

Received: 13 June 2017

Revised: 6 February 2019

Accepted: 11 February 2019

DOI: 10.1111/fwb.13293

ORIGINAL ARTICLEWILEY **Freshwater Biology**

The impacts of changing nutrient load and climate on a deep, eutrophic, monomictic lake

Alan D. Radbourne¹  | J. Alex Elliott² | Stephen C. Maberly² | David B. Ryves¹ | Nicholas John Anderson¹

¹Geography and Environment, Loughborough University, Loughborough, U.K.

²Centre for Ecology & Hydrology, Lancaster Environment Centre, Bailrigg, U.K.

Correspondence

Alan D. Radbourne, Geography and Environment, Loughborough University, Loughborough, U.K.

Email: aradbourne@ceh.ac.uk

Funding information

Natural Environment Research Council, Grant/Award Number: NE/L002493/1

Abstract

1. Nutrient availability and climate have substantial effects on the structure and function of lakes. Predicted changes to climate (particularly temperature) over the 21st century are expected to adjust physical lake functions, changing thermal and nutrient use processes. Both increasing anthropogenic nutrient inputs and net reductions following remediation will also drive ecological change. Therefore, there is an increasing necessity to disentangle the effects of nutrient and temperature change on lakes to understand how they might act in additive and antagonistic ways.
2. This study quantified internal and external nutrient loads at Rostherne Mere, U.K., a deep ($z_{\max} = 30$ m), monomictic eutrophic lake (average annual total phosphorus >100 $\mu\text{g/L}$) that has a long, stable period of stratification (c. 8.5 months). A lake biophysical model (PROTECH) was used to assess the effect of changes in these loads and climate change on lake productivity in a factorial modelling experiment.
3. During the summer, phosphorus released from the sediment is largely restricted to the hypolimnion and phytoplankton production is supported by the external load. On overturn, phosphorus at depth is distributed throughout the water column with the elevated concentration persisting to support algal productivity in the following spring.
4. Consequently, the model showed that internal nutrient loading was the main driver of current and future changes in the concentration of phosphorus (responsible for up to 86% P reduction), phytoplankton chlorophyll *a* and cyanobacterial blooms. However, although the external phosphorus load had a relatively small influence on annual mean phosphorus concentration, it had a statistically significant effect on chlorophyll *a* concentration, because it supported algal production during summer stratification.
5. Climate had minimal direct impact, but a substantial indirect impact by altering the timing, depth and length of lake stratification (c. 14 days longer by 2100), and therefore altered nutrient cycling and phosphorus availability.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Freshwater Biology* Published by John Wiley & Sons Ltd.

6. In summary, the recovery trajectory at Rostherne Mere is limited by the annual internal soluble reactive phosphorus load replenishment that realistically is unlikely to change greatly on a shorter time-scale. Therefore, the external soluble reactive phosphorus load has the potential to play an important role as it can be managed further, but is complicated by the indirect impact of climate changing stratification and flushing patterns.

KEYWORDS

internal loading, multiple stressors, PROTECH modelling, Rostherne Mere, stratification

1 | INTRODUCTION

Nutrient availability is a major factor affecting lake ecosystem functioning including productivity, the development of potentially toxic algal blooms and oxygen depletion (Sas, 1989). Anthropogenic nutrient enrichment has increased nutrient loads, causing many lakes to become eutrophic (Smith, Joye, & Howarth, 2006). Climate also has a major effect on lakes via water temperature and stratification (Hutchinson & Löffler, 1956) and climate change has increasingly been recognised to have a substantial impact on lake structure and function globally (Paerl & Huisman, 2008; Tranvik et al., 2009; Williamson, Saros, Vincent, & Smol, 2009). Long-term incremental increase of air temperature influences the thermal structure (Gauthier, Prairie, & Beisner, 2014; Liu, Bocaniov, Lamb, & Smith, 2014) and timing of stratification in lakes (Izmest'eva et al., 2016; Meis, Thackeray, & Jones, 2009). The shorter-term impact of heatwaves, droughts, and flooding can alter the hydrological balance and ecological structure in many lakes (Bakker & Hilt, 2016; Bertani, Primicerio, & Rossetti, 2016; Wigdahl-Perry et al., 2016). Thus, if future projections of U.K. climatic warming are correct, with annual average temperatures rising by +1.4°C from 2020 to 2060 and +3.4°C from 2020 to 2100 (UKCP09 projections; Murphy et al., 2009), there are likely to be substantial effects on lakes across the U.K. However, the precise direction and magnitude of change is uncertain since multiple stressors may interact in synergistic, antagonistic, or additive ways (Coors & De Meester, 2008). Lakes are differentially sensitive to system stressors (i.e. George, Maberly, & Hewitt, 2004) further complicating the assessment of how an individual lake will respond to environmental change or management intervention.

Rostherne Mere, Cheshire, U.K. is a prime example of a eutrophic lake that has undergone a significant change in trophic status over the last century caused by the direct impact of human activity (Moss et al., 2005). Like many such lakes (Schindler, 2006; Zamparas & Zacharias, 2014), Rostherne Mere has recently undergone catchment-scale management intervention to limit nutrient load and reduce lake nutrient concentrations. While reducing the external phosphorus load improved ecological condition in some lakes (Jeppesen et al., 2005; Sondergaard, Jensen, & Jeppesen, 2005), many have only witnessed a slow recovery as a result of internal

loading of soluble reactive phosphorus (SRP) derived from historic SRP inputs stored within the upper sediment (Jarvie et al., 2013; Schindler, 2006). Rostherne Mere is a small but deep lake permitting a particularly long and strong summer stratification (Radbourne, Ryves, Anderson, & Scott, 2017). In conjunction with high productivity, this drives rapid oxygen depletion at depth following spring stratification (Scott, 2014), favouring the release of large quantities of remobilised P from the sediment into the hypolimnion, potentially slowing the rate of recovery and extending the requirement for management intervention.

This study used observed catchment and lake monitoring data from 2016 to assess contemporary nutrient dynamics at Rostherne Mere. These data are used in the biophysical PROTECH model (Phytoplankton RespOnses To Environmental CHange; Reynolds, Irish, & Elliott, 2001; Elliott, Irish, & Reynolds, 2010) to simulate a range of future nutrient (internal SRP load and external SRP load) and climate (air temperature) scenarios (UKCP09 projections; Murphy et al., 2009). The aim was to determine the importance of internal nutrient loads, external nutrient loads and changing climate on key biophysical lake properties and dynamics. Using a factorial model design, the key drivers were tested to see how they individually and collectively changed the lake properties in either additive or antagonistic ways to better identify future possible recovery pathways.

2 | METHODS

2.1 | Site description

Rostherne Mere (53°20'N, 2°24'W) is one of the largest (area 48.7 ha) and deepest lakes, (max depth 31 m; mean depth 13.6 m) of the Shropshire–Cheshire Meres (Carvalho, Beklioglu, & Moss, 1995) with an average water retention time of about 9–10 months. It develops a long, stable summer stratification (thermocline average depth March to November c. 10 m) with an anoxic hypolimnion. With a long history of eutrophication (defined as >100 µg P/L; Carlson, 1977; Radbourne et al., 2017), Rostherne Mere received a substantial nutrient load from upstream sewage treatment works, with effluent discharged directly into the upstream watercourse between the 1930s and June 1991, when it was then diverted out of the

catchment (catchment size: 9 km²). However, the reduced P inputs did not lead to a similar reduction of P export, resulting in the lake becoming a large net source of P following sewage treatment works diversion. This net export is sustained to the present day with a net 552 kg total phosphorus (TP)/year exported during 2016. The net export of P is fed by the internally loaded P from lake sediments during anoxic stratification (Nurnberg, 1984). Internal loading produces high concentrations of SRP in the hypolimnion of Rostherne Mere during stratification (>800 µg/L), which, at autumn overturn, replenishes the whole lake SRP pool and persists into the next spring. This internal loading explains the slow long-term recovery trajectory of Rostherne Mere over the last 25 years (Moss et al., 2005).

Phytoplankton blooms are dominated in spring by diatoms (largely *Asterionella formosa* Hassall and *Stephanodiscus* spp.), followed by summer cyanobacterial blooms (largely *Aphanizomenon* spp. and *Microcystis* spp.; Reynolds, 1979; Moss et al., 2005). Since 2010, an automated water quality monitoring station has been located at a central buoy, being part of the U.K. Lake Ecological Observatory Network (UKLEON) project (see <https://www.ceh.ac.uk/our-science/projects/uk-lake-ecological-observatory-network-ukleon>). The buoy measures various in-lake parameters and lake-surface meteorological variables at high resolution (every 4 min) with the data uploaded in real-time. This study used lake temperature readings and surface wind speed data.

2.2 | Collection and analysis of field data

Between January 2016 and January 2017, water samples were collected approximately every 3 weeks from Rostherne Brook (the main inflow, draining 79% of the catchment), Blackburn's Brook (outflow) and the central lake surface (UKLEON buoy site; water depth c. 26 m), with multiple column depth water samples (6, 12, 18, and 24 m) added to the 3-weekly collection programme from September 2016. Water samples were shipped to an external certified laboratory (National Laboratory Service, U.K.) for orthophosphate (SRP), TP, dissolved inorganic nitrogen (DIN), and dissolved silicate (DSi) nutrient analysis. Additionally, an integrated water column sample (0–8 m) from the central lake location was collected for live phytoplankton identification and chlorophyll *a* (chl-*a*) analysis. Phytoplankton community composition was analysed after concentrating a 1-L sample using a sequence of settling procedures and the gridded cell abundance count method (Brierley, Carvalho, Davies, & Krokowski, 2007). Chlorophyll-*a* analysis involved a standard spectrophotometer approach, with recordings taken at wavelengths of 630, 645, 665, and 750 nm and an extraction solvent of 80% acetone (Sartory & Grobbelaar, 1984).

Inflow and outflow discharge was determined by calculating a linear discharge relationship between cross-sectional profiles and sectional velocities recorded for a range of stage heights over 2016. This empirical stage–discharge relationship was then applied to continuous stage height measurements recorded using a Van Essen mini-diver data logger (www.vanessen.com), recording water pressure every 5 min and calibrated to a barometer located at the lake

shore, to provide a high-resolution record of inflow and outflow discharge for the whole year.

The standard outflow method for water residence time (WRT) was estimated as the annual average outflow rate against the total lake volume. An adjusted method (WRT_m) was also used, calculated as the monthly average outflow rate against the monthly available mixed lake volume (i.e. during the stratified period from April to November, this is the epilimnion, but during the mixed period from December to March, this is the entire lake).

2.3 | The PROTECH model

PROTECH is a mechanistic model, i.e. its predictions emerge from the biological processes simulated within the model, which allow a better understanding of potential cause and effect relationships. It also simulates at the species level, so allows community level simulations to be conducted rather than just a simulation of total chl-*a*. The model simulates the responses of a number of phytoplankton populations (here representing a genus) distributed in a one-dimensional vertical water column (described by 0.1-m layers, reflecting the bathymetry of the lake) at daily time steps, but also calculates key physical limnological parameters such as thermocline development, stratification pattern, and nutrient concentrations. A full description of the model's equations and concepts has been already published (Elliott et al., 2010; Reynolds et al., 2001) but the main biological component of the model is the daily change in chl-*a* concentration ($\Delta X/\Delta t$) attributable to each phytoplankton population:

$$\Delta X/\Delta t = (r' - S - G - D)X, \quad (1)$$

where r' is the growth rate defined as a proportional increase over 1 day, S is the loss caused by settling out from the water column, G is the loss caused by *Daphnia* grazing (it is assumed only phytoplankton <50 µm diameter are grazed) and D is the dilution loss caused by hydraulic exchange.

The growth rate (r') is further refined by:

$$r' = \min\{r'_{(\theta, I)}, r'_{P'}, r'_{N'}, r'_{Si'}\}, \quad (2)$$

where $r'_{(\theta, I)}$ is the growth rate at a given water temperature and light intensity and $r'_{P'}$, $r'_{N'}$, $r'_{Si'}$ are the growth rates determined by SRP, N, and DSi concentrations below these respective threshold concentrations: <3, 80, and 500 µg/L (Reynolds, 2006). The r' values are phytoplankton-dependent (e.g. non-diatom taxa are not limited by silica concentrations below 500 µg/L and nitrogen-fixing cyanobacteria are not limited by nitrogen) and, crucially, relate to the morphology of the taxon. The phytoplankton communities used in the model were selected from analysis of the most abundant species observed in the lake (Radbourne, 2018), giving a total of seven phytoplankton taxa: *Asterionella*, *Stephanodiscus* (diatoms), *Cryptomonas* (cryptophyta), *Gomphosphaeria*, *Microcystis*, *Aphanizomenon*, and *Dolichospermum* (cyanobacteria).

Water temperature and light (i.e. cloud cover and seasonal irradiance) are varied at each time-step throughout the simulated water

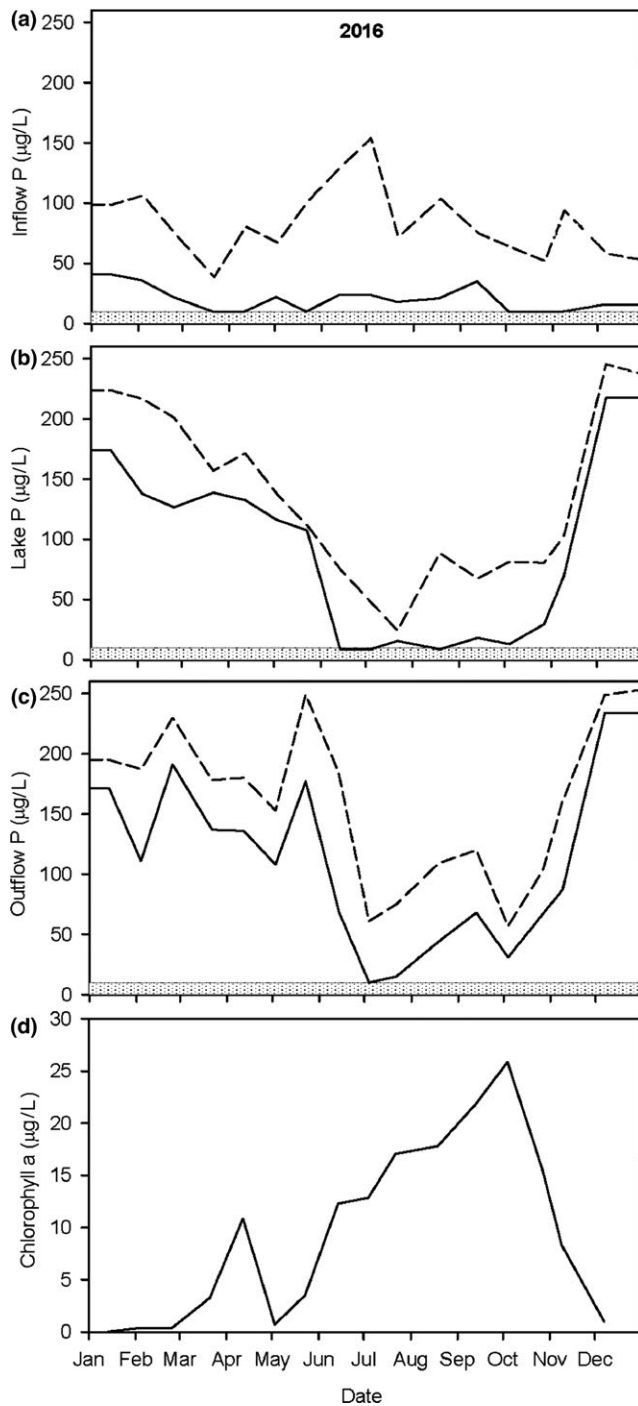


FIGURE 1 Seasonal changes in concentration of phosphorus (P) and chlorophyll *a* at Rostherne Mere for 2016. (a) P inflow concentration, (b) P lake epilimnion concentration, (c) P outflow concentration and (d) epilimnion chlorophyll *a* concentration. Solid line represents soluble reactive P and dashed line total P. Analysis detection limit represented by shaded area at 10 µg/L

column in response to external meteorological drivers. The value of $\Delta X/\Delta t$ (Equation 1) is modified on a daily time-step for each algal taxon in each 0.1 m deep layer of the water column.

The model was run and compared to the observed data recorded from the lake during 2016 by using the coefficient of determination

(R^2 and RMSE). After the initial simulation, as expected, it became clear that an internal hypolimnetic nutrient supply of SRP needed to be added to simulate the internal loading of P. This being cited previously as an important component of P dynamics at Rostherne Mere (Carvalho et al., 1995; Moss et al., 2005). Therefore, incremental daily amounts of SRP were added to the bottom 15 m of the water column from 1 June for 90 days until the hypolimnion concentration matched those observed from the depth profiles: $7.8 \mu\text{g SRP L}^{-1} \text{ day}^{-1}$ was found to be optimal. The model assumes the internally loaded SRP is not mixed into the surface water until stratification breaks down, a suitable simplifying assumption in a strongly stratifying lake such as Rostherne Mere (Mackay, Folkard, & Jones, 2014). The internal load period of 90 days was fixed to ensure that the internal load only occurs during anoxic stratification (a feature of Rostherne Mere; Radbourne et al., 2017) for all climate change scenarios, because anoxia promotes the sediment release of iron bound P for replenishment into the water column (Nurnberg, 1984). This P will only be redistributed throughout the water column at stratification overturn due to the strong summer stratification within the lake.

2.4 | Future climate scenarios

The calibrated 2016 simulation was taken as a baseline and then re-run through a combination of progressive changes to air temperature and nutrient load. Each future projection scenario was run in daily time steps for 10 years using the 2016 driving data repeatedly, and the final year only was used for the analysis to allow the simulation time to move away from the baseline and stabilise under the new driving conditions. The different scenarios were created by application of UKCP09 future temperature change projections (with 11 model simulations), forecasting daily temperatures using years 360 days long, as used by the UKCP09 models, between 2011–2020, 2051–2060, and 2091–2100 for the 25 km² grid reference of Rostherne Mere (the U.K. Met Office Hadley Centre Regional Model Perturbed Physics Ensemble simulations HadRM3-PPE; Murphy et al., 2009). Temperature change was combined with decreasing SRP loads compared to 2016, through calculating a percentage of measured internal and external SRP loads in 2016, these being 100% (i.e. no change from 2016; referred to as high), 60% (referred to as mid), and 20% (referred to as low) from the 2016 baseline. Furthermore, a single simulation of the current 2016 baseline with a 10-fold increase in external SRP concentration was modelled, from an annual average of 20 to 200 µg/L, designed to simulate an unmanaged catchment similar to that of pre-sewage treatment work diversion in 1991 (Carvalho et al., 1995). In total, this produced 298 scenario combinations (i.e. 11 different temperature models at three time frames, with three external SRP loadings and with internal SRP loadings, plus on increased external load simulation).

Model simulation results were statistically analysed using a single factor ANOVA, testing the significance of the difference between the 11 temperature forecast models with external load change, internal load change, and temperature change.

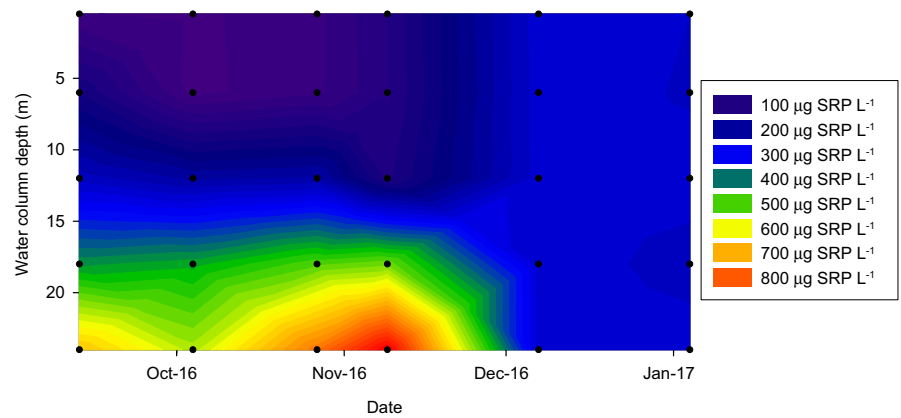


FIGURE 2 Internal concentration of soluble reactive phosphorus (SRP) building in the hypolimnion during stratification and released into the whole water column upon stratification overturn. Black dots represent sampling points

3 | RESULTS

3.1 | Seasonal changes in Rostherne Mere

The ratio of TP to SRP concentrations at Rostherne Mere was fairly constant throughout 2016 (Figure 1b), thus SRP was used in this study because available reactive P is important for phytoplankton ecology and its use here will not significantly underestimate the P budget. The concentration of SRP in Rostherne Mere was high at the start of 2016 ($>150 \mu\text{g/L}$; Figure 1b), but then decreased as it became diluted by the inflow ($c. 20 \mu\text{g SRP/L}$; Figure 1a) and through algal uptake (observed chl-*a* increase; Figure 1d). By mid-June, the concentration of SRP within the lake had fallen to levels near (or below) analysis detection limits ($<10 \mu\text{g/L}$; Figure 1b). Low SRP concentrations ($<18 \mu\text{g/L}$) in the epilimnion from mid-June to November (Figure 1b) limit algal growth, as seen in the chl-*a* production reaching a maximum $25.8 \mu\text{g/L}$ (Figure 1d), with production sustained, and thus limited, by the inflow SRP load (mean June to November inflow SRP concentration $22 \mu\text{g/L}$; Figure 1b). During summer, anoxic stratification in the hypolimnion establishes a high concentration of sediment-derived SRP at depth ($>800 \mu\text{g/L}$; Figure 2), which is dispersed throughout the water column at overturn in late November, returning the whole lake to the similar high SRP concentrations found at the start of the year (Figure 1b). The mass balance of P during 2016 (Radbourne, Ryves, Madgewick, & Anderson, In review) shows that Rostherne Mere was a net source of P (inflow 864 kg TP/year , outflow $1,416 \text{ kg TP/year}$ = net loss 552 kg TP/year ; Figure 1a,c), supporting the inference that the major source of this large quantity of P replenishing the water column annually is derived internally from the sediment P store, not from inflows draining the managed pastureland catchment. DIN and DSi were deemed not to be important for annual chl-*a* production as concentrations were high throughout the year in both the inflow (annual mean 2.2 mg DIN/L , 7.4 mg DSi/L ; minima 0.2 mg DIN/L , 0.5 mg DSi/L ; data not shown) and lake (annual mean 2.9 mg DIN/L , 2.7 mg DSi/L ; minima 0.2 mg DIN/L , 0.2 mg DSi/L ; data not shown).

The WRT for Rostherne Mere calculated for 2016 using the standard method was 0.82 years ($c. 10$ months). The mixed lake WRT (WRT_m) that takes account of the strong stratification for 8.5 months (mid-March to end-November), which limits the available lake volume for outflow export, gave an annual estimate of 0.57 years ($c. 7$ months).

3.2 | Calibration and validation of PROTECH

The only adjustment of PROTECH that was required was to include sediment released SRP into the hypolimnion between 1 June and 30 August, to reflect its build up over the period of stratification and subsequent mixing throughout the water column at overturn (see Section 2). Other coefficients were left at their standard values. The resulting comparisons between observed and simulated variables for the year 2016 were good for surface water temperature ($R^2 = 0.98$, $p < 0.001$, $\text{RMSE} = 0.64$; Figure 3a), the epilimnion concentration of SRP ($R^2 = 0.76$, $p < 0.001$, $\text{RMSE} = 48.7$; Figure 3b) and total epilimnion chl-*a* ($R^2 = 0.93$, $p < 0.001$, $\text{RMSE} = 4.68$; Figure 3c).

3.3 | Response of SRP concentration to future change

Model simulations of possible future changes altered annual mean lake SRP concentrations. Reduction of the internal loading had the greatest effect on epilimnion SRP concentration (Figure 4), with a 48.9% and 85.6% reduction for high-mid and high-low, respectively (Table 1); all scenario results being statistically significant (Table 2). Lower external load scenarios in conjunction with a reduction in internal load slightly decreased SRP concentrations further, by an additional 1.3% and 2.2% for high-mid and high-low, respectively (Table 1). Increases in air temperature to 2060 also reduced SRP further when combined with a reduction of internal loads, yet there was a slight rise in SRP concentration with further warming to 2100 (Table 1). All three scenarios (i.e. internal, external, and temperature) combined led to the largest decline in SRP concentration (Table 1).

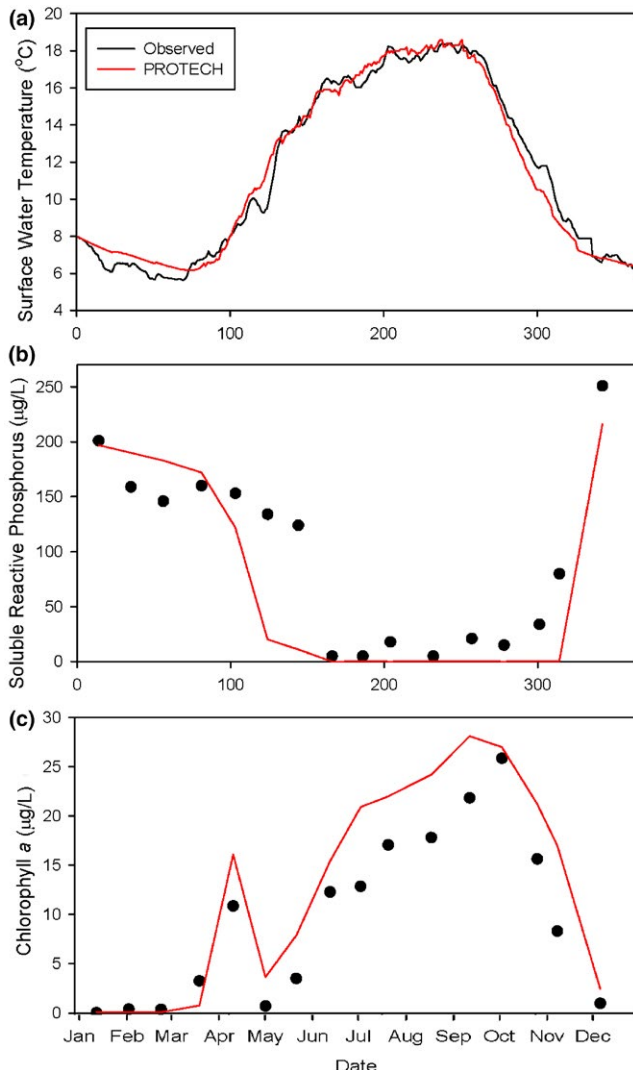


FIGURE 3 Validation plots comparing measured and modelled changes in Rostherne Mere during 2016: (a) surface water temperature ($^{\circ}\text{C}$; $R^2 = 0.98$, $p < 0.001$); (b) soluble reactive phosphorus concentrations in the epilimnion (SRP $\mu\text{g/L}$; $R^2 = 0.76$, $p < 0.001$), (c) chlorophyll *a* epilimnion integrated sample (chl-*a*, $\mu\text{g/L}$; $R^2 = 0.93$, $p < 0.001$)

Altering external load alone (i.e. maintaining current baseline of high internal load) had a much smaller impact on SRP concentration compared to changing internal load, with a 3.4% and 6.4% fall in concentration from high-mid and high-low, respectively (Table 1). These changes are not statistically significant (Table 2). However, the relative impact of the external load increased in scenarios where the internal load was lower (under low internal load: 10.2% reduction high-mid and 20.3% reduction high-low external loads; Table 1), thus external load became increasingly statistically significant (Table 2). Increasing temperature alone (i.e. nutrient loads remain the same over time) did not have a statistically significant effect on SRP concentration (Table 2), marginally altering SRP concentration ($\pm < 2\%$ 2020–2060, $< 6\%$ 2020–2100; Table 1).

3.4 | Response of chl-*a* concentration to future change in climate and nutrient load

The concentration of chl-*a* responded to the alterations in SRP concentration (Figure 5). Reduced internal loading led to the greatest chl-*a* reduction (51.0% high-mid, 65.0% high-low; Table 1). All scenarios of internal load change were statistically significant (Table 3). Like SRP, the chl-*a* reduction is amplified by a reduced external load. However, temperature increased chl-*a* in the 2060 scenarios, yet is shown to support reduction to 2100 (Table 1). The impact of changed external load on chl-*a* was statistically significant in all scenarios, with increasing significance in future temperature scenarios and at reduced internal loads (Table 3).

Changes in air temperature increased chl-*a* concentrations between 2020 and 2060, with the biggest alterations in higher nutrient load scenarios (Table 1). However, from 2060 to 2100, all nutrient scenarios suggested a decline in chl-*a* concentrations with the largest reduction in the low nutrient scenarios (3.5% to 27.8%; Table 1). Statistical significance of temperature change was only evident in the high nutrient load scenarios (Table 3).

3.5 | Response of phytoplankton to future change in climate and nutrient load

Annual modelled phytoplankton assemblages differed among future scenarios (Figure 6a,b). Cyanobacteria showed a substantial decrease in bloom size (represented as chl-*a*) and proportional chl-*a* dominance in reducing internal load scenarios (Figure 6a). External load reduction had a greater influence by reducing cyanobacterial dominance in lower internal load scenarios, while temperature slightly increased the cyanobacterial dominance in future warmer climates (Figure 6a). The additional simulation of future change with a 10-fold external SRP concentration increase showed an increase in SRP and chl-*a*, with the predominant increase found in cyanobacterial abundance (up to 88% of total chl-*a*; Table 4).

Annual modelled diatom abundance (in terms of chl-*a*) showed little change under all future change scenarios (Figure 6b). Due to the limited response in chl-*a* production, the relative contribution to total algal chl-*a* increased with a decreasing total chl-*a* (Figure 5) and cyanobacterial bloom size (Figure 6a).

3.6 | Response of lake thermal structure and stratification to future climate change

Future temperature changes represented an annual average increase of air temperature of 1.4°C by 2060 and 3.4°C by 2100, compared to the 2020 baseline (i.e. final year of 2011–2020 future temperature scenario). Increases in temperature altered the water column mixing and stratification patterns, with the annual average mixing depth increasing by 0.48 and 1.12 m by 2060 and 2100, respectively (Figure 7a; statistically significant $F(2,$

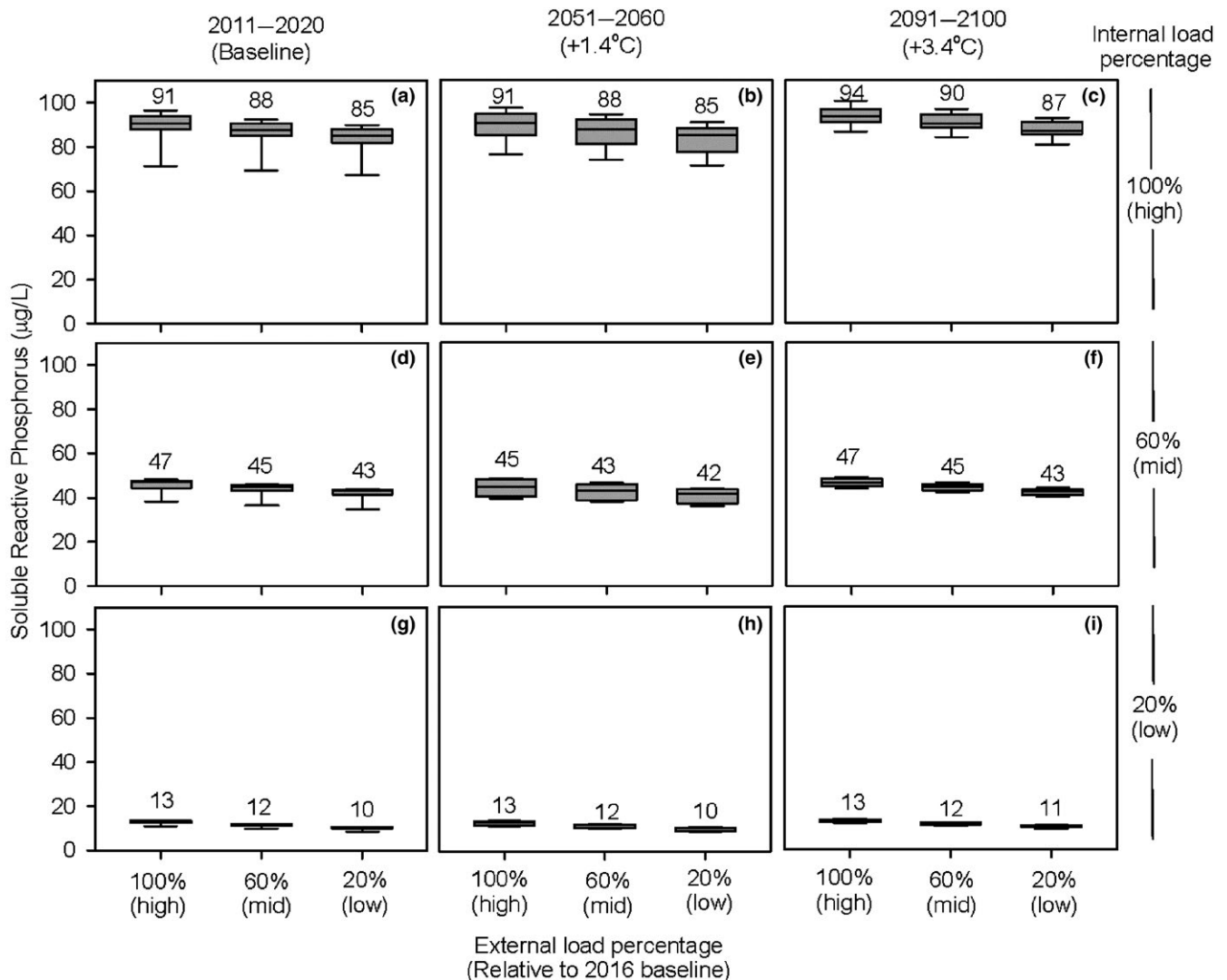


FIGURE 4 Response of annual average soluble reactive phosphorus concentration to altered external and internal phosphorus loads under three climate scenarios. Final modelled year average for each time frame is divided into an internal load percentage and external load percentage with a box and whisker plot representing the quartile range, 5th/95th percentiles and median values for the 11 UKCP09 climate model projections. Median values annotated above each box

30) = 6.08, $p = 0.01$). Consequently, the WRT_m increased slightly from 0.57 years (2016 baseline) to 0.58 and 0.60 years by 2060 and 2100, respectively.

The increase in air temperature also led to a statistically significant earlier onset of stratification, Figure 7c; $F(2, 30) = 5.30$, $p = 0.01$. This was 6 days earlier by 2060 and 14 days earlier by 2100. Thus, overall stratification duration increased significantly, Figure 7b; $F(2, 30) = 5.09$, $p = 0.01$, because the timing of stratification breakdown was unchanged (Figure 7d). Longer periods of stratification altered the WRT_m from 0.57 years (2016 baseline) to 0.56 years by 2060 and 0.55 years by 2100. However, the combination of deeper mixing (lengthening WRT_m) and longer stratification (shorter WRT_m) offset each other so WRT_m was 0.58 years in both 2060 and 2100.

A small number of individual model scenarios of climatic warming suggested stratification overturn may not occur until early January

the following year (shown here as the final day of the modelled year, day 360; Figure 7d). These scenarios forecasted the late stratification end time and in turn led to a slightly later stratification onset the following year, explaining the range of stratification periods projected by the 11 climate model scenarios and the benefit of using the average of these models.

4 | DISCUSSION

4.1 | Phosphorus legacy of the sediment limiting future recovery

The PROTECH projections of possible future change scenarios clearly show that the main driver of substantial change at Rostherne Mere would be the reduction of the large internal SRP load, producing a 10-fold greater percentage reduction than

TABLE 1 Modelled annual mean values ($\mu\text{g/L}$) for soluble reactive phosphorus (SRP), chlorophyll *a* (chl-*a*) and the ratio between chl-*a*:SRP for different internal and external SRP loads and climate scenarios

Internal load	High external load			Mid external load			Low external load		
	SRP	Chl- <i>a</i>	Ratio	SRP	Chl- <i>a</i>	Ratio	SRP	Chl- <i>a</i>	Ratio
2011–2020									
High	89.0	20.0	0.22	86.0	18.1	0.21	83.0	16.0	0.19
Mid	45.5	9.8	0.22	43.5	8.3	0.19	41.5	6.3	0.15
Low	12.8	7.0	0.55	11.5	5.7	0.50	10.2	4.6	0.45
2051–2060									
High	89.6	22.6	0.25	86.7	21.2	0.24	83.5	19.2	0.23
Mid	44.8	10.6	0.24	43.0	9.1	0.21	40.9	7.4	0.18
Low	12.7	7.2	0.57	11.4	5.7	0.50	10.0	4.7	0.47
2091–2100									
High	93.6	21.8	0.23	90.9	20.0	0.22	87.6	18.2	0.21
Mid	46.7	9.5	0.20	44.6	7.6	0.17	42.4	5.2	0.12
Low	12.9	6.6	0.51	11.7	5.3	0.45	10.4	4.2	0.40

Note. Values based on the final year annual averages for 11 temperature model forecasts.

Significance of external load change			
Internal load	Future time frame		
	2011–2020	2051–2060	2091–2100
High	1.53 ns	2.36*	29.46***
Mid	3.70 ns	3.79*	26.32***
Low	5.56**	17.28***	47.52***
Significance of internal load change			
External load	Future time frame		
	2011–2020	2051–2060	2091–2100
High	617.51***	669.4***	679.89***
Mid	851.28***	854.34***	885.94***
Low	2,275.43***	2,509.7***	2,509.70***
Significance of temperature change			
Internal load	External load		
	High	Mid	Low
High	1.63 ns	1.95 ns	1.81 ns
Mid	1.08 ns	0.94 ns	0.81 ns
Low	0.26 ns	0.47 ns	0.58 ns

Note. *F*-values ($df_{2,30}$) and significance from single factor ANOVA ($n = 33$) are presented. Highly significant values in bold. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; ns $p > 0.05$.

similar changes in the external load. The substantial difference between the importance of internal and external loads is explained by the relative change in load size, with a much larger reduction in internal loading (baseline c. 200 $\mu\text{g/L}$) than external loading (baseline c. 20 $\mu\text{g/L}$).

TABLE 2 Significance of external load change, internal load change and temperature change on the final modelled year annual soluble reactive phosphorus for 11 future temperature models

4.2 | Contribution of internal and external loads to the concentration of chl-*a*

A reduction in SRP concentration is anticipated to reduce chl-*a* production, ultimately improving the wider lake ecosystem. It has

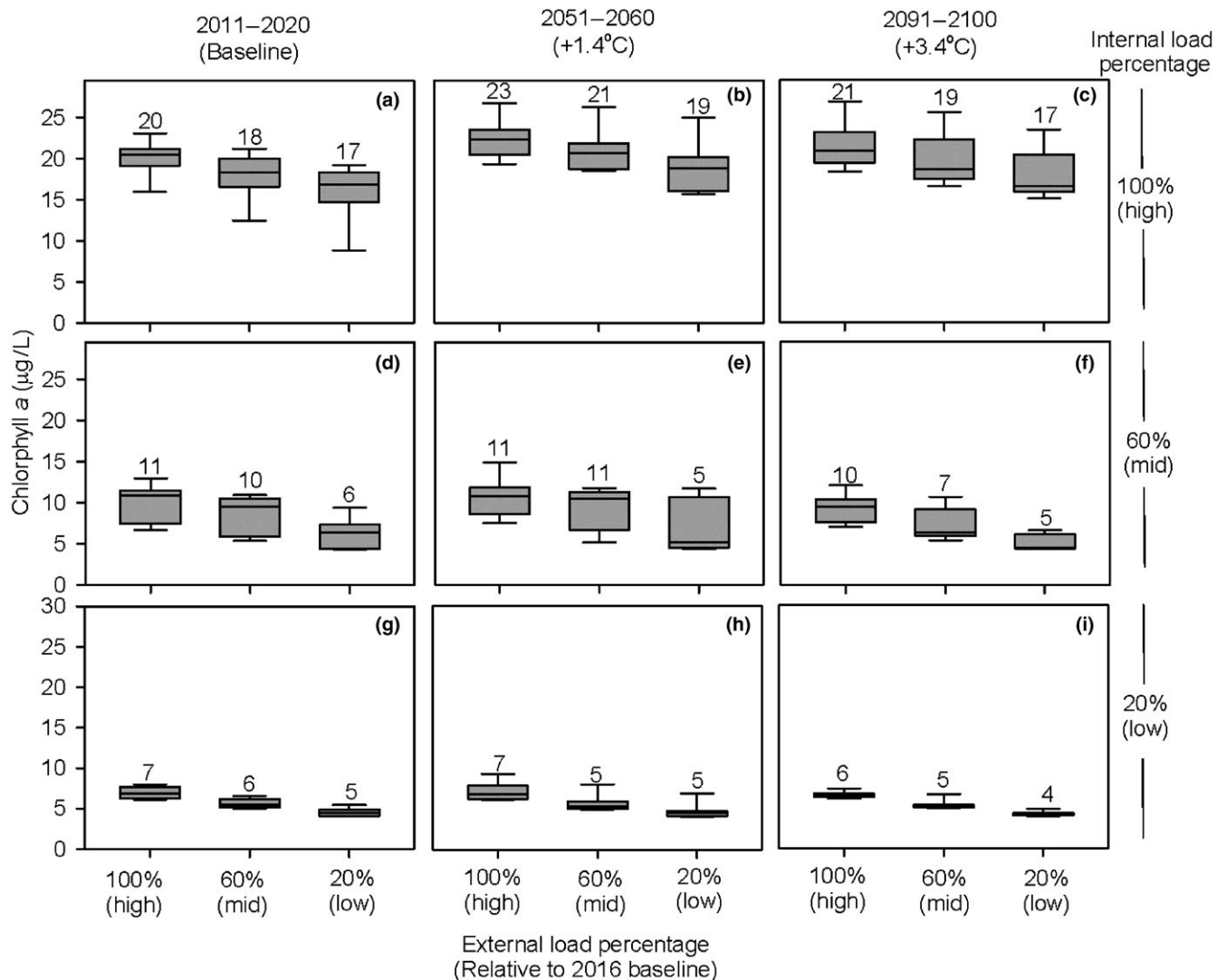


FIGURE 5 Response of annual average chlorophyll-*a* concentration to altered external and internal phosphorus loads under three climate scenarios. Final modelled year average for each time frame is divided into an internal load percentage and external load percentage with a box and whisker plot representing the quartile range, 5th/95th percentiles and median values for the 11 UKCP09 climate model projections. Median values annotated above each box

been suggested that a reduced external SRP load will starve internal load replenishment, eventually exhausting the standing SRP store (assuming sediment oxygen condition does not change). However, it may take decades or longer before internal P store is exhausted and full lake recovery occurs (Reddy, Newman, Osborne, White, & Fitz, 2011; Sharpley et al., 2013).

The response between the reduction of chl-*a* and SRP concentrations was non-linear. The model simulations show that there is a greater proportional reduction of SRP than chl-*a* with a reduced internal load, whereas a reduced external load alone results in a similar proportional chl-*a* reduction, suggesting that external load is a key driver in chl-*a* production, despite its small impact on SRP load. Similar non-linear patterns between chl-*a* and SRP were evident in all nutrient scenarios. External loading was only significant for SRP when internal loading was low, predominantly due to the increasing relative ratio of load size (i.e. the external load forms a

greater proportion of the total nutrient input), or with the influence of future temperatures.

Here, we propose that the non-linear responses of chl-*a* to SRP following changes in external load are caused by seasonal nutrient availability and the importance of nutrient replenishment from the stream inflow during summer. At Rostherne Mere, the high winter/spring nutrient concentrations decline with dilution by the (low SRP concentration) inflowing stream and phytoplankton use; by mid-June SRP concentrations are similar to the inflow. Therefore, from this point SRP will be replenished predominantly from the inflow, because rates of SRP generation from the decomposition of dead, moribund and senescent phytoplankton in the water column (Radbourne et al., 2017) and entrainment from the hypolimnion are both very low. Thus within an individual year under current scenarios, a reduction in the external SRP load (although having a minor impact for much of the year: following overturn, November to mid-June) will

Significance of external load change			
Internal load	Future time frame		
	2011–2020	2051–2060	2091–2100
High	5.71**	7.02***	47.42***
Mid	4.70*	3.63*	15.79***
Low	4.19*	19.85***	84.44***
Significance of internal load change			
External load	Future time frame		
	2011–2020	2051–2060	2091–2100
High	144.75***	103.98***	85.62***
Mid	180.50***	145.82***	95.39***
Low	202.10***	151.37***	216.16***
Significance of temperature change			
Internal load	External load		
	High	Mid	Low
High	3.40*	3.41*	2.99 ns
Mid	0.81 ns	1.09 ns	2.91 ns
Low	1.84 ns	0.87 ns	2.03 ns

Note. *F*-values ($df_{2,30}$) and significance from single factor ANOVA ($n = 33$) are presented. Highly significant values in bold. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; ns $p > 0.05$.

have a greater importance in replenishing SRP later in the year, driving late-summer phytoplankton blooms (and chl-*a* concentrations).

The future scenario of a 10-fold increase in external SRP concentration, designed to simulate an unmanaged catchment, showed a substantial increase in SRP and chl-*a*, driven by a rise in summer algal blooms. This confirms the role of the external load in replenishing the late summer SRP and highlights its importance for catchment management in lakes such as Rostherne Mere. Additionally, whilst not modelled here, the UKCP09 model projections suggest that precipitation will increase with future climate change, especially during the summer (Murphy et al., 2009). Thus, given the diffuse nature of the sources, external SRP (and TP) load is likely to rise (Andersen et al., 2006; Jeppesen et al., 2011), increasing the overall importance of the external load and further highlighting the necessity for continued catchment management.

4.3 | The effect of climatic warming on the concentration of chl-*a*

Rising air temperatures to 2060 resulted in a slight increase in chl-*a* concentration, under current nutrient loads and a smaller increase in lower nutrient scenarios. Some studies have found that temperature increase has no effect on chl-*a*, only increasing the cyanobacterial dominance (Kosten et al., 2012), whereas others found an increase in chl-*a*, but the mechanistic reason is unknown (Elliott, McElarney, & Allen, 2016; Izmet'seva et al., 2016). However, in Rostherne Mere at the highest temperature,

TABLE 3 Significance of external load change, internal load change and temperature change on the final modelled year annual chlorophyll *a* (chl-*a*) for 11 future temperature models

corresponding to the 2100 time period, chl-*a* concentrations were forecast to be lower than those in 2060. This reduction in chl-*a* with continued warming is counter to other modelling studies simulating warming, that reported a step change increase with higher warming scenarios in similar deep, stratifying eutrophic lakes (Elliott et al., 2016; Tadonleke, 2010). Although the mechanism linking chl-*a* change and temperature change is unclear, we suggest that the response at Rostherne Mere is based on the indirect impact on nutrient cycling caused by altered stratification and its effect on the hydrology of the lake, leading to a changing species dominance that produces a variation in chl-*a* (discussed below).

4.4 | Phytoplankton assemblage change driven by climate and nutrient loads

Cyanobacterial blooms responded to environmental change in a similar way to chl-*a* since they are the dominant algal group, unlike diatoms, which represent a smaller proportion of total chl-*a*. Temperature change altered diatom phenology, but not the population size. At Rostherne Mere, diatom assemblages predominantly form in spring when concentrations of SRP and dissolved Si are still high following entrainment from depth, explaining why the diatoms are largely unaffected by reduced internal and external nutrient load. The relatively small response of diatom chl-*a* compared with the reduction seen in cyanobacterial blooms under lower nutrient load scenarios, results in diatoms contributing a greater proportion of the total chl-*a*.

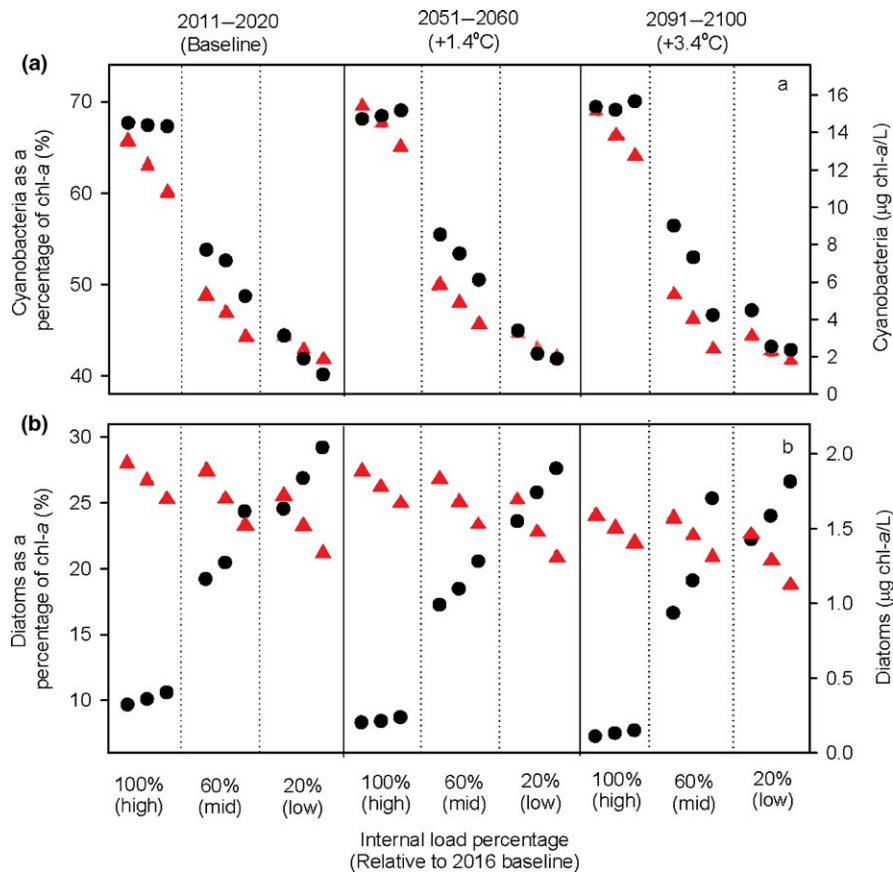


FIGURE 6 Annual average modelled phytoplankton blooms in future nutrient and climate scenarios. (a) Cyanobacterial bloom assemblage size (red triangles; μg chlorophyll [chl]-a/L) and bloom dominance as a percentage of modelled chl-a values (black dots; %). (b) Diatom bloom assemblage size (red triangles; μg chl-a/L) and bloom dominance as a percentage of modelled chl-a values (black dots; %). The three symbols in each segment represent high, mid and low external nutrient load scenarios (from left to right). Note that the sum of cyanobacteria and diatoms do not equal 100% as do not include cryptophytes, which showed little response so were not graphically represented

TABLE 4 Annual mean values ($\mu\text{g/L}$) for soluble reactive phosphorus (SRP) and total, cyanobacteria and diatom chlorophyll *a* (chl-*a*)

	SRP	Total Chl- <i>a</i>	Cyanobacteria Chl- <i>a</i>	Diatom Chl- <i>a</i>
2016 baseline	94.4	9.5	5.3	0.9
PROTECH validation	78.2	12.2	7.2	1.4
10 x external SRP	118.0	38.3	33.7	1.3

4.5 | Climatic warming alters stratification depth, length and timing

The large range of SRP concentrations in Rostherne Mere across the annual cycle is predominantly driven by the long stratification (0.71 years) and rapid flushing rate (0.82 years WRT method; 0.57 years WRT_m method). Strong stratification allows anoxia to develop at depth, promoting SRP release and minimising the entrainment of SRP into the surface layer during the growing season. Stratification breaks down late in the year and consequently SRP is released into the upper water column after the end of the growing season. Therefore, a change in the development of stratification at Rostherne Mere could influence the cycling and availability of nutrients.

A warming climate could potentially lead to a shallower thermocline with enhanced stability in the water column (Butcher, Nover, Johnson, & Clark, 2015). Here, the statistically significant increase in epilimnion depth at Rostherne Mere under future scenarios of a warmer climate, suggests warming at the surface (and greater energy input to the lake) is transferred deeper into the water column deepening the thermocline depth, as has been found in other studies (Gauthier et al., 2014; Liu et al., 2014; Luoto & Nevalainen, 2013). This deepening increases the water column available for flushing and hence increases retention time, increasing nutrient availability, as epilimnetic flushing will take longer. However, here the increase in WRT_m is small (+0.01 to +0.03 years) and thus would be unlikely to have a large influence on algal populations.

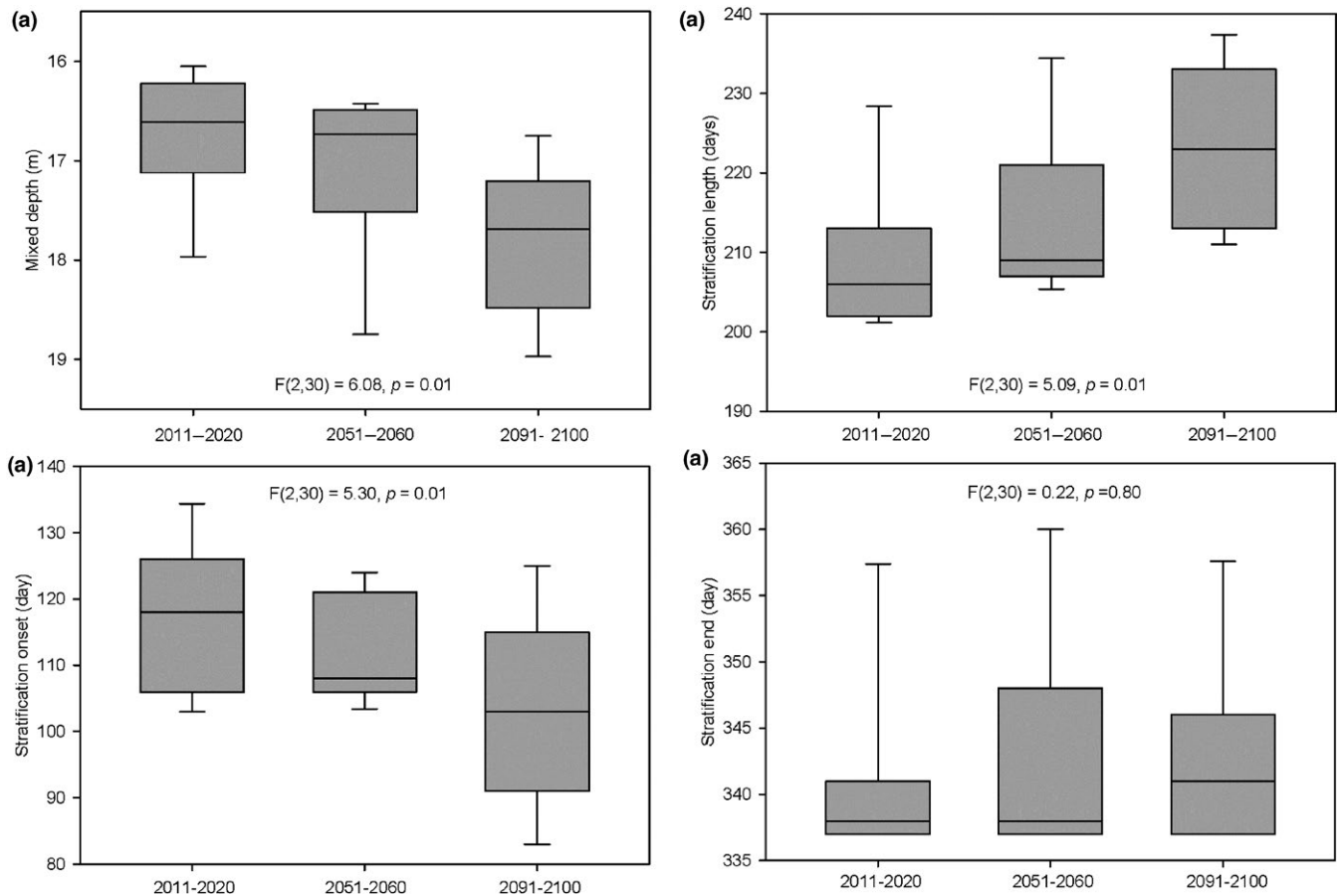


FIGURE 7 Response of annual average stratification patterns to future climate change. Box and whisker plots summarise the quartile range, 5th/95th percentiles and median of the 11 UKCP09 climate model projections for three future time frames and the impact on; (a) average stratified mixed depth (i.e. thermocline depth), (b) time of stratification onset, (c) stratification length, (d) time of stratification end (overturn). Single factor ANOVA f -values and significance included as annotation for each plot

In warmer future climates, the duration of stratification may be increased, as found here and by others (Izmest'eva et al., 2016; Liu et al., 2014). A longer stratification time would lead to a faster flushing rate with a smaller mean lake volume available for flushing (i.e. epilimnion) for a longer period of the year. In this study, the impact of the future projected increased duration of stratification led to a slight decrease in WRT_m that would reduce nutrient availability, leading to smaller phytoplankton blooms. However, the decrease is again minor and is not likely to be significant in isolation. The combination of deeper stratification lengthening the WRT_m and a longer stratification shortening the WRT_m , in the case of Rostherne Mere, is forecast to result in a net offset and so will have a minimal effect.

An earlier onset of stratification would lead to a reduction in nutrient availability in the early part of the year, because the nutrients stored in the hypolimnion become unavailable for the remainder of the water column at an earlier stage. Therefore, the size of summer cyanobacterial blooms will decrease. Evidence of such reductions is seen in the lower chl-*a* concentrations in the 2100 scenarios compared to the 2060 scenarios. Earlier onset of stratification in the 2100 scenarios leads to earlier nutrient limitation and thus lower productivity for a larger part of the summer period.

5 | CONCLUSIONS

Rostherne Mere's trophic trajectory towards recovery, monitored since 1991, has been limited by the large annual internal load of SRP from the profundal sediment. Future scenarios of changes in internal SRP load, external SRP load and air temperature over the rest of the 21st century show that this legacy of phosphorus stored in the sediment will control the extent of lake recovery, with alterations in internal load leading to the greatest change in concentration of SRP, chl-*a*, and cyanobacterial populations. Realistically, internal load reductions are unlikely to occur within the next century on the large scale modelled in this study. Conversely, external SRP loading may have the potential to be reduced by management within a much shorter timeframe (i.e. <10 years). Therefore, external SRP loading, although having a relatively small influence on future SRP scenarios, does have an important role in future chl-*a* production at Rostherne Mere, due to the replenishment of SRP throughout the summer, sustaining the summer cyanobacterial blooms. The summer reduction in SRP is brought about by the combination of a long stratification time and fast flushing rates, leading to the mixed epilimnion being diluted by the managed external contribution. Climate

appears to have a small direct influence on the future of nutrient use and change at Rostherne Mere. However, the indirect impact of changing stratification patterns (i.e. mixing depth, length, and onset timing) and potential for increased internal loading, could decrease the available nutrients in the epilimnion in late summer and autumn, yet increase the internal load contribution for winter replenishment, subsequently adjusting the rate and trajectory of future recovery and potentially altering algal community structure.

ACKNOWLEDGMENTS

This study was supported by the Natural Environment Research Council (NERC) [grant number NE/L002493/1] and ADR acknowledges the support of the research studentship award from Central England NERC Training Alliance (CENTA). Additionally, we thank the UKLEON network for providing access to monitoring station data. Finally, we thank Natural England as especially the warden, Rupert Randall, for allowing regular access to the wider site area at Rostherne Mere.

ORCID

Alan D. Radbourne  <https://orcid.org/0000-0003-3167-5783>

REFERENCES

- Andersen, H. E., Kronvang, B., Larsen, S. E., Hoffmann, C. C., Jensen, T. S., & Rasmussen, E. K. (2006). Climate-change impacts on hydrology and nutrients in a Danish lowland river basin. *Science of the Total Environment*, 365, 223–237. <https://doi.org/10.1016/j.scitotenv.2006.02.036>
- Bakker, E. S., & Hilt, S. (2016). Impact of water-level fluctuations on cyanobacterial blooms: Options for management. *Aquatic Ecology*, 50, 485–498. <https://doi.org/10.1007/s10452-015-9556-x>
- Bertani, I., Primicerio, R., & Rossetti, G. (2016). Extreme climatic event triggers a lake regime shift that propagates across multiple trophic levels. *Ecosystems*, 19, 16–31. <https://doi.org/10.1007/s10021-015-9914-5>
- Brierley, B., Carvalho, L., Davies, S., & Krokowski, J. (2007). Guidance on the quantitative analysis of phytoplankton in freshwater samples. Report to SNIFFER (Project WFD80), Edinburgh, December 2007.
- Butcher, J. B., Nover, D., Johnson, T. E., & Clark, C. M. (2015). Sensitivity of lake thermal and mixing dynamics to climate change. *Climatic Change*, 129, 295–305. <https://doi.org/10.1007/s10584-015-1326-1>
- Carlson, R. E. (1977). Trophic state index for lakes. *Limnology and Oceanography*, 22, 361–369. <https://doi.org/10.4319/lo.1977.22.2.0361>
- Carvalho, L., Beklioglu, M., & Moss, B. (1995). Changes in a deep lake following sewage diversion – A challenge to the orthodoxy of external phosphorus control as a restoration strategy. *Freshwater Biology*, 34, 399–410. <https://doi.org/10.1111/j.1365-2427.1995.tb00898.x>
- Coors, A., & De Meester, L. (2008). Synergistic, antagonistic and additive effects of multiple stressors: Predation threat, parasitism and pesticide exposure in *Daphnia magna*. *Journal of Applied Ecology*, 45, 1820–1828. <https://doi.org/10.1111/j.1365-2664.2008.01566.x>
- Elliott, J. A., Irish, A. E., & Reynolds, C. S. (2010). Modelling phytoplankton dynamics in fresh waters: Affirmation of the PROTECH approach to simulation. *Freshwater Reviews*, 3, 75–96. <https://doi.org/10.1608/frj-3.1.4>
- Elliott, J. A., McElarney, Y. R., & Allen, M. (2016). The past and future of phytoplankton in the UK's largest lake, Lough Neagh. *Ecological Indicators*, 68, 142–149. <https://doi.org/10.1016/j.ecolind.2015.07.015>
- Gauthier, J., Prairie, Y. T., & Beisner, B. E. (2014). Thermocline deepening and mixing alter zooplankton phenology, biomass and body size in a whole-lake experiment. *Freshwater Biology*, 59, 998–1011. <https://doi.org/10.1111/fwb.12322>
- George, D. G., Maberly, S. C., & Hewitt, D. P. (2004). The influence of the North Atlantic Oscillation on the physics, chemistry and biology of four lakes in the English Lake District. *Freshwater Biology*, 49, 760–774. <https://doi.org/10.1111/j.1365-2427.2004.01223.x>
- Hutchinson, G. E., & Löffler, H. (1956). The thermal classification of lakes. *Proceedings of the National Academy of Sciences*, 42, 84–86. <https://doi.org/10.1073/pnas.42.2.84>
- Izmeteva, L. R., Moore, M. V., Hampton, S. E., Ferwerda, C. J., Gray, D. K., Woo, K. H., ... Silow, E. A. (2016). Lake-wide physical and biological trends associated with warming in Lake Baikal. *Journal of Great Lakes Research*, 42, 6–17. <https://doi.org/10.1016/j.jglr.2015.11.006>
- Jarvie, H. P., Sharpley, A. N., Spears, B., Buda, A. R., May, L., & Kleinman, P. J. A. (2013). Water quality remediation faces unprecedented challenges from “Legacy Phosphorus”. *Environmental Science & Technology*, 47, 8997–8998. <https://doi.org/10.1021/es403160a>
- Jeppesen, E., Kronvang, B., Olesen, J. E., Audet, J., Sondergaard, M., Hoffmann, C. C., ... Ozkan, K. (2011). Climate change effects on nitrogen loading from cultivated catchments in Europe: Implications for nitrogen retention, ecological state of lakes and adaptation. *Hydrobiologia*, 663, 1–21. <https://doi.org/10.1007/s10750-010-0547-6>
- Jeppesen, E., Sondergaard, M., Jensen, J. P., Havens, K. E., Anneville, O., Carvalho, L., ... Winder, M. (2005). Lake responses to reduced nutrient loading – An analysis of contemporary long-term data from 35 case studies. *Freshwater Biology*, 50, 1747–1771. <https://doi.org/10.1111/j.1365-2427.2005.01415.x>
- Kosten, S., Huszar, V. L. M., Bécares, E., Costa, L. S., Van Donk, E., Hansson, L.-A., ... Scheffer, M. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, 18, 118–126.
- Liu, W. T., Bocaniov, S. A., Lamb, K. G., & Smith, R. E. H. (2014). Three dimensional modeling of the effects of changes in meteorological forcing on the thermal structure of Lake Erie. *Journal of Great Lakes Research*, 40, 827–840. <https://doi.org/10.1016/j.jglr.2014.08.002>
- Luoto, T. P., & Nevalainen, L. (2013). Climate-driven limnological changes determine ecological thresholds in an alpine lake. *Aquatic Biology*, 18, 47–58. <https://doi.org/10.3354/ab00487>
- Mackay, E. B., Folkard, A. M., & Jones, I. D. (2014). Interannual variations in atmospheric forcing determine trajectories of hypolimnetic soluble reactive phosphorus supply in a eutrophic lake. *Freshwater Biology*, 59, 1646–1658. <https://doi.org/10.1111/fwb.12371>
- Meis, S., Thackeray, S. J., & Jones, I. D. (2009). Effects of recent climate change on phytoplankton phenology in a temperate lake. *Freshwater Biology*, 54, 1888–1898. <https://doi.org/10.1111/j.1365-2427.2009.02240.x>
- Moss, B., Barker, T., Stephen, D., Williams, A. E., Balayla, D. J., Beklioglu, M., & Carvalho, L. (2005). Consequences of reduced nutrient loading on a lake system in a lowland catchment: Deviations from the norm? *Freshwater Biology*, 50, 1687–1705. <https://doi.org/10.1111/j.1365-2427.2005.01416.x>
- Murphy, J. M., Sexton, D. M. H., Jenkins, G. J., Booth, B. B. B., Brown, C. C., Clark, R. T., ... Wood, R. A. (2009). *UK Climate Projections Science Report: Climate Change Projections*. Exeter, UK: Meteorological Office Hadley Centre.
- Nurnberg, G. K. (1984). The prediction of internal phosphorus load in lakes with anoxic hypolimnia. *Limnology and Oceanography*, 29, 111–124. <https://doi.org/10.4319/lo.1984.29.1.0111>

- Paerl, H. W., & Huisman, J. (2008). Climate – Blooms like it hot. *Science*, 320, 57–58. <https://doi.org/10.1126/science.1155398>
- Radbourne, A. D. (2018). *Disentangling the impacts of nutrient enrichment and climatic forcing as key drivers of change at Rostherne Mere*. PhD, Loughborough University.
- Radbourne, A. D., Ryves, D. B., Anderson, N. J., & Scott, D. R. (2017). The historical dependency of organic carbon burial efficiency. *Limnology and Oceanography*, 62, 1480–1497. <https://doi.org/10.1002/lno.10512>
- Radbourne, A. D., Ryves, D. B., Madgewick, G., & Anderson, N. J. (In review). Increasing climatic influence following nutrient load stabilisation in a deep stratifying lake. *Ecosystems*.
- Reddy, K. R., Newman, S., Osborne, T. Z., White, J. R., & Fitz, H. C. (2011). Phosphorous cycling in the Greater Everglades ecosystem: Legacy phosphorous implications for management and restoration. *Critical Reviews in Environmental Science and Technology*, 41, 149–186. <https://doi.org/10.1080/10643389.2010.530932>
- Reynolds, C. S. (1979). The limnology of the eutrophic meres of the Shropshire-Cheshire Plain: A review. *Field Studies*, 5, 93–173.
- Reynolds, C. S. (2006). *Ecology of phytoplankton*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/cbo9780511542145>
- Reynolds, C. S., Irish, A. E., & Elliott, J. A. (2001). The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecological Modelling*, 140, 271–291. [https://doi.org/10.1016/s0304-3800\(01\)00330-1](https://doi.org/10.1016/s0304-3800(01)00330-1)
- Sartory, D. P., & Grobbelaar, J. U. (1984). Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, 114, 177–187. <https://doi.org/10.1007/bf00031869>
- Sas, H. (1989). *Lake restoration by reduction of nutrient loading: Expectation, experiences, extrapolation*. Berlin, Germany: Academia.
- Schindler, D. W. (2006). Recent advances in the understanding and management of eutrophication. *Limnology and Oceanography*, 51, 356–363. https://doi.org/10.4319/lo.2006.51.1_part_2.0356
- Scott, D. R. (2014). *Carbon fixation, flux and burial efficiency in two contrasting eutrophic lakes in the UK (Rostherne Mere & Tatton Mere)*. PhD Thesis, Loughborough University.
- Sharpley, A., Jarvie, H. P., Buda, A., May, L., Spears, B., & Kleinman, P. (2013). Phosphorus legacy: Overcoming the effects of past management practices to mitigate future water quality impairment. *Journal of Environmental Quality*, 42, 1308–1326. <https://doi.org/10.2134/jeq2013.03.0098>
- Smith, V. H., Joye, S. B., & Howarth, R. W. (2006). Eutrophication of freshwater and marine ecosystems. *Limnology and Oceanography*, 51, 351–355. https://doi.org/10.4319/lo.2006.51.1_part_2.0351
- Sondergaard, M., Jensen, J. P., & Jeppesen, E. (2005). Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. *Freshwater Biology*, 50, 1605–1615. <https://doi.org/10.1111/j.1365-2427.2005.01412.x>
- Tadonleke, R. D. (2010). Evidence of warming effects on phytoplankton productivity rates and their dependence on eutrophication status. *Limnology and Oceanography*, 55, 973–982. <https://doi.org/10.4319/lo.2010.55.3.0973>
- Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R. G., Ballatore, T. J., ... Weyhenmeyer, G. A. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography*, 54, 2298–2314. https://doi.org/10.4319/lo.2009.54.6_part_2.2298
- Wigdahl-Perry, C. R., Saros, J. E., Schmitz, J., Calcote, R., Rusak, J., Anderson, D., & Hotchkiss, S. (2016). Response of temperate lakes to drought: A paleolimnological perspective on the landscape position concept using diatom-based reconstructions. *Journal of Paleolimnology*, 55, 339–356. <https://doi.org/10.1007/s10933-016-9883-5>
- Williamson, C. E., Saros, J. E., Vincent, W. F., & Smol, J. P. (2009). Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*, 54, 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273
- Zamparas, M., & Zacharias, I. (2014). Restoration of eutrophic freshwater by managing internal nutrient loads. A review. *Science of the Total Environment*, 496, 551–562. <https://doi.org/10.1016/j.scitotenv.2014.07.076>

How to cite this article: Radbourne AD, Elliott JA, Maberly SC, Ryves DB, Anderson NJ. The impacts of changing nutrient load and climate on a deep, eutrophic, monomictic lake. *Freshwater Biol.* 2019;00:1–14. <https://doi.org/10.1111/fwb.13293>