



## Estimating nutrient thresholds for eutrophication management: Novel insights from understudied lake types



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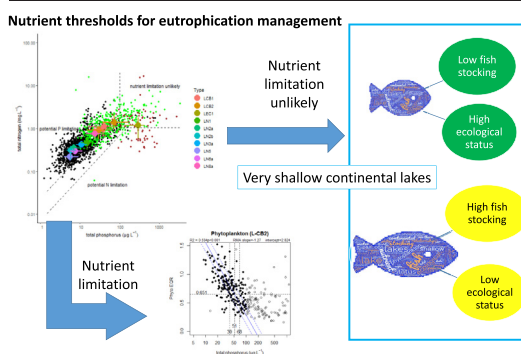
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### HIGHLIGHTS

- Nutrient concentration thresholds based on pressure-response models are needed for management.
- Nutrient thresholds were derived from relationships of phytoplankton and macrophytes against nutrients.
- Very shallow eastern continental lakes do not demonstrate a strong response to nutrients.
- Fish stocking is the dominant pressure in these highly eutrophic shallow lakes.
- These understudied lakes challenge the dominant paradigm of lake assessment and management.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Nutrient targets based on pressure-response models are essential for defining ambitions and managing eutrophication. However, the scale of biogeographical variation in these pressure-response relationships is poorly understood, which may hinder eutrophication management in regions where lake ecology is less intensively studied. In this study, we derive ecology-based nutrient targets for five major ecoregions of Europe: Northern, Central-Baltic, Alpine, Mediterranean and Eastern Continental. As a first step, we developed regressions between nutrient concentrations and ecological quality ratios (EQR) based on phytoplankton and macrophyte communities. Significant relationships were established for 13 major lake types; in most cases, these relationships were stronger for phosphorus than for nitrogen, and stronger for phytoplankton than for macrophytes. Using these regressions, we estimated the total phosphorus (TP) and total nitrogen (TN) concentrations at which lakes of different types are likely to achieve good ecological status. However, in the very shallow lakes of the Eastern Continental region, relations between nutrient and biological communities were weak

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or non-significant. This can be attributed to high nutrient concentrations (in the asymptotic zone of phosphorus-phytoplankton models) suggesting other factors (light, grazing) limit primary production. However, we also show that fish stocking is a major pressure on Eastern Continental lakes, negatively affecting ecological status: lakes with low fish stocking show low chlorophyll-a concentrations and good ecological status despite high nutrient levels, while the lakes with high fish stocking show high chlorophyll-a and low ecological status. This study highlights the need to better understand lakes in biogeographic regions that have been, for historical reasons, less studied. This, in turn, helps reveal factors that challenge the dominant paradigms of lake assessment and management.

## 1. Introduction

Nutrient pollution and the associated process of eutrophication affect lake ecosystems and human welfare through multiple impacts on ecosystem services. While moderate nutrient enrichment can increase biodiversity and fish production (Jeppesen et al., 2000; Persson et al., 1991), high concentrations of nutrients causes significant environmental degradation, including harmful cyanobacterial blooms, loss of submerged vegetation, hypoxic events, and periodic fish kills along with direct effects on ecosystem services, including drinking water supply and recreational uses (Bennett et al., 2001; Wurtsbaugh et al., 2019).

Since the early 1970s, scientists have linked algal blooms in lakes to increased nutrient inputs from catchments caused by human activities (Schindler, 1974). Empirical models predicting phytoplankton biomass from nutrient concentrations coupled to lake-phosphorus loading models provide a scientific basis for eutrophication management. The need to control eutrophication has led to a huge proliferation of phosphorus-chlorophyll models, most of them expressed as log–log linear regressions (Dillon and Rigler, 1974; Phillips et al., 2008) with chlorophyll-a used as a surrogate for phytoplankton biomass and total phosphorus assumed to be the key limiting nutrient in most freshwaters (Carvalho et al., 2013a). However, the relationship between phosphorus and productivity is more complex and follows resource limitation theory, which predicts that chlorophyll increases linearly only until some other factor (e.g., nitrogen, light) becomes limiting (Hutchinson, 1975; Reynolds, 1992). Therefore, if a long gradient is covered, phosphorus-chlorophyll relationships typically exhibit a sigmoidal shape (Filstrup et al., 2014; McCauley et al., 1989) with three distinct phases: (1) an initial zone with low phosphorus concentrations and low phytoplankton biomass, probably linked to low phosphorus bioavailability (Chow-Fraser et al., 1994); (2) a linear phase where chlorophyll concentrations increase rapidly with increasing TP concentrations; and (3) an asymptotic or plateau zone where phytoplankton production is controlled by other factors, e.g. nitrogen or other nutrients, light limitation due to phytoplankton self-shading and/or suspended solids (Huisman and Weissing, 1994; Reynolds, 1992) and biotic interactions such as grazing (Benndorf et al., 2002). When using load reduction as a restoration strategy, it is usually assumed that the target lake is on the linear portion of this nutrient-phytoplankton model, where a change in phosphorus concentration should generate a corresponding response in phytoplankton biomass. This type of approach, however, might not be appropriate for lakes with high phosphorus concentrations (Quinlan et al., 2021). This relates especially to shallow lowland lakes which, due to their morphometry, climate and geology (Borics et al., 2013; Robarts et al., 2005), exhibit high nutrient concentrations and are characterized as “naturally eutrophic” or even “naturally hypertrophic” (Krasznai et al., 2008).

Another caveat relates to multiple pressures. There is no doubt that eutrophication is the most widespread cause of lake degradation in Europe and worldwide. However, there are other pressures which also have severe impacts on lake ecosystems (e.g. water level fluctuations, shoreline modification, invasions of non-native species) which have been less-intensively studied (Poikane et al., 2020). One such pressure is fish stocking for recreational and commercial fishing, leading to significant negative changes to lake ecosystems through various mechanisms (Skeate et al., 2021). There is, for example, ample evidence that the effects of widely-stocked common carp interact with nutrients, causing a shift from clear macrophyte-vegetated conditions to turbid waters (Weber and Brown, 2009). Despite

this, there is a clear consensus that nutrient reduction is the most effective way to control eutrophication and mitigate its effects (Conley et al., 2009; Jeppesen et al., 2005) and, therefore, it is necessary to set nutrient targets to guide lake restoration and management, even though this presents a major challenge (Poikane et al., 2019).

In Europe, elevated concentrations of nutrients are a major reason why many European lakes are degraded (EEA, 2018). In 2000, the Water Framework Directive (2000/60/EC) (WFD; EC, 2000) mandated, among other things, a comprehensive ecological status assessment of all surface waters based on a variety of biological, hydromorphological, chemical, and physicochemical quality elements (Annex V 1.1 and V 1.2). Many of these quality elements are traditionally used for assessing lake eutrophication, in particular nutrients, phytoplankton and macrophytes. The Directive requires Member States to classify the ecological status of surface water bodies into one of five ecological status classes following common definitions. Phytoplankton and macrophyte communities at ‘good’ status are characterized by only slight changes in composition and abundance of communities compared to non-disturbed conditions and there should be no undesirable disturbance to the aquatic ecosystem (i.e. development of cyanobacteria blooms, loss of macrophyte vegetation and impairment to fisheries, EC, 2009). In recent decades, all European countries have developed approaches that follow this definition (Poikane et al., 2014a; Wolfram et al., 2009).

The WFD also required Member States to intercalibrate status class boundaries (specifically the high-good and good-moderate boundaries) for biological quality elements (BQEs) in order to ensure that the diverse assessment methods in use reflect similar ecological status and thus a shared level of ambition.

Even where anthropogenic pressures are minor, lake ecology differs, reflecting the physical, geological and chemical characteristics of their catchments, and these differences determine the response of lakes to nutrient enrichment. This recognition led to the first trophic classification of lakes in the early decades of the last century (Naumann, 1919) and also to the development of new lake typologies in recent years (Lyche Solheim et al., 2019). Combining basic hydrological and morphological characteristics of lakes such as a lake area, depth, altitude, residence time, alkalinity allows hundreds of lake types to be created. However, the need to compare and harmonise classifications among countries necessitated the formation of so-called common intercalibration types (i.e. similar lake types shared by countries) and Geographic Intercalibration Groups (i.e., groups of countries sharing common types) which reflect the climatic differences and similarities of countries and broadly corresponds with the established biogeographic regions of Europe (EC, 2011; Poikane et al., 2014b).

To deliver good ecological status the pressures affecting status must be managed. To achieve this, it is necessary to establish targets which may differ between biogeographic regions and water body types (Dolman et al., 2016; Kelly et al., 2021). Member States are required to establish threshold nutrient concentrations and use these as part of the assessment of ecological status. Unlike biological quality elements, the WFD does not require these boundary values to be compared and harmonized across Member States, but simply requires that these boundaries should be set at concentrations that support good ecological status. However, setting such boundaries is complicated, with many countries facing obstacles including short pressure gradients, confounding pressures, and weak relationships between nutrients and biology (Borics et al., 2013). Therefore, there is still uncertainty within and among countries about where critical thresholds should lie

(Poikane et al., 2019, 2021). Since many river basins are transboundary, while individual lake types are rarely confined to single Member States, there is a need to harmonise nutrient thresholds between countries lest natural differences hinder successful management.

In this study, we aim to determine nutrient (phosphorus and, where available, nitrogen) concentration thresholds which support good status for phytoplankton and, where available, macrophytes for the major lake types in Europe, by examining pressure response relationships using data collated from several European countries for the intercalibration process. These have been grouped into broad biogeographical units (“Geographic Intercalibration Groups”, subsequently referred to as “regions”) thus providing longer pressure gradients than were available in many national data sets. Additionally, as countries use different assessment methods for status assessment, we use ecological quality ratios (EQRs) derived from common metrics developed during the intercalibration process rather than national EQR values, thus removing a major source of variability. In the Eastern Continental region, where the relationships were weak or non-significant thus hindering the setting of nutrient thresholds, we explore the impact of fish stocking as angling is a popular recreational activity in these lakes.

## 2. Material and methods

### 2.1. Data and lake types

Data for mean lake TP, TN and biological status were originally collated for the intercalibration (comparison and harmonization) of phytoplankton and macrophyte assessment systems. Lakes were allocated to ecoregions (Central Baltic, Northern, Mediterranean, Alpine and Eastern Continental) consisting of countries having similar biogeophysical drivers (EC, 2011; Poikane et al., 2014b). The common lake types were delineated by their altitude, mean depth, alkalinity and other factors, as humic content for Northern region and climatic factors for Mediterranean region (Table 1; Poikane et al., 2015). All types refer to natural lakes, except Mediterranean reservoirs (“heavily modified water bodies” sensu WFD) as in this region, due to the high variety of lake characteristics, it was not possible to define common lake types (Poikane et al., 2015). Altogether, data of 4306 lake-years were collated, with higher number from Northern (2425) and Central Baltic (1363) regions.

For each region, biological status was expressed as an EQR using common metrics (for detailed description see Table 2) to express each member state's boundaries on a common scale (EC, 2011; Poikane et al., 2014b, 2015). The EQR expresses the ratio between observed values of metrics

**Table 2**

Description of phytoplankton and macrophyte common metrics. Chl-a – chlorophyll-a; BV – Biovolume; EQR - Ecological Quality Ratio, IGA – Algal Group Index; MedPTI - Mediterranean Phytoplankton Trophic Index; PTI - Plankton Trophic Index; PT<sub>OT</sub> - phytoplankton oligotrophic-eutrophic index; PTSI - Phytoplankton Taxa Lake Index.

Region	Common metrics	References
<b>Phytoplankton</b>		
Alpine	Average of national EQR values: - Multimetrics of chl-a, phytoplankton BV and Brettum index; - Multimetrics of chl-a, phytoplankton BV, algal class metrics and PTSI index; - Multimetrics of chl-a, phytoplankton BV and PT <sub>OT</sub> index;	Wolfram et al., 2014; Mischke et al., 2008 Salmaso et al., 2006
Central Baltic	Multimetrics of chl-a and PTI EQR	Phillips et al., 2013; Phillips et al., 2014
Eastern Continental	Multimetrics of chl-a, Cyanobacteria abundance and Q index	Padisák et al., 2006; Borics et al., 2018
Mediterranean	Average of national EQR values: - Multimetrics of chl-a, phytoplankton BV, Cyanobacteria BV and IGA index; - Multimetrics of chl-a, phytoplankton BV, percentage of Cyanobacteria BV and IGA index; - Multimetrics of chl-a, phytoplankton BV, Cyanobacteria BV and MedPTI index	de Hoyos et al., 2014; Pahissa et al., 2015 Marchetto et al., 2009
Northern	Multimetrics of chl-a and PTI EQR	Phillips et al., 2013; Lyche Solheim et al., 2014
<b>Macrophytes</b>		
Central Baltic	Average of national EQR values: National assessment systems of Belgium-Flanders, Denmark, Estonia, France, Germany, Latvia, Lithuania, the Netherlands, Poland, United Kingdom	Portielje et al., 2014; Poikane et al., 2018
Eastern Continental	Average of national EQR values: - Hungarian Adapted Reference Index - Bulgarian Adapted Reference Index - Romanian Adapted Reference Index	Pall et al., 2018; Gecheva et al., 2010
Northern	Intercalibration common metric for lake macrophytes	Hellsten et al., 2014; Kolada et al., 2014

and their values at “reference conditions”. Values range from zero to one (or greater): high ecological status is represented by values close to one and bad ecological status by values close to zero. Two types of common metrics were used:

**Table 1**

Description of shared lake types.

Type code	Type description	Altitude (m a.s.l.)	Mean depth (m)	Alkalinity (meq/L)	Additional characteristics
<b>Alpine region</b>					
LAL3	Lowland or mid-altitude, deep, calcareous, large	50–800	>15	>1	Area > 50 ha
LAL4	Mid-altitude, shallow, calcareous, large	200–800	3–15	>1	Area > 50 ha
<b>Central Baltic region</b>					
LCB1	Lowland, shallow, high alkalinity	<200	3–15	>1	Residence time 1–10 years
LCB2	Lowland, very shallow, high alkalinity	<200	<3	>1	Residence time 0.1–1 years
<b>Northern region</b>					
LN1	Lowland, shallow, moderate alkalinity, clear	<200	3–15	0.2–1	Colour <30 mg Pt/L
LN2a	Lowland, shallow, low alkalinity, clear	<200	3–15	<0.2	Colour <30 mg Pt/L
LN2b	Lowland, deep, low alkalinity, clear	<200	>15	<0.2	Colour <30 mg Pt/L
LN3a	Lowland, shallow, low alkalinity, meso-humic	<200	3–15	<0.2	Colour 30–90 mg Pt/L
LN6a	Mid-altitude, shallow, low alkalinity, meso-humic	200–800	3–15	<0.2	Colour 30–90 mg Pt/L
LN8a	Lowland, shallow, moderate alkalinity, meso-humic	<200	3–15	0.2–1	Colour 30–90 mg Pt/L
<b>Mediterranean region</b>					
LM5/7	Reservoirs, deep, large, siliceous, ‘wet’ areas	<800	>15	<1	Annual mean precipitation >800 mm and/or Annual mean T < 15 °C
LM8	Reservoirs, deep, large, calcareous	<800	>15	>1	Area 0.5–50 km <sup>2</sup> (for both Mediterranean types)
<b>Eastern Continental region</b>					
L-EC1	Lowland, very shallow, hardwater	<200	<6	1–4	Conductivity 300–1000 μS/cm

- Intercalibration common metrics (ICM), derived specially for the purposes of Intercalibration and used as ‘international currencies’ into which the national definitions of good status had to be converted before being compared (Lyche-Solheim et al., 2013); and,
- Average of EQRs of countries participating in an intercalibration exercise (“pseudo-common metric”) (Poikane et al., 2014b).

For phytoplankton, in the Alpine and Mediterranean regions, the average of national EQR values were used as common metrics, while in the Central Baltic and Northern regions, a common metric was developed comprising two submetrics - chlorophyll-a and a composition index, the Phytoplankton Trophic index, PTI; (Phillips et al., 2013). In the Eastern Continental region, all Member States used the same method: the Lake Phytoplankton Index, comprising chl-a, cyanobacteria abundance and the Q-index (Padisák et al., 2006).

For macrophytes, a common metric was developed in the Northern region (Hellsten et al., 2014; Kolada et al., 2014), while other regions used the average of national EQRs (Portielje et al., 2014; Pall et al., 2018). Nutrient concentrations were growing season or annual mean total phosphorus (TP) and total nitrogen (TN) values for each lake or lake-year.

## 2.2. Data analysis

### 2.2.1. Deriving nutrient thresholds

We used the EQRs to establish relationships with nutrients and thus derive nutrient concentrations corresponding to good-moderate and high-good class boundaries for the common metric agreed during the intercalibration process. We followed Kelly et al. (2021) and Phillips et al. (2018) and used both univariate and multivariate linear models. The univariate models were fitted using a type II ranged major axis (RMA) regression (Legendre and Legendre, 2012). Multivariate models were fitted using ordinary least squares (OLS) regressions. After fitting univariate relationships, the value of the nutrient concentration was solved for Y where X was the value of the common metric EQR value at the boundary between good and moderate status. Only linear parts of the relationship were used for fitting regressions. Linearity was assessed using a combination of GAM models (mgcv package) and segmented regression (segmented package). The significance of potential break points was determined using the Davies test.

Regression models were fitted for TP and TN independently and (where data was available) in combination with multivariate OLS. The multivariate analysis results in an infinite range of potential TN and TP concentrations at the specified boundary EQR values. These are presented as contour lines overlaid on a scatter plot of mean TP vs mean TN. The values identified as boundaries were those where the contour line intersected with an RMA regression line fitted to the relationship between TN and TP.

In all cases, uncertainty in the predicted nutrient boundary values is indicated by the upper and lower quartiles of the residuals of the regression lines. Thus, the range of boundary values will contain 50% of the observed data and the most likely value associated with a particular status will be given by the regression line itself.

All statistical analyses were carried out with R with RMA fitted using the lmodel2 package (Legendre, 2011). TP and TN were log transformed prior to analyses.

### 2.2.2. Modelling the impacts of fish stocking and nutrients

Since recreational fishing sustained by fish stocking and associated feeding is the most important lake-use in the Eastern Continental region (Borics et al., 2013), lakes in this region were categorised into three subsets, depending on the intensity of fish stocking based on the data provided by the lake users and the regional water authorities:

- Lake group 1: no fishing activity and no artificial stocking of fish, fish biomass <50 kg ha<sup>-1</sup>;
- Lake group 2: moderate fishing activity with occasional artificial fish stocking, fish biomass is between 50 and 200 kg ha<sup>-1</sup>; and,

- Lake group 3: intensive fishing, regular fish stocking, fish biomass >200 kg ha<sup>-1</sup>.

Linear models including a dummy variable representing these different levels of fish stocking activity were fitted using phytoplankton EQR against nutrient concentration. Three models were fitted using TP and TN independently, and TP and TN together and compared using the Akaike Information Criterion, AIC.

## 3. Results

### 3.1. Data overview

The dataset spanned a wide range of concentrations (TP 1–3000 µg/L, TN 0.02–16.5 mg/L). The range of TP and TN was similar in the different intercalibration types but spanned different portions of the nutrient gradient (Fig. 1). Lakes from the Northern region generally had the lowest concentrations, those from the Central Baltic were typically higher, but the highest values were found in the Eastern Continental region. TP and TN were significantly correlated in all regions except Eastern Continental (Tables S1 and S2). Most lakes had a high TN:TP ratio (Redfield molar ratio > 16:1), with low values mostly found at higher TP concentrations (>100 µg/L). While ratios of total nutrients alone are not good predictors of nutrient limitation (Ptacnik et al., 2010), they can provide broad indications of regions of potential nutrient limitation (Fig. 1). Based on Redfield ratios, the majority of lakes in this study are either co-limited by N and P or P-limited.

### 3.2. Relationships between nutrients and biota

For phytoplankton, the relationships between ecological status, expressed as EQR, and TP concentration were generally relatively strong ( $r^2 = 0.28–0.79$ ;  $P < 0.001$ ), the exception being Eastern Continental region where the relationship was very weak ( $r^2 = 0.06$ ;  $P = 0.035$ ). Where the range for TP was high (>100 µg/L) relationships were curved, with decreasing change in EQR at higher concentrations necessitating selection of a linear range for modelling (Fig. 2).

Univariate relationships for TN generally explained less variance than equivalent relationships for TP ( $r^2 = 0.10–0.53$ ,  $p < 0.001$ ). Most of the  $r^2$  values for univariate TN models were less than the threshold ( $r^2 = 0.36$ ) below which it is unsafe to predict boundary values (Phillips et al., 2018; Smith, 2009). In particular, weak relationships for TN were observed in some Northern types (LN2a:  $r^2 = 0.1$ ;  $P < 0.001$ ; LN2b:  $r^2 = 0.26$ ;  $P = 0.003$ ) and in Eastern Continental very shallow lakes ( $r^2 = 0.16$ ;  $P = 0.005$ ) where the range of TP was relatively narrow.

Including both TP and TN in models increased the  $R^2$  value significantly relative to the use of TN alone, and marginally relative to the use of TP alone (Table S1). As multivariate OLS regression tended to have higher  $R^2$  values (ranging from 0.37 to 0.80;  $P < 0.001$ ), these bivariate models were used for setting nutrient thresholds where they were available (Northern and Central-Baltic regions: Fig. 3).

For macrophytes, the relationships for total phosphorus in the Central Baltic region were highly significant but explained variance was lower than that for phytoplankton (LCB1:  $r^2 = 0.43$ ,  $p < 0.001$ ; LCB2:  $r^2 = 0.40$ ,  $p < 0.001$ ), while explained variance for nitrogen was similar or higher than for phytoplankton (Table S2).

In the Northern region, the pressure gradient was too short to produce an adequate model for low alkalinity clear water lakes so the data for both low and moderate alkalinity clear lakes were combined for analysis, producing a moderately strong relationship between total phosphorus and macrophyte common metrics ( $r^2 = 0.41$ ,  $p < 0.001$ ). The low alkalinity humic lakes had a short pressure gradient with considerable scatter, meaning that a significant regression model could not be fitted to these data, either independently or in combination with the moderate alkalinity lake type. In contrast, moderate alkalinity humic lakes had a long pressure gradient and a moderately strong relationship with TP ( $r^2 = 0.31$ ,  $p < 0.001$ ).



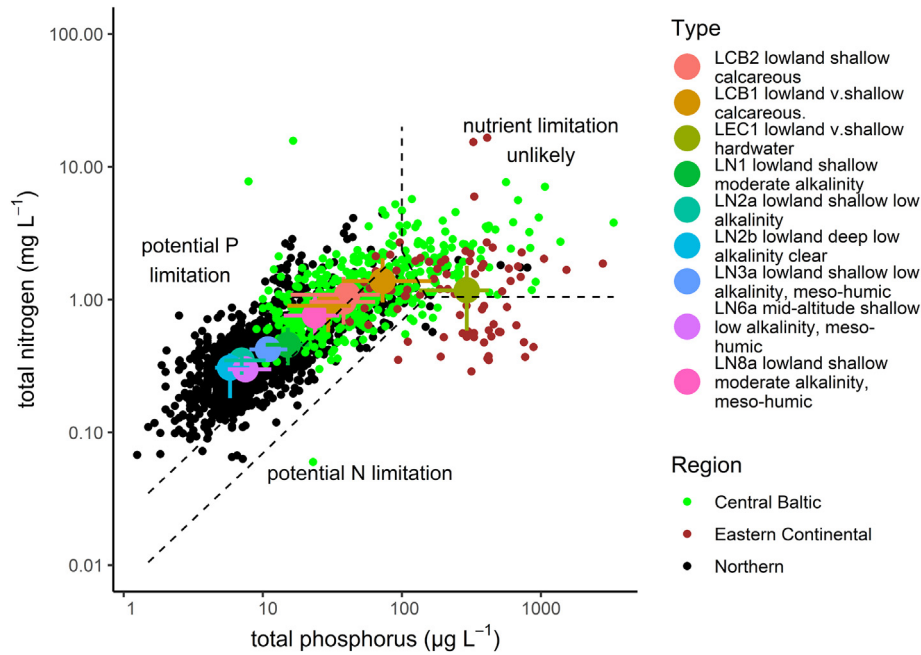


Fig. 1. Scatter plot showing the relationship between phosphorus and nitrogen concentration in the data set (points coloured by region: green = Central Baltic region, brown = Eastern Continental region, black = Northern region) overlain by points showing the median and interquartile ranges for each of the intercalibration lake types. Lines show N:P ratios where N, P or co-N&P limitation may occur:  $<16$  molar ratio N limitation,  $>53$  molar ratio P limitation (Ptcnik et al., 2010).

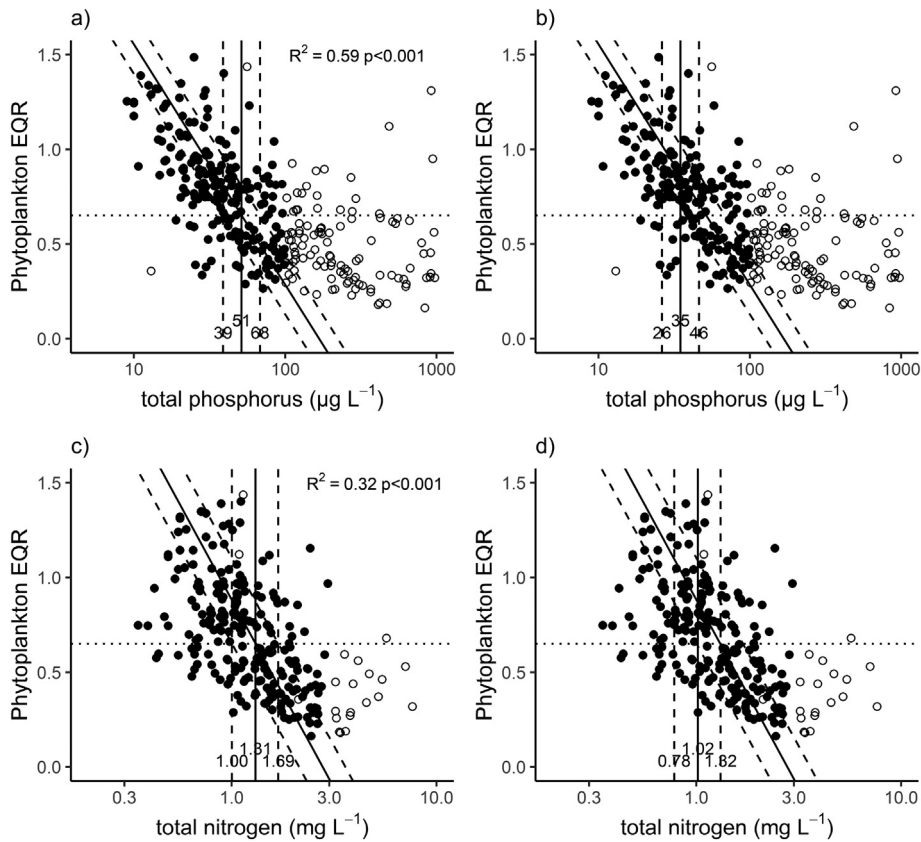
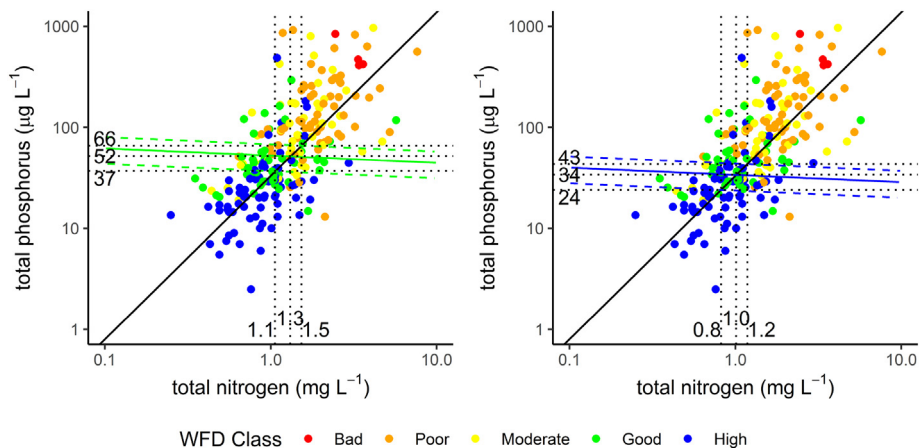


Fig. 2. Relationship between common metric for phytoplankton and total phosphorus (upper panel) and total nitrogen (lower panel) for high alkalinity very shallow Central Baltic region lakes (type L-CB2) showing good/moderate boundary (left) and high/good boundary (right) values. Line shows type II RMA regression, dotted lines show area containing 50% of the data, open circles data points excluded from regression.



**Fig. 3.** Relationship between mean TP and TN, points coloured by WFD class for phytoplankton in high alkalinity very shallow Central Baltic region lakes (type L-CB2). Dotted lines contours of predicted TN & TP concentration when phytoplankton common metric EQR is at good/moderate boundary (left panel) and high/good boundary (right panel), dotted lines show  $\pm 25$ th and 75th residuals of prediction.

As for phytoplankton, the relationships between macrophytes and TP was very weak in Eastern Continental lakes ( $r^2 = 0.12, p = 0.013$ ). The relationship between macrophytes and TN was slightly stronger ( $r^2 = 0.22, p < 0.001$ ) but still weaker than observed in Central Baltic lakes.

### 3.3. Fish stocking in the lakes of eastern continental region

Fish stocking is an important factor in Eastern Continental lakes where the weakest relationships were found (Tables S1 and S2). Models including three levels of fish stocking intensity in addition to nutrients showed much higher  $R^2$  values than those that did not (Table 3) (TP + Fish stocking:  $R^2 = 0.63$ , TN + Fish stocking:  $R^2 = 0.57$ , TP + TN + Fish stocking:  $R^2 = 0.62$ ). The relationship between nutrients, phytoplankton EQRs and fish stocking pressure are shown in Fig. 4 and the best model, based on AIC (Table 3) excluded TN which, once the effect of fish stocking was accounted for in the model, showed no relationship with EQR.

Judged by the coefficients from model 1 (Table 3), there is a significant effect of fish stocking pressure along with an interaction with TP on lake ecological status, as assessed by phytoplankton. Thus, the effect of TP is greatest in lakes with high fish stocking and decreases to no effect in lakes where fish stocking is low.

To achieve an EQR of 0.6 (good-moderate class boundary) these models imply that a very low TP would be required in lakes with intensive fish

**Table 3**

Analysis of variance table comparing models predicting Phytoplankton EQR from TP, TN and intensity of fish stocking, together with AIC values for each model. AIC - Akaike information criterion., EQR – Ecological Quality Ratio, TN - total nitrogen, TP - total phosphorus.

Model	AIC	Variable	Sum of squares	Degree of freedom	Variance ratio (F)	Probability (P)
1	-103.38	logTP	0.06	1	3.94	0.051
		Fish stocking	1.62	1	108.61	0.000***
		logTP: fish stocking	0.13	1	8.49	0.005**
		Residuals	1.14	76		
2	-92.03	logTN	0.01	1	0.71	0.401
		Fish stocking	1.36	1	78.71	0.000***
		logTN: fish stocking	0.00	1	0.02	0.888
		Residuals1	1.31	76		
3	-100.07	logTP1	0.07	1	4.81	0.031*
		Fish stocking	1.13	1	74.34	0.000***
		logTN1	0.01	1	0.50	0.484
		logTP: fish stocking	0.11	1	7.20	0.009**
		logTN: fish stocking	0.00	1	0.14	0.710
		Residuals2	1.13	74		

Significance level: \* - significant ( $P < 0.05$ ); \*\* - very significant ( $P < 0.01$ ); \*\*\* - highly significant ( $P < 0.001$ ).

stocking, while for lakes with lower levels of fish stocking good status is apparently independent of nutrients and can be sustained at surprisingly high TP.

Comparison of Eastern Continental very shallow lakes with those from other regions.

As well as being influenced by fish stocking, Eastern Continental very shallow lowland lakes also tend to have higher nutrient concentrations than similar lakes in other regions of Europe (Fig. 1). Given the shape of the relationships found for very shallow lowland lakes in the Central Baltic (Fig. 2), it is therefore not surprising that the relationships were weak.

To explore this, we compared the relationships between mean chlorophyll-a concentration and nutrients using data from Northern, Central-Baltic and Eastern-Continental regions (Fig. 5). Chlorophyll-a was used as it is a metric that is common to all of the region-specific phytoplankton common metrics. Scatter plots (Fig. 5) demonstrate that the data from these different European regions generally overlap but with an increasing scatter in mean chlorophyll as TP increases. In particular, a large number of sites had lower than predicted chlorophyll concentrations. Such sites were found in all three regions but, proportionally, were much commoner in the Eastern-Continental region. GAM models fitted to each region clearly demonstrated this overlap and a curvilinear relationship, which started to reach an asymptote at TP concentration above 100  $\mu\text{g/L}$  (Fig. 5a).

The sites with the lower levels of chlorophyll relative to TP from the Eastern Continental region were sites with low and moderate fish stocking (Fig. 5b). In contrast, sites with high fish stocking do show a positive response of chl-a to TP increase even at high TP concentrations, resulting in very high chlorophyll a concentrations. The situation for TN is a little less clear. The very shallow lakes from the Central Baltic and Northern regions show relatively linear relationship between chl-a and TN (Fig. 5a), while the Eastern Continental region data set show a weaker relationship (Fig. 5a), even after allowing for the effect of fish stocking (Fig. 5b).

### 3.4. Deriving nutrient thresholds supporting high and good ecological status

Predicted threshold values for TP and TN, and their possible ranges are shown in Tables 4 and 5 and compared in Fig. 6. For phytoplankton, good-moderate (G-M) thresholds for TP range from 16 to 52  $\mu\text{g/L}$ , with the lowest thresholds in the Alpine and Northern region and highest in the Mediterranean and Central Baltic regions. For Eastern Continental very shallow lakes, the regressions suggest high threshold values, but the explained variance is low and therefore, these values are unlikely to be reliable.

In the Northern region, the lowest TP threshold for good status (14  $\mu\text{g/L}$ ) was derived for deep low alkalinity clear-water lakes (LN2b type). Similarly, low values were derived for other clear-water types:

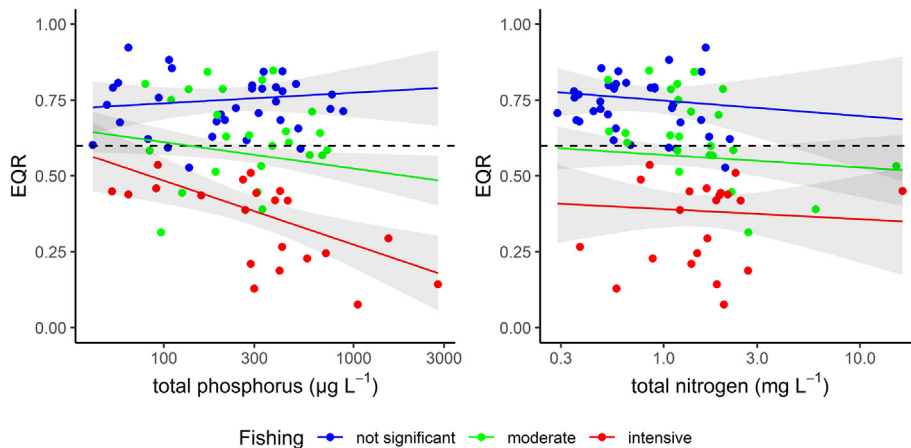


Fig. 4. Scatter plots showing relationship between phytoplankton EQR and total phosphorus (left panel) and total nitrogen (right panel) split by intensity of fish stocking. Lines show the fit from model 1 (left panel) and model 2 (right panel). For model description see Table 5. Horizontal dotted line shows good-moderate boundary value.

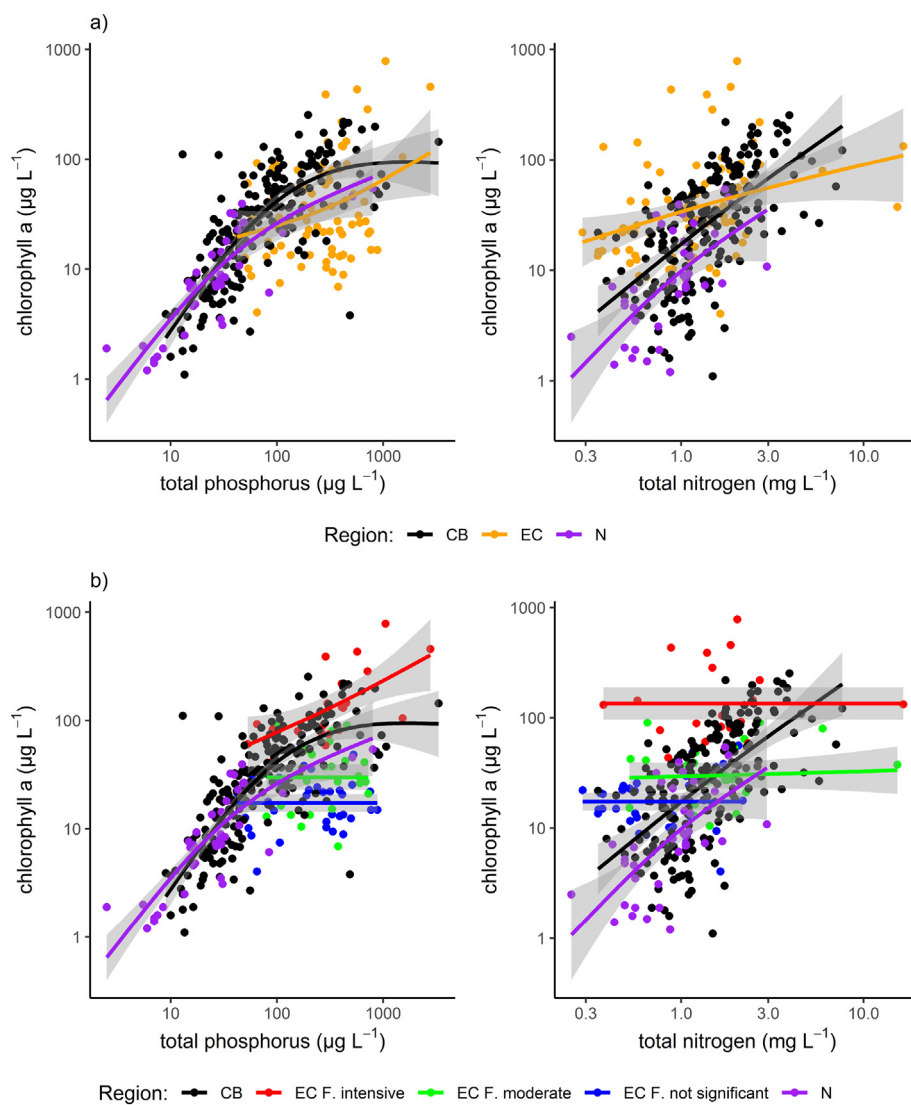


Fig. 5. Scatter plots showing the relationships between chlorophyll-a and total phosphorus (left panel) and total nitrogen (right panel) split by region (a) and in addition (for the Eastern Continental region) by fish stocking (F) intensity (b). Lines show gam models together with standard error in grey. CB – Central Baltic region, EC – Eastern Continental region, N – Northern region.

**Table 4**

Predicted total phosphorus boundary values (TP µg/L) using regression models. Predictions from models where  $R^2 < 0.36$  shown in *italic* as potentially less reliable. OLS - ordinary least squares regression; RMA - ranged major axis regression. Explanation for lake type codes given in Table 1.

Region	Lake type	Model	$r^2$	Type of regression	Good-moderate TP µg/L		High-good TP µg/L	
					Predicted	25–75th	Predicted	25th–75th
Central-Baltic	LCB1	Phytoplankton	0.55	OLS	39	28–55	22	16–31
		Macrophytes	0.40	OLS	44	24–84	16	9–30
	LCB2	Phytoplankton	0.68	OLS	52	37–66	34	24–43
		Macrophytes	0.46	OLS	69	36–132	29	15–56
Northern	LN1	Phytoplankton	0.81	OLS	18	16–22	11	10–14
	LN2a	Phytoplankton	0.37	OLS	20	15–26	9	7–12
	LN2b	Phytoplankton	0.37	OLS	14	10–18	8	6–10
	LN1 + 2a + 2b	Macrophytes	0.41	RMA	22	14–29	14	10–19
	LN3a	Phytoplankton	0.61	OLS	22	18–27	12	10–15
	LN6a	Phytoplankton	0.41	OLS	26	18–34	14	10–18
	LN8a	Phytoplankton	0.80	OLS	27	23–33	16	13–19
		Macrophytes	0.31	RMA	36	19–54	20	10–29
Alpine	LAL3	Phytoplankton	0.63	RMA	16	12–21	6	5–8
	LAL4	Phytoplankton	0.73	RMA	31	23–44	13	10–19
Mediterranean	LM5/7	Phytoplankton	0.53	RMA	46	40–52	32	28–36
	LM8	Phytoplankton	0.28	RMA	43	33–60	27	50–37
Eastern Continental	L-EC1	Phytoplankton	0.25	OLS	246	143–511	80	46–165
		Macrophytes	0.33	OLS	195	142–297	65	47–99

shallow, low alkalinity (LN2a: 20 µg/L) and shallow, moderate alkalinity (LN1: 18 µg/L). For meso-humic lakes (colour 30–90 mg Pt/L), TP threshold values were higher than for the clear-water lakes with moderate alkalinity waters (L-N8a), having a good-moderate threshold of 27 µg/L. Similar low G-M threshold values were derived for TP for Alpine deep (LAL3; 16 µg/L) and shallow (LAL4; 31 µg/L) lake types.

Analysis of the available data for high alkalinity Central-Baltic lakes demonstrates a relatively wide range of potential G-M threshold values. Threshold predictions from the very shallow lake type (L-CB2) produced higher values (52 µg/L) than the deeper LCB1 type (39 µg/L). Thresholds predicted using macrophytes were generally slightly higher than those derived from phytoplankton (Fig. 6), ranging from 22 µg/L for Northern clear water lakes to 69 µg/L for very shallow calcareous Central-Baltic lakes.

For nitrogen, data from Central-Baltic and Northern regions produced thresholds of 0.6–0.9 mg/L in the Northern region and 1.0–1.4 mg/L in the Central Baltic region (Table 5).

## 4. Discussion

### 4.1. Nutrient threshold values in lakes

In this study, we derived nutrient thresholds below which lakes of different types are likely to achieve good ecological status. Phytoplankton was most sensitive to TP, providing good-moderate class threshold of 14–52 TP µg/L while macrophyte-based boundaries were higher at 22–69 TP µg/L. The lowest threshold values were derived using data from the Northern and Alpine region, and the highest using data from the Central

Baltic and Mediterranean regions. In general, thresholds were higher in shallow lakes than in deep lakes, in high alkalinity lakes than in low alkalinity lakes, and in humic lakes than in non-humic lakes, confirming the influence of depth, alkalinity and lake colour reported elsewhere (Cardoso et al., 2007; Carvalho et al., 2008; Poikane et al., 2014a). Other studies have also highlighted differences between regions: lakes in the Central-Baltic and Mediterranean regions have higher background levels compared to the Northern and Alpine region (Cardoso et al., 2007; Poikane et al., 2010). However, this is a complex issue, as the effect can include both a lake type effect (e.g. CB lake types are high alkalinity, shallow and very shallow), as well as coarser scale latitude and continentality effects related to temperature and other factors (Abell et al., 2012). This is all in accord with the reference condition approach (Stoddard et al., 2006) which is an integral part of the WFD. Assessments of ecological status should take into account the variation expected in undisturbed conditions and, as background nutrient concentrations are a function of geology, morphology and hydrology, among other factors, we should accept that some ecosystems may be more productive than the others by nature, therefore nutrient concentrations that equate to a “slight change” (i.e. “good status”) might be higher than those for the less productive ones.

This study is the first to apply the same analyses to datasets collected using very similar approaches on a continental scale in Europe. The results could be compared with standards set by different European countries and used to justify or amend these values. However, while such comparisons may be useful, it is important to remember that, in most cases, national standards have been derived from data sets that are more closely attuned to national conditions and we caution against an over-simplistic interpretation.

**Table 5**

Predicted total nitrogen boundary values for different lake types using regression models. Predictions from models where  $R^2 < 0.36$  shown in *italic* type as potentially less reliable. OLS - ordinary least squares regression; RMA - ranged major axis regression. Explanation for lake type codes given in Table 1.

Region	Type	Model	$r^2$	Type of regression	Good - moderate status criteria TN mg/L		High - good status criteria TN mg/L		
					Pred	25th–75th	25th–75th	Pred	
Central-Baltic	LCB1	Phytoplankton	0.55	OLS	1.11	0.79–1.57	0.63	0.45–0.89	
		Macrophytes	0.40	OLS	1.03	0.59–1.85	0.40	0.23–0.72	
	LCB2	Phytoplankton	0.68	OLS	1.32	1.06–1.54	1.01	0.81–1.18	
		Macrophytes	0.46	OLS	1.37	0.91–2.04	0.80	0.54–1.20	
Northern	LN1	Phytoplankton	0.81	OLS	0.65	0.54–0.82	0.36	0.30–0.45	
	LN3a	Phytoplankton	0.61	OLS	0.71	0.62–0.83	0.46	0.40–0.54	
	LN6a	Phytoplankton	0.41	OLS	0.59	0.49–0.70	0.41	0.33–0.48	
	LN8a	Phytoplankton	0.80	OLS	0.86	0.71–1.05	0.47	0.39–0.58	
	Eastern Continental	LEC1	Phytoplankton	0.25	OLS	1.10	0.44–3.83	0.16	0.06–0.56
			Macrophytes	0.33	OLS	1.82	1.33–2.78	0.60	0.44–0.92



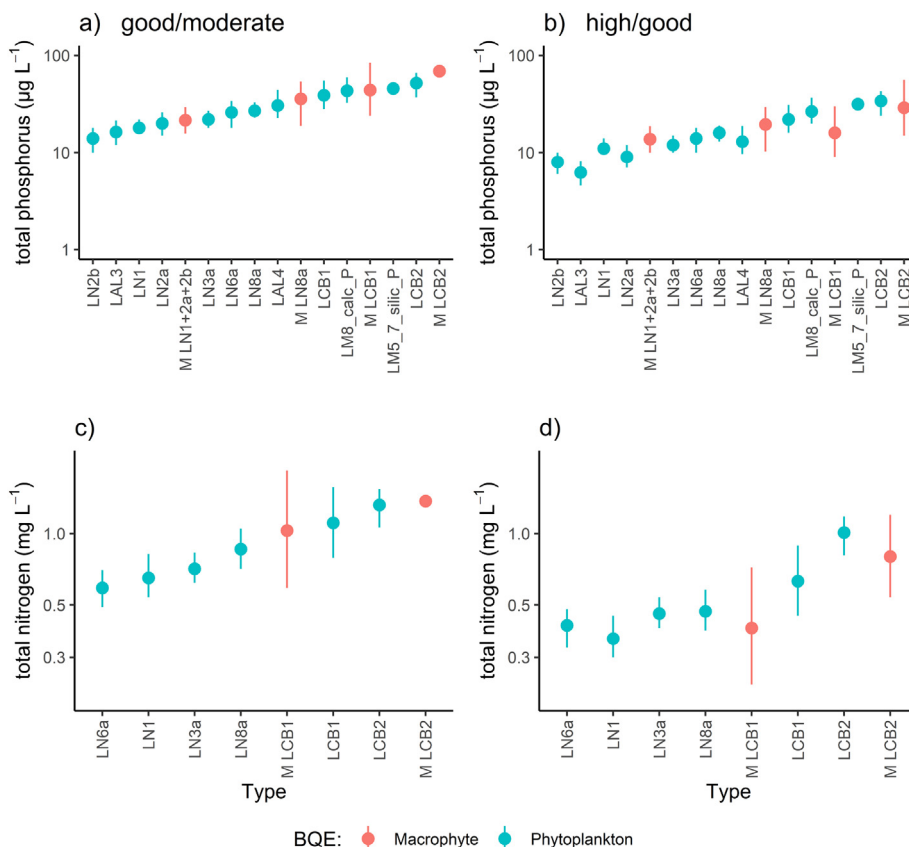


Fig. 6. Thresholds for total phosphorus (upper panel) and total nitrogen (lower panel) good-moderate (left panel) and high-good (right panel) class boundaries for different types of lakes derived from macrophyte and phytoplankton biological quality elements (BQE).

Nonetheless, results from this study are generally in line with results of other studies, which have explored nutrient thresholds supporting good ecological status in different countries (Table 6). These studies also stress the contrast between shallow/deep and clear/humic lakes.

In some cases national thresholds were based on the regressions between chl-a and nutrients (without considering phytoplankton community structure). These generally have higher explained variance and therefore can be considered more reliable (Direktoratgruppen vanndirektivet, 2018). However, while relationships with chlorophyll-a provides a higher  $r^2$ , chlorophyll represents only a part of the whole phytoplankton quality element. As

chlorophyll thresholds alone have not been harmonized around Europe, these cannot be used for the purpose of pan-European threshold setting.

There is a need to explain the meaning of good status and convey its meaning to the public and stakeholders, which can be done linking status to ecosystem services important for human wellbeing. For example, good status boundaries are set to prevent/control Cyanobacteria blooms (EC, 2009; Poikane et al., 2014a) since these are well known to disrupt ecosystem service provision (Carvalho et al., 2013b). These thresholds converge around a TP range 20–60 µg TP/L (Chorus and Schauser, 2011; Downing et al., 2001; Fastner et al., 2016, Xu et al., 2015) depending both on lake

Table 6

Nutrient thresholds set by different ecology-based methods supporting good ecological status (GES). TP – total phosphorus, TN – total nitrogen.

Reference	Lakes	Good-moderate boundary		Approach to setting criteria
		Total phosphorus (TP)	Total nitrogen (TN)	
Dolman et al., 2016	German lakes, - Stratified - Polymictic	20–35 µg TP/L 35–75 µg TP/L	0.4–0.5 mg TN/L 0.5–1.1 mg TN/L	Supporting GES using phytoplankton Linear and piecewise regression ( $r^2 = 0.44–0.62$ )
Free et al., 2016	Irish lakes, all types combined	24–28 µg TP/L		Supporting GES using phytoplankton Linear regression ( $r^2 = 0.65$ )
Kagalou et al., 2021	Greek lakes, - Shallow (3–9 m) - Deep (>9 m)	41 (27–56) µg TP/L 32 (28–38) µg TP/L		Supporting GES using phytoplankton Linear regression ( $r^2 = 0.51–0.71$ )
Direktoratgruppen vanndirektivet, 2018	Norwegian lakes, for different types	9–17 µg TP/L	0.40–0.68 TN/L	Supporting GES using chlorophyll-a – nutrient regressions ( $r^2 = 0.46–0.81$ )
Søndergaard et al., 2019	Danish high alkalinity lakes - Low colour, deep (>3 m) - Low colour, shallow (<3 m) - High colour (>60 mg Pt L), shallow - High salinity (>0.5‰), shallow	24 µg TP/L 55 µg TP/L 73 µg TP/L –	0.75 mg N/L 1.1 mg TN/L 1.4 mg TN/L 0.95 TN/L	Supporting GES using chlorophyll-a – nutrient regressions TP $r^2 = 0.37–0.59$ TN $r^2 = 0.22–0.30$

type (Vuorio et al., 2020) and the criteria used (Carvalho et al., 2013b) and are in line with our study.

#### 4.2. Why are Eastern Continental lakes different?

We found significant relationships between nutrients and phytoplankton and macrophyte EQRs in most lake types (including very shallow lakes from Central Europe) but only weak associations in Eastern Continental lakes. The first, and potentially the simplest explanation, for this is that the nutrient concentrations, particularly TP, in these lakes are generally higher (median 292  $\mu\text{g}/\text{TP L}$ ; 81.2% values > 100  $\mu\text{g}/\text{TP L}$ ) than in other lake types/regions and many lakes are in the range where the TP–phytoplankton relationship is asymptotic. However, stocking omnivorous/benthivorous fish for recreational angling is also a major pressure on Eastern Continental lakes, and has a negative effect on ecological status (Borics et al., 2013). This is clearly therefore a factor that needs to be considered when setting nutrient thresholds. The question it raises is whether the socio-economic benefits derived from fish stocking outweigh the negative effects caused by excessive nutrients and how fish stocking might influence the derivation of appropriate nutrient thresholds in these lakes.

##### 4.2.1. Asymptotic range of TP-phytoplankton model

The non-linear response of chlorophyll-a and phytoplankton (and Cyanobacteria) biovolume to phosphorus is a well-documented phenomenon in lakes worldwide (Brown et al., 2000; Carvalho et al., 2013b; Dolman et al., 2012; Jones et al., 2011; McCauley et al., 1989; Quinlan et al., 2021; Phillips et al., 2008; Watson et al., 1992). However, opinions diverge on: (i) the TP breakpoint concentration beyond which further increases of phosphorus do not notably raise chl-a levels; and (ii) the mechanisms behind the nonlinearities in the phosphorus–phytoplankton relationship. A TP concentration of 100  $\mu\text{g}/\text{TP L}$  has often been suggested as a break point (Brown et al., 2000; Carvalho et al., 2013b; Phillips et al., 2008). However, other research has suggested different breakpoints: 50  $\mu\text{g}/\text{TP L}$  (Dolman et al., 2012; McCauley et al., 1989), 75  $\mu\text{g}/\text{TP L}$  (Jones et al., 2011), and 230  $\mu\text{g}/\text{TP L}$  (Quinlan et al., 2021). Our data shows the breakpoint to occur at around 100  $\mu\text{g}/\text{TP L}$  (Fig. 5), in line with other studies on European lakes (Carvalho et al., 2013b; Phillips et al., 2008).

Explanations are linked to the factors (other than P) controlling productivity in these high-P systems:

- (1) Nitrogen limitation, or co-limitation, at high TP concentrations (Brown et al., 2000; Dolman et al., 2012; Phillips et al., 2008). According to N:P ratios, N limitation is more likely in the Eastern Continental lakes (Fig. 1). Maberly et al. (2002) suggested that N limitation is only an issue when inorganic N levels are <0.01 mg DIN/L, a concentration widely exceeded in Eastern Continental lakes (Borics et al., 2013).
- (2) Light limitation due to self-shading from dense algal blooms and/or light attenuation by suspended solids (Huisman and Weissing, 1994; Mischke, 2003; Reynolds, 1992). It is well established that increased light attenuation by algal accumulation/non-algal turbidity reduces light availability to a point where further increase of nutrients does not increase phytoplankton biomass. However, we lack data on the underwater light climate to confirm the importance of this mechanism in the Eastern Continental lakes.
- (3) Top-down effects such as grazing by zooplankton or competition with macrophytes (Benndorf et al., 2002; Jeppesen et al., 1997, 2003). This can be linked to fish stocking through a cascading effect of fish predation on zooplankton and grazing invertebrates influencing the biomass of phytoplankton and periphyton and hence, vegetation (as well as other effects, e.g., direct feeding on macrophytes). Thus, where fish stocks are low, phytoplankton growth is suppressed by zooplankton grazing, uncoupling the direct effect of nutrient elevation (Carpenter et al., 1985; Brönmark and Weisner, 1992; Jeppesen et al., 1997, 2003; Jones and Sayer, 2003). This effect depends on the body size and composition of the fish community, but is particularly important in small and very shallow lakes, which often have elevated

nutrient concentrations and thus contributes to the asymptotic response of our dataset.

##### 4.2.2. Fish stocking - the main pressure in Eastern Continental lakes

The dominant paradigm in freshwater science is that enrichment by nutrients, particularly phosphorus, is the most important human-induced pressure on lake ecosystems (Carvalho et al., 2013a, 2013b; Phillips et al., 2008). However, while well established, there are exceptions. Several other pressures can play a major role in lake degradation, both independently and through interactions with eutrophication: water level fluctuations (Mjelde et al., 2013; Zohary and Ostrovsky, 2011), lakeshore developments (Brauns et al., 2011; Jusik and Macioł, 2014), introduction of invasive taxa (Volta et al., 2013; Walsh et al., 2016), and lake uses including shipping, boating, and bathing (Mehner et al., 2005; Poikane et al., 2017). Such pressures may occur in the lakes within our dataset and, as we have no data to quantify these, this is reflected in the uncertainty around our pressure response models. However, in the case of the Eastern Continental lakes we have good information relating to fish stocking.

Fish stocking is a commonly used (and abused) management tool in freshwater recreational fisheries (Eby et al., 2006; Moss et al., 2002) or to enhance commercial production. It is the most common use of lakes in the Eastern Continental region of Europe (Borics et al., 2013; Specziár and Erős, 2015) as well as in some other regions (Skeate et al., 2021). The most commonly stocked species include common carp *Cyprinus carpio* (comprising more than half of the catch), common bream *Abramis brama*, white bream *Blicca bjoerkna*, roach *Rutilus rutilus* and gibel carp *Carassius gibelio* (Specziár and Erős, 2015). These species consume macroinvertebrates, macrophytes, zooplankton and detritus in varied proportions depending on species and life stage or body size.

The effects of stocking on lake ecosystems have been well documented, but the consequences for ecological status assessment are seldom quantified (Borics et al., 2013; Kelly et al., 2019). Here, we showed that fish stocking is a potentially important factor affecting ecological status in very shallow lakes in Eastern Europe. Lakes with low fish stocking show low chlorophyll-a concentrations and good ecological status despite high nutrient levels (Figs. 4 and 5), while those with high fish stocking have high chlorophyll-a and low ecological status. Using multivariate models, we show that fish stocking is the strongest predictor of ecological status and that clear effects of phosphorus (but not nitrogen) are only seen in lakes with high fish stocking pressure. Lakes with low or moderate fish stocking show no significant effects of nutrients.

Stocking with benthivores, although obviously much more widespread in the Eastern Continental region, is not a pressure/use that is unique and can impact lakes all over Europe (Skeate et al., 2021). Various factors may explain this impact. The most widely-reported mechanism is fish predation on zooplankton/macroinvertebrates reducing the grazing pressure on phytoplankton/epiphytes (Brönmark and Weisner, 1992; Carpenter et al., 1985; Jeppesen et al., 1997, 2003; Jones and Sayer, 2003). Many studies have shown that changes in fish communities caused by intentional removal of planktivorous fish (biomanipulation) or fish kill (Borics et al., 2000; Oh et al., 2019) can induce great changes in lower trophic levels, leading to higher grazing pressure, lower phytoplankton biomass and recovery of macrophytes. These findings are corroborated by numerous mesocosm studies and lake-scale manipulations (Van De Bund and Van Donk, 2002; Razlutskiy et al., 2021). However, other mechanisms can also contribute. Benthic-feeding fish such as common carp (*Cyprinus carpio*), the most widely-stocked fish in eastern Europe, exert a strong detrimental effect on the macrophytes by increasing sediment re-suspension (thus increasing turbidity and enhancing shading); by direct feeding on and uprooting of macrophytes and by releasing nutrients into the water column thus favouring phytoplankton and epiphytic alga (Huser et al., 2016).

Overall, several studies show that the effect of introduced fish on nutrient and phytoplankton dynamics can be complex in shallow lake ecosystems (Breukelaar et al., 1994; Chumchal et al., 2005; Driver et al., 2005). Our findings point to the adverse effects of fish stocking on lake ecosystems, arising both via direct top-down effects on zooplankton/epiphytic

invertebrates and by intensive bioturbation, excretion and feeding on macrophytes by large benthivorous fish. These and associated factors help drive the transition from a clear-water to turbid-water state, a phenomenon observed in lakes worldwide (Scheffer and Jeppesen, 2007). Bioturbation on one hand releases nutrients stored in the sediment into water column; on the other hand, it directly increases non-algal turbidity of water and thus, leads to light limitation (Adámek and Maršálek, 2013). This may be the reason why, despite the high concentration of available nutrients, the phytoplankton biomass in the very shallow Eastern Continental lakes remains far below the theoretical maxima, which should be around 300–600 µg/L chl-a, assuming a water column no deeper than two metres (Reynolds, 2006).

#### 4.2.3. Implications for lake management

These findings have important implications for lake management. In lakes where strong relationships between nutrients and ecological quality exist, nutrient loads should be reduced in order to improve their ecological quality (Jeppesen et al., 2005). However, this strategy might not be sufficient in lakes where nutrient-phytoplankton links are weak or non-existent, as in the very shallow Eastern Continental lakes. In theory, targeted removal of benthivorous/zooplanktivorous fish might be used (Mehner et al., 2002), and the use of fish bait restricted. However, such measures invariably cause conflict with lake owners, anglers and fishery management authorities (Moss et al., 2002; Skeate et al., 2021; Tiberti and Cardarelli, 2021). Angling is a very popular recreational activity in Eastern Europe with an additional benefit of providing protein through diet. As a result, these lakes provide an important ecosystem service for society, albeit at the expense of realising ecological objectives. The solution at least partly lies in stocking with piscivores, controlled fishery, and co-operation of all lake users (Mehner et al., 2004). This last point is, indeed, critical and applies far more widely than just fisheries: achievement of WFD goals very often conflicts with other policy objectives (Carvalho et al., 2019) and there is an urgent need for water policy to be more thoroughly integrated with other policy sectors. This, in turn, implies a need to make good status and its benefits understood by the public and stakeholders. In part, this can be done linking status to ecosystem services important for human wellbeing (e.g. good status boundaries are set to prevent/control Cyanobacteria blooms, EC, 2009; Poikane et al., 2014a). However, as our study demonstrates, interactions between ecological status and ecosystem services may occasionally be antagonistic rather than additive or synergistic.

## 5. Conclusions

With 60% of European lakes having less than good ecological status, it is clear that eutrophication remains a significant problem. In most regions, phosphorus and nitrogen are negatively associated with lake ecological status, as assessed by phytoplankton and macrophytes. In general, relationships were stronger for phytoplankton than for macrophytes, and stronger for phosphorus than for nitrogen. Regression models allowed thresholds to be set for 12 large transnational lake types (Tables 4 and 5).

However, in the very shallow lakes of the Eastern Continental region relationships between nutrients and biota were weak or non-existent. This can be attributed to high nutrient concentrations in the asymptotic zone of phosphorus-phytoplankton model suggesting other factors (light, grazing, nitrogen) limiting primary production. In addition, we show that fish stocking is the main pressure negatively affecting ecological status in these highly eutrophic lakes. This study highlights that the dominant paradigms should be transferred cautiously to less-well studied regions with due consideration of factors that may confound the nutrient-biota relationship. Our study also raises questions about the potential for conflicts between ecological targets and ecosystem services, and the necessary trade-offs between them.

### CRedit authorship contribution statement

SP: Conceptualization, Methodology, Data curation, Writing - original draft, Writing - review & editing, Supervision, Project administration.

MGK: Conceptualization, Methodology, Data curation, Writing - original draft, Writing - review & editing. GV: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. GB: Methodology, Data curation, Writing - review & editing. TE: Conceptualization, Writing - review & editing. SH: Data curation, Writing - review & editing. AK: Conceptualization, Writing - review & editing. BAL: Data curation, Writing - review & editing. ALS: Conceptualization, Writing - review & editing. JPL: Data curation, Writing - review & editing. NJW: Data curation, Writing - review & editing. GW: Data curation, Writing - review & editing. GP: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.154242>.

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