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To cite this article: Stephen C. Maberly , Jo-Anne Pitt , P. Sian Davies & Laurence Carvalho (2020) Nitrogen and phosphorus limitation and the management of small productive lakes, Inland Waters, 10:2, 159-172, DOI: [10.1080/20442041.2020.1714384](https://doi.org/10.1080/20442041.2020.1714384)

To link to this article: <https://doi.org/10.1080/20442041.2020.1714384>



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Nitrogen and phosphorus limitation and the management of small productive lakes

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ABSTRACT

Many inland waters are enriched with nutrients, causing deleterious effects to their ecology and the benefits they provide for society, but their effective management first requires identification of the nutrient(s) that limit algal production. Concentrations of nutrients and chlorophyll *a* (Chl-*a*) were used to assess nutrient limitation seasonally at 17 meres over 2 time periods: historic (2005–2009; 1995–1998 at one site) and contemporary (2014–2018). Different approaches were used to assess nutrient limitation because they reflect different aspects of nutrient availability and their conversion into biomass. In the historic period, 3 meres were phosphorus (P) limited, 3 nitrogen (N) limited, 5 co-limited; the remaining 6 meres were not nutrient limited. For this period, ecological status assessed using phytoplankton Chl-*a* was only at good or high ecological status (*sensu* the Water Framework Directive) at 2 sites. The contemporary period was slightly improved, with 4 sites at good status. At the sites that failed to meet good ecological status, the required reduction in P concentration was least in P-limited sites and, conversely, the reduction in N was least in N-limited sites, suggesting that remediation by nutrient reduction would be most efficient if it was targeted using site-specific information. Even in primarily P-limited sites, once input of P has been reduced, further ecological benefit of reducing N at targeted sites should be explored.

ARTICLE HISTORY

Received 5 September 2019
Accepted 4 January 2020

KEYWORDS

eutrophication; meres; nutrient limitation; phytoplankton; remediation; Water Framework Directive

Introduction

Lakes are highly connected systems impacted by a range of anthropogenic pressures: locally from inputs of material from the catchment; regionally from atmospheric deposition of acids, nitrogen (N), and large-scale weather effects; and globally from climate change (Maberly and Elliott 2012, Richardson et al. 2018). Of these, nutrient enrichment, derived from local point sources and diffuse sources as well as regional atmospheric deposition, has had the longest and largest effect on the ecological structure and function of lakes (Moss et al. 2011, Moss 2018, Le Moal et al. 2019). The symptoms of this eutrophication include increased growth of planktonic and attached algae, blooms of cyanobacteria, a decline in macrophyte abundance, and deoxygenation at depth during stratification (Moss et al. 2011). These changes can substantially affect the biodiversity of fresh waters (Zhang et al. 2019) and degrade the diverse benefits they provide to society.

For several reasons, the main focus of nutrient enrichment studies, and attempts to remediate its effects, have

been on phosphorus (P). First, early large-scale comparisons across temperate lakes found broad relationships between phytoplankton biomass, commonly expressed as the concentration of the ubiquitous photosynthetic pigment chlorophyll *a* (Chl-*a*), and P expressed as total phosphorus (TP; e.g., Dillon and Rigler 1974, Vollenweider and Kerekes 1980, Vollenweider 1989, Phillips et al. 2008). This finding is expected because phytoplankton typically comprise a large fraction of the TP. Second, the history of eutrophication in the well-studied US Lake Washington (e.g., Edmondson and Lehman 1981) and in UK lakes such as Windermere (Talling and Heaney 1988, Pickering 2001), Lough Neagh (Wood and Smith 1993), and Loch Leven (Carvalho and Kirika 2003) is related to an increase in the availability of P rather than N. Third, the seminal whole-lake experiments on Canadian Shield lakes (Schindler 1977, Schindler et al. 1978) demonstrated that, in these lakes, P was the prime limiting nutrient. Fourth, the management of P loading is generally more practical than that of N loading because much anthropogenic P often arises from point-source discharges (Reckhow and Simpson 1980). Such

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 Supplemental data for this article can be accessed <https://doi.org/10.1080/20442041.2020.1714384>.

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powerful evidence and practicality has guided the management of eutrophication toward a focus on P control through legislation acting on point and diffuse sources (Janus and Vollenweider 1981, Rast and Lee 1983).

Despite this focus on P, from an early stage other nutrients were known to limit overall or specific components of freshwater phytoplankton, including N (Sakamoto 1966), silicon (Reynolds 1984), or minor trace elements such as molybdenum, iron, and cobalt (Goldman 1965). N is the primary or co-limiting nutrient for phytoplankton production in some lakes in North America (Elser et al. 1990), South America (Diaz and Pedrozo 1996), northern Sweden (Jansson et al. 1996), acidified lakes in central Sweden (Blomqvist et al. 1993), and some lowland German (Sommer 1989) and Dutch lakes (van der Molen et al. 1998). N limitation may be more widespread in tropical than in cooler lakes (Vincent et al. 1984, Talling and Lemoalle 1998). Within the United Kingdom, N limitation has been observed in some Cheshire meres and other shallow eutrophic and mesotrophic lowland lakes (Moss et al. 1992, 1994, James et al. 2003) and in upland lakes (Maberly et al. 2002). Even where lakes are not predominately N limited, N limitation of phytoplankton can occur for short periods (Sommer 1989, Maberly et al. 2002, Fisher 2003, Carvalho et al. 2012). A meta-analysis of nutrient enrichment experiments from >500 freshwater studies showed that, on average, freshwater phytoplankton are as commonly N limited as P limited, and addition of both nutrients typically produced the strongest response, indicating co-limitation (Elser et al. 2007). A similar conclusion was reached by Lewis and Wurtsbaugh (2008) based on a review of the available literature. Bergstrom and Jansson (2006) raised the intriguing possibility that in the Northern Hemisphere the anthropogenic increase in atmospheric N deposition has driven some lakes from their natural N-limited state toward P limitation; in other words, before human intervention, more lakes in the Northern Hemisphere would have been N limited, a finding supported by more recent work (Elser, Andersen et al. 2009a, 2009b). The steady accumulation of P in lakes over the last century has tended to drive lakes in the opposite direction, toward N limitation.

In this study, we build on the ground-breaking work carried out by Brian Moss and his students and colleagues at Liverpool University on nutrient limitation in the Shropshire and Cheshire meres to examine seasonal variability in nutrient limitation and the implications for their effective management and restoration. Globally, small shallow lakes are more numerous than large deep lakes (Messenger et al. 2016) and can be particularly sensitive to nutrient enrichment (Phillips et al. 2008). Furthermore, because they generally have a higher

sediment area to water volume ratio than large lakes, processes such as denitrification, leading to N loss as N_2 or N_2O , or release of nutrients from the sediment into the water, especially P, are likely to be particularly influential, potentially shifting the likelihood of P limitation toward co-limitation or N limitation, as may the recent finding that N limitation tends to increase with trophic state (Scott et al. 2019).

Study sites

The meres of the North-West Midlands in the United Kingdom lie on the Shropshire–Cheshire Plain in the West Midlands of England (Reynolds 1979). Geologically, the plain comprises Carboniferous limestones, grits, and shales around the perimeter and Triassic sandstones and marls in the centre. However, most of these rocks lie beneath glacial drift deposited during the Pleistocene glaciation, comprising boulder clay, sands, and gravels. They have a complicated hydrology often dominated more by groundwater than by surface water (Reynolds 1979), and at least some are believed to be chronically nutrient rich as a result of efficient retention of nutrients (Fisher et al. 2009).

Methods

Data sources and analysis

Data were compiled from 3 major sources. A substantial report (Moss et al. 1992) based on data collected every 3 weeks in 1991 and 1992 provided background information on each site. Approximately monthly water chemistry data from the Environment Agency (UK), collected between 2005 and 2009, apart from at Berrington Pool where the data derived from 1995 to 1998, provided the main data analysed. Contemporary monthly data from 2014 to 2018 from the Environment Agency were also analysed to determine current ecological conditions.

TP and total nitrogen (TN) were determined colorimetrically after persulphate digestion. Soluble reactive phosphorus (SRP), ammonium (NH_4-N), and total oxidised nitrogen (TON) were measured by colorimetric analysis after filtration through $0.45\ \mu m$ filters. Chl-*a* was measured spectrophotometrically after filtration onto Whatman GF/C filters and extraction with cold acetone. Details of these methods are available online (<http://www.standingcommitteeofanalysts.co.uk/archive/librarylist.html>). TP data were only used from January 2008 when the detection limit improved to $3\ \mu g\ L^{-1}$, apart from the earlier data from Berrington Pool where the detection limit was $20\text{--}50\ \mu g\ L^{-1}$ and most values were above it. Concentrations reported at the detection

limit were halved in value. Missing data for a few sites were estimated from relationships derived from the other sites. Mean depth where unknown was estimated from a power regression: mean depth (m) = $0.324 \times \text{maximum depth (m)}^{0.712}$; $R^2 = 0.90$. Mean retention time where unknown was estimated from a power regression: retention time (y) = $0.132 \times (\text{lake volume (m}^3\text{)}/\text{catchment area (m}^2\text{)})^{0.730}$; $R^2 = 0.83$. Only one site, Aqualate Mere, had retention time estimated using an estimated mean depth. Four meres (Betley, Chapel, Cop, and Hatch) lacked TN data. At these sites, TN (mg L^{-1}) was estimated from a linear regression between dissolved inorganic nitrogen (DIN) and TN: $\text{TN (mg L}^{-1}\text{)} = \text{DIN (mg L}^{-1}\text{)} \times 0.97 + 1.03$; $R^2 = 0.89$.

Several approaches were used to diagnose nutrient limitation to account for different aspects of limitation and the use of both seasonal and annual measures. Data were analysed seasonally because the ratios represent different things in each season. For example, ratios in winter represent the balance of supply when biological demand is low while ratios in summer represent potential limitation during the growing season. For seasonal analyses, the data were divided into meteorological seasons: winter is December to February, spring is March to May, summer is June to August, and autumn is September to November.

Nutrient ratios

Redfield (1958) showed that, on average, marine algae require N and P in a molar ratio of about 16:1 (7.2:1 by weight). The N:P ratio has been used to identify nutrient limitation (e.g., OECD 1982). However, its interpretation is complicated by different algal groups varying in their nutrient requirements (Ho et al. 2003); uncoupling of concentration from limitation at high, saturating concentrations so ratios are no longer relevant (Reynolds 1999); unavailability of some forms of the total nutrient (Axler et al. 1994); luxury uptake of nutrients (Mackereth 1953); and the ability to exploit dissolved organic nutrients (Bronk et al. 2007) or N gas in the case of N-fixing organisms (Vitousek et al. 2002). To assess nutrient availability, we used concentrations of readily bioavailable inorganic nutrients: SRP and DIN comprising TON (nitrate plus nitrite) and ammonium. N limitation was considered probable when molar N:P < 10 and P limitation when N:P > 20. Potential co-limitation was indicated by intermediate ratios.

Seasonal nutrient minima

Ratios do not necessarily indicate limitation, especially in lakes like meres where nutrient concentrations can be extremely high. A more reliable measure of potential

limitation can be obtained from the nutrient concentrations themselves (SRP and DIN or TON) and how they change seasonally. P limitation is possible in months when $\text{SRP} < 10 \mu\text{g L}^{-1}$, and N limitation is possible in months when $\text{DIN} < 0.1 \text{mg L}^{-1}$ (Maberly et al. 2002). Concentrations of $\text{NH}_4\text{-N}$ were not available at all dates at 5 meres, and so on these occasions DIN is an underestimate when based only on TON, although TON was the dominant form of DIN. Limitation was assigned when concentrations fell below the thresholds.

Chlorophyll a to nutrient ratios

The efficiency of conversion of nutrients to Chl-*a* is a potential measure of nutrient limitation. The ratio of Chl-*a* to a limiting nutrient tends to be high when the nutrient is limiting because that nutrient is in demand. The ratio will be lower when the nutrient is in excess because production is controlled by other limiting factors. No objective cut-off exists to separate nutrient limitation from nutrient sufficiency, but here we used a ratio of $>0.3 \text{mg Chl-}a \text{ mg}^{-1} \text{TP}$ to indicate P limitation and a ratio of $>0.042 \text{mg Chl-}a \text{ mg}^{-1} \text{DIN}$ to indicate N limitation based on an assessment of the relationship between Chl-*a* to nutrient ratio and nutrient concentration (Maberly and Carvalho 2010). Because a low ratio could result from a multitude of reasons, lakes with low Chl-*a* to TP or Chl-*a* to DIN ratios were not allocated to a nutrient limitation category in the “consensus” summary.

Stoichiometric modelling: Metabolake

The stoichiometric approach outlined by Reynolds and Maberly (2002) is based on the relative amount of energy and different material resources needed to produce new algal biomass. The supportive capacity of each potentially limiting resource is defined by the theoretical biomass yield in terms of phytoplankton carbon or Chl-*a*, assuming standard stoichiometric compositional ratios of healthy algal cells. Working through these in turn, the smallest yield is produced by the resource most likely to control local maxima of the phytoplankton, an application of “Liebig’s Law of the Minimum” (see Reynolds and Maberly 2002 for more details). The maximum concentration of phytoplankton Chl-*a* that could be supported by the available P was estimated from the mean Chl-*a* concentration in January and February plus the Chl-*a* concentration calculated from the concentration of SRP in these months: $\text{Chl-}a = \text{Jan-Feb Chl-}a + (6.32 [\text{SRP}]^{0.585})$ (concentrations in $\mu\text{g L}^{-1}$). The maximum concentration of phytoplankton Chl-*a* that could be supported by the N available was estimated

from the mean Chl-*a* concentration in January and February plus the Chl-*a* concentration calculated from the concentration of DIN in these months: $\text{Chl-}a = \text{Jan-Feb Chl-}a + ([\text{DIN}]/0.11)$. Light limitation was estimated using the equations in (Reynolds 1992) based on a photosynthesis to respiration ratio of 15, a photon flux I_k for the onset of saturation of photosynthesis of $20 \mu\text{mol m}^{-2} \text{s}^{-1}$, lake depth, a Chl-*a* specific attenuation coefficient of $0.01 \text{ m}^2 \text{ mg}^{-1} \text{ Chl-}a$, and a background attenuation of 0.5 m^{-1} for lakes designated as “clear” (clear lakes defined as having a colour $<30 \text{ mg L}^{-1} \text{ Pt}$) and 1.5 m^{-1} for lakes designated as “humic” (Table 1), a day length of 12 h, and a maximum daytime photon irradiance at the surface of $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Although Metabolake can also estimate the phytoplankton carrying capacity based on silica, this method was not implemented here because it only applies to diatoms that typically compose $\sim 20\%$ of the phytoplankton at these sites (Moss et al. 1992).

Consensus nutrient limitation

All sites where seasonal nutrient minima did not fall below the threshold concentrations for P or N were scored as having no nutrient limitation. At the other sites, the most frequent result from the 4 different approaches was used to allocate the site to a nutrient limitation type. At 4 sites with a tie for 2 types of limitation, the seasonal nutrient minimum assessment was judged to be the most direct assessment.

Ecological status and the Water Framework Directive

The European Water Framework Directive (WFD; European Commission 2000) requires Member States to achieve good ecological status in all surface waters. Good status is based on biological quality elements, including phytoplankton for lakes. Standards for supporting physicochemical elements, including nutrient conditions, should be set to support good ecological status. The United Kingdom has developed a lake phytoplankton classification tool (PLUTO; WFD UKTAG 2014) that includes a Chl-*a* metric, together with taxonomic and cyanobacterial biomass metrics. In this analysis, we used the Chl-*a* metric alone as an indicator of status, although it produces a less certain result (and usually a slightly higher status) than the full classification tool (WFD UKTAG 2014). TP standards have been set on a site-specific basis (WFD UKTAG 2008). Type-specific TN standards (based on lake depth and humic type), developed but not yet officially adopted for formal reporting purposes (WFD UKTAG 2019), were used

here. More information on WFD environmental standards and classification methods is available at the UKTAG website (www.wfduk.org).

Results

Site characteristics

The 17 meres in this study are small, with areas 2.5–59 ha, and generally shallow, with maximum depths 1–27.5 m and mean depths 0.3–13.6 m (Table 1). Generally, their water has a high ionic strength with a median conductivity of $474 \mu\text{S cm}^{-1}$. Excluding Oak Mere where the alkalinity is $0.03 \text{ mequiv L}^{-1}$ and Bomere Pool where it is $0.56 \text{ mequiv L}^{-1}$, the water is hard with an overall median alkalinity of $2.45 \text{ mequiv L}^{-1}$. These sites are nutrient-rich with a median TP concentration of $163 \mu\text{g L}^{-1}$ and DIN concentration of $980 \mu\text{g L}^{-1}$, and productive with a median annual Chl-*a* concentration of $25 \mu\text{g L}^{-1}$ (Table 1) and a median maximum Chl-*a* concentration of $76 \mu\text{g L}^{-1}$.

Limitation assessed from nutrient ratios

Seasonal and annual ratios of DIN to SRP were used to assess nutrient limitation. For the historic period, the ratios ranged ~ 3000 -fold, from 0.4 in White Mere in summer to 1229 in Hatch Mere in spring (Table 2). P limitation was indicated in 53% of the combinations of season and mere (Table 2) and was more frequent in winter and spring, whereas N limitation was indicated on 20% of occasions and was more frequent in summer and autumn; intermediate ratios, perhaps indicating potential co-limitation, occurred on 27% of occasions. The summary limitation was based on the most frequent limitation between spring and autumn, and co-limitation was also assigned when co-, P, and N limitation occurred in the 3 seasons. Using this approach, P limitation was detected at 7 sites, N limitation at 4 sites, and co-limitation at 6 sites.

Limitation assessed from nutrient concentrations

Because a nutrient ratio may not indicate nutrient limitation when concentrations are high, we also analysed seasonal changes in absolute concentrations. At White Mere (Fig. 1), SRP (as P) was always substantially higher than 0.01 mg L^{-1} , the notional concentration for the onset of P limitation, while concentrations of DIN and TON (as N) fell below the equivalent concentration for N limitation of 0.1 mg L^{-1} during summer and autumn. These results indicate this site is potentially N limited during the bulk of the growing season. By contrast, Hatch Mere concentrations of DIN and TON substantially exceeded

Table 1. Summary characteristics for the 17 meres in this study. Annual mean conductivity and alkalinity derived largely from Moss et al. (1992) and nutrient chemistry from the Environment Agency (2005–2009), apart from Berrington Pool (1995–1998). Mean depth and retention times in parentheses are calculated (see methods).

Site	Elevation (m)	Lake area (ha)	Catchment area (km ²)	Max depth (m)	Mean depth (m)	Mean retention (y)	Conductivity (µS cm ⁻¹)	Alkalinity (mequiv L ⁻¹)	TP (µg L ⁻¹)	DIN (µg L ⁻¹)	Chl- <i>a</i> (µg L ⁻¹)	WFD category	WFD humic type
Aqualate Mere	67	59	58	1.0	(0.3)	(0.07)	610	3.59	250	6820	25	HAVS	H
Berrington Pool	78	2.5	0.36	12.2	6.7	(2.1)	392	1.80	180	1020	20	HAS	—
Betley Mere	58	9.3	8.3	1.8	(0.6)	0.07	659	3.93	480	2180	74	HAVS	H
Betton Pool	75	6.4	1.3 ^a	10.9	3.6	1.9	231	2.14	60	450	11	HAS	C
Bomere Pool	75	10.3	1.3 ^a	15.2	5.1	4.5	120	0.56	40	220	23	MAS	C
Chapel Mere	88	6.5	2.4	2.4	(0.8)	0.15	721	4.68	300	1030	25	HAVS	H
Cole Mere	88	28	1.7	11.5	3.3	1.3	239	1.49	130	330	25	HAS	C
Comber Mere	78	51.5	8.1	11.8	(4.6)	1.7	513	3.00	190	980	31	HAS	C
Cop Mere	88	16.8	13.6	2.7	1.0	0.08	457	2.95	163	3490	9	HAVS	C
Croze Mere	88	15.2	3.6	9.3	4.8	(2.3)	474	3.05	110	610	25	HAS	C
Hatch Mere	76	4.7	2.2	3.8	(1.4)	0.4	484	2.36	70	3180	44	HAVS	PH
Oak Mere	73	22.9	3.5	5.6	2.0	0.8	187	0.03	80	200	29	LAVS	—
Rostherne Mere	27	48.7	10	27.5	13.6	1.1–3.4	474	2.65	180	960	30	HAS	C
Tabley Mere	32	19.4	8.1	4.4	(1.6)	0.33	701	2.45	350	1950	92	HAVS	H
Tatton Mere	46	31.7	5.5	11.0	(4.2)	0.88	518	2.60	160	410	17	HAS	C
The Mere	42	15.8	3.8	8.1	2.8	0.5	523	1.51	70	1090	28	HAVS	H
White Mere	96	25.5	0.93	13.8	4.4	(4.0)	309	1.88	470	360	32	HAS	C
Median	75	16.8	3.8	9.3	3.3	1.25	474	2.45	163	980	25	—	—

Sites are designated for the Water Framework Directive (WFD): LA = low alkalinity (<0.2 meq L⁻¹); MA = moderate alkalinity (0.2–1.0 meq L⁻¹); HA = high alkalinity (>1.0 meq L⁻¹); S = shallow (3–15 m mean depth); VS = very shallow (<3 m mean depth); C = clear (≤30 mg L⁻¹ of Pt); H = humic (>30–90 mg L⁻¹ of Pt); PH = polyhumic (>90 mg L⁻¹ of Pt); — = missing or not appropriate.

Table 2. Nutrient limitation of phytoplankton in the historic period assessed using seasonal and annual molar ratios of DIN:SRP. Ratios <10 indicating potential N limitation are shaded gold, ratios >20 indicating potential P limitation are shaded blue, and intermediate ratios indicating potential co-limitation are shaded grey. The summary in the final column is based on the limitation in spring, summer, and autumn (for colour version, please see online article).

Site	Winter	Spring	Summer	Autumn	Annual	Summary
Aqualate Mere	134	181	39	44	75	P-limited
Berrington Pool	37	13	16	20	24	Co-limited
Betley Mere	95	56	4	19	28	Co-limited
Betton Pool	39	80	22	14	31	P-limited
Bomere Pool	46	29	31	12	29	P-limited
Chapel Mere	36	46	1	3	9	N-limited
Cole Mere	17	12	4	8	11	N-limited
Comber Mere	17	30	12	8	15	Co-limited
Cop Mere	83	273	18	33	53	P-limited
Crose Mere	54	121	62	27	50	P-limited
Hatch Mere	170	1229	543	222	344	P-limited
Oak Mere	22	24	11	9	17	Co-limited
Rostherne Mere	15	18	19	13	16	Co-limited
Tabley Mere	73	68	3	18	24	Co-limited
Tatton Mere	14	12	2	4	8	N-limited
The Mere	71	324	223	49	102	P-limited
White Mere	4	2	0.4	1	2	N-limited

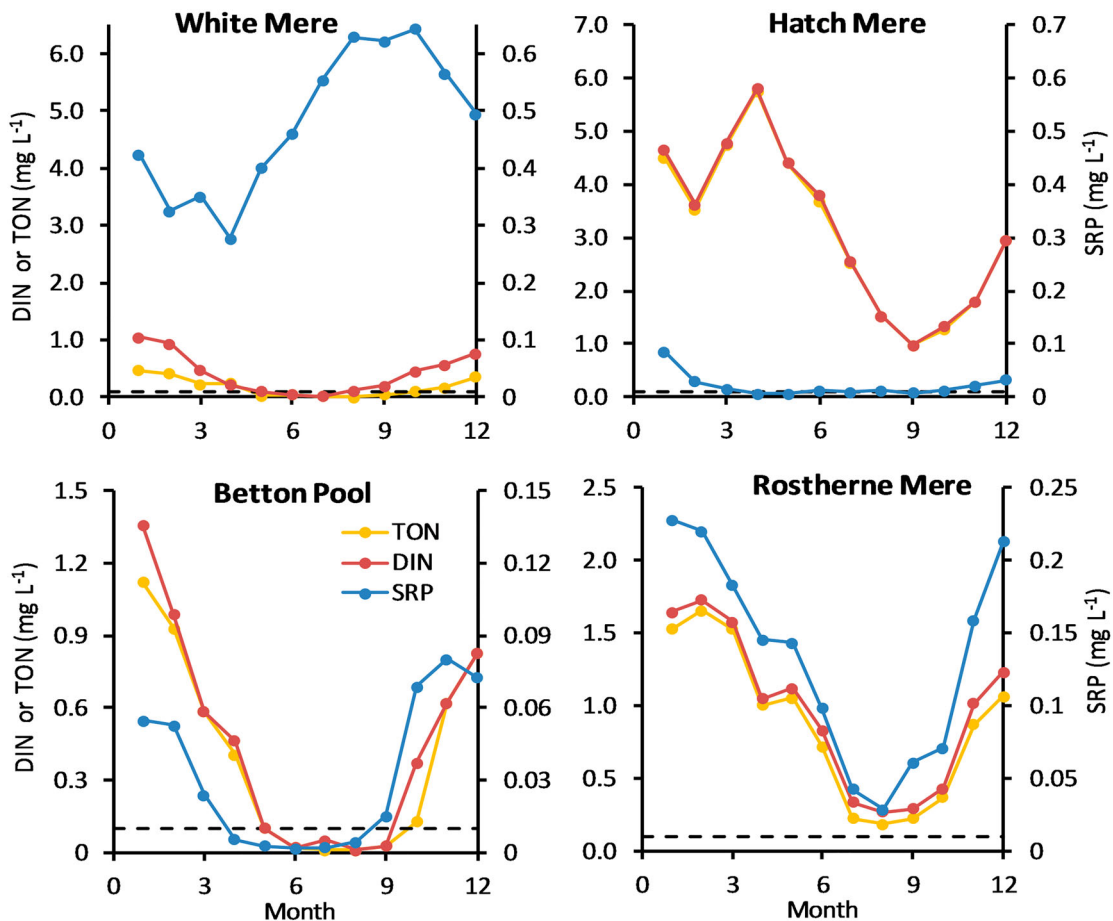


Figure 1. Seasonal changes in nutrient concentration in 4 meres with contrasting nutrient availability. The horizontal dashed line represents potentially limiting concentrations for N (0.1 mg L⁻¹) and P (0.01 mg L⁻¹). Data based on monthly means between 2005 and 2009.

Table 3. Nutrient limitation of phytoplankton in the historic period based on nutrient concentrations and Chl-*a* to nutrient ratios. For concentration, the number of months are shown when TON, DIN, or SRP are below a potentially limiting threshold concentration of 0.001 mg L⁻¹ for P and 0.1 mg L⁻¹ for N. For the Chl-*a* ratio, the number of months when the Chl-*a*:TP ratio is >0.3 mg mg⁻¹ and when the Chl-*a*:TN ratio is >0.042 mg mg⁻¹. For each, the summary limitation requires more than 1 month to fall below the nutrient concentration or ratio threshold. N = N limitation, None = no nutrient limitation, P = P limitation, Co = Co-limitation.

Site	Concentration			Summary	Chl- <i>a</i> :nutrient ratio		
	TON	DIN	SRP		Chl- <i>a</i> :TP	Chl- <i>a</i> :TN	Summary
Aqualate Mere	0	0	0	None	2	0	P
Berrington Pool	0	0	0	None	0	0	None
Betley Mere	0	0	0	None	1	1	Co
Betton Pool	4	4	5	Co	5	0	P
Bomere Pool	8	5	6	Co	10	1	Co
Chapel Mere	1	1	1	Co	3	1	Co
Cole Mere	6	3	0	N	5	1	Co
Comber Mere	2	0	0	N	4	3	Co
Cop Mere	0	0	0	None	1	0	P
Croze Mere	2	1	5	Co	5	0	P
Hatch Mere	0	0	4	P	12	0	P
Oak Mere	6	3	0	N	10	2	Co
Rostherne Mere	0	0	0	None	4	4	Co
Tabley Mere	0	0	0	None	3	5	Co
Tatton Mere	4	2	0	N	2	1	Co
The Mere	2	1	6	Co	7	1	Co
White Mere	6	2	0	N	0	2	N

the limitation threshold, but SRP concentrations were at the P limitation threshold for many months during the growing season, indicating that P limitation is likely. At Betton Pool, both N and P seemed to be limiting during the growing season, indicating co-limitation, and at Rostherne Mere, neither N nor P seemed to be limiting. Analysis of the 17 sites where suitable data are available suggests that P limitation occurred at one site, N limitation at 5 sites, co-limitation at 5 sites, and no nutrient limitation at 6 sites (Table 3).

Limitation assessed from chlorophyll *a* to nutrient ratios

Lakes where the ratio of Chl-*a* to TP is high are potentially P limited because the conversion of TP to Chl-*a* is efficient. Based on these ratios, 5 sites were classified as P limited, 1 site as N limited, 10 sites as co-limited, and 1 site as not nutrient limited (Table 3).

Limitation assessed using Metabolake

Calculations using Metabolake suggest that light is not an important limiting factor except at Rostherne Mere, although here strong summer stratification is likely to minimise or overcome light limitation (Reynolds and Bellinger 1992; Fig. 2a). Thirteen meres were diagnosed as P limited, 1 (White) as N limited, and 3 (Cole, Oak, and Tatton) as co-limited (Fig. 2b).

Nutrient limitation consensus

The overall consensus nutrient limitation (see methods) recorded 6 sites with no nutrient limitation, 5 with co-

limitation, and 3 each with N or P limitation (Table 4). Seasonal patterns of nutrient and Chl-*a* concentrations helped explain these allocations (Fig. 3). At P-limited sites, the concentration of SRP was lower in all seasons than in sites with other types of limitation. Conversely, the concentration of DIN was lower in N-limited sites than in sites with other types of limitation. For both SRP and DIN, these differences were greater during summer than at other times of the year, and nutrient concentrations of the second nonlimiting nutrient (i.e., N in P-limited sites and P in N-limited sites) were substantially higher in all months while co-limited sites had intermediate concentrations. Sites without nutrient limitation had high concentrations of SRP and DIN in all months. The seasonality of the TN:TP ratio generally declined during the growing season in all types of limitation and was lowest in summer and increased in autumn and winter. Seasonal patterns of Chl-*a* to TP and TN showed broad seasonal peaks of high ratios between about March and October, the growing period, and the expected greater production of Chl-*a*:TP in P-limited sites and Chl-*a*:TN in N-limited sites. Despite the differences in nutrient availability and limitation, the seasonality of phytoplankton Chl-*a* was similar, apart from a large spring bloom in the sites with no nutrient limitation, and these sites had the highest concentration of Chl-*a* in 7 of the 12 months.

Status and targets

The thresholds between different status levels for concentrations of Chl-*a*, TP, and TN are reported for each of the 17 meres (Supplementary Table S1). The status for each mere was recorded based on the data analysed

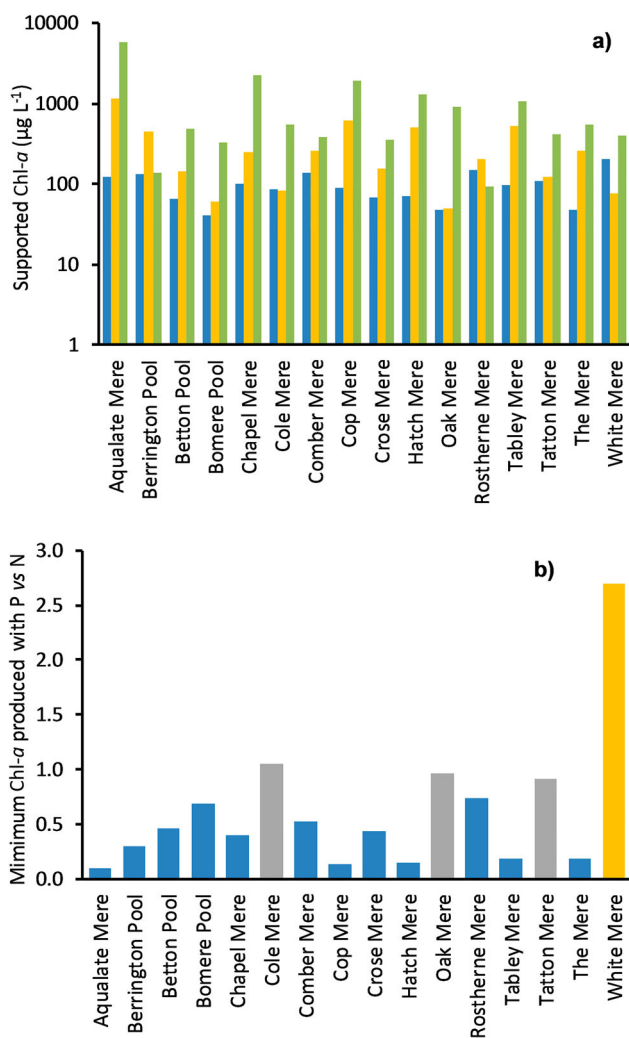


Figure 2. Nutrient limitation based on calculations using Metabolake. (a) Amount of phytoplankton as Chl- α that can be supported by availability at the start of the year of P (blue), N (gold), or by light (green). (b) Ratio of minimum amount of Chl- α produced based on P vs. N, showing P limitation (blue), N limitation (gold), or co-limitation (grey). SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, TON = total oxidised nitrogen (for colour version, please see online article).

here from before 2010 and for the contemporary period from 2014 to 2018 (Fig. 4). For both time periods, the ecological status, based solely on Chl- α , was on average better than those based on nutrients (Fig. 4), although use of Chl- α alone without taking phytoplankton composition into account is likely less stringent than the approved WFD approach. Two lakes were at high or good status in the historic period for Chl- α while no lakes were at or above good status based on TP, and only one lake for N. Changes in status for the 2 time periods were relatively small. Based on Chl- α , the number of lakes at high or good status increased to 4 in the contemporary period, and the number of lakes at poor or bad status decreased from 9 to 8. The number of lakes in

Table 4. Summary of nutrient limitation based on different approaches. Nutrient limitation shown as P = P limitation, N = N limitation, Co = co-limitation, None = no nutrient limitation or not determined. The consensus was produced at each site by scoring limitation as “none” based on seasonal minima and using the most frequent limitation based on all criteria at the other sites and using the seasonal minimum for a tie (see methods).

Site	Seasonal minima	Chl- α :TP or Chl- α :DIN	N:P	Metabolake	Overall consensus
Aqualate Mere	None	P	P	P	None
Berrington Pool	None	None	Co	P	None
Betley Mere	None	Co	Co	P	None
Betton Pool	Co	P	P	P	P
Bomere Pool	Co	Co	P	P	Co
Chapel Mere	Co	Co	N	P	Co
Cole Mere	N	Co	N	Co	N
Comber Mere	N	Co	Co	P	Co
Cop Mere	None	P	P	P	None
Crose Mere	Co	P	P	P	P
Hatch Mere	P	P	P	P	P
Oak Mere	N	Co	Co	Co	Co
Rostherne Mere	None	Co	Co	P	None
Tabley Mere	None	Co	Co	P	None
Tatton Mere	N	Co	N	Co	N
The Mere	Co	Co	P	P	Co
White Mere	N	N	N	N	N

poor or bad status was reduced by 1 based on TP and reduced by 2 based on TN over the 2 time periods.

The reduction in nutrient concentration needed to reach good ecological status differed depending on the nutrient limitation in each mere. Unsurprisingly, less P would need to be removed from P-limited lakes to reach good ecological status than from N-limited lakes (Fig. 5a). Conversely, less N would need to be removed from P-limited lakes. To quantify this further, based on the contemporary period, at N-limited sites the mass-based ratio of TN to TP to reach good ecological status was 3.2, 0.4 times the mass-based Redfield ratio, while at P-limited sites the TN:TP ratio was 69, 9.5 times the mass-based Redfield ratio. An obvious corollary of this is that the amount of P removal needed would be much higher at sites with bad P status compared to sites at moderate status (Fig. 5c); the same pattern occurs when comparing bad versus moderate sites for N (Fig. 5d). While this result is not surprising, it highlights the benefit of knowing the nature of nutrient limitation to manage a site effectively.

Discussion

Approaches to diagnose nutrient limitation

The diagnostic method used to identify the primary limiting nutrient tended to vary with the approach, dependent in part on the extent that seasonal variation was

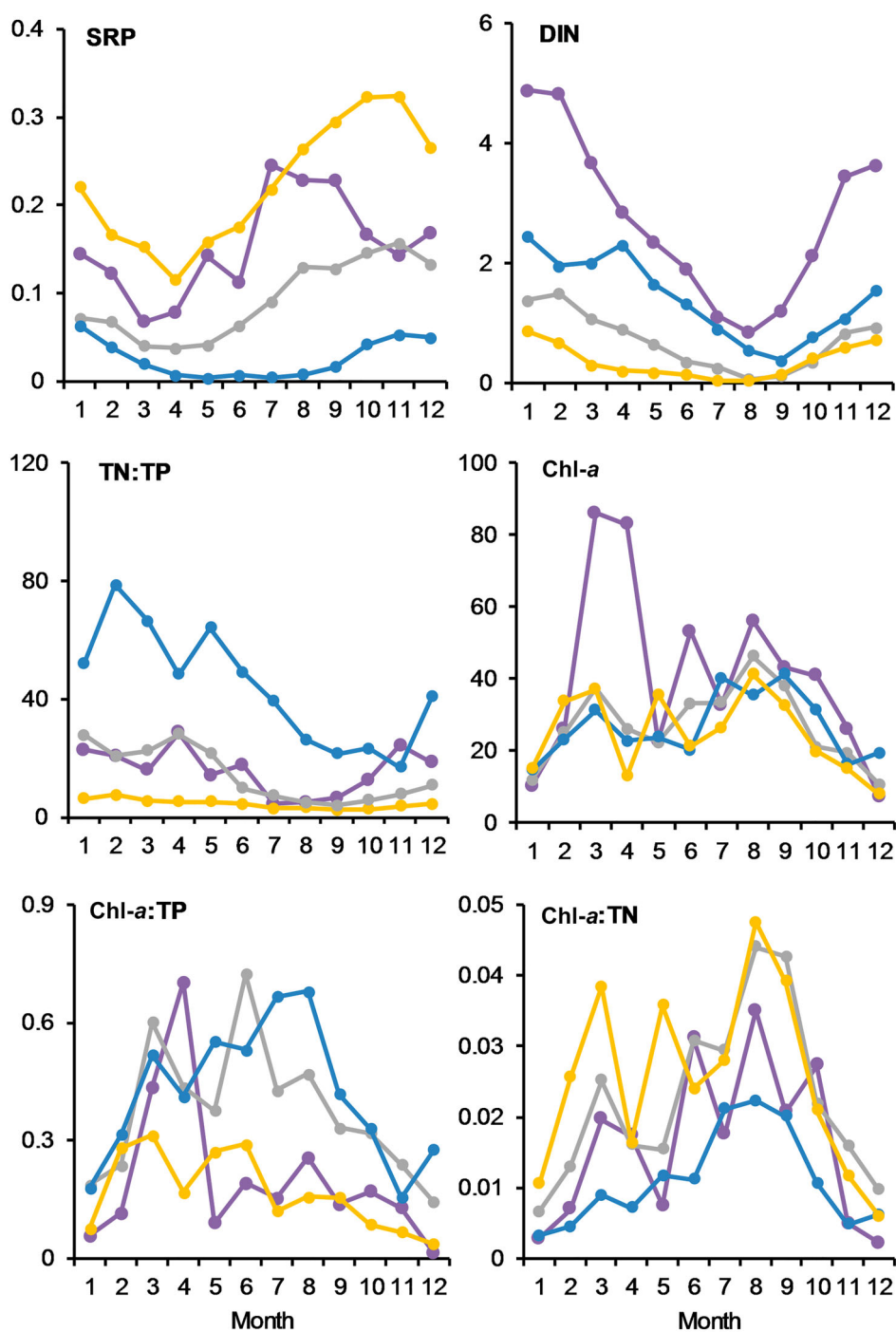


Figure 3. Contrasting seasonal changes in concentrations and ratios for sites with different types of nutrient limitation, based on monthly averages for the historic period. SRP (mg L^{-1}); DIN (mg L^{-1}), Chl-*a* ($\mu\text{g L}^{-1}$), other reported as mass ratios. Co-limited (grey, 5 sites), N limited (gold, 3 sites), P limited (blue; 3 sites), and no limitation (purple, 6 sites) (for colour version, please see online article).

taken into account. For example, the Metabolake approach had the lowest agreement with the consensus nutrient limitation. However, it estimates nutrient limitation using winter concentrations of nutrients, which may be appropriate for large lakes with relatively long retention times but probably less so for small shallow lakes with short retention times and a large sediment

area to water volume ratio that show extremely large changes in nutrient concentration over a year. Compared to the consensus, the N:P method and the Chl-*a* to nutrient ratio method frequently agreed with the consensus, and indeed nutrient concentrations at the start of the year were strongly linked to the type of nutrient limitation (Fig. 3). Direct and relatively time-consuming lake

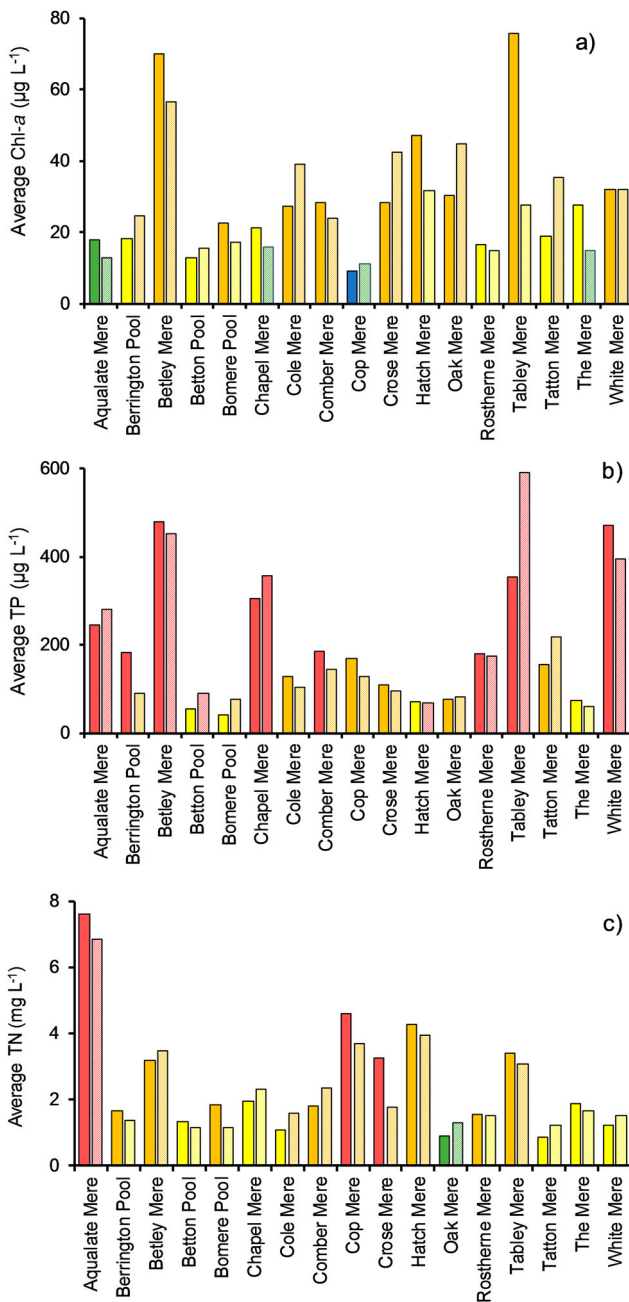


Figure 4. Annual average Water Framework directive ecological status. (a) Phytoplankton Chl-*a* based on a geometric mean, (b) total phosphorus (TP), and (c) total nitrogen (TN), for the 17 meres in the period before 2010 (solid colour) and 2014–2018 (horizontal hatching). Status shown as high (dark blue), good (green), moderate (yellow), poor (orange), and bad (red) (for colour version, please see online article).

enrichment experiments, such as bioassays in the laboratory or use of nutrient diffusing substrates in the field (e.g., Fairchild et al. 1985, Maberly et al. 2002), have limitations but are best for determining which nutrients limit the algal population. In their absence, the approaches used in this study represent a practical and relatively robust method to estimate nutrient limitation

using routinely monitored determinands. In particular, compared with using just N:P ratios, the approach using actual concentrations of bioavailable N and P, in relation to potential limitation thresholds, offers a more realistic and visual indication of the different forms of limitation over the whole growing season (Fig. 1). More modern and rapid techniques such as nutrient-induced fluorescence transients may provide promising future approaches to identify nutrient limitation (Beardall et al. 2001, Spijkerman et al. 2016).

Environmental factors controlling nutrients and nutrient limitation

The environmental factors that control phytoplankton abundance include those that promote growth rates such as light and nutrient concentrations and those that control loss rates such as sinking, grazing by zooplankton, and hydraulic flushing (Reynolds 1984). The 17 meres studied are generally nutrient rich and can support large populations of phytoplankton. Sites that were not nutrient limited had seasonally high nutrient concentrations and a low ratio of Chl-*a* to total P and N. Some of these sites have large catchment areas and relatively short retention times, suggesting that phytoplankton biomass may be limited by the high rate of flushing because retention times of 0.07–0.08 years are likely short enough to reduce phytoplankton populations while resupplying nutrients from the catchment. At other sites, such as Rostherne Mere with a long retention time, substantial internal loading can occur when stratification breaks down and the long retention time permits elevated concentrations to persist into the growing season (Radbourne et al. 2019). N limitation may become more prevalent as trophic state increases (Elser et al. 2007, Paerl et al. 2016, Scott et al. 2019). However, in the lake we studied, which had a relatively limited trophic range (annual mean Chl-*a* = 9–92 µg L⁻¹), we found no significant differences in annual mean Chl-*a* among limitation types (ANOVA, $p = 0.60$).

Although N limitation is becoming recognised as more widespread than hitherto thought (Elser et al. 2007), in the case of the meres, the frequently high concentrations of TP, originally attributed to input from glacial deposits (Reynolds 1979) but more recently to high rates of internal recycling of TP (Carvalho and Moss 1995, Kilinc and Moss 2002), coupled with potential loss of N to the atmosphere through denitrification, will tend to favour N limitation. This trend was reflected in the analysis: an equal number of meres were N limited and P limited, and many were co-limited.

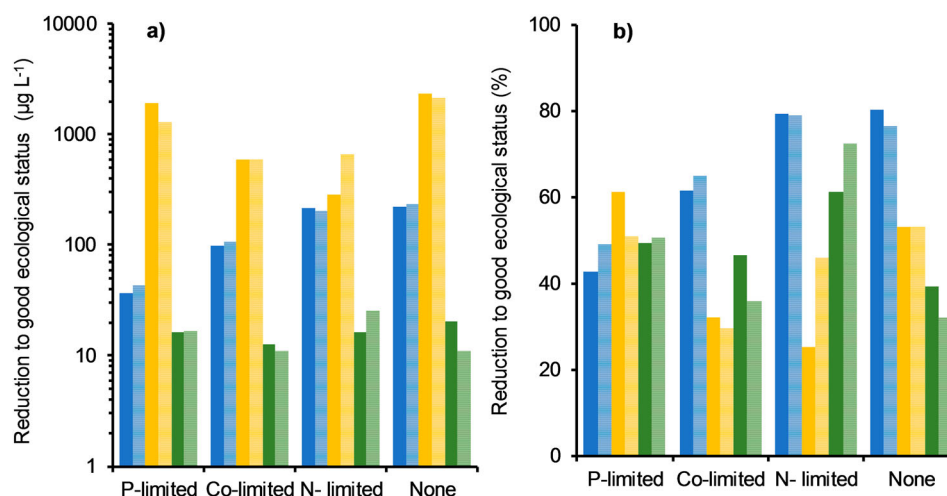


Figure 5. Reduction in concentration of P, N, or Chl-*a* required to meet good ecological status. Sites are aggregated according to their overall consensus nutrient limitation in Table 4. Reduction given as (a) concentration on a log scale, or (b) percent of current concentration. Values are based on total phosphorus (blue), total nitrogen (orange), and Chl-*a* (green). Values before 2010 in solid colour, those from 2014–2018 with horizontal hatching (for colour version, please see online article).

Implications of nutrient limitation status and management

Site-specific Water Framework Directive TP targets for the meres at the good/moderate boundary range from 22 to 56 $\mu\text{g L}^{-1}$ (Supplementary Table S1). Proposed type-specific standards for TN range from 0.77 to 1.46 mg L^{-1} , a 26–35-fold higher concentration on a mass basis, well in excess of the Redfield ratio of N to P. A recent controversy concerns how to manage nutrient enrichment in lakes and whether just P or both N and P should be targeted (Howarth and Paerl 2008, Schindler et al. 2008, Schindler and Hecky 2008, Paerl et al. 2014, Hamilton et al. 2016). One reason for focusing on P rather than N is the belief that N fixation by certain cyanobacteria may allow an escape from N limitation (Schindler 1977). However, evidence is growing that N fixation is inadequate to overcome N limitation (Shatwell and Kohler 2019, van Gerven et al. 2019). A Policy Forum Review in Science concluded that amelioration of the negative impacts of nutrient enrichment should be made by control and reduction of both N and P (Conley et al. 2009); more recent work supports this contention (Lewis et al. 2011, Paerl et al. 2016, Wurtsbaugh et al. 2019). Recent considerations on the Water Framework Directive (Poikane et al. 2019) also recognise the importance of considering N as well as P reduction. Although seemingly counterintuitive, sites failing P targets (high P) might be most effectively managed by reducing N, evidenced by our finding that the phytoplankton are most likely to be N limited, and those failing N targets (high N) may be best managed by reducing P, evidenced by our finding that the

phytoplankton are most likely to be P limited. Managing N loads may provide additional benefits as well, with evidence that lower nitrate levels lead to increased species richness of macrophytes (James et al. 2005). For shallow plant-dominated lakes, like many of the meres, nutrient management for plants may therefore require a different perspective than management in deeper lakes dominated by planktonic communities.

Much effort has been exerted within the region to reduce diffuse inputs of nutrients from the land, yet disappointingly little improvement was realized in ecological quality in 2014–2018 compared to the data from before 2010, further highlighting the high degree of inertia in the ecological status of many lakes (Carpenter 2005, European Environment Agency 2018). This inertia results in part from “legacy P” stored in the sediment over many decades because of high loading and the lack of a gaseous loss to the atmosphere. For many of the chronically enriched meres, much more substantial nutrient reductions, and time, will be required to bring them to good ecological status. This target may be impossible to achieve because the concentrations of TP at the good–moderate boundary are generally lower than the inferred TP concentrations from ca. 1850, which range between 31 and 50 $\mu\text{g L}^{-1}$ (McGowan 1996, Brooks et al. 2001). The higher mobility of N, and because it can be lost to the atmosphere in different forms, provides an opportunity to control lake nutrient enrichment by aggressive reductions in N loading. This regional study is typical of the challenges facing nutrient management in well-established agricultural landscapes, but it also highlights how a greater understanding of nutrient limitation may help achieve success.

Acknowledgements

This paper is dedicated to Brian Moss for his inspirational teaching, lucid and thought-provoking talks, and scientific insights, especially on the ecological consequences of nutrient enrichment in small lakes. We thank the Reviewers for their helpful comments.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The work was partly funded by Natural England and was supported by Natural Environment Research Council, Hydro-scape Project: Grant Number NE/N00597X/1.

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