



The Influence of Climate Change on the Restoration Trajectory of a Nutrient-Rich Deep Lake

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ABSTRACT

Nutrient reduction in impacted lowland freshwater systems is ecologically and culturally important. Gaining a greater insight into how lakes respond to lowering nutrient loads and how climate-driven physical limnology affects present and future cycling of available nutrients is important for ecosystem resource management. This study examines the nutrient decline in a hypereutrophic freshwater lake (Rostherne Mere, Cheshire, UK) 25 years after sewage effluent diversion, a uniquely long-term analysis of a recovering nutrient-rich deep lake. Using nutrient, phytoplankton, climate and catchment hydrological monitoring, the contemporary lake system is compared to previous studies from 1990 to 2002. Nutrient change since point source load diversion showed annual average and maximum phosphorus (P) concentrations decreased significantly for the first 10 years (1992: $\sim 600 \mu\text{g P L}^{-1}$; 2002: $\sim 200 \mu\text{g P L}^{-1}$), but have since stabilised due to a substantial legacy sediment P internal load. Dissolved inorganic nitrogen (DIN) concentrations have not substan-

tially changed since diversion, resulting in the alteration of the DIN/SRP ratio from a system characterised by N limitation (N:P ~ 5), to one predominantly P limited (N:P > 20). Nutrient changes over this time are shown to drive ecological change, especially in the cyanobacterial and algal communities. Furthermore, very high-resolution monitoring of lake inflow and outflow (every 5 min during 2016) shows that water residence time at this lake is significantly shorter than previously estimated (~ 0.8 years compared to previous estimates of ~ 1.6 – 2.4 years). Together with long-term data demonstrating that the stratification period at Rostherne Mere has increased by 40 days over the last ~ 50 years (due to later autumnal mixing), we show that a rapid rate of epilimnetic flushing together with a long stratification period substantially reduces the available epilimnetic P during the summer cyanobacterial bloom. This is of growing importance for many such lakes, given widespread climate-driven lengthening of stratification and a national trend of decreasing summer rainfall (decreasing seasonal flushing) but more intense summer storm events (resulting in short-term flushing events).

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Author's Contribution ADR and DBR conceived this study, and it was designed with contributions from all authors. ADR performed the research and analysed the data. All authors contributed to new methods and models and wrote the paper.

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Key words: Rostherne Mere; management intervention; lake phosphorus budget; internal loading; flushing; water residence time.

HIGHLIGHTS

- Climate influence on lake ecology evident after nutrient load stabilisation
- Large nutrient load reduction has historically been major driver of change
- Complex interactions between nutrients, climate and ecology affect lake restoration trajectory

INTRODUCTION

Eutrophication continues to be a problem in lowland freshwater catchments, due to excessive nutrient loads from anthropogenic sources, such as wastewater effluent and agricultural runoff, leading to changes in trophic state and community structure (Spears and others 2012; Withers and others 2017). As understanding of the catchment-scale issues has developed, management intervention has attempted to reduce point source nutrient loads entering freshwater systems with the purpose of restoring surface waters to a good ecological status, as required by law across the European Union for example (European Commission 2000). Such efforts have been heavily biased towards phosphorus (P) control (Schindler 2006), being successful in some lakes, especially those that are shallow and flush quickly, while others (especially deeper, stratifying lakes) have been slow to respond (Jeppesen and others 2005; Fraterrigo and Downing 2008; Kusmer and others 2018).

However, lakes respond to multiple stressors at a variety of timescales (Smith and others 2006; Williamson and others 2009; Emmerton and others 2018). In temperate ecosystems in their natural state, the effect of climate forcing is mediated by soil and vegetation processes. In strongly disturbed systems, where both catchment and lake have been impacted, it may be difficult to assign ecological change to a key driver unambiguously (Nõges and others 2016).

Climate-driven changes (for example, altered heat budgets and flushing rates) overlay both catchment and in-lake management scenarios, resulting in complex synergistic and antagonistic interactions. Moreover, although climate-driven changes in thermal budgets are becoming more obvious with the increasing frequency of warmer summers (for example, Lowe and others 2018), altered precipitation is changing nutrient delivery from catchment soils and hydrological budgets with unpredictable results (Ockenden and others 2017). For example, at White Lough (Northern Ireland),

the 1975–1976 drought reduced hydrological runoff, so the internally derived lake P was not flushed from the lake at overturn, increasing inter-annual P retention and having a profound impact on in-lake nutrient concentration and algal abundance (Rippey and others 1997). At Lough Neagh, reduced Si delivery during the dry summer of 1995 affected diatom abundance, changing the pattern of annual phytoplankton succession and nutrient resource use (Gibson and Guillot 1997). There is a subtle interplay between precipitation and hydrologically mediated input of nutrients from the catchment, and the impact of changes in lake water retention time on nutrient concentrations, especially in deep lakes where P is derived from internal loading associated with anoxia.

Here, we assess the impact of nutrient reduction strategies on a hypertrophic, deep, monomictic lake (Rostherne Mere, Cheshire, UK) against a background of regional warming, increasing summer precipitation and changing stratification patterns focusing on two more intensive periods of monitoring some 25 years apart. The complex interactions of managed nutrient decrease, and climate-driven changes on ecosystem function are discussed in the context of their applicability to other eutrophic deep lakes.

METHODS

Study Site

Rostherne Mere (53°20'N, 2°24'W) is the largest (area 48.7 ha) and deepest, (max depth 31 m; mean depth 13.6 m) of a regional group of lakes known as the Shropshire-Cheshire Meres (Reynolds 1979). This is the last of a chain of three lakes lying sequentially along a single stream, draining a small catchment (940 ha) of agricultural, urban and parkland (Carvalho and others 1995). Rostherne Mere is a hypertrophic, monomictic lake, with a stable summer stratification (thermocline average depth March/April to November ~ 10 m from 2004 to 2016; Radbourne and others 2019) that leads to hypolimnetic anoxia within ~ 3 weeks of stratification (Scott 2014), predominantly due to decomposition of sedimented phytoplankton crops.

Rostherne Mere is a SSSI (Site of Special Scientific Interest), National Nature Reserve (NNR) and Ramsar site, and therefore is of great ecological value, and has been studied extensively for over a century (Tattersall and Coward 1914; Pearsall 1923; Lind 1944). However, the lake has been hypereutrophic at least since the 1970s (defined as $> 100 \mu\text{g P L}^{-1}$, Carlson 1977), largely due to

anthropogenic P loading from two sewage treatment works (STWs) discharging effluent upstream of Rostherne Mere between the 1930s and June 1991 (when all STW effluent was diverted outside the catchment), although the lake also has a long history of cultural eutrophication through land-use change (agriculture, settlement). The effect of nutrient point source removal and wider catchment management intervention were examined by several studies spanning 1990 to 2002. These focussed on in-lake P response to changes in external P loading, comparing the nutrient budgets immediately before and after STW diversion (Carvalho 1993; Carvalho and others 1995; Moss and others 2005).

Climate and Lake Temperature Data

Air temperature, wind speed and precipitation data were taken from the closest reliable meteorological station (Manchester Airport, UK; situated 7.4 km north-east of Rostherne Mere). Wind speed at the airport (V_{MA}) was corrected for local sheltering (V_{RM}) through comparison with the available wind speed data from the UK Lake Ecological Observatory Network project buoy on Rostherne Mere (UKLEON; see <http://www.ceh.ac.uk/our-science/projects/uk-lake-ecological-observatory-network-ukleon>; comparable daily data from February 2013 to January 2017; correction factor of $V_{RM} = 0.55 V_{MA} - 0.12$, $r^2 = 0.82$, $n = 1417$, $p < 0.0001$). Additionally, the UKLEON buoy measures various in-lake parameters (for example, temperature profiles, chlorophyll) and lake-surface meteorological variables at high temporal resolution (every 4 min) with data uploaded in real-time. This buoy has provided daily average water column temperatures since 2010, from thermistor readings at 2 m intervals from 2 m to 24 m depth at a central lake location (Figure 1). The date of stratification onset was taken as the day a greater than 3% difference in epilimnion, and hypolimnion temperature develops and is maintained throughout the summer, with stratification end taken as the first day, and the difference in epilimnion and hypolimnion temperatures drops to a less than 3% range.

Sample Collection and Analysis

Two 250 ml water samples were collected for nutrient analysis into new PTFE sealable bottles approximately every 3 weeks for each sampling location from January 2016 to January 2017. Sampling locations included Rostherne Brook (main inflow, 250 m upstream from the lake), Harper's Bank Spring (groundwater inflow),

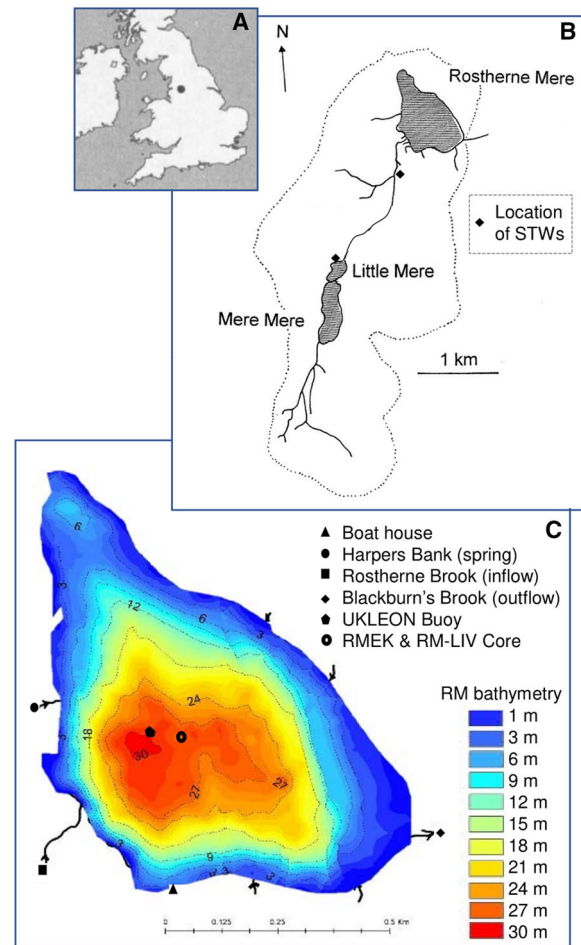


Figure 1. Location in UK (A), catchment map (B; adapted from Moss and others 2005) and bathymetric map of Rostherne Mere with sample sites labelled (C; adapted from Scott 2014).

Blackburn's Brook (outflow, 350 m downstream from the lake) and surface water samples from a central lake location, with multiple water column depth samples (6 m, 12 m, 18 m and 24 m) added to the collection programme from September 2016 (Figure 1). Additionally, an 8 m integrated water column sample from the central lake location (Figure 1) was collected into two opaque 500 ml bottles and two opaque 250 ml bottles, with 2 ml of Lugol's iodine added to each 500 ml bottle to preserve phytoplankton for identification. All samples were sealed and placed in a cool box for transport back to Loughborough University. Secchi depth was recorded at this central lake location during each visit.

On the same day as collection, one of the 250 ml water samples per site was frozen as collected, with the other filtered using GF/F filter paper (0.45 μm) before being stored frozen, which previous work

has suggested is a suitable method at this lake (see Supplementary Information). Periodically (~ 2 month intervals), samples were shipped to an external certified laboratory (National Laboratory Service, UK) for orthophosphate (that is, soluble reactive phosphate, SRP), DIN and total P (TP) nutrient analysis.

Nutrient Budget and Water Residence Time

Discharge into and out of Rostherne Mere was estimated by measuring the cross-sectional profile and sectional velocities for a range of stage heights for both inflow (Rostherne Brook) and outflow (Blackburn's Brook) at the water sampling points. This discharge/stage relationship was then applied to continuous stage height recordings taken throughout the study period (Jan 2016–Jan 2017) from the inflow and outflow using a Van Essen mini-diver data logger (www.vanessen.com), recording water pressure every 5 min, corrected to changes in air pressure by a barometer located in the boat house (Figure 1). Application of the measured discharge to stage relationship to the mini-diver data provides a very high-resolution total discharge measurement for both the inflow and outflow. Total nutrient fluxes were calculated by applying a daily nutrient concentration estimate through linear interpolation between two sample dates, although another algorithm was also applied and gave similar results (see Supplementary Information). The estimated daily nutrient concentration was then multiplied by monitored average daily flow rate to provide a total inflow and outflow load of each nutrient on a daily basis (SRP, TP, DIN). Loadings from the 21% of the lake catchment (to the north) not drained by the inflow ("catchment north drainage" and "catchment north groundwater") were estimated using the same methods as Carvalho and others (1995), with estimation of cormorant bird roost nutrient inputs kept the same as 1992 values, in the absence of evidence to suggest substantial changes in bird population size.

The TP budget was calculated using a mass balance equation as in Carvalho and others (1995), with flux balance as follows:

$$\begin{aligned} \text{Output} = & \text{external inputs} \\ & \pm \text{internal source} / \sin k \\ & - \Delta \text{lake storage} \end{aligned} \quad (\text{Eq.1})$$

The internal source represents the release of P to the hypolimnion, and the sink includes sedimentation of particulate matter. The internal source/

sink contribution was calculated by balancing Equation (Eq. 1).

The standard outflow method for water residence time (WRT) was estimated as the total lake volume ($6.85 \cdot 10^6 \text{ m}^3$) divided by the annual outflow discharge ($8.33 \cdot 10^6 \text{ m}^3 \text{ yr}^{-1}$). As the lake is strongly seasonally stratified (following the classic monomictic pattern), a second, adjusted WRT for the mixed part of the water column (denoted WRT_m) was calculated. This is the monthly available mixed lake volume during the stratified period from April to November, which is the epilimnion, but during the mixed period from December to March, this is the entire lake. To calculate WRT and WRT_m from 2010 to 2016, the UKLEON buoy data were used to determine the period of stratification and the thermocline depth (that is, to calculate the available outflow lake volume), while we used 2016 data for the monthly outflow rate.

Chl-a and Phytoplankton Data Collection

Chl-*a* was determined by a standard spectrophotometer approach with pigments extracted from filtered water samples (Sartory and Grobbelaar 1984). Phytoplankton enumeration was undertaken by concentrating the total 1 L sample to 50 ml via a sequence of settling procedures. The concentrated sample was then well mixed and a measured 1 ml sub-sample was extracted and placed on a gridded Sedgwick-Rafter cell for identification and absolute abundance counts using an inverted microscope at $400 \times$ magnification (Lund and others 1958). Four of the initial 16 algal samples were counted in triplicate to allow an estimate of sample reproducibility and counting error (with $1\sigma = \pm 15\%$ total number of cells).

RESULTS

Climate and Meteorological Data

Air temperature, precipitation and wind speed have varied seasonally during the past 43 years (Figure 2). Precipitation varied greatly, with successions of drier and wetter years, with a non-significant trend towards increasing annual precipitation since 1973 ($y = 1.48x - 2290.5$, $r^2 = 0.04$, $p = 0.15$; Figure 2A). Every season showed a long-term increase in precipitation (Figure 2B), but with the greatest rise in summer ($+15.9$ mm between 1973 and 2016; $y = 0.37x - 677.7$, $r^2 = 0.06$, $p = 0.06$; Figure 2B). Wind speed showed seasonal peaks, with a strongly significant decreasing trend ($y = -0.0053x + 12.7$, $r^2 = 0.22$, $p < 0.001$; Figure 2C),

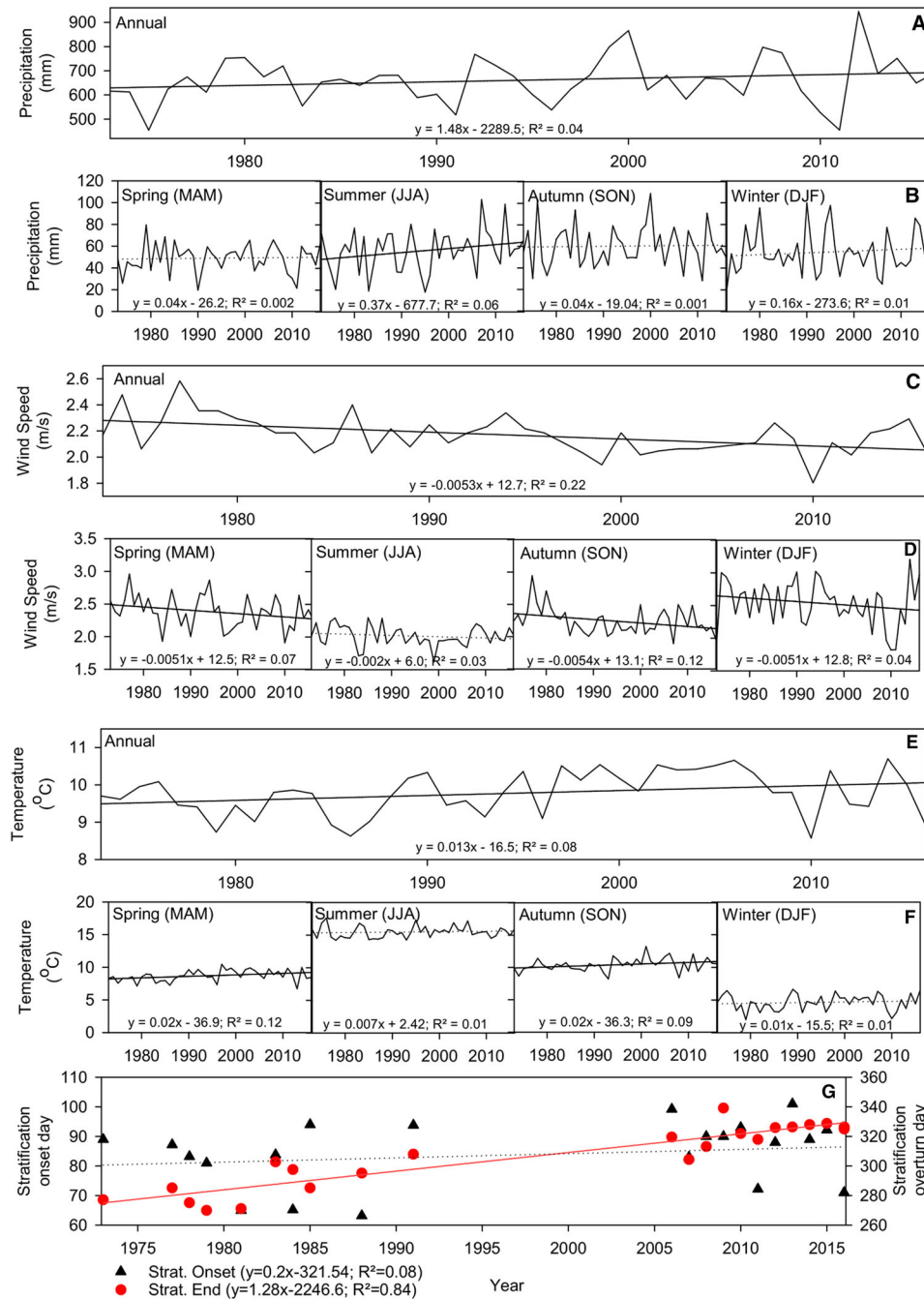


Figure 2. Climate and stratification timing data. **A–F** Annual and seasonal meteorological data at Rostherne Mere over the last 43 years, including the 43 year regression lines (solid = significant; dotted = not significant). **A** annual precipitation, **B** seasonal precipitation, **C** annual wind speed, **D** seasonal wind speed, **E** annual air temperature, **F** seasonal air temperature. **G** stratification onset (black triangles) and overturn dates (red circles) including regression lines (onset = dotted black line, overturn = solid red line), with data from 1973 to 1988 taken from Reynolds and Bellinger (1992), 1991 from Carvalho (1993) and 2006–2016 from the UKLEON thermistor data.

with the on-lake to regional wind speed correction highlighting the sheltered position of the lake ($\sim 45\%$ lower wind speed on the lake compared to Manchester Airport). Air temperature varied seasonally and inter-annually, with a warming trend

present annually ($+0.72^\circ\text{C}$ between 1973 and 2016; $y = 0.013x - 16.5$, $r^2 = 0.08$, $p = 0.22$; Figure 2E) and for every season, although only significant for spring and autumn (Figure 2F).

Physical Limnological Data

The UKLEON thermistor data show stratification onset, and overturn date during the last 10 years has varied from year to year (Figure 2G) and comparison with stratification timings in Reynolds and Bellinger (1992) and Carvalho (1993) confirm stratification onset that has frequently ranged from early-March to mid-April. The stratification overturn date is shown to have become gradually later in the year ($y = 1.28x - 2246.6$, $r^2 = 0.84$, $p < 0.0001$), extending the total time of stratification at Rostherne Mere by ~ 40 days over the past 43 years ($y = 1.07x - 1918.9$, $r^2 = 0.66$, $p < 0.0001$; Figure 2G).

The WRT estimated in this study (0.82 years) suggests Rostherne Mere flushes substantially quicker than it was previously thought (estimated as 1.6–2.4 years; Harrison and Rogers 1977; Moss and others 2005), likely due to higher-resolution monitoring data available with technological advances (that is, use of pressure transducers recording stream stage every 5 min, rather than just 2-weekly flow measurements). Furthermore, 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, reduces the summer residence time to an annual estimate of 0.57 years in 2016 (see Supplementary Information). This suggests that the epilimnion will flush completely during thermal stratification in the contemporary system (7–8 months, ~ 0.65 years), but would not have done so some 30 or 40 years ago.

2016 NUTRIENT CYCLING AND ALGAL ASSEMBLAGES

At the beginning of 2016, lake P and N concentrations were high ($> 150 \mu\text{g L}^{-1}$ SRP and $> 1000 \mu\text{g L}^{-1}$ DIN; Figure 3), with in-lake SRP concentration being diluted by the inflow ($< 50 \mu\text{g L}^{-1}$ SRP; Figure 3), although inflow N concentrations are substantially higher than the lake ($> 1300 \mu\text{g L}^{-1}$ DIN; Figure 3). Nutrient draw-down from the spring diatom bloom (predominantly *Asterionella formosa* Hassall, Figure 4) and the early summer cyanobacterial blooms (predominantly *Aphanizomenon* and *Dolichospermum*, Figure 4) utilises the available P and N within the mixed part of the lake (epilimnion), which is also rapidly being flushed out of the lake and diluted by the lower inflow nutrient concentrations, consequently decreasing levels to near (or below) detection limits by mid-June (Figure 3A and B).

The faster fall of SRP (Figure 3A) compared to DIN in June (Figure 3B) results in a short-term high DIN/SRP ratio (maximum $> 88:1$; Figure 3C). Yet, DIN decreases shortly after, and both DIN and SRP are below detection limits for a majority of the summer, making ratio assessment impossible until later in the year (\sim late-October). The phytoplankton summer maximum was $25.8 \mu\text{g chl-}a \text{ L}^{-1}$ (Figure 4).

With consistently higher outflow compared to inflow, the net export of P (635 kg TP; Table 1) is driven by internal loading, with a large store of P developing during stratification in the hypolimnion (maximum $> 800 \mu\text{g SRP L}^{-1}$ in deepest water; Figure 5) and dispersed throughout the water column at overturn, returning the lake system to high concentrations for the following spring ($\sim 250 \mu\text{g SRP L}^{-1}$; Figure 3A and 6). Outflow N and P concentrations were often slightly greater than the epilimnion (Figure 3) due to the impact of an additional water source contributing nutrients from the catchment between the lake and the site of outflow sampling. This additional supply is most notable in November with an inflow and outflow DIN peak, showing the impact of localised catchment sources in these water courses.

Updated Rostherne Mere Phosphorus Budget

With the WRT estimate in this study about 40% of that calculated in previous studies (0.8 to ~ 2 years), it can be assumed the previous nutrient budget calculations for the inflow and outflow were also substantially underestimated. Therefore, the previous P budget from 1990 to 1992 was adjusted by linking the 2016 measured discharge to flow data provided in Carvalho (1993) and correcting for the higher precipitation in 2016, which suggests a $\times 1.73$ factor difference is needed to account for the increased flow rates. This correction in turn increases the net TP loading to the lake pre-STW diversion (933 kg TP; Table 1) and the net TP export post-STW diversion (2140 kg TP; Table 1). We use these corrected figures hereafter.

In comparison, the 2016 nutrient budget showed an almost identical TP external source total input as the post-STW diversion values in 1991–1992 (1991–1992 total external inputs 958 kg TP, 2016 total external inputs 959 kg TP; Table 1), dominated by the inflowing load from the Rostherne Brook catchment (88–91%; see Supplementary Information Table S2). These post-STW values are substantially reduced from the pre-STW diversion external inputs (1990–1991 total external inputs

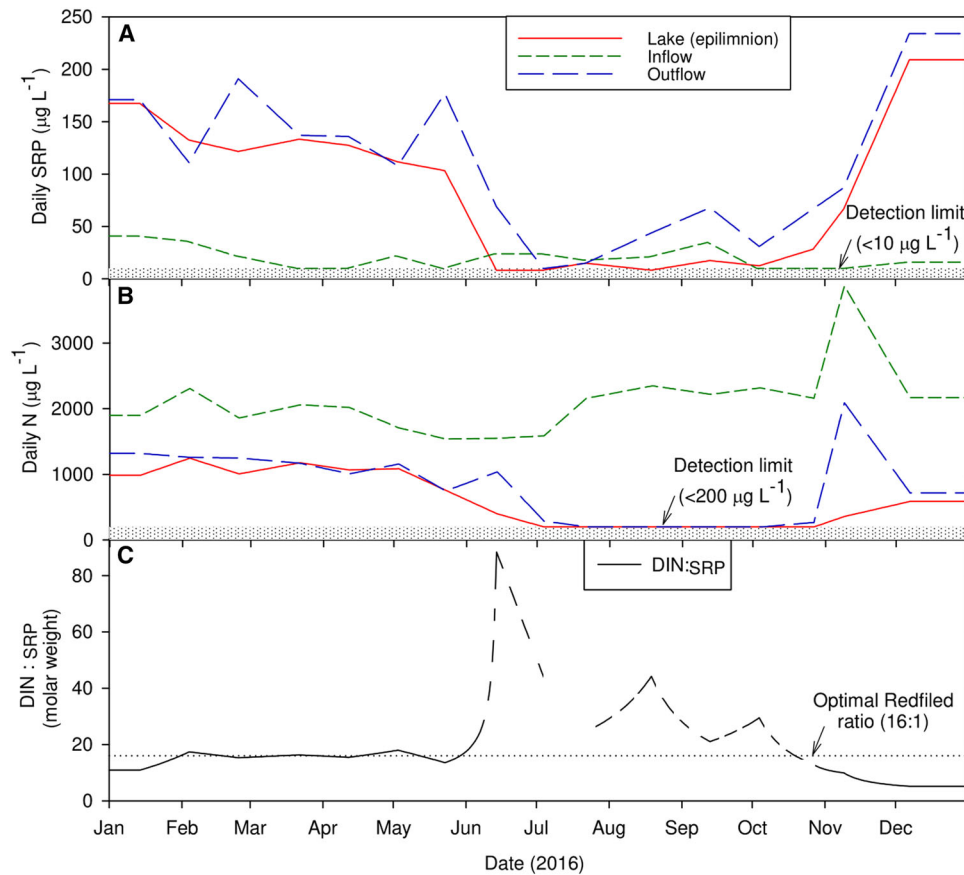


Figure 3. Estimated daily SRP (**A**) and N (**B**) concentrations for the major inflow, lake (epilimnion) and outflow. Analysis detection limits $< 10 \mu\text{g SRP L}^{-1}$ and $< 200 \mu\text{g N L}^{-1}$, samples below detection values set as $10 \mu\text{g}$ or $200 \mu\text{g}$, respectively. DIN/SRP (molar weight) ratio (**C**) with optimal Redfield ratio (16:1) reference line (dotted line). Dashed line when one analysis below detection limit; no line when both analyses were below detection limits.

3999 kg TP; Table 1), driven by inflow load (97% total external inputs; see Supplementary Information Table S2). The outflow load between 1990–1991 and 1991–1992 did not fall in the same way as the inflow load; however, by 2016 the outflow load had substantially decreased (1991–1992 outflow 3443 kg TP, 2016 outflow 1416 kg TP; Table 1), resulting in a declining net TP balance, that is, loss of TP from the system through the outflow (1991–1992 loss of + 2140 kg TP, 2016 loss of + 635 kg TP; Table 1).

Nutrient, Chl-*a* and Phytoplankton Change Over the Last 25 Years

Following STW diversion upstream of Rostherne Mere, the concentration of in-lake P (TP and SRP) declined rapidly for approximately 11 years. Values stabilised to current levels (annual average $\sim 160 \mu\text{g P L}^{-1}$; Figure 6C) from ~ 2002 , the end of the study period of Moss and others (2005).

With a decrease in the external TP loads following STW diversion (Table 1), the annual replenishment of P at Rostherne Mere has been driven by internal sediment P loading, as evident in the 2016 water column TP profile (Figure 5). DIN showed seasonal variability with no long-term trend in concentration change following STW diversion (Figure 6B). A trend of increasing DIN/SRP ratios highlights the stable DIN and decreasing P concentrations, with values over the last 25 years increasing from those implying N limitation in the 1990s, to those suggestive of potential P limitation, especially in the summer of some years (for example, 2002–2004 and 2016; Figure 6D). However, low N concentrations in these years make it difficult to argue unequivocally for P limitation. Chl-*a* showed annual peaks each summer, yet no change of note is seen in the 2016 data compared with the 1990s and early 2000s (mean annual chl-*a*: 1990–2003 = $15 \mu\text{g L}^{-1}$, 2016 = $13 \mu\text{g L}^{-1}$; Figure 6A). However, long-term trends in the chl-*a* data were

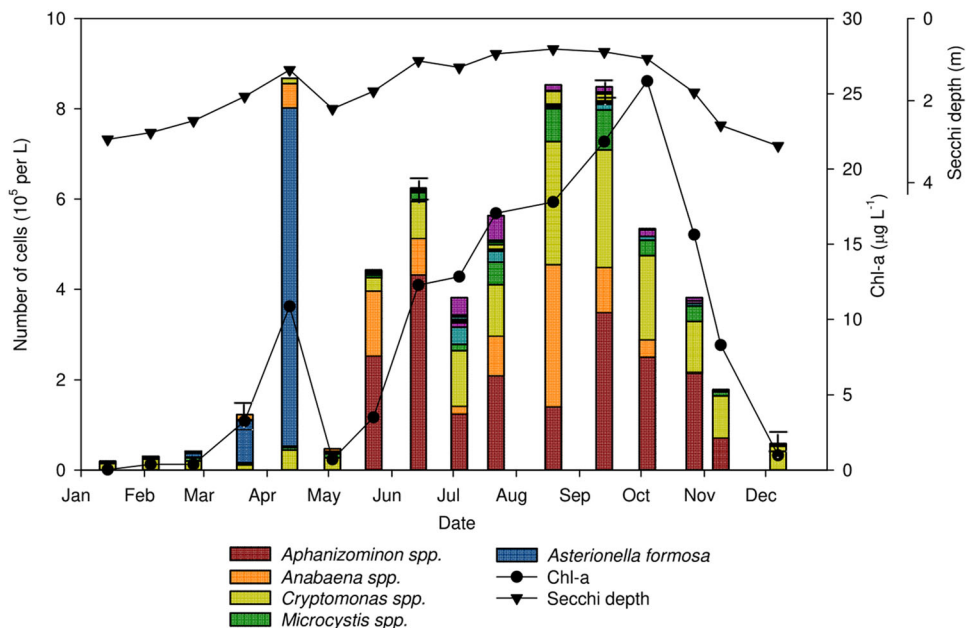


Figure 4. Epilimnion integrated samples total algal cells present (including triplicate count error bars for samples 4, 8, 12 and 16), chl-a concentration and measured Secchi depth.

Table 1. Rostherne Mere Nutrient Budget Summary

Period	Inflow	Total inputs	Δ P lake	Out flow	Balance
5/2/90–14/5/91	2250	2356	– 100	1830	– 626
23/7/91–21/7/92	504	590	– 345	1990	+ 1055
5/2/90–14/5/91 (WRT corrected)	3893	3999	– 100	3166	– 933
23/7/91–21/7/92 (WRT corrected)	872	958	– 345	3443	+ 2140
14/1/16–4/1/17	864	959	+ 178	1416	+ 635

Total phosphorus budget for Rostherne Mere. Values in kg. 1990 to 1992 data taken from Carvalho and others (1995). A correction of inflow*1.73 based on comparison of water budgets from this study and Carvalho (1993). For balance, + values are net losses from lake system, – are net gains. Shading indicates pre-STW diversion. Full budget table available in Supplementary Information Table S1

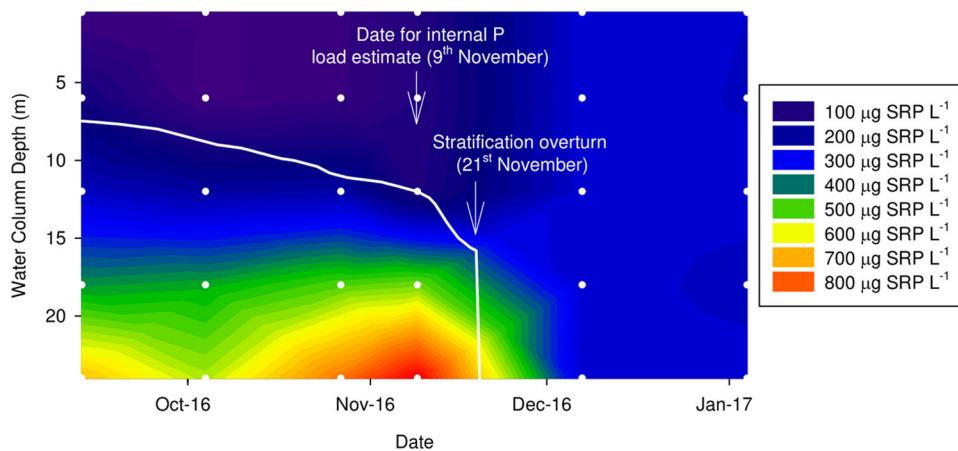


Figure 5. Internal concentration of SRP building in the hypolimnion during stratification and released into the whole water column upon stratification overturn in 2016. White dots represent sampling points. White line represents thermocline depth estimated using UKLEON daily thermistor data.

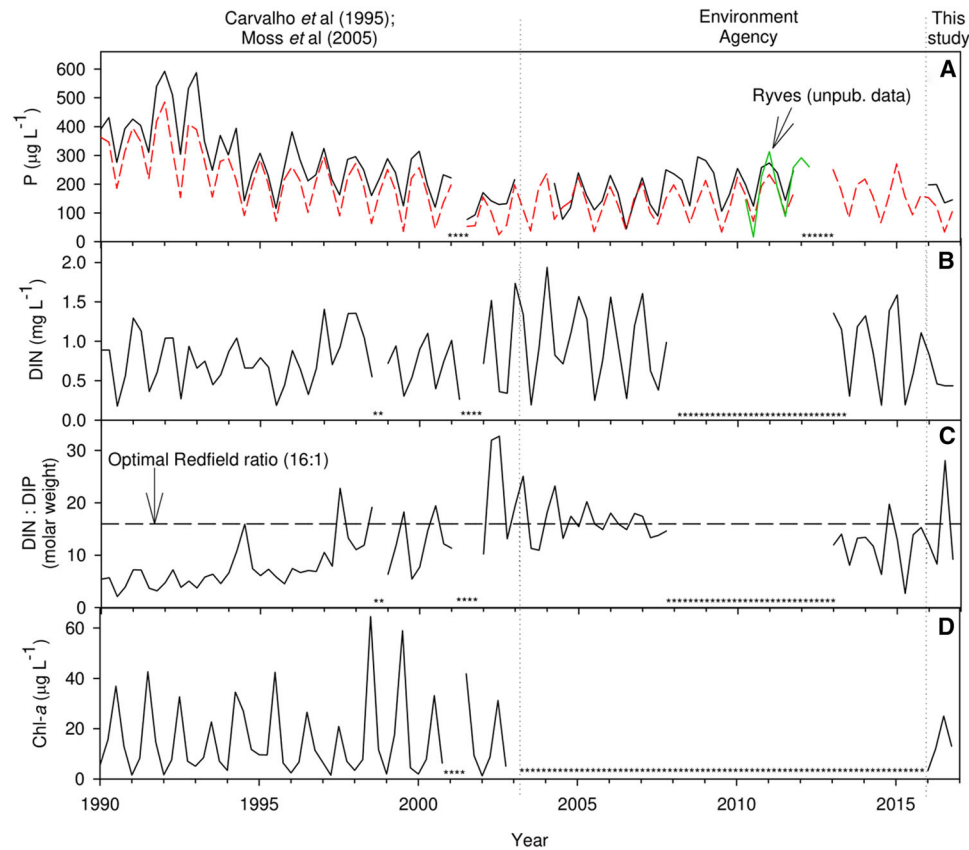


Figure 6. Seasonal (quarterly) nutrient, nutrient ratios and chl-*a* values at Rostherne Mere during the last 25 years. Data sources include Carvalho and others (1995), Moss and others (2005), Environment Agency and this study, with independent SRP data from 2010 to 2012 confirming data reliability from D. B. Ryves. Dashed red line in 'C' signifies SRP. Asterisks signify unavailable data.

difficult to assess due to a long period (2003–2015) when data were not available.

Cyanobacterial summer blooms following STW diversion in 1991 initially showed a rapid decline in *Microcystis* spp. (Figure 7C), a gradual decline in *Dolichospermum* spp. (Figure 7B), and a consistent presence of *Aphanizomenon* spp. with 2 years of high abundance (1996 and 1998; Figure 7A). Phytoplankton collections in 2016 showed summer phytoplankton assemblages still include the same cyanobacterial species at abundances consistent with earlier observations (Figure 7).

DISCUSSION

Climatic-Driven Change Increasing Epilimnion Flushing

With the caveat that the focus of this study is on two shorter periods of more intensive monitoring 25 years apart, there is nonetheless clear evidence that climate has driven physical limnological change, altering the stratification and flushing rates

within Rostherne Mere. During the last 43 years, there has been a weak trend of warming in every season (Figure 2). Like many other lakes globally, Rostherne Mere has responded dynamically through physical limnological change (Williamson and others 2009). Rostherne Mere's stratification has extended predominantly through a delay in the autumnal overturn date by around 6 weeks (40 days). Changing stratification timing is a common feature under global warming for deep lakes, with several previous studies also showing a change in timing as stratification onset becomes earlier in the year (Thackeray and others 2008; Meis and others 2009) and/or increases the duration of stratification (Liu and others 2014; Izmet'eva and others 2016). A significant decreasing trend of wind speed over this time (Figure 2D) may also have an influence on the timing of stratification. In particular, the timing of autumnal overturn may be delayed with reduced wind speeds in both autumn and winter (Figure 2D and E), because less water turbulence is created from wind shear stress

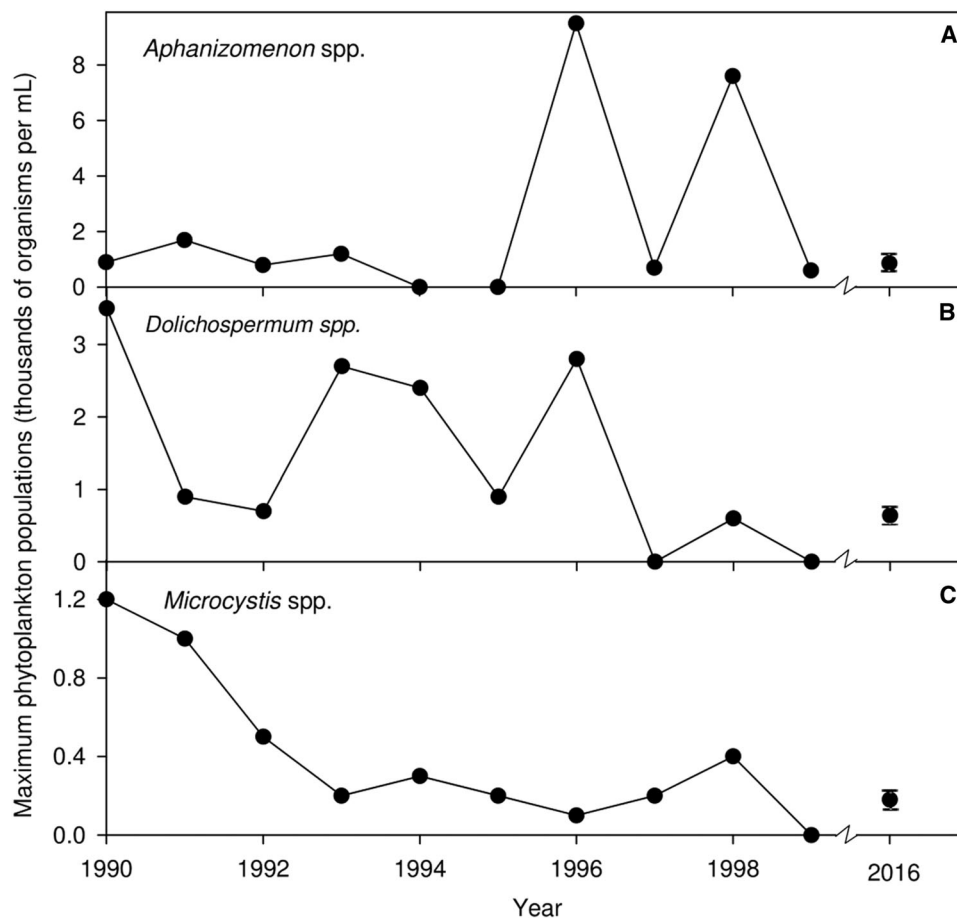


Figure 7. Maximum annual cyanobacteria populations for the three most abundant species. 1990s data taken from Moss and others (2005), with 2016 data from this study.

that can lead to stratification breakdown. Indeed, Rostherne Mere's sheltered position (relative to nearby Manchester Airport, which experiences about twice average wind speeds as Rostherne) may impose a threshold wind speed for effective wind-induced turbulence that has been crossed less frequently as wind speeds have fallen regionally.

Changes in the timing of stratification result in a longer period of epilimnetic nutrient reduction. Although climatic changes over time will have driven some alteration to stratification at Rostherne Mere, it is not the sole reason for the large difference in the reported WRT here and in previous studies. Rather this study found the WRT to be 0.8 years, only $\sim 40\%$ of previously published estimates (that is, flushing rate is faster), likely due to the availability of higher-resolution data that picks up significant periods of higher inflows and outflows. Past studies relied only on fortnightly flow sampling, whereas this study used pressure transducers to estimate stage height every 5 min, allowing the inclusion of "flashy" stream flows

(that is, highly responsive to precipitation events) in the calculation. The new, faster flushing rate calculated for Rostherne Mere is further exaggerated with consideration of the WRT_m (that is, available water column flushing rate). Although the WRT_m is only estimated for 2016 due to data availability, we argue this is similar for previous years as there is no reason to expect that the inflow hydrograph has changed in its response to precipitation. This approach is applicable for other stratifying lakes with an epilimnion outflow.

At Rostherne Mere, the WRT_m calculated for 2016 is shorter than the length of stratification. This implies that the epilimnion may be completely flushed each summer, with P sequestered in algae both sedimenting to the lake floor and being washed out, together with dissolved P in outflow discharge reducing the nutrient concentration to that of the managed (low nutrient) inflow. A longer period of lower epilimnion nutrient concentrations will impact algal growth and succession in the lake. For example, lakes that have tended

towards an earlier onset of stratification, such as Windermere (Thackeray and others 2008), will flush and utilise the available nutrient load earlier in the growing season, resulting in greater limitation of summer algal growth, causing substantial impacts on algal ecological succession (and cascading to higher trophic levels). Lakes that tend to extend their stratification later into autumn, as seen here at Rostherne Mere, will show a longer reduction in available nutrients later into the year, delaying autumnal blooms (for example, diatom blooms reliant on dissolved Si upwelling from the hypolimnion; Jewson and others 2015; Roberts and others 2018), perhaps to an extent where other factors, such as ambient (seasonal) light, may become an important factor in limiting growth.

However, nutrient limitation in cyanobacteria is further complicated by the ability of several buoyant species to migrate diurnally from the nutrient-poor epilimnion to the nutrient-rich hypolimnion (Reynolds and others 1987; Reynolds 2006). This strategy could mean that factors other than those suggested above are limiting algal populations, such as light (that is, algal crop self-shading). Comparison of Rostherne Mere's phytoplankton summer maximum to other published data for deep lake systems undergoing nutrient reduction suggests that (epilimnetic) P is not necessarily limiting growth throughout the summer, with a similar biomass (chl-*a*) as reported from other lakes (such as; Cattaneo and others 1998; Hansson and others 1998; Guildford and Hecky 2000; Jeppesen and others 2005; Langdon and others 2006). It should also be noted here that towards the mid- to late-summer, a number of samples for N and P analysis were below the analysis detection limit, making the assessment of the DIN/SRP ratio insecure as a means to determine P or N limitation at these times.

Although the timing and length of stratification impact the period of sustained epilimnion nutrient reduction, catchment precipitation is a key influence on its development through the mechanism of flushing. Theoretically, increased precipitation will lead to an increased flushing rate, if other variables such as changes in land-use or catchment saturation or runoff rates remain consistent. Future climate projections under UKCP18 modelling suggest the UK will have warmer, wetter winters and hotter, drier summers, with more intense storms (Lowe and others 2018). Warmer, wetter winters will result in an earlier stratification and increased flushing rate, both reducing epilimnion nutrient concentrations earlier in the year under a regime of P-managed catchment inflow, as at Rostherne. This

increased flushing rate can impact lake ecology, with studies attributing increases in rainfall to low abundances of siliceous diatoms (McGowan and others 2012; Reynolds and Irish 2000). By contrast, in the hotter, drier summer, the flushing rate will fall, leading to lowering water levels, less efficient nutrient flushing pathways and reduced nutrient inputs from the catchment (for example, Si), resulting in increased cyanobacterial growth. Rippey and others' (1997) study of White Lough (Northern Ireland) during the drought of 1975–1976 provides an example where observed reduced hydrological runoff failed to flush the internally derived lake P, having a profound impact on in-lake nutrient concentration and algal abundance.

The development of more intense storms and prolonged extreme weather will also have an important influence on lake ecology. Storms create a hydrological flushing pulse that has been linked to reduce lake biomass (Tolotti and others 2010; Cross and others 2014), whereas increasing water turbulence can impact certain cyanobacterial standing crops that prefer calm waters for reproduction (Godlewska and others 2003). Additionally, changes in the light environment can impact ecological succession with increased water turbidity from sediment plumes near to the catchment inflow during high precipitation events (Aryal and others 2014). The impacts on lake hydrology and ecology of future short-term precipitation extremes (flood and drought), or longer-term unusual weather patterns, for example the dry 2010–2011 followed by the wet 2012 summer in the UK (Parry and others 2013), are likely to be substantial.

The climatic influence on lake ecology and ecosystem functioning found in this study has major implications for other deep, stratifying, eutrophic lakes, given future climatic projections. If the recent projections of warming and increased precipitation in this region of the UK are correct, changes to flushing rates, stratification onset and overturn, and longer summer and autumn periods of nutrient reduction, as seen at Rostherne, can be expected more widely, dynamically shifting lake nutrient availability and ecological organisation (Lowe and others 2018; Williamson and others 2009).

Nutrient-Driven Change: Updated Phosphorus Budget 25-Year Post-STW Diversion

The P mass balance changes between pre-STW diversion, immediately post-STW diversion and 25-year post-STW diversion highlight the dynamic

response of Rostherne Mere to management intervention. There was a rapid fall in the incoming P load following STW diversion, yet a stable out-flow load, resulting in a switch from a net burial of P in lake sediments to a net loss of P from the lake system.

The consistent export of P from Rostherne Mere since STW diversion is a result of internal sediment P release that has replenished lake P values annually at overturn, as in many other such eutrophic and stratifying lakes (Sondergaard and others 2005; Spears and others 2012). Sediment P release in Rostherne Mere is high due to the long period of thermal stratification and rapid onset of anoxic conditions, which promotes the sediment release of iron-bound P into the water column (Nurnberg 1984). This morphometrically enhanced anoxic release, in the context of over a century of eutrophication sedimenting large quantities of P-rich organic matter, results in a large pool of sedimentary P that can be released over a long time frame (Radbourne and others 2017). Since \sim 2002, lake P concentrations have stabilised, implying the internal load contribution is consistent (as the inflow TP load remained approximately the same following STW diversion, see Table 1). This is not an unusual scenario, as seen in other deep stratifying lake systems undergoing managed catchment nutrient reduction, and similarly driven by major internal legacy source contributions (Jeppensen and others 2005; Spears and others 2012).

The 25-year DIN concentrations at Rostherne Mere show no trend following STW diversion, implying DIN is from a source other than the STW, likely runoff from the agricultural catchment. Therefore, with a reduction in P over this time, there has been a shift in the DIN/SRP ratio, from N limitation (that is, 1990–1994; as suggested by Moss and others 1997), to potential short-term summer P limitation, in certain years (that is, 2002–2004 and 2016; Figure 7D). However, summer N concentrations also fall below detection levels shortly after P, hampering a valid assessment of nutrient limitation.

The change in available nutrients during the summer months can directly influence the phytoplankton assemblage, causing cascading impacts across the lake ecosystem (Dolman and others 2012). At Rostherne Mere, a change in algal community is evident with the abundance of *Dolichospermum* spp. and *Microcystis* spp. blooms declining in line with falling lake P concentrations, as has been found in other experimental and observational studies (Carvalho and others 2013; Richardson and others 2018). However, chl-*a* showed little change

over this time, possibly due to the impact of migrating cyanobacteria (discussed earlier), or other factors such as zooplankton grazing and fish population dynamics on algal community structure (Jeppensen and others 2005). Alternatively, climate change may also offset the expected nutrient-driven decline in chl-*a*. It can be assumed that rising temperatures will stimulate phytoplankton growth, especially cyanobacteria (Paerl and Huisman, 2008). Yet, temperature can also affect zooplankton grazing numbers, either increasing or decreasing grazing of chl-*a*, depending upon seasonal timing and zooplankton response (Reynolds 2006; Carvalho and others 2012). Alterations in grazing pattern can have implications on water clarity, in turn impacting the growth of other aquatic plants.

Although higher-resolution monitoring datasets presented here for Rostherne Mere, in the context of the longer record of stratification, do suggest an important role of climate change in lake ecosystem functioning, expectations for other similar stratifying and eutrophic systems should be tempered until more contemporary data are collected. Bearing this in mind, we argue that climate (both temperature and precipitation) has impacted Rostherne Mere's physical limnology over at least the last 43 years, altering flushing rates and length of stratification. This has changed nutrient cycling and availability, impacting seasonal algal succession and causing changes in crop size, timing and dominance. This could cascade further across trophic levels, as the zooplankton and fish communities may have less (or possibly at times more) edible algae available at critical times of the year. The climatic influence on lake ecology, although potentially having an impact for decades, is only clearly evident since nutrient load stabilisation following STW diversion, with the large reduction in nutrient load (that is, P) following management intervention initially being the major driver of change. Increasingly, however, more subtle and complex interactions between nutrients, climate, physical limnology and lake ecology are becoming apparent, which will together determine the potential for sustained nutrient reduction, and its possible pathways, at Rostherne Mere and other such deep, stratifying lakes.

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DATA AVAILABILITY

Data used in this study have been made available at <https://doi.org/10.5285/5c6b2bcb-6b10-4c57-a595-ce94a655e709>.

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