



Research paper

Trophic gradient is the main determinant of species and large taxonomic groups representation in phytoplankton of standing water bodies



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ABSTRACT

We used the newly formed database of phytoplankton samples from the Czech Republic, containing 696 taxa from 662 samples of various types of stagnant waters (fishponds, alluvial backwaters, flooded sand- and gravel pits, lakes in abandoned quarries in former coal mines, reservoirs and others) to test for the relationships between phytoplankton composition and productivity, geographical and climatic variables (elevation, temperature, precipitation) and season of the year. As a surrogate of productivity, the number of cells/ml and the total biovolume [μm^3]/ml, both spanning over more than six orders of magnitude (from 10^1 to 10^7 for the number of cells and from 10^2 to 10^9 for the biovolume) were used. The phytoplankton was characterized by its species composition and also by the composition of large taxonomic groups. The data were analysed by constrained ordination (Canonical Correspondence Analysis), including variation partitioning, and by ANOVA of the estimates of species optima based on weighted averages of environmental characteristics.

All the explanatory variable groups, i.e. productivity, geography/climate, and season have significant effects on both the species composition and the composition of large taxonomic groups. Productivity is the best predictor of both species and large taxonomic group composition, followed by climatic variables and finally season. The relative effectiveness of productivity as a predictor was considerably greater for large taxonomic groups. The productivity characterized by the number of cells was always a better predictor than when characterized by biovolume. The species optima estimated as weighted averages of corresponding environmental variables show consistent patterns according to large taxonomic groups, but also according to the genera within the groups: in particular, the cyanobacteria and Chrysophyceae preferred on average the most and the least productive environments respectively, however, there were large differences in species preferences also within groups and even within genera. The optima of species on the trophic gradient are suitable characteristics for ecological indication and are presented for more than 400 taxa in the appendix together with estimates of species tolerance.

1. Introduction

The species composition of phytoplankton communities usually corresponds well to the environmental conditions (Maileht et al., 2013), and thus, the phytoplankton organisms are also suitable ecological indicators (Bellinger and Sigee, 2015). In comparison with communities of perennial plants, where the study of the community composition–environment relationship and the use of community composition for bioindication have the longest tradition (Ellenberg, 1974), the phytoplankton communities are highly variable in time, undergoing pronounced seasonal dynamics (Weithoff et al., 2015) and exhibit fast changes in response to the change of environmental conditions

(particularly fast and pronounced response to nutrient input). In contrast to macroscopic plant communities, phytoplankton is composed of a phylogenetically highly diverse mix of organisms. Typically, phytoplankton communities are composed of a combination of prokaryotes and eukaryotes, and within each group, we can find a phylogenetically diverse selection of taxonomic units.

The diversity of life is a result of evolution. Clades will share many common traits originating from their ancestral species. Whereas sharing common morphological traits is obvious, we can also expect that the species within clades will also have similar niches, i.e. they will prefer similar ecological conditions (De Bello et al., 2015). This will create a phylogenetic signal in composition of ecological communities, and can

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lead to a pattern called niche conservatism (compare Losos, 2008 and Wiens et al., 2010 for concepts of niche conservatism). If this assumption is correct, phylogenetically close organisms will have similar environmental preferences, and not only the species composition, but also the composition of large taxonomic groups should reflect the environment well (and thus can be used for ecological indication). On the other hand, the more similar the species niches are (i.e. the more similar are their ecological requirements), the more the species will compete for resources (e.g. nutrients). According to the limiting similarity concept MacArthur and Levin, (1967), species must differ in their niches to coexist; consequently, we can expect also some phylogenetic divergence among co-occurring species.

In phytoplankton, organisms differing in their phylogenetic origin have often very similar habitat preferences and phytoplankton functional groups are usually composed of taxonomically diverse organisms (Reynolds et al., 2002; Salmaso and Padisák, 2007; Kruk et al., 2010; Borics et al., 2016). Still, we can expect some phylogenetic niche conservatism, some taxonomic groups will prevail in some functional groups. Thus, in this paper, we ask whether the phylogeny is a good predictor of species ecological preferences (and thus, do the phylogenetic groups differ in their ecological preferences)? And, if so, are the differences more consistent on the level of large taxonomic groups, or on much more detailed taxonomic classification (e.g. on the level of individual genera)? And can the composition of major taxonomic groups be predicted from environmental conditions?

For phytoplankton, various parameters connected with productivity (sometimes subsumed under the trophic status or trophic level of the water body) are usually among the best predictors (Ptacnik et al., 2009). It has also been shown that large planktonic groups have their optima at a certain trophic level (e.g. Watson et al., 1997) but many of them show also clear seasonal dynamics throughout the year (e.g. Salmaso et al., 2006; Lampert and Sommer, 2007; Devlin et al., 2009). Nevertheless, it seems that the local environment effect is more pronounced than the seasonal variability, both for the species and taxonomic group compositions (Anneville et al., 2004). In addition to the trophic status and seasonality, the phytoplankton composition and its dynamics is also affected by a series of other abiotic and biotic factors, including biotic interactions (Reynolds, 1998), particularly the zooplankton grazing (Watson et al., 1997; Colina et al., 2016).

In general, the trophy of the water body is the basic characteristic of water quality for both the drinking water supply and recreational purposes (Chorus and Bartram, 1999). Accordingly, there are efforts to use phytoplankton groups, genera or species as indicators of the trophic level in lakes or other types of standing water bodies (Rawson, 1956; Reynolds, 1998; Padisák et al., 2006; Salmaso et al., 2006; Carvalho et al., 2013; Borics et al., 2014; Lumberras et al., 2016). Various metrics characterizing the trophic status are based on the complete species composition of the phytoplankton community (Ptacnik et al., 2009; Mischke et al., 2008; Katsiapi et al., 2016) or on the composition of genera (Anneville et al., 2004; Phillips et al., 2013), but in many cases on some general characteristics like proportion of cyanobacteria (Silva et al., 2014; Hutorowicz and Pasztalaniec, 2014; Carvalho et al., 2013), total chlorophyll (Carlson, 1977; Sun and Huang, 1993 in Chen et al., 2003; Felip and Catalan, 2000; Carvalho et al., 2008), total biovolume (Felip and Catalan, 2000) or both in combination (Carlson and Havens, 2005). Facca et al. (2014) attempted to also use diversity to create Multimetric PhytoIndex for assessment of transitional waters. Nevertheless, this approach might be difficult to apply as we have demonstrated the unimodal response of diversity to trophy level (Skácelová and Lepš, 2014), where low diversity corresponds either to extremely low, or extremely high productivity. Lugoli et al. (2012) use phytoplankton size classes, chlorophyll concentration and taxonomic richness for multimetric phytoplankton index for ISS-Phyto (Index of Size Spectra Sensitivity of Phytoplankton) in marine and transitional waters.

The interest in the phytoplankton communities of standing water, based on both practical (water quality) and theoretical interests, led in

last decades to large international programs (REBECCA, WISER) resulting in large databases of phytoplankton samples from European lakes (e.g. Salmaso et al., 2006; Moe et al., 2008; Ptacnik et al., 2009). Czech Republic is not represented in these databases, partially because there are very few real lakes in the Czech Republic. The fairly most common water bodies in the Czech Republic are fishponds, artificial waterbodies of usually small size (typically several hectares), and, in the Czech Republic often several centuries old. Our study is based on the Database of phytoplankton samples of the Czech Republic, which we started to build several years ago (Skácelová and Lepš, 2014). The database is growing continuously, and is based on a sets of phytoplankton samples, collected for various purposes (including various environmental monitoring, nature conservation projects). Its advantage is the fact that all samples were analysed by the same person (first author of this paper), which guarantees taxonomic consistency and precision – indeed, unifying the taxonomic concepts is one of the most challenging tasks in building large international databases based on results of many researchers, sometimes resulting in aggregation of species for data analyses, e.g. at the genus level (e.g. Phillips et al., 2013). We have used this database to test for the dependence of species and higher taxonomic units composition on selected available environmental characteristics.

Here, we aim to disentangle the effect of trophic status (often reflecting management), climatic/geographic variables, and season on species composition and on the composition of major taxonomic groups of phytoplankton samples. Because the trophic status appeared to be the strongest determinant of both composition of species and trophic groups, we further concentrated on the response of organisms to trophic level. We have determined the optima of individual species on the trophic gradient (which might be also used for bioindication purposes), and tested whether they are conservative within genera and within large taxonomic groups.

2. Material and methods

2.1. Phytoplankton composition and productivity data

The species composition of the phytoplankton samples was retrieved from our database of phytoplankton samples of the Czech Republic containing 662 samples collected during various monitoring programs (in which quantitative data on the abundance of individual species were required) during the period 1987–2014. Total number of taxonomic units in the database is 696. Of these, 615 taxa are identified to the species level, 77 to the genus level, and rest to the higher taxonomic units (this level is called species level in further text). Studied localities cover a broad spectrum of stagnant water habitats from dystrophic to hypertrophic sites from lowlands to mountains (altitude from 160 to 720 m a.s.l.). The majority of samples come from the most frequent stagnant water body type in Czech Republic – fishponds (599), others from alluvial backwaters (10), flooded sand- and gravel pits (25), lakes in abandoned quarries in former coal mines (11), reservoirs (12) and others (5). Some waterbodies were sampled repeatedly in various seasons, across different years, and also in different parts of the waterbody.

Samples with volume 0.1 l (hypertrophic conditions) to 1 l (oligotrophic waters) were taken from depth 0.1–0.3 m, fixed with Lugol's iodine solution and afterwards all sedimentation was decanted. Cell counts were carried out in a Bürker chamber and recalculated to cell numbers per milliliter and converted into biovolumes using cell dimensions from the internal database of institute of Hydrobiology, CAS, provided by Jaroslava Komárková (Skácelová and Lepš, 2014). For species missing from the database we used our own data.

All the analyses (species determination and cell counting) were done by the same person (first author), which ensures taxonomic consistency throughout the dataset and ensures that the differences are not confounded by differences in identification ability, varying concepts of

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