Impact of climate warming on phenological asynchrony of plankton dynamics across Europe

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Abstract

Climate warming alters the seasonal timing of biological events. This raises concerns that species-specific responses to warming may de-synchronize co-evolved consumer-resource phenologies, resulting in trophic mismatch and altered ecosystem dynamics. Here we explore effects of warming on the temporal coherence of two key phenological events in lakes across Europe: The onset of the phytoplankton spring bloom and the spring/summer maximum of the grazer Daphnia. Simulation of 1,891,744 lake years revealed that, under the current climate, the phenological delay between the two events varies greatly (20-190 days) across lake types and geographic locations. Warming moves both phenological events forward in time and can predictably lengthen or shorten the delay between them by up to 60 days. Our findings expose large extant variation in phenological synchrony of planktonic organisms, provide quantitative predictions of its dependence on physical lake properties and geographic location, and highlight research needs concerning its ecological consequences.

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Data accessibility statement: All data underlying the study will be available on the open repository Zenodo after acceptance of the manuscript without any restriction on data availability.

Abstract

Climate warming alters the seasonal timing of biological events. This raises concerns that species-specific responses to warming may de-synchronize co-evolved consumer-resource phenologies, resulting in trophic mismatch and altered ecosystem dynamics. Here we explore effects of warming on the temporal coherence of two key phenological events in lakes across Europe: The onset of the phytoplankton spring bloom and the spring/summer maximum of the grazer *Daphnia* . Simulation of 1,891,744 lake years revealed that, under the current climate, the phenological delay between the two events varies greatly (20-190 days) across lake types and geographic locations. Warming moves both phenological events forward in time and can predictably lengthen or shorten the delay between them by up to 60 days. Our findings expose large extant variation in phenological synchrony of planktonic organisms, provide quantitative predictions of its dependence on physical lake properties and geographic location, and highlight research needs concerning its ecological consequences.

MAIN TEXT

Introduction

Some of the earliest and most consistent observations of ecological responses to climate warming come from shifts in the timing of seasonal events (Parmesan & Yohe 2003; Thackeray et al. 2010). This has raised concerns that asynchronous responses to a changing climate could disrupt co-evolved consumer-resource phenologies, resulting in phenological mismatch (Stenseth & Mysterud 2002). Phenological mismatch occurs when the seasonal peak in consumer demand for a resource does not coincide with the seasonal peak in the availability of that resource (Visser & Gienapp 2019; Samplonius et al. 2021). While several studies have identified cases where climate change has led to phenological asynchrony with negative consequences for consumers, recent literature surveys concluded that the available evidence is weak and insufficient to draw general conclusions about the future prevalence of climate-mediated phenological asynchrony (Thackeray 2012; Kharouba & Wolkovich 2020; Samplonius et al. 2021).

A major reason for this lack of robust evidence is that most studies to date cannot answer one or more of the following questions (Kharouba & Wolkovich 2020). 1 - What is the reference state of phenological synchrony prior to climate change, and how variable is the degree of phenological synchrony in time and space under reference conditions? 2 - What are the climatic drivers of the phenology of different species, and do interacting species respond to the same drivers? 3 - How does climate change affect these drivers, and do interacting species respond equally strongly to these changes? Here, we address these questions in a

study of phenological synchrony of an aquatic producer-grazer interaction that is central to pelagic ecosystem dynamics in most temperate to arctic freshwater lakes.

A conspicuous seasonal event in many lakes is the spring phytoplankton bloom. Its onset is usually triggered by the alleviation of light limitation, while its termination is often caused by grazing by zooplankton of the genus *Daphnia* (Sommer et al. 2012). The end of the spring bloom, the so-called clear water phase, therefore often closely coincides with the spring/summer maximum in *Daphnia* abundance (Straile & Adrian 2000; Berger et al. 2007). The onset of the spring phytoplankton bloom and the timing of the *Daphnia* maximum are not phenological life history events (such as the timing of flowering or breeding in longer-lived organisms) but numerical responses to changes in temperature, resource availability, and predation pressure (Thackeray 2012). The period between the two events thus correlates with both the overall duration of the spring bloom (an ecosystem characteristic) and the spring growth period of *Daphnia* (a characteristic of predator-prey dynamics). Warming-induced advances in the timing of the phytoplankton bloom have been suggested to result in phenological asynchrony and thus in a reduction of *Daphnia* population size (Winder & Schindler 2004; George 2012). Yet, other studies did not find a general relationship between warming and phenological asynchrony (Berger et al. 2014; Straile et al. 2015), and more research is needed to reconcile these contrasting findings.

Both the onset of the algal bloom and the timing of the *Daphnia* maximum correlate closely with physical events. The onset of the algal bloom (OAB) depends primarily on light and typically takes place once underwater light availability exceeds a specific threshold (Siegel et al. 2002; Diehl et al. 2015). In contrast, spring population growth of *Daphnia* is most strongly influenced by temperature, and the timing of the *Daphnia* maximum (TDM) coincides closely with the seasonal exceedance of thresholds in near-surface water temperature that are similar across entire hemispheres (Gillooly & Dodson 2000; Straile et al. 2012). The tightness of these empirical relationships makes it possible to infer the phenology of OAB and TDM from physical conditions which, in turn, are amenable to process-based hydrodynamic modelling (Straile et al. 2015; Gronchi et al. 2021). We exploited this opportunity and used a numerical modelling to explore the phenologies of phytoplankton and *Daphnia* , as well as their synchrony, over a vast range of climatic conditions and physical lake properties.

Specifically, we simulated the physical drivers of OAB and TDM in 16 model lake types at the spatial scale of Western Europe and North Africa over three decades of the driving meteorology and two climatic conditions: the ambient climate and a constant warming scenario of + 4°C. We used the resulting 1,891,744 lake year simulations to address the three questions raised in (Kharouba & Wolkovich 2020) in the following specific ways. 1 - What are the phenological patterns of OAB and TDM across Europe under current climatic conditions? 2 - Which climatic and lake-specific factors determine the delay in the timings between the two events and, thus, their phenological asynchrony? 3 - How is warming expected to alter the magnitude of this phenological asynchrony in different lake types and at different geographic locations? To identify general, continental-scale and lake type-specific patterns of phenologies and their responses to warming, we focus, throughout the manuscript, on the median values of the predicted time series of OAB, TDM, and of the delay between these two phenological events. We compare these medians between lake types, locations and climate scenarios.

Materials and Methods

Definition of OAB and its controlling processes

As winter and early spring mixing typically replenish nutrients in the photic zone of most European lakes, the onset of the algal bloom (OAB) is primarily determined by light availability in the water column (Sommer et al. 2012; Peeters et al. 2013). We define the timing of the OAB as the first day of the year when the intensity of the average photosynthetically active radiation in the mixed surface layer, I_{mix} , exceeds a critical light intensity, I_{crit} , above which net phytoplankton growth is positive. We used the empirically determined value (Siegel et al. 2002; Sommer & Lengfellner 2008; Mignot et al. 2014) $I_{crit} = 1.3$ mol photons[?]m^{-2}[?]d^{-1}. I_{mix} was calculated as

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$$I_{\text{mix}} = I_{\text{ws}} \cdot \frac{(1 - e^{-K_d \cdot z_{\text{mix}}})}{(K_d \cdot z_{\text{mix}})} (\text{eq. 1})$$

where I_{ws} [mol photons[?]m^{-2}[?]d^{-1}] is the incident radiation penetrating the water surface, K_d[m^{-1}] the light attenuation coefficient, and z_{mix} [m] the depth of the mixed surface layer. z_{mix} was defined as the shallowest depth at which the water density exceeds the surface water density by 0.04 kg[?]m^{-3}. This threshold is in the range of values used in numerous studies on stratified water bodies (de Boyer Montegut et al. 2004; Read et al. 2011; Giling et al. 2017). I_{ws} was calculated from incident solar radiation, taking into account reflection from the lake surface as in (Peeters et al. 2007). We furthermore assumed that $I_{mix} < I_{crit}$ whenever a lake is ice-covered. While phytoplankton can develop under clear ice conditions (Kalinowska & Grabowska 2016; Hampton et al. 2017), clear ice is uncommon at the end of the ice season when snow cover and/or low ice transparency often cause light limitation of phytoplankton growth (Weyhenmeyer et al. 1999; Adrian et al. 2006).

Underwater light levels required for the calculation of the OAB timing were derived from numerical simulations (see below). We distinguished three processes controlling this timing. For each of the 1.9 million simulated lake years, the simulated OAB (OAB$_s$) was compared with a hypothetical timing (OAB$_h$), which was determined analogous to OAB$_s$ but assuming fully mixed conditions and no ice cover. OAB$_h$, therefore, provides a phenological 'null model' where the seasonal change in incident radiation is the sole factor controlling OAB. The process controlling OAB was then identified as: (I) the timing of ice-off if OAB$_s$ occurs after OAB$_h$, i.e. if OAB$_s$ > OAB$_h$ + 2 days, (II) the onset of thermal stratification if OAB$_s$ occurs before OAB$_h$, i.e. if OAB$_s$ < OAB$_h$ + 2 days, and (III) the seasonal increase in incident radiation if OAB$_s$ occurs within two days of OAB$_h$, i.e. if |OAB$_s$–OAB$_h$| [?] 2 days. The +-2-day time window made the categorization robust against minor inaccuracies in the meteorological data. Similar results were obtained with different time windows between +-1 and +-5 days. In years when I_{mix} exceeded I_{crit} already on the first day of the year (suggesting that light was not limiting) the OAB was set to day 1. Lakes where this occurred in [?]16 of the simulated 31 years were categorized as not light-limited and were excluded from further statistical analyses.

Definition of TDM and phenological delay (PLD)

It is well established that *Daphnia* growth in spring is predominantly controlled by water temperature (Gillooly & Dodson 2000; Schalau et al. 2008; Straile et al. 2012). It has been shown that the timing of the annual *Daphnia* abundance maximum (TDM) can be predicted from a temperature threshold ($TT_{13,5m}$), i.e. the first day of the year when the mean temperature in the upper 2 m of a lake exceeds 13degC (Straile et al. 2012):

$$TDM = 0.99 \cdot \text{TT}_{13,5m} + 22.25 \ days \ (\text{eq. 2})$$

This relationship has been successfully applied to predict TDM in 62 northern hemisphere lakes of various depth and trophic status, as well as inter-annual variation in TDM in three lakes ranging from 5 to 100 m mean depth (Straile et al. 2012). We therefore used eq. 2 as our definition of TDM.

Water temperatures required for the calculation of this proxy were obtained from numerical simulations (see below). In years when the simulated mean water temperature in the upper 5 meters did not reach 13degC, the TDM was set to day 366. Lakes where this occurred in [?]16 of the simulated 31 years were excluded from further statistical analyses. Finally, we quantified the degree of phenological synchrony between OAB and TDM as the phenological delay (PLD) between the two phenologies, i.e. the difference in days

$$PLD = TDM - OAB \ (\text{eq. 3})$$

Model description, lake types, and climate scenarios

The quantification of OAB and TDM requires knowledge of the timing of ice off, the seasonal development of the underwater light climate in the mixed surface layer, and the temperature in the top 5 m of the water column. We derived this information from numerical simulations of the seasonal development of ice cover

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and underwater light and temperature profiles with the model LAKEoneD. This model combines a one-dimensional hydrodynamic model with an ice model (Johnk & Umlauf 2001; Hutter & Johnk 2004; Yao et al. 2014; Gronchi et al. 2021) (Supplement S2 Hydrodynamic model) and requires meteorological data, lake depth and water clarity as input variables.

In the reference scenario, LAKEoneD was driven with meteorological data from the global atmospheric re-analysis dataset ERA-Interim (Dee et al. 2011) produced by the European Centre of Medium-Range Weather Forecasts (ECMWF). We extracted from this dataset 3-hourly data on wind speed, air temperature, incident solar radiation, relative cloud cover, and relative humidity for a total of 1907 terrestrial locations covering Europe from 35deg to 70deg North and -10deg to 20deg East at a 0.5deg resolution. All meteorological variables covered the period from 1979-2009 and were linearly interpolated to hourly values.

In addition to the reference scenario, we explored a warming scenario that used the same 31 years of meteorological data as the reference scenario except for assuming an increase in air temperature by +4degC at all locations and times. Similar simplified warming scenarios have been employed in earlier lake studies (Peeters et al. 2007; Trolle et al. 2011; Kupisch et al. 2012; Wahl & Peeters 2014; Straile et al. 2015), and warming by 4degC is within the range of pessimistic projections (Rajendra K. 2014).

At each location, we considered 16 different lake types defined by the factorial combination of four maximum lake depths (z_{max} = 5, 10, 30, and 100 m) with four light attenuation coefficients (K_d = 0.3, 0.6, 1.2, and 2.4 m^{-1}). These values of z_{max} and K_d cover the ranges encountered in a majority of lakes >1 ha (Perez-Fuentetaja et al. 1999; Cael et al. 2017; Seekell et al. 2018). For certain statistical analyses (see below), we characterized the underwater light climate in each of the 16 lake types by its optical depth (OD) defined as

$$OD = K_d \cdot z_{\max} \quad (4)$$

For each lake type and at each geographic location, we simulated 31 years of vertical temperature profiles for both climate scenarios, yielding a total of 1,891,744 simulated lake years. All simulations were performed by first simulating a spin-up period of 5 years using meteorology from 1979 to 1984. Vertical temperature profiles from the final day of the pre-run period were used as initial conditions for the main simulations, which were restarted on the 1st of January 1979 and run through 2009. In the warming scenario, the +4degC temperature increase was applied to both the pre-run and the main simulation periods. Based on these simulations and local incident radiation from the meteorological data, we generated for each lake type, geographic location, and climate scenario a 31-year time series of OAB, TDM, and PLD, respectively. We expressed the impact of climate warming on the individual phenologies by their respective time differences (warming minus reference scenario) OAB$_{diff}$, TDM$_{diff,}$ and PLD$_{diff}$.

Model validation

We validated the model by comparing simulated (= predicted) timings of TDM and OAB to observations from lakes for which relevant data on phytoplankton (15 lakes) and *Daphnia* (18 lakes) could be extracted from the literature (Supplement S3 Model validation). Linear regressions of observed vs. predicted timings of both OAB and TDM give good statistical fits (R^2 [?] 0.6) and indicate that the predictions are unbiased, i.e. regression slopes are not significantly different from 1 and intercepts not different from zero (Supplement S3 Model validation). A similar analysis based on observations of PLD was not meaningful, because we were unable to find data with sufficient temporal resolution on both OAB and TDM for more than five lakes.

Focal results and statistical analyses

Throughout the manuscript, we focus on the median values of the 31-year time series of OAB, TDM and PLD in both climate scenarios and compare them between lake types. We do so because the objective of our work is to identify general, continental-scale and lake type-specific patterns of phenology and their responses to warming, and not to describe phenological responses to interannual variation in the weather. Similarly, we define the dominant controlling process of OAB in a given lake type at a given geographic location as the process (seasonal change in incident radiation, ice-off, or thermal stratification) which controls OAB in most of the 31 simulated years.

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We analyzed the influence of environmental drivers on predicted phenology metrics with generalized additive models (GAMs) (R package mgcv (Wood 2017)). Environmental drivers included geographic location (described by latitude, longitude, and elevation), OD, and the dominant process controlling OAB. Predicted phenology metrics included OAB, TDM, and PLD in both climate scenarios as well as OAB_{diff}, $TDM_{diff,}$ and PLD_{diff}. Since OAB and TDM could not be determined for all lake types at all geographical locations and scenarios (see above), GAMs were run on a slightly reduced data set including those 24501 (our of 30512 possible) combinations of lake types x geographic locations for which OAB and TDM were defined in both the reference and warming scenarios (i.e. PLD_{diff} could be calculated).

We used GAMs to allow for non-linear relationships between environmental drivers and phenology metrics. As we were interested in main effects, we did not model any interactions between environmental drivers. Hence, for each phenology metric, we compared three different models: 1 - a model including only smooth functions of latitude, longitude, and elevation, 2 - a model including only a smooth function of log-transformed OD, and 3 - a model including smooth functions of all four independent variables. For OAB_{diff}, TDM_{diff}, and $PLD_{diff,}$ we ran additional models using the dominant process controlling OAB as the sole independent variable. For all models, we report R^2 and plot the component smooth functions +- 1 standard error. We do not report p-values as metrics were calculated from the results of deterministic models. Furthermore, due to the large number of observations (grid points x lake types), p values are always highly significant and standard errors are usually too small to show on the plots.

Results

Drivers of plankton phenology under the current climate

Under the current climate, simulated OAB and TDM show similar geographic variation across Europe. Both events occur later at higher latitudes and altitudes but are only weakly affected by longitude (Fig. 1a-h; Fig. 2a-b, d-e, g-h; Fig. S1-2). Still, with increasing continentality (eastern longitude), OAB gets slightly delayed whereas TDM shifts marginally forward in time (Fig. 2 d-e). OAB occurs earlier than TDM and varies considerably more among lake types and geographic locations (Fig. 1a-h; Fig. 2m-n; Fig. S1-2). The Europe-wide overall median values are Julian day-of-year 87 vs. 157 for OAB and TDM, respectively, and the corresponding 20th-80th percentiles are day-of-year 53-130 (OAB) vs. 140-183 (TDM). At a given geographic location, OAB can vary up to 46 days with lake type (Fig. 2m). A major driver of this variation is a lake type's optical depth (Fig. 2j). In contrast, TDM at a given geographic location varies much less with lake type ([?] 26 days, Fig. 2n) and is independent of optical depth (Fig. 2k). Consequently, variance in TDM is almost exclusively explained by latitude, longitude, and altitude, whereas optical depth contributes almost 20% to the Europe-wide variance in OAB (Fig. 2p-q).

The similarities and differences between the phenologies of OAB and TDM can be explained by the proximate factors controlling them, i.e. underwater light availability and surface water temperature, respectively. Both increase seasonally, which explains the common latitudinal and altitudinal patterns in OAB and TDM (Fig. 2a-b, g-h, see also Fig. S5 in (Gronchi et al. 2021) and Supplement S3 Model validation). While the seasonal increase in surface water temperature is well described by the seasonal increase in air temperature and largely independent of lake type (Toffolon et al. 2014), underwater light availability also depends on ice cover, water transparency, and mixed layer depth, all of which vary with lake type. Depending on geographic location and lake type, the dominant process controlling OAB can therefore be the seasonal increase in incident radiation, the timing of ice-off, or the onset of thermal stratification (Fig. 1m-p; Fig. S3; (Gronchi et al. 2021)).

Phenological asynchrony varies greatly across locations and lake types

The simulated current Europe-wide variation in phenological asynchrony, expressed as the phenological delay (PLD) between OAB and TDM, is strikingly large, ranging from 20 to 190 days across geographic locations and lake types (Fig. 1i-l, Fig. S4, S9). PLD decreases towards more northern and eastern locations and with increasing elevation (Fig. 1i-l, Fig. 2c, f, i), indicating shorter spring bloom periods in regions with a higher probability of ice cover in winter. Because OAB and TDM show strong but similar latitudinal and altitudinal trends and weak but opposite longitudinal trends, the influence of these three geographical

factors on PLD is of comparable magnitude (Fig. 2a-i). The longitudinal trends can be explained by the more continental climate at eastern longitudes, where cold winters delay ice-off and thus OAB while warm summers promote an earlier TDM (Fig. 1a-l, Fig. 2d-f, Fig. S1, S2, S4).

For both OAB and TDM, optical depth explains much less of the variability than geographic location (Fig. 2p-q). Yet, because latitudinal and elevation effects on OAB and TDM are similar, geographic location explains only a relatively small fraction of the variance in PLD (Fig. 2r), which instead is primarily driven by the effect of optical depth on OAB (Fig. 2j, l). With increasing optical depth, OAB occurs later while TDM remains approximately unchanged (Fig. 2j-k). Consequently, PLD decreases with increasing optical depth (Fig. 2l). The differences in the sensitivities of the phenologies to optical depth are also reflected in location-specific standard deviations, which are small for TDM and large for OAB and PLD (Fig. 2m-o). Large PLDs are typically observed in lakes with optical depth [?] 12 in which OAB occurs early because it is controlled by the seasonal increase in incident radiation (Fig. 1; Fig. 2l; Fig S1, S3, S4). In contrast, small PLDs are observed in lakes with optical depth [?] 36, where OAB is controlled by the onset of stratification (Fig. 1l, p; Fig. 2l; Fig S3, S4).

Impact of climate warming on phenological asynchrony at the European scale

Our model simulations predict that uniform warming by +4degC will advance OAB and TDM by similar median values of 19 and 24 days, respectively. Yet, the variability in the response of OAB and TDM to warming differs. While the advancement of OAB with warming varies substantially between geographic locations and lake types (20th-80th percentiles 0-35 days; Fig. 3a-d; Fig. S5), the advancement of TDM is spatially more uniform and considerably less variable between lake types (20th-80th percentiles 19-30 days; Fig. 3e-h; Fig. S6). Consequently, the net effect of warming on phenological asynchrony (PLD) is on average close to zero (median -3 days), but can range from -60 to +60 days (Fig. 3i-l; Fig. 4b; Fig. S7).

How phenological asynchrony (expressed as PLD) changes with warming depends on the dominant process controlling OAB (Fig. 4a, b) and thus on lake type and geographic location, because these properties determine which process controls OAB before and after warming (Fig. 3i-p; Fig. S7-S9). In northern, eastern, or high-elevation lakes with optical depth [?] 6, where OAB is controlled by ice-off (Fig. 3m; Fig. S8), asynchrony will increase because OAB advances more with warming than TDM (Fig. 4a-f; Fig. S9). In contrast, in low-elevation, southern and western lakes with optical depth 6-18, where OAB is controlled by incident radiation (Fig. 3n, o; Fig. S8), asynchrony will decrease because only TDM advances with warming (Fig. 4a-f; Fig. S9). In lakes with optical depth [?] 36, where OAB is controlled by the onset of stratification (Fig. 3p, Fig. S8), asynchrony will not change systematically because OAB and TDM advance similarly with warming (Fig. 4a-f; Fig. S9). Finally, lakes in which the dominant process controlling OAB will shift with warming – either from ice-cover to radiation (optical depth 6-12) or from radiation to stratification (optical depth 24-30) – OAB will advance at a slightly faster or slower pace than TDM, respectively, leading to intermediate shifts in asynchrony (Fig. 4a-b, Fig. S9). Intriguingly, warming will thus decrease asynchrony in lakes in which it is currently largest (radiation controlled lakes), but will not change asynchrony in lakes in which it is currently shortest (stratification controlled lakes; Fig. 4b; Fig. S9).

Overall, the OAB controlling factors explain more than 60% of the variance in the warming-induced changes in both OAB and PLD in the 16 lake types across Europe (Fig. 4g, i). The controlling factors thus describe the impact of warming on phenological asynchrony equally well as does the combination of geographic coordinates and optical depth (Fig. 4g, i).

Discussion

In freshwater systems, the description of patterns and drivers of plankton phenology - and the projection of climate change effects - has been largely limited to verbal scenarios and qualitative graphical models (Sommer et al. 2012; De Senerpont Domis et al. 2013; Berger et al. 2014). Our study takes a step forward towards both a deeper understanding of underlying drivers and a quantitative prediction of key phenological events across climatic gradients, lake types and climate change scenarios. With respect to the three questions raised in (Kharouba & Wolkovich 2020), our model makes the following predictions.

1 - Phenological asynchrony, defined as the delay between the onset of the phytoplankton bloom and the population maximum of *Daphnia* , is highly variable across climatic gradients and lake types under current climatic conditions. 2 - The degree of phenological asynchrony varies systematically across Europe and is co-determined by physical lake properties (in particular water transparency, lake depth, and their product optical depth) that mediate how climate controls the onset of the algal bloom. 3 - Under constant, uniform warming, phenological asynchrony can predictably increase, remain unchanged or decrease, again driven by on the factors that control the onset of the algal bloom.

In evaluating these predictions, one must keep in mind that the main objective of our work is to identify general, continental-scale and lake type-specific patterns of phenology and phenological synchrony, and not to predict phenologies and their synchrony in any existing, real lakes. Modeled lake types were simplified to one-dimensional water columns with temporally constant light attenuation properties, and the driving meteorology was obtained at a spatial grid resolution of 0.5deg. Observations from real lakes can therefore deviate from model predictions, especially in lakes where local climatic conditions diverge substantially from the grid-averaged meteorology. In Supplement S3 (Model validation), we illustrate this with an example from Lake Windermere, where use of the local rather than grid-averaged meteorology greatly improved the accuracy of TDM predictions. In contrast, our approach successfully captures general trends in phenology related to large-scale climatic gradients and their interaction with lake depth and water transparency. Below, we illustrate this by comparing modelled with observed phenologies from lakes covering a broad range of climate regions and optical depths.

First, linear regressions of observed vs. predicted timings of both OAB and TDM suggest that model predictions are unbiased, i.e. regression slopes are not significantly different from 1 and intercepts not different from zero (Supplement S3 Model validation). Unfortunately, empirical data on the phenological delay between OAB and TDM are too scarce for a similar regression analysis. Yet, the predicted wide range in phenological asynchrony across lake types and geographic gradients – as well as its inferred dependence on the dominant controlling processes of OAB – are supported by observations from a broad range of lake types.

For example, the longest delays are expected in lakes where our model predicts that OAB is controlled by incident radiation. This is in line with data from Loch Leven in northern Britain collected in 1979-2007, where the median predicted, radiation-controlled, phenological delay of ˜140 days compares well with the observed median delay of ˜120 days (Carvalho et al. 2015; Gunn et al. 2015). Intermediate phenological delays are expected in lakes where our model predicts that OAB is controlled by the timing of ice-off. In such lakes, the phenological delay should thus increase in warmer years without ice cover. Both of these expectations are in line with observations from Lake Muggelsee in eastern Germany, where the phenological delay was ˜74 days in the ice-covered year 1987 and ˜98 days in the ice-free year 1988 (Shatwell et al. 2008), close to model predictions of 75 to 88 days, respectively. Similar observations were made in Lower Lake Constance in southern Germany, where phenological asynchrony was ˜92 days in the ice-covered year 2011 and ˜116 days in ice-free year 2014 (IGKB 2012, 2016). Finally, the shortest phenological delays are expected in lakes where our model predicts that OAB is triggered by the onset of stratification. In such lakes, the phenological delay is also predicted to be largely independent of optical depth. Both of these expectations are in line with observations from the Sicilian Lake Arancio (OD ˜ 24) in 1991 and 1993 and Upper Lake Constance (OD ˜ 75) in 2011 and 2014, where both observed (Naselli-Flores & Barone 1997; IGKB 2012, 2016) and predicted phenological delays were ˜60 days for these two lakes.

Our predictions are also in line with the general observation that phenological responses to warming can vary greatly across space and between different taxa at the same locations (Kharouba et al. 2018; Roslin et al. 2021). More specifically, our analyses provide a mechanistic understanding of why simple, ubiquitous phenological responses to warming are not to be expected in pelagic producer-grazer systems, and can thus explain why studies of the impacts of warming on phytoplankton-*Daphnia* dynamics in different systems have come to different conclusions (Winder & Schindler 2004; George 2012; Berger et al. 2014; Straile et al. 2015).

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The predicted extent of the variation in phenological asynchrony suggests that *Daphnia* populations must be able to cope with large temporal and spatial variability in the phenology of their resource and that a single, optimal type of co-evolved phytoplankton-*Daphnia*phenology may not exist. It, therefore, seems unlikely that warming-induced changes in phenological asynchrony must always have negative effects on pelagic grazer populations. Consumer performance does indeed not only depend on the degree of phenological synchrony with its resources but also on the magnitude of the resource peak, which in the case of phytoplankton strongly depends on the availability of mineral nutrients and light (Jager et al. 2008; Winder et al. 2012). A recent review emphasized that, to date, almost no empirical study of temperature-mediated phenological asynchrony has addressed the most important consumer performance measure, i.e. population size (Samplonius et al. 2021). Further steps in the projection of climate effects on seasonal plankton dynamics, therefore, require a merging of the purely physical approach presented here with models that quantitatively describe trophic interactions in the plankton and their dependence on temperature, light, and nutrient supply (Jager et al. 2008; Schalau et al. 2008; Kerimoglu et al. 2013; Uszko et al. 2017).

Changes in the phenological delay between the onset of the spring phytoplankton bloom and the *Daphnia* population maximum have consequences for lake ecosystem processes far beyond the phytoplankton-*Daphnia* interaction. For example, a shorter spring bloom implies a more rapid control of algal biomass by *Daphnia* , suggesting that sedimentation losses are less important under such circumstances (Maier et al. 2019). Thus, changes in phenology and spring bloom duration can affect algal export production to deeper waters and the sediment, with consequences for food webs and biogeochemistry (Kienel et al. 2017; Maier et al. 2019). Similarly, a shorter bloom period and faster *Daphnia* growth can decrease grazing by protozoans (Tirok & Gaedke 2006), and thus increase trophic transfer from primary producers to fish (Caldwell et al. 2020) as well as impede the development of toxic cyanobacteria in the bloom (Shatwell et al. 2008). The wide range of phenological asynchrony exposed in our study, and its predicted responses to warming, are thus likely to affect lake food web dynamics, energy, and nutrient fluxes in ways that remain yet to be systematically explored. Our study provides predictions of the phenological patterns that drive these processes as a function of geographic location and lake type, and thus identifies space-for-time (Pickett 1989) and lake type-for-time substitutions that can address the ecological consequences of phenological delay.

Acknowledgements

References

Adrian, R., Wilhelm, S. & Gerten, D. (2006). Life-history traits of lake plankton species may govern their phenological response to climate warming. *Glob. Chang. Biol.* , 12, 652–661.

Berger, S.A., Diehl, S., Stibor, H., Sebastian, P. & Scherz, A. (2014). Separating effects of climatic drivers and biotic feedbacks on seasonal plankton dynamics: no sign of trophic mismatch. *Freshw. Biol.* , 59, 2204–2220.

Berger, S.A., Diehl, S., Stibor, H., Trommer, G., Ruhenstroth, M., Wild, A., *et al.* (2007). Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton.*Oecologia* , 150, 643–654.

de Boyer Montegut, C., Madec, G., Fischer, A.S., Lazar, A. & Iudicone, D. (2004). Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *J. Geophys. Res. C Ocean.* , 109, 1–20.

Cael, B.B., Heathcote, A.J. & Seekell, D.A. (2017). The volume and mean depth of Earth's lakes. *Geophys. Res. Lett.* , 44, 209–218.

Caldwell, T.J., Chandra, S., Feher, K., Simmons, J.B. & Hogan, Z. (2020). Ecosystem response to earlier

ice break-up date: Climate-driven changes to water temperature, lake-habitat-specific production, and trout habitat and resource use. *Glob. Chang. Biol.* , 26, 5475–5491.

Carvalho, L., Bailer-Watts, A.E. & Kirika, A. (2015). Loch Leven diatom counts 1968-2007. *NERC Environ. Inf. Data Cent.*

Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S., *et al.* (2011). The ERA-Interim reanalysis: Configuration and performance of the data assimilation system. *Q. J. R. Meteorol. Soc.* , 137, 553–597.

Diehl, S., Berger, S.A., Soissons, Q., Giling, D.P. & Stibor, H. (2015). An experimental demonstration of the critical depth principle.*ICES J. Mar. Sci.* , 72, 2051–2060.

George, D.G. (2012). The effect of nutrient enrichment and changes in the weather on the abundance of Daphnia in Esthwaite Water, Cumbria.*Freshw. Biol.* , 57, 360–372.

Giling, D.P., Staehr, P.A., Grossart, H.P., Andersen, M.R., Boehrer, B., Escot, C., *et al.* (2017). Delving deeper: Metabolic processes in the metalimnion of stratified lakes. *Limnol. Oceanogr.* , 62, 1288–1306.

Gillooly, J.F. & Dodson, S.I. (2000). Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans.*Limnol. Oceanogr.* , 45, 22–30.

Gronchi, E., Johnk, K.D., Straile, D., Diehl, S. & Peeters, F. (2021). Local and continental-scale controls of the onset of spring phytoplankton blooms: Conclusions from a proxy-based model. *Glob. Chang. Biol.* , 27, 1976–1990.

Gunn, I.D.M., George, D.G., Johnson, D., Jones, D.H. & May, L. (2015). Crustacean zooplankton data from Loch Leven, 1972-2007. *NERC Environ. Inf. Data Cent.*

Hampton, S.E., Galloway, A.W.E., Powers, S.M., Ozersky, T., Woo, K.H., Batt, R.D., *et al.* (2017). Ecology under lake ice. *Ecol. Lett.* , 20, 98–111.

Hutter, K. & Johnk, K. (2004). *Continuum Methods of Physical Modeling* . Springer Berlin Heidelberg, Berlin, Heidelberg, Heidelberg.

IGKB. (2012). Limnologischer Zustand des Bodensees. *Jahresbericht Int. Gewasserschutzkommission fur den Bodensee - Gruner Bericht* , 39, 1–95.

IGKB. (2016). Limnologischer Zustand des Bodensees. *Jahresbericht Int. Gewasserschutzkommission fur den Bodensee - Gruner Bericht* , 1–119.

Jager, C.G., Diehl, S., Matauschek, C., Klausmeier, C.A. & Stibor, H. (2008). Transient dynamics of pelagic producer grazer systems in a gradient of nutrients and mixing depths. *Ecology* , 89, 1272–1286.

Johnk, K.D. & Umlauf, L. (2001). Modelling the metalimnetic oxygen minimum in a medium sized alpine lake. *Ecol. Modell.* , 136, 67–80.

Kalinowska, K. & Grabowska, M. (2016). Autotrophic and heterotrophic plankton under ice in a eutrophic temperate lake. *Hydrobiologia* , 777, 111–118.

Kerimoglu, O., Straile, D. & Peeters, F. (2013). Seasonal, inter-annual and long term variation in top-down versus bottom-up regulation of primary production. *Oikos* , 122, 223–234.

Kharouba, H.M., Ehrlen, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E., *et al.* (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proc. Natl. Acad. Sci.* , 115, 5211–5216.

Kharouba, H.M. & Wolkovich, E.M. (2020). Disconnects between ecological theory and data in phenological mismatch research. *Nat. Clim. Chang.* , 10, 406–415.

Kienel, U., Kirillin, G., Brademann, B., Plessen, B., Lampe, R. & Brauer, A. (2017). Effects of spring warming and mixing duration on diatom deposition in deep Tiefer See, NE Germany. *J. Paleolimnol.* , 57, 37–49.

Kupisch, M., Moenickes, S., Schlief, J., Frassl, M. & Richter, O. (2012). Temperature-dependent consumer-resource dynamics: A coupled structured model for Gammarus pulex (L.) and leaf litter. *Ecol. Modell.* , 247, 157–167.

Maier, D.B., Diehl, S. & Bigler, C. (2019). Interannual variation in seasonal diatom sedimentation reveals the importance of late winter processes and their timing for sediment signal formation. *Limnol. Oceanogr.* , 64, 1186–1199.

Mignot, A., Claustre, H., Uitz, J., Poteau, A., D'Ortenzio, F. & Xing, X. (2014). Understanding the seasonal dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments: A Bio-Argo float investigation. *Global Biogeochem. Cycles* , 28, 856–876.

Naselli-Flores, L. & Barone, R. (1997). Importance of water-level fluctuation on population dynamics of cladocerans in a hypertrophic reservoir (Lake Arancio, south-west Sicily, Italy).*Hydrobiologia* , 360, 223–232.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* , 421, 37–42.

Peeters, F., Kerimoglu, O. & Straile, D. (2013). Implications of seasonal mixing for phytoplankton production and bloom development.*Theor. Ecol.* , 6, 115–129.

Peeters, F., Straile, D., Lorke, A. & Livingstone, D.M. (2007). Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Glob. Chang. Biol.* , 13, 1898–1909.

Perez-Fuentetaja, A., Dillon, P.J., Yan, N.D. & McQueen, D.J. (1999). Significance of dissolved organic carbon in the prediction of thermocline depth in small Canadian shield lakes. *Aquat. Ecol.* , 33, 127–133.

Pickett, S.T.A. (1989). Space-for-Time Substitution as an Alternative to Long-Term Studies. In: *Long-Term Studies in Ecology* . Springer New York, New York, NY, pp. 110–135.

Rajendra K., P. (2014). IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)].*IPCC, Geneva, Switz.* , 155.

Read, J.S., Hamilton, D.P., Jones, I.D., Muraoka, K., Winslow, L.A., Kroiss, R., *et al.* (2011). Derivation of lake mixing and stratification indices from high-resolution lake buoy data.*Environ. Model. Softw.* , 26, 1325–1336.

Roslin, T., Antao, L., Hallfors, M., Meyke, E., Lo, C., Tikhonov, G.,*et al.* (2021). Phenological shifts of abiotic events, producers and consumers across a continent. *Nat. Clim. Chang.* , 11, 241–248.

Samplonius, J.M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S.J., Assmann, J.J., *et al.* (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts.*Nat. Ecol. Evol.* , 5, 155–164.

Schalau, K., Rinke, K., Straile, D. & Peeters, F. (2008). Temperature is the key factor explaining interannual variability of Daphnia development in spring: A modelling study. *Oecologia* , 157, 531–543.

Seekell, D.A., Bystrom, P. & Karlsson, J. (2018). Lake morphometry moderates the relationship between water color and fish biomass in small boreal lakes. *Limnol. Oceanogr.* , 63, 2171–2178.

De Senerpont Domis, L.N., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E., *et al.* (2013). Plankton dynamics under different climatic conditions in space and time. *Freshw. Biol.* , 58, 463–482.

11

Shatwell, T., Kohler, J. & Nicklisch, A. (2008). Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring. *Glob. Chang. Biol.* , 14, 2194–2200.

Siegel, D.A., Doney, S.C. & Yoder, J.A. (2002). The North Atlantic Spring Phytoplankton Bloom and Sverdrup's Critical Depth Hypothesis.*Science (80-.).* , 296, 730–733.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J.J., Gaedke, U., Ibelings, B., *et al.* (2012). Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession. *Annu. Rev. Ecol. Evol. Syst.* , 43, 429–448.

Sommer, U. & Lengfellner, K. (2008). Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom.*Glob. Chang. Biol.* , 14, 1199–1208.

Stenseth, N.C. & Mysterud, A. (2002). Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. *Proc. Natl. Acad. Sci. U. S. A.* , 99, 13379–13381.

Straile, D. & Adrian, R. (2000). The North Atlantic Oscillation and plankton dynamics in two European lakes–two variations on a general theme. *Glob. Chang. Biol.* , 6, 663–670.

Straile, D., Adrian, R. & Schindler, D.E. (2012). Uniform Temperature Dependency in the Phenology of a Keystone Herbivore in Lakes of the Northern Hemisphere. *PLoS One* , 7, e45497.

Straile, D., Kerimoglu, O. & Peeters, F. (2015). Trophic mismatch requires seasonal heterogeneity of warming. *Ecology* , 96, 2794–2805.

Thackeray, S.J. (2012). Mismatch revisited: What is trophic mismatching from the perspective of the plankton? *J. Plankton Res.* , 34, 1001–1010.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., *et al.* (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments.*Glob. Chang. Biol.* , 16, 3304–3313.

Tirok, K. & Gaedke, U. (2006). Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *J. Plankton Res.* , 28, 361–373.

Toffolon, M., Piccolroaz, S., Majone, B., Soja, A.M., Peeters, F., Schmid, M., *et al.* (2014). Prediction of surface temperature in lakes with different morphology using air temperature. *Limnol. Oceanogr.* , 59, 2185–2202.

Trolle, D., Hamilton, D.P., Pilditch, C.A., Duggan, I.C. & Jeppesen, E. (2011). Predicting the effects of climate change on trophic status of three morphologically varying lakes: Implications for lake restoration and management. *Environ. Model. Softw.* , 26, 354–370.

Uszko, W., Diehl, S., Englund, G. & Amarasekare, P. (2017). Effects of warming on predator–prey interactions – a resource-based approach and a theoretical synthesis. *Ecol. Lett.* , 20, 513–523.

Visser, M.E. & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* , 3, 879–885.

Wahl, B. & Peeters, F. (2014). Effect of climatic changes on stratification and deep-water renewal in Lake Constance assessed by sensitivity studies with a 3D hydrodynamic model. *Limnol. Oceanogr.* , 59, 1035–1052.

Weyhenmeyer, G.A., Blenckner, T. & Pettersson, K. (1999). Changes of the plankton spring outburst related to the North Atlantic Oscillation.*Limnol. Oceanogr.* , 44, 1788–1792.

Winder, M., Berger, S.A., Lewandowska, A., Aberle, N., Lengfellner, K., Sommer, U., *et al.* (2012). Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. *Mar. Biol.* , 159, 2491–2501.

Winder, M. & Schindler, D.E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* , 85, 2100–2106.

Wood, S.N. (2017). *Generalized Additive Models: An Introduction with R, 2nd Edition* . Chapman and Hall/CRC.
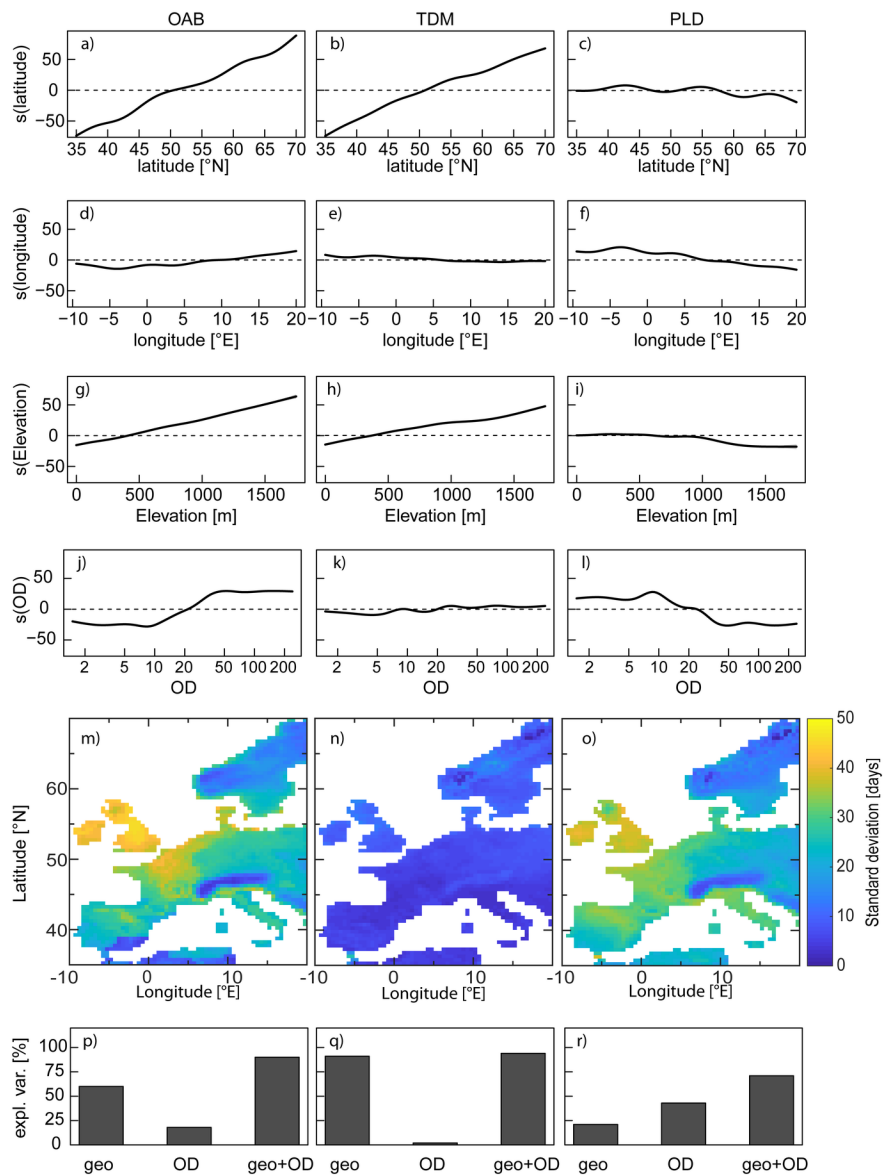
Yao, H., Samal, N.R., Joehnk, K.D., Fang, X., Bruce, L.C., Pierson, D.C., *et al.* (2014). Comparing ice and temperature simulations by four dynamic lake models in Harp Lake: Past performance and future predictions. *Hydrol. Process.* , 28, 4587–4601.
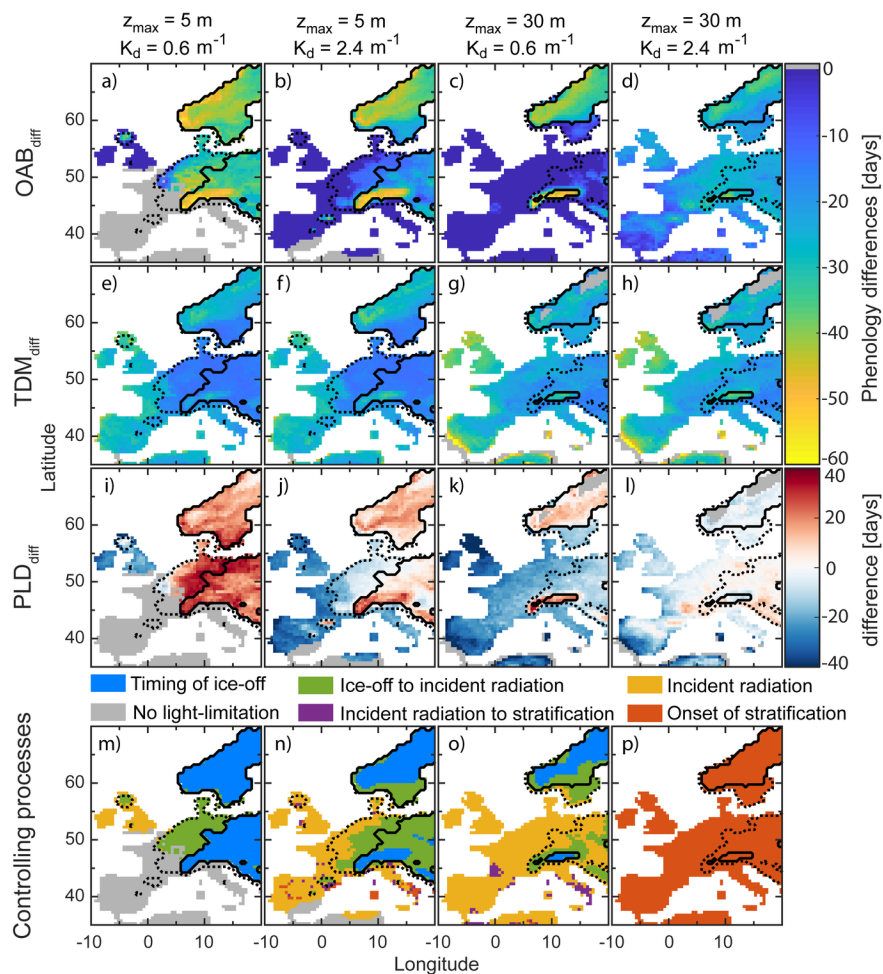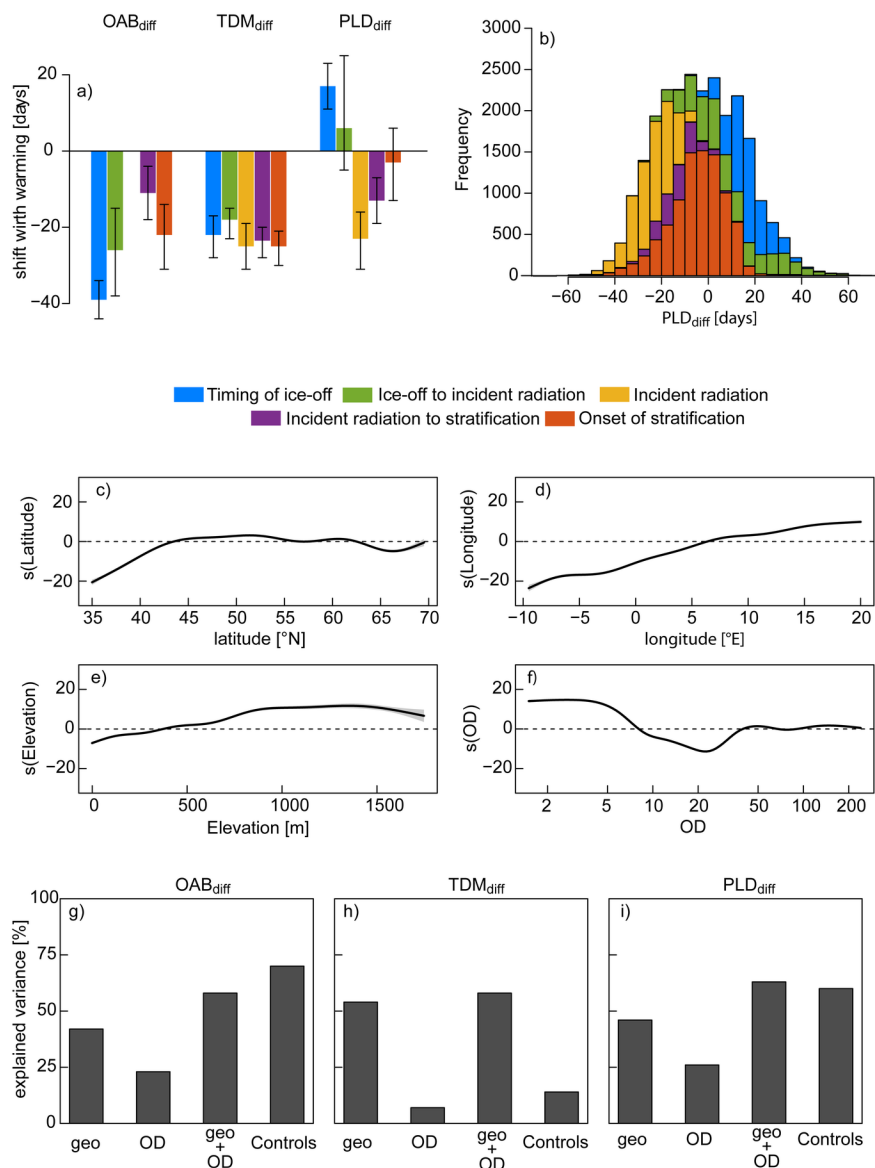
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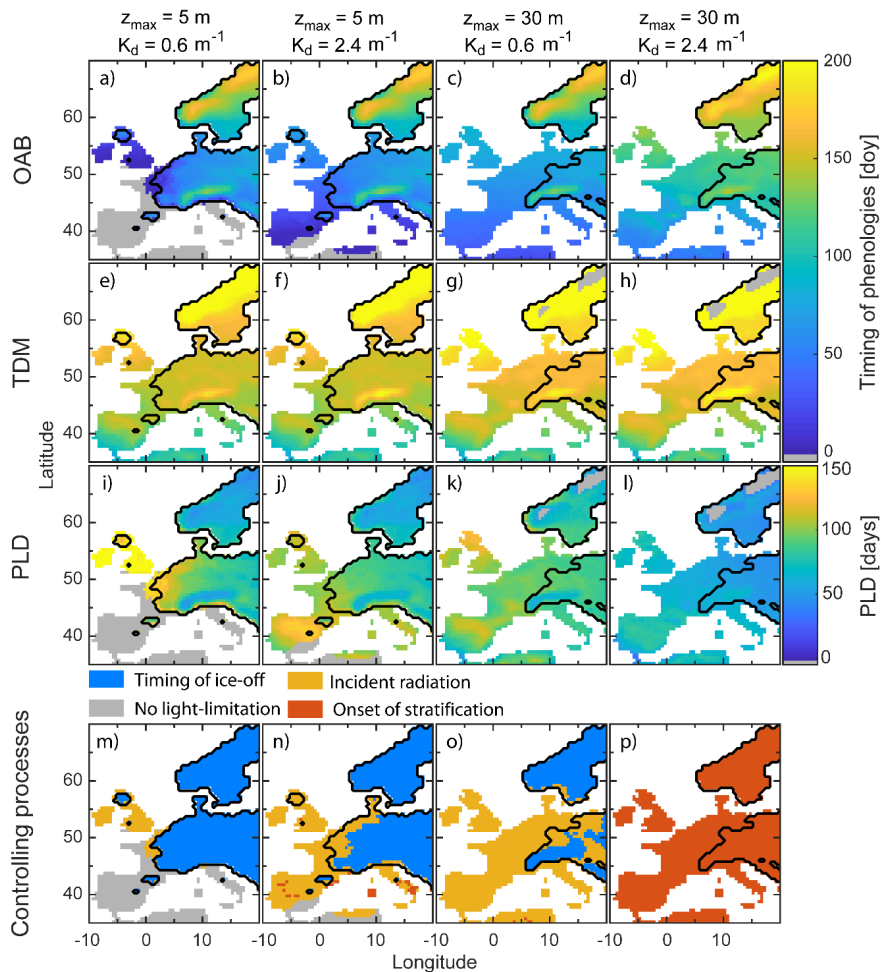
Fig. 3

Fig. 4

Figure legends

Fig. 1. Predicted timings of phenological events and the phenological delay between them in four representative lake types across Europe under reference climate conditions (median values for 1979-2009). Lake types are indicated by their maximum depth (z_{max}) and light extinction coefficient (K_d). Shown are **(a-d)** the onset of the algal bloom (OAB) in day of year (doy), **(e-h)** the timing of the *Daphnia* maximum (TDM, doy), **(i-l)** the phenological delay between TDM and OAB (PLD, days), and **(m-p)** the dominant process controlling OAB. Black lines delimit regions in which lakes develop ice cover in at least 16 out of the 31 simulated years. Regions, where the light threshold for OAB is exceeded already on the first day of the year or where the temperature threshold for TDM is not reached in more than 50% of the simulated years, are marked in grey. Supplement S1 provides figures on the geographic distributions of OAB, TDM, PLD, and the controlling processes for all 16 lake types investigated.

Fig. 2. Impact of geographical factors (latitude, longitude, elevation) and optical depth (OD) on the

timing and asynchrony of phenological events across 1907 European locations and 16 lake types.**(a-l)** The relationships ($\pm$ 1 standard error) of the onset of the algal bloom (OAB), the timing of the *Daphnia* maximum (TDM), and the phenological delay between them (PLD), with latitude, longitude, elevation and OD, as determined by general additive models (GAM) including these four factors as smooth functions. Y-axes scale in days, where the dashed line at 0 indicates the isoline of no effect of the respective independent variable. Standard errors are too small too be visible in all panels. Standard deviations (days) of OAB **(m)** , TDM **(n)** and PLD **(o)** across the 16 lake types at each location. Proportion of the variance in OAB **(p)** , TDM**(q)** and PLD **(r)** that is explained by GAMs including as independent variables only geographical factors ('geo'), only 'OD', or both (i.e. the full model, 'geo+OD').

Fig. 3. Predicted effects of a uniform temperature increase by +4°C on the timings of phenological events and the phenological delay between them in four representative lake types (median values of 31 simulation years). Lake types are indicated by their maximum depth (z_{max}) and light extinction coefficient (K_d). Shown is the difference in days between the warming and reference scenarios for **(a-d)** the onset of the algal bloom (OAB$_{diff}$), **(e-h)** the timing of the *Daphnia* maximum (TDM$_{diff}$), and **(i-l)** the phenological delay between them (PLD$_{diff}$).**(m-p)** Dominant processes controlling OAB in the reference and warming scenarios. The controlling process changes between the two scenarios in green and purple regions but remains the same in blue, yellow and red regions. Black lines delimit regions in which lakes develop ice cover in the reference (dotted lines) and warming (solid lines) scenarios. Regions, where the light threshold for OAB is exceeded already on the first day of the year or where the temperature threshold for TDM is not reached in more than 50% of the simulated years in at least one of the scenarios, are marked in grey. Supplement S1 provides corresponding figures on OAB$_{Diff}$, TDM$_{Diff}$, PLD$_{Diff}$ and the controlling processes for all 16 lake types investigated.

Figure 4: Factors and processes mediating predicted shifts in phenology between the reference and warming scenarios. **(a)**Median temporal shifts (days, with error bars indicating the 20 % and 80 % quantiles) between the warming and reference scenarios for the onset of the algal bloom (OAB$_{diff}$), the timing of the *Daphnia* maximum (TDM$_{diff}$), and the phenological delay between them (PLD$_{diff}$) in lakes that differ in the dominant processes controlling OAB in the two scenarios. **(b)**Frequency distribution of PLD$_{diff}$ in lakes that differ in the dominant processes controlling OAB in the two scenarios.**(c-f)** The relationship of PLD$_{diff}$ to latitude, longitude, elevation and optical depth (OD), as determined by a general additive model (GAM) including these four factors as smooth functions. Grey shading (only visible in panel e) indicates $\pm$ 1 standard error. Y-axes scale in days, where the dashed line at 0 indicates the isoline of no effect of the respective independent variable. Proportion of the variance in OAB$_{diff}$ **(g)** , TDM$_{diff}$ **(h),** and PLD$_{diff}$**(i)** that is explained by GAMs including as independent variables only latitude, longitude and elevation ('geo'), only 'OD', both ('geo+OD'), or, alternatively, the five categories of dominant processes controlling OAB from panels (a) and (b).