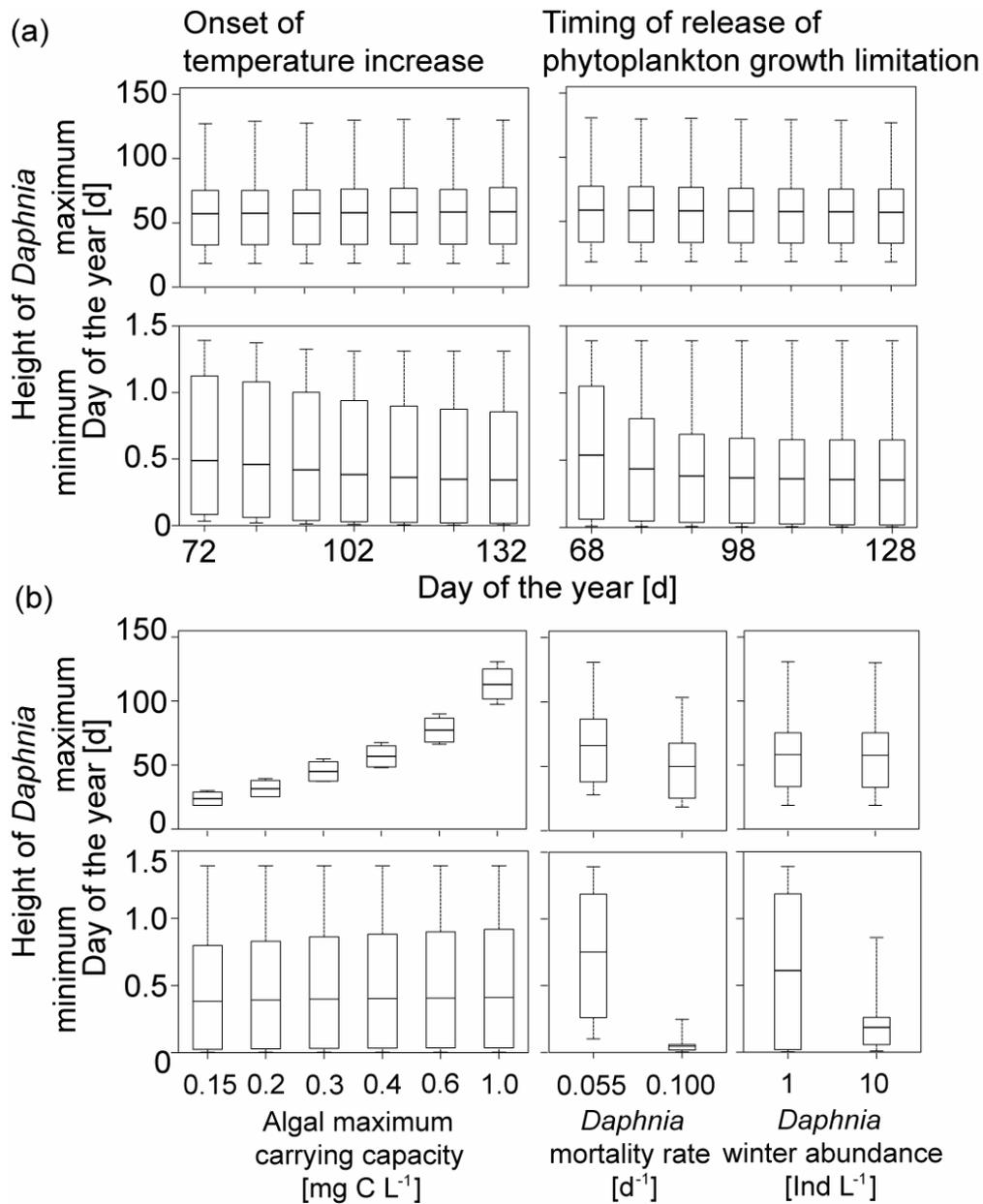


Fig.S2. Response of the height of *Daphnia* spring maximum and late winter minimum to external (a) and internal factors (b). Note that the horizontal line within a box represents the mean value, whiskers show the minimum and the maximum values and boxes describe 50 % of the values.