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Water colour, phosphorus and alkalinity are the major determinants of the dominant phytoplankton species in European lakes

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Abstract

Analysis of phytoplankton data from about 1500 lakes in 20 European countries has revealed that two-thirds of the species that dominate lakes during the summer are dominant right acrossEurope. Using Canonical Correspondence Analyses, we have examined how both habitat conditions within lakes and environmental factors over broad geographical scales explained the distribution of the 151 most common summer dominant species. The distributions of these species were best explained by water colour and latitude, although alkalinity and total phosphorus also appeared to be important explanatory factors. Contrary to our original hypothesis, summer water temperatures had a negligible impact on the distribution of dominants, although, due to the restricted summer season we examined, only a limited temperature gradient was present in the dataset. Cryptophytes occurred more frequently among dominants in Northern Europe whereas cyanobacteria and dinophytes dominated more in Central and Southern Europe. Our analyses suggest that besides nutrient concentrations, other water chemistry variables, such as alkalinity and the content of humic substances, have at least as important a role in determining the distribution of the dominant phytoplankton species in European lakes.

Introduction

Despite continuous efforts of generations of algologists studying individual lakes, the biogeographical distribution of freshwater phytoplankton and its driving factors are still largely unknown. Padisák et al. (2003) pointed out that this may because taxonomic and floristic work has had a stronger focus in small lakes, the bulk of our knowledge on the ecology of phytoplankton is derived from relatively large lakes. The major problem in biogeographical studies has been the absence of phytoplankton data of a comparable resolution and harmonized taxonomy covering broad continental scales. Variability in phytoplankton composition and abundance is driven by local environmental factors, such as lake morphometry, as well as broad latitudinal, longitudinal and altitudinal gradients. Phytoplankton abundance and taxa richness may display some regularity in spatial distribution, but these patterns are often blurred because of regionally different taxonomic resolution, counting routines and traditions in taxonomic work. Nevertheless, a number of important studies have been carried out on a relatively large numbers of lakes, generally at a national level (Table 1).

Table 1. Examples of broad-scale studies on phytoplankton community composition

Scope of study	Selection of lakes	Reference
Gradients in phytoplankton community structure with increasing lake trophic status	165 lakes in Florida	Duarte et al. (1992)
Patterns in phytoplankton taxonomic composition across lakes of differing nutrient status	91 temperate lakes	Watson et al. (1997)
Responses of three major phytoplankton classes to eutrophication	850 lakes from Scandinavia and the United Kingdom	Ptacnik et al. (2008)
Relationship between phytoplankton species richness and productivity including six major taxonomic groups	33 well-studied lakes on different continents	Dodson et al. (2000)
Geographic gradients in phytoplankton biodiversity at species-level over a continental scale	540 lakes and reservoirs on the continental U.S.	Stomp et al. (2011)
Community structure of summer phytoplankton	73 nutrient-poor Swedish lakes	Willén et al. (1990)
Dominant species and functional assemblages in late summer phytoplankton	80 Hungarian small shallow lakes	Padisák et al., 2003
Type-specific and indicator taxa of phytoplankton as a quality criterion for assessing the ecological status	55 Finnish boreal lakes	Lepistö et al. (2004)

In Europe the implementation of the Water Framework Directive (Directive, 2000) has given a new impetus to freshwater ecological studies at species and community level and the need for comparisons over broad geographical ranges shifted to the forefront of research. Chemical and biological data from more than 5,000 lakes in 20 European countries were compiled into databases within the EU REBECCA Project (Moe et al., 2008) and complemented by new data during the EU WISER Project (www.wiser.eu). This database is now the largest combined dataset on phytoplankton composition in Europe.

It is always challenging to study phytoplankton community responses to changes in the environment due to the high variability of phytoplankton species structure. Common ways to cope with this complexity is to “boil it down” to major taxonomic groups (e.g. Duarte et al., 1992; Ptacnik et al., 2008), functional groups (Reynolds et al., 2002, Padisák et al., 2003) or strategist groups (Grime, 1979; Reynolds, 1988) or to calculate various indices to characterize different aspects of the community structure, such as diversity (Shannon, 1948; Simpson, 1949; Margalef, 1958) or evenness (Pielou, 1975). For many purposes even the simplest parameter, the number of species (Hill, 1973), may be the most useful measure of local or regional diversity. In our study, we follow a different approach and focus on the dominant species. Studying the dominants is interesting for several reasons: Firstly, the stability of ecological communities often depends greatly upon the population dynamics of the dominant species (Grime, 1998; Flöder et al., 2010); and secondly, as the winners of competition for resources, the dominants can give a robust picture of resource availability. In this respect, studying the summer phytoplankton is most promising, as community equilibria occur most prominently during summer when higher growth rates and less flushing allows competitively stabilized associations to develop (Padisák et al., 2003). Many of the dominants tend to be nuisance species, so the distribution and understanding of their controlling factors remains a high priority research topic. Finally, selecting just to examine the dominant species should guarantee reduced taxonomic uncertainty, as researchers tend to pay more attention to abundant species and their high abundance in the sample should minimize misidentification errors as sufficient material is observed to cover phenotypic variability in the species.

A recent analysis of the 1,337 lakes included in the European Environment Agency (EEA) database (Nõges, 2009) showed that lakes at higher latitudes are larger but shallower and have smaller catchment areas. Northern lakes have lower alkalinity, pH and conductivity, and also lower concentrations of nitrogen and phosphorus while the concentration of organic matter is higher compared to southern lakes. Several gradients in lake environments were found also along longitudinal and altitudinal scales. As Europe extends from arctic to sub-tropical areas, and from maritime to continental climates, the temperature and ice regimes of inland waters vary within a wide range. The present study aims to assess the impact of these hydrochemical, climatic, and morphometric factors on the dominant taxa of lake phytoplankton and their functional attributes, over broad geographical scales,. As differences in humic matter content and alkalinity have been shown to be the major factors modifying phytoplankton response to eutrophication within the Nordic countries (Ptacnik et al., 2008), we hypothesise that expanding the geographical range to the south and west, and focusing on dominant species, we should see an even stronger impact of these factors. We also hypothesise that the effect of water temperature will be clearly manifested in the occurrence of different phytoplankton dominants.

Materials and methods

Twenty countries provided data to the EU 7th Framework Programme project WISER. Data were gathered spanning a long time period (1972-2009). Data from samples taken only in July, August and September were selected for analysis, comprising a total of 6120 samples from 1558 water bodies from Belgium (BE) 11, Cyprus (CY) 7, Germany (DE) 217, Denmark (DK) 64, Estonia (EE) 46, Spain (ES) 135, Finland (FI) 156, France (FR) 5, Greece (GR) 1, Hungary (HU) 13, Ireland (IE) 40, Italy (IT) 14, Lithuania (LT) 36, Latvia (LV) 58, The Netherlands (NL) 43, Norway (NO) 401, Poland (PL) 39, Romania (RO) 10, Sweden (SE) 113 and United Kingdom (UK) 149. More than half of these data (62%) originated from the last ten years.

Phytoplankton and chemical data were largely based on integrated samples from either the epilimnion or euphotic zone. Samples were analyzed according to the Utermöhl technique (CEN EN 15204, 2006). Very seldomly, additional slide preparation for identification of diatom species was carried out in parallel, so the diatom taxa list is based on different analytical approaches. Therefore, for example, the diatom genus *Cyclotella* is identified to species level in only a small proportion of samples. The European WISER phytoplankton list was created as an operational list to merge European data (http://www.freshwaterecology.info/). This list is not kept up to date with new names, but was harmonized based on the status of common determination keys in Europe in 2010.

We focused our study on the most dominant taxa, which we defined as the single species with the largest biovolume from each sampling date. Only species which were recorded as dominants in at least five of the 6120 samples in the dataset were included in our analysis. We also examined the dominant species in terms of their belonging to 11 algal classes: Bacillariophyceae (Bac), Chlorophyceae (Chlor), Chrysophyceae (Chrys), Conjugatophyceae (Conj), Cryptophyceae (Crypt), Cyanophyceae (Cyan), Dictyochophyceae (Dict), Dinophyceae (Dino), Euglenophyceae (Eug), Prymnesiophyceae (Prym) and Raphidophyceae (Raph).

To study the occurrence of dominant species in Europe, we split the data into two parts – countries belonging to the Nordic Geographical Intercalibration Group (N-

GIG: FI, SE, NO, IE, part of UK) and countries located in Central and Southern Europe, belonging to the Central Baltic (CB-GIG), Alpine (AL-GIG), East Continental (EC-GIG) and Mediterranean (M-GIG) Geographical Intercalibration Groups. The GIG boundaries were delineated within the WFD implementation process and reflect the eco-regions which share common types of surface water bodies. This split divided the data into relatively comparable parts with 4071 samples collected from 859 N-GIG lakes and 2049 samples collected from 699 lakes located in Central and Southern parts of Europe. The fact that many lakes were represented by a number of samples in which the dominant species could either be the same or different, complicated the calculation of occurrence frequencies of different dominant species: calculation by lakes became impossible whereas calculating by samples would have caused a bias towards lakes for which there were more samples in the dataset. To overcome this, we considered the occurrences of different dominant species in the same lake as different counting units or occasions, but if the same species dominated in all samples from a lake, it was considered as one counting unit. We got 1897 such counting units for N-GIG and 1341 counting units for Central and Southern part of Europe that were analyzed for the frequency of dominant species belonging to different algal classes.

The database included the following environmental parameters: latitude, longitude, altitude, alkalinity, maximum depth, mean depth, surface area, colour (Pt-Co scale), total nitrogen (TN), total phosphorus (TP) and water temperature.

For evaluation of the relationships between the distribution of dominant species and the environmental variables, we ran a Canonical Correspondence Analysis (CCA), using CANOCO 4.5 (Ter Braak & Šmilauer, 2002).

Results

In Northern Europe, lakes are generally larger, but shallower, have lower alkalinity, total N and total P and are generally more coloured than in Central and Southern European lakes. A difference in summer water temperatures between the two regions was not so apparent (Table 2).

Altogether 151 phytoplankton taxa were recorded as dominants in 5 or more samples, 130 of which were identified to species level and 21 to genus level. We handled all of them as unique taxa. The occurrence of these dominant taxa by country is presented in electronic annex 1.

The frequency distribution of the dominant taxa among the 20 countries had a positive skew (Fig. 1) with many of the dominant taxa only shared by 2-4 countries. The most widespread taxa, occurring as dominant in 15 or more countries, were *Ceratium hirundinella, Cyclotella* sp., *Aulacoseira granulata* and *Cryptomonas* sp. Among dominants, 132 taxa occurred in N-GIG lakes, with only 29 of these being restricted to the N-GIG and 126 dominant taxa occurred in Central and Southern Europe, with only 16 taxa restricted to this area. About two-thirds of the dominant taxa, therefore, dominated in both regions of Europe.

The division of the dominant taxa between algal classes was rather similar in the two parts of Europe (Fig. 2). There were slightly more diatom, chrysophyte and chlorophyte taxa and slightly less cyanobacterial taxa among dominants in the North than in Central and Southern Europe. The same differences appear much stronger in terms of the frequency of occurrence of dominants between the two regions. Chrysophytes occurred 3 times and cryptophytes nearly twice as frequently among dominants in the N-GIG than in Central and Southern part of Europe and cyanobacteria and dinophytes occurred about twice less frequently. The biggest difference, however, was revealed for *Gonyostomum semen*, the single representative of Raphidophyta, which dominated in N-GIG lakes 5 times more frequently than elsewhere. Our dataset revealed that *Gonyostomum semen* was a dominant species of soft water lakes (alkalinity between -0,067 to 1,055 meq/l) in DK, EE, ES, FI, LV, NO, SE and UK. The highest biovolumes of *G. semen* were recorded in humic lakes in SE, NO, EE and DK(average water colour of these lakes was 112 mg/l Pt). Our analysis highlighted other species as being capable of dominating dark acid waters, like *Chrysosphaerella longispina* (Dillard, 2008; Trigal et al., 2011), *Botryococcus terribilis* (Trigal et al., 2011), *Peridinium inconspicuum* (Willén, 2003) and *Dinobryon sociale var. americanum* (Canter-Lund & Lund, 1995). Species which showed a good relationship with longitude, like *Dinobryon pediforme*, were also a common dominant in acid lakes (Willén, 2003).

Cumulutive percentage variance of species and environmental relations in two CCA axes was 36.0. Monte Carlo permutation test showed that the most significant parameters explaining the taxa ordination in rank order were maximum depth, latitude, alkalinity, colour, longitude, altitude, total P, total N, surface area and mean depth ($p \leq 0.024$). The only insignificant parameter was water temperature ($p = 0.242$). The CCA biplot (Fig. 3a,b) revealed a strongly intercorrelated group of factors describing lake morphometry (mean depth, maximum depth, surface area), which was positively related to altitude and negatively to TP and TN. Water colour increased strongly with increasing latitude and longitude and was negatively related to alkalinity. Water temperature, which was the weakest of the explanatory variables tested, increased with decreasing lake size and depth and showed no relationship with geographic location (latitude and longitude).

The cloud of the dominant species had a strongly elongated shape in the gradient determined by water colour,alkalinity and TP. Taxa associated with high water colour were in rank order *Crucigenia tetrapedia*, *Peridinium umbonatum var. goslaviense* and *Urosolenia longiseta* and those associated with high alkalinity *Aphanizomenon aphanizomenoides, Cryptomonas curvata* and *Staurastrum pingue. A. aphanizomenoides* and *Cylindrospermopsis raciborskii* showed very good relationships with water temperature, TP and alkalinity.

At low latitudes and longitude, i.e. Southern Europe, there is another cluster of species such as *Planctonema lauterbornii*, *Dictyosphaerium subsolitarium*, *Cyclotella ocellata*, *Mougeotia* sp., *Coenochloris fotti* and *Cryptomonas erosa*. All these species had their peak biovolume in southern countries, most of these in ES. One of these species, *Planctonema lauterbornii*, has been shown in other studies to have a strong relationship with temperature (Gomes et al., 2004).

The diatoms *Asterionella formosa, Tabellaria fenestrata and Cyclotella comensis* were strongly related with lake size and depth. If plotted by algal class, the stronger dependence of diatoms on lake morphometry compared to other algal classes was expressed in the much broader vertical spread of the cloud (not shown). Chrysophytes (Fig. 4) instead had a strongly skewed distribution towards increasing latitude and water colour.

Discussion

Dominant taxa

The fact that, in general, about two-thirds of the dominant species in Northern Europe were the same taxa that dominated in Central and Southern part of Europe is surprising. This suggests that broad geographical-scale gradients, such as the effects of climate and day length or length of growing season are less important in determining the dominant species than more local lake- and catchment-specific factors, such as depth and alkalinity. Less surprising is that dominant species spanned many algal classes, reflecting the diverse range of lake types and broad alkalinity and nutrient gradients across Europe. The fact that chrysophytes, cryptophytes, diatoms and raphidophytes were more frequently dominant in Northern Europe, whilst cyanobacteria and dinoflagellates more frequently dominated Central and Southern Europe reflected the broad distinction between dominant lake types in these two regions. Northern lakes are generally larger and shallower with smaller catchment areas, lower alkalinity, pH and conductivity and with less nutrients and more dissolved organic compounds than southern lakes (Nõges, 2009). Chrysophytes are common in softwater lakes with low or moderate productivity and lakes with low pH (Nicholls & Wujek, 2003), which is in good correspondence with our analyses (Fig. 3). Cryptophytes are common species with a widespread distribution in many lake types, but our analysis supports individual lake studies that show they often dominate in the summer and autumn in humic lakes (Arvola et al., 1999). The higher frequency of cyanobacteria and dinophytes (Fig. 2) as dominants in Southern Europe is clearly explained by the distribution of lakes of higher nutrient concentrations and higher alkalinity in this region. The impact of these specific individual gradients in geography, morphology and water quality on species is discussed in more detail below.

Colour, latitude and longitude

Latitude, longitude and colour gradients in European lakes are correlated, but the strongest factor was colour, since the other two simply describe location. The majority of Scandinavian lakes have acid and coloured waters in correspondence with catchment areas covered mostly by forests, swamps and mires. Thin soils lie directly on bedrock and buffer capacities are relatively low (Arvola et al., 1999). Hereafter colour and latitude, and to a lesser degree longitude, are discussed together, not as separate parameters.

Many taxa common in highly productive lakes, are also more frequently recorded in lakes of higher humic content (Arvola et al., 1999). Arvola et al. (1999) presented a list of species that occur more frequently in brown coloured lakes. The following species also occurred as the dominant species in our dataset: *Acanthoceras zachariasii*, *Anabaena planktonica*, *Aphanizomenon flos-aquae*, *Eunotia zasuminensis*, *Mallomonas caudata*, *Melosira varians*. *Gonyostomum semen*, *Botryococcus braunii*, *Crucigenia tetrapedia*, *Tabellaria flocculosa, Monoraphidium griffithii, Dinobryon pediforme, Synura* sp., *Aulacoseira alpigena, Spondylosium planum, Peridinium umbonatum, Urosolenia longiseta* and *Aulacoseira italica*. Additionally, *Anabaena lemmermannii*, known as a characteristic species of soft water lakes (Ott & Kõiv, 1999) was also found as a dominant predominantly in Northern Europe, whereas we observed that *Trichormus catenula* is widely distributed (Zabelina et al., 1951). Most of these species dominate in northern parts of Europe, in countries like NO, SE, FI, UK, EE and DK, with some exceptions like *Trichormus catenula* and *Synura* sp.

Rosen (1981) identified *Oocystis submarina* (Arvola et al., 1999) and small naked chryso- and dinoflagellates as typical of humic conditions. *Anabaena macrospora* and

Woronichinia compacta are also common in the northern temperate zone (Komárek & Anagnostidis, 1999; Komárek & Zapomelova, 2008).

Gonyostomum semen is a well-known nuisance alga with widespread distribution in Northern Europe (Figueroa & Rengefors, 2006) and has been recorded as increasing in Scandinavian (Willén, 2003; Figueroa & Rengefors, 2006; Trigal et al., 2011) and Baltic soft water lakes (Rakko et al., 2008).

Polyhumic lakes usually have a very specific phytoplankton composition, where dominant species are adapted to low light and large fluctuations and gradients of temperature and oxygen. Higher humic content has been observed to be associated with higher phytoplankton biovolume (Arvola et al., 1999; Carvalho et al., 2008; 2009). In polyhumic lakes (>100 g Pt m^{-3}) this trend stops (Arvola et al., 1999). Moderate content of humic matter seems to positively affect phytoplankton abundance. One explanation of this is that environmental resources are enriched in humic waters. If besides moderate humic matter, the supply of mineral nutrients is enriched, and there is enough carbon resource, phytoplankton have been shown to be richer in comparison with low colour lakes (Ott & Kõiv, 1999).

Water temperature, TP and alkalinity

The wide distribution of *C. raciborskii* and *A. aphanizomenoides* in the temperate zone is widely cited as a response to global warming (Briand et al., 2004; Stüken et al., 2006). *C. raciborskii* is a common species in tropical and pantropical regions (Cronberg & Annadotter, 2006). Our analyses showed that *C. raciborskii* was now a dominant species in samples from ES, HU and NL. This species has rapidly increased all over the world from tropical to temperate zones (Fabbro & Duivenvoorden., 1996; Chapman & Schelske., 1997; Lagos et al., 1999; Shafik et al., 2001; Briand et al., 2004; Valerio et al., 2005; Bouvy et al., 2006; Fastner et al., 2007; Moustaka-Gouni et al., 2009; Alster et al., 2010; Kokociński et al., 2010; Moisander et al., 2012) except Antarctica (Padisák et al., 2003). *C. raciborskii* prefers highly eutrophic waters, when water temperature is high and light conditions are poor (Moustaka-Gouni et al., 2006; 2009), but it can also survive in water bodies with lower trophic status, because of its effective storage capacity for phosphorus. This species can also dominate under varied abiotic conditions, such as high concentrations of dissolved minerals or variable salinity. Temperature appears to be the most important factor. *A. aphanizomenoides* is also recorded from tropical and subtropical regions, but has expanded its distribution into the temperate zone (Stüken et al., 2006). Our database showed that *A. aphanizomenoides* is now a dominant in Germany (DE) and Spain (ES).

Water temperature, TP and alkalinity also showed a strong relationship with many cyanobacteria, such as *Microcystis flos-aquae*, *Anabaena viguieri*, *Aphanizomenon gracile*, *Planktothrix agardhii*, *Pseudanabaena limnetica*, *M. viridis*, *Limnothrix redekei*, *Chroococcus limneticus* and *Anabaena danica*. All these species, except *C. limneticus*, are particularly known from meso- and eutrophic water bodies and may form water blooms (Mischke & Nixdorf 2003; Nixdorf et al., 2003; Reynolds et al., 2002; Cronberg & Annadotter, 2006; Willén, 2007). Phillips et al. (2012) classified phytoplankton genera into very tolerant, tolerant, sensitive and very sensitive taxa of high nutrient conditions. Many of the cyanobacterial genera were classified as very tolerant or tolerant. Only *Chroococcus* sp. was classified as a slightly sensitive genus of nutrient concentrations. The dominance by *Euglena* sp. also showed a strong relationship with water temperature and TP. This taxon does not generally reach a high biovolume in large lakes, but in small lakes its biovolume can be great (Padisák et al., 2003), as was supported in this study. *Pandorina morum* and *Cryptomonas curvata* are common in nutrient rich water bodies (Reynolds et al., 2002; Padisák et al., 2003) and *C. curvata* is tolerant of low light (Reynolds et al., 2002). *Ceratium furcoides* and *Aphanizomenon gracile* dominance showed strong relationships with alkalinity in our study but both species are described by Reynolds et al. (2002) as tolerant of low carbon concentrations, although this may be the case in waters of very high alkalinity.

Lake morphometry (surface area, mean and maximum depth) and altitude

Lake morphometry and altitude appeared important in favouring the dominance of the following species in rank order: *Asterionella formosa*, *Tabellaria fenestrata*, *Cyclotella comensis* and *Dinobryon bavaricum*. *Asterionella formosa* and *Tabellaria fenestrata* showed very strong relationship with mean depth, surface area and maximum depth. Both species are dominant in deep lakes with large surface area. Despite heavy frustules they are best adapted to float in the water column due to long, thin cells, or the belt- and star-like structure of their colonies. *Cyclotella comensis* showed a particularly strong relationship with surface area. This species is common in alpine lakes (Zabelina et al., 1951; Hausmann & Lotter, 2001; Scheffler & Morabito, 2003). Our analyses supported this, showing that it was dominant in higher altitude locations of ES, IT, NO and SE (with average altitude 397.6 m). The average maximum depth of these lakes was also relatively high (164.7 m).

Conclusions

We recorded 151 phytoplankton taxa mostly identified to species level, which occurred as the most dominant taxa by biovolume in at least five of the 6120 samples collected between July and September from 1558 lakes in 20 countries of Europe.

Two-thirds of the dominant species in Northern Europe (including Finland, Sweden, Norway, Ireland and part of UK) were the same taxa that dominate in Central and Southern regions of Europe. The dominant species spanned all algal classes in both regions reflecting a diverse range of lake types across Europe. There were slightly more diatom, chrysophyte, crypotophyte and chlorophyte taxa and slightly less cyanobacteria and dinophyte taxa among dominants in the north than in the south.

Chrysophytes occurred 3 times and cryptophytes nearly twice more frequently among dominants in the North European lakes than in Central and Southern part of Europe whereas cyanobacteria and dinophytes occurred about twice less frequently.

The CCA ranked water colour, alkalinity, and TP as the most influential factors determining the large-scale distribution patterns of lake phytoplankton dominants in Europe. This suggests that, besides trophic conditions, other hydrochemical variables, have at least as important a role in determining phytoplankton community composition in lakes. Water temperature from July to September had only a negligible impact on the distribution of dominants, showing the prevalence of rather homogeneous thermal conditions throughout Europe for this period of year.

Cryptophytes and especially chrysophytes revealed a clear affinity to more coloured and less alkaline waters of Northern Europe. The higher frequency of cyanobacteria and dinophytes as dominants in Southern Europe can be explained by the higher trophic state and higher alkalinity of lakes in this region.

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Fig. 1 Histogram of the number of dominant phytoplankton taxa that are shared by increasing numbers of European countries

Fig. 2 Distribution of the dominating lake phytoplankton taxa among algal classes (two left columns) and their relative frequency of occurrence (two right columns) compared between countries belonging to the Nordic Geographical Intercalibration Group (N-GIG) and in Central and Southern part of Europe belonging to Central Baltic (CB-GIG), Alpine (AL-GIG), East Continental (EC-GIG) and Mediterranean (M-GIG) Geographical Intercalibration Group

Fig. 3 Biplot of the Canonical Correspondence Analysis (CCA) results on factors determining the distribution of dominant phytoplankton taxa in lakes of Europe. a – the large picture, b – the central part magnified. The arrows in the biplot representing the environmental variables indicate the direction of maximum change of that variable across the diagram and the length of the arrow is proportional to the rate of change. Each point representing a dominant species lies at the centroid of the samples in which it was found

Fig. 4 CCA biplot showing the factors determining the distribution of Chrysophytes in lakes of Europe

Table 1. Examples of studies on phytoplankton community composition based on analyses of published data

Table 2. Information of range of maximum and mean depth, surface area, alkalinity, colour, total N, total P and water temperature in two different parts of Europe: Nordic Geographical Intercalibration Group (Nordic GIG) and Central and Southern part of Europe belonging to Alpine (AL-GIG), Central Baltic (CB-GIG), East-Continental (EC-GIG) and Mediterranean (M-GIG) Geographical Intercalibration Group

Electronic annex 1. Occurrence of the most dominant species in European countries