MICROALGAL FUNCTIONAL TRAITS

Review Paper

Trait-based ecology of microalgae

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Abstract   This paper introduces and summarises the main outcomes of the 19th workshop of the International Association for Phytoplankton Taxonomy and Ecology held in Tiszafüred, Hungary, Tisza Balneum Hotel, from 23 to 30 September 2022. The selected theme of the workshop was "Trait-Based Approaches in Micro-Algal Ecology". The discussions presented during the workshop sessions resulted in the 18 articles contained in this Special Issue. There are 6 main thematic aspects developed by the participants: 1. Shape and size: are these traits easy to measure? 2. Spatial scales: when and where to look for microalgae? 3. Climate and extremes of ecological gradients: hot topics of this century. 4. Metaphyton and metaphytic habitats: life beyond plankton and benthos. 5. Microalgae in water management: phycology in practice. 6. Traditional and new methods: perspectives and comments. Trait-based approaches in microalgae ecology, although requiring further investigation and methodological development, represent a valid tool for refining the analysis of environmental variability in aquatic ecosystems. The papers presented in this Special Issue demonstrate that these approaches are extremely useful not only in the study of planktic algae but constitute a thoughtful method for the analysis of benthic and metaphytic microalgae in a wide variety of aquatic ecosystems.

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Introduction

"There are more things in heaven and earth,
Horatio,
Than are dreamt of in our philosophy."
(Shakespeare: The Tragedy of Hamlet, Prince
of Denmark, 919–920, web1)

An immeasurable number of species have evolved
on our Earth since life appeared in the Hadean eon,
more than 4 billion years ago, as suggested by the
earliest stromatolite microfossils found in Greenland,
dating back to around 3.7 billion years ago (Nutman
et al., 2016). After the "father of taxonomy", Carl
von Linné (Linnaeus, 1753) elaborated the classifi-
cation system and the binomial nomenclature, the
number of described species started to grow expo-
nentially. Still, we have millions of species that have
not been described yet, and this is especially apparent
for microbiota. It was recognized quite early that we
have more species than functions therefore a need for
"grouping", other than taxonomic, arose.

The term "trait" appeared very early in the biologi-
cal literature and has been used as a proxy of organ-
ismal performance (Darwin, 1859). The recognition
that natural selection, which determines the compo-
sition of the assemblages in the presence of various
environmental constraints, acts on traits rather than
species has inspired the development of trait-based
approaches in ecology. The approach has spread to
every level of biological organisation, from individ-
uals to ecosystems, and has contributed to help our
understanding of how ecological systems function.

To avoid the ambiguous definitions often found in
the literature, the following list summarises the inter-
pretations accepted and widely used by ecologists:

- Functional traits are defined as those components
  of an organism's phenotype that determine its
  effect on ecosystem processes (Petchey & Gaston,
  2006).
- Functional traits are defined as the characteristics
  of an organism that determine its performance in
  response to the environment and/or its effects on
  ecosystem functioning (Bulleri et al., 2008).

- Traits are defined here as species characters that
  are quantifiable. There is obviously a large num-
  ber of potentially relevant traits for a given eco-
  system process that are measured on a mixture of
  scales (binary, nominal, ordinal, and quantitative)
  (Ricotta & Moretti, 2011).
- Traits are evolutionarily selected characteristics
  (morphological, physiological, behavioural and
  phenological), that can be measured at individual
  level and that govern the ecological functions of
  organisms (Violle et al., 2007).

In the common language of phytoplankton ecolo-
gists the term "trait" has only appeared in recent
years, but in fact the use of traits has always been
present in phytoplankton studies. When the rela-
tive abundance of diazotrophic and non-diazotrophic
algae, or that of flagellated and non-motile algae are
contrasted, the performance of the traits is compared
(e.g., Naselli-Flores & Barone, 2000). This, however,
is not always obvious because in many case studies
the emphasis is on taxonomic groups, even though
these might represent traits or combinations of traits.
Litchman and Klausmeier (2008) provided a con-
ceptual framework that illustrates the nexus between
various types of algal traits and their ecological func-
tion. That study was a big step towards trait-based
approaches. However, in phytoplankton ecology,
approaches that are based on functional groups (FGs)
received considerable attention in recent years. In
Reynolds's system (Reynolds et al., 2002) the empha-
sis has been put on functional aspects of microalgae,
and species with different morphological properties
were assigned to the same functional groups, with
the awareness that the adaptations of organisms to a
given environmental scenario can find multiple paths.
In other classification systems (Salmaso & Padisák,
2007; Kruk et al., 2010, 2011) the grouping of micro-
algae was based on the similarities in their morpho-
logical and physiological traits. Although the setting
of the groups differs, all these approaches have been
successfully used in both theoretical and practical
studies (Salmaso et al., 2015).

In the 1990s and 2000s, the main focus of benthic
diatom research was on disentangling the relation-
ships between species-level community structure
and environmental factors. Those efforts were moti-
vated by the assessment of ecological status of inland
waters required by the Water Framework Directive

(Kelly et al., 2014). In the past decade, the recognition of the species-level methodologies of benthic diatoms-based water quality assessment sparked an interest in alternative approaches (Tapolczai et al., 2016). This demand motivated the development of the diatom guild concept (Passy, 2007). The cornerstone of this concept (Biggs & Stokseth, 1996; Biggs et al., 1998) was that physical disturbance and nutrient availability are the primary factors controlling the colonisation of substrates and biofilm formation of benthic diatoms. Based on these recognitions, three guild categories were created, which were modified and completed by Rimet and Bouchez (2012). These guilds (as functional groups) are now widely used in diatom studies. In addition, easy-to-measure traits (e.g. cell size, biovolume, length/width ratio; Rimet & Bouchez, 2012; Stenger-Kovács et al., 2018), life forms, attachment types, mobility traits (Rimet & Bouchez, 2012; Lange et al., 2016) as well as combined trait groups (B-Béres et al., 2016; Lukács et al., 2018; Stenger-Kovács et al., 2018) have been regularly involved in diatom research. Recent studies have demonstrated that the implementation of diatom trait- and functional group- or guild-based approaches in ecological studies can help recognizing global forces and processes jeopardising aquatic ecosystems all over the World (e.g., see B-Béres et al., 2023; Stenger-Kovács et al., 2023).

Motivation of the special issue: the 19th international association for phytoplankton taxonomy and ecology (IAP) workshop

The recent development in plant and animal community ecology was largely due to the widespread use of trait-based approaches, therefore the organisers asked the participants of the 19th IAP Workshop to focus on these approaches, and to place their results in a functional context. The aim was to enhance the communication amongst experts of each functional approach, and to provide an elementary basis for combining the "group" and "trait" approaches for the development of phytoplankton ecology. Although IAP meetings are considered as forums where phytoplankton ecologists share their new results and ideas with their colleagues, experts working on trait-based approaches in benthic microalgal assemblages were also invited to participate in the workshop.

Table S1 (Supplementary materials) lists the papers included in this Special Issue and are here briefly reviewed. In the table, papers are numbered in the order in which they are discussed in this review paper.

Shape and size: are these traits easy to measure?

The ecological theme of the 14th IAP Workshop, held in September 2005 in Sapanca, Turkey, was "Morphological plasticity of phytoplankton under different environmental constraints" (Naselli-Flores et al., 2007). Almost twenty years have passed since then but that theme have remained very topical in the ecology of phytoplankton (perhaps more today than that time). In fact, morphological traits of organisms are considered master traits in phytoplankton ecology since they govern most of the physiological and ecological features of this group of organisms (Litchman & Klausmeier, 2008). Both shape and size concur in defining the morphology of phytoplankton. These are a group of unicellular or colonial organisms (made up of cells similar to each other) adapted to live in apparent suspension in turbulent water masses (Reynolds, 2006). Each species on our planet is subjected to a multitude of independent selective pressures. With regard to phytoplankton, if the problem considered was only the acquisition of resources (nutrients and light), phytoplankton were only be made up of small and spherical cells (Reynolds, 1997). It is therefore reasonable to think that:

(i) the variability in shape and size of these cells have contributed to regulate their fitness with respect to resource acquisition and avoidance of predation (Lürling, 2021) whilst constantly transported in "apparent suspension" in turbulent water masses;

(ii) hydrodynamic variability, given their short life, represents the most important driver of environmental change for phytoplankton populations, and

(iii) size and shape are the main cellular characteristics on which evolution operates.

The lower limit of size that planktic algae may attain depends on the minimum space required by a cell to accommodate all the organelles (eukaryotes)

and biological molecules necessary to carry on its vital functions. The upper limit is strongly constrained by the hydrodynamic characteristics (i.e., turbulence) of the fluid within which phytoplankton is adapted to live in apparent suspension (Naselli-Flores et al., 2021). For most microalgae, the size range is therefore between 0.5 and 200 μm (Reynolds, 2006). However, as shown in the **first paper** of this Special Issue (see Table S1), size alone does not explain the amazing shape variability of phytoplankton. These organisms live at low Reynolds' numbers, i.e., in a world dominated by viscous rather than by inertial forces. Viscous forces proportionally act on the surface of objects. Modifications in shape represent a way to regulate the exposition of cells or colonies to the effects of such forces, and is the main evolutionarily adaptation addressed at influencing their sinking velocity and their entrainment in turbulent water motion. Finally, the authors suggest that the morphological variability of phytoplankton is able to cover all possible turbulent conditions of water masses on our planet.

However, it is not an easy task to find a geometrically correct and precise representation of the morphological variability of phytoplankton. This is an extremely important task since cell ornamentations as papillae, spines, bristles, even mucilage are generally not considered when surface area is computed, but they can have an important role in modulating the effects of viscosity on cell surface. Phytoplankton ecologists are familiar with formulas aimed at calculating cell surface area and cell volume, as biovolume calculation is widely used to estimate phytoplankton fresh weight biomass. Unfortunately, the methods traditionally used and available in literature (e.g., Hillebrand et al., 1999) are not sufficient to offer a numerical characterisation of the real phytoplankton shape variability. A way to overcome this problem has been proposed by Borics et al. (2021) who carried out size measurements on shape-realistic 3D models of microalgae and proposed species-specific constants to calculate surface area and biovolume of microalgae that keep in account the real surface of the organisms. The **second contribution** of this Special Issue (see Table S1) goes further in this direction by identifying six interconnected shape metrics and providing mathematical formulas to numerically investigate the shape of phytoplankton species also from an evolutionary perspective. The authors investigated

not only how the shape metrics relate to each other and how they are linked to size but also how these values change along the size (length and biovolume) scale, showing that surface area to volume ratio of the microalgae are hyperbolic functions of the length and volume for each shape. Furthermore, the authors demonstrated that the different shapes of phytoplankton actually derive from the spherical shape. Random deviations from the spherical shape have enabled phytoplankton to cope with the wide range of turbulent conditions under which microalgae must access resources and escape predation. "Contingently useful" shape changes have thus persisted and given rise to the astonishing morphological diversity of phytoplankton. All in all, the authors could show that the proposed shape metrics can serve as suitable quantitative traits capturing the shape characteristics of microalgae and paving the way to a quantitative analysis of morphological traits. This approach can offer a better understanding of how the different morphologies contribute to the assembly of phytoplankton under various ecological conditions.

Spatial scales: when and where to look for microalgae?

Small organisms like microalgae can disperse in various ways, by air or water, using epi- or endozoochory, or by human vectors (Padisák et al., 2016). Therefore, not surprisingly, the Baas-Becking view of microbiology (Baas-Becking, 1934), i.e., "everything is everywhere but environment selects" was a widely accepted central paradigm and shaped our thinking on the distribution of microalgae until the last decades. For a long time, the general notion prevailed that diversity and composition of phytoplankton depended exclusively on the processes occurring below the water surface. For this reason, in most cases the lakes and ponds were studied as if they were isolated environments. Due to the accumulation of evidence on the distribution of phytoplankton species (i.e., the presence of endemic species (Popovskaya et al., 2006), the well-defined distribution regions (Graff et al., 2016), vicariance patterns (Filatov et al., 2021), etc.), researchers' view on the importance of wider spatial scales have changed in recent decades. Using the tools of metabarcoding, a comparison between Arctic, sub-Antarctic, and Antarctic lacustrine benthic

samples Tytgat et al. (2023) proved that microbiota, including cyanobacteria and eukaryotic algae have distinct evolutionary histories further supporting the limitations of the Baas-Becking hypothesis.

Metapopulation biology, that has had a major impact on the development of ecology since the 1980s (Hanski & Gaggiotti, 2004; Leibold et al., 2017), has appeared in the field of phytoplankton ecology and has shown, that similarly to terrestrial systems, dispersal-dependent processes in the assembly of phytoplankton community cannot be neglected (Leibold & Norberg, 2004). The other relevant field of phytoplankton ecology where spatial scales have great importance is the study of species area relationship. Recent studies of the topic yielded meaningful results at both global (Smith et al., 2005) and regional scales (Várbíró et al., 2017; Bolgovics et al., 2019). As the previous reasoning suggests, the compositional characteristics of phytoplankton deserve to be studied at various spatial scales from microhabitats size (10^{-2} m) to global scale (10^7 m). However, it is an open question how the involvement of functional traits or functional groups can facilitate the understanding of spatial processes (Xiao et al., 2018).

The study shown in the **3rd paper** of this Special Issue (see Table S1) encompasses the smallest spatial scale. The authors investigated how the representatives of the various functional groups positioned in the different vertical layers of a linearly stratified oxbow. They found a distinct separation within the water layer: a photic layer with several peaks of various functional groups, and an aphotic highly inhospitable realm dominated by purple sulphur bacteria. Light intensity did not have an impact on the diversity of phytoplankton or on the vertical distribution of biomass. However, it has been shown that the number of vertically separated assemblages correlates with the depth of the photic layer. The authors also found that diversity is not a good measure to characterise compositional differences; similarity metrics reflect these differences better.

The authors of the **4th paper** of this Special Issue (see Table S1) investigated the impacts of spatial and local variables on the phytoplankton of 14 coastal lakes by applying species-, functional trait-, and functional group-based approaches. Differences were found at both fine and broad spatial scales. Environmental filtering (i.e. local environmental variables) had a pronounced impact on the metacommunity

structure independently of the selected approaches. Amongst the applied traits, phytoplankton biovolume appeared to be the best predictor for both local and spatial variables.

The contribution of habitat size to algal distribution—from thelmatas ($10^{-2}m^2$) to large lakes ($10^{11}m^2$) and rivers—was highlighted in the **5th paper** of this Special Issue (see Table S1). The authors, in an ecoregion-scale study, investigated the similarities of traits and functional groups amongst different habitats, and showed that creation of habitat clusters using the functional group approach had great overlap with the clusters established by hydro-morphological and chemical habitat characteristics. In accordance with previous findings (Borics et al., 2014) rivers and river-connected habitats had the most species-rich microflora. The results suggest that habitat template of some species that are assigned to a certain functional group could be wider than it was specified in the original descriptions (Reynolds et al, 2002; Borics et al., 2007; Padisák et al., 2009).

The three papers summarised in this section demonstrate that functional group-based and trait-based approaches highlight those characteristics of microalgae (specific tolerances and preferences, traits that help their survival during dispersion) that enhance our understanding of their spatial dynamics and patterns.

Climate and extremes of ecological gradients: hot topics of this century

In the recent past, humans are having a significant impact on almost all ecosystems including aquatic ones. Our activities have dramatically altered food webs and nutrient cycles by changing the composition and biodiversity of communities from the local landscape to the receiving waters, from producers (including planktic and benthic algae) to consumers (Smith, 2003; Reid et al., 2019). In the twentieth century, surface waters were exposed to pressures (e.g., nutrient loads) that led to spectacular changes (e.g., algal blooms, even potentially toxic cyanobacterial biomass peaks) and serious economic damages (Paerl et al., 2001; Carvalho et al., 2013). It was recognised early that one of the key limiting factors for algal mass-production is the phosphorus content of the water (Pearsall, 1920), however, the relationship

between nutrients and algal biomass began to be intensively studied from the 1960s and 1970s (Vollenweider & Kerekes, 1980). In the following decades, the primary water management efforts were aimed at reducing the nutrient loads and minimising their ecological and economic consequences (Scholten et al., 2005). Exploring the environmental background of potentially or actually toxic cyanobacterial water blooms and monitoring the spread of invasive cyanobacterial species have remained a hot spot in algal ecology (Chorus & Welker, 2021), as does preventing these processes (Huisman et al., 2018; Sukenik & Kaplan, 2021). For example, most of the metrics developed by the EU member countries following the advice of the Water Framework Directive (EC, 2000) concentrated on trophic indicators whilst disregarding other ones (e.g., salinization; Poikane et al., 2011, 2015). From an ecological and nature conservation point of view, another important and exciting scientific topic is to highlight how changes in biodiversity are related to biomass growth. Laboratory experiments in the 1980s (Sommer, 1984) revealed that source fluctuation, which is also a common phenomenon in nature (see Reynolds, 1992), affects community diversity much more than the absolute amount of nutrients. Field observations in the 1990s suggested that intermittent disturbances maintain diverse algal communities (Padisák et al., 1988, 1990; Reynolds et al., 1993). Assessing, the relationships between biomass and taxonomic/functional diversity have remained an exciting scientific question (Török et al., 2016; T-Krasznai et al., 2022b), and have also yielded conflicting results (Jeppesen et al., 2000; Borics et al., 2014; Török et al., 2016), enlightening the complex mechanisms between algal blooms and food web structure (Paerl et al., 2001; Naselli-Flores et al., 2003b). In the 1970s-1990s, as a result of very strong government pressure (intensive legislative processes – EC, 1976; CEC, 1991), nutrient loads to surface waters began to decline. Oligotrophication has started in both lakes (Anderson et al., 2005) and streams (Stockner et al., 2011; Ibanez et al., 2012; Ibanez & Penuales, 2019). Long-term studies revealed that structural change in phytoplankton accompanied this process. A positive correlation was found between the decrease in total phosphorus concentration and the dominance of small species within the assemblages (lakes—Willén, 1987; Alvarez-Cobelas et al., 1998; rivers—Abonyi et al., 2018). Oligotrophication may

also result in desirable consequences just because of the size and shape of the beneficiary species (*Mougeotia*; Tapolczai et al., 2015).

Whereas eutrophication was the main focus of surface water research in the second half of the twentieth century, one of the major ecological, economic and social challenges of the twenty-first century is the need to address global climate change. The World we will live in the future depends on how and how quickly we respond to changes caused by climate extremes. Freshwater ecosystems, whose role in providing ecosystem services is unquestioned (Magand et al., 2020; Vári et al., 2022), are particularly vulnerable to climate-related stress factors such as increasing water temperature, changes in precipitation distribution and intensification of extreme climatic events (flash floods, drastic water level declines or even the complete drying up of the riverbed). However, a neglected area in major climate change projections is the study of processes in these ecosystems, in contrast to the oceans and seas. These extreme events directly or indirectly exert strong selective pressures on aquatic communities, including planktic algae and benthic diatoms (Kasprzak et al., 2017; Abonyi et al., 2018; Novais et al., 2020; Várbíró et al., 2020). However, it is important to emphasise that these environmental changes do not individually affect the populations or the community composition, but have a complex effect. *De facto*, an increase in temperature may lead to size reduction of cells at the population level (e.g., diatoms, dinoflagellates—Montagnes & Franklin, 2001; Atkinson et al., 2003), but this is only one of the possible adaptation strategies of algae. Centric and fragilaroid diatoms have been shown to change their temperature optimum and shift their temperature range (Jin & Agusti, 2018) as does one of the invasive flagship cyanobacterium species, *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera et al. (Dokulil, 2016). At the same time, however, it must be stressed that this is not a win–win situation. By adapting to the higher temperature, their reproduction rate or photosynthetic efficiency decrease, or they find it more difficult to tolerate higher light intensities.

In addition to the direct effect of temperature increase, climate change can also have an impact on algal communities through other factors. It alters water cycles, energy flows and nutrient cycles. It can be accompanied by an increase in the depth of

the thermocline, which has a fundamental effect on the stability and stratification of lakes, and can induce anoxic periods and water blooms (Kraemer et al., 2015; Selmeczy et al., 2019). In Arctic ponds, prolonged ice-free periods may be associated with changes in biofilm composition: biodiversity increases as new habitats (macrophytic) develop and light conditions become more favourable. The phytoplankton here will be dominated by small-sized centric diatoms, which favour the thermal stability and the longer period of the thermal stratification (Rühland et al., 2015). In rivers, increasing water temperature and residence time (low flow) can alter water viscosity and water mass turbulence. These can lead to changes in the taxonomic and functional composition of the phytoplankton: Abonyi et al. (2018) found that the phytoplankton in the middle section of the Danube River significantly altered with the dominance of flagellated, elongated and/or filamentous taxa from **X2**, **Y** and **E** coda (Reynolds et al., 2002), whilst eutrophic taxa from **W1**, **W2** and **WS** coda became less significant. A further functional shift was also observed, with an increase in the relative abundance of benthic diatoms.

Another aspect of climate change that has been intensively studied in recent years is the effect of flow intermittence and stream drying on benthic algae (Novais et al., 2014, 2020; B-Béres et al., 2016, 2019, 2022; Falasco et al., 2016; Lukács et al., 2018, 2021). Globally, approximately 50–60% of lotic ecosystems are considered to be intermittent (Messager et al., 2021), but for small streams this value can exceed 70% (Datry et al., 2014), and is projected to increase regionally (Pissaridou et al., 2021; B-Béres et al., 2022) and globally in the coming decades (Pumo et al., 2016). Whilst drought in the Mediterranean and arid regions can be traced back to historical times, it is a recent phenomenon in continental areas (Acuña et al., 2017; Várbíró et al., 2020). There is no doubt that drought acts as a strong environmental filter for diatoms regardless of region, but little is known about how the duration of drought and, in the continental regions (B-Béres et al., 2016, 2019, 2022; Lukács et al., 2021), the drought itself, affects community adaptation (Tornés et al., 2021). There is also little information available on ecoregional differences caused by streambed drying (but see Várbíró et al., 2020). These changes affect the ecological status of watercourses,

which raises direct economic and social problems in addition to ecological issues. However, a long-term study of a large, perennial river in the Carpathian Basin has shown that decreasing precipitation in recent years has already had a significant impact on the taxonomic and functional composition of benthic diatoms (Nemes-Kókai et al., 2023).

These issues are thoroughly detailed in four case studies in this special issue (Table S1; phytoplankton—papers #6–8 and benthic diatoms—paper #9). In the **6th paper** of this Special Issue (see Table S1), the need for long-term research is emphasised. Here, over half a century, significant changes in phytoplankton have been observed in Mondsee as a result of eutrophication, oligotrophication and, more recently, climate-induced changes in abiotic environments. Long-term study was also presented in the **7th paper** of this Special Issue (see Table S1). The effect of drastic discharge and water level fluctuations caused by climatic extremes on the functional structure of the phytoplankton over a period of 10 years in a semi-arid, tropical reservoir has been shown in this paper. Not only the lentic but also the lotic phytoplankton community is significantly altered by discharge fluctuations. This was highlighted in the **8th paper** of this Special issue (see Table S1), examining the Loire phytoplankton community. Significant changes in the structure of the phytoplankton caused by the hydrological regime could be detected even within a short period of time. To understand what changes in diversity can be expected even within a few years, and whether this may affect the role of phytoplankton in ecosystem services, it is important to know the direction of compositional changes in algal assemblages, and short-term studies can help to deepen this understanding. Benthic diatom assemblages can also be structurally altered by water supply and flow conditions. This is illustrated, *inter alia*, in the **9th paper** of this Special Issue (see Table S1) by examining the diatom community of a small, drying lowland stream. Water supply also had a significant effect on the diatom-based ecological status of the stream, highlighting the need for water management to pay special attention to these small water bodies.

Metaphyton and metaphytic habitats: life beyond plankton and benthos

Limnological research has focused on deep, stratified lakes for a long time (Scheffer, 2001). Meanwhile, shallow natural lakes are more common worldwide than deep lakes, and their number is increased by the creation of shallow man-made lakes (Scheffer, 2001). There is a delicate and more or less well-defined relationship between key producers, i.e., between phytoplankton and submerged aquatic macrophytes in these shallow lakes (e.g., Scheffer & Jeppesen, 2007). Scheffer's model describes two stable states, clear water and turbid water states, in which nutrient load (especially phosphorus content), water level fluctuations, and food web structure are critical environmental factors (Scheffer & Jeppesen, 2007). Several studies have highlighted that eutrophication promotes turbid state resulting even in algal blooms, and reduces submerged macrophyte biomass and diversity (see more in Scheffer & Jeppesen, 2007).

As mentioned above, significant efforts have been made in recent decades to reduce eutrophication (see Section entitled "Climate and extremes of ecological gradients: hot topics of this century"). This favours the growth of aquatic plants and thus increases the ecosystem services provided by these communities in shallow lakes (Hossain et al., 2017; Thomaz, 2023). The plant cover creates unique environments, which can be particularly favourable for shade-adapted, even mixotrophic, and/or small flagellated species (Reynolds et al., 2002; Padisák et al., 2009). It provides a high degree of habitat heterogeneity in the littoral region, allowing the development of a diverse metaphyton (Borics et al., 2003), which contributes to the maintenance of highly diverse phytoplankton even under unfavourable conditions. Although the metaphyton is a unique realm, it is not sharply separated from the phytoplankton and phytobenthos. It is rather a refugium. It is constantly present as a source of species and provides propagules for the open habitats (Stoyneva, 1994; Naselli-Flores & Barone, 2012; Leibold & Chase, 2018; Görgényi et al., 2019).

The extensive and diverse macrophytic vegetation not only provides habitat for the metaphyton communities but also serves as a substrate for benthic algae (Hossain et al., 2017; Thomaz, 2023). The fractal complexity of aquatic plants strongly determines the composition and diversity of benthic communities,

either benthic algae or macroinvertebrates (Dibble & Thomaz, 2009; Hinojosa-Garro et al., 2010; Do Nascimento Filho et al., 2021). In general, emergent macrophytes are the less complex forms, therefore, benthic algal assemblages formed on these plants are usually less species-rich and less functionally diverse especially compared to those formed on submerged plants (Do Nascimento Filho et al., 2021). The submerged species, characterised by high functional complexity (Dibble & Thomaz, 2009), can fill the entire water column (Temmink et al., 2021) and can form a large biomass. This significant plant biomass contributes to the formation of a large amount of benthic and metaphytic microflora, and inhibits algal blooms by reducing nutrient content and shading the water column (Seto et al., 2013). Like submerged aquatic plants, rooted-floating species also play a crucial role in reducing water temperature, light availability, and water turbulence (Frodge et al., 1990). However, in contrast to submerged species, macrophytes with leaves floating on the water surface can be considered as disturbed habitat for benthic algal flora. The leaf' surface, protruding from the water and exposed to wave motion, may facilitate the settlement of aerophilic and/or disturbance-tolerant benthic diatoms, similarly to other intermittently drying substrates (Falasco et al., 2016). Overall, aquatic macrophyte species with different life forms play a varied yet equally important role in sustaining a complex benthic and metaphytic algal community that also enhances the biodiversity in waters.

All this information is vital for the implementation of water management projects aimed at reducing the impacts of those actions that could be a threat to the survival of the diverse macrophyte communities. Undesirable changes in plant community structure and diversity can have negative consequences for the entire lake ecosystem, e.g., the formation of algal blooms. Although reducing eutrophication locally is beneficial, several human-induced global processes remain a significant threat to the maintenance of diverse aquatic macrovegetation. Global climate change and salinisation pose threats that can result in the decline of microhabitats provided by macrophytes (Alahuhta et al., 2011; Phillips et al., 2016; Hossain et al., 2017), ultimately leading to the reduction of species and functional diversity in algal communities.

In this Special Issue, the above topics are presented in detail in three papers (Table S1;

phytoplankton-macrophytes' relationship—paper #10; metaphyton realm—paper #11; benthic diatoms-macrophytes' relationship—paper #12). The **10th paper** of this Special Issue (see Table S1) emphasised a clear compositional difference in the phytoplankton depending on the habitat studied, i.e. the open water habitat or the areas covered by macrophytes. Within each habitat, characteristic functional groups and species have been identified. In the **11th paper** of this Special Issue (see Table S1), a whole pond experiment was implemented, in which the exclusion of source-sink dynamics was investigated. There is clear evidence that the metaphyton can be considered as a refuge for open water phytoplankton and plays a pivotal role in within-lake metacommunity processes. The **12th paper** of this Special Issue (see Table S1) highlighted the importance of microhabitat heterogeneity provided by macrophytes of different life forms in the complexity of benthic diatom assemblages in a multi-purpose reservoir.

Microalgae in water management: phycology in practice

In (1962), 'Silent Spring' an impressive book by Rachel Carson was published, which highlighted the human responsibility for living Earth and as a public consequence resulted in the establishment of the United States Environmental Protection Agency (the EPA) in 1970 (web2). In addition to the United States, efforts have also been made in Europe to reduce human impacts on ecosystems and to create a uniform legal framework since the 1970s (EC, 1976, 2000; CEC, 1991). The latter, the Water Framework Directive (WFD; EC, 2000), enabled the establishment of a fairly uniform monitoring system in the Member States, which also considered ecoregional differences. This was necessary, *inter alia*, because many of the river basins of the European large rivers are of international interest, i.e., Danube, Elbe, Ems, Rhine, etc. As a result of the introduction of the WFD, the interest of algologists has been focused for years, if not decades, on ecological status assessment, which has remained an ongoing project. Thousands of papers have been written on this topic (see more e.g.: Nixdorf et al., 2008; Nõges et al., 2009; Birk et al., 2012; Bergkemper & Weisse, 2018), pointing out its scientific and economic importance. The use

of phytoplankton taxa for water quality assessment dates back almost one hundred years (see more in Padisák et al., 2006).

Chlorophyll-a content and algal biomass are the most commonly included metrics in phytoplankton indices. This requires an accurate and precise biomass estimation, a high level of taxonomic expertise and knowledge of the autoecological needs of the species. The limitations of this method are discussed in the "Traditional and new methods: perspectives and comments" section. In other phytoplankton indices (Padisák et al., 2006; Borics et al., 2007), the Reynolds functional groups (RFGs) have been involved, which is based on deep ecological knowledge of planktic algae pooling phytoplankton species with very similar characteristics and demand into RFGs (coda; Reynolds et al., 2002). During a year, phytoplankton communities undergo a seasonal succession (Sommer et al., 1986, 2012), which creates a strong competitive situation for the taxa. Given the lake morphology and the annual cycle of the main environmental variables, as well as the competitive exclusion mentioned above, one or a few best-adapted species repeatedly dominate in a given habitat and in a certain period of the year (Padisák et al., 2006). This means that there is a snapshot of the composition of the phytoplankton, which can be used to characterise the ecological state of the habitat in question. Although phytoplankton rarely reach a steady-state condition (Naselli-Flores et al., 2003a), there are periods in all climate zones when the biomass and chlorophyll content change little (e.g., Melack, 1979; Padisák et al., 2003). Using information from this period, habitat types and their characteristics can be inferred from group proportions, and *vice versa*, which is key information from a water management perspective.

The above highlights the strong policy pressure to monitor the trophic status of waters using phytoplankton data (national and ecoregional scales—Padisák et al., 2006; Borics et al., 2007; long-term data of lakes—Hajnal & Padisák, 2008; Ostrovsky et al., 2013; Znachor et al., 2020). In recent years, however, factors and processes other than eutrophication have been recognised and identified as having the potential to threaten entire aquatic ecosystems (Reid et al., 2019). In the United States alone, freshwater algal blooms, mostly of cyanobacteria, cause more than $4 billion in economic losses each year, primarily

through impacts on aquatic food production, recreation and tourism, and drinking water supplies (Ho et al., 2019). Their monitoring is hampered by uncertainties in species identification and estimation of cell numbers and biomass (T-Krasznai et al., 2022a). The latest studies have shown that even freshwater diatoms, both planktic and benthic, are capable of producing secondary metabolites that bioaccumulate in the food web and even directly cause neurodegenerative human diseases (Violi et al., 2019). However, climate-induced changes in freshwater hydrology and physical and chemical characteristics may favour these potentially harmful algal blooms in phytoplankton and phytobenthos (Reid et al., 2019; Violi et al., 2019). Although secondary salinisation of freshwaters is not a new phenomenon (Stenger-Kovács et al., 2023), its scale and extent are increasing at an unprecedented rate and are expected to escalate further due to climate change (e.g., decrease in precipitation, increase in evaporation) (Reid, et al., 2019). In phytoplankton, significant structural changes can be predicted with an increase in the number of small, tolerant species (Astorg et al., 2021). Benthic diatom assemblages are predicted to be dominated by extremely small or large species, mucilaginous colony-forming and/or halophilic (e.g., Kókai et al., 2015; B-Béres et al., 2016) and over time aerophilic and terrestrial taxa, and/or motile taxa capable of moving to the upper sediment layer (e.g., Sabater et al., 2016).

Water management needs to respond quickly to these phenomena, as they impose serious environmental and economic burden for several countries. However, this requires well-coordinated monitoring work based on a solid and regular financial background, even across administrative and territorial boundaries. It must be emphasised, however, that data from monitoring should not be buried in a desk drawer, but should enable intelligent, scientific analyses and their use in legislation.

The importance and current relevance of this topic is underlined by two papers in this special issue (Table S1; papers #13–14). The **13th paper** of this Special Issue (see Table S1) presents the result of the 4th Joint Danube Survey organised by the International Commission for the Protection of the Danube River (ICPDR), which was aimed at supporting the quality improvement of the Danube. At the same time, the paper also highlights that the Iron Gate notably reduces water flow and extends the residence time resulting in modification to the phytoplankton structure which finally indicates hydrological degradation. The **14th paper** of this Special Issue (see Table S1) focuses on the effects of salinization on the phytoplankton assemblages in Mediterranean shallow lakes. The study highlights that in future water management planning, particularly those affecting the hydrological regime, it is crucial to consider the lakes' natural state, and the focus must be on preserving it.

Traditional and new methods: perspectives and comments

The first publications appeared in the field of microalgal research focused on the description of new taxa or exploration of the microflora of aquatic habitats. At that time, the plankton net and the traditional upright microscope were the basic research devices that algologists used in their every-day work. Investigation of net samples provided floristic data for a given lake or river, and in the middle of the last century these data were used for water quality assessment (Thunmark, 1945; Nygaard, 1949). In their indices, the authors applied the ratios of species richness values of various algal groups as measures of water quality. However, these so-called taxonomic indices are not robust measures because they are sensitive to differences in sampling and taxonomic skills of the observers. Application of the settling method (Utermöhl, 1931), and elaboration of standardised counting protocol (Lund et al., 1958; Rott, 1981) enabled the use of quantitative phytoplankton data which gave a great impetus to both basic and applied algological researches. The next important step was when algal counts were converted to biovolume data. This procedure approximates the shape of algae with equivalent geometric forms and calculates their volume with the well-known formulas (Kovala & Larrance, 1966; Kellar et al., 1980; Hillebrand et al., 1999). The standardised Utermöhl technique combined with biovolume estimation (CEN-EN 16695, 2015) has been considered currently the most accurate species abundance acquisition approach. However, it has two serious shortcomings: it is time consuming, and requires well-trained staff who are familiar with microscopy,

taxonomy and algal counting. Providing mean biovolume data for the most frequent species is an option by which the work of monitoring staff can be made somewhat easier (Olrik, 1994), but undoubtedly it reduces the accuracy of biovolume estimation. Recent advances in 3D imagery enabled the use of 3-dimensional models of microalgae and measurement on these objects provide a more accurate and quicker way of biovolume estimation (Borics et al., 2021).

To avoid hardships of microscopy the researchers have been seeking for instrumental solutions aimed at estimating the biomass and taxonomic composition of the samples. The technological innovations of the last decades allowed the use of photometric, chromatographic (Jeffrey et al., 1999), or fluorescence-based techniques (Holm-Hansen et al., 1965; Lorenzen, 1966) to measure the concentration of photosynthetic pigments in the water as proxies of phytoplankton biomass. Due to the improvement in detection of fluorescence signals, satellite colour imagery became an extensively used tool in large-scale limnological and oceanological studies (Behrenfeld et al., 2006; Tóth, 2023). These advanced techniques also have the potential to yield information on the taxonomic composition of phytoplankton assemblages. Besides chlorophyll-a, several so-called marker pigments (photosynthetic or photoprotective pigments) are characteristic for certain taxa, thus their relative abundance in water depends on the phytoplankton composition. Several studies demonstrated that applying high-performance liquid chromatography (Mackey et al., 1996), solar- (Catherine et al., 2012) or laser-induced fluorescence techniques (Babichenko et al., 1993), the compositional pattern of major phytoplankton classes showed good correlation with the results of traditional microscopy (Gregor et al., 2005; Izydorczyk et al., 2009). Flow cytometry combined with video technology has been successfully applied for rapid identification and measurement of phytoplankton cells or trait clusters in low diversity systems with stable phytoplankton composition (Thomas et al., 2018). However, these approaches allow only a rough taxonomic resolution, and understanding the functioning of the planktic assemblages, fine-scale taxonomic resolution is still required. The revolutionary development in molecular tools, including the various DNA and RNA sequencing approaches, opened new perspectives in the identification of species in the last decades (Johnson & Martiny, 2015). Two papers in this special issue (Table S1; papers #15–16) used these approaches

to reveal diversity of eukaryotic phytoplanktic assemblages in karstic (**15th paper** of this Special Issue—see Table S1) and cyanobacteria in Alpine and Sub-Alpine (**16th paper** of this Special Issue—see Table S1) lakes. In the karst lakes there was only a weak overlap between the observed functional groups derived from the traditional microscopy and molecular approaches (paper #15). These results highlighted the still existing gaps in the completeness of the NCBI GenBank taxonomic reference database. Meanwhile, differences in the trophic status of Alpine lakes (paper #16) appeared in the distribution of amplicon sequence variants. The **17th paper** of this Special Issue (see Table S1) pointed out that molecular approaches in cyanobacterial taxonomy considerably increased our understanding of their ecology, large scale distribution and cryptic diversity. Both the literature review (paper #17) and the study on Alpine and pre-alpine lakes' cyanobacterial assemblages (paper #16) revealed that the lakes' pelagial provides more uniform habitats for cyanobacteria compared to those that are associated to solid substrate, like terrestrial habitats and benthic ones in lakes, therefore these latter habitats have considerably larger cyanobacterial diversity. It has also been emphasised that precise estimation of taxa abundances using molecular approaches still has not been solved, which hinders the application of functional group-based water quality assessment.

Majority of phytoplankton samples investigated by the algologists serve for monitoring of water quality. The sample processing is a time consuming task that does not allow investigating as many samples as would be necessary to reduce the uncertainty caused by the hectic temporal changes in the composition and biomass of the phytoplankton. **The 18th paper** of this Special Issue (see Table S1) provided a semi-quantitative counting approach as an alternative of the traditional counting. This approach works with ordinal scale data, and thus it is similar to the frequency estimates that were successfully applied in saprobiological analyses (Pantle & Buck, 1955), to the cover classes of the Braun Blanquet method (Braun-Blanquet, 1964), and to estimate values of the Kohler scale (Kohler, 1978) applied in terrestrial and aquatic macrophyte surveys. The proposed method can be useful for quick assessment of morpho-functional groups or indicator species as well. Although this approach requires some practice from the observer, it can be improved, as it was demonstrated in the case

of cyanobacterial colony size estimation (T-Krasznai et al., 2022a).

Concluding remarks

As briefly mentioned earlier, case studies in this Special Volume assembled trait-, guild- or functional group (T/G/F) approaches along a wide array of spatial and temporal scales and aquatic habitat types. It is also apparent that the applied grouping methods varied from paper to paper sharing only one common feature: the T/G/F approach.

It is historical evidence that, in microalgal ecology, phytoplankton ecologists were the first group of scientists to greet the publication of the first coherent functional group system (RFG – Reynolds et al., 2002; Padisák et al., 2009; Kruk et al., 2021), and that it was applied almost immediately in the studies presented at the 13th IAP meeting (e.g., Naselli-Flores et al., 2003b; Padisák et al, 2003). This need was so apparent that others were also working on elaboration of such systems, based on different theoretical (MFG—Salmaso & Padisák, 2007) or statistical (MBFG—Kruk et al., 2010) approaches and published them not very long after. All these three methods were successfully applied for understanding phytoplankton patterns compared to spatially or temporally arising environmental forcing (Salmaso et al., 2015). Later, and by offering appropriate quantitative metrics these systems were applied for assessing ecological status of freshwater ecosystems (Padisák et al., 2006; Borics et al., 2007). A majority of papers in this volume applied these systems. In phytoplankton studies, the RFG system was the most frequently used method either alone or in comparison with the MBFG or the MFG. A paper also used the life strategy types (CSR—Reynolds, 1988). Besides, a number of authors applied different traits like maximal linear dimension, volume, volume fractions.

Historically, diatom researchers have primarily focused on the taxonomy and distribution of species, whilst trait and functional-based perspectives, as well as their ecological significance, have been somewhat overlooked. Despite attempt in the late 1990s (Biggs et al., 1998) to adapt Grime's CSR system for terrestrial plants (Grime, 1979) to benthic diatom communities (C/C-S/S/R), the approach only received significant interest in the late 2000s/early 2010s. In 2007,

Passy used this, *inter alia*, to elaborate the T/F/G concept, sorting stream diatoms into guilds according to their adhesion strategies, which was followed by definition of a number of trait and trait categories (Berthon et al., 2011; Rimet & Bouchez, 2012; Lange et al., 2016; Stenger-Kovács et al., 2018). In papers where attached diatoms were analysed, a number of traits were used to explore patterns related to processes: length/width ratio, cell size, attachment type, life form, guild affiliation, pioneer character, endangered taxa.

It is apparent that the trait-based approach is more intensively used by diatom- than by phytoplankton ecologists, probably because a single taxonomic group (diatoms) have, understandably, less ecophysiological diversity than phytoplankton where some functional properties (like ability for dinitrogen fixing, flagellar movements and specific gravity to cope with vertical gradients in the pelagic or the mixotrophy) are of prior importance besides morphometric features. In addition, diatoms can be relatively well identified under the microscope, so the specification of easy to measure characteristics is more straightforward than for planktic algae and cyanobacteria, or even for other benthic algal taxonomic groups, although there are limitations. The correct calculation of biomass, as well as the precise identification of the life form or attachment type, or even the assignment to the appropriate guild, remain outstanding tasks to be resolved. Last but not least, habitat-based approach, similar to Reynolds' system, is still awaiting in diatom research. Because the current ones are primarily made up of species with similar traits from related taxonomic groups, and do not focus on the functional response of taxa with different properties but the same ecological needs, as the habitat concept does. However, in studies comparing the T/G/F approach to taxonomic affiliation, the T/G/F described better the observed patterns compared to environmental drivers than the merely taxonomic. The contribution where DNA metabarcoding was also applied has shown that, at present, the operative taxonomic units (OTUs) display only poor overlap with either T/F/G or taxonomic compositions pointing out to the need to further develop the reference data-bases.

Declarations

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