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Chlorophyll - nutrient relationships of different lake types using a large European dataset

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Abstract

In Europe there is a renewed focus on relationships between chemical determinands and ecological impact as a result of the Water Framework Directive. In this paper we use regression analysis to examine the relationship of growing season mean chlorophyll a concentration with total phosphorus and total nitrogen using summary data from over 1000 European lakes. For analysis, lakes were grouped into types with three categories of mean depth, alkalinity and humic content. The lakes were also divided into broad geographic regions covering Atlantic, Northern, Central/Baltic and for some types the Mediterranean areas of Europe. Chlorophyll a was found to be significantly related to both total phosphorus and total nitrogen, although total phosphorus was almost always found to be the best predictor of chlorophyll. Different nutrient chlorophyll relationships were found for lakes according to mean depth and alkalinity, although no significant effect of geographic region or humic content was found for the majority of lake types. We identified three groups of lakes with significantly different responses. Deep lakes had the lowest yield of chlorophyll per unit of nutrient, low and moderate alkalinity shallow lakes the highest and high alkalinity lakes were intermediate. We recommend that the regression models provided for these three lake groups should be used for lake management in Europe and discuss the limitations of such models.

Introduction

The introduction of the Water Framework Directive (2000/60/EC) in Europe has focused the attention of many lake managers and scientists on relationships between ecological status and anthropogenic pressures. For lakes, nutrients remain one of the key pressures influencing European lakes and one of the most obvious and well known effects that need to be quantified is the impact that elevated nutrients have on phytoplankton biomass.

Chlorophyll a concentration is a widely used measure of phytoplankton biomass and since the founding papers of Sakamoto (1966) and Dillon & Rigler (1974) there have been many studies showing strong empirical links between chlorophyll and nutrients, particularly phosphorus (cf. Prairie et al., 1989). The most widely known relationships are those from the OECD study (Vollenweider & Kerekes, 1980) and these are often used to underpin decisions about lake management (Ryding & Rast, 1989). Reynolds (1980) has highlighted the limitations of such models for individual lake predictions, but their value to lake managers, who need to make decisions with limited data, is undeniable.

One problem with the published relationships is the substantial variability of the parameters generated from different regression analyses. These differences are due to the many influences on the nutrient chlorophyll relationship. Regressions drawn from specific lake districts are particularly appropriate for making predictions about lakes within those districts, but they may be of less use for lakes in other areas. Conversely, large data sets will be influenced by many and various factors, all of which will appear as increased variation. In this paper we present the results of the analysis of a large data set drawn from a wide variety of national European data archives. In particular we explore the variation of nutrient chlorophyll relationships in different lake types with a view to providing a set of regression equations that can be used to underpin lake nutrient management decisions for European lakes.

Materials and Methods

Data for this study were gathered from national data archives from individual European countries, as a basis for studying relationships between biological and chemical elements in European lakes as part of the EU project REBECCA (Moe et al., this issue). As part of the WFD Common Implementation Strategy (Van de Bund et al., 2004) lakes have been divided into 6 geographic regions. Individual sample data were available from 16 countries, spanning a period from 1988 to 2004. Five of the six regions were represented, although relatively few data were available from the Mediterranean region, and the data set was dominated by data from countries in northern, and to a lesser extent central Europe.

Chlorophyll a (Chl), total phosphorus (TP) and total nitrogen (TN) data were summarised for each lake as a single mean value for a common "growing season" of April – September. In a large data set drawn from many different sources, different sampling frequencies could influence summary statistics. To minimise noise, only lakes with more than three sampling occasions during this growing season were selected, and data were summarised by site year and month and the above three determinands matched prior to calculation of a single mean for each lake. This ensured that only matched summary data for Chl, TP and TN contributed to the final mean value. Data for all available years and sites within a lake contributed to a final single lake average value for each of Chl, TP and TN, thereby obtaining only one single value per lake for each parameter in the regression analyses.

This resulted in a data set of 1138 lakes, substantially larger than any other reported in the literature that we are aware of (cited in table 2). As pointed out by Praire et al. (1989) this brings with it additional uncertainties, caused by different geographical regions, climate and sampling strategies. We will examine the effect of region and lake types, and thus assigned each lake into one of 9 core types based on alkalinity and mean depth and 3 sub-types based on colour (Table 1). Data for alkalinity, depth and colour were taken from national data archives, collated by Moe et al. (2008, this issue). These types were identified by a range of European experts during the WFD intercalibration process and represent the best available agreed typology that is likely to minimise natural biological variation in European lakes.

Chlorophyll nutrient relationships , denoted as Chl = f(TP), Chl = f(TN) and Chl = f(TP,TN), were derived using linear least squares regression. Prior to analysis all data were logarithmically transformed (base 10) to ensure their homogeneity of variance, as is common practice for data of this type. We investigated the effects of categorical variables lake type, geographic region and humic content on these relationships using univariate General Linear Modelling (GLM). The model was run with Chl as dependent variable, TP as covariate and each of the above categorical variables as fixed factors. Analysis of Variance (ANOVA) was used to test the significance of the factor on the slope, intercept and their interactions. Type III sums of squares were used to test significance, which had the advantage that they are not dependent on the frequency of observations in each group (Field, 2005).

Having identified which type factors significantly influenced the regression, we compared the resulting regression equations to identify which types had similar regression coefficients. Lake types with similar coefficients were then re-grouped and the general linear model (GLM) repeated to check that the type factor was no longer significantly influencing the regression relationship. Thus, we were able to identify the key factors influencing the nutrient Chl relationship and identify appropriate groups of lake types.

Prior to analysis, we investigated the general shape of the relationships between variables using LOWESS techniques (Cleveland, 1979). This enabled us to restrict regression to a range of nutrient concentrations where the data were linearly related. For Chl = f(TP) we therefore restricted regression to data where TP < 100 $\mu g\ l^{-1}$ and for Chl = f(TN) where TN < 1700 $\mu g\ l^{-1}$. For Chl = f(TP,TN) no restrictions were made as our purpose was to identify if the use of both nutrients provided an effective model for the whole data range. We tested the significance of including a second predictor variable using ANOVA. As TP and TN might be correlated, we tested for the variance inflation factor (VIF), which is a good indicator of whether one predictor has a strong linear relationship with other predictors. Where the VIF was <10 we concluded that predictor variables were not strongly related (Myers 1990).

We investigated the relative power of TP and TN in predicting Chl for different lake types using stepwise multiple regression, comparing regression coefficients as values standardised by standard deviation units (β coefficients) to make them independent of scale. Prior to analysis, the data were screened by removing samples with reported values of Chl or TP of <1.0 $\mu g\ l^{-1}$ as we considered these were likely to be errors in the source data. We also excluded results where the Chl: TP ratio was >1.0, which was the 99th percentile of the whole data set.

To explore the effect of TN:TP ratios, proposed by several studies as important factors influencing the relationship between nutrients and chlorophyll (Nűrnberg & Shaw, 1999), we grouped data into 5 TN:TP categories (≤10, >10≤17, >17≤25, >25≤50, >50). We chose the first two categories as they are widely reported values at which nitrogen limitation of phytoplankton biomass may occur (Forsberg & Ryding 1980); the others are convenient categorical divisions. Analysis was carried out using SPSS v14.

Results

After data screening > 1000 typed pairs of data were available for analysis (1129 TP vs. Chl; 1138 TN vs. Chl and 1077 TN & TP vs. Chl). Chlorophyll, phosphorus and nitrogen concentrations ranged over 2 orders of magnitude, increasing markedly as lakes get shallower and to a lesser extent as alkalinity increases (Fig 1a-c). In low and moderate alkalinity lakes there was also a marked effect of humic content with the highest concentrations of all of these parameters in polyhumic lakes and the lowest in clear water lakes. In high alkalinity lakes, however, the effect of humic content was either non-existent or even reversed in high alkalinity very shallow lakes. The ratio of TN:TP ranged from <2 to >100, with different ranges characteristic of each lake type (Fig 1d). TN:TP was highest in low and moderate alkalinity, deep lakes and became progressively lower as depth decreased and alkalinity increased. Polyhumic and humic lakes nearly always had lower TN:TP ratios than clear water lakes, and a substantial proportion of lakes in the coloured, very shallow lake categories had values below 17 and a minority of lakes below 10. The effect of colour on the TN:TP ratio was confirmed by 2 way ANOVA, which showed significant effects of both lake type (F =

12.1 p <0.001) and humic type ($F=9.7$ $p<0.001$) with post hoc Bonferroni tests showing significant differences in mean N:P ratios for all comparisons of humic categories.

Regression relationships

Scatter plots for the relationships Chl = f(TP) and Chl = f(TN) are shown in figure 2. The LOESS fitted line shows non-linearity in both relationships. There is slight indication of a sigmoidal response, but the most marked non-linearity is the reduction in slope at high nutrient levels. This is most marked for TN, but also occurs for TP. The upper point of inflection for Chl = f(TP) occurs at ca. TP = 100 $\mu g\ l^{-1}$ and for Chl = f(TN) at TN =1700 $\mu g\ l^{-1}$. Asymptotic behaviour of Chl=f(TP) is widely reported, occurring typically at around this TP concentration (Prarie et al., 1989; Canfield, 1983), although in our case the LOESS fits do not give as clear an indication of a plateau in chlorophyll as do those of others. However, because of this we restricted the range of TP and TN concentrations in our least square regressions to concentrations of <100 $\mu g\ l^{-1}$ (TP) and <1700 $\mu g\ l^{-1}$ (TN) (Fig 3).

The regressions of all lakes taken together regardless of type were the following:

1. $\mathrm{Log_{10}\,Chl} = -0.455(\pm0.020)+1.026(\pm0.016)\ \mathrm{Log_{10}TP}$ $\quad R^2 = 0.78$ (TP <100 $\mu g\ l^{-1}$)
2. $\mathrm{Log_{10}\,Chl} = -2.828(\pm0.093)+1.355(\pm0.035)\ \mathrm{Log_{10}TN}$ $\quad R^2 = 0.58$ (TN <1700 $\mu g\ l^{-1}$)
3. $\mathrm{Log_{10}\,Chl} = -1.028(\pm0.083) + 0.792(\pm0.027)\ \mathrm{Log_{10}TP} + 0.324(\pm0.039)\ \mathrm{Log_{10}TN}$ $\quad R^2 = 0.77$

All regressions were significant ($p<0.001$) and the coefficients of determination (R^2) were similar to those reported in other published studies (Table 2). Scatter plots with the regressions are shown in Fig 4. Within the linear range of these functions, TP was a better predictor than TN, although over the full data range the combined Chl – f(TN,TP) model gave almost as good a prediction.

We also tested the use of a Chl = f(TN,TP) model restricted to the linear portion of both the TP and TN relationships.

4. Log_{10} Chl = -1.135(±(0.026) + 0.896(±0.026) Log_{10} TP + 0.322(±0.039) Log_{10} TN

R^2 = 0.80 (TP <100 μg l^{-1}, TN < 1700 μg l^{-1})

In both models collinearity was found to be low (VIF 2.6 model 3 and 2.5 model 4). For both models 3 & 4 the addition of TN provided a small, but significant (F = 68.2 $p<0.001$ model 3 and 67.4 $p<0.001$ model 4) increase in predictive power. The standardised β regression coefficients for TP were however much higher than those for TN (βTP = 0.71 βTN = 0.20 model 3; βTP = 0.75 βTN = 0.18 model 4) indicating that TP was the more influential variable.

There is a significant degree of scatter in these data and we now explore whether dividing lakes into types can account for this variation and thus provide more useful regression models. The general linear model (GLM) demonstrated that while geographic region did not influence the regressions, lake type was a significant factor in the regression models, so we repeated the regression analysis on lakes split by type (Table 3). Few of the resulting R^2 were higher than those obtained for the whole data set, but significantly different regression parameters were found. We give particular attention to the differences in slope (Fig 4). For a log-log relationship this characterises the relative rate of increase of two variables and thus the highest slopes indicate lake types where there is the greatest positive response to TP or

TN. Our all lake relationships had slopes for TP close to 1, slightly higher for TN, but in several cases the type-specific slopes were significantly different. Differences were greatest for Chl = f(TN), but for both Chl = f(TP) and Chl = f(TN), deep lakes had significantly lower slopes. In general the chlorophyll response to nutrients increases significantly as depth decreases and for shallow and very shallow lakes it decreases with alkalinity. These results suggest that predictions made without reference to type may significantly over or under estimate chlorophyll concentrations. Type specific relationships seem to offer the best approach for TN, but for TP we have divided lakes into 3 groups: 1) deep lakes, 2) moderate and low alkalinity shallow and very shallow lakes, and 3) high alkalinity shallow and very shallow lakes. Within these groups the GLM confirmed that lake type did not significantly influence the regression and the following equations (all significant $p<0.001$) represent what we consider are appropriate models for these lake groups.

5. Low and moderate alkalinity (<1mekv l^{-1}), shallow (3-15 m mean depth) and very shallow (< 3m mean depth) lakes:

   $\mathrm{Log_{10}\,Chl} = -0.528(\pm0.03) + 1.108(\pm0.02)\,\mathrm{Log_{10}\,TP}$ $R^2 = 0.81$
6. High alkalinity (>1 mekv l^{-1}), shallow (3-15 m mean depth) and very shallow (< 3m mean depth) lakes: $\mathrm{Log_{10}\,Chl} = -0.306(\pm0.10) + 0.868(\pm0.07)\,\mathrm{Log_{10}\,TP}$ $R^2 = 0.52$
7. All deep lakes (>15 m mean depth):

   $\mathrm{Log_{10}\,Chl} = -0.286(\pm0.04) +0.776(\pm0.041)\,\mathrm{Log_{10}\,TP}$ $R^2 = 0.65$

Colour from humic compounds is another factor which has been reported to influence the Chlorophyll nutrient relationship (Havens and Nűrnberg, 2004). In our data we found that TP, TN and Chl were higher in humic lakes, but GLM showed no significant effect of colour on Chl = f(TN) in any lake types. For Chl = f(TP) only one lake type (low alkalinity deep lakes) showed a humic type effect with a significantly higher slope and intercept in the humic lakes than in the clear water lakes (Fig 5). The regression equations were both significant ($p<0.001$) and are given below:

8. LAD Humic: $\log_{10} Chl = -0.733(\pm0.14) + 1.261(\pm0.15) \log_{10} TP$ $R^2 = 0.75$
9. LAD Clear: $\log_{10} Chl = -0.208(\pm0.05) + 0.639(\pm0.07) \log_{10} TP$ $R^2 = 0.42$

Effect of TN:TP ratio on regression

Lakes were also grouped in categories based on TN:TP ratio to investigate the effects of this on the regression relationships. This ratio should indicate the potential for nitrogen or phosphorus limitation, at least at the seasonal scale, and we thus might expect that where TN:TP is low, nitrogen may limit algal growth and thus TN would provide a better prediction of chlorophyll. Conversely when TN:TP is high, phosphorus is more likely to limit growth and TP would be the better predictor. To an extent we found these predictions were true. Where TN:TP is <10, TN provided a better prediction of Chl with a higher R^2 and regression slope (Fig 6). As TN:TP increased this difference is rapidly reduced, with similar R^2 and regressions slopes for either TN or TP. The highest category (TN:TP >50) Chl = f(TP) provides a better fit and has a higher slope than Chl = f(TN), indicating the clear dominance of phosphorus limitation.

Finally, using stepwise multiple regression, we investigate the relative predictive power of TP and TN if lakes were split into alkalinity, depth and humic categories. Table 4 shows the resulting values for R^2 together with the standardised β regression coefficients (in standard deviation units), which can be used to compare the relative importance of each predictor variable independent of scale. Stepwise regression selected Chl = f(TP) for the majority of lake types, but for those lake types with the lowest TN:TP ratios (humic HAVS and polyhumic MAVS) Chl = f(TN) was the preferred model. In 7 of the 19 types, Chl = f(TP,TN) was selected and for three of these (polyhumic LAS, polyhumic LAVS & humic LAVS) the β coefficients were very similar indicating that both TP and TN had equal predictive power. All of these lake types had relatively low TN:TP ratios where it might be expected that nitrogen limitation would occur. The remaining types either had TP as the single predictor variable, or if both TP and TN were selected, the β coefficients suggested that TN played a minor role in the model.

Discussion

There is a relatively wide range of parameter values available in the literature relating to regression models which can be used to estimate chlorophyll a concentration from phosphorus (Table 2). Several studies (Prairie et al., 1989; White, 1983) report values that generally predict lower chlorophyll values than those we found when we grouped all lakes together. These include the widely used equations from the OECD study (cited in Vollenweider & Kerekes, 1980). Other studies (Dillon & Rigler, 1974; Jones & Bachmann, 1976) report models yielding higher predictions of chlorophyll and these matched our all lake results more closely. Both of these studies reported slopes significantly > 1, which on a log log plot produces an increasing yield of chlorophyll as TP increases, in contrast our all lakes model had a slope close to 1, showing that the relationship was close to linear. There are less reported models for total nitrogen, but those of Nürnberg (1996) and Prairie et al. (1989) are very similar to our all lakes combined model. However, our type-specific nutrient models produced values that correspond to the full range of those reported.

For Chl=f(TP) our deep lakes model predicted the lowest chlorophyll concentrations, that are only slightly higher than those from the OECD equations. Our high-alkalinity lake model predicted higher values while the models for the other lake types, (low and moderate alkalinity shallow and very shallow lakes), predict chlorophyll values that are similar to the highest reported values. For Chl = f(TN) our deep-lake equations provide lower predicticted values than those in the literature, while the low and moderate alkalinity very shallow lakes are significantly higher. These discrepancies highlight some of the issues of log log regression relationships: they hide within them a relatively wide range of values. Reynolds (1980) identified this when he pointed out that regression models can only describe the general behaviour of lake populations, and that in reality any particular lake will have a chlorophyll yield that is influenced by a number of factors other than nutrients. None the less, these models are in many cases the only method for lake managers to determine the relationship between a nutrients, a factor they can potentially control, and algal biomass. What is important, is that managers should use an equation that is derived using data from a lake type that matches as closely as possible the lake they are concerned with.

Our data show that lake depth is a key factor, with deep lakes generally less responsive to nutrient enrichment. Stauffer (1991) pointed out the importance of self-shading and suggests this is responsible for the levelling of Chl at the highest TP concentrations. We might expect this in deep lakes if they are light limited with a euphotic depth less than the mixing depth, however as we do not have data on these parameters we were unable to explore these relationships further. Shallow lakes, in particular very shallow lakes, are less likely to be light limited, particularly when chlorophyll values are low, as we found for low and moderate alkalinity lakes, and it is not surprising that in these lakes chlorophyll yield per unit of nutrient was generally higher.

We found the weakest relationships for Chl = f(TP) in high alkalinity shallow lakes. Håkanson et al. (2005) also reported that the predictive power of Chl TP models increased markedly if hardwater lakes were omitted from their model and concluded that this was linked to bio-availability of particulate phosphorus. Calcium may have a role to play in precipitating phosphorus, making it less bioavailable. High alkalinity lakes also generally have the highest levels of phosphorus which will have two effects that could influence the relationships: Firstly, chlorophyll will also be high, and even in shallow lakes could result in light inhibition, particularly for mixed or weakly stratified lakes. Secondly, at high TP the TN:TP ratio can be very low leading to nitrogen, rather than phosphorus limitation and thus a poor Chl=f(TP) relationship. Prairie et al. (1989) concluded that variability in published relationships between Chl and nutrients can be accounted for by TN:TP ratios. We found similar results, but only for lakes where TN:TP was <10. In these lakes, contrary to the findings of Prairie, we found that TN provided a better predictor of Chl than TP. A TN:TP ratio <10 is generally interpreted as evidence of nitrogen limitation (Downing & McCauley, 1992, Smith 1982) so this observation is not surprising and may account for at least some of the scatter in the Chl=f(TP) relationship in high alkalinity lakes.

For very shallow lakes, interactions with macrophytes are also likely to be important (Phillips, 2003), and in lakes dominated by macrophytes, top-down control mediated through zooplankton grazing is also likely to play a key role in reducing chlorophyll concentrations below that predicted by their nutrient status (Scheffer, 1990). We do not have sufficient information in our database to identify lakes likely to be influenced by top-down controls, but grazing by zooplankton is likely to introduce additional variability into the nutrient chlorophyll relationship and could be particularly strong in high alkalinity lakes where TP is within the range where top-down effects are strongest (Jeppesen et al 2000). It is thus not surprising that we find the greatest variability in Chl=f(TP) and we suggest that a combination of top-down influences, light inhibition and nitrogen limitation all contribute to limiting Chl in high alkalinity lakes.

Humic substances have also been shown to influence the nutrient chlorophyll relationships in lakes. Edmundson & Carlson (1998) and Havens (2003) both reported lower yields of chlorophyll concentration per unit of TP. This may result from lower availability of light, due to increased water colour (Havens, 2003) or to lower bioavailability of phosphorus (Jones 1998) In our study we found that low and moderate alkalinity humic lakes had higher Chl concentrations. This was accompanied by higher TN and TP concentrations, but we could find no evidence of a reduced yield of chlorophyll. Nürnberg & Shaw (1999) also reported elevated nutrients in humic lakes, but in this case a small but significant positive effect on the Chl=f(TP) relationship. We only found this for low alkalinity deep humic lakes, despite the fact that TN:TP ratios in humic low and moderate alkalinity lakes is lower than those in clear waters. Havens & Nürnberg (2004) pointed out the interactions between humic substances and mixing regime, demonstrating that the Chl concentration in mixed humic lakes is marginally reduced. They propose that in stratified lakes phytoplankton is able to adjust to reduced light availability by migration, resulting in elevated Chl level in surface layers. We can only speculate as to the explanation of the positive effect on the Chl = f(TP) relationship we found in deep low alkalinity humic lakes, as we have insufficient information to identify stratified and mixed lakes. However, it is reasonable to assume that this lake type is very likely to be stratified, and the higher yield we observed may be a result of vertical migration of phytoplankton, an effect not seen in shallow mixed lakes. Also light-adaptation in humic lakes yielding higher Chla:biomass ratios may contribute to explaining why deep low-alkalinity humic lakes have steeper Chla=f(TP) slope than the comparable clearwater lakes.

We found a clearer effect of TN:TP ratios on Chl = f(TP), particularly when combined with humic content. TN:TP was low in humic lakes and a substantial proportion of the very shallow humic lakes had values low enough to suggest TN rather than TP limitation. This is in contrast to Nürnberg & Shaw (1999), who found no evidence of changes to TN:TP ratios in humic lakes. In our data set stepwise multiple regression demonstrated that TN rather than TP provided the best predictor of Chl in humic high alkalinity and polyhumic moderate alkalinity very shallow lakes and it seems likely that these lakes are more likely to be limited by nitrogen rather than phosphorus. We also conclude from our data that there is no significant effect of geographic region on our regression models, despite the relatively wide area from which our data were drawn. A similar conclusion was reached by Seip et al. (2000), who concluded that trophic level, mediated via the TN:TP ratio is more important in influencing the Chl = f(TP) relationship than geographic region.

Use for Lake Management

Regression models relating TP and TN to Chl are useful tools for lake managers as they enable management decisions to be made. For example, standards for nutrients can be established and actions taken within the catchment to achieve them. This is particularly important in the context of the Water Framework Directive where nutrient conditions capable of supporting good ecological status need to be defined. However, it is important to recognise the limitations of such models and consider the most appropriate way to use them.

Firstly, a linear model is only an approximation to what is more likely a curvilinear or sigmoidal relationship. The effects of this can be minimised by using type-specific regression relationships and restricting the regression to the linear regions of the response. In most cases Chl = f(TP) provided the best model, but where TN:TP ratios are low (≤10) Chl = f(TN) may be more reliable.

Secondly, it is important to be aware of the relative high degree of scatter hidden in log log relationships. Many factors can influence this as we have discussed above and lake managers need to know how to deal with this uncertainty. For example, they may often need to assess permissible levels of nutrients necessary to prevent deterioration in ecological quality. A typical situation is the need to establish a target TP which would maintain a currently acceptable Chl concentration. By using an appropriate type specific regression equation it would be possible to determine a TP concentration that would correspond to the desired Chl. However, there is significant uncertainty associated with this decision. It should be noted that Prairie (1996) cautions that regressions with $R^2 < 0.65$ should not be used for predictions, as they have limited predictive power. Our combined lake model has an R^2 which exceeds this value, but has the disadvantage that it does not distinguish the significantly different responses that lakes of different types have. Although some of our type-specific models have R^2 values >0.65 we suggest that it is more appropriate to use the models derived from grouped lake types where the effect of type on the regression equations within the group was not significant. Two of these models have R^2 values >0.65, but the high alkalinity lake model should be used with more caution.

While a prediction from a regression model provides the most likely outcome, for any particular lake, the outcome is uncertain with a chance that 50% of cases would yield higher or lower Chl concentrations than that predicted. In situations where it is important to reduce the risk of exceeding a given level of Chl, a target TP value could be determined using the upper confidence limit of the regression (e.g. 90^{th} percent confidence of individual points). If TP targets were based on this relationship then on average only 10% of sites might exceed the desired Chl concentration, a more precautionary approach. In contrast, faced with setting a restoration target and justifying significant financial expenditure this might be interpreted as a too precautionary value. In this case, the regression line might be a more appropriate choice, as 50% of lakes are likely to achieve the desired Chl at the TP value predicted. To assist in this application to management, we provide figures containing both regression lines and confidence limits for our three type specific models on a linear scale in appendix 1, together with equations to predict both the regression line and values similar to the 90% confidence intervals based on the 5^{th} and 95^{th} percentiles of the residuals of the regression (appendix 2).

Conclusion

In conclusion we propose that chlorophyll nutrient regression models can provide useful tools for lake management, provided the uncertainty associated with them is clearly recognised. Total phosphorus and total nitrogen can be used to predict chlorophyll a concentration, although phosphorus is the better predictor for all types, with the exception of humic lakes.

We show that except for deep lakes, the widely used OECD models predict much lower concentrations of chlorophyll than what is predicted with our regressions, which are based on a large European data set. We thus present 3 models for a) deep lakes, b) low and moderate alkalinity shallow and very shallow lakes and c) high alkalinity shallow and very shallow lakes, which we suggest are the most appropriate for lake management in Europe, where more detailed regional models are not available.

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Legends

Figure 1a & 1b. Box plots showing type specific ranges of seasonal (April – September) mean values for a) chlorophyll a (µg l^{-1}), b) total phosphorus (µg l^{-1}), Lakes split into 3 alkalinity classes (low L, moderate M and high H) and 3 depth classes (deep D, shallow S, very shallow VS). Boxes represent polyhumic (dotted), humic (striped) and clear water (clear) lakes and show median, interquartile range and outliers.

Figure 1c & 1d Box plots showing type specific ranges of seasonal (April – September) mean values for c) total nitrogen (µg l-1) d) total nitrogen to total phosphorus ratio in lakes of different humic class. Lakes split into 3 alkalinity classes (low L, moderate M and high H) and 3 depth classes (deep D, shallow S, very shallow VS). Boxes represent polyhumic (dotted), humic (striped) and clear water (clear) lakes and show median, interquartile range and outliers. Horizontal lines in figure 1d represent ratios of 10 and 17 marking probable region of N limitation and NP co-limitation respectively.

Figure 2. Relationship between growing season chlorophyll a concentration (µg l^{-1}) and a) total phosphorus concentration (µg l^{-1}), b) total nitrogen concentration (µg l^{-1}). Solid line is the LOESS fitted curve.

Figure 3. Relationship between growing season chlorophyll a concentration (µg l^{-1}) and (a) total phosphorus concentration (µg l^{-1}) (b) total nitrogen concentration (µg l^{-1}). Lines are best fit regression and 95% confidence limits.

Figure 4. Change in regression slope for Chl = f(TP) and Chl = f(TN) relationships in lakes of different types.

Figure 5. Scatter plot and regression lines (± 95% confidence intervals) for Chl = f(TP) for lakes of different humic content in a)low and moderate alkalinity shallow and very shallow lakes (solid line all humic types), b)low alkalinity deep lakes (solid line clear water (L), dotted line humic (H) types).

Figure 6. Changes in a) the coefficient of determination (R^2) and b) the slope of Chl = f(TP) and Chl = f(TN) for lakes grouped by total nitrogen to total phosphorus ratios (TN:TP).

Table 1 Details of lake types used to categorise lakes.

Type	**Abbreviation**	**Determinand**
Alkalinity types		
High	HA	alkalinity >1.0 mEq l^{-1}
Moderate	MA	alkalinity 0.2 – 1.0 mEq l^{-1}
Low	LA	alkalinity <0.2 mEq l^{-1}
Depth types		
Deep	D	mean depth >15.0 m
Shallow	S	mean depth 3.0-15.0 m
Very Shallow	VS	mean depth <3.0 m
Colour types		
Polyhumic	VH	colour >90 mgPt l^{-1}
Humic	H	colour 30-90 mgPt l^{-1}
Clear	L	colour <30 mgPt l^{-1}

Table 2. Regression equations from this study (in italics) compared to those taken from the literature for $\log_{10}$ chlorophyll a concentration as a function of total phosphorus (TP) and total nitrogen (TN). To facilitate comparison of non-linear functions the predicted chlorophyll concentration (µg l^{-1}) is given when TP = 35µg l^{-1} and TN = 875ug l^{-1} (N:P ratio of 25).

Reference	Constant	Slope Log TP	Log TN	R^2	Comment	Predicted Chlorophyll
				Chlorophyll a f(TP)		
OECD 1982	-0.432	0.79		0.77		5.4
Classen 1980 (OECD shallow lakes and reservoirs)	-0.268	0.720		0.76		6.3
White 1983	-0.638	0.940		0.45		6.5
This study (deep lakes)	*-0.286*	*0.776*		*0.65*		*8.2*
Rast & Lee 1978	-0.260	0.760		0.59		8.2
Prairie et.al. 1989	-0.390	0.874		0.69		9.1
Vollenweider 1976	-0.432	0.910		0.76		9.4
Havens & Nűrnberg 2004	-0.156	0.738		0.60	Humic	9.6
Nűrnberg 1996	-0.250	0.799		0.64		9.6
Havens & Nurnberg 2004	-0.240	0.813		0.59	Clear	10.4
This study (High alkalinity shallow & very shallow lakes)	*-0.306*	*0.868*		*0.52*		*10.8*
Dillon & Rigler 1974	-1.136	1.449		0.92		12.6
This study (all lakes)	*-0.455*	*1.026*		*0.78*		*13.5*
Jones & Bachmann 1976	-1.090	1.460				14.8
This study (Low & moderate alkalinity shallow & very shallow lakes)	*-0.528*	1.108		0.81		15.2
Seip et.al. 2000	-0.443	1.123		0.93		19.5
				Chlorophyll a f(TN)		
Nűrnberg 1996	-2.180		1.114	0.38		12.5
Prairie et.al. 1989	-3.131		1.445	0.69		13.2
Prairie et.al. 1989	-2.888		1.371		N:P 20-30	14.0

This study (all lakes)	*-2.828*		*1.355*	*0.58*		*14.4*
This study (lakes N:P 10-17)	*-1.761*		*1.034*	*0.53*	*N:P <10*	*19.1*
White 1983	-2.699		1.410	0.74	N:P < 17	28.1
Prairie et.al. 1989	-1.627		1.072		N:P <10	33.6
			Chlorophyll a f(TP,TN)			
Smith 1982	-1.517	0.653	0.548	0.76		12.7
Prairie et.al. 1989	-2.213	0.517	0.838	0.81		11.2
This study (all lakes)	*-1.135*	*0.896*	*0.322*	*0.80*		*15.7*

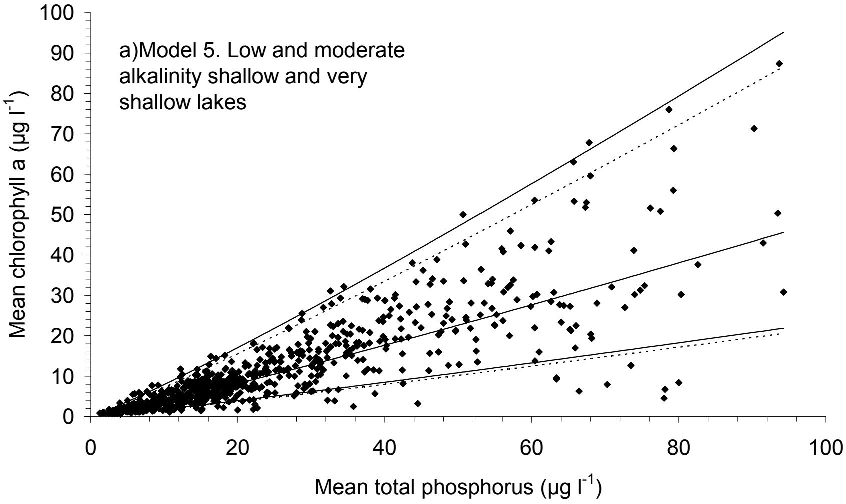
Table 3. Regression equations for relationship between mean growing season chlorophyll a ($\mu g\ l^{-1}$) and total phosphorus ($\mu g\ l^{-1}$) and total nitrogen ($\mu g\ l^{-1}$) for different European lake types (*** p<0.001, * p<0.05).

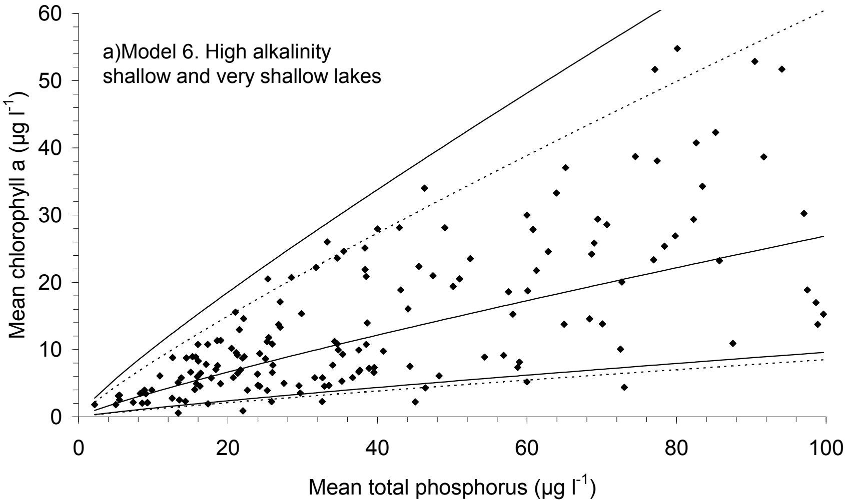
Type	Equation	R^2	n
High alk Deep	not significant too few data	0.334 0.75^{*}	10 7
High alk Shallow	Log_{10} Chl = -0.216(±0.13) + 0.806(±0.09) Log_{10} TP Log_{10} Chl = -2.177(±0.35) + 1.096(±0.12) Log_{10} TN	0.42^{***} 0.51^{***}	115 78
High alk Very Shallow	Log_{10} Chl = -0.521(±0.15) + 1.000(±0.09) Log_{10} TP Log_{10} Chl = -2.575(±0.87) + 1.205(±0.30) Log_{10} TN	0.71^{***} 0.37^{***}	48 29
Mod alk Deep	Log_{10} Chl = -0.243(±0.05) + 0.822(±0.05) Log_{10} TP Log_{10} Chl = -1.609(±0.31) + 0.813(±0.12) Log_{10} TN	0.86^{***} 0.53^{***}	41 42
Mod alk Shallow	Log_{10} Chl = -0.434(±0.05) + 1.062(±0.04) Log_{10} TP Log_{10} Chl = -2.158(±0.19) +1.091(±0.07) Log_{10} TN	0.77^{***} 0.54^{***}	201 194
Mod alk Very Shallow	Log_{10} Chl = -0.501(±0.15) + 1.081(±0.09) Log_{10} TP Log_{10} Chl = -3.189(±0.40) + 1.538(±0.14) Log_{10} TN	0.57^{***} 0.53^{***}	109 115
Low alk Deep	Log_{10} Chl = -0.283(±0.05) + 0.745(±0.06) Log_{10} TP Log_{10} Chl = -0.783(±0.20) + 0.448(±0.08) Log_{10} TN	0.50^{***} 0.18^{***}	146 146
Low alk Shallow	Log_{10} Chl = -0.561(±0.04) + 1.125(±0.03) Log_{10} TP Log_{10} Chl = -2.866(±0.19) + 1.361(±0.07) Log_{10} TN	0.77^{***} 0.49^{***}	344 363
Low alk Very Shallow	Log_{10} Chl = -0.596(±0.10) + 1.149(±0.06) Log_{10} TP Log_{10} Chl = -3.904(±0.36) + 1.812(±0.13) Log_{10} TN	0.74^{***} 0.61^{***}	114 123

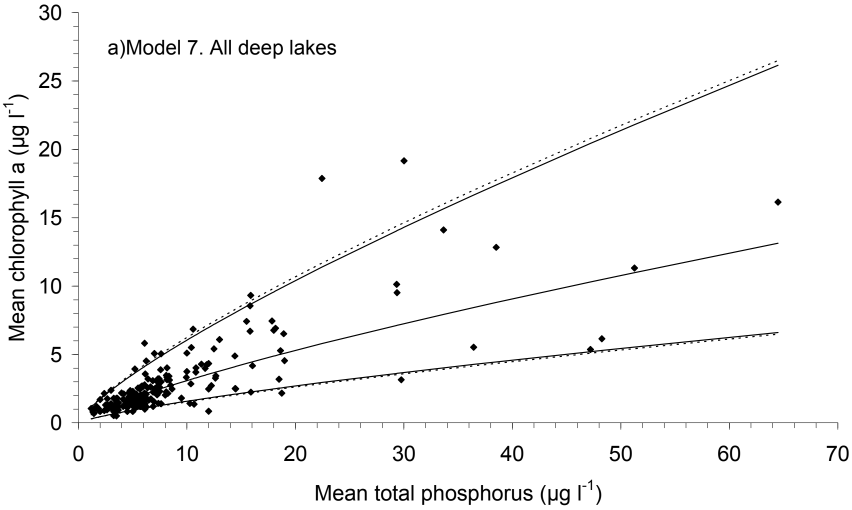
Table 4. Coefficient of determination (R^2) and standardised regression (β) coefficients for stepwise multiple regression model for total phosphorus and total nitrogen with chlorophyll in lakes split by alkalinity, depth and humic substances.

Type	Clear			Humic			Polyhumic		
		Standardised coefficients			Standardised coefficients			Standardised coefficients	
	R^2	TP	TN	R^2	TP	TN	R^2	TP	TN
HS	0.46	0.47	0.28	0.34	0.59	-			
HVS	0.43	-	0.64	0.53	-	0.73			
MD	0.81	0.90	-	0.88	0.94	-			
MS	0.84	0.92	-	0.67	0.70	0.19			
MVS	0.81	0.90	-	0.73	0.63	0.28	0.63	-	0.80
LD	0.43	0.66	-	0.46	0.68	-			
LS	0.62	0.69	0.15	0.60	0.77	-	0.55	0.44	0.41
LVS	0.87	0.94	-	0.73	0.57	0.37	0.45	0.33	0.41

Appendices


a)Model 5. Low and moderate alkalinity shallow and very shallow lakes
Mean chlorophyll a (μg l-1)
Mean total phosphorus (μg l-1)


a)Model 6. High alkalinity shallow and very shallow lakes
Mean chlorophyll a (μg l-1)
Mean total phosphorus (μg l-1)


a)Model 7. All deep lakes
Mean chlorophyll a (μg l-1)
Mean total phosphorus (μg l-1)

Appendix 1. Relationship between summer mean total phosphorus (μg l^{-1}) and chlorophyll a (μg l^{-1}) in lakes grouped by alkalinity and mean depth. Solid lines show modelled regressions, upper and lower 90% confidence intervals. Dotted lines show modelled regressions ± 95th percentile of regression residuals.

Appendix 2. Equations to calculate expected chlorophyll a from total phosphorus. The upper and lower boundary values are very similar to the 90% confidence limit of the regression and are determined by adding the 95th and 5th percentiles of the regression residuals. For any particular TP value approximately 90% of lakes will have a chlorophyll concentration below the upper boundary and above the lower boundary.

Model 5 Low and moderate alkalinity, shallow and very shallow lakes

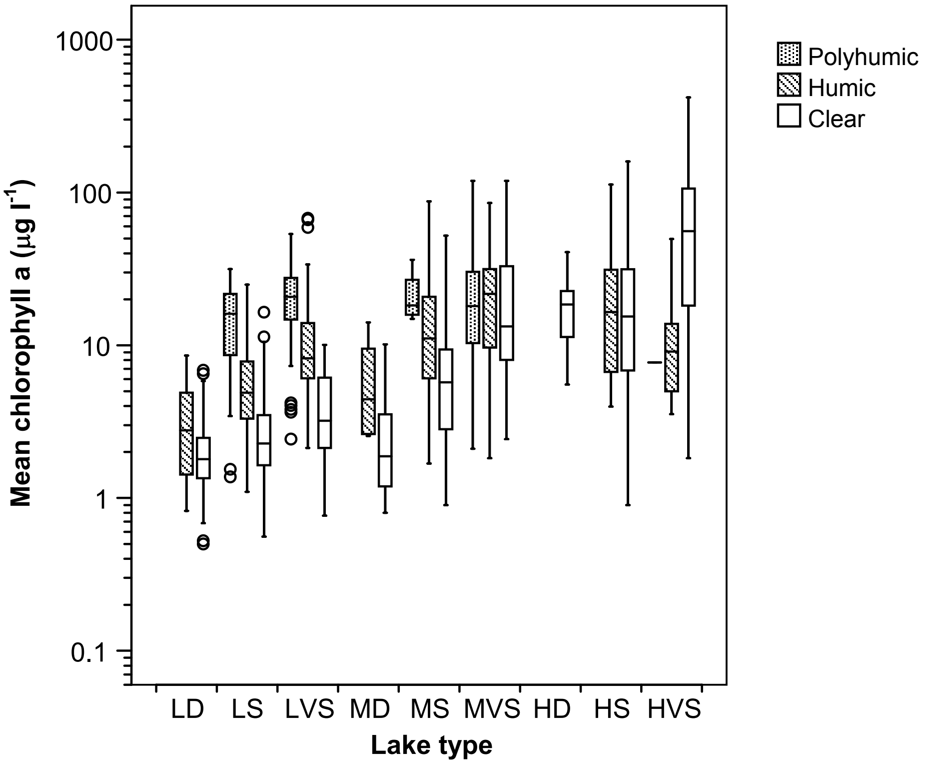
Upper boundary	$Log_{10}[Chl] = -0.528 + 1.108\ Log_{10}[TP] + 0.278$
Regression	$Log_{10}[Chl] = -0.528 + 1.108\ Log_{10}[TP$
Lower boundary	$Log_{10}[Chl] = -0.528 + 1.108\ Log_{10}[TP] - 0.346$

Model 6 High alkalinity shallow and very shallow lakes

Upper boundary	$Log_{10}[Chl] = -0.306 + 0.868\ Log_{10}[TP] + 0.352$
Regression	$Log_{10}[Chl] = -0.306 + 0.868\ Log_{10}[TP$
Lower boundary	$Log_{10}[Chl] = -0.306 + 0.868\ Log_{10}[TP] + -0.500$

Model 7 All deep lakes

Upper boundary	$Log_{10}[Chl] = -0.286 + 0.776\ Log_{10}[TP] + 0.306$
Regression	$Log_{10}[Chl] = -0.286 + 0.776\ Log_{10}[TP]$
Lower boundary	$Log_{10}[Chl] = -0.286 + 0.776\ Log_{10}[TP] + 0.305$



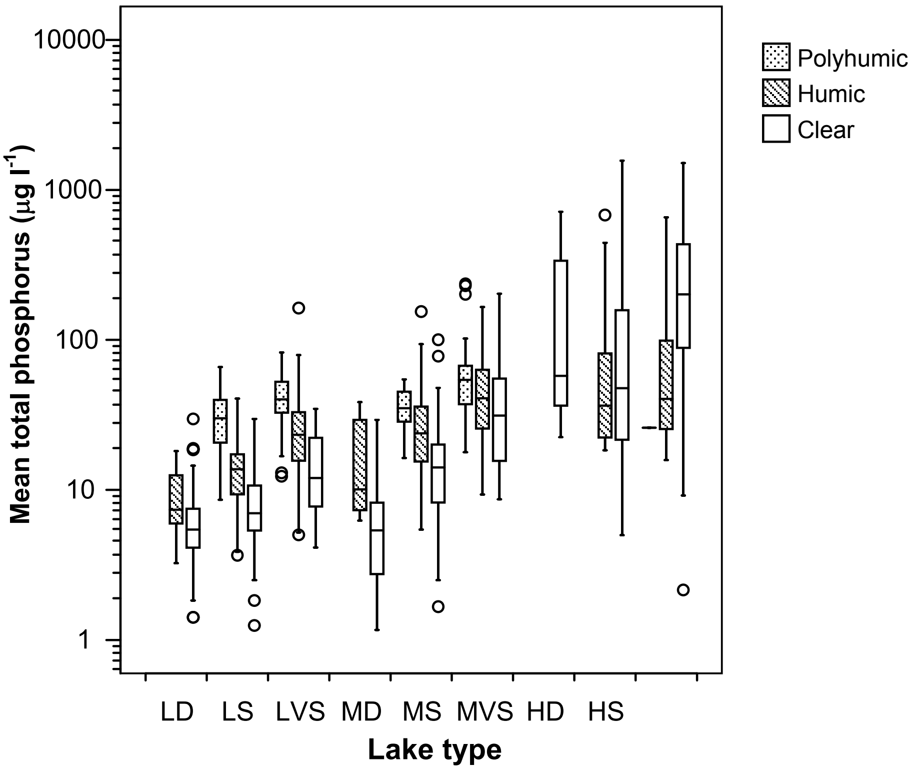
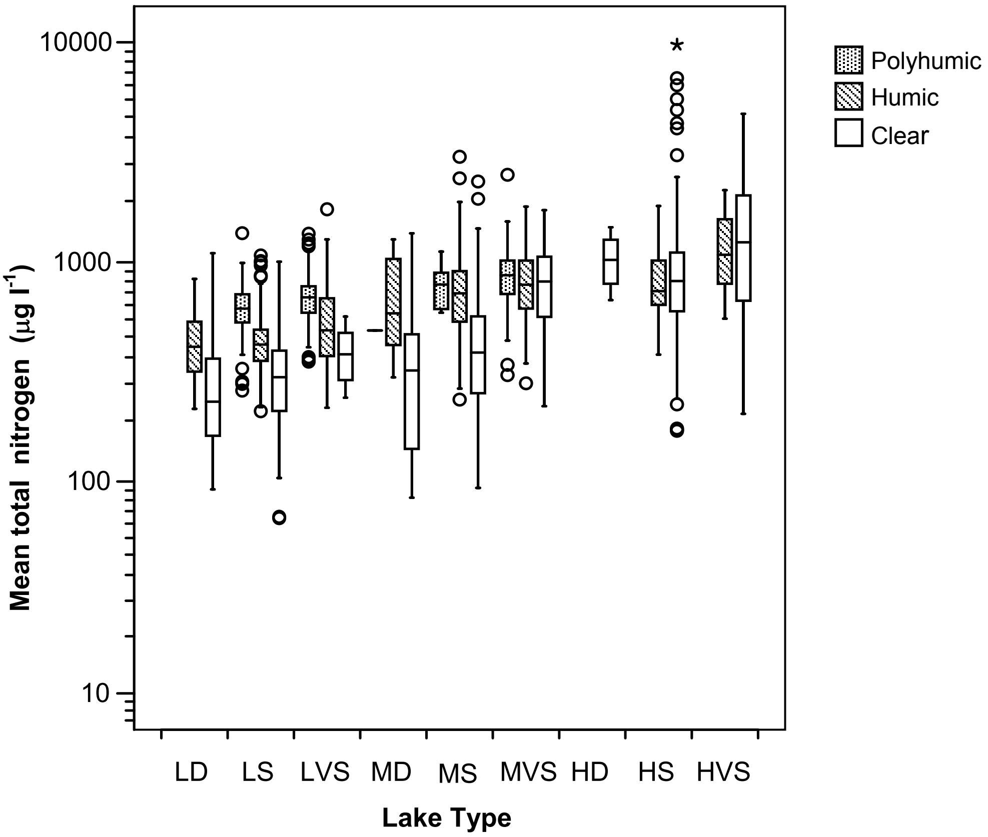


Figure 1a & b. Box plots showing type specific ranges of seasonal (April – September) mean values for a) chlorophyll a (μg l^{-1}), b) total phosphorus (μg l^{-1}), Lakes split into 3 alkalinity classes (low L, moderate M and high H) and 3 depth classes (deep D, shallow S, very shallow VS). Boxes represent polyhumic (dotted), humic (striped) and clear water (clear) lakes and show median, interquartile range and outliers



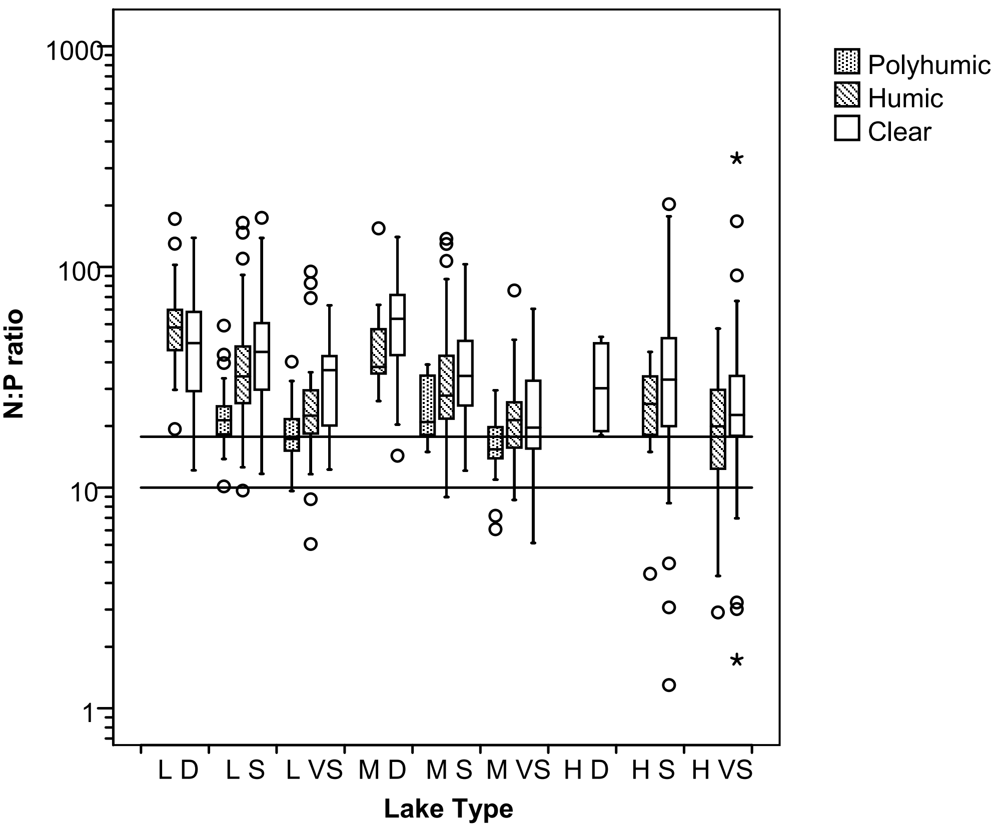
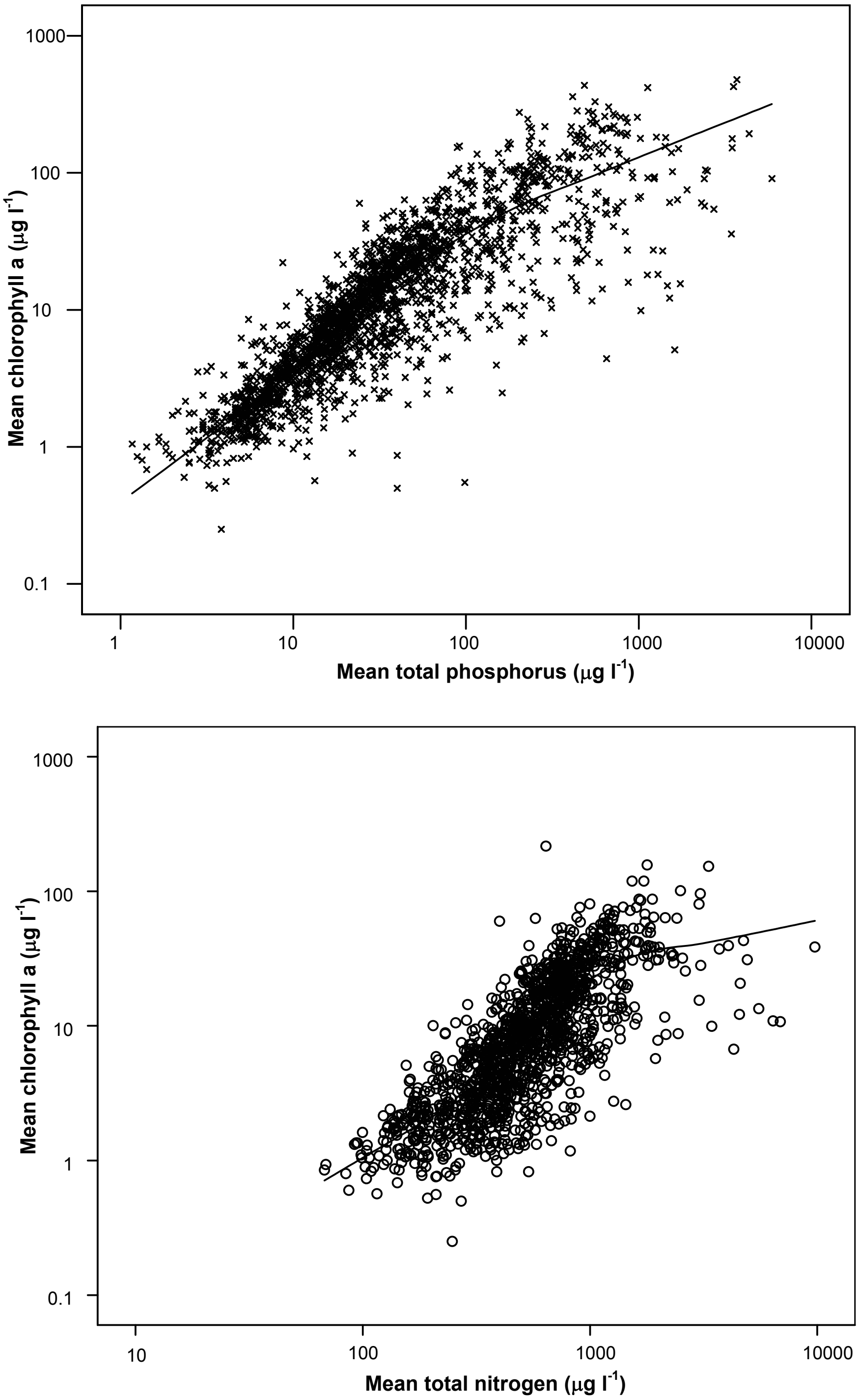


Figure 1c & d Box plots showing type specific ranges of seasonal (April – September) mean values for c) total nitrogen (µg l-1) d) total nitrogen to total phosphorus ratio in lakes of different humic class. Lakes split into 3 alkalinity classes (low L, moderate M and high H) and 3 depth classes (deep D, shallow S, very shallow VS). Boxes represent polyhumic (dotted), humic (striped) and clear water (clear) lakes and show median, interquartile range and outliers Horizontal lines in figure 1d represent ratios of 10 and 17 marking probable region of N limitation and NP co-limitation respectively.



d

Fig 2. Relationship between growing season chlorophyll a concentration (µg l^{-1}) and a) total phosphorus concentration (µg l^{-1}) . b) total nitrogen concentration (µg l^{-1}). Solid line is the LOESS fitted curve

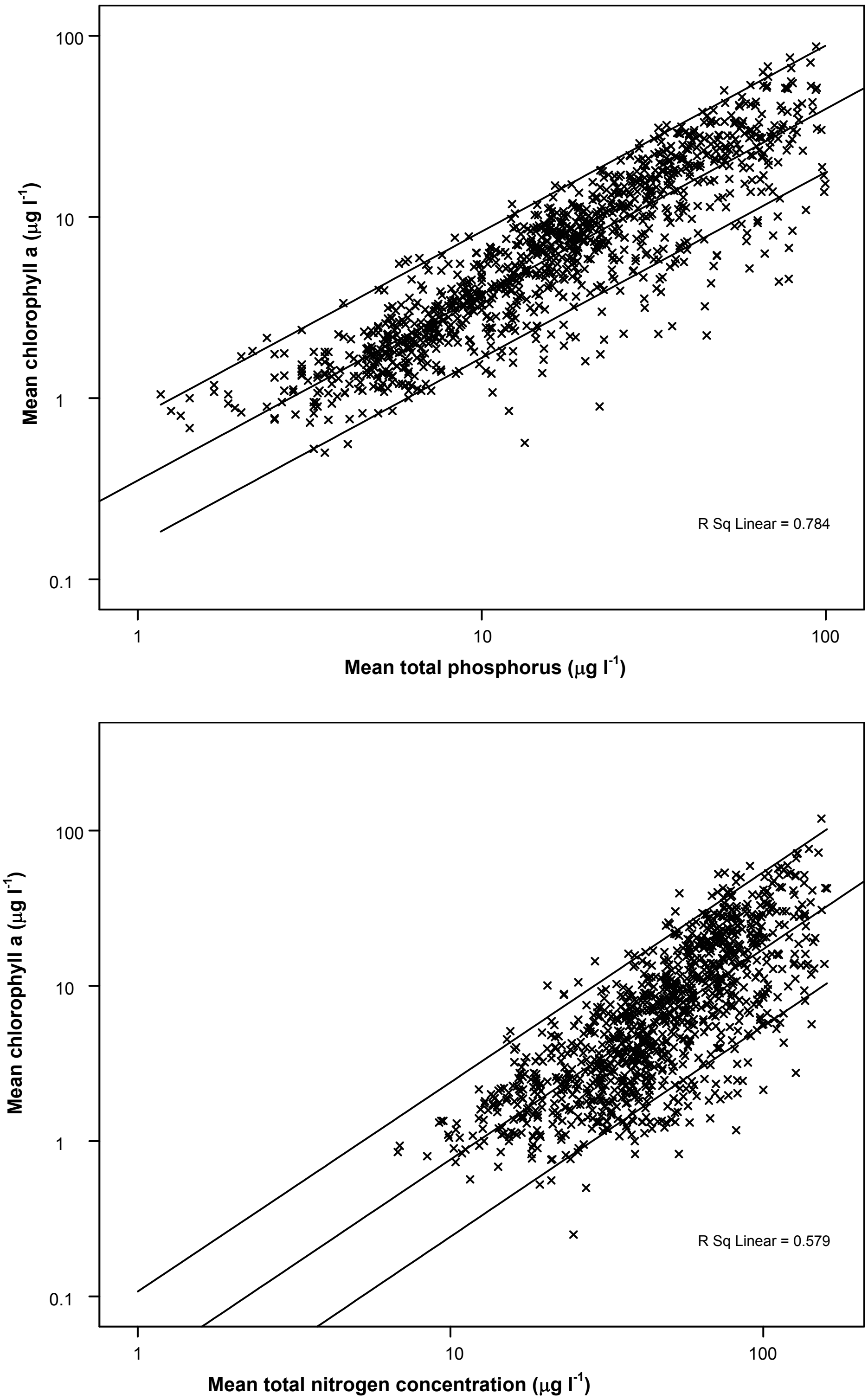


Figure 3. Relationship between growing season chlorophyll a concentration (μg l-1) and (a) total phosphorus concentration (μg l-1) (b) total nitrogen concentration (μg l-1). Lines are best fit regression and 95% confidence limits.

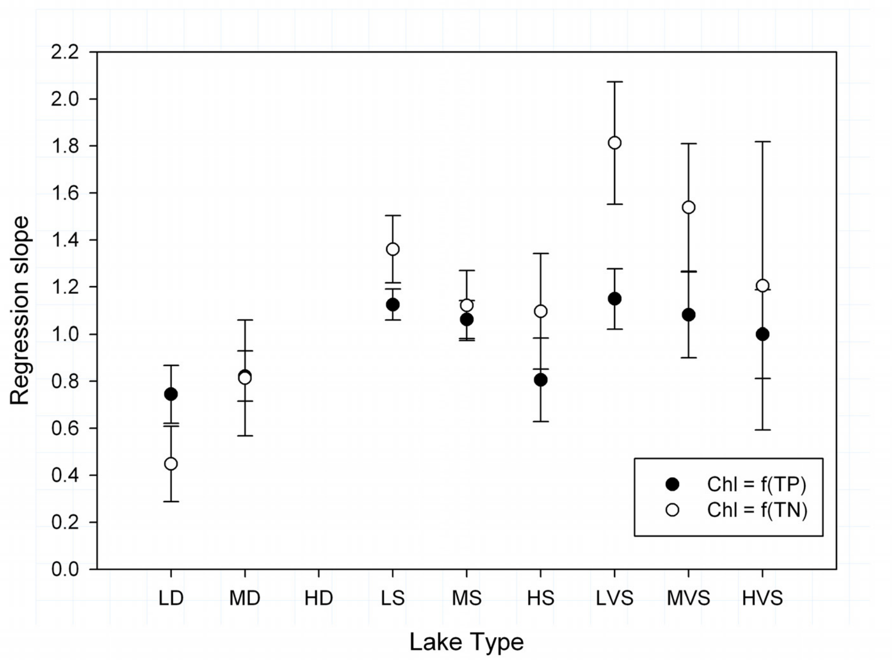
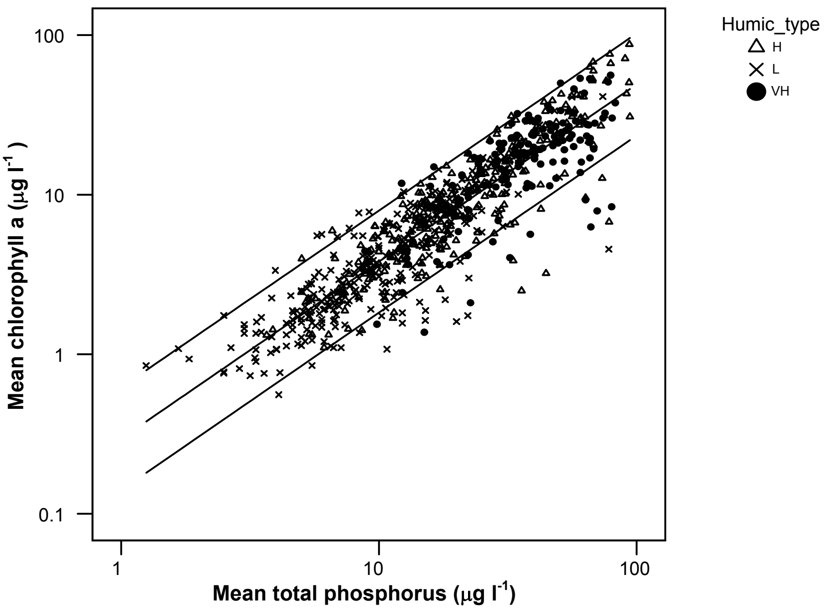


Figure 4. Change in regression slope for Chl = f(TP) and Chl = f(TN) relationships in lakes of different types.



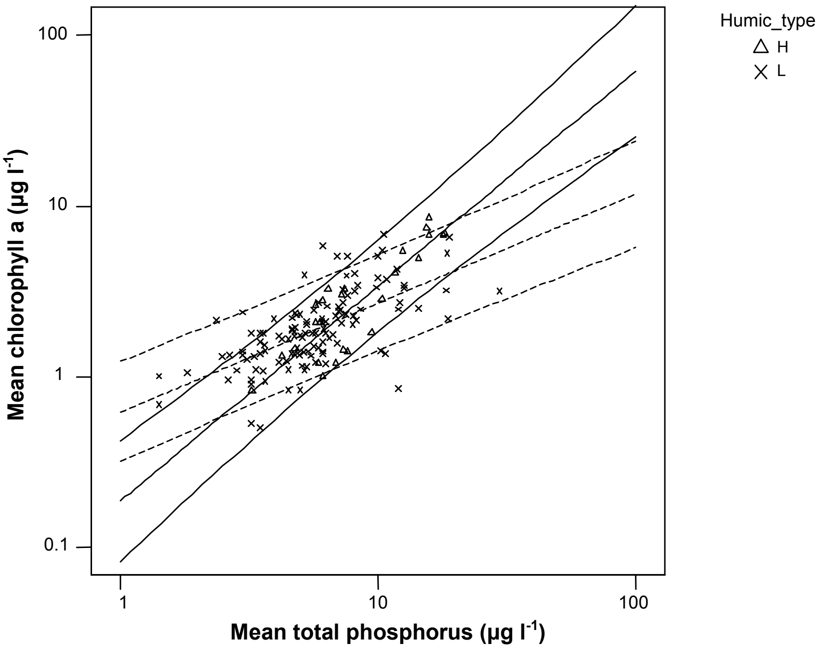


Figure 5. Scatter plot and regression lines (± 95% confidence intervals) for Chl = f(TP) for lakes of different humic content in a)low and moderate alkalinity shallow and very shallow lakes (solid line all humic types); b)low alkalinity deep lakes (solid line clear water (L), dotted line humic (H) types).

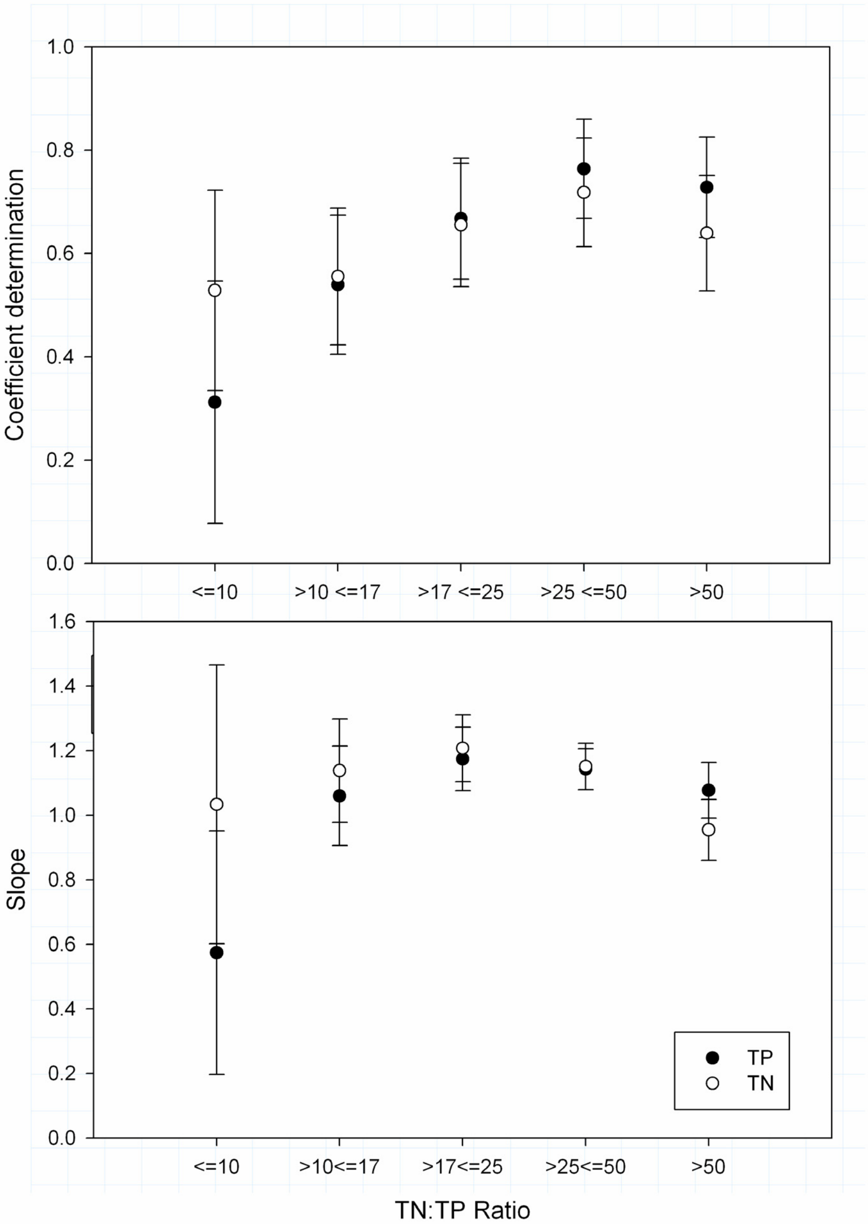


Figure 6 Changes in a) the coefficient of determination (r^2) and b) the slope of Chl = f(TP) and Chl = f(TN) for lakes grouped by total nitrogen to total phosphorus ratios (TN:TP).