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Quantitative responses of lake phytoplankton to eutrophication in Northern Europe

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Abbreviations: Chlorophyll-a – Chl-a

Abstract

Based on the currently largest available dataset of phytoplankton in lakes in northern Europe, we quantified the responses of three major phytoplankton classes to eutrophication.

Responses were quantified by modeling the proportional biovolumes of a given group along the eutrophication gradient, using generalized additive models. Chlorophyll-*a* was chosen as a proxy for eutrophication because all classes showed more consistent responses to Chlorophyll-*a* than to total phosphorus.

Chrysophytes often dominate in (ultra-) oligotrophic lakes, and showed a clear decrease along the eutrophication gradient. Pennate diatoms were found to be most abundant at moderate eutrophication level (spring-samples). Cyanobacteria often dominate under eutrophic conditions, especially in clear-water lakes at chlorophyll-*a* levels $> 10 \mu\text{g L}^{-1}$ (late summer samples).

We compare the relationships among types of lakes, based on the lake typology of the northern geographic intercalibration group, and among countries sharing common lake types. Significant differences were found especially between humic and clear-water lakes, and between low- and moderately alkaline lakes, but we could not identify significant differences between shallow and deep lakes.

Country-specific differences in response curves were especially pronounced between lakes in Norway and Finland, while Swedish lakes showed an intermediate pattern, indicating that country-specific differences reflect large-scale geographic and climatic differences in the study area.

Introduction

Phytoplankton community composition responds sensitively to changes in waters quality (Reynolds 1980, Sommer 1991, Lepistö et al. 1999), making phytoplankton a useful biological quality parameter for lake monitoring. The indicative value of phytoplankton assemblages to eutrophication has been recognized already for long time (Naumann 1919, Nygaard 1949), and numerous researchers have developed indices for using phytoplankton composition for assessing water quality (e.g. Teiling 1955; Hornström 1981; Orlik et al.1998; Willén 2000).

A general problem with many proposed indicators is the lack of a critical statistical evaluation. Often, indicators are based on small datasets in combination with expert knowledge, and have not been evaluated by statistical methods. Also, indicators are often based on rather regional datasets, which were accessible to the person performing the analysis, and a wider applicability of such indicators appears questionable.

A indicator should be representative for the area where it is going to be used. For the WFD, this means that indicators must be applicable to multinational areas. Because different experts in different countries often use different taxonomic keys, combined datasets often cause problems with respect to taxonomic identity of the biological elements (e.g. Moe et al. 2008, this issue). This causes considerable problems when one develops indicators based on such datasets. On the contrary, datasets aggregated on higher taxonomic levels (classes, orders) may be expected to be less affected by identifier-specific traits.

One of the key steps in the Water Framework Directive (WFD) implementation process is the assessment of ecological status of water bodies according to biological parameters and supporting physico-chemical elements (European Commission 2000). The ecological status of the water bodies should be given as deviations from type-specific reference conditions. In order to develop WFD compliant classification systems for the assessment of ecological status, we need to know

quantitative the relationships between biological and physico-chemical factors for different types of water bodies. According to the boundary setting protocol given by the intercalibration steering group (Intercalibration technical report 2007) type-specific response curves of different biological indicators /indices along the pressure gradient should be used as a basis to recommend boundaries between the different classes of ecological status. This is the core of the pan-European intercalibration process of comparing and harmonizing ecological assessment systems (Intercalibration guidance 2005).

According to the WFD, phytoplankton is one of the biological key elements for assessment of ecological status in lakes. Both biomass as well as taxonomic composition should be used to assess ecological status (WFD Annex V). The most important environmental factor affecting phytoplankton biomass and community composition is eutrophication (Vollenweider 1989).

The main objective of this study thus is to quantify responses of phytoplankton indicators to eutrophication in major lake types in Northern Europe, as a basis for identification of type-specific ecological status class boundaries. A sub-objective is to test whether relationships are comparable among different countries and among lake types. For this purpose, we used a large dataset from Northern European lakes to model responses of phytoplankton classes, expressed by their proportional biovolumes, along the eutrophication gradient, and test if these response curves vary between lake types. In addition to comparison among lake-types, we analyze where responses differ among countries.

We focus on highly aggregated groups (classes) rather than genera and species in order to warrant wide applicability of our metrics. Furthermore, this approach yields a more user-friendly index, since classes are easier to monitor than lower taxonomic levels, such as genera or species.

Material and Methods

1) Datasets

The Northern European part of the REBECCA phytoplankton database consists of close to 5000 phytoplankton samples from app. 850 different lakes, mainly collected from various monitoring programs in Norway, Sweden and Finland in the period from 1988 to 2003. To the best of our knowledge, this dataset, which has been assembled as a part of the EU-project REBECCA (Moe et al. 2008, this issue), is at present the largest combined dataset on phytoplankton composition in Northern Europe. Additionally United Kingdom (UK) also provided data from a few sites for comparison. Samples were mostly taken from the upper mixed surface layer of the lakes during the growing season. Thus, metalimnetic samples and winter samples are not included in our dataset. Except for the UK, all samples from each country were counted by only one single expert from each country, ensuring high comparability of data within each country. These experts have for many years participated in an ongoing process of standardization of phytoplankton counting methods among the specialists from the Scandinavian countries (Vuorio et al. 2006), thereby providing good comparability of data also between the countries.

2) Selection of indicator classes

Initial analyses showed that especially chrysophytes, pennate diatoms and cyanobacteria respond clearly to lake eutrophication, as observed earlier by Watson et al. (1997). We therefore focus here on these three taxonomic group indicators. Some taxa, which behave differently from the bulk of species within a class, were excluded from the indicator groups. The genera *Synura* and *Uroglena* were excluded from the chrysophytes, because these genera are not indicative for oligotrophic conditions, but may indeed form blooms under eutrophic conditions (Brettum 1989). From the cyanobacteria, all chroococcales were excluded with exception of the genera *Microcystis* and *Woronichinia*, because chroococcales include mainly small-sized taxa which are common in oligotrophic lakes (Komarek and Anagnostidis 1999). The selection of the taxa was preliminarily

based on expert knowledge, and later evaluated and confirmed by statistical analysis, using weighted averaging of each taxon's abundance along the pressure gradient (data not shown).

3) Lake types

The intercalibration of ecological assessment systems is based on the division of European water bodies into regions and lake types which are similar in their hydromorphological and geochemical properties and therefore expected to have similar reference conditions (Table 1; see also Moe et al. 2008, this issue). However, we combined lowland with upland lakes (L-N2a+L-N5, L-N3a+L-N6a, Table 1), because initial analyses did not show clear differences between those types.

4) Chlorophyll-a as a proxy for eutrophication

Chl-*a* was chosen as a proxy to express the level of eutrophication. because this proxy has been shown to correlate well with total phosphorus (Phillips et al. 2008, this issue and references therein), and because preliminary analyses indicated more sensitive responses of phytoplankton classes to Chl-*a* as compared to total phosphorus. Chl-*a* also has the advantage of being independent of whether nitrogen or phosphorus is the limiting factor for phytoplankton production. Moreover, Chl-*a* also represents a more immediate measure for the effect of eutrophication than phosphorus, since phosphorus concentrations can be quite high without causing high algal biomass (e.g. in lakes with low retention time, in which there is too little time to build up a large phytoplankton biomass, or in lakes with high mineral turbidity, in which most of the phosphorus is unavailable for phytoplankton). Moreover, Chl-*a* has also been used as a measure for phytoplankton biomass and for boundary settings within the northern geographic intercalibration group (EU Intercalibration report 2007).

5) Data selection for statistical analysis and seasonality

In order to analyse type-specific responses, we only used data from lakes that belonged to one of the Northern GIG intercalibration types, thereby reducing the dataset to less than half of the total

dataset. Statistical evaluation was performed on basis of single samples, i.e. single samples from each lake were not averaged prior to analysis. In order to prevent the dataset from being dominated by sites (lakes) with a very large number of samples, we randomly selected four samples from sites with more samples, but kept all observations from sites with up to four samples.

For pennate diatoms, which peak during the spring bloom, a dataset ranging from May to July was selected, using above outlined sample selection approach. This 'spring bloom' dataset contained 967 samples (Table 1). For the two remaining algal groups, samples taken from the period July to September were selected by the same process. The final dataset used for analyses of these classes contained 1000 samples (Table 1).

6) *Generalized additive models (GAM)*

Responses of each taxonomic indicator group (chrysophytes, pennate diatoms and cyanobacteria) were modeled using generalized additive models (GAMs; Wood 2006). GAMs allow non-linear regressions to be fitted to the dataset, based on linear thin plate splines. In contrast to conventional smoothing functions, GAMs include cross validation in the model-fitting routine (Wood 2006), which makes them robust against non-normal distribution of data and outliers. Also, GAMs give confidence intervals for the regression line, which allow visual inspection of the significance of a relationship.

7) *AIC model comparison*

We tested whether relationships differ among lake-types and among countries using the Akaike Information criterion (AIC; Sakamoto et al. 1986). For this purpose, two models were built, one with the predictor (Chl-*a*) and the response variable estimated from the whole dataset for two lake types or two countries (e.g. proportion cyanobacteria vs. Chl-*a* concentration), and a second model, where a covariable split this dataset into two components (lake-type A and B, or country A and B). If the AIC-value of the split model was clearly lower (at least by -2), the split model gave a

significantly better fit to the data than the joint model (Sakamoto et al. 1986). In these cases the split model was preferred, otherwise the simple (joint) model was preferred. All statistical analyses were performed using the R software (R Development Core Team 2007).

Results

Response curves

Distinct patterns were found along the eutrophication gradient (as expressed by Chl-*a*) for all the three indicator groups, and the patterns were qualitatively similar for most lake types (Fig. 1). The narrow confidence intervals (Fig.1) show that the responses are significantly different from random patterns.

Chrysophytes – The relative biomass of chrysophytes decreased along the eutrophication gradient for all Nordic lake types. While the proportion of chrysophytes was on average close to 40% below 3 $\mu\text{g Chl-}a \text{ L}^{-1}$ in all lake types except L-N8a (Fig.1), their proportion became insignificant above ca. 20 $\mu\text{g Chl-}a \text{ L}^{-1}$.

Pennate diatoms – In the clear-water lakes, the relative biomass of pennate diatoms increased between 2 and 10 $\mu\text{g L}^{-1}$ Chl-*a*. However, their share in the total biomass leveled off or even decreased as Chl-*a* concentration increased further. The response was comparable among lake types except for the moderate alkaline humic lakes (LN-8a), where the response of pennate diatoms fluctuated and was less distinct (Fig. 1b).

Cyanobacteria – The proportions of cyanobacteria increased with increasing Chl-*a* concentration in all Nordic lake types, but relationships were overall less pronounced in humic compared to clear-water lakes (Fig. 1). Compared to pennate diatoms, cyanobacteria started to increase at considerably higher Chl-*a* levels. The increase was not linear, but showed a sharp threshold that differed between lake types, at ca. 5-6 $\mu\text{g L}^{-1}$ Chl-*a* in the low alkalinity clearwater lakes (LN-2a,

LN-5) and at ca. 9-10 $\mu\text{g L}^{-1}$ Chl-*a* in the moderate alkalinity clear-water type (LN-1) and in the low alkalinity humic lake types (LN-3a, LN-6a).

Differences between lake types

Using the AIC statistics, differences between lake types were tested for the three phytoplankton class indicators (Table 2). The response of cyanobacteria in clearwater lakes was significantly different from humic lakes, in terms of showing a weaker response in humic compared to clearwater lakes. Within the clearwater lakes, the moderately alkaline lakes, L-N1, showed different phytoplankton responses from the low alkalinity lakes, L-N2 and L-N5, with respect to chrysophytes and cyanobacteria, while the deep low alkalinity lakes, L-N2b, did not differ significantly from the other clearwater types for any of the tested indicators. Within the humic lake group, the moderately alkaline lakes (LN-8a) differed significantly only with respect to the cyanobacteria response curves.

Difference between countries

Due to the large number of possible combinations, and due to limited number of observations for some lake types and countries (Table 1), this comparison was restricted to the two major lake types (humic and clearwater lakes, Table 2). UK lakes were excluded from this comparison due to low number of observations (Table 1).

Responses differed quite clearly between countries. 9 out of 18 pairwise comparisons differed significantly (Table 3). Only the pennate diatoms did not differ significantly among the three countries. Differences were most pronounced between Norway and Finland (4 of 6 comparisons different) but less between Norway and Sweden (3 of 6) and between Finland and Sweden (2 of 6), corresponding to geographic distances between countries. For chrysophytes, all pairwise comparisons different significantly, except for the humic lakes in Sweden and Finland. For

Cyanobacteria, the responses were different in each country for both the major lake types, except in Finland and Sweden for clearwater lakes, and for Norway and Sweden for humic lakes. Responses appear to be more pronounced in Norway compared to the other countries (Fig. 1) in the sense that proportions of Chrysophytes and Cyanobacteria both showed higher contrasts between oligo- and eutrophic conditions than in Sweden and Finland. However, the Norwegian data covered a larger part of the Chl-*a* gradient than the Swedish and Finnish data, making the comparison difficult.

In addition to differences seen in mean trends, also variations seem to differ among countries. The Norwegian data generally seems to be more variable compared to the data from Sweden and Finland (see range in proportions of cyanobacteria and chrysophytes at moderate Chl-*a* levels; Fig. 1). However, the statistical evaluation applied here is restricted to comparisons of mean trends, thus significant differences as identified by the AIC criterion should reflect differences in mean trends, but not in variations around the trend lines.

Discussion

Major response patterns and general ecological traits

The general decrease along the trophic gradient found for chrysophytes is a well-known ecological feature of this class of often mixotrophic phytoplankton prevailing in the waters of oligotrophic lakes (Sandgren 1988, Lyche 1990). The underlying mechanism explaining the high relative abundance of chrysophytes in oligotrophic lakes is related to severe limitation in dissolved inorganic nutrients, and to the ability of chrysophytes to supplement their nutrient uptake with phagotrophy of bacteria and small phytoplankton. This ability allows mixotrophic chrysophytes to maintain positive growth rates under nutrient-poor conditions (Raven 1995).

Large-sized, pennate diatoms were found to have their peak relative abundance at intermediate trophic levels. The underlying causal factors for this response pattern may be related to the ability

of these algae to grow fast when there are more inorganic nutrients available (references in Andersen 1997). Moreover, their large cell size makes pennate diatoms less vulnerable to grazing compared to smaller taxa.

The dominance of Cyanobacteria at the upper end of the trophic gradient is also a well-known response pattern (Lyche 1990, Downing et al. 2001), often explained by their adaptation to low light conditions, and their low vulnerability to grazing (Reynolds 1984).

Deep vs. shallow lakes

Our analyses did not show any significant differences between deep and shallow lakes among the low alkalinity clear water lakes. Our data did not include observations from the metalimnion of deep lakes. Thus, sub-surface blooms of cyanobacteria, which may be characteristic for moderately eutrophicated deep lakes (e.g Teubner et al. 2001), are not represented in our dataset, limiting our possibilities to find potential differences between deep and shallow lakes in our study.

Impact of humic substances

The lake typology of the WFD reflects major environmental gradients, and we therefore expected differences in responses among lake types. The weaker response of cyanobacteria in humic compared to clearwater lakes is probably related to reduced supply of inorganic carbon as HCO_3^- in those often acidic humic lakes in the Northern countries, as well as to shifts in light quality towards red light. Most cyanobacteria depend on HCO_3^- as inorganic carbon source (Kohl and Nicklisch 1988), making them poor competitors at low pH. Moreover, the light conditions in humic lakes diminish the competitive advantage of cyanobacteria with respect to utilization of the light in the 'green gap' (Britton 1983).

Impact of alkalinity

Among clearwater lakes, cyanobacteria exhibited the most abrupt response to eutrophication in low-alkaline lakes (L-N2a, L-N2b, L-N5, L-N6a), while the responses seem more buffered in the

moderate alkaline lakes (L-N1, L-N8a). This phenomenon may be related to the more stable supply of inorganic carbon in the form of HCO_3^- found in moderately alkaline lakes. The Chl-*a* threshold above which there was an abrupt increase in the relative abundance of Cyanobacteria was also lower in low alkalinity lakes (ca. 6 $\mu\text{g/L}$) than in moderately alkaline lakes (ca. 9 $\mu\text{g/L}$) (Fig.1a). Response of cyanobacteria generally seems to be more variable, i.e. less predictable in low alkaline compared to moderate alkaline lakes.

Altogether, the results show that humic substances and alkalinity do have considerable impact on the phytoplankton responses to eutrophication, and thus confirms that the WFD lake typology, which is mainly based on these two chemical factors, reflects ecological meaningful gradients, and may be useful for lake management.

Geographical differences –

Differences in the datasets caused by methodological differences should be small, both due to the ongoing standardization work among the phytoplankton experts in the Nordic countries (Vuorio et al. 2006), and due to the low taxonomic resolution applied for definition of the indicator groups (class level). Thus, the observed differences between the countries most likely reflect true differences, caused by geological and climatic gradients producing differences in hydrology and water quality.

Humic matter, pH, alkalinity and retention time all increase from west to east across the study area (Skjelkvåle et al. 2001). This was further supported by results found for our dataset that pH and alkalinity increase from west to east in Scandinavia (Spearman rank correlation between longitude and alkalinity (n=700) and pH (n=947); $\rho=0.36$ (alk.), 0.56 (pH), $p(\text{alk.}, \text{pH}) < 0.001$). pH and alkalinity are essential factors affecting phytoplankton dynamics and composition (see *low vs*

moderate alkaline lakes, above). The study area is also characterized by a strong east-west gradient in climate, with mild winters and wet and cool summers in western Norway, and pronounced seasonality with cold winters and dry and sunny summers in the eastern Sweden and Finland. Moreover, lake morphometry differs systematically among the Nordic countries (Fig. 2). The lakes tend to be large and shallow in Finland, but deep and small in Norway. Swedish lakes are similar in size to Norwegian lakes, but more shallow. Also the humic substances increase from west to east and give more coloured lakes in Finland than in Norway, again with Sweden in the middle. This difference in humic content has implications both for the carbon source available for phytoplankton, as well as for the underwater light climate. Thus, the climatic, morphometric, as well as the physico-chemical variability across the study area likely causing systematic trends in important variables such as light conditions, mixing depth and stability of the upper mixed layer, which may have substantial effects on phytoplankton communities (Reynolds 1984, Ptacnik et al. 2003).

A recent study shows that phytoplankton diversity and predictability of community composition are positively related (Ptacnik et al. 2008). Because phytoplankton diversity increases from west to east in the study area (Fig. 1 in Ptacnik et al. 2008), the differences in variation seen between countries may well relate to differences in phytoplankton diversity in the study area.

Conclusions

Since these phytoplankton classes show significant trends along the eutrophication gradient, they may be useful as indicators for eutrophication in lakes in Northern Europe. As we have shown, the three classes indicate different levels of productivity, with chrysophytes, pennate diatoms and cyanobacteria dominating in oligotrophic, mesotrophic and eutrophic lakes respectively. The thresholds shown for cyanobacteria may be especially useful for setting boundaries between good and moderate ecological status in Northern lakes. Provided that geographic gradients are taken into account, our data also show that the WFD typology system is useful in lake management.

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Tables

Table 1. Overview of lake types, dataproviders and number of observations per lake-type and country. A slash separates number of spring samples (first) from number of summer samples. The lake types 2a & 5, and 3a & 6a, respectively, have been combined into one group each, since we were not able to find significant differences between 2a & 5, nor between 3a & 6a.

Lake type	Type characteristics				Country (data provider)				
	alkalinity (mEq/L)	colour (mg peat/L)	depth (m)	altitude (m above sea level)	FI (SYKE)	NO (NIVA)	SE (SILU)	UK (CEH)	All per type
L-N1	0.2-1	<30	3-15	<200	39/49	87/89	0/6	0/1	126/145
L-N2b	<0.2	<30	>15	<200	18/18	241/185	0/0	2/8	261/211
L-N2a*	<0.2	<30	3-15	<200	55/55	128/115	0/26	1/2	184/198
L-N5*	<0.2	<30	3-15	200-800	1/1	84/69	20/65	0/0	105/135
L-N3a [†]	<0.2	30-90	3-15	<200	89/93	73/66	0/9	0/0	162/168
L-N6a [†]	<0.2	30-90	3-15	200-800	15/15	29/29	4/7	0/0	48/51
L-N8a	0.2-1	30-90	3-15	<200	41/50	40/36	0/6	0/0	81/92
All per country					258/281	682/589	24/119	3/11	967/1000

*, †, : types with common symbols were treated as one combined lake type.

Table 2. Results from pairwise comparison of response curves for cyanobacteria, chrysophytes and pennate diatoms among different lake types. AIC values for the combined types model (1st number) and the split types model (2nd number) are shown. Significant differences are emphasized by bold letters.

	Chrysophytes	Pennales	Cyanobacteria
All clear / clear moderate alkaline (L-N1)	-637,-644	-663.4,-664.8	-1169,-1194
All clear/ clear deep (L-N2b)	-636.8,-635.4	-663.4,-661.7	-1169.6,-1166.8
All clear/ all humic	-1096,-1092	-925.2,-926.6	-1314,-1453
All humic/ humic moderate alkaline (L-N8a)	-497.8,-498.3	-261,-258	-324,-345

Table 3. pairwise comparison of GAM regression models among countries for clearwater and humic lakes, respectively. The AIC values for the combined lake types (1st number) and for the split lake types model (2nd number) are given for each pair of countries (UK lakes excluded due to low no. of lakes). Significant differences are given in bold letters.

Lake-type		Chrysophytes		Pennaes		Cyanobacteria	
		FI	SE	FI	SE	FI	SE
L-N2a, 5	NO	-192/ -232	-252/ -261	-293/-291	-224/-224	-362/ -366	-416/-457
& 2b	FI		-187/ -203		-224/-224		-509/ -509
L-N3a & 6a	NO	-318/ -361	-148/ -154	-262/ -263	-120/ -116	-386/ -392	-143/ -143
	FI		-266/ -264		-161/ -157		-260/ -270

Figure captions

Fig. 1. Relationships for all three indicator groups along the Chl-*a* gradient, split into lake types that exhibited significant differences (Table 2). 1a, clearwater lakes; 1b, humic lakes. In each panel, the lakes are split into low alkaline (left column) and moderate alkaline lakes (right column). The graphs show from top to bottom proportions of the total phytoplankton biovolume for chrysophytes, pennate diatoms and cyanobacteria, respectively. The grey lines show the GAM regressions fitted to each relationship, with dotted lines giving the confidence interval of the mean trend line. The dots represent single samples taken during spring/early summer (May-July) for pennate diatoms and during late summer (July-Sept) for chrysophytes and cyanobacteria.

Fig. 2. Mean depth plotted against surface area of lakes in the study area. Note the difference between Finnish and Norwegian lakes.

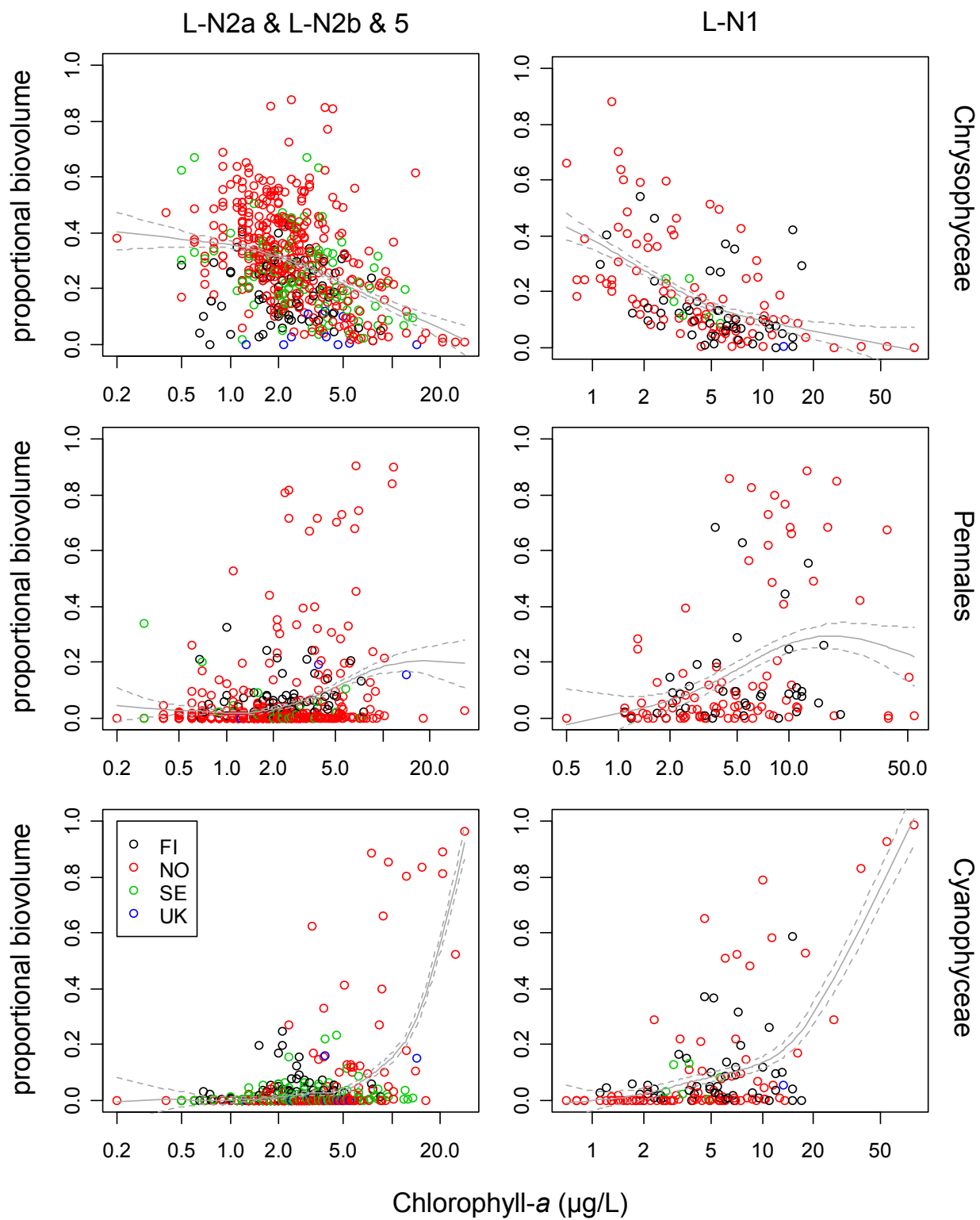


Fig. 1a.

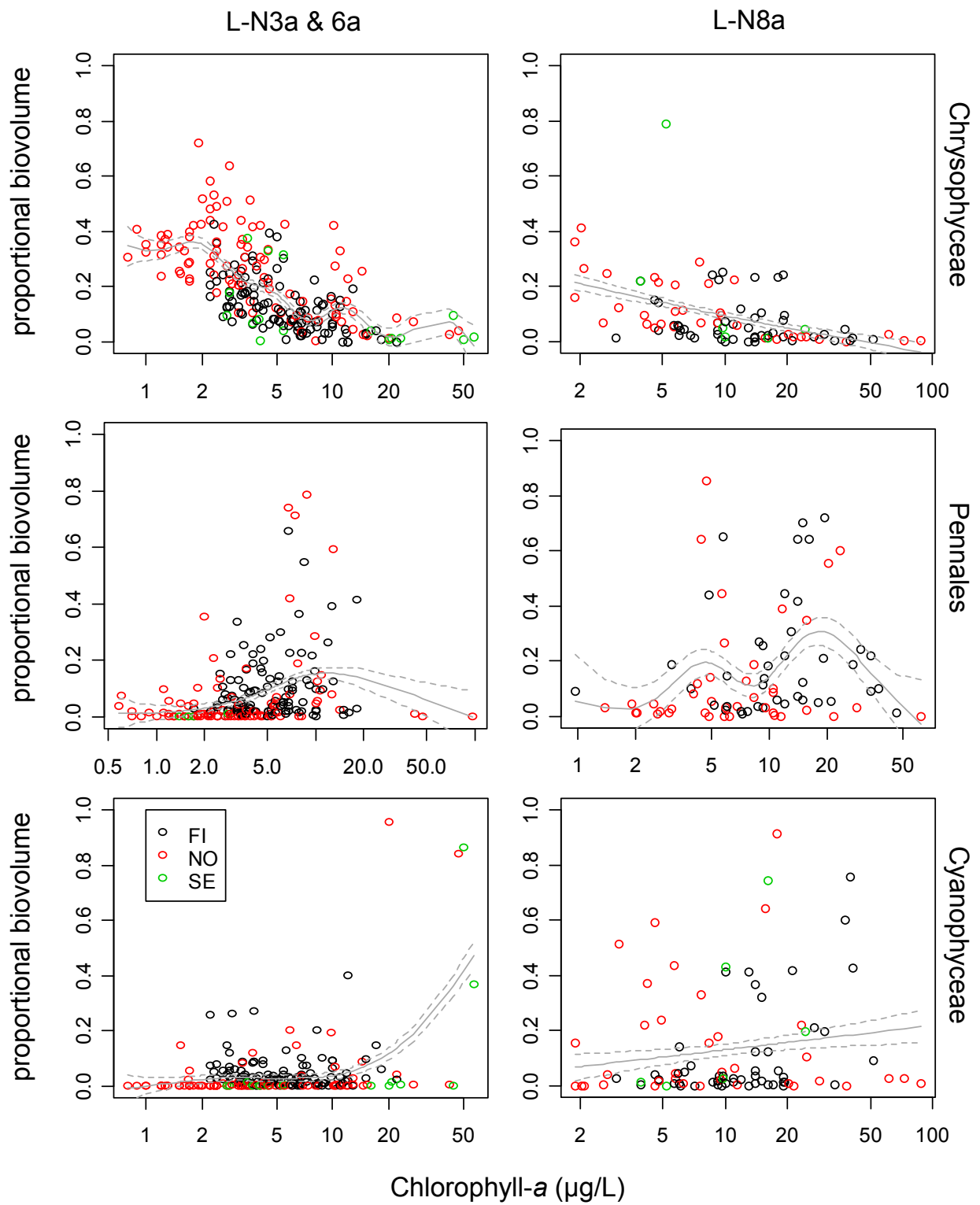


Fig. 1b.

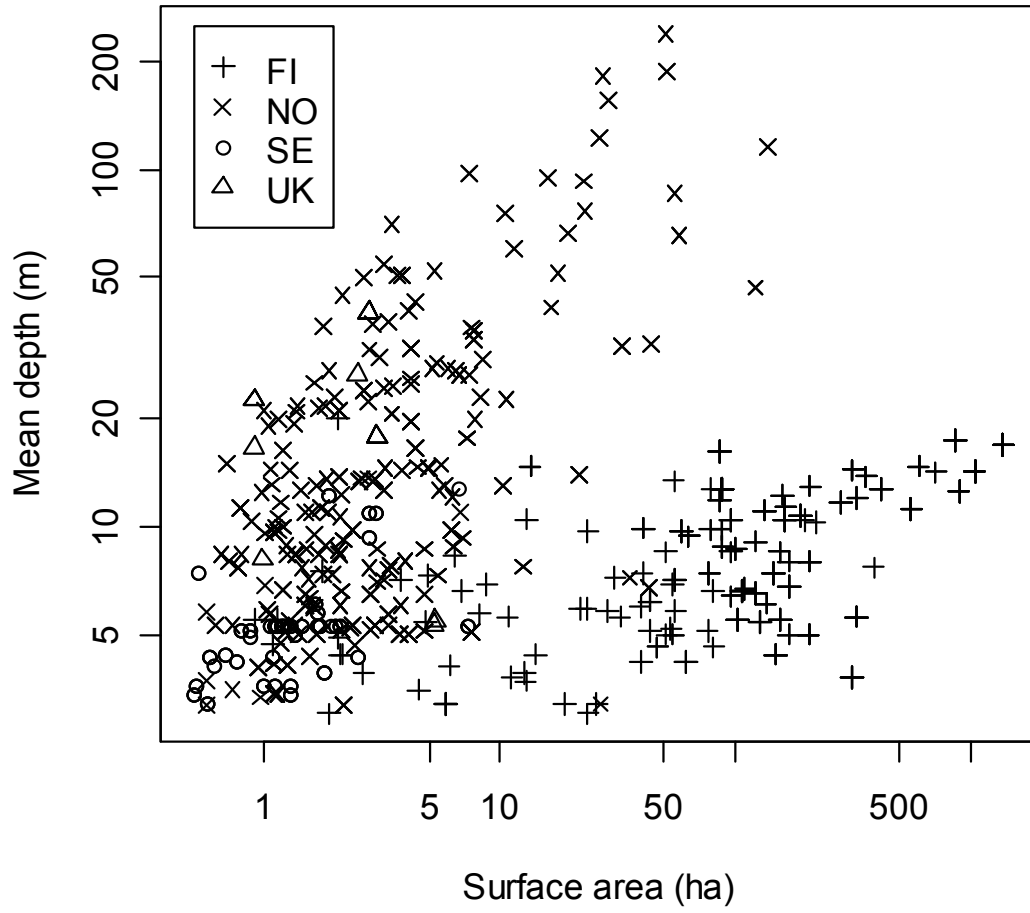


Fig. 2.