

Blowing in the wind: how many roads can a phytoplankton walk down? A synthesis on phytoplankton biogeography and spatial processes

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Abstract The selected theme of the 17th Workshop of the International Association for Phytoplankton Taxonomy and Ecology (IAP), “Biogeography and Spatial Patterns of Biodiversity of Freshwater Phytoplankton,” offered the opportunity to explore one neglected aspect of phytoplankton ecology: the distribution of species in the geographic space. This paper summarizes the outcomes of 20 selected contributions among those presented at the workshop. The articles report the results from studies carried out in five continents (only Oceania is not represented) and on a wide array of aquatic ecosystems (deep and shallow natural lakes, man-made lakes, temporary and permanent ponds, rivers). The topics analyzed by the

contributors are related to Island Biogeography paradigms, dispersal vectors, survival strategies, environmental filters, dispersal distances, vertical and horizontal spatial variability of phytoplankton between and within water bodies, and of course, invasive algae. The overall analysis of the results presented clearly demonstrates that, as for many other organisms, there are “rules” governing freshwater phytoplankton spatial patterns and that these organisms also have a true biogeography, as nowadays is quite evident for several other groups in the same range of size. We can definitively conclude that the statement “Everything is everywhere” is obsolete, even though human activities tend to homogenize species distribution in the biosphere.

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Biogeography and Spatial Patterns of Biodiversity of
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Introduction

According to Krebs (2009), ecology is the scientific analysis of the factors that determine the abundance and the distribution of biological populations. Biogeography, the branch of Ecology studying the distribution of species in geographic space and through geological time, is thus an essential part of Ecology often neglected in the studies related to the ecology of phytoplankton. A great many of the

scientific publications produced on this topic study the factors determining the abundance of phytoplankton in a given environment. Incomparably less is the amount of literature produced on the geographic distribution and spatial patterns of phytoplankton. To fill this gap, the International Association for Phytoplankton Taxonomy and Ecology (IAP) centered its most recent triennial workshop on the topic “Biogeography and Spatial Patterns of Biodiversity of Freshwater Phytoplankton.”

The present paper summarizes the outcomes of the workshop, which were mainly devoted to demonstrate the hypothesis that, as for many other organisms, there are “rules” governing phytoplankton spatial patterns and that these organisms also have a true biogeography, as nowadays is quite evident for several other groups in the same range of size (Fontaneto & Hortal, 2008). The first ideas about a biogeography of freshwater algae were collected in a special issue published in this journal by one of the founders of the IAP, Jørgen Kristiansen, exactly 20 years ago (Kristiansen, 1996a). This ground-breaking volume has not received the recognition it deserved when it was published. Actually, several lines of evidence tended to sustain the so-called “Cosmopolitanism Paradigm” for phytoplankton and other micro-organisms for a long time. This belief was caused by inadequate taxonomical tools, as well as by the idea that, because of their very high population size and small body size there were no real barriers to the dispersal of freshwater microorganisms (for a review see Incagnone et al., 2015). This idea, first raised by Darwin (1859), was formally summarized by the renowned statement “Everything is Everywhere, but the environment selects” (EiE hypothesis) by the Dutch microbiologist Baas-Becking (1934; see Williams, 2011 for a review). We dedicate the present paper to our friend and colleague Jørgen Kristiansen with all our gratitude for having inspired most of the work contained in this special issue.

The assumption that organisms smaller than 2 mm have cosmopolitan distribution has been often supported by traditional taxonomy. However, the increased spreading of DNA taxonomy has challenged the EiE hypothesis. This relatively new methodology is adding new information about the high degree of cryptic diversity in the microscopic world at an almost daily rate supporting that spatial patterns of distribution exist also for the “smallest” organisms (Fontaneto & Hortal, 2012, 2013).

As demonstrated for other microorganisms (Heger et al., 2013), DNA taxonomy is a very promising tool to unravel the puzzle of distribution and diversity of phytoplankton species and strains (for the role of different “cryptic adaptive traits” found in different phytoplankton strains see Salmaso et al., 2015). However, as with all tools, it has to be used in a proper way (see Fontaneto et al., 2015) and the reliability of the results achieved by these new molecular methods still needs to be carefully checked and assessed (e.g., Morgan et al., 2014). Compiling appropriate DNA libraries for freshwater phytoplankton, as is done by Kaplan-Levy et al. (this volume), is thus an important starting point to assemble the amount of molecular references we still need to clarify the real extent of species identity, distribution, and occurrence and to solve the phylogenetic position of phytoplankton genera and species (e.g., Krienitz & Bock, 2012; Komárek, this volume). Clarifying molecular diversity can also offer the possibility to improve the traditional, morphology-based taxonomic approaches (de Tezanos Pinto et al., this volume). Such methods help to disclose physiological adaptation of species, like the existence of the H-gen in *Limnorphis robusta* (Paracutty) Komárek, Zapomelová, Smarda, Kopecky, Rejmánková, Woodhouse, Neilan et Komárková (Komárková et al., this volume) which may, to a large extent, explain the dominance of an “unusual” species in specific environments. As reviewed by Padisák et al. (this volume), genetic tools or analyses of secondary metabolites of different strains of the same species may help to disclose migration patterns, especially when there is a lack of reliable historical floristic records. Exploring physiological fingerprints of peculiar species, for example, *Borghiella dodgei* Moestrup, Hansen et Daugbjerg, has been a great help in understanding geographic distributions (Flaim et al., 2010). Indeed, some lakes, like Lake Tovel in the southern high Alps (Cellamare et al., this volume) seem to be a collector of rare species with remarkable geographic distributions and physiological adaptations.

However, once ascertained that biogeographical and spatial patterns exist in phytoplankton, traditional ecological studies and analyses are needed to understand the reasons leading to the patterns themselves, as observed in field studies. In the next paragraphs of this paper, we present an overview of the most updated research carried out, on a worldwide perspective and at

different spatial scales, on the geographic distribution of phytoplankton, its dispersal vectors and strategies, the colonization patterns, and the survival strategies adopted by species to cross the barriers existing between different water bodies. In this respect, as outlined by many contributors to this volume, inland waters may be considered as islands scattered in a terrestrial ocean of environments, unsuitable for phytoplankton. As discussed by Triantis & Sfenthourakis (2012), island biogeography is not a single-variable discipline. Accordingly, authors tested several concepts deriving from insular biogeography i.e., distance effect, species–area curves, small island and target effects, rescue effect, habitat suitability and environmental filters, connectivity and serendipity, which were explained and found to be valid also for phytoplankton under a variety of spatial and temporal scales.

Last but not least, since wind may effectively collect and transport phytoplankton when it is blowing on water surface (see the paragraph “Distances, in situ environmental filters and dispersal agents”), we took the liberty to pay a tribute to Bob Dylan’s song “Blowing in the wind” when we had to think of a title for the present contribution.

Geographic distribution of different types, patterns of colonization, invasions

Geographic distribution maps are commonly available for macrobiota, with birdwatcher guides being the most popular example for amateur ornithologists (like the “Collins Pocket Guide to Birds Britain and Europe,” Heinzl et al., 1995). Such maps are notoriously rare in phytoplankton ecology, with some recent refreshing exception (Roelke, this volume; Wilk-Woźnak et al., this volume). Although the Baas-Becking (1934) hypothesis (“everything is everywhere, but the environment selects”) repeatedly gained support for free-living microbiota (e.g., Finlay, 2002; Souffreau et al., 2015) and is also known as the “ubiquity hypothesis,” the opposing “moderate endemism” hypothesis (Foissner, 2006) is also supported from field observations. As discussed by Padisák et al. (this volume), such field support is limited, for example because (i) the microscopic size of the organisms often prevents a complete census of the entire habitat (Bolgovics et al., this volume), (ii) inexperience in organisms’

identification, or (iii) insufficient diacritical recognizable features in fixed samples (often not accompanied by observation of corresponding living samples). Moreover, there is also a general lack of systematic floristic surveys in most parts of the world. This way, revealing geographic distribution and area expansion of individual species must rely on competent floristic surveys that provide “bricks in the wall” (Stoyneva, this volume), which eventually may lead to solving the “jigsaw puzzle” (Wilk-Woźnak et al., this volume). Difficulties arise when one has to decide if a species is alien (invasive, exotic) or not. As discussed by Wilk-Woźnak et al. (this volume) this requires both a proper taxonomic identification and a good description of the native range of the species. An analysis of the floristic surveys of the last 25 years covering 161 water bodies, with comparison to older data, allowed Stoyneva (this volume) to reach basic results on spatial limitation of algal dispersal at least in a restricted area (Bulgaria, 110,994 km²). Of the 1,393 infrageneric taxa in that study, 318 (23%) exhibited restricted distributions which is quite a large number taking the size of the country into account. The thorough analysis of the data revealed some important mechanisms and highlighted the importance of migrating birds as main dispersal agents (see below in the paragraph “Distances, in situ environmental filters and dispersal agents”).

Analysis of spatial and temporal patterns of geographic distribution and range expansion of three species *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, *Raphidiopsis mediterranea* Skuja, *Cuspidothrix issatschenkoi* (Usatchev) Rajinemi, Komárek, Williame, Hrouzek, Kastovská, Hoffmann & Sivonen (Wilk-Woźnak et al., this volume) supported the African origin of *Cylindrospermopsis raciborskii* as was hypothesized earlier (Padisák, 1997) and although no testable hypothesis on migration routes of the other two species could be provided, the paper shows important geographic distribution maps with an apparent bipolar distribution of *Cuspidothrix issatschenkoi*.

Success of colonization of a habitat by a newcomer species in a given ecosystem requires some important conditions:

- the species must reach the habitat either by active or passive dispersal (for phytoplankton active migration can be ruled out);

- interspecific interactions (grazers, parasites, competitors) must not ultimately prevent successful establishment; and
- the habitat properties and the species-specific tolerance limits of the species must meet.

Stoyneva (this volume) provides an example where the first condition was met (probably by birds as carriers), but the habitat properties and the species' niche requirements are strikingly different. This example concerns the presence of a single specimen of the subaerophytic peat-bog species *Tolypothrix distorta* Kützing ex Bornet et Flahault in a hyperhaline water basin of the Black Sea coastal saltworks. Lack of competitors may allow “unfit” species to become even dominant as mentioned by Padišák et al. (this volume) for example when observing a high dominance of *Entomoneis paludosa* var. *subsalina* (Cleve) Krammer, a species typical of inland saline lakes, in a newly built small freshwater reservoir. Another signal that indicates series of arrivals and extinctions is multiple introductions. As already supposed by analyzing the history of *Cylindrospermopsis raciborskii* in North America (Padišák, 1997), Stoyneva (this volume) also supported the occurrence of repeated introductions of some species like *Anabaenopsis knipowitschii* (Usachev) Komárek and *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová et Cronberg. Roelke et al. (this volume) also discussed under this perspective the fast range expansion of *Prymnesium parvum* N. Carter in North America.

Successful establishment of a species and especially the numerical increase of its population up to bloom are often attributed to changes of trophic status or to global climate change. Roelke et al. (this volume) listed a number of rarely considered human-induced habitat changes that might facilitate blooms of *P. parvum*, such as increasing salinity as a consequence of increasing frequency and length of dry periods, reservoir construction expanding the residence time of continental waters and facilitating inter-basin transfer, increasing water hardness due to sand erosion, and herbicide use. In this case, a direct relationship between toxic blooms and the increased external nutrients loadings (eutrophication) could not be supported. Increasing evidence substantiates that in some cases it is rather the trophic change itself and not its direction that may lead to blooms of some species. For instance, blooms of *Mougeotia* have repeatedly been

reported from a number of deep lakes when external phosphorous load reduction reached a certain threshold (Tapolczai et al., 2015).

Island biogeography and associated species–area relationships for algae

Why are there so many kinds of “species”? To find an answer to this question, G.E. Hutchinson produced one of the most iconic papers in the history of modern ecology (Hutchinson, 1959; Naselli-Flores & Rossetti, 2010). Hutchinson's student Robert MacArthur, probably among those mostly influenced by the question, co-authored with Edward Wilson a book, *The Theory of Island Biogeography*, which analyzes the factors affecting species richness of isolated communities (MacArthur & Wilson, 1967). This work is considered a milestone which has driven ecology from a merely descriptive science to an experimental one, making biogeography one of its essential components.

Lentic inland waters, which are isolated environments surrounded by relatively dry ecosystems, perfectly fit the paradigms set by the theory formulated by MacArthur and Wilson and several studies have investigated under this perspective the species distribution patterns of their macrobiota (for a review see Incagnone et al., 2015). However, because of the reasons explained before and briefly reviewed by Bolgovics et al. (this volume), a few attempts have been made to analyze the distribution patterns of (freshwater) micro-autotrophic species although, numerically, they are the major component of aquatic communities.

Two papers in this volume directly deal with theoretical aspects of insular biogeography confirming that its paradigms are also valid for the autotrophic microbiota. In particular, by collecting data in 64 water bodies with a surface spanning between 10^{-2} and 10^9 m², Borics et al. (this volume) could demonstrate that

- larger water bodies have higher species number since they have greater possibility of “intercepting” the arrival of new invaders and of maintaining stable populations;
- lake size, by acting on morphological, kinetic, and chemical properties of the water body, also has a major importance in shaping the composition of phytoplankton assemblages.

These authors showed that specific adaptations (i.e., sinking velocity, swimming ability, or photosynthetic performances) allow some algal groups to develop in larger water bodies (e.g., dinoflagellates or heterocytic cyanobacteria), whereas some others are better fitted to smaller environments (e.g., euglenophytes). They also found that some groups (e.g., large colonial flagellated chlorophytes, non-heterocytic filamentous cyanobacteria, and filamentous chlorophytes) occasionally occur in high relative abundance both in small- and large-sized water bodies.

The above results are in accordance with the findings of Bolgovics et al. (this volume), who investigated species–area relationships (SAR) in benthic diatoms. While reviewing important conceptual issues related to SAR, they found that for these microscopic taxa, when the size-range of investigated environments spans over three order of magnitude, SAR cannot be conveniently described by a sigmoid model, as postulated in many theoretical works (see Bolgovics et al., this volume, for more details). Conversely, they demonstrated that the relationship could be best described by breakpoint regression applying a single breakpoint at 10^4 m². This implies that a considerable increase in species number can be expected in lakes larger than this threshold. Therefore, they could clearly show that water bodies falling in the surface range 10^{-2} – 10^4 m² were characterized by a Small-Island Effect (SIE), as theorized by insular biogeography. SIE postulates that very small islands do not follow the general rule of species number increasing with area. In these environments, the relationship appears to break down with species number varying independently of island area (Morrison, 2014).

The general theory of island biogeography also posits that species numbers tend to remain constant (although species identities may vary) on islands in an equilibrium state (MacArthur & Wilson, 1967). The concept of equilibrium in this case refers to the available pool of species, the availability of niches in a given island, and to the balance between immigration and extinction among the species in the pool. It is, thus, different from the equilibrium concept in phytoplankton ecology as reported in Naselli-Flores et al. (2003). Islands with no species may hide SIE (for more details see Triantis & Sfenthourakis, 2012) and, as shown in Naselli-Flores et al. (this volume), the occurrence and frequency of colonization events

cannot be simply related to the surface area of the receiving ecosystems but to several other factors as, e.g., the number of suitable ecosystems in a given area (the number of islands in the archipelago) and their relative distance, the size of inocula, the nature and availability of dispersal vectors, and the extent of environmental filters (see next chapter). An increase in the degree of connectivity was considered as a major factor contributing to the fast dispersal of *Prymnesium parvum* in North America (Roelke et al., this volume).

Distances, in situ environmental filters, and dispersal agents

Spatial patterns of biodiversity of freshwater phytoplankton depend on both determinism, mediated by environmental filters, and stochasticity, mediated by dispersal. Immigration of phytoplankton species in a new environment firstly depends on the ability to disperse over the physical barrier represented by the surrounding dry land. Although dispersal mechanisms for phytoplankton are quite elusive, some evidences exist on the role exerted by wind and aquatic birds as potential dispersal agents (Kristiansen, 1996b; Genit-saris et al., 2011; Incagnone et al., 2015). As stated by Stoyneva (this volume), occasional and isolated findings of phytoplankton species in a given environment often occur and represent a “proof of dispersal,” even though these events do not lead to the establishment of a permanently resident population. The successful colonization of a new environment and the establishment of a permanent population imply that, once arrived, organisms have to pass a series of environmental filters (linked to the different physical, chemical, and biological features of the recipient ecosystem) that may prevent the establishment of the immigrant species (Incagnone et al., 2015, Němcová et al., this volume). Biological interactions, e.g., predation, competition, and allelopathy, are also frequently reported as strong filters; these interactions historically determine the composition of a community, strengthen the relationships existing among its members during time, and make difficult for newcomers to colonize “already occupied” environments. These biological interactions altogether are named as “priority effects” (i.e., species or lineages already present in a community affect the establishment of later arriving immigrants) and are often considered as

powerful inhibitors of colonization success (Louette & De Meester, 2007; Symons & Arnott, 2014). Priority effects along with local adaptations achieved by resident population (which may be formed by a genetically different strains) may represent a “barrier” to colonization as described by the “Monopolization Hypothesis” (De Meester et al., 2002), a cornerstone in the interpretation of the distribution of the genetic diversity in freshwater organisms.

Phytoplankton can be passively dispersed by physical (e.g., wind, water) and biological vectors (e.g., animals) (see Incagnone et al., 2015, and literature therein; Padišák et al., this volume, and literature therein). As regards microalgae, vegetative cells can be released from water by bubble-burst processes generated by the action of the wind blowing on the water surface (Hamilton & Lenton, 1998). Due to their small dimensions, phytoplankton taxa can be trapped in the water bubbles and transported by the wind (anemochory). Hydrochory (water transport) is commonly occurring among floodplain lakes in river valleys (Devercelli et al., this volume; Stoyneva, this volume) or among man-made lakes connected through canals or pipelines (Xiao et al., this volume). Animals may transport phytoplankton organisms attached to their body (epizoochory) or in their gut (endozoochory). Dispersal, therefore, may occur “outside” and “inside” the aquatic medium. The first one implies that phytoplankton cells may resist desiccation when transported by wind or non-aquatic animal vectors (for more details see the next paragraph “Survival strategies of species, the importance of physiological adaptations”). Dispersal occurring through the aqueous medium is certainly easier for the involved organisms: it does not require specific adaptations since it is mediated by water connections between aquatic environments or by animal vectors permanently or semi-permanently living in the aquatic medium like fish, mollusc, pond turtles, crustaceans, etc. Görgényi et al. (this volume), by culturing samples collected from the hindgut of filter-feeding Asian carps, introduced in Hungary for recreational purposes, found a number of phytoplankton species which demonstrated viability despite the expected physical and chemical digestion by fish. This finding underlines the importance of human-mediated introduction of animals and plants, by accident or on purpose, which may contemporarily bring on or inside them a variety of “colonizers” whose effect on the receiving ecosystems is beyond human control.

With regard to dispersal mediated by water connections, Devercelli et al. (this volume), by studying 22 lakes with different hydrological connectivity and morphological features in the Paraná River floodplain system, elegantly showed that both deterministic and stochastic processes affect the structure of phytoplankton metacommunities. As expected, these authors suggested the preponderance of stochastic organization (mediated by drift dispersal during flood periods) as a structuring force for the local assemblages, which contributed to keep dissimilarity low. Although, in some cases a clear distinction between determinism and stochasticity is not immediate, the relative importance of these two groups of factors can be strictly linked to the typology of investigated systems. As an example, the investigation by Xiao et al. (this volume), carried out on a phytoplankton metacommunity in a system formed by two reservoirs connected through a pipeline, suggested that the length of the pipeline, and thus the amount of time that phytoplankton had to spend in the dark when transported from a reservoir to another had a great impact on the composition of the assemblages, keeping dissimilarity high, in these two connected reservoirs. These two cases show how the same factor (drift dispersal) may result in two contrasting effects.

Spatial scales and the relative distances among aquatic ecosystems may also confound the balance between deterministic and stochastic factors. On a continental scale, Izaguirre et al. (this volume), by studying 60 lakes scattered along a 2,150 km latitudinal gradient spanning from Patagonia to Antarctic, found a significant decrease of species richness with increasing latitude. This result could suggest a distance-limit to passive dispersal, even though the different climates along the latitudinal gradient can also be considered an environmental filter. Evenness, however, was not affected suggesting that the local biological context had an important role in structuring the assemblages. This was confirmed by analyzing the effects exerted at a local scale by environmental filters (i.e., trophic state, conductivity, pH), which were found to have a shaping effect on the structure of the studied assemblages in relation to the pool of available species as set by the latitudinal gradient.

However, large geographic scales alone may not represent a limit to dispersal, especially when the suitable receiving ecosystems are not distributed over a latitudinal gradient and thus without significant

climatic differences. Therefore, even when phytoplankton beta diversity is studied at large geographic scales, the distinction between deterministic and stochastic factors may remain unresolved. Accordingly, Santos et al. (this volume), in a group of 8 Brazilian lakes over a large geographical scale (1,500 km) but all located under tropical climate, found that phytoplankton structure was strictly linked to local niche differentiation. This effect was explained by the high dispersal potential of phytoplankton (see Padisák et al., this volume). Conversely, these authors found that zooplankton assemblages were much more affected by dispersal limits linked to distances. The difference between the distribution patterns in phyto- and zooplankton observed in this study can be explained by the different dispersal mechanisms in these two groups of organisms, also related to, e.g., relative numerical abundance of populations, mechanisms of resting stage production, size of resting stages, and mating behavior (Incagnone et al., 2015).

Naselli-Flores et al. (this volume) showed that, at small geographic scales, passive dispersal of phytoplankton is influenced by the geographical distribution of water bodies in a given area (i.e., their relative distance and their number: structural connectivity) and by the effective movements of vector animals among the water bodies (functional connectivity). Phytoplankton in pond-networks forms, therefore, a meta-community that enhances rescue effects by (i) maintaining a continuous flux of species among single environments, and (ii) compensating local extinctions.

Survival strategies of species, the importance of physiological adaptations

As recognized in literature (e.g., Incagnone et al., 2015), the key component of algal dispersal is the ability of crossing the “dry ocean.” Many species have desiccation tolerant resting stages facilitating dispersal, but some, and among them many phytoplankton species, do not have. Mucilage of phytoplankton individuals or colonies has multiple functions (Reynolds, 2007): density reduction, dynamic streamlining, sequestration and storage of nutrients, resistance to grazing and digestion, and protection against desiccation. Analyzing morphological properties of species

where long-distance transport is supposed, Stoyneva (this volume) found that more than 90% of them had mucilage sheets and concluded that mucilage is especially important for both forms of bird dispersal: endozoochory (when algae are ingested) and epizoochory (when algae are transported on the body surface); examined taxa include, for example, species of *Planktolyngbya* and *Woronichinia*. Though fish are seldom considered as dispersal agents, introduction of alien species (like Asian carps) or fish species migrating up- or downstream, may facilitate algal dispersion. Testing the viability of algae from hindgut samples proved that filter-feeding fish can harvest and disperse all algal taxa, irrespective of size, that are available in the ambient water except for those few groups that possess intracellular coverings (Görgényi et al., this volume) like flattened, cellulose-containing vesicles (dinoflagellates), proteinaceous plates (cryptophytes), and pelli-cles (euglenophytes).

As reviewed by Padisák et al. (this volume), little is known about resistance of planktic algae to river transport where algae are exposed to turbulent flow, shear forces, unstable light climate, and flocculation of sediment (Estrada & Berdalet, 1997). On the example of pipeline transport between two reservoirs (40 km), Xiao et al. (this volume) demonstrated a differential survival of algal taxa, which contributed to the high dissimilarity of the investigated phytoplankton assemblages.

For most species with distribution at low latitudes (tropical, subtropical climate) temperature is considered as the main barrier of expansion to higher latitudes. Analyzing data of occurrence of *Cylindrospermopsis raciborskii* at low temperatures, Dokulil (this volume) concluded that vegetative existence of populations is possible at temperatures below 12 °C and may play a key role in re-establishment of populations when water temperatures rise again. The strain persistence at low temperature can eventually promote an earlier growth in the season. The study by Selmečzy et al. (this volume) provides a direct support to these observations. By studying *Aphanizomenon flos-aquae* Ralfs ex Bornet et Flahault dynamics, these authors found that the germination of akinetes occurs at 16–17 °C; therefore, lacking overwintering populations, mass growth in Lake Stechlin can start only in June. Conversely, when an overwintering population is present in the lake, blooms start much earlier in the year (Üveges et al., 2012; Bižić-Ionescu et al., 2014).

Both the above observations on *Cylindrospermopsis raciborskii* and *Aphanizomenon flos-aquae* noted the absence of heterocytes in vegetative populations that indicates the unnecessary of energy consumption in N-fixation. An unusual form, the fixation during night by diazocytes, might have a basic role in development of *Limnographis robusta* in oligotrophic tropical lakes with low N/P ratios (Komárková et al., this volume). Adaptation to cold environments has been an under-represented issue in phytoplankton ecology and, as shown by the above quoted examples, it not only facilitates survival but also may trigger bloom events. Another example is *Pseudotetraedriella kamillae* Hegewald et Padisák, an eustigmatophycean alga with oily storage material in Lake Tovel, a cold-monomictic lake. The species is cold stenotherm needing deep mixing. Therefore, it is found (but often overlooked) in pre-stratification plankton of both deep and shallow temperate lakes for a short period (Hegewald et al., 2007). The species is perennial and occurs in high relative abundance in the high-mountain cold oligotrophic Lake Tovel, where deep mixing and cold temperatures are prevailing all the year (Cellamare et al., this volume).

Vertical and horizontal spatial variability of phytoplankton

Phytoplankton species are small and they live their relatively short lives suspended in the water. These features make phytoplankton an ideal object to study and experiment the temporal scale of ecological processes (e.g., Passarge et al., 2006) but do not ease the understanding of the processes governing their spatial distribution. Many strips of within-lake spatial distribution of phytoplankton indicate the importance of a variety of processes, i.e., (i) the diurnal vertical migration of certain species like *Ceratium* spp. (e.g., Heaney & Furnass, 1980) or *Microcystis* spp. (e.g., Hunter et al., 2008); (ii) the abundance and compositional differences along trophic gradients (Istvánovics et al., 2007); (iii) the wind-driven horizontal patchiness of bloom-forming cyanobacteria (e.g., Rolland et al., 2013) or other ephemeral blooms (Reynolds et al., 1993); (iv) the development of dense phytoplankton layers in the metalimnion or upper hypolimnion (DCM; e.g., Clegg et al., 2012).

Since Nauwerck's (1963) seminal work, Lake Erken became a kind of etalon for phytoplankton research and numerous important mechanisms were explored by studying the Erken phytoplankton such as the importance of P-storage and internal loads (Pettersson et al., 1993) and the key role of alkaline phosphatases in P-uptake (Pettersson, 1980). However, a systematic work describing seasonal patterns of phytoplankton in this lake was missing until now because of two reasons (Yang et al., this volume). The first explanation is the uncommon behavior of the summer dominant cyanoprokaryote, *Gloeotrichia echinulata* P. G. Richter. The species occurs in large colonies that makes difficult to perform reliable counting. In addition, it accumulates on the surface where it is easily blown away by winds, this way being unevenly distributed on the lake surface (Pettersson et al., 1995). The second reason is the relatively small density difference between the epi- and hypolimnetic water that makes stratification unstable, strongly influencing the annual development of phytoplankton. The robust statistical analysis on the long-term data set from Lake Erken (Yang et al., this volume) described the disturbance-sensitive temporal development of phytoplankton in a rarely considered stratification-type, the discontinuous polymixis. Importance of mixing events and stratification strength is also demonstrated on the example of the high mountain Lake Tovel (Cellamare et al., this volume) where markedly different assemblages were found in the two different parts of the lake characterized by different stratification patterns.

Existence of chlorophyll maxima (DCM) in the meta- or upper hypolimnetic layers has long been known along with the reasons resulting in such layering of phytoplankton. These layers are mostly monospecific but in some cases more species (commonly various filamentous cyanoprokaryotes) contribute to the DCM (Padisák et al., 2003). However, it has not been considered whether or not these multispecies DCM were structured into fine layers. Selmečzy et al. (this volume) demonstrated that not only spatial segregation existed between three populations forming DCM in Lake Stechlin but also niche segregation. This study urges a more careful investigation of DCM that has been performed so far and supports the necessity of parallel use of automated fluorescence measurements and microscopic investigations.

The above three contributions (Cellamare et al., this volume; Selmečy et al., this volume; Yang et al., this volume) highlight the importance of the physical environment (main topic of the 15th IAP Workshop; Zohary et al., 2010) on various ways. In case of Lake Erken (Yang et al., this volume) instability of the stratification results in some different, but repetitive seasonal phytoplankton sequences. In Lake Stechlin relative permanency of metalimnetic and upper hypolimnetic layers provide opportunity for spatial- and niche differentiation of sufficiently adapted DCM species Selmečy et al., this volume). Within Lake Tovel, different morphologies of its two basins governs differences in phytoplankton assemblages (Cellamare et al., this volume) without physical barrier between the basins. This observation calls the attention to the different physical regimes that may act as an environmental filter since in this case spatial barrier certainly does not exist. Borics et al. (this volume) concludes similarly: by adopting a sufficiently sensitive trait classification system, it is also possible to observe that there are size-dependent variables (like lake size and fetch) that filter functional traits.

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