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Local and continental-scale controls of the onset of spring phytoplankton blooms: Conclusions from a proxy-based model

Enzo Gronchi[1] | **Klaus D. Jöhnk**[2] | **Dietmar Straile**[1] | **Sebastian Diehl**[3,4] | **Frank Peeters**[1]

[1]Limnological Institute, University of Konstanz, Konstanz, Germany

[2]CSIRO Land and Water, Canberra, ACT, Australia

[3]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

[4]Integrated Science Lab – IceLab, Umeå University, Umeå, Sweden

Correspondence
Enzo Gronchi, Limnological Institute, University of Konstanz, Konstanz, Germany.
Email: enzo.gronchi@uni-konstanz.de

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Abstract

A key phenological event in the annual cycle of many pelagic ecosystems is the onset of the spring algal bloom (OAB). Descriptions of the factors controlling the OAB in temperate to polar lakes have been limited to isolated studies of single systems and conceptual models. Here we present a validated modelling approach that, for the first time, enables a quantitative prediction of the OAB and a systematic assessment of the processes controlling its timing on a continental scale. We used a weather-driven, one-dimensional lake model to simulate the seasonal dynamics of the underwater light climate in 16 lake types characterized by the factorial combination of four lake depths with four levels of water transparency. We did so at 1962 locations across Western Europe and over 31 years (1979–2009). Assuming that phytoplankton production is light-limited in winter, we identified four patterns of OAB control across lake types and climate zones. OAB timing is controlled by (i) the timing of ice-off in ice-covered clear or shallow lakes, (ii) the onset of thermal stratification in sufficiently deep and turbid lakes and (iii) the seasonal increase in incident radiation in all other lakes, except for (iv) ice-free, shallow and clear lakes in the south, where phytoplankton is not light-limited. The model predicts that OAB timing should respond to two pervasive environmental changes, global warming and browning, in opposite ways. OAB timing should be highly sensitive to warming in lakes where it is controlled by either ice-off or the onset of stratification, but resilient to warming in lakes where it is controlled by incident radiation. Conversely, OAB timing should be most sensitive to browning where it is controlled by incident radiation, but resilient to browning where it is controlled by ice-off or the onset of stratification. Available lake data are consistent with our findings.

KEYWORDS
browning, ice phenology, *k*-ε turbulence model, phenology, phytoplankton, regional modelling, spring bloom, warming

1 | INTRODUCTION

One of the most conspicuous events on Earth is the spring phytoplankton bloom in lakes and oceans of temperate to polar regions (Siegel et al., 2002; Sommer et al., 2012). The life cycles of important fish species are linked to the timing of the spring bloom (Cushing, 1990) and its magnitude is a main determinant of the annual export of photosynthetically fixed carbon to deep waters and sediments (Beaulieu, 2002). Changes in the phenology of spring phytoplankton blooms can lead to mismatches with growth processes of higher trophic levels (Straile et al., 2015; Thackeray et al., 2010; Winder & Schindler, 2004). Such mismatches can, in turn, feed back on bloom magnitude and export production, because the latter are partly controlled by grazers (Sarnelle, 1999). Understanding the processes controlling phytoplankton bloom phenology is therefore crucial to the prediction of ecosystem-wide consequences of environmental changes such as global warming, eutrophication and browning.

A critical event in the annual cycle of pelagic ecosystem production is the onset of the spring phytoplankton bloom (in the following OAB, onset of algal bloom) when, after a period of decline or stagnation during winter, phytoplankton production starts to exceed losses and sets off the vernal plankton succession (Sommer et al., 2012). Despite the importance of phytoplankton blooms, controversies on the mechanisms triggering the onset of vernal algal blooms still exist (Behrenfeld & Boss, 2014). Empirical studies in specific systems have identified a variety of factors controlling the timing of the OAB, such as the seasonal change in incident radiation (Sommer et al., 2012; Sommer & Lengfellner, 2008), the break-up of shading ice cover (Adrian et al., 2006; Weyhenmeyer et al., 1999) or the shallowing of the mixed surface layer (Diehl et al., 2015; Peeters, Straile, Lorke, & Livingstone, 2007; Peeters, Straile, Lorke, & Ollinger, 2007; Straile et al., 2015). A systematic characterization of the main processes controlling the OAB in different systems has, however, been lacking.

Common to all of the above studies is an underlying assumption that the OAB hinges critically on the alleviation of light limitation of phytoplankton production. This assumption has been formalized in the concept of the critical light intensity, I_{crit}, which is the depth-integrated intensity, I_{mix}, of photosynthetically active radiation (PAR, mol photons·m^{-2} day^{-1}) above which phytoplankton growth, averaged over the mixed surface layer, exceeds losses (Siegel et al., 2002; Sommer & Lengfellner, 2008; Sverdrup, 1953; Winder et al., 2012). I_{mix} depends on incident radiation penetrating the water surface, I_{ws} (mol photons·m^{-2} day^{-1}), on the light attenuation coefficient, K_d (m^{-1}), and the depth of the mixed surface layer, z_{mix} (m):

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

Importantly, the three parameters in Equation (1), I_{ws}, K_d, and z_{mix}, are controlled by a variety of proximate and ultimate drivers, some of which depend on seasonally varying, regional-scale climatic conditions (e.g. incident radiation, air temperature, wind), while others depend on local lake characteristics (e.g. lake depth, water clarity; Table 1). Because the OAB occurs when $I_{mix} > I_{crit}$, the timing of OAB depends on the proximate and ultimate drivers of the three parameters affecting I_{mix}, and on their interplay. This interplay is changing at local, regional and continental scales. For example, global warming is altering the extent to which lakes are shaded by ice cover in winter (affecting I_{ws}; Hewitt et al., 2018) and is shifting the timing and depth of thermal stratification in spring (affecting z_{mix}; Peeters, Straile, Lorke, & Livingstone, 2007), whereas more localized changes in the input of dissolved and suspended matter from the catchment (eutrophication, browning, soil erosion) alter water clarity (affecting K_d; Canfield Jr. & Bachmann, 1981; Creed et al., 2018; Donohue & Garcia Molinos, 2009; Solomon et al., 2015). A broader understanding of the processes controlling OAB across current climatic conditions and lake types will, therefore, enhance our ability to predict future changes in OAB at local to continental scales.

TABLE 1 Proximate and ultimate drivers of average light intensity in the mixed surface layer (I_{mix}), calculated as $I_{mix} = I_{ws}\left(1 - e^{-K_d \cdot z_{mix}}\right) / \left(K_d \cdot z_{mix}\right)$, and their implementation in the modelled scenarios across Western Europe (right column)

Parameter	Proximate driver(s)	Ultimate drivers	Drivers are lake specific or regional?	Drivers of model scenarios
I_{ws}	Seasonal course of incident radiation	Latitude, cloud cover, season	Regional	Incident light intensity obtained from regional climatologies
	Ice cover and timing of ice-off	Climate	Regional	Meteorological data obtained from regional climatologies
		Water column depth	Lake specific	Four prescribed levels: 5, 10, 30, 100 m Ice model
K_d	Water clarity	Dissolved and suspended material from catchment	Lake specific	Four prescribed levels: 0.3, 0.6, 1.2, 2.4 m^{-1}
z_{mix}	Timing and depth of thermal stratification	Climate	Regional	Meteorological data obtained from regional climatologies
		Water column depth	Lake specific	Four prescribed levels: 5, 10, 30, 100 m
		Water clarity (and its ultimate drivers)	Lake specific	Four prescribed levels: 0.3, 0.6, 1.2, 2.4 m^{-1} Hydrodynamic model

In this study, we used numerical simulations to investigate the influence of local lake characteristics and continental-scale climatic gradients on the timing of OAB in lakes across Western Europe. We explored two lake-specific drivers, water clarity and lake depth, and three processes that vary seasonally and geographically: (a) the occurrence of ice cover and the timing of ice-off, (b) the seasonal increase of incident radiation at the lake surface and (c) the seasonal development of thermal stratification causing a shallowing of the mixed surface layer.

We assessed the timing of OAB and the processes controlling it in different lakes from numerical simulations of the underwater light climate with a one-dimensional hydrodynamic model coupled to an ice model (Joehnk & Umlauf, 2001; Yao et al., 2014). The model was driven by 31 years of meteorological data at 1962 locations across Western Europe. At each of these locations and for all 31 years, the timing of OAB was determined from simulations of the underwater light climate in 16 different lake types obtained from a factorial combination of four lake depths and four light attenuation coefficients resulting in a total of 937,152 simulation years.

We hypothesized that the local factors, lake depth and water clarity, would interact with continental-scale meteorological forcing in a complex, but predictable, way in determining the timing of OAB and the processes controlling it. Specifically, we hypothesized that the dominant processes controlling the OAB are: (1) the timing of ice-off in shallow lakes of northern and alpine areas, (2) the seasonal course of incident radiation in shallow lakes that do not freeze and (3) the timing of the onset of stratification in deep lakes. We subsequently analysed inter-annual variability in OAB timing within lakes and compared OAB timing between lakes of different transparency to explore how OAB timing should change in response to global warming and browning. We expected that the resilience, that is the ability to resist changes (Holling, 1973), of OAB timing to warming and browning should differ depending on which of the three controlling processes is currently the dominant one, and on whether warming or browning would lead to a shift in the dominant controlling process.

2 | MATERIALS AND METHODS

2.1 | Definition of OAB timing and its dominant controlling process

In temperate to arctic lakes, nutrient concentrations are typically high after the late winter/early spring mixing period, and algal growth is primarily limited by light (Sommer et al., 2012). While light-saturated algal growth can be strongly temperature dependent, temperature has only a very weak influence on algal growth at light levels below 1.7 mol photons m^{-2} day^{-1} (Edwards et al., 2016). Natural phytoplankton communities are furthermore adapted to local climatic conditions such that phytoplankton in colder regions show positive growth at lower temperatures (Thomas et al., 2016). We therefore focus exclusively on light as the dominant growth limiting factor and assume that the onset of the spring phytoplankton bloom occurs on the first day of the year when the average light intensity in the mixed surface layer, I_{mix}, has stably exceeded the critical light intensity, I_{crit}, above which net growth of light-limited phytoplankton is positive. We used an empirically derived value of I_{crit} of 1.3 mol photons·m^{-2} day^{-1} (Mignot et al., 2014; Siegel et al., 2002; Sommer & Lengfellner, 2008) and calculated I_{mix} from Equation (1), where z_{mix} was defined as the shallowest depth at which the water density exceeds the density at the lake surface by 0.04 kg m^{-3}. This threshold value is similar to the ones used in other studies of stratified water bodies (de Boyer Montégut et al., 2004; Giling et al., 2017; Read et al., 2011).

Incident radiation penetrating the water surface, I_{ws}, was calculated from incident radiation at the lake surface taking into account time variable reflection from the lake surface as described in Peeters, Straile, Lorke, and Ollinger (2007). In ice-covered lakes, I_{ws} is often low because of snow cover and/or low transparency of the ice itself. Consequently, algal growth can be strongly light-limited under ice (Adrian et al., 2006; Weyhenmeyer et al., 1999). While phytoplankton can develop under clear ice conditions (Hampton et al., 2017; Kalinowska & Grabowska, 2016), the occurrence of such ice conditions especially at the end of the ice season is uncommon. Usually, ice cover including snowpack will strongly limit light penetration into a lake. We thus make the simplifying assumption that $I_{mix} < I_{crit}$ whenever a lake is ice-covered. We also make the simplifying assumption that ice break-up is a discrete event that occurs instantaneously across the entire lake.

In the numerical simulations described below and based on the above assumptions, we defined the simulated timing of OAB (OAB_s) as the first day of the year (doy, expressed as the number of days since 1 January) when the following two conditions are fulfilled: (i) the lake is ice-free and (ii) I_{mix} lastingly exceeds I_{crit}. The latter condition excludes short-lived transients where an initial exceedance of the criterion $I_{mix} > I_{crit}$ is not maintained, as would be the case when a short period of inverse temperature stratification after ice-out is followed by a longer period of deep mixing during spring overturn. We furthermore distinguished four cases with respect to the dominant process alleviating phytoplankton light limitation by comparing, for each lake and each geographical location, the simulated timing OAB_s with a hypothetical timing OAB_h that would have been observed in the absence of ice cover and seasonal stratification. We calculated OAB_h in exactly the same way as OAB_s, except that the water column was assumed to be fully mixed and ice-free. OAB_h thus corresponds to a 'null model' where the seasonal change in incident radiation is the sole factor controlling OAB. In the case of OAB_s occurring after OAB_h, ice cover must have prevented the penetration of light in the water and has thus controlled the timing of OAB. In the case of OAB_s occurring before OAB_h, stratification must have caused z_{mix} to be shallower than the maximum lake depth and thus reduced the incident light intensity required for the OAB in the respective lake. Hence, the onset of stratification has controlled the timing of OAB. If OAB_s and OAB_h occur at about the same time, the seasonal increase in incident radiation is the only controlling process of the timing of OAB. We, therefore, defined the dominant process controlling the timing of OAB as: (1) The timing of ice-off if OAB_s occurred more than 2 days after OAB_h, that is OAB_s – OABh >2 days; (2) The seasonal increase of incident radiation if OAB_s and OAB_h occurred within a 2-day interval, that is | OAB_s – OAB_h | ≤2 days; (3) The onset of stratification if OAB_s occurred more than 2 days before OAB_h, that is OAB – OABh <2 days (see Figure S1). We used a 2-day time window to make this categorization robust against minor inaccuracies in the meteorological data. The results were, however, very similar when time windows between 1 and 5 days were chosen (data not shown). Finally, in some shallow and clear southern lakes, I_{mix} exceeded I_{crit} already on the first doy, suggesting that light was not a limiting factor. These lakes were categorized as (4) 'Not light-limited'.

2.2 | Model description and lake scenarios

Our definition of the timing of OAB in a given lake requires knowledge of the seasonal development of ice cover and the underwater light climate in the mixed surface layer. We numerically simulated underwater light climate and ice cover with the hydrodynamic model LAKEoneD combined with the ice model SIM, which requires meteorological data and information on water column depth and water clarity as input variables (Table 1). Below, we briefly describe the two models, as well as the meteorological data and lake type scenarios used in this study.

LAKEoneD is a one-dimensional lake model that simulates hydrodynamics and the vertical temperature distribution. The model is described in Joehnk and Umlauf (2001) and Hutter and Jöhnk (2004) and has been successfully applied in a range of lakes (Jöhnk et al., 2008; Samal et al., 2009; Stepanenko et al., 2013; Thiery et al., 2016; Yao et al., 2014). The model is driven by hourly meteorological data on air temperature, wind speed, relative humidity, solar radiation and cloud cover for the simulation of heat fluxes and wind stress at the lake surface. Water vapour pressure (which depends on altitude and affects latent heat fluxes) is calculated from relative humidity and air temperature, which both were provided in the meteorological data set at the average altitude of the respective geographical region (see below). Heat is transported vertically by turbulent diffusion. Turbulent diffusion coefficients are estimated from turbulent kinetic energy k and energy dissipation ε which are both simulated dynamically. Coriolis effects were not considered.

The ice model SIM (Yao et al., 2014) uses an empirical degree-day approach to determine the timing of ice-on and an ice-model for the dynamic simulation of ice thickness from which the timing of ice-off is inferred (Ashton, 2011). To allow for the simulation of lakes of different depths, we extended the original degree-day approach in a way similar to Shuter et al. (2013). Specifically, we calculated the timing of ice-on from an empirical description relating the number of negative degree days (i.e. the integral of daily average air temperature below 0°C after 1 October) required for ice-on to the square root of mean lake depth, where greater depth implies more heat storage and slower surface cooling as demonstrated in Franssen and Scherrer (2008). In addition, a minimum of two consecutive days with daily mean air temperatures below zero was required to freeze over (see Supporting Information SI2 for a detailed description). Lateral inhomogeneities in lake ice cover are not considered. The development of the ice-cover, that is ice thickness, was calculated from an ice-model which is based on the steady-state solution of the 1D heat conduction equation through homogenous ice (Ashton, 2011) and is driven by hourly time series of air temperature. The timing of ice-off was determined from the simulated ice thickness assuming that ice break-up does not necessarily require ice thickness to become zero but can occur earlier if wind speed exceeds a certain threshold. Following Yao et al. (2014) we used threshold values of 0.02 m for ice thickness and 1 m s^{-1} for wind speed.

The meteorological data used to drive the numerical models were taken from the global atmospheric reanalysis data set ERA-Interim produced by the European Centre of Medium-Range Weather Forecasts (ECMWF; Dee et al., 2011). We extracted from this data set values from 1962 terrestrial locations covering Western Europe from 35° to 70° North and −20° to 20° West with a spatial resolution of 0.5°. For each of the 1962 locations, we extracted three-hourly values of the following data over the period 1979–2009: wind speed at 10 m above the ground (m s^{-1}), air temperature (°C), incident solar radiation (W m^{-2}), relative cloud cover (%) and relative humidity (%). All data were then linearly interpolated to hourly values for model input.

To explore how local lake characteristics interact with continental-scale climatic conditions in affecting underwater light intensities (Equation 1), we simulated seasonal temperature profiles for 16 different lake types at each of the 1962 grid locations and all 31 years, yielding a total of 937,152 simulated lake years. Lake types were characterized by the factorial combination of four different maximum lake depths (z_{max} =5, 10, 30 and 100 m) with four different, temporally constant, light attenuation coefficients (K_d = 0.3, 0.6, 1.2 and 2.4 m^{-1}; see right-hand column in Table 1). These values bracket mean lake depths and water clarities encountered in the majority of lakes >1 ha (Cael et al., 2017; Pérez-Fuentetaja et al., 1999; Seekell et al., 2018).

For each lake type and at each location, we simulated a 31-year long time series of vertical temperature profiles based on the driving meteorology and the lake type's water column depth and water clarity. All simulations were performed with a 5-year spin-off simulation using the meteorology from 1979 to 1984. The profiles of the state variables (temperature, turbulent kinetic energy and energy dissipation) from the final day of the spin-off period were used as initial conditions for the main simulation which was started again on 1 January 1979 and run through 31 December 2009. From this, we obtained, for each lake type at each location, a 31-year long time series of simulated ice-cover and solar radiation within the mixed part of the water column, which we converted to I_{mix} by assuming that 45.6% of solar radiations is PAR (Jacovides et al., 2003) and using a conversion factor from W m^{-2} to mol photons·m^{-2} day^{-1} of 0.395 (McCree, 1972). We determined OAB timing by finding the first day in each year on which a given lake was ice-free and the condition $I_{mix} > I_{crit}$ was stably fulfilled. In a few simulations, ice-covered lakes exceeded I_{crit} on the day of ice-off because of inverse temperature stratification, but soon thereafter experienced a reversal to $I_{mix} < I_{crit}$ during spring overturn. In those lakes, we defined OAB timing as the first day following spring overturn on which $I_{mix} > I_{crit}$.

We subsequently used the medians of these 31 simulated OAB timings to explore general patterns in OAB timing, and the processes controlling it, in different lake types across Western Europe.

2.3 | Resilience of OAB timing to climate change and browning

In order to explore the effects of changing climatic conditions and of browning on the timing of OAB, we evaluated the inter-annual variability of the timing of OAB and its sensitivity to changes in K_d. Inter-annual variability was operationally defined as the time difference between the 80th and 20th percentiles of the timings of OAB in the 31 simulated years. Sensitivity to changes in K_d, that is Sens_{OAB}, was calculated for each geographical location and lake depth as the relative difference (days per unit of K_d) between the timings of OAB of consecutive K_d scenarios (Equation 2).

$$\text{Sens}_{\text{OAB}(i)} = \frac{\text{OAB}_{K_d(i+1)} - \text{OAB}_{K_d(i)}}{K_d\,(i+1) - K_d\,(i)}. \quad (2)$$

Here, i indicates a scenario with a lower K_d, $i+1$ the scenario with the next higher K_d and OAB_{Kd} the median timing of OAB at this K_d.

2.4 | Model validation

We validated our approach by comparing the simulated timings of ice-off to observations from 14 lakes from the Global Lake and River Ice Phenology Database (Benson et al., 2012). Similarly, we compared simulated OAB timings to observations from 15 lakes for which data on the seasonal dynamics of phytoplankton biomass (or proxies thereof) could be extracted from the literature. Both comparisons involved lakes covering a broad range of depths and climate regions (see Tables S1 and S2) and were based on simulations using values of maximum lake depth, water clarity and geographical location that were most similar to the empirically studied lakes. We assessed model performance with respect to the timings of ice-off and OAB with the multiple linear regression model:

$$T_o = a + bT_p + cE_d, \quad (3)$$

where T_o is the median of the observed timing of ice-off or OAB in a given lake, T_p is the median of the corresponding timing predicted by our simulation model, E_d accounts for the effect of the elevation difference between the observed lake and the corresponding ERA-Interim grid point used in the simulations, and a, b and c are fitted coefficients. Elevation difference (or an appropriate transform thereof) was included as an explanatory variable to account for the up to 600 m difference between the actual elevation of a lake in the validation data set and the grid cell elevation used in the simulations. Further details of the validation procedure are described in Supporting Information SI3.

3 | RESULTS

3.1 | Model validation

Predicted phenologies agreed well with observations for both ice-off (see Figure S3) and OAB (Figure 1). Predicted ice-off in combination with the elevation difference between lake and grid cell explained 93% of the variance in observed ice-off ($p < 0.0001$) with an intercept of a = 20.9 days (standard error [SE] of ±7.6), a slope of b = 0.83 [±0.07 SE] in respect of predicted ice-off and a slope of c = −0.03 [±0.02 SE] in respect of elevation difference (see Table S3a). Predicted ice-off thus slightly underestimates the observed ice-off in lakes where ice-off occurred on doy 60 or earlier (see Figure S3). Predicted OAB together with elevation difference explained 89% of the variance in observed OAB ($p < 0.0001$) with an intercept of a = 0.63 days (±6.4 SE), a slope of b = 0.93 (±0.1 SE) in respect of predicted OAB and a slope of c = −6.6 (±1.8 SE) in respect of log-transformed elevation difference (see Table S4b). With estimates of a not significantly different from zero (p = 0.92) and b

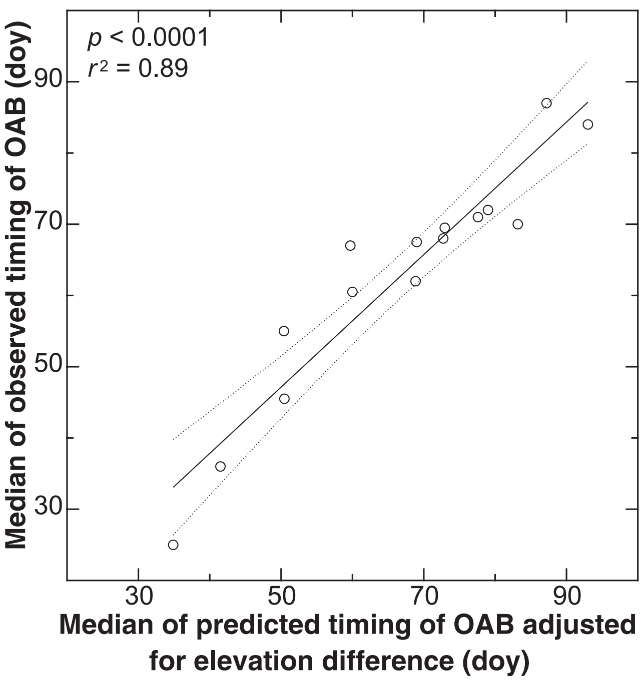

FIGURE 1 Relationship between median timing of observed (T_o) onset of algal bloom (OAB) and median timing of predicted OAB adjusted for elevation difference (T_{pa}). To visualize the model performance, the OAB predicted by the model (T_p) was adjusted for differences in elevation between the actual, observed lakes, and the grid cells used in the simulation model (see details in Supporting Information SI3). T_{pa} was determined from $T_{pa} = T_p + \frac{c}{b}\log_{10}(\Delta E)$, where ΔE is the difference in elevation between the simulated grid cell and the observed lake, and a, b and c are the coefficients obtained from multiple linear regression (Equation 3 using $E_d = \log_{10}(\Delta E)$). The thick solid line equals $T_o = a + bT_{pa}$ and the dashed lines are the 95% confidence intervals (see regression statistics in Table S4b)

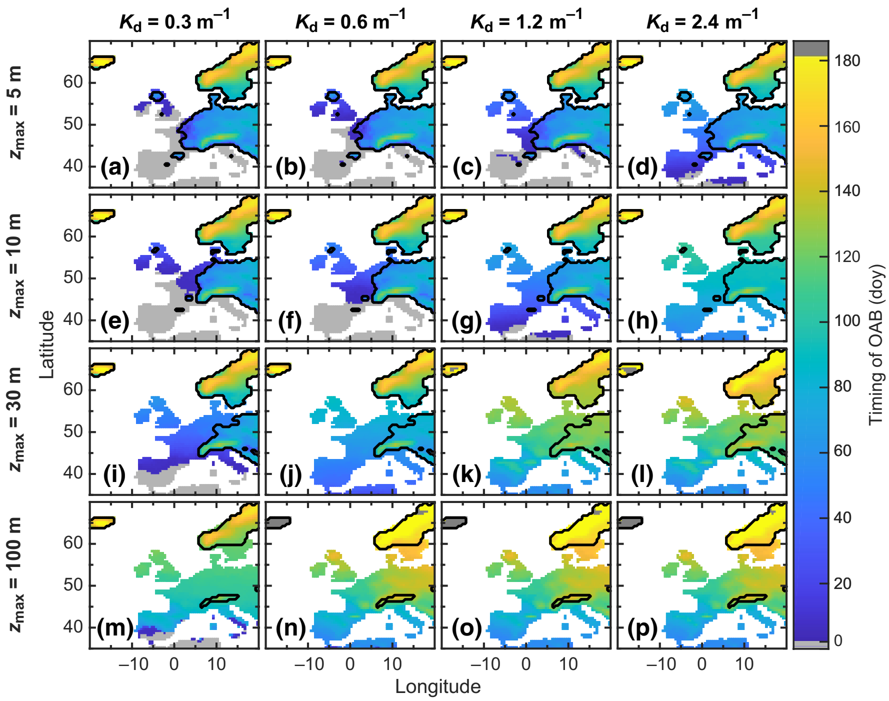

FIGURE 2 Predicted timing of the onset of algal bloom (OAB) across Western Europe for 16 different lake types. Shown is the median day of the year (doy) of OAB timing from a 31-year time series covering the period 1979–2009. Lake types are characterized by the factorial combination of four maximum lake depths (z_{max}, rows of panels) with four light attenuation coefficients (K_d, columns of panels). Black lines delimit regions in which lakes develop ice cover in at least 16 out of the 31 simulated years. In regions marked in light grey, the critical light intensity required for an algal bloom, I_{crit}, is exceeded already on the first day of the year. In regions marked in dark grey, I_{crit} is not reached during the entire year

not significantly different from 1 (p_1 = 0.46), the model thus gives an unbiased prediction of OAB (Figure 1).

3.2 | Continental distribution of OAB

For the 31 simulated years, the median predicted timing of OAB ranges from 1 January (doy 0; i.e. absence of light limitation) in shallow and clear lakes of southern and south-western Europe to end of June (doy ~ 180) in deep and turbid lakes of northern Scandinavia (Figure 2). On the continental scale, three general trends in OAB timing are visible in each of the 16 panels of Figure 2: The OAB occurs earliest at the most south-western latitudes and gets increasingly delayed towards (i) more northern latitudes, (ii) more eastern longitudes and (iii) higher altitudes, all of which are characterized by an increasingly colder winter climate. Furthermore, two effects of lake-specific drivers become visible when comparing given geographical locations across the 16 panels of Figure 2: The OAB occurs earliest in clear, shallow lakes and gets increasingly delayed with both increasing maximum lake depth and light attenuation. Finally, the presence of ice cover often implies a discrete delay in OAB timing compared to nearby ice-free regions.

3.3 | Continental distribution and underlying mechanisms of the processes controlling OAB

How do climate, water clarity and water column depth interact in determining whether OAB timing is controlled by the seasonal increase in incident radiation, the timing of ice-off or the onset of stratification? The answer to this question is largely determined by only two factors as suggested by Figure 3: (i) presence or absence of ice cover and (ii) the optical depth of the lake, that is OD, which is the product of maximum lake depth and water clarity (OD = $z_{max} \times K_d$). Specifically, in lakes with an OD ≤18, the controlling process of OAB depends strongly on the absence or presence of an annual ice cover but never on stratification (Figure 3a–g,i,j). In contrast, in lakes with an OD ≥60, the controlling process of OAB is almost everywhere independent of ice cover but strongly dependent on stratification (Figure 3l,n–p). Lakes in the OD range 24–36 take on an intermediate position, where the timing of OAB is controlled by ice cover in the north-east and by stratification in the south-west (Figure 3h,k,m). These patterns and their underlying mechanisms can be further described as follows.

In the optically shallowest lakes (OD ≤9, Figure 3a–c,e,f,i), the condition $I_{mix} > I_{crit}$ requires only modest incident radiation even when the water column is fully mixed. Under ice-free conditions, these lakes are therefore either not light-limited at all (at southern latitudes) or have the OAB triggered by the seasonal increase in incident radiation at a time when seasonal warming has not yet been sufficient to stratify the water column. In contrast, under ice-covered conditions, OAB is typically delayed and triggered by ice break-up, indicating that the solar radiation and atmospheric heat required to melt a shading ice cover are higher than the solar radiation required to reach $I_{mix} > I_{crit}$ in an ice-free, optically shallow lake. Similar patterns exist in lakes where 12 ≤ OD ≤18 (Figure 3d,g,j), except in ice-covered regions with relatively mild winter temperatures such as the lowlands of Central and Eastern Europe. Here, ice break-up occurs sufficiently early that I_{mix} is still below I_{crit} in these optically deeper lakes, and a further increase in incident radiation is required to trigger the OAB (yellow areas in ice-covered regions in Figure 3d,g,j).

At the other end of the optical depth spectrum (OD ≥60, Figure 3l,n–p), incident radiation alone is never sufficient to trigger an OAB, because, in a fully mixed lake with OD ≥60, $I_{mix} < I_{crit}$ at any time of the year. Such lakes must therefore thermally stratify prior

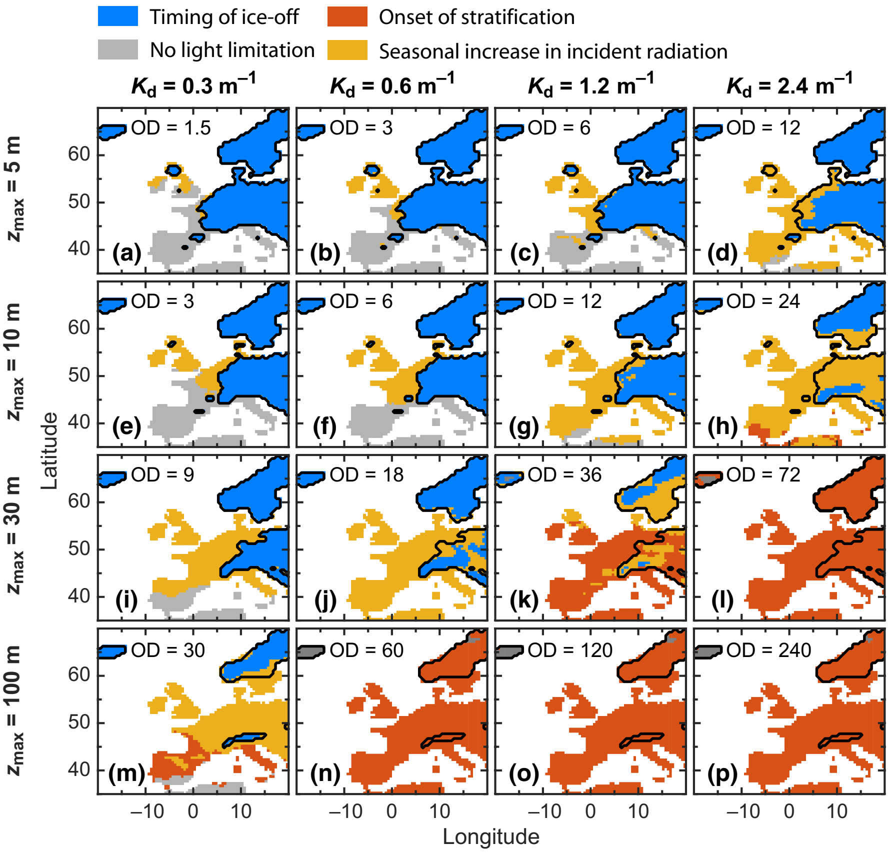

FIGURE 3 Geographical distribution of the dominant processes controlling the onset of algal bloom (OAB) in 16 different lake types. Lake types are characterized by the factorial combination of four maximum lake depths (z_{max}, rows of panels) with four light attenuation coefficients (K_d, columns of panels), and by the resulting optical depth (OD = $z_{max} \cdot K_d$). Black lines delimit regions in which lakes develop ice cover in at least 16 out of the 31 simulated years. Depending on lake type and geographical location, the dominant process controlling OAB timing can be the timing of ice-off (blue), the seasonal increase in incident radiation (yellow) or the onset of stratification (red). In regions marked in light grey, the critical light intensity required for an algal bloom, I_{crit}, is exceeded already on the first day of the year. In regions marked in dark grey, I_{crit} is not reached during the entire year. The colour coding is based on the median values of the difference between OAB_s and OAB_h in the 31-year time series

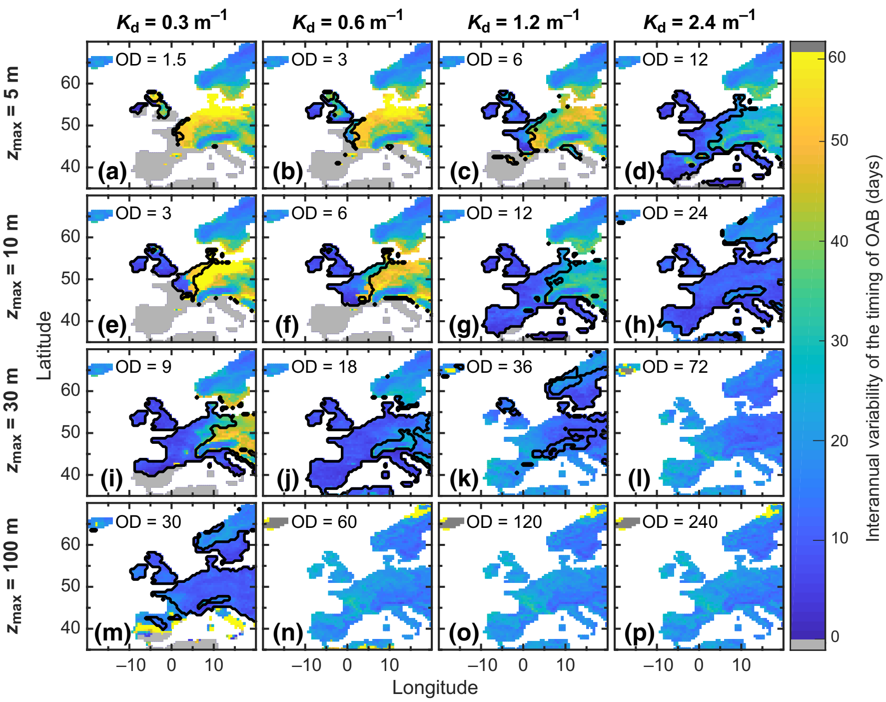

FIGURE 4 Geographical distribution of the inter-annual variability in the timing of onset of algal bloom (OAB) in 16 different lake types. Inter-annual variability is defined as the difference between the 80th and 20th percentiles of the OAB timings in the 31 simulated years. Lake types are characterized by the factorial combination of four maximum lake depths (z_{max}, rows of panels) with four light attenuation coefficients (K_d, columns of panels). Black lines delimit regions in which the timing of OAB is controlled by the seasonal increase in incident radiation in at least 16 out of the 31 simulated years. Light and dark grey shading have the same meaning as in Figure 2

to OAB, regardless of their geographical location and ice cover. OAB timing is therefore tightly coupled to the onset of stratification in these lakes. Finally, in lakes in the OD range 24–36 (Figure 3h,k,m), the controlling process of OAB depends on how much heat is required to stratify a water column compared to how much incident radiation is needed to reach $I_{mix} > I_{crit}$ under full mixing. Which of the two events comes first depends on air temperature and optical depth, with milder temperatures and larger OD favouring a relatively earlier stratification (see also Section 4.1). With increasing optical depth, the geographical extent of the area in which lakes do not stratify prior to OAB, therefore, becomes increasingly limited to colder regions in the northeast (Figure 3h,k,m).

3.4 | Inter-annual variability

A comparison of Figures 3 and 4 shows very clearly that inter-annual variability in the timing of OAB (Figure 4) depends on the process controlling the OAB (Figure 3). Inter-annual variability is the largest (often 30–60 days) in lakes with an OD ≤12 in which OAB timing is controlled by ice-off (green to yellow areas in Figure 4a–g,i). It is intermediate (often 20–40 days) in lakes with an OD ≥36 in which OAB timing is controlled by the onset of stratification (light blue to green areas in Figure 4k–p). It is the smallest (often 0–5 days) in lakes with an OD ≤30 in which OAB timing is controlled by incident radiation (dark blue areas in Figure 4a–j,m). Exceptions from these patterns can be found in lakes in which the controlling process shifts from incident radiation to ice-off between warmer and colder years, such as shallow lakes in the north-west of Central Europe (Figure 4c,e,f).

3.5 | Resilience of the timing of OAB to the light extinction coefficient K_d

The sensitivity of the timing of OAB to changes in the light attenuation coefficient depends also on the process controlling the OAB, but the pattern is opposite to the one observed for inter-annual variability. Thus, sensitivity of the timing of OAB to changes in K_d is highest in lakes in which OAB timing is controlled by incident radiation either before and/or after the change in K_d has taken place (the vast majority of the coloured areas in Figure 5), where OAB timing can be delayed by 30–150 days per unit of increase in K_d. In these lakes, sensitivity is highest if K_d is initially low, suggesting that the rate of change of OAB timing increases logarithmically with increasing K_d (see Figure S4). In contrast, sensitivity of the timing of OAB to changes in K_d is typically very low in lakes in which OAB timing is controlled by ice-off or by the onset of stratification. In the vast majority of these lakes, an increase in K_d will have either no effect at all or slightly advance OAB timing by a few days per unit of K_d (grey areas in Figure 5), that is the timing of OAB is rather resilient towards changes in K_d.

4 | DISCUSSION

Plankton blooms are common features of many aquatic systems where they drive important ecosystem and community processes (Beaulieu, 2002; Hjermann et al., 2007; Smayda, 1997). Bloom impacts on ecosystem dynamics can, however, vary greatly depending on bloom timing (Maier et al., 2019; Malick et al., 2015; Winder & Schindler, 2004). Correctly identifying the processes that lead to the initiation of a bloom is therefore crucial to an understanding of pelagic ecosystem dynamics. Descriptions of the factors controlling the spring phytoplankton bloom in temperate to polar lakes have, until now, been largely limited to isolated studies of single

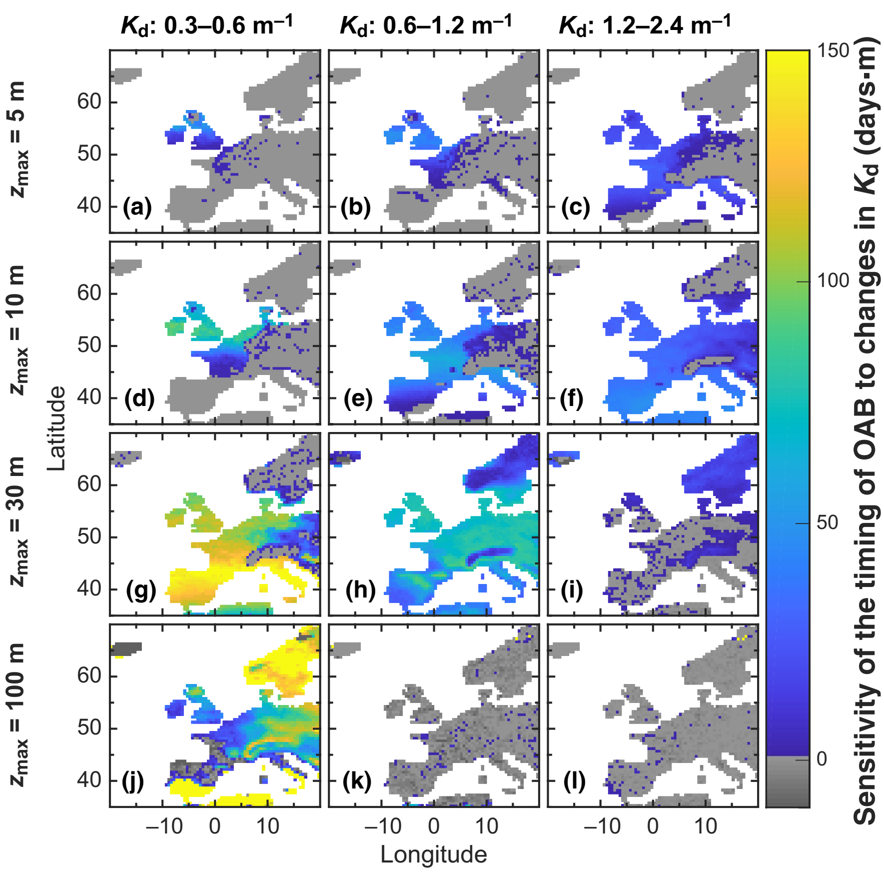

FIGURE 5 Geographical distribution of the sensitivity of the timing of onset of algal bloom (OAB) to changes in water transparency in lakes of different maximum depth (z_{max}, rows of panels). Sensitivity was calculated from Equation (2) as the relative change in OAB timing (days per unit of the light attenuation coefficient K_d) in response to a stepwise increase in K_d between the panels in Figure 2, as indicated at the top of each column of panels. Zero and negative changes in OAB timing with increasing K_d are indicated in shades of grey

systems (Adrian et al., 2006; Berger et al., 2010; Diehl et al., 2015; Meis et al., 2009; Peeters et al., 2013; Peeters, Straile, Lorke, & Livingstone, 2007; Thackeray et al., 2008; Weyhenmeyer et al., 1999) and to conceptual models (Berger et al., 2014; De Senerpont Domis et al., 2013; Sommer et al., 2012). In contrast, our proxy-based hydrodynamic modelling approach constitutes a first step towards a truly quantitative prediction of plankton succession in lakes.

Our study makes two major advances. First, it provides a tool for the quantitative prediction of the onset of the OAB in lakes, using continental-scale meteorological data and a few local lake characteristics as input variables. Second, the new tool enables us to identify the processes that most strongly influence OAB timing in different types of lakes across Western Europe. Knowledge of the controlling processes of OAB is particularly useful when making projections of how environmental change will affect OAB timing in the future. We will therefore first briefly discuss how ice cover, ice break-up and stratification are influenced by climate, water clarity and maximum lake depth. We subsequently ask how these three factors interact in determining whether OAB timing is controlled by the seasonal increase in incident radiation, the timing of ice-off or the onset of stratification. The remainder of the discussion will then focus on how two pervasive environmental changes, climate warming and browning, are expected to affect OAB timing across lake types and geographical locations.

4.1 | Determinants of ice cover, ice-off and stratification

If the seasonal change in incident radiation was the sole factor controlling OAB, then, for any given lake type (i.e. within each panel in Figure 2), OAB timing would simply follow the latitudinal gradient, because geographical variations in cloud cover along a given latitude are small compared to seasonal variation in incident radiation. Instead, the rate of change of predicted OAB timing along the latitudinal climate gradient varies with latitude, water clarity and water column depth in highly non-linear ways (Figure S5). Understanding these deviations of OAB timing from a simple latitudinal pattern driven by incident radiation requires understanding how lake depth and water clarity interact with the climate in shaping ice cover and stratification as alternative controlling processes of OAB.

Both the formation and the break-up of ice cover depend on the heat balance at the lake–atmosphere interface. The probability of a lake to become ice-covered—and the timing of ice-off—therefore increase with latitude, altitude and continentality of the climate (Figure 2). The probability of ice formation also decreases with lake depth (Table 1; Figure 2), because deeper water columns contain more heat at the onset of winter. Deep lakes, therefore, become ice covered in a much smaller geographical region than shallow lakes, independently of water clarity (Figure 2). Because the timing of ice-off is well described by meteorological conditions, that is air temperature (Korhonen, 2006; Lopez et al., 2019; Weyhenmeyer et al., 2004) or a combination of air temperature and wind speed (Yao et al., 2014), our model assumes that feedback of water temperature, light attenuation and lake depth on ice decay is negligible once the lake is frozen. For lakes that develop ice cover, the predicted timing of ice-off is therefore independent of lake depth and water clarity (see Figure S6).

All 16 lake types are predicted to stratify everywhere on the continent at some point during the open-water season, except for some lake types in Iceland (see Figure S7). Whether stratification contributes to the OAB, therefore, depends on how early in the year the water column stratifies. The timing of the onset of stratification depends, in turn, primarily on three factors: winter to spring climate, ice-cover (which depends partly on lake depth) and water clarity (Table 1; Figures S7 and S8). In regions with a mild winter climate, lakes are ice-free and relatively warm and therefore require only a minor heat transfer for stratification. In contrast, ice-covered lakes are colder and cannot absorb much solar radiation prior to ice break-up. Finally, in the absence of ice-cover, turbid waters require less heat input for stratification, because they absorb solar radiation (and subsequently stratify) at shallower depths than clear waters (see Figure S10). An early onset of stratification is therefore favoured by the absence of an ice cover, warm climate early in the season and low water clarity (see Figures S7 and S9).

4.2 | Identification of different regimes of OAB-controlling processes

We identified four different regimes with respect to the OAB-controlling processes. These regimes depend on a complex interplay between the seasonal increase in incident radiation, local meteorological conditions affecting ice cover and the onset of stratification, and on maximum lake depth and water clarity. The latter two factors modulate the consequences of incident radiation and meteorological conditions for the development of ice cover and stratification and thus also for the seasonal course of I_{mix}. This complex interplay will ultimately determine which process controls the timing of OAB. Despite these complex interdependencies, the prevalence of the four regimes depends on only two factors—geographical location and optical depth (Figure 3). While comparative lake data that can discriminate among these processes are rare, we found evidence for all four regimes in regions and lake types that are consistent with model predictions.

4.2.1 | Seasonal increase in incident radiation

For lakes in the English lake district with an optical depth ≤30, our model predicts that OAB timing is determined by the seasonal increase in incident radiation (Figure 3), with the OAB being delayed in deeper lakes compared to shallower ones (Figure 2). This is exactly what has been observed in lakes in this region, which do not develop ice-cover except for shallow lakes in exceptionally cold years

(Feuchtmayr et al., 2012). In deep Lake Windermere (z_{max} = 42 and 64 m; OD ~ 21 and 25 for the southern and northern basin respectively), net growth rates of phytoplankton during early spring were closely related to surface irradiance (Neale et al., 1991) suggesting radiation control of OAB timing. Also as predicted, OAB in shallow Esthwaite Water (z_{max} = 14 m; OD ~ 16) occurs earlier compared to Windermere (Talling, 1993).

4.2.2 | *Timing of ice-off*

For lakes in Central, Eastern and Northern Europe with an optical depth ≤12, our model predicts that the timing of OAB is controlled by the timing of ice-off (Figure 3). This has indeed been observed in most years in Lake Erken, Sweden (z_{max} = 21 m, OD ~ 12; Weyhenmeyer et al., 1999) and Müggelsee, Germany (z_{max} = 8 m, OD ~ 9; Adrian et al., 2006). However, during very warm winters, Müggelsee can be ice-free, which results in a much advanced OAB timing (Adrian et al., 2006). This is, again, consistent with our model, which predicts that in lakes with an OD ≤ 9, ice-cover delays the OAB substantially at any given latitude (Figure 2).

4.2.3 | Onset of stratification

For deep lakes characterized by an OD ≥ 60, our model predicts that everywhere in Western Europe, the timing of OAB depends on the onset of stratification (Figure 3; Bouffard et al., 2018; Peeters, Straile, Lorke, & Ollinger, 2007) and is delayed considerably compared to lakes with an OD ≤ 36 (Figure 2). These predictions are supported by observations from Lake Constance, where the OAB in deep Upper Lake Constance (z_{max} = 251, OD ~ 75) is controlled by the onset of stratification and occurs substantially later (i.e. in March or April; Peeters, Straile, Lorke, & Ollinger, 2007) than in the more shallow basins of Lower Lake Constance (e.g. in the Gnadensee basin [z_{max} = 19, OD ~ 7] the OAB typically occurs in February [Güde & Straile, 2016]).

4.2.4 | Absence of light limitation

Finally, our model predicts that light availability should exceed the threshold for the onset of an algal bloom throughout the entire year in Mediterranean lakes with an OD ≤ 6 (Figure 3). Hence, in these lakes, phytoplankton phenology should be controlled by other factors such as seasonal changes in water level, nutrient inflows and grazing (Romo et al., 2005; Segura et al., 2013). Absence of light limitation was confirmed in a study of Greek lakes by Moustaka-Gouni et al. (2014), who also showed that winter biomass of phytoplankton was high in these lakes, and that phytoplankton seasonality was very different from that of temperate and boreal lakes (De Senerpont Domis et al., 2013).

4.3 | How will warming and browning affect OAB timing?

In many Northern Hemisphere lakes, ongoing global change is causing a rise in both surface water temperature and the concentration of coloured ('brown') dissolved organic matter (Clark et al., 2010; O'Reilly et al., 2015). Temperature and coloured dissolved organic matter are powerful drivers of numerous physical, chemical and biological properties of lakes (Read & Rose, 2013; Seekell et al., 2015; Woodward et al., 2010). Their projected increase, therefore, raises the question of how continued warming and browning will affect the timing of the onset of the OAB. Our model predicts that the answer to this question should depend on the process controlling the timing of the OAB under current environmental conditions. Intriguingly, the model predicts that lakes in which OAB timing is most sensitive to warming should be least sensitive to browning and vice versa.

4.3.1 | Sensitivity to warming

We expect that the timing of the OAB is more sensitive to climate warming in lakes, in which the OAB is controlled by either the timing of ice-off or by the onset of stratification than in lakes in which the OAB is controlled by the seasonal increase in incident radiation. Both ice-off and the onset of stratification are predicted to advance in a warmer world (Peeters, Straile, Lorke, & Livingstone, 2007; Weyhenmeyer et al., 2011), whereas the seasonal increase in incident radiation should remain largely unaffected by warming. Warming should, therefore, advance OAB timing in most lakes that are ice-covered in winter and in optically deep lakes that require thermal stratification prior to the OAB, but not in lakes where OAB timing is controlled by incident radiation. In the latter lakes, the timing of OAB is expected to be rather resilient to warming.

These expectations are consistent with observational data and with predictions from our model. For example, in ice-covered lakes Erken and Müggelsee, inter-annual variation in the timing of OAB (or proxies thereof such as the timing of the spring phytoplankton peak) was positively correlated with the timing of ice-off, which occurred earlier in warmer springs (Adrian et al., 2006; Weyhenmeyer, 2009). Similarly, the timing of OAB in deep Upper Lake Constance was positively related to the onset of stratification, which also occurred earlier in warmer springs (Peeters, Straile, Lorke, & Livingstone, 2007; Straile et al., 2015). In contrast, in lakes in which the OAB is controlled by the seasonal increase in incident radiation, its timing should not be very sensitive to inter-annual variation in spring temperature. This expectation is supported by our model, which hindcasts that inter-annual variation in OAB timing in the years 1979–2009 was much larger in lakes where OAB timing is controlled by ice-off or stratification than by incident radiation (Figure 4).

4.3.2 | Sensitivity to browning

Coloured dissolved organic matter is a major driver of both light climate and primary production in many nutrient-poor lakes (Thrane et al., 2014; Vasconcelos et al., 2018; Williamson et al., 1999). As for climate warming, our model predicts that the sensitivity of the OAB to browning depends on the process controlling its current timing, but the predicted pattern is exactly opposite to that for warming. Thus, we expect that OAB timing should be most sensitive to browning in lakes in which the OAB is controlled by incident radiation, but should be rather resilient to browning in lakes where the OAB is controlled by ice-off or the onset of stratification (Figure 5). These expectations are based on three patterns that emerge from a comparison of Figures 3 and 5.

First, browning can cause a considerable delay of the OAB, but only in lake types and at geographical locations where the OAB is currently controlled by the seasonal increase in incident radiation (compare Figure 5d,g,h with Figure 3e,i,j). Also, if the OAB is controlled by the seasonal increase in incident radiation, the same amount of browning causes a stronger delay in systems that are initially relatively clear (K_d = 0.3–0.6 m^{-1}) than in systems that are already relatively brown ($K_d \geq 1.2$ m^{-1}; see Figure S4). This is a consequence of the near-inverse, non-linear relationship between I_{mix} and K_d (Equation 1). Consistent with these expectations, a recent model application for the North Sea calculated that an increase in K_d from 0.02 to 0.1 m^{-1} due to browning and sediment resuspension has delayed the OAB by 3 weeks during the last century (Opdal et al., 2019. The low values of K_d in that study imply a corresponding change in OD from 4 to 20, for which our model would predict that OAB timing should be controlled by the seasonal increase in incident radiation at the studied location (58°N, 8.5°E).

Second, in lakes where the OAB is controlled by ice-off, browning and the associated increase in K_d will have essentially no effect on the timing of the OAB, i.e. the timing of OAB will be resilient to browning, as long as the OAB controlling factor does not change (cf. Figures 3 and 5). This is a consequence of the (realistic) model assumption that the timing of ice-off is not affected by the clarity of the water below the ice cover.

Finally, browning will also have hardly any effects on the timing of OAB if the latter is controlled by the onset of stratification (cf. Figures 3 and 5). An increase in K_d causes an earlier onset of stratification and a faster shallowing of the surface mixed layer (Figures S7–S9; Creed et al., 2018; Read & Rose, 2013; Solomon et al., 2015). These effects compensate for increased light absorption at increased K_d, leaving the product $K_d \cdot z_{mix}$ approximately constant (Heiskanen et al., 2015). As a consequence, our model predicts that browning can even cause a slight advance of the OAB indicated by a negative $Sens_{OAB}$, but should, more commonly, have only minor effects in lakes where OAB timing is dependent on stratification (Figure 5i,k,l).

4.3.3 | Sensitivity when OAB-controlling factors change

The above analyses indicate that in lakes in which the OAB is controlled by the timing of ice-off or by the onset of stratification, the timing of OAB is sensitive to warming but resilient to browning, whereas it is resilient to warming and sensitive to browning in lakes in which the OAB is controlled by the seasonal increase in incident radiation. Note that this conclusion is valid under the assumption that the factor controlling the OAB does not change with warming or browning. Yet, a large number of lakes are predicted to lose ice-cover completely in a warmer climate (Sharma et al., 2019), suggesting that the control of the OAB will shift in these lakes from the timing of ice-off to either the seasonal increase in incident radiation or to the onset of stratification. In such lakes, OAB timing should become resilient to additional warming but more sensitive to browning. A similar effect can be expected in Central, Eastern and Northern European lakes with OD ≤18, in which browning is predicted to shift the OAB controlling factor from ice-off to incident radiation (Figure 3). Finally, in sufficiently deep lakes ($z_{max} \geq 30$), browning can shift the control of OAB timing from the seasonal increase in incident radiation to the onset of stratification (Figure 3j,k,m,n), which can cause a substantial shift in the timing of OAB indicated by large $Sens_{OAB}$ (Figure 5j). However, after the transition to the more turbid conditions, OAB timing in these lakes should be more resilient to further browning (Figure 5k) but less resilient to future warming.

The type of OAB control does not only determine the resilience of lakes to future warming and browning, but also the currently observed inter-annual variability in OAB timing. As the OAB is important to many ecosystem processes, inter-annual variability in OAB timing will likely also affect inter-annual variability in processes such as the transfer of primary production to the upper layers in the food chain (Cushing, 1990) or export production (Beaulieu, 2002). OAB timing might be more predictable for consumers when it is controlled by incident radiation rather than by stratification or ice-off. Hence, we predict that mismatches between the timing of the OAB and consumer phenology might be more common and/or more strongly expressed in lakes in which the OAB is ice-off or stratification controlled rather than incident radiation controlled. On the other hand, consumers relying on phytoplankton in high-variability OAB lakes may have developed specific adaptations to cope with high inter-annual variability in bloom timing (e.g. Seebens et al., 2009).

5 | CONCLUSIONS

Long-term monitoring is of fundamental importance to the identification of patterns in the responses of lake ecosystems to global change (Adrian et al., 2009). Yet, it is very challenging to draw general conclusions about the effects of changing environmental conditions on ecosystem dynamics based on observations alone. For example, an important seasonal event such as the onset of the OAB not only depends on various climatic drivers but also on lake characteristics such as lake depth and water clarity, and on the complex interaction between the drivers and the lake characteristics. Causal inference from observations is further hampered because several environmental drivers or lake characteristics may be changing simultaneously (Jacobson et al., 2017; Tanentzap et al., 2008).

The numerical modelling approach taken in this study integrates the effects of the different drivers and lake characteristics and allows for a quantitative comparison of the timing of the onset of the OAB in different regions across Europe and in lakes of different depths and turbidities. Thus, the model results do not only contribute to a better understanding of the consequences of changing conditions for the timing of the OAB, but also enable the identification of lakes in which the timing of the OAB will be most strongly affected by environmental changes such as climate warming and brownification. We thus predict that climate warming will advance OAB timing only in lakes where the OAB is controlled by ice-off or the onset of stratification, whereas browning will delay OAB timing only in lakes where the OAB is controlled by incident radiation. Importantly, there is not *one* specific lake type or *one* geographical region that would be particularly sensitive to warming or browning, but it is the combination of lake type and regional climate that makes certain lakes more or less resilient to these global changes.

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DATA AVAILABILITY STATEMENT

The model output on which the manuscript is based was generated with the hydrodynamic model LAKEoneD (described in Joehnk & Umlauf (2001) and Hutter & Jöhnk (2004) and the ice model SIM (described in Yao et al., 2014). The cited references are listed in the reference list of the manuscript. The model simulations used meteorological input data from the global atmospheric reanalysis dataset ERA-Interim produced by the European Centre of Medium-Range Weather Forecasts (ECMWF; Dee et al., 2011). These data are openly available at https://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/.

ORCID

Enzo Gronchi https://orcid.org/0000-0002-9901-4829
Klaus D. Jöhnk https://orcid.org/0000-0002-5972-4201
Dietmar Straile https://orcid.org/0000-0002-7441-8552
Sebastian Diehl https://orcid.org/0000-0002-3860-5051

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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