https://doi.org/10.5194/egusphere-2023-1679
Preprint. Discussion started: 25 September 2023

Timing of spring events changes under modelled future climate scenarios in a mesotrophic lake

Jorrit P. Mesman[1], Inmaculada C. Jiménez-Navarro[2], Ana I. Ayala[1], Javier Senent-Aparicio[2], Dennis Trolle[3], Don Pierson[1]

[1]Department of Ecology and Genetics, Uppsala University, Uppsala, 75236, Sweden

[2]Department of Civil Engineering, Catholic University of San Antonio, Guadalupe, 30107, Spain

[3]WaterITech, Døjsøvej 1, Skanderborg, 8660, Denmark

Correspondence to: Jorrit P. Mesman (jorrit.mesman@ebc.uu.se)

Keywords: Phenology, Climate change, Ice, Stratification, Phytoplankton, Runoff, Process-based modelling

Correspondence emails: jorrit.mesman@ebc.uu.se; icjimenez@ucam.edu; isabel.ayala.zamora@ebc.uu.se; jsenent@ucam.edu; dt@wateritech.com; don.pierson@ebc.uu.se

Abstract. Lakes experience shifts in the timing of processes as a result of climate warming, and especially relative changes in the timing of events may have important ecological consequences. Spring in particular is a period in which many key processes that regulate the ecology and biogeochemistry of lakes occur, and also a time which may experience significant changes under influence of global warming. In this study, we used a coupled catchment-lake model forced by future climate projections to evaluate changes in the timing of spring discharge, ice-off, the spring phytoplankton peak, and the onset of stratification, in a mesotrophic, temperate lake. All these events showed a clear trend towards earlier occurrence with climate warming, with ice cover tending to disappear at the end of the century in the most extreme climate scenario. Moreover, relative shifts in the timing of these springtime events also occurred, with the onset of stratification tending to advance slower than the other events, and the spring phytoplankton peak and ice-off advancing faster in the most extreme climate scenario. The outcomes of this study stress the impact of climate change on the phenology of processes in lakes and especially the relative shifts in timing during spring. This can have profound effects on food-web dynamics as well as other regulatory processes, and influence the lake for the remainder of the growing season.

1. Introduction

A changing timing of lake processes is one of the many consequences of climate change. Long-term changes in the timing of processes have been reported for, for instance, the onset and end of stratification (Woolway et al., 2021; Moras et al., 2019), the onset and end of ice cover (Sharma et al., 2019), lake metabolism (Ladwig et al., 2022), the spring phytoplankton bloom (Peeters et al., 2007a; Gronchi et al., 2021; Meis et al., 2009), the spring zooplankton peak (Straile, 2000; Anneville et al., 2002) and fish spawning (Jeppesen et al., 2012; Lyons et al., 2015). Such shifts in timing are highly relevant for lake ecosystem functioning, as they may lead to an altered duration of the growing season (Rouse et al., 1997), changed biogeochemical conditions during key biological events (Weyhenmeyer et al., 2013; Prowse and Brown, 2010), or a trophic mismatch in cases where the relative timing of multiple processes changes (Donnelly et al., 2011; but see Berger et al., 2014; Thackeray et al., 2010). Especially in spring, key events for the food web occur (Sommer et al., 2012) that may resonate for the remainder of the season (Straile, 2005), and observations and simulations suggest that, in general, there will be an earlier occurrence of springtime events in mid- to high-latitudes lakes with climate warming (e.g. Winder and Schindler, 2004; Woolway et al., 2021; Feldbauer et al., 2022). These changes can influence ecosystem functioning for the remainder of the growing season and thus represent a latent consequence of climate warming.

While there are several key metrics of ecosystem functioning at play during spring, previous studies have typically focused only on one or few of these. Hence, we do not know if the changes in the timing of these spring metrics are changing synchronically as a consequence of climate change. In this study, we investigated and compared changes of several key metrics during spring, namely the timing of ice-off, spring discharge, the spring phytoplankton bloom, and onset of stratification, in a mesotrophic lake in Sweden. These processes are all influenced by meteorological conditions, but they also influence each other. Break up of snow-covered or white ice strongly increases light penetration into the water (Weyhenmeyer et al., 2022), which is important both for phytoplankton growth and formation of thermal stratification. In catchments with snow cover, spring high flows are common due to snowmelt, and these may provide an important source of nutrients for the phytoplankton community (Hrycik et al., 2021). Lastly, following turbulent water conditions in deep lakes, the onset of stratification is often a prerequisite for the spring phytoplankton bloom (Huisman et al., 1999; Peeters et al., 2007b). Despite this, these processes are rarely studied together in a single lake, and the separate projected trends in timing are seldom compared to each other within the same study site.

We used a coupled catchment-lake model framework to make future projections of the timing of these four processes and additionally to compare the projected trends between each of them. We hypothesised that all events would occur earlier in the year in a future, warmer climate, which is in line with previous studies, but also that relative changes in the timing of these events would occur. The latter expectation was partially due to the different processes driving each event, for example rain and air temperature would have the greatest importance in affecting snow and ice melt, while wind and temperature later in the season would affect the onset of stratification. Moreover, the effect of the strong seasonal cycle of solar radiation at the latitude of our study site would provide different physical constraints on phytoplankton, stratification, ice-off, and discharge. An earlier occurrence of spring events has several major consequences for lakes, but relative shifts could also result in previously unforeseen ecosystem effects, as ecological niches may close or open due to changing time windows. The use of process-based models can provide a robust framework for future projections of the timing of these springtime events, and the numerical coupling of lakes to their catchment allows a more thorough evaluation of climate change impacts and environmental changes (Kong et al., 2022).

2. Material & Methods

2.1. Study site

Lake Erken is located in eastern Sweden (N 59.8°, E 18.6°) and has a mean depth of 9 m, a maximum depth of 21 m, and covers 24 km^2 (Fig. 1). It is considered mesotrophic, with a summer average Secchi depth of 4.2 m, a surface total phosphorus concentration of 21.9 mg/m^3, and a surface chlorophyll concentration of 5.6 mg/m^3. The catchment of the lake has a maximum elevation difference of around 50 m and is covered mostly by pine forest, interspersed by deciduous forest and farmland. Around 50% of the catchment is drained by a stream that enters the lake at its western end (Fig. 1) and the hydraulic retention time is around 7 years. Weather data were collected on an island in the lake and missing data were supplemented with nearby weather stations (Moras et al., 2019). Lake data were collected near the deepest point of the lake (Fig. 1) and all data are publicly available at the Sites Data Portal (2022).

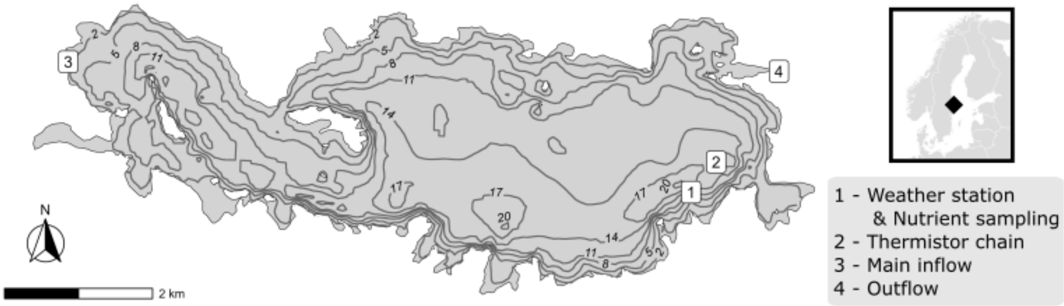

Figure 1. Bathymetric map of Lake Erken and the locations where data were collected.

2.2. Model framework and model performance

A coupled catchment-lake model setup was used to simulate catchment discharges, nutrient loads, and in-lake conditions under present and future conditions. SWAT+ is a catchment model that takes into account meteorological forcing and catchment characteristics, such as land use and soil type, to reproduce catchment hydrology (Bieger et al., 2017) and was used to simulate discharges into Lake Erken. Stream nutrient concentrations and temperatures were estimated statistically using LOADEST (Runkel et al., 2004; Runkel and De Cicco, 2017) and air2stream (Toffolon and Piccolroaz, 2015; Piccolroaz et al., 2018), respectively. The coupled GOTM-WET model was used to simulate lake physics and biogeochemistry. GOTM simulates one-dimensional lake physics based on meteorological and hydrological boundary conditions (Umlauf et al., 2005) and WET is a modular biogeochemical model that can simulate amongst others nutrient, phytoplankton, zooplankton, and fish dynamics (Schnedler-Meyer et al., 2022). The simulated food web composition for this study involved four phytoplankton groups (diatoms, cyanobacteria, green algae, and flagellates), one macrophyte group, and one zooplankton group. The models were calibrated using data collected locally as part of the Lake Erken monitoring program using the time period 2000-2015 (2007-2015 for inflow data), and the period 2016-2021 was used for model validation. The calibrated models were then run under future climate projections, where SWAT+ output was used as input into GOTM-WET. These future climate projections were based on five GCMs (General Circulation Models, models used: BCC-CSM2-MR, CanESM5, INM-CM5-0, MiroC6, MRI-ESM2-0) from CMIP6 (Coupled Model Intercomparison Project, Eyring et al., 2016) and ran from 1985 until the end of the 21st century. Two socioeconomic pathways, SSP 2-45 and SSP 5-85 were used, corresponding to a future with moderate or no climate mitigation efforts, respectively. The period 1985-2014 was the same for both scenarios (historical period) and the two pathways diverged over the period 2015-2100. A full description of the different models, the coupling of the models and the employed calibration techniques, can be found in Jiménez-Navarro et al. (2023).

A comparison between simulated and observed inflow and lake data, spanning 2000-2021 for most variables, confirmed that the models reproduced the dynamics of the system with reasonable accuracy (see Jiménez-Navarro et al., 2023). Discharge, lake temperature and oxygen concentrations were simulated well, with R^2 values over 0.6, whereas nutrient and chlorophyll were more uncertain (R^2 values between 0.1 and 0.6 for NH_4, NO_3, PO_4, and chlorophyll), although the model still reproduced convincing seasonal cycles (for a more detailed assessment of model performance, see S1 and Jiménez-Navarro et al. (2023)). As such, we took the calibrated SWAT+-GOTM-WET model framework as an acceptable representation of the ecosystem and used it as a basis to look at springtime phenology. Here, we provided a separate assessment of the model's reproduction of the springtime phenology in the Results section.

2.3. Springtime events and other lake variables

Four different springtime events were considered in this study: ice-off, date of 50% cumulative spring discharge, the spring phytoplankton bloom, and stratification onset.

Ice-off dates in the lake were recorded when the majority of the lake had thawed. The GOTM-WET model contained an ice module, but because snow was not considered, ice-on dates were typically accurate (mean absolute error 10 days, mean error -4 days), but ice-off dates were simulated consistently too early (mean absolute error 22 days, mean error -22 days, using the GOTM ice module). We therefore instead used a threshold of surface water temperature to decide the day of modelled ice-off. Multiple thresholds were tested with intervals of 0.5 °C and we settled on 2 °C, which showed the lowest bias. The first day the modelled surface water temperature passed this threshold was set to be the day of ice-off. The date of ice-off was set to the day of the year with lowest surface water temperature in case no ice was simulated, which was necessary to account for ice-free years under future climate simulations.

The date of 50% cumulative spring discharge was chosen as indicator of the timing of spring snowmelt runoff. We followed an identical approach to Hrycik et al. (2021), where discharge was summed between January 1 and May 31, and the day that the cumulative runoff passed 50% of the total was calculated.

A peak of chlorophyll was used as indication for the spring phytoplankton bloom. In most years, a single spring peak in chlorophyll was visible in the observed data in spring, but in several years, there were similar, separate peaks, necessitating a different approach than simply choosing the date of the highest peak, as we wanted to assess the timing of first spring peak. Instead, we first determined the highest chlorophyll peak in the period January-May, and in the case of multiple peaks then took the first peak that had at least 90% of the chlorophyll of the highest peak. Although we applied this method to both the simulated and observed data, it should be noted that observed chlorophyll data were available at roughly weekly intervals during the spring period. Therefore, there was an uncertainty in the timing of the observed peak of about 1 week, in addition to the possibility of missing a short-lived bloom.

Onset of summer thermal stratification was taken as the day that a density difference between the surface and bottom of more than 0.1 kg/m^3 formed (Wilson et al., 2020), at a surface water temperature above 4 °C, for at least seven consecutive days.

In addition to these springtime events, several other variables were calculated, that could shed light on the reason behind the simulated trends. These were the chlorophyll concentration during the spring peak, the cumulative discharge in spring (January-May), the average ice thickness during ice cover, the average strength of stratification (Schmidt stability, Schmidt, 1928; calculated with the R package "rLakeAnalyzer", Winslow et al., 2019) and mixed layer depth during the stratified period (using a density difference of 0.1 kg/m^3 from the surface, following Wilson et al., 2020). Moreover, the end of stratification was calculated in the same way as its onset, and onset of ice cover was based on the GOTM ice module. Finally, the total number of stratified or ice-covered days per year was evaluated as well.

2.4. Trend estimation

The timing of the springtime events and the other variables were calculated for each year in the climate scenarios and determined for each GCM separately. Following this, the results from the GCMs were averaged and a Mann-Kendall test was done to estimate trends over time, expressed as Sen’s slope, using the R package “modifiedmk” (Patakamuri and O'brien, 2021). An intercept was estimated in addition to the Sen’s slope, following Helsel et al. (2020); this intercept refers to the value at the start of the simulation in 1985. For the cross-comparison of the timing of springtime events, Mann-

https://doi.org/10.5194/egusphere-2023-1679
Preprint. Discussion started: 25 September 2023

Kendall tests were additionally done for the trends in timing relative to other springtime events (e.g. the number of days the spring chlorophyll peak occurred before the onset of stratification).

All analyses were done in R version 4.1.3 (R Core Team, 2022).

3. Results

3.1. Model performance

In most years, the timing of the spring events was simulated closely to observations (70% of the events within 10 days of observed) and showed little bias (mean error < 5 days) (Fig. 2). However, only 29 - 47% of the variation was explained by the model, which was largely due to several years showing large discrepancies between observed and modelled results (Fig. 2). We investigated all events that were missed by more than 14 days, to discern whether this would invalidate the use of our model under future conditions (see S2). Upon this further inspection, we concluded that for the five badly simulated years for discharge and chlorophyll, the model did indeed not capture the dynamics of the lake or catchment. However, for ice-off, poor fits were rather caused by the method of determining the date of ice-off, as the well-simulated surface water temperature (see S1) was not always a useful predictor of the date of ice-off. Similarly, for onset of stratification, sometimes a temporary period of stratification was identified as onset in the simulation, whereas in the observations a following period was taken as onset, despite bottom-top density difference being simulated accurately by the model. Since the simulation provided good results in the majority of the years and the metrics only occasionally gave false impressions, we concluded that the method would overall give reliable estimates under future climate scenarios. Moreover, the lack of bias indicates that the model can provide the average timing of spring events under prevailing atmospheric conditions, even though year-to-year variability may be missed.

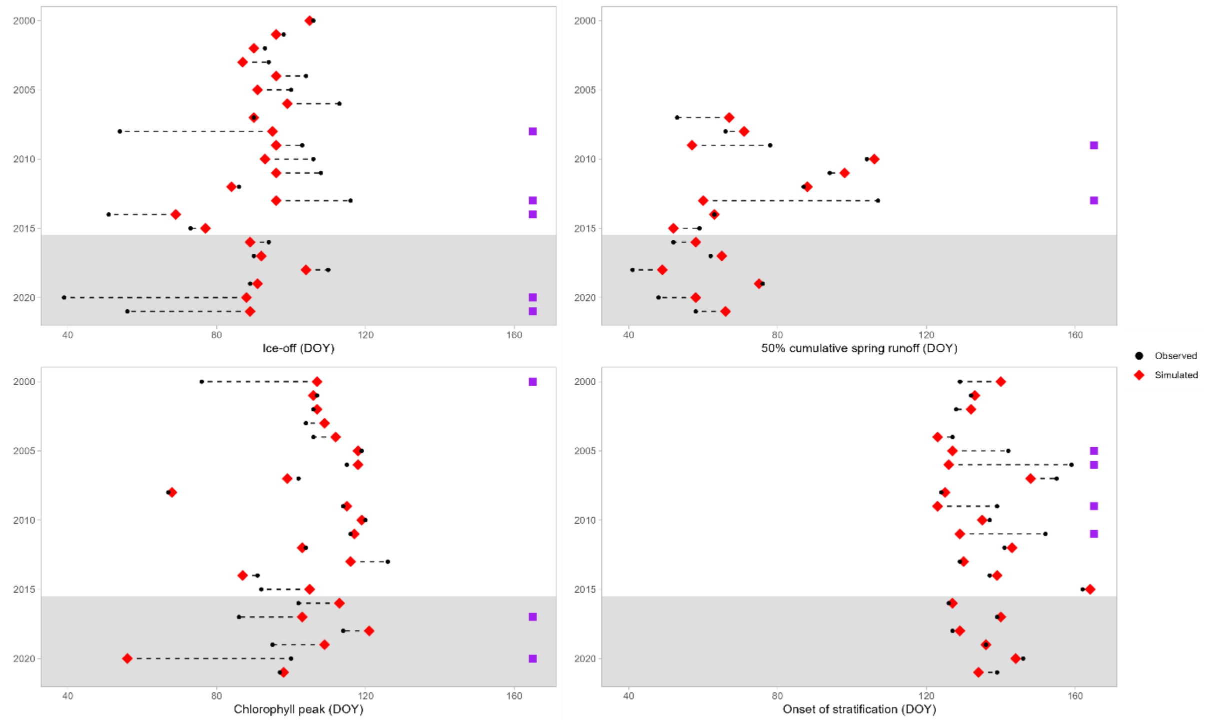

Figure 2. Simulated (red) and observed (black) timing of ice-off, 50% cumulative spring runoff, spring chlorophyll peak, and onset of stratification. The years are on the y-axis, and the difference in timing is shown by a dashed line. The units on the x-axis are in day-of-year (DOY). The light grey area indicates the validation period. Purple squares denote the years that were fitted badly (> 14 days error) and that are further investigated in S2.

3.2. Trends over time under climate scenarios

The duration of stratification increased (1.95 and 3.27 more stratified days per decade for SSP 2-45 and 5-85, respectively, Table 1), as did the strength of stratification, expressed as Schmidt stability (6.35 and 10.49 J/m^2/decade, Table 1). The mixed layer depth showed a tendency to shoal slightly (-0.02 and -0.06 m/decade, Table 1). The magnitude of the spring chlorophyll peak decreased, by 0.37 (SSP 2-45) and 0.35 (SSP 5-85) mg/m^3/decade, while the cumulative spring discharge increased ($3.05 \cdot 10^5$ and $4.65 \cdot 10^5$ m3/decade for SSPs 2-45 and 5-85, Table 1). Winter conditions became less severe, as the number of days with ice cover decreased (-5.68 and -7.02 days/decade, Table 1) and average ice thickness decreased by 0.0012 and 0.014 m/decade. The percentage of ice-free winters increased from 3% in the first 30 years of the simulation to

38% under SSP 2-45 or 70% under SSP 5-85 at the end of the century, though the results varied strongly between the different GCMs (between 43% and 97% for the SSP 5-85 scenario).

Table 1. Results of Mann-Kendall trend tests for trends during the future climate scenarios. DOY stands for day-of-the-year.

		SSP 2-45			**SSP 5-85**		
Variable	**Unit**	**p-value**	**Sen's slope (/decade)**	**Intercept**	**p-value**	**Sen's slope (/decade)**	**Intercept**
Chlorophyll peak date	DOY	<0.0001	-2.45	109.22	<0.0001	-3.71	112.11
Peak spring chlorophyll concentration	mg/m^3	<0.0001	-0.37	14.42	<0.0001	-0.35	14.06
50% spring discharge date	DOY	<0.0001	-2.21	77.61	<0.0001	-2.26	73.31
Cumulative spring discharge	m^3	<0.0001	$3.05 \cdot 10^5$	$8.69 \cdot 10^6$	<0.0001	$4.65 \cdot 10^5$	$8.39 \cdot 10^6$
Ice-off date	DOY	<0.0001	-2.13	105.93	<0.0001	-3.75	107.95
Ice-on date	DOY	<0.0001	3.75	2.05	<0.0001	4.73	1.74
Number of days with ice	days	<0.0001	-5.68	73.34	<0.0001	-7.02	67.91
Average ice thickness	m	<0.0001	-0.012	0.14	<0.0001	-0.014	0.13
Stratification onset	DOY	<0.0001	-1.20	140.94	<0.0001	-1.88	141.68
End of stratification	DOY	<0.0001	0.74	261.73	<0.0001	1.42	260.74
Number of stratified days	days	<0.0001	1.95	121.87	<0.0001	3.27	118.02
Average Schmidt stability during stratification	J/m^2	<0.0001	6.35	175.19	<0.0001	10.49	163.07
Average mixed layer depth during stratification	m	0.023	-0.02	6.47	<0.0001	-0.06	6.50

3.3. Spring events timing

The investigated spring events were without exception projected to occur earlier in the year, with stronger changes predicted for SSP 5-85 compared to SSP 2-45 (Fig. 3). Although there was substantial variation between the different GCMs, the negative Sen's slope was significant for all variables and climate scenarios (Table 1). However, the magnitude of the projected slope was different between the investigated variables, with for example the trend in chlorophyll peak advancing

roughly twice as fast as the trend in onset of stratification. A cross-comparison of the relative trends revealed that some
185 timings of spring events indeed significantly changed relative to each other (Fig. 4). More specifically, the rate of change of the onset of stratification was slower than that of other events, while for the SSP 5-85 climate scenario, the advance of the spring chlorophyll peak and ice-off were faster than that of other two events.

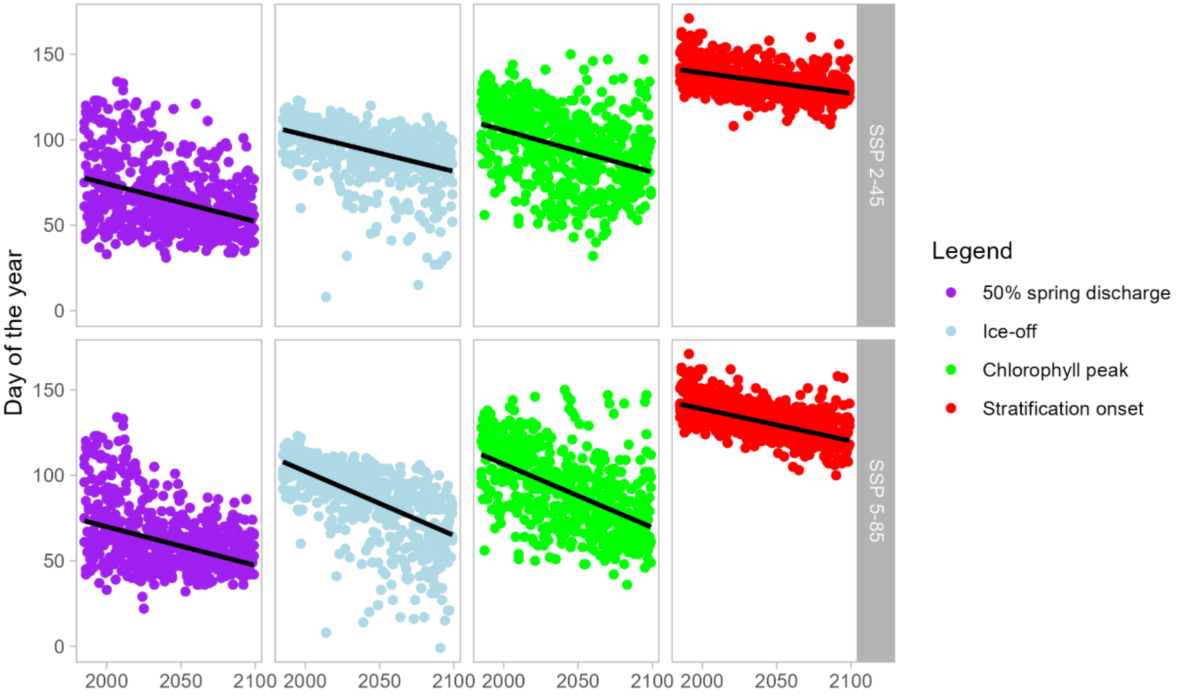

Figure 3. Projected timings of spring events for 1985-2100, with the upper row showing the projections for SSP 2-45 and the lower
190 **row for SSP 5-85. Results for all GCMs are plotted here. The black line indicates the fit of the Mann-Kendall trend test on the ensemble mean (details of the Mann-Kendall test results can be found in Table 1).**

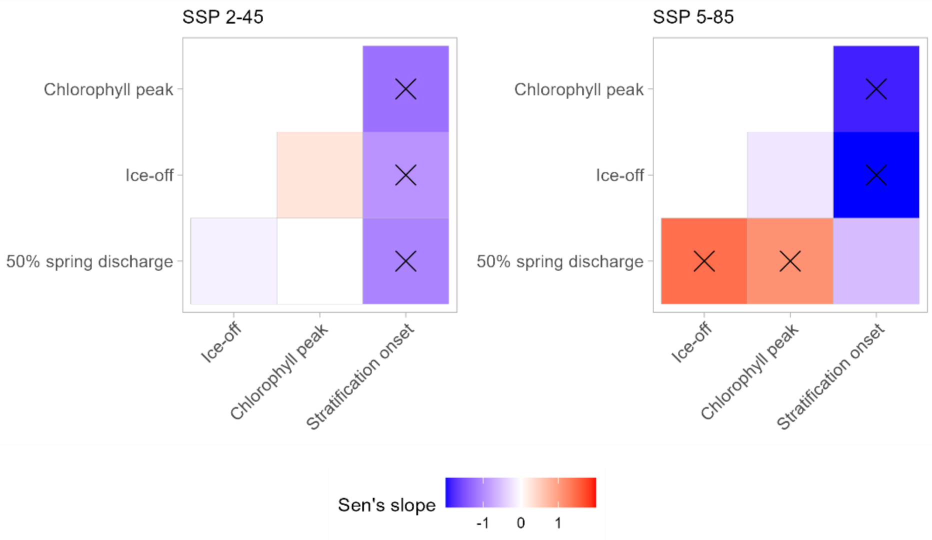

Figure 4. Sen's slopes (days/decade) of timings of spring events relative to the other spring events. The colour scale indicates Sen's slope of the day-of-the-year of the event on the y-axis relative to the timing of the corresponding event on the x-axis. A positive slope therefore means that the variable on the x-axis advanced to earlier dates faster than the variable on the y-axis. Crosses indicate a significant difference from 0 (Mann-Kendall test, p-value < 0.05). For the exact values of the slopes and the p-values, see S3.

4. Discussion

Each of the investigated spring events was projected by the model simulations to occur earlier in the year. As air temperatures in our climate scenarios were rising (Jiménez-Navarro et al., 2023), the earlier occurrence of ice-off and stratification onset was unsurprising and the rates of change were indeed in line with previous studies (Woolway et al., 2021; Magee and Wu, 2017; Shatwell et al., 2019; Feldbauer et al., 2022; Li et al., 2022). Under SSP 5-85, ice cover is projected to largely disappear in Lake Erken at the end of the century. Together with the shifting precipitation and runoff patterns, this will mean a complete transformation of the lake's winter conditions, with both societal and ecological relevance (Cavaliere et al., 2021; Knoll et al., 2019). Regarding the earlier discharge, the Lake Erken catchment is commonly snow-covered in winter, and future increasing air temperatures lead to earlier snowmelt and a concurrent discharge peak, a process common at high latitudes (Hrycik et al., 2021). Moreover, the future climate scenarios suggested that an increase in precipitation will

https://doi.org/10.5194/egusphere-2023-1679
Preprint. Discussion started: 25 September 2023

occur during winter for the location of Lake Erken (Jiménez-Navarro et al., 2023), but projections of such precipitation patterns in future climate vary geographically (e.g. IPCC, 2021). As such, the earlier occurrence of spring discharge should be viewed as a phenomenon linked to areas where the accumulation of snow has an important effect on the regional hydrology and where winter precipitation is predicted to increase. Lastly, the earlier occurrence of the spring chlorophyll peak with climate change could be due to a combination of factors. Earlier ice-off promotes an earlier onset of phytoplankton growth, if light obstruction by ice is the main limiting factor for growth (Gronchi et al., 2021). Earlier spring discharge into Lake Erken also provides an earlier supply of nutrients, but in this lake, the majority of spring discharge occurs prior to ice-off and the spring chlorophyll peak. In Lake Erken, the spring chlorophyll peak tends to occur prior to onset of stratification, an order of events which is commonly reversed in deeper lakes where stratification is required to overcome light limitation (Huisman et al., 1999; Gronchi et al., 2021). Altogether, the earlier chlorophyll peak therefore seems to be mostly attributable to the increased availability of light due to earlier ice-off, causing growth to commence earlier. The peak of the spring chlorophyll bloom (i.e. the end of net growth) in the model seemed to have been dictated mostly by nutrient limitation, as nutrient concentrations reached low concentrations around the time of the simulated peak, with a potential shift to more light limitation at the end of the century (see S4). The role of zooplankton grazing was predicted to increase under future climate projections as well, although a clear link between simulated spring chlorophyll and zooplankton concentrations was not observed (see S5), leading to nutrient and light limitation as the major determinants of the spring chlorophyll peak in the model.

The absolute changes in the timing of spring events were comparable to findings in other studies, but relative changes (other than phytoplankton-zooplankton dynamics) have received much less attention in the scientific literature, despite their potential impact on lake ecosystem functioning. One of the few studies to look at relative changes, Meis et al. (2009) found no effects of timings of ice-off and stratification on phytoplankton spring phenology, but rather a secondary effect of temperature on the dominant phytoplankton species. Earlier onset of stratification is a well-known consequence of climate warming (Woolway et al., 2021), but our findings suggest that other events in spring will advance at an even higher rate in our study lake. This leads to an increased gap between onset of stratification and the three other events evaluated here. Such a differential effect on lake processes can lead to marked changes in lake dynamics, potentially affecting food web dynamics

https://doi.org/10.5194/egusphere-2023-1679
Preprint. Discussion started: 25 September 2023

(e.g. Thackeray et al., 2008; Yang et al., 2016). In the SSP 5-85 scenario, the rate of an earlier spring chlorophyll peak and an earlier ice-off exceeded that of the two other spring events. The similar trend of ice-off and the spring chlorophyll peak is in line with findings by Gronchi et al. (2021), who postulated that the onset of the spring bloom in lakes like Lake Erken (i.e. light-limited, but phytoplankton growth not reliant on stratification) is either dependent on ice-off or the seasonal increase in solar radiation. The former option would suggest that the trend in the onset of the spring bloom follows that of ice-off, whereas the latter option implies only a weak response to climate warming. Although Gronchi et al. (2021) looked at the onset of the growth, whereas we looked the peak of the spring phytoplankton bloom, the similar trend in our study would confirm ice-off as main determinant for the timing of the spring chlorophyll peak. The timing of the spring bloom in Lake Erken indeed tended to occur around or shortly after the time of ice-off (Fig. 3, Weyhenmeyer et al., 1999). The earlier spring chlorophyll peak coincided with a lower chlorophyll concentration during the spring peak. The earlier occurrence of ice-off would move the start of phytoplankton growth to days with less incoming solar radiation, a strong effect due to Lake Erken's high latitude, and shorter, less intense winters may cause higher zooplankton concentrations at ice-off (Hebert et al., 2021), which could both partially explain the less intense spring peaks.

The climate change scenarios reveal pertinent changes in the conditions of Lake Erken towards the end of the century, including longer and stronger stratification, shorter ice cover, and absolute and relative changes in the timing of springtime events. The longer period between ice-off and the spring bloom on one hand and the onset of stratification on the other, could open up new niches for species adapted to well-mixed water columns, such as diatoms (Yang et al., 2016). Regarding summer phytoplankton dynamics, the earlier onset of stratification lengthens the period of nutrient limitation in the epilimnion and this may partially explain the lower summer chlorophyll concentrations at the end of the century, despite higher yearly average nutrient values (Jiménez-Navarro et al., 2023). Indeed, previous studies have shown that climate warming and a shifting timing of spring events may alter food web composition (Beare and McKenzie, 1999; Winder and Schindler, 2004; Thackeray et al., 2008), and that events in winter and spring can have effects well into the following summer and beyond (Straile, 2005; Hampton et al., 2017).

Methods to make future projections of ecological conditions are by definition uncertain, and the present study is no different. For example, the method of determining the timing of events was sometimes not in line with the observed data, where real patterns are often more complex than a single peak or event. Zooplankton grazing can be an important factor for spring phytoplankton (e.g. Peeters et al., 2007b), but the simulated zooplankton could not be validated due to a lack of long-term, high-frequency zooplankton data. Moreover, scenarios of future nutrient loads were done in a simple approach (Jiménez-Navarro et al., 2023), which did not consider, for example, potential changes in land use policies. Regardless, the models showed clear signs of earlier spring events under warmer climate conditions, in line with previous studies, and the coupled setup of the catchment and lake allowed future projections that took into account the interdependency of the lake and its catchment. Changing phenology is an important aspect of ecosystems' response to climate change and this study provides more insight into relative temporal changes between different springtime events in lakes under future climate scenarios.

Conclusions

We analysed future climate projections of the timing of spring discharge, ice-off, spring chlorophyll peak, and onset of stratification in a mesotrophic lake. While all events occurred earlier in the year under a warmer climate, there were marked changes in the relative timing of events as well, with the onset of stratification advancing slower than the other events and both the spring chlorophyll peak and ice-off advancing faster under the most severe climate scenario. Phenological changes in individual lake processes in response to climate change have been well-established, but relative changes and future projections of the timing of multiple interdependent processes in the same lake have received little attention so far. While changes in the timing of events have important consequences for ecosystems, relative changes may present a secondary, perhaps unforeseen, effect that can influence food web dynamics and lake functioning. The simulations in the present study imply that both absolute and relative changes in the timing of springtime lake events are likely to occur in response to climate warming, and that this should be considered when assessing climate change impacts on lakes.

Code and Data availability

Lake Erken meteorological and lake data are available at the SITES data portal (SITES Data Portal, 2022). The future climate scenarios were generated by the CMIP6 project (Eyring et al., 2016) and downloaded from the DKRZ ESGF-CoG node.

A repository containing the files, model setups, and scripts that were used to produce the results of this study, has been made available by Mesman et al. (2023).

Author contributions

JPM and DCP designed the study. JPM and ICJN set up and ran the model simulations. JPM created the visualisations and wrote the original draft. All authors were involved in discussions throughout the course of the study and in reviewing and editing the final manuscript.

Competing interest statements

The authors declare that they have no conflict of interest.

Acknowledgements

This study was funded by the European Union's Horizon 2020 research and innovation program, grant agreement number 101017861 (SMARTLAGOON). The study has been made possible by data provided by the Swedish Infrastructure for Ecosystem Science (SITES).

We acknowledge the World Climate Research Programme, which, through its Working Group on Coupled Modelling, coordinated and promoted CMIP6 and the Earth System Grid Federation (ESGF) for archiving the data and providing access.

References

Anneville, O., Souissi, S., Ibanez, F., Ginot, V., Druart, J. C., and Angeli, N.: Temporal mapping of phytoplankton assemblages in Lake Geneva: annual and interannual changes in their patterns of succession, Limnology and Oceanography, 47, 1355-1366, 2002.

Beare, D. and McKenzie, E.: Connecting ecological and physical time-series: the potential role of changing seasonality, Marine Ecology Progress Series, 178, 307-309, 10.3354/meps178307, 1999.

Berger, S. A., Diehl, S., Stibor, H., Sebastian, P., and Scherz, A.: Separating effects of climatic drivers and biotic feedbacks on seasonal plankton dynamics: no sign of trophic mismatch, Freshwater Biology, 59, 2204-2220, 10.1111/fwb.12424, 2014.

Bieger, K., Arnold, J. G., Rathjens, H., White, M. J., Bosch, D. D., Allen, P. M., Volk, M., and Srinivasan, R.: Introduction to SWAT+, a completely restructured version of the soil and water assessment tool, JAWRA Journal of the American Water Resources Association, 53, 115-130, 10.1111/1752-1688.12482, 2017.

Cavaliere, E., Fournier, I. B., Hazuková, V., Rue, G. P., Sadro, S., Berger, S. A., Cotner, J. B., Dugan, H. A., Hampton, S. E., Lottig, N. R., McMeans, B. C., Ozersky, T., Powers, S. M., Rautio, M., and O'Reilly, C. M.: The Lake Ice Continuum Concept: Influence of Winter Conditions on Energy and Ecosystem Dynamics, Journal of Geophysical Research: Biogeosciences, 126, 10.1029/2020jg006165, 2021.

Donnelly, A., Caffarra, A., and O'Neill, B. F.: A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems, International Journal of Biometeorology, 55, 805-817, 10.1007/s00484-011-0426-5, 2011.

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., and Taylor, K. E.: Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization, Geoscientific Model Development, 9, 1937-1958, 10.5194/gmd-9-1937-2016, 2016.

Feldbauer, J., Ladwig, R., Mesman, J. P., Moore, T. N., Zündorf, H., Berendonk, T. U., and Petzoldt, T.: Ensemble of models shows coherent response of a reservoir’s stratification and ice cover to climate warming, Aquatic Sciences, 84, 10.1007/s00027-022-00883-2, 2022.

Gronchi, E., Johnk, K. D., Straile, D., Diehl, S., and Peeters, F.: Local and continental-scale controls of the onset of spring phytoplankton blooms: Conclusions from a proxy-based model, Global Change Biology, 27, 1976-1990, 10.1111/gcb.15521, 2021.

Hampton, S. E., Galloway, A. W., Powers, S. M., Ozersky, T., Woo, K. H., Batt, R. D., Labou, S. G., O'Reilly, C. M., Sharma, S., Lottig, N. R., Stanley, E. H., North, R. L., Stockwell, J. D., Adrian, R., Weyhenmeyer, G. A., Arvola, L., Baulch, H. M., Bertani, I., Bowman, L. L., Jr., Carey, C. C., Catalan, J., Colom-Montero, W., Domine, L. M., Felip, M., Granados, I., Gries, C., Grossart, H. P., Haberman, J., Haldna, M., Hayden, B., Higgins, S. N., Jolley, J. C., Kahilainen, K. K., Kaup, E., Kehoe, M. J., MacIntyre, S., Mackay, A. W., Mariash, H. L., McKay, R. M., Nixdorf, B., Noges, P., Noges, T., Palmer, M., Pierson, D. C., Post, D. M., Pruett, M. J., Rautio, M., Read, J. S., Roberts, S. L., Rucker, J., Sadro, S., Silow, E. A., Smith, D. E., Sterner, R. W., Swann, G. E., Timofeyev, M. A., Toro, M., Twiss, M. R., Vogt, R. J., Watson, S. B., Whiteford, E. J., and Xenopoulos, M. A.: Ecology under lake ice, Ecol Lett, 20, 98-111, 10.1111/ele.12699, 2017.

Hebert, M. P., Beisner, B. E., Rautio, M., and Fussmann, G. F.: Warming winters in lakes: Later ice onset promotes consumer overwintering and shapes springtime planktonic food webs, Proceedings of the National Academy of Sciences, 118, 10.1073/pnas.2114840118, 2021.

Helsel, D. R., Hirsch, R. M., Ryberg, K. R., Archfield, S. A., and Gilroy, E. J.: Chapter 3 of Section A, Statistical Analysis Book 4, Hydrologic Analysis and Interpretation [Supersedes USGS Techniques of Water-Resources Investigations, book 4, chap. A3, version 1.1.], in: Statistical methods in water resources: U.S. Geological Survey Techniques and Methods, edited by: Helsel, D. R., and Hirsch, R. M., 458, 10.3133/tm4a3, 2020.

Hrycik, A. R., Isles, P. D. F., Adrian, R., Albright, M., Bacon, L. C., Berger, S. A., Bhattacharya, R., Grossart, H. P., Hejzlar, J., Hetherington, A. L., Knoll, L. B., Laas, A., McDonald, C. P., Merrell, K., Nejstgaard, J. C., Nelson, K., Noges, P., Paterson, A. M., Pilla, R. M., Robertson, D. M., Rudstam, L. G., Rusak, J. A., Sadro, S., Silow, E. A., Stockwell, J. D., Yao, H., Yokota, K., and Pierson, D. C.: Earlier winter/spring runoff and snowmelt during warmer winters lead to lower summer chlorophyll-a in north temperate lakes, Global Change Biology, 27, 4615-4629, 10.1111/gcb.15797, 2021.

Huisman, J., van Oostveen, P., and Weissing, F. J.: Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms, Limnology and Oceanography, 44, 1781-1787, 10.4319/lo.1999.44.7.1781, 1999.

IPCC: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, IPCC, Geneva, Switzerland, 2021.

Jeppesen, E., Mehner, T., Winfield, I. J., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H. J., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandström, A., Blanco, S., Kangur, A., Ragnarsson Stabo, H., Tarvainen, M., Ventelä, A.-M., Søndergaard, M., Lauridsen, T. L., and Meerhoff, M.: Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes, Hydrobiologia, 694, 1-39, 10.1007/s10750-012-1182-1, 2012.

Jiménez-Navarro, I. C., Mesman, J. P., Pierson, D., Trolle, D., Nielsen, A., and Senent-Aparicio, J.: Application of an integrated catchment-lake model approach for simulating effects of climate change on lake inputs and biogeochemistry, Science of the Total Environment, 885, 163946, 10.1016/j.scitotenv.2023.163946, 2023.

Knoll, L. B., Sharma, S., Denfeld, B. A., Flaim, G., Hori, Y., Magnuson, J. J., Straile, D., and Weyhenmeyer, G. A.: Consequences of lake and river ice loss on cultural ecosystem services, Limnology and Oceanography Letters, 4, 119-131, 10.1002/lol2.10116, 2019.

Kong, X., Ghaffar, S., Determann, M., Friese, K., Jomaa, S., Mi, C., Shatwell, T., Rinke, K., and Rode, M.: Reservoir water quality deterioration due to deforestation emphasizes the indirect effects of global change, Water Research, 221, 118721, 10.1016/j.watres.2022.118721, 2022.

Ladwig, R., Appling, A. P., Delany, A., Dugan, H. A., Gao, Q., Lottig, N., Stachelek, J., and Hanson, P. C.: Long-term change in metabolism phenology in north temperate lakes, Limnology and Oceanography, 67, 1502-1521, 10.1002/lno.12098, 2022.

Li, X., Peng, S., Xi, Y., Woolway, R. I., and Liu, G.: Earlier ice loss accelerates lake warming in the Northern Hemisphere, Nature Communications, 13, 5156, 10.1038/s41467-022-32830-y, 2022.

Lyons, J., Rypel, A. L., Rasmussen, P. W., Burzynski, T. E., Eggold, B. T., Myers, J. T., Paoli, T. J., and McIntyre, P. B.: Trends in the Reproductive Phenology of two Great Lakes Fishes, Transactions of the American Fisheries Society, 144, 1263-1274, 10.1080/00028487.2015.1082502, 2015.

Magee, M. R. and Wu, C. H.: Response of water temperatures and stratification to changing climate in three lakes with different morphometry, Hydrology and Earth System Sciences, 21, 6253-6274, 10.5194/hess-21-6253-2017, 2017.

Meis, S., Thackeray, S. J., and Jones, I. D.: Effects of recent climate change on phytoplankton phenology in a temperate lake, Freshwater Biology, 54, 1888-1898, 10.1111/j.1365-2427.2009.02240.x, 2009.

Mesman, J. P., Jiménez-Navarro, I. C., Ayala, A. I., Senent-Aparicio, J., Trolle, D., and Pierson, D. C.: Timing of spring events changes under modelled future climate scenarios in a mesotrophic lake [dataset], 10.48546/workflowhub.workflow.511.2, 2023.

Moras, S., Ayala, A. I., and Pierson, D. C.: Historical modelling of changes in Lake Erken thermal conditions, Hydrology and Earth System Sciences, 23, 5001-5016, 10.5194/hess-23-5001-2019, 2019.

Patakamuri, S. K. and O'Brien, N.: modifiedmk: Modified Versions of Mann Kendall and Spearman's Rho Trend Tests. R package version 1.6. [code], 2021.

Peeters, F., Straile, D., Lorke, A., and Livingstone, D. M.: Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate, Global Change Biology, 13, 1898-1909, 10.1111/j.1365-2486.2007.01412.x, 2007a.

Peeters, F., Straile, D., Lorke, A., and Ollinger, D.: Turbulent mixing and phytoplankton spring bloom development in a deep lake, Limnology and Oceanography, 52, 286-298, 10.4319/lo.2007.52.1.0286, 2007b.

Piccolroaz, S., Healey, N. C., Lenters, J. D., Schladow, S. G., Hook, S. J., Sahoo, G. B., and Toffolon, M.: On the predictability of lake surface temperature using air temperature in a changing climate: A case study for Lake Tahoe (U.S.A.), Limnology and Oceanography, 63, 243-261, 10.1002/lno.10626, 2018.

Prowse, T. D. and Brown, K.: Hydro-ecological effects of changing Arctic river and lake ice covers: a review, Hydrology Research, 41, 454-461, 10.2166/nh.2010.142, 2010.

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing [code], 2022.

Rouse, W. R., Douglas, M. S. V., Hecky, R. E., Hershey, A. E., Kling, G. W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B. J., Roulet, N. T., and Smol, J. P.: Effects of Climate Change on the Freshwaters of Arctic and Subarctic North America, Hydrological Processes, 11, 873-902, 10.1002/(sici)1099-1085(19970630)11:8<873::Aid-hyp510>3.0.Co;2-6, 1997.

Runkel, R. and De Cicco, L.: rloadest: River Load Estimation. R package version 0.4.5. [code], 2017.

Runkel, R. L., Crawford, C. G., and Cohn, T. A.: Load Estimator (LOADEST): A FORTRAN program for estimating constituent loads in streams and rivers2328-7055, 2004.

Schmidt, W.: Über die Temperatur- und Stabilitätsverhältnisse Von Seen, Geografiska Annaler, 10, 145-177, 10.1080/20014422.1928.11880475, 1928.

Schnedler-Meyer, N. A., Andersen, T. K., Hu, F. R. S., Bolding, K., Nielsen, A., and Trolle, D.: Water Ecosystems Tool (WET) 1.0 – a new generation of flexible aquatic ecosystem model, Geoscientific Model Development, 15, 3861-3878, 10.5194/gmd-15-3861-2022, 2022.

Sharma, S., Blagrave, K., Magnuson, J. J., O'Reilly, C. M., Oliver, S., Batt, R. D., Magee, M. R., Straile, D., Weyhenmeyer, G. A., Winslow, L., and Woolway, R. I.: Widespread loss of lake ice around the Northern Hemisphere in a warming world, Nature Climate Change, 9, 227-231, 10.1038/s41558-018-0393-5, 2019.

Shatwell, T., Thiery, W., and Kirillin, G.: Future projections of temperature and mixing regime of European temperate lakes, Hydrology and Earth System Sciences, 23, 1533-1551, 10.5194/hess-23-1533-2019, 2019.

SITES Data Portal: SITES Data Portal - Swedish Infrastructure for Ecosystem Science [dataset], 10.17616/R31NJNC5, 2022.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J. C., Mooij, W. M., van Donk, E., and Winder, M.: Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession, Annual Review of Ecology, Evolution, and Systematics, 43, 429-448, 10.1146/annurev-ecolsys-110411-160251, 2012.

Straile, D.: Meteorological forcing of plankton dynamics in a large and deep continental European lake, Oecologia, 122, 44-50, 10.1007/PL00008834, 2000.

Straile, D.: Food webs in lakes—seasonal dynamics and the impact of climate variability, in: Aquatic food webs. An ecosystem approach. Oxford University Press, New York, edited by: Belgrano, A., Scharler, U. M., Dunne, J., and Ulanowicz, R. E., Oxford University Press, New York, United States, 41-50, 2005.

Thackeray, S. J., Jones, I. D., and Maberly, S. C.: Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change, Journal of Ecology, 96, 523-535, 10.1111/j.1365-2745.2008.01355.x, 2008.

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T. I. M., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., Roy, D. B., Scott, W. A., Smith, M., Smithers, R. J., Winfield, I. J., and Wanless, S.: Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments, Global Change Biology, 16, 3304-3313, 10.1111/j.1365-2486.2010.02165.x, 2010.

Toffolon, M. and Piccolroaz, S.: A hybrid model for river water temperature as a function of air temperature and discharge, Environmental Research Letters, 10, 114011, 10.1088/1748-9326/10/11/114011, 2015.

Umlauf, L., Burchard, H., and Bolding, K.: GOTM: Sourcecode and Test Case Documentation, 2005.

Weyhenmeyer, G. A., Blenckner, T., and Pettersson, K.: Changes of the plankton spring outburst related to the North Atlantic Oscillation, Limnology and Oceanography, 44, 1788-1792, 10.4319/lo.1999.44.7.1788, 1999.

Weyhenmeyer, G. A., Peter, H., and Willén, E.: Shifts in phytoplankton species richness and biomass along a latitudinal gradient - consequences for relationships between biodiversity and ecosystem functioning, Freshwater Biology, 58, 612-623, 10.1111/j.1365-2427.2012.02779.x, 2013.

Weyhenmeyer, G. A., Obertegger, U., Rudebeck, H., Jakobsson, E., Jansen, J., Zdorovennova, G., Bansal, S., Block, B. D., Carey, C. C., Doubek, J. P., Dugan, H., Erina, O., Fedorova, I., Fischer, J. M., Grinberga, L., Grossart, H. P., Kangur, K., Knoll, L. B., Laas, A., Lepori, F., Meier, J., Palshin, N., Peternell, M., Pulkkanen, M., Rusak, J. A., Sharma, S., Wain, D., and Zdorovennov, R.: Towards critical white ice conditions in lakes under global warming, Nature Communications, 13, 4974, 10.1038/s41467-022-32633-1, 2022.

Wilson, H. L., Ayala, A. I., Jones, I. D., Rolston, A., Pierson, D., de Eyto, E., Grossart, H.-P., Perga, M.-E., Woolway, R. I., and Jennings, E.: Variability in epilimnion depth estimations in lakes, Hydrology and Earth System Sciences, 24, 5559-5577, 10.5194/hess-24-5559-2020, 2020.

Winder, M. and Schindler, D. E.: Climatic effects on the phenology of lake processes, Global Change Biology, 10, 1844-1856, 10.1111/j.1365-2486.2004.00849.x, 2004.

Winslow, L. A., Read, J. S., Woolway, R. I., Brentrup, J. A., Leach, T., Zwart, J., Albers, S., and Collinge, D.: rLakeAnalyzer: Lake Physics Tools. R package version 1.11.4.1. [code], 2019.

Woolway, R. I., Sharma, S., Weyhenmeyer, G. A., Debolskiy, A., Golub, M., Mercado-Bettín, D., Perroud, M., Stepanenko, V., Tan, Z., Grant, L., Ladwig, R., Mesman, J., Moore, T. N., Shatwell, T., Vanderkelen, I., Austin, J. A., DeGasperi, C. L., Dokulil, M., La Fuente, S., Mackay, E. B., Schladow, S. G., Watanabe, S., Marcé, R., Pierson, D. C., Thiery, W., and Jennings, E.: Phenological shifts in lake stratification under climate change, Nature Communications, 12, 2318, 10.1038/s41467-021-22657-4, 2021.

Yang, Y., Pettersson, K., and Padisák, J.: Repetitive baselines of phytoplankton succession in an unstably stratified temperate lake (Lake Erken, Sweden): a long-term analysis, Hydrobiologia, 764, 211-227, 10.1007/s10750-015-2314-1, 2016.