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Sustaining recreational quality of European lakes: minimizing the health risks from algal blooms through phosphorus control

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Summary

- 1. A safe, clean water supply is critical for sustaining many important ecosystem services provided by freshwaters. The development of cyanobacterial blooms in lakes and reservoirs has a major impact on the provision of these services, particularly limiting their use for recreation and water supply for drinking and spray irrigation. Nutrient enrichment is thought to be the most important pressure responsible for the widespread increase in cyanobacterial blooms in recent decades. Quantifying how nutrients limit cyanobacterial abundance in lakes is, therefore, a key need for setting robust targets for the management of freshwaters.
- 2. Using a data set from over 800 European lakes, we highlight the use of quantile regression modelling for understanding the maximum potential capacity of cyanobacteria in relation to total phosphorus (TP) and the use of a range of quantile responses, alongside World Health Organisation (WHO) health alert thresholds for recreational waters, for setting robust phosphorus targets for lake management in relation to water use.
- 3. The analysis shows that cyanobacteria exhibit a nonlinear response to phosphorus with the sharpest increase in cyanobacterial abundance occurring in the TP range from about $20 \mu g L^{-1}$ up to about $100 \mu g L^{-1}$.
- 4. The likelihood of exceeding the World Health Organisation (WHO) 'low health alert' threshold increases from about 5% exceedance at 16 μ g L⁻¹ to 40% exceedance at 54 μ g L⁻¹. About 50% of the studied lakes remain below this WHO health alert threshold, irrespective of high summer TP concentrations, highlighting the importance of other factors affecting cyanobacteria population growth and loss processes, such as high flushing rate.
- 5. Synthesis and applications. Developing a more quantitative understanding of the effect of nutrients on cyanobacterial abundance in freshwater lakes provides important knowledge for restoring and sustaining a safe, clean water supply for multiple uses. Our models can be used to set nutrient targets to sustain recreational services and provide different levels of precaution that can be chosen dependent on the importance of the service provision.

Key-words: algal bloom, blue-green algae, ecosystem services, freshwater, lake, nutrient, quantile regression, WHO

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Introduction

Currently, there is much political drive to quantify ecosystem services provided by freshwaters (Assessment Millennium Ecosystem 2005) although there is still a great deal of debate as to what primary data can best be used to map the provision and quality of services (Eigenbrod et al. 2010). In this respect, for freshwaters, a safe, clean water supply is a critical need. Cyanobacteria, specifically the toxins they produce, represent one of the most hazardous waterborne biological substances that produce a range of adverse health effects from mild skin irritations to severe stomach upsets and even fatal consequences (Codd, Morrison & Metcalf 2005). The widespread development of large cyanobacterial populations, or blooms, in lakes and reservoirs, therefore, has a major impact on the provision of many ecosystem services, particularly limiting their use for recreational activities in and around freshwaters (WHO 2003) and water supply for drinking and spray irrigation (WHO 2004). A diverse array of cyanotoxins is produced with differing impacts on health (Codd, Morrison & Metcalf 2005). The concentration of particular toxins is dependent on both the species or strain of cyanobacteria present and the environmental conditions (Dolman et al. 2012). Currently, many cyanotoxins are not routinely measured, so the majority of assessments of health risks associated with cyanobacterial blooms in lakes and reservoirs are based on the abundance of cyanobacteria as cell densities or biovolume, rather than cyanotoxin concentrations (WHO 1999, 2003, 2004). Their abundance can, therefore, be used as a direct indicator of the 'functional quality' of freshwater services.

There is strong evidence that the development of cyanobacterial blooms has been increasing in recent decades (Smith 2003), and this is widely believed to be primarily due to nutrient enrichment, especially phosphorus (Downing, Watson & McCauley 2001; Schindler et al. 2008), but also in response to warmer and drier summer conditions (Weyhenmeyer et al. 2002; Paerl & Huisman 2008) and more stable stratification (Wagner & Adrian 2009). Nutrient concentrations in the water, often phosphorus, set the capacity for cyanobacteria standing crops and are probably the most manageable pressure affecting their abundance (Schindler et al. 2008). Developing a more quantitative understanding of the effect of nutrients on cyanobacterial capacity within freshwaters would, therefore, provide important knowledge for restoring and sustaining a safe, clean water supply. Having clear management targets for nutrients to limit cyanobacteria could also support mitigation strategies in relation to the less manageable pressure of climate change.

There is a vast amount of quantitative empirical evidence demonstrating increasing phytoplankton abundance under increasing nutrient concentrations, with particularly strong relationships with total phosphorus (Dillon & Rigler 1974; OECD 1982; Phillips *et al.* 2008). There are also a few studies examining more specifically the relative

(%) abundance of cyanobacteria in relation to nutrients (Downing, Watson & McCauley 2001; Ptacnik et al. 2008; Wagner & Adrian 2009). There are, however, far fewer extensive empirical studies quantifying the actual abundance of cyanobacteria in relation to nutrients, despite this being directly relevant to water use. Most studies of actual abundance are of individual or small groups of lakes (Mischke 2003; Nõges et al. 2008), although Carvalho et al. (2011), De Hoyos, Negro & Aldasoro (2004) and Dolman et al. (2012) examined cyanobacteria abundance in relation to nutrients in about 150 UK lakes, 47 Spanish reservoirs and 100 German lakes, respectively. In this paper, we analyse the actual abundance of cyanobacteria from a data set of over 1500 European lakes, substantially larger than any other analysis reported in the literature. With this data set, we are able to provide robust quantification of the abundance of cyanobacteria in relation to total phosphorus (TP) concentrations. In particular, we highlight the novel use of quantile regression modelling for understanding the maximum potential capacity, or upper quantile response, of cyanobacteria in relation to phosphorus and the use of a range of quantile responses, alongside the World Health Organisation (WHO) cyanobacteria thresholds for recreational waters (WHO 2003), for setting robust phosphorus targets for lake management in relation to water use. The focus on phosphorus is because phytoplankton and specifically cyanobacteria appear to be more strongly related to total phosphorus concentrations, rather than total nitrogen (Phillips et al. 2008; Carvalho et al. 2011). For this reason, total phosphorus is the most widely targeted nutrient for management of eutrophication and particularly for minimizing algal blooms.

Materials and methods

DATA

The EC Water Framework Directive has enabled the collation of large biological data sets following standard sampling and counting methodologies. As part of the EC WISER Project (http://www. wiser.eu/), phytoplankton composition data were collated from >1500 lakes spanning 4 European biogeographical regions and 16 countries (Table 1 and Appendix S1 in Supporting Information) (Moe et al. 2012). The bulk of the data was from low and mediumalkalinity lakes in Northern Europe (855 lakes) and high-alkalinity lakes in Central-European or Baltic countries (599 lakes) (Table 1). Both cyanobacterial abundance (biovolume) and nutrient data were summarized as a summer mean using data spanning the months July, August and September. For each lake, only the last year of available data was used in the analysis to avoid bias of lakes with many years of data. Samples for phytoplankton and TP were predominantly collected by integrated tube samples from the middle of the lake. Phytoplankton samples were counted after preservation with Lugol's iodine solution. In general, 400 counting units were measured across magnifications usually using a combination of low-magnification full-chamber counts, intermediate-magnification transects and high-magnification fields of view.

Table 1. Number of lakes with cyanobacteria and total phosphorus (TP) data, by region, country and alkalinity type (L = low, M = medium, H = high and U = unknown) and percentage of these lakes where recreational use is at risk (mean summer biovolume exceeding the World Health Organisation (WHO 1999) low risk threshold of 2 mm³ L⁻¹)

Region	Country	L	M	Н	U	Total	% at risk
Central	Belgium			9		9	33
	Germany			223		223	47
	Denmark		1			1	0
	Estonia	3	5	46		54	17
	France		3			3	0
	Ireland		1	33	10	44	8
	Lithuania				39	39	15
	Latvia				63	63	32
	Netherlands			47		47	53
	Poland			49		49	27
	United		3	64		67	17
	Kingdom						
Central Total	C	3	13	471	112	599	37
Eastern	Hungary			18		18	22
Mediterra- nean	Spain	9	8	16	1	34	23
Northern	Finland	104	47		5	156	5
	Ireland	6	2			8	8
	Norway	308	147	44	3	502	3
	Sweden	97	21	7		125	3
	United	51	12	1		64	17
	Kingdom						
Northern Total	J	566	229	52	8	855	5
Grand Total		578	250	557	121	1506	15

Counts and biovolume estimates of cells, colonies and filaments broadly followed the Utermöhl approach outlined by CEN (2004). TP analysis was carried out by spectrometric determination using ammonium molybdate (ISO 2004).

STATISTICAL ANALYSIS

The majority of biological response modelling approaches in current use [e.g. simple linear least-squares regression, generalized linear models (GLM) or generalized additive modelling (GAM)] are based on the estimation of mean or median responses to environmental factors. One method that models the relationship between variables at different levels of a distribution is quantile regression (Koenker & Bassett 1978). Quantiles can be estimated and can be used to identify relationships that least-squares regression of mean responses may not effectively represent. In this study, we used quantile regression to model responses of cyanobacterial abundance (actual biovolume) against TP concentrations. A number of percentile cyanobacterial responses were modelled: 10%, 25%, the median (50%), 75%, 90% and 95%. Modelling high quantiles, such as the 95%, may better represent the maximum capacity of cyanobacteria for a given TP concentration in comparison with lower quantiles. Linear and nonlinear parametric and nonparametric quantile regressions were all applied to the data in R (R Development Core Team 2010), using routines available in the quantreg package (Koenker 2009). Nonparametric quantile regression was applied using the function rass in the quantreg package which fits a smoothing spline using a roughness penalty term. The parametric nonlinear quantile regression models are described further below. Simple linear regression and GAMs of the mean response (Wood 2006, 2008) were also examined for comparison with the quantile models. Cubic regression splines were used as the type of smooth function. The GAM was fitted using a normal distribution and an identity link function.

Nonparametric regression models are based on rank differences and, therefore, cannot be used to describe or visualize the relationship and do not enable predictions from model equations. Therefore, parametric, nonlinear quantile regression was applied to the data sets to enable this using the interior point algorithm for finding the best-fitting model solution (Koenker & Park 1994). For the significant quantiles, the following 3-parameter asymptotic exponential equation was generally used:

 $Log_{10}(Cyanobacteria\ biovolume\ +1) = a/[1 + b*exp(-c*Log_{10})]$

where a = cyanobacteria biovolume where the fitted curve begins to reach a maximum.

b = a - position on the y-axis where the convex curve starts.

c = position of x-axis where the initial change in slope occurs, that is, where the concave curve starts.

For the 25% quantile model, a 2-parameter asymptotic exponential model was fitted to the data:

 $Log_{10}(Cyanobacteria biovolume+1) = [a * exp(b * log_{10}(TP))]$ where a is the intercept of the line and b is the slope of the line

Akaike information criterion (AIC) values for the linear and the nonparametric quantile regression models were used to compare the different quantile model fits to the data to distinguish the best models for prediction purposes, the model having the lowest AIC being the best. For parametric nonlinear quantile regression, AIC values cannot be calculated for each quantile; therefore, deviance is reported as a measure of goodness-of-fit. For a continuous variable, such as cyanobacterial biovolume, deviance is calculated as:

$$D = \sum_{i=1}^{n} (y_i - \mu)^2$$

where n is the sample size, y_i is the observed data point, and μ is the mean of the v variable. The lower the deviance value, the better the fit of the model to the data set.

WHO GUIDELINES

In this study, the quantile modelling approach is combined with WHO thresholds for cyanobacterial abundance in recreational waters to identify the likelihood of exceeding health alert thresholds. WHO (1999, 2003) recommend 'a series of guideline values associated with incremental severity and probability of health effects', and these values are then defined for three health alert categories: low, moderate and high. A high alert (or high probability of adverse health effects) is assigned when surface scums are present, where cell densities and toxin concentrations can be very high and severe health risks are possible. Cyanobacteria cell densities of 20,000 and 100 000 cells mL⁻¹, respectively, are associated with 'low' and 'moderate' probabilities of adverse

health effects, associated with less severe symptoms such as skin irritations and gastrointestinal illness. These cell densities can be converted to a biovolume (mm 3 L $^{-1}$) by multiplying by a typical cyanobacterial cell volume. We have adopted here the equivalent biovolumes of 2 mm 3 L $^{-1}$ and 10 mm 3 L $^{-1}$, outlined in WHO (1999), based on a spherical cell with a diameter of 5.7 μ m.

Results

Exploratory analysis of the data highlighted that cyanobacteria are generally absent, or in very low abundance, in low-alkalinity lakes (<200 μ equiv. L^{-1}) with the summer median abundance and upper percentiles all clearly increasing with increasing alkalinity class (Fig. 1). Low-alkalinity lakes are predominantly found in Northern Europe, where only 5% of lakes have mean summer biovolumes exceeding the WHO low risk threshold of 2 mm 3 L^{-1} ; a much higher proportion of lakes (37%) are at risk in Central Europe, where high-alkalinity lakes predominate (Table 1).

MEAN RESPONSE

Considering the whole lake data set together, there is a positive linear relationship between (\log_{10}) cyanobacterial biovolume and (\log_{10}) TP concentrations ($r^2 = 0.295$, P < 0.001, deviance 138-7). Despite the significance, the relationship is still relatively weak. Because of the general absence or low abundance of cyanobacteria in low-alkalinity lakes, further analysis was, therefore, carried out on a subset of 807 medium- and high-alkalinity lakes drawn from all regions. A GAM (Fig. 2; $r^2_{adj} = 0.342$, P = <0.001, deviance = 128-9) and a 3-parameter nonlinear model (Fig. 3; deviance = 129-4) of the mean cyanobacterial response fit the data better. Both nonlinear models indicate a take-off in the mean cyanobacterial response above a TP concentration of approximately 10 µg L⁻¹. For the GAM model, a strong positive

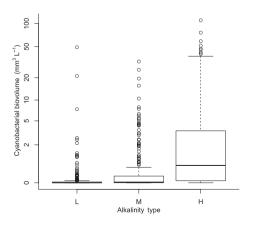


Fig. 1. Boxplot of cyanobacterial biovolume (\log_{10} mm³ L⁻¹) in lakes of low, medium and high alkalinity (<0·2, 0·2–1·0, >1·0 mequiv. L⁻¹, respectively).

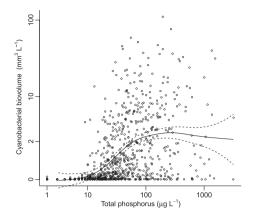


Fig. 2. Generalized additive model (GAM) for cyanobacteria biovolume in response to total phosphorus for medium- and high-alkalinity lakes (n = 807).

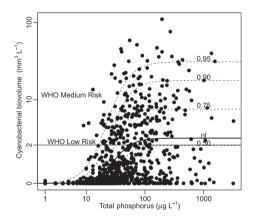


Fig. 3. Scatter plot for \log_{10} cyanobacteria and \log_{10} total phosphorus for medium- and high-alkalinity lakes (n = 807). Quantile regression curves (0·50–0·95) using a fitted 3-parameter sigmoid nonlinear model are displayed. nl = nonlinear regression fit to mean of data. Thresholds relating to approximate WHO (2003) low and medium risk thresholds are also indicated.

response is apparent up to about 300 $\mu g \ L^{-1}$ (Fig. 3), whereas for the parametric nonlinear model, there is a flattening of the mean response at a threshold of about 100 $\mu g \ L^{-1}$ (Fig. 2). Below about 5 $\mu g \ L^{-1}$ and above about 300 $\mu g \ L^{-1}$, there are few data points and, therefore, less confidence in the modelled relationships outside this TP range (Fig. 2).

QUANTILE RESPONSES – MEDIUM- AND HIGH-ALKALINITY LAKES

Comparison of AIC values for linear and nonlinear non-parametric quantile regression models highlight the much poorer fit of linear models for most quantiles (Table 2). The exceptions to this were the models for the lowest quantiles examined (0.05, 0.10 and 0.25), which were linear and had the lowest AIC values (best fit). This was, however, a statistical artefact due to the very large

Table 2. Akaike information criterion (AIC) values for both linear and nonparametric quantile regression models relating cyanobacterial biovolume to TP concentrations in medium- and high-alkalinity lakes

	Quantile								
Model type	0.05	0.10	0.25	0.50	0.67	0.75	0.83	0.90	0.95
Linear quantile Nonparametric quantile	-185·5 6·5	-99·1 20·4	160·2 205·1	549·6 496·4	812·2 685·4	952·1 798·6	1110·1 962·2	1315·8 1184·2	1560·9 1427·4

proportion of low or zero values for cyanobacteria biovolume. These lower-quantile relationships between cyanobacteria biovolume and TP were more or less flat, and there was, therefore, no significant relationship between the two variables, for example 0.05 (P = 0.98), 0.10 (P = 1.00) quantiles. For all higher quantiles examined (0.25 and above), nonlinear, nonparametric regression models all had a highly significant relationship between cyanobacteria biovolume and TP (P < 0.001).

Three-parameter asymptotic exponential models were the best fit for the 0.50-0.95 quantile models and the nonlinear mean response, whereas only a 2-parameter model was selected for the 0.25 quantile (Table 3). The resulting nonlinear parametric regression models for quantiles 0.5-0.95 are shown in Fig. 3, and deviance values and parameter estimates are given in Table 3. The models shown are those with the deviance minimized. Like the nonlinear model for the mean response, all the quantile models indicate a take-off in the cyanobacterial response above a threshold TP of approximately 10 µg L⁻¹ and a flattening of the response at a threshold of about $100 \mu g L^{-1}$ (Fig. 3). The biggest difference between the different quantiles is in the slope of the increase, with the 0.95 quantile showing the steepest increase whilst the 0.50 quantile the shallowest increase. Additionally the quantiles differ greatly in terms of parameter a: the estimated cyanobacteria value where the fitted curve begins to reach a maximum (Table 3, Fig. 3). For example, the 0.50 quantile plateaus at just below 2 mm3 L-1, the WHO

(1999) low risk threshold, at TP concentrations of 100 μ g L⁻¹ or greater.

APPLICATION OF QUANTILE RESPONSES FOR PREDICTING BLOOM CAPACITY

The upper quantiles (e.g. 0.95) provide estimates of the potential maximum capacity of cyanobacteria in response to increasing TP concentrations (Table 4). The capacity for cyanobacteria increases with increasing TP, with the relationship levelling off at TP concentrations $>150 \mu g L^{-1}$. The 95% quantile model indicates that at 16 μ g L⁻¹, 5% of lakes will exceed the low risk threshold and at 32 µg L⁻¹ 5% of lakes will exceed the medium risk threshold (Table 4).

NUTRIENT TARGETS IN RELATION TO HEALTH THRESHOLDS

The equations in Table 3 can be used to determine the proportion of lakes exceeding the low and medium risk WHO thresholds for cyanobacteria for a given TP concentration (Table 5; Fig. 4). Only significant quantile curves that pass through these risk threshold levels can be used. The results indicate that at a TP concentration of about 22 µg L⁻¹, 10% of lakes exceeded the WHO low risk threshold, at 31 µg L⁻¹ this increased to 25% of lakes, and at 41 μ g L⁻¹ 33% of lakes were above the WHO low risk threshold. Similarly 10% of lakes exceeded

Table 3. Parameter estimates derived using nonlinear quantile regression for medium- and high-alkalinity lakes. Estimates for nonlinear mean response are also shown.

	Deviance	Parameter a	Parameter b	Parameter c	
Model		$\pm SE$	$\pm { m SE}$	$\pm SE$	
0.25	61.95	-5.41 ± 0.42	1.04 ± 0.38		
0.50	97.23	0.47 ± 0.05	1500579 ± 0	8.97 ± 0.23	
Mean (nonlinear)	102-92	0.56 ± 0.03	9493 ± 15020^{NS}	$6\cdot23\pm1\cdot12$	
0.60	100.91	0.64 ± 0.06	86850 ± 0	$7{\cdot}18\pm0{\cdot}18$	
0.67	98.90	0.80 ± 0.05	99913 ± 0	$7{\cdot}38\pm0{\cdot}21$	
0.75	90.22	0.92 ± 0.04	98649 ± 0	7.78 ± 0.16	
0.83	75.51	1.03 ± 0.05	17577 ± 0	6.79 ± 0.15	
0.90	55-48	1.28 ± 0.08	3695 ± 0.4	5.77 ± 0.17	
0.95	34.15	1.51 ± 0.07	$1219 \pm 529*$	5.23 ± 0.36	

Coefficients in bold all highly significant (P < 0.01).

^{*=} P < 0.05, NS = not significant.

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Table 4. 95% quantile fitted values showing the changing cyanobacterial biovolume (mm 3 L $^{-1}$) with change in total phosphorous (μ g L $^{-1}$). The fitted quantile reaches an asymptote at 31·5 mm 3 L $^{-1}$ of cyanobacteria biovolume

Total Phosphorus $(\mu g \ L^{-1})$	Cyanobacteria capacity (95%) (mm 3 L $^{-1}$)		
0	0		
10	0.5		
12	1		
16	2		
24	5		
32	10		
50	20		
150	30		
350	31		

Table 5. Total phosphorus (TP) concentrations for a given likelihood (quantile) of being below low and medium risk World Health Organisation (WHO 1999) threshold levels for cyanobacteria volume. TP concentrations are obtained from the fitted quantile regression models to the medium- and high-alkalinity lakes

WHO Threshold	Quantile	% exceeded	TP
Low	0.57	43	57.8
	0.60	40	54.4
	0.63	37	45.8
	0.67	33	41.0
	0.75	25	30.7
	0.78	22	29.4
	0.83	17	26.2
	0.87	13	22.8
	0.90	10	21.6
	0.95	5	16.3
	0.98	2	13.2
Medium	0.87	13	58.3
	0.90	10	47.7
	0.95	5	32.4
	0.98	2	22.7

the WHO medium risk threshold, at TP concentrations of 48 $\mu g \ L^{-1}$.

Discussion

Despite the wide variety of life strategies between different cyanobacterial species and the consequent variety of environmental factors shaping their abundance (Dokulil & Teubner 2000; Reynolds 2006), it is still of great importance to understand more fully the response of this whole group of algae in relation to nutrient pressures. The reason for this is that many cyanobacterial species produce hazardous toxins and this has led to the WHO guidance for recreational and drinking waters that outline threshold densities of cyanobacteria as a whole, rather than for individual species, in relation to threats to water usage (WHO 1999, 2003, 2004). There is widespread acceptance amongst freshwater ecologists that cyanobacteria increase in abundance with increasing nutrient concentrations.

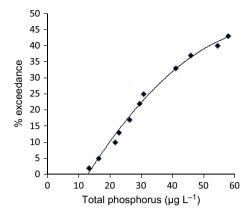


Fig. 4. Relationship between% lakes exceeding World Health Organisation (WHO 1999) low/medium risk threshold for cyanobacterial biovolume (2 mm 3 L $^{-1}$) in relation to total phosphorus (TP)

Most published literature quantifying the relationship has, however, focused on the relative percentage abundance of cyanobacteria (e.g. Downing, Watson & McCauley 2001; Ptacnik et al. 2008). It is, however, the actual biomass of cyanobacteria that affects the provision of safe, clean water for recreation and water supply (WHO 2003, 2004). Our study specifically addresses this, providing robust quantitative relationships between TP and actual cyanobacterial biovolume in European lakes and reservoirs. The exploratory analysis highlighted that cyanobacteria are generally absent, or in very low abundance, in low-alkalinity lakes, particularly in Northern Europe. The preference of cyanobacteria for neutral to alkaline waters is generally recognized and has been nicely demonstrated in previous in-lake experimental studies (Reynolds & Allen 1968; Shapiro 1984), but our exploratory analysis highlights effectively that this is a broad pattern that holds true for many lakes. It was for this reason that our further analysis was carried out on data from medium- and high-alkalinity lakes only. A previous study (Carvalho et al. 2011) of lakes in the UK, of which 97 were mediumand high-alkalinity lakes, indicated that the mean response of cyanobacteria to TP was linear, although with cyanobacteria largely absent below 20 µg L⁻¹. Our current more extensive analysis of more than 800 mediumand high-alkalinity lakes also covers a broader nutrient gradient than that of Carvalho et al. (2011). In this study, the mean response indicated a nonlinear relationship with TP. One reason for the better fit of the nonlinear model to the mean response in this study appears to be because there were more lakes included with very low (<10 μ g L⁻¹) and very high (>100 μ g L⁻¹) TP concentrations, and the response appears to flatten out at these extremes. Dolman et al. (2012) also show a flattening out of the median cyanobacteria response above 100 μ g L⁻¹ TP, in a study of 102 German lakes. Even though the relationship between TP and the mean response of cyanobacteria biovolume was highly significant, it was evident that there was a large amount of scatter in the data. For this reason, modelling the mean response is not the ideal approach to adopt; quantile regression is more appropriate when several factors may limit a population at many sites (Cade & Noon 2003).

QUANTILE MODELS

There are many possible factors limiting cyanobacteria abundance in freshwaters, and many of these, such as water retention time or water colour, are not routinely recorded. Given this reality, there will be unequal variation across a data set when describing the relationship between a population response and only one of these factors. Examining a number of quantile responses allows us to compare how a range of cyanobacteria responses, from the minimum to maximum response, are affected by TP. This range in responses was demonstrated by the fact that linear models fitted the lower quantiles, a 2-parameter nonlinear model was the best fit for the 25%, and 3-parameter nonlinear models were the best fit for mean, median and higher quantiles. The fact that the lowerquantile relationships between cyanobacteria biovolume and TP were more or less flat, and not significant, indicates that a small percentage of lakes always have no, or little, cyanobacteria, irrespective of TP concentrations. Clearly other factors limit cyanobacteria populations in the summer months in these lakes. This could include factors limiting population growth (e.g. competition with macrophytes or other algae for light), or factors affecting population loss processes (e.g. flushing, grazing, parasitism) (Reynolds 2006; Carvalho et al. 2011). For example, long-term monitoring of individual lakes has demonstrated that cyanobacteria are never abundant in lakes or reservoirs with a retention time <30 days (Reynolds & Lund 1988).

Variability may also reflect the fact that a number of cyanobacterial genera that contribute significantly to total biovolume in European lakes may be affected by TP, or other limiting factors, differently from each other and also differently in different lake types. For example, colonial gas-vacuolate genera, such as Microcystis, are known to migrate vertically in response to nutrient limitation, potentially allowing them to exploit deep, hypolimnetic sources of P, irrespective of epilimnion concentrations (Brookes & Ganf 2001). The slopes and plateaus of the different quantile models all vary, although all models show that the biggest increase in cyanobacterial abundance occurs in the TP range from about 20 μ g L⁻¹ up to about 100 µg L⁻¹. This is an important finding for achieving successful restoration, as it indicates that nutrient concentrations need to be within this range before any significant declining response is likely to be observed in cyanobacterial abundance. The use of these different quantile responses to two specific applications for lake management in relation to recreational services is described further below.

APPLICATION OF QUANTILE RESPONSES FOR PREDICTING BLOOM CAPACITY

In the context of harmful cyanobacterial blooms, it is important to know the maximum cyanobacterial abundance that a lake could potentially support, rather than the mean or relative% abundance. Modelling the upper bounds of species-environment relationships relates much more to the most limiting resource (Cade & Noon 2003; Vaz et al. 2008), and for phytoplankton in many temperate lakes this is often phosphorus (Phillips et al. 2008; Schindler et al. 2008). The wide scatter of points around the mean or median responses clearly indicate that TP is not the single dominating factor limiting cyanobacterial abundance in lakes, but the higher quantile models may still better represent the capacity for cyanobacterial abundance in relation to phosphorus, given a lack of other limiting factors, such as loss rates to grazing or flushing. Using the 95% quantile to represent the potential maximum capacity, our results clearly demonstrate that there are small probabilities for quite substantial cyanobacterial populations that exceed WHO (1999) health thresholds at relatively low TP concentrations. The fact that 5% of medium- and high-alkalinity lakes exceeded the low and medium risk thresholds at TP concentrations less than 35 $\mu g L^{-1}$ supports anecdotal accounts of blooms in relatively nutrient-poor waters that often cause surprises to local lake managers. At the other extreme, the 95% quantile shows that, in medium- and high-alkalinity lakes, cyanobacterial populations reach a maximum capacity of about 30 mm3 L-1 at TP concentrations of about 150 μg L⁻¹. Further increases in TP have little effect on capacity, indicating that some other factor is limiting their abundance, in particular light limitation (self-shading) (Reynolds & Maberly 2002) or nitrogen (Dolman et al. 2012).

NUTRIENT TARGETS IN RELATION TO RECREATIONAL **HEALTH THRESHOLDS**

Given our extensive data set, the quantiles can also be used to represent the likelihood of cyanobacterial abundance exceeding the WHO recreational health alert thresholds for a given TP concentration. Although only a small proportion of lakes exceed the low risk threshold at low TP concentrations, the steepest rise in% exceedance occurs between TP concentrations of about 20 and 30 $\mu g L^{-1}$ TP (approximately 10–25% exceedance). It was also clear that in about 50% of lakes the low risk threshold is not exceeded, irrespective of summer TP concentrations above $100 \mu g L^{-1}$. What level of precaution is chosen in terms of nutrient management is a local, social or economic decision and will be affected by the use of the water body. A TP target of 20 µg L⁻¹ should result in a low probability of risk (<10% exceedance) and may be appropriate for lakes or reservoirs of high importance for recreation or water supply. It is, however, important to

point out that the nutrient targets outlined here are based on the analysis of a population of medium- and highalkalinity lakes and reservoirs and are, therefore, most applicable for setting nutrient targets in these lake types at a national, regional or European landscape scale. Given the approach used to derive them, these models are less certain for individual lake management, as discussed by Reynolds (1980) in relation to the limitations of Vollenweider models for predicting chlorophyll concentrations in lakes. For individual lake management, it is advisable that these targets are considered in relation to other site-specific factors that can affect sensitivity to cyanobacteria (e.g. retention times). For example, Wagner & Adrian (2009) in a detailed single lake study highlighted that climatic factors had significant positive effects on cyanobacterial dominance when TP concentrations rose above 70 μ g L⁻¹. This further emphasizes the value of setting nutrient targets that minimize the potential capacity for cyanobacterial blooms to help mitigate future climate changes.

APPLICATION FOR ASSESSING RECREATIONAL QUALITY OF FRESHWATERS

Currently, inland bathing water quality in the European Union (EU), and many other countries around the world, is formally assessed using only microbiological parameters (e.g. intestinal enterococci and E. coli concentrations). Article 8 of the EU Bathing Water legislation (EC 2006) does mention that appropriate monitoring should be carried out to enable timely identification of cyanobacterial health risks, but provides no formal guidelines on how this should happen. Our study highlights the magnitude of the number of European lakes exceeding WHO health thresholds, with 7 countries reporting over 25% of monitored lakes exceed the WHO low risk threshold (Table 1). There is clearly, therefore, a need for more informed assessment of bathing water quality or other recreational activities involving water contact. The WHO thresholds adopted in this study (WHO 1999, 2003, 2004) are not the only targets that exist. For example, recent guidelines from Australia (NHMRC 2008) have a level 1 alert threshold set at a total cyanobacterial biovolume equivalent of 4 mm³ L⁻¹, although they do recognize that skin irritations have been observed at densities as low as $0.4 \text{ mm}^3 \text{ L}^{-1}$ (Pilotto et al. 2004) and that swimmers wearing wetsuits often accumulate more algae and are more prone to skin irritations. The parameterized quantile models can be applied to any agreed cyanobacterial thresholds, to indicate the likely risk of exceedance of the specific threshold for a given TP. This is particularly useful for current or future predictions of recreational quality at broad geographical scales. Nutrient data are much widely available than phytoplankton data for many lakes and reservoirs and can also be readily modelled from catchment data (Duethmann et al. 2009). So, based on an agreed risk level of exceeding the cyanobacterial

threshold, the parameterized models can also be used to assess recreational quality across broad geographical scales. One example where this could be applied is in current attempts at mapping ecosystem services of different habitats, including recreational quality, across Europe (Maes *et al.* 2012). Irrespective of specific uses, developing a more quantitative understanding of the effect of phosphorus on cyanobacterial abundance in freshwaters provides important knowledge for restoring and sustaining a safe, clean water supply for multiple uses. Our models can be used to set phosphorus targets for sustaining the delivery of services and provide different levels of precaution that can be chosen dependent on the importance of the service provision.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed description of dataset.

Table S1. Number of lakes with cyanobacteria and TP data, by region, country and alkalinity type (L = Low, M = Medium, H = High and U = Unknown). Statistics on mean depth (minimum, mean and maximum) and surface area (minimum, mean and maximum) of lakes within each country are provided.

Table S2. Number of lakes sampled by country and year.