

LETTER

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. We explored the effects of warming on the synchrony of two events: the onset of the phytoplankton spring bloom and the spring/summer maximum of the grazer *Daphnia*. Simulation of 16 lake types over 31 years at 1907 North African and European locations under 5 climate scenarios revealed that the current median phenological delay between the two events varies greatly (20–190 days) across lake types and geographic locations. Warming moves both events forward in time and can lengthen or shorten the delay between them by up to ± 60 days. Our simulations suggest large geographic and lake-specific variations in phenological synchrony, provide quantitative predictions of its dependence on physical lake properties and geographic location and highlight research needs concerning its ecological consequences.

KEYWORDS

climate change, *Daphnia*, phenology, phytoplankton, regional modelling

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 a 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 (Samplonius et al., 2021; Visser & Gienapp, 2019). 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 (Kharouba & Wolkovich, 2020; Samplonius et al., 2021; Thackeray, 2012).

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 the 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 (Berger et al., 2007; Straile & Adrian, 2000). The onset of the spring phytoplankton bloom and the timing of the *Daphnia* maximum are not phenological life history events 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 (George, 2012; Winder & Schindler, 2004). Yet, other studies did not find a general relationship between warming and phenological asynchrony (Berger et al., 2014; Straile et al., 2015). 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 (Diehl et al., 2015; Siegel et al., 2002). In contrast, the 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 temperatures 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 (Gronchi et al., 2021; Straile et al., 2015). We exploited this opportunity and used numerical modelling to explore the phenologies of phytoplankton and *Daphnia*, as well as their synchrony, over a vast range of climatic conditions.

Specifically, we simulated the physical drivers of OAB and TDM in 16 model lake types (hypothetically assumed to exist in each pixel of the studied geographic range) over three decades of driving meteorology covering the full range of Mediterranean to subarctic, oceanic, continental and alpine climates of Western Europe and North Africa using an ambient climate and various climate warming scenarios. We used the resulting 4,729,360

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 a reference scenario of 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 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 (Peeters et al., 2013; Sommer et al., 2012). 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 (Mignot et al., 2014; Siegel et al., 2002; Sommer & Lengfellner, 2008) $I_{\text{crit}} = 1.3 \text{ mol photons} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. I_{mix} was calculated as

$$I_{\text{mix}} = I_{\text{ws}} \cdot (1 - e^{-K_d \cdot z_{\text{mix}}}) / (K_d \cdot z_{\text{mix}}) \quad (1)$$

where I_{ws} [$\text{mol photons} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$] is the incident radiation penetrating the water surface, K_d [m^{-1}] is the light attenuation coefficient, and z_{mix} [m] is 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 $0.04 \text{ kg} \cdot \text{m}^{-3}$. This density threshold is in the range of values used in numerous studies on stratified water bodies (de Boyer Montégut et al., 2004; Giling et al., 2017; Read et al., 2011). I_{ws} was calculated from incident solar radiation, taking into account reflection from the lake surface (Peeters et al., 2007). We furthermore assumed that $I_{\text{mix}} < I_{\text{crit}}$ whenever a lake is ice-covered. While phytoplankton can develop under clear ice conditions (Hampton et al., 2017; Kalinowska & Grabowska, 2016), 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 (Adrian et al., 2006; Weyhenmeyer et al., 1999).

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 4.7 million simulated lake years, the simulated OAB timing (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. For a given lake type and geographical location, if OAB_s occurs after OAB_h , this means that favourable light conditions for a phytoplankton bloom were delayed by an ice cover. The process controlling OAB was then identified as: (I) the timing of ice-off if $OAB_s > OAB_h + 2$ days. Conversely, if OAB_s occurs before OAB_h , this means that favourable light conditions were met earlier in the year due to a shallowing of the surface mixed layer. The controlling process was then identified as (II) the onset of thermal stratification if $OAB_s < OAB_h + 2$ days. Finally, if OAB_s and OAB_h coincide, this implies that the controlling process is (III) the seasonal increase in incident radiation, defined by $|OAB_s - OAB_h| \leq 2$ days. The ± 2 -day time window made the categorization robust against minor inaccuracies in the meteorological data. Similar results were obtained with 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) 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 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; Schallau et al., 2008; Straile et al., 2012). Correspondingly, the timing of the annual *Daphnia* abundance maximum (TDM) can be empirically predicted from a temperature threshold ($TT_{13,5m}$), i.e. the first day of the year when the mean temperature in the upper 5 m of a lake exceeds 13°C (Straile et al., 2012):

$$TDM = 0.99 \cdot TT_{13,5m} + 22.25 \text{ days} \quad (2)$$

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 Equation 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 m did not reach 13°C, 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 events, i.e. the difference in days

$$PLD = TDM - OAB \quad (3)$$

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 and underwater light and temperature profiles with the model LAKEoneD. This model combines a one-dimensional hydrodynamic model with an ice model (Gronchi et al., 2021; Hutter & Jöhnk, 2004; Jöhnk & Umlauf, 2001; Yao et al., 2014) (see Supplementary Information S1) 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 reanalysis 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 35° to 70° North and -10° to 20° East at a 0.5° resolution. All meteorological variables covered the period 1979–2009 and were linearly interpolated to hourly values.

In addition to the reference scenario, we explored four warming scenarios that used the same 31 years of meteorological data as the reference scenario except for assuming an increase in air temperature at all locations and times. The increase in air temperature was either seasonally constant at +2°C or +4°C, or seasonally varying (see Supporting Information S2). Similar simplified warming scenarios have been employed in earlier lake studies (Kupisch et al., 2012; Peeters et al., 2007; Straile et al., 2015; Trolle et al., 2011; Wahl & Peeters, 2014), and warming by 4°C is within the range of pessimistic projections (Rajendra, 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 (Cael et al., 2017; Pérez-Fuentetaja et al., 1999; 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 the 16 lake type and at 1907 geographic location, we simulated 31 years of vertical temperature profiles for the 5 climate scenarios, yielding a total of 4,729,360 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 reference state simulations, which were restarted on the 1st of January 1979 and run through 2009. In the warming scenarios, the temperature treatments were 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} . Note that our reference period 1979–2009 was already influenced by global warming. The historical state of phenological synchrony prior to anthropogenic climate warming may therefore deviate from the reference scenario in our study.

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 (see Supporting Information S3). Linear regressions of observed vs. predicted timings explain about 90% of the variance of OAB ($R^2 = 0.89$, predicted range: 44–98 days, RMSE = 5.76 days) and 60% of the variance of TDM ($R^2 = 0.60$, predicted range: 100–191 days, RMSE = 25.9 days). Moreover, predictions are unbiased, i.e. regression slopes are not significantly different from 1, intercepts not different from zero, and fitted regression lines deviate very little from the 1:1 line within the range of predicted values (see Supporting Information S3). Unbiasedness is important because we aim at identifying general, continental-scale and lake-type-specific patterns of phenology rather than making accurate predictions for real lakes at specific locations where local climatic conditions can diverge from the coarse, grid-averaged meteorology that drives the model.

Focal results and statistical analyses

Throughout the manuscript, we focus on median values of the 31-year time series of OAB, TDM and PLD and compare them between lake types and climate scenarios. Again, 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) that controls OAB in most of the 31 simulated years.

We analysed the influence of environmental drivers on predicted phenology metrics with generalized additive models (GAMs) (R package mgcv (Wood, 2017)) to allow for non-linear relationships. Environmental drivers included geographic location (described by latitude, longitude, and elevation), OD, and the dominant process controlling OAB. Further details are provided in Supporting Information S4. For all models, we report R^2 and plot the component smooth functions. Due to a 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 variations across Europe. Both events occur later at higher latitudes and altitudes but are only weakly affected by longitude (Figure 1a–h; Figure 2a,b,d,e,g,h; Figures S5 and S6). Still, with increasing continentality (eastern longitude), OAB gets slightly delayed whereas TDM shifts marginally forward in time (Figure 2d,e). OAB occurs earlier than TDM and varies considerably more among lake types and geographic locations (Figure 1a,h; Figure 2m,n; Figures S5 and S6). The Europe-wide overall median values are Ordinal day-of-year 87 versus 157 for OAB and TDM, respectively, and the corresponding 20th–80th percentiles are day-of-year 53–130 (OAB) versus 140–183 (TDM). At a given geographic location, OAB can vary considerably with lake type (standard deviation ≤ 46 days, Figure 2m). A major driver of this variation in OAB is OD (Figure 2j). In contrast, TDM at a given geographic location varies much less with lake type (standard deviation ≤ 26 days, Figure 2n) and is independent of OD (Figure 2k). Consequently, variance in TDM is almost exclusively explained by latitude, longitude and altitude, whereas OD contributes almost 20% to the Europe-wide variance in OAB (Figure 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 (Figure 2a,b,g,h, see also Figure S5 in (Gronchi et al., 2021) and Supporting Information S3). While the seasonal increase in surface water

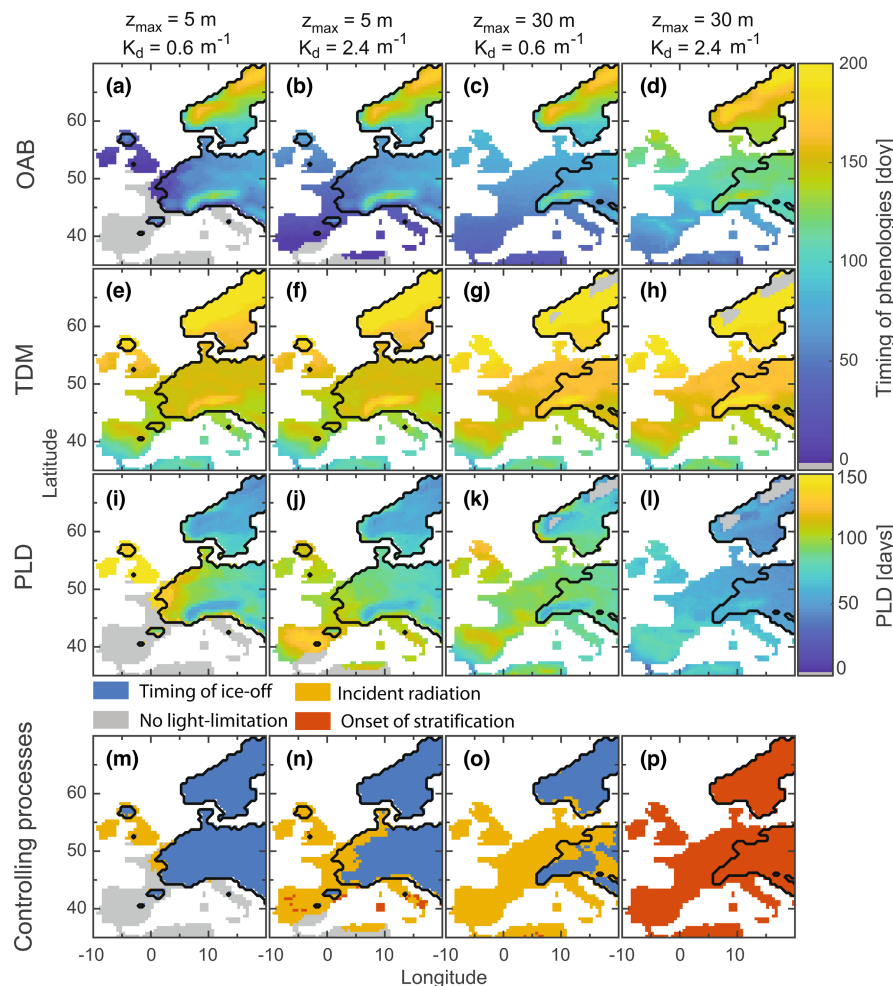


FIGURE 1 Predicted timings of phenological events and the phenological delay between them in four representative lake types across Europe under reference climate conditions (median values for 1979–2009). Lake types are indicated by their maximum depth (z_{\max}) and light attenuation coefficient (K_d). 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. Each pixel represents the simulation results at a single geographical position/grid cell. 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 S5 provides figures on the geographic distributions of OAB, TDM, PLD, and the controlling processes for all 16 lake types investigated.

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 (Figure 1m–p; Figure S7; (Gronchi et al., 2021)).

Phenological asynchrony varies greatly across locations and lake types

The simulated current Europe-wide variation in the phenological delay (PLD) between OAB and TDM, is

strikingly large, ranging from 20 to 190 days across geographic locations and lake types (Figure 1i–l, Figure S8, S13). PLD decreases towards more northern and eastern locations and with increasing elevation (Figure 1i–l, Figure 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 (Figure 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 (Figures 1a–l, 2d–f, Figures S5, S6 and S8).

For both OAB and TDM, OD explains much less of the variability than geographic location (Figure 2p,q).

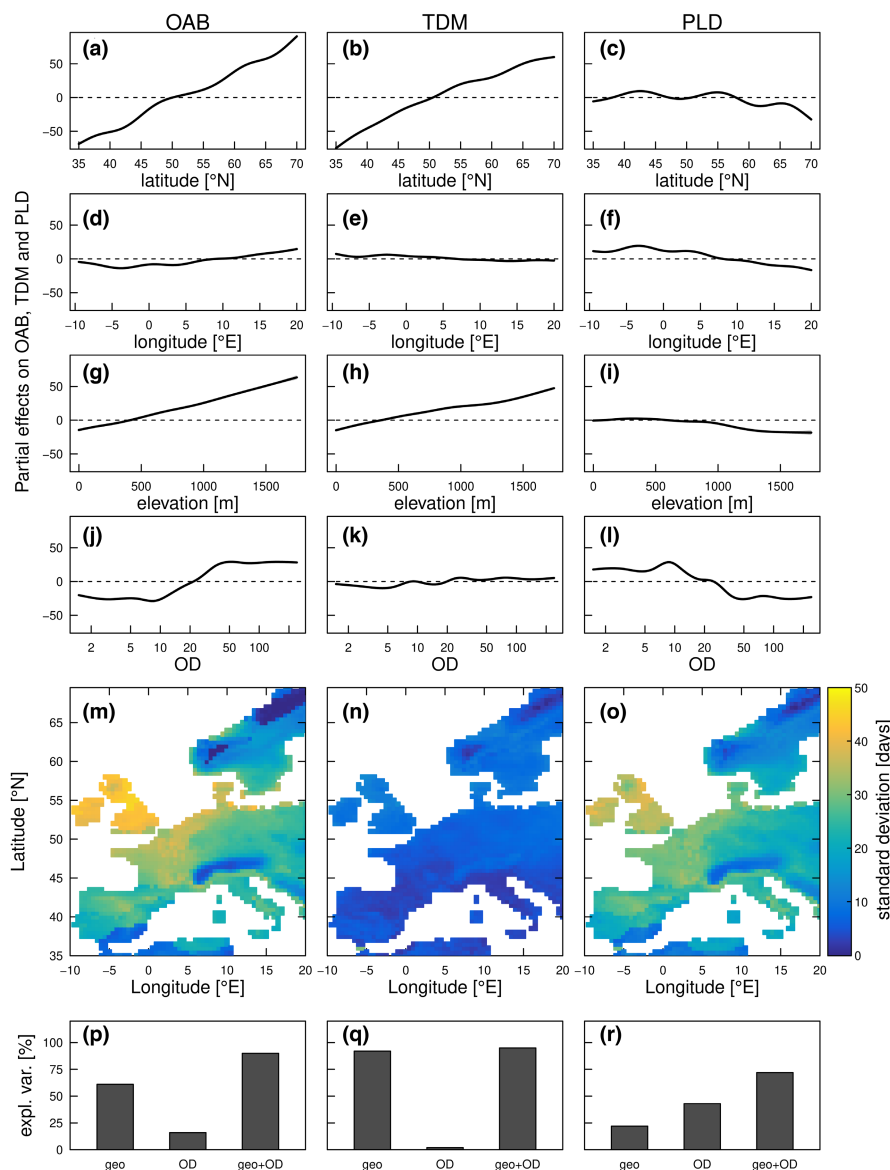


FIGURE 2 Impact of geographical factors (latitude, longitude, elevation) and optical depth (OD) on the timing and asynchrony of phenological events across 1907 European locations and 16 lake types. (a–l) Smooth functions (± 2 standard error) of the partial effect of latitude, longitude, elevation and optical depth (OD) on the onset of the algal bloom (OAB), the timing of the Daphnia maximum (TDM), and the phenological delay between them (PLD) determined by general additive models (GAM). 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 to be visible on all panels. Standard deviations (days) of OAB (m), TDM (n) and PLD (o) across the 16 lake types at each location. Each pixel represents the simulation results at a single geographical position/grid cell. 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'), optical depth (log10-transformed) 'OD', or both (i.e. the full model, 'geo+OD').

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 (Figure 2r), which instead is primarily driven by the effect of OD on OAB (Figure 2j,l). With increasing OD, OAB occurs later while TDM remains approximately unchanged (Figure 2j,k). Consequently, PLD decreases with increasing OD (Figure 2l). The differences in the sensitivities of the phenologies to OD are also reflected in location-specific standard deviations, which are small for TDM and large for OAB and PLD (Figure 2m–o). Large PLDs are typically observed in lakes with $OD \leq 12$ in which

OAB occurs early because it is controlled by the seasonal increase in incident radiation (Figures 1; 2l; Figures S5, S7 and S8). In contrast, small PLDs are observed in lakes with $OD \geq 36$, where OAB is controlled by the onset of stratification (Figures 1l,p; 2l; Figures S7 and S8).

Impact of climate warming on phenological asynchrony at the European scale

Because of the trends being qualitatively similar across all four warming scenarios, we focus on illustrating them with

the +4°C scenario (see [Figures S1–S3](#) for the other scenarios). Our model simulations predict that uniform warming by +4°C 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; [Figure 3a–d](#); [Figure S9](#)), the advancement of TDM is spatially more uniform and considerably less variable between lake types (20th–80th percentiles 19–30 days; [Figure 3e–h](#); [Figure S10](#)). Consequently, the effect of warming on phenological asynchrony (PLD) is on average close to zero (median –3 days), but can range from –60 to +60 days ([Figures 3i–l](#); [4b](#); [Figure S11](#)).

How phenological asynchrony (expressed as PLD) changes with warming depends on the dominant process controlling OAB ([Figure 4a,b](#)) and thus on lake type and geographic location, because these properties determine which process controls OAB before and after warming ([Figure 3i–p](#); [Figures S11–S13](#)). In northern, eastern, or high-elevation lakes with OD ≤6, where OAB is controlled by ice-off ([Figure 3m](#); [Figure S12](#)), asynchrony will increase because OAB advances more with warming than TDM ([Figure 4a–f](#); [Figure S13](#)). In contrast, in low-elevation, southern and western lakes with OD 6–18, where OAB is controlled by incident radiation ([Figure 3n,o](#); [Figure S12](#)), asynchrony will decrease because only TDM advances with warming ([Figure 4a–f](#); [Figure S13](#)). In lakes with OD ≥36, where OAB is controlled by the onset of stratification ([Figure 3p](#); [Figure S12](#)), asynchrony will not change systematically because OAB and TDM advance similarly with warming ([Figure 4a–f](#); [Figure S13](#)). Finally, in lakes in which the dominant process controlling OAB will shift with warming—either from ice-cover to radiation (OD 6–12) or from radiation to stratification (OD 24–30)—OAB will advance at a slightly faster or slower pace than TDM, respectively, leading to intermediate shifts in asynchrony ([Figure 4a,b](#); [Figure S13](#)). 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; [Figure 4b](#); [Figure S13](#)).

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 ([Figure 4g,i](#)). The controlling factors thus describe the impact of warming on phenological asynchrony equally well as does the combination of geographic coordinates and OD ([Figure 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 (Berger et al., 2014; De Senerpont Domis et al., 2013; Sommer et al., 2012). 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, i.e. OD) 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 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. Modelled 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 0.5°. 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 Supporting Information S3, we illustrate this with an example from Lake Windermere, where the 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 OD.

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 (see Supporting Information S3). Unfortunately, empirical data on the phenological delay between OAB and TDM are too scarce for 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.

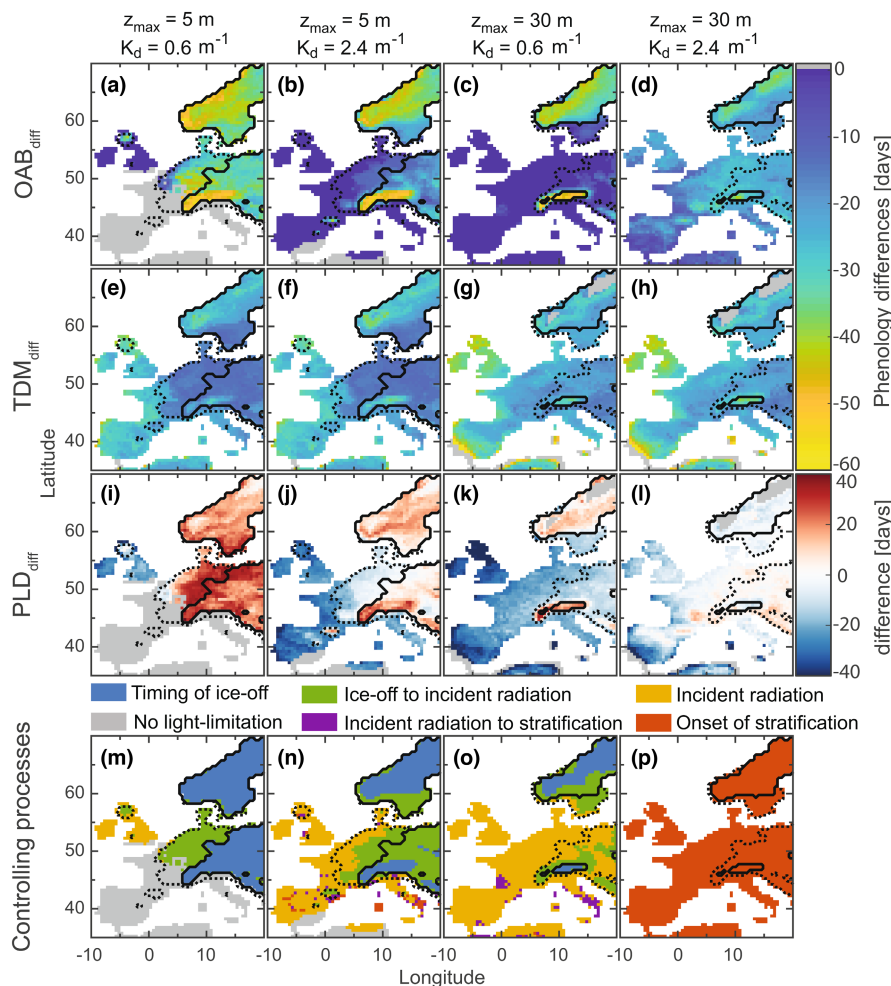


FIGURE 3 Predicted effects of an uniform temperature increase by +4°C on the timings of phenological events and the phenological delay between them in four representative lake types (median values of 31 simulation years). Lake types are indicated by their maximum depth (z_{\max}) and light attenuation 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. Each pixel represents the simulation results at a single geographical position/grid cell. 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 S5 provides corresponding figures on OAB_{diff} , TDM_{diff} , PLD_{diff} and the controlling processes for all 16 lake types investigated.

For example, the longest phenological delays between the two trophic levels 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 Müggelsee 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 75–88 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 the 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 OD. 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 (IGKB, 2012, 2016; Naselli-Flores & Barone, 1997) and predicted phenological delays were ~60 days for these two lakes.

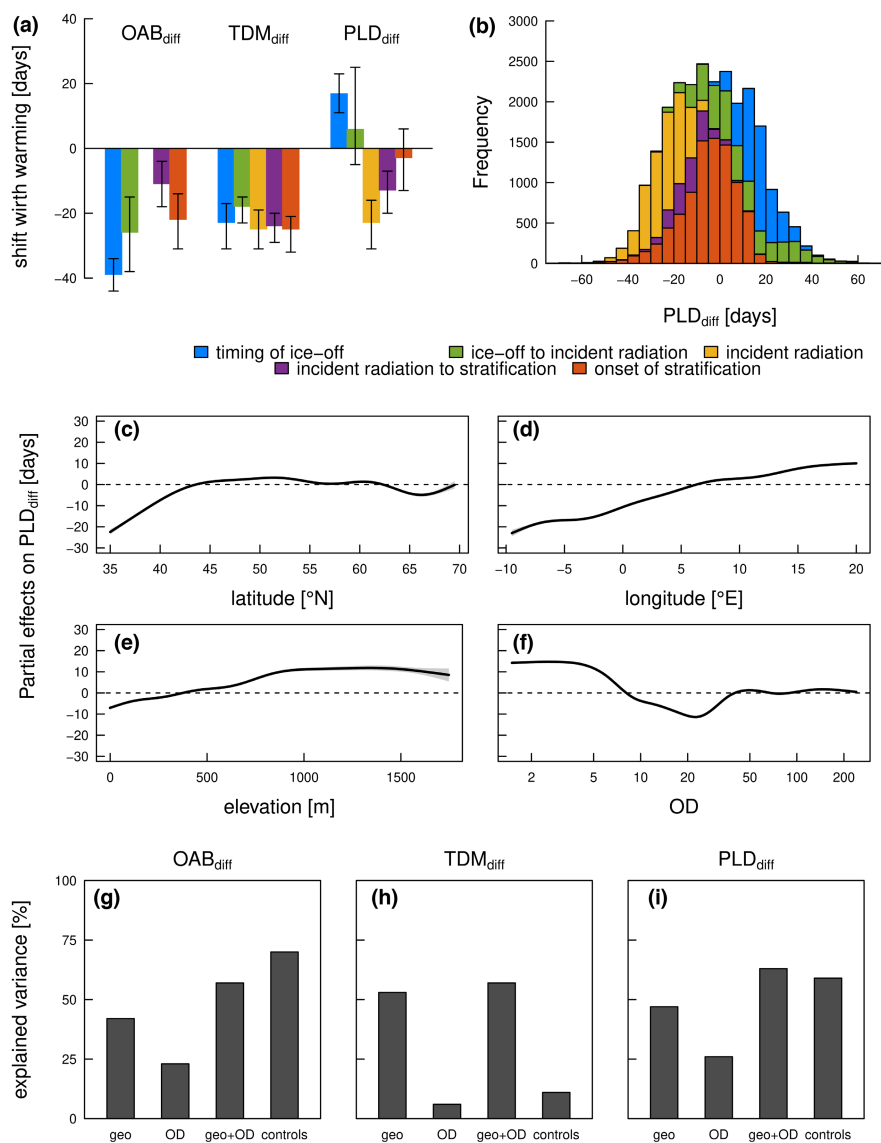


FIGURE 4 Factors and processes mediating predicted shifts in phenology between the reference and warming scenarios. (a) Median temporal shifts (days, with error bars indicating the 20% and 80% quantiles) between the warming and reference scenarios for the onset of the algal bloom (OAB_{diff}), the timing 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) Smooth function (± 2 standard error) of the partial effect of latitude, longitude, elevation and optical depth (OD) on PLD_{diff} determined by a general additive model (GAM). Grey shading (only visible in panel e) indicates ± 2 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'), optical depth (log10- transformed) 'OD', both ('geo+OD') or, alternatively, the five categories of dominant processes controlling OAB from panels (a) and (b).

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 (Berger

et al., 2014; George, 2012; Straile et al., 2015; Winder & Schindler, 2004).

The predicted large 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. While it seems plausible that *Daphnia* can adapt to local climatic conditions and/or show some plasticity in its phenology (possibilities that are not accounted for in our model but would be in line with the relatively large RMSE of the TDM model validation), the large extend (20–190 days) of the predicted

range in phenological asynchrony suggests 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 (Jäger 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 (Jäger et al., 2008; Kerimoglu et al., 2013; Schallau et al., 2008; 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 substitutions (Pickett, 1989) (e.g. with respect to northward-shift of climate zones) and lake type-for-time substitutions (e.g. with respect to browning) that can address the ecological consequences of phenological delay.

AUTHOR CONTRIBUTIONS

KDJ and DS conceptualized the study, EG and KDJ designed the methodology and EG performed the modelling work. EG and DS analysed output data and all authors contributed to the visualization of the results. EG,

FP and SD wrote the first draft of the manuscript and all coauthors contributed substantially to revisions and editing of the manuscript.

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PEER REVIEW

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OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: <https://doi.org/10.5281/zenodo.7627042>.

DATA AVAILABILITY STATEMENT

All data and code underlying the study can be found on Zenodo: <https://doi.org/10.5281/zenodo.7627042>

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SUPPORTING INFORMATION

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