



From historical backgrounds towards the functional classification of river phytoplankton sensu Colin S. Reynolds: what future merits the approach may hold?

Andras Abonyi · Jean-Pierre Descy · Gábor Borics · Evangelia Smeti

Received: 26 January 2020 / Revised: 9 May 2020 / Accepted: 14 May 2020 / Published online: 23 May 2020
© The Author(s) 2020

Abstract River phytoplankton has been studied to understand its occurrence and composition since the end of the nineteenth century. Later, pioneers addressed mechanisms that affected river phytoplankton by “origin of plankton”, “turbulent mixing”, “flow heterogeneity”, “paradox of potamoplankton maintenance” and “dead zones” as keywords along the twentieth century. A major shift came with the recognition that characteristic units in phytoplankton compositions could be linked to specific set of environmental conditions, known as the “Phytoplankton Functional Group concept” sensu Reynolds. The FG concept could successfully be applied to river phytoplankton due to its close resemblance to shallow lakes phytoplankton. The FG approach enables one to

separate the effects of “natural constraints” and “human impacts” on river phytoplankton and to evaluate the ecological status of rivers. The FG classification has mainly been advocated in the context of how the environment shaped the functional composition of phytoplankton. It may be further developed in the future by a trait-based mechanistic classification of taxa into FGs, and by the exact quantification of FGs on ecosystem functioning. These improvements will help quantify how global warming and human impacts affect river phytoplankton and corresponding alterations in ecosystem functioning.

Keywords Benthic diatoms · Ecological indication · Ecosystem functioning · Functional groups · Functional traits · River plankton · Potamoplankton · River ecosystems

Guest editors: Judit Padišák, J. Alex Elliott, Martin T. Dokulil & Luigi Naselli-Flores / New old and evergreen frontiers in freshwater phytoplankton ecology: the legacy of Colin S. Reynolds.

A. Abonyi (✉)
Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány u 2-4, Vácrátót 2163, Hungary
e-mail: abonyiand@gmail.com

A. Abonyi
WasserCluster Lunz, Dr. Kupelwieser-Prom. 5,
3293 Lunz am See, Austria

J.-P. Descy
Unit of Chemical Oceanography, University of Liège,
Allée du 6 Août, 19, 4000 Liège, Belgium

G. Borics
Department of Tisza Research, Danube Research Institute,
Centre for Ecological Research, 18/c Bem tér,
Debrecen 4026, Hungary

E. Smeti
Hellenic Centre for Marine Research, Institute of Marine
Biological Resources and Inland Waters,
19013 Anavissos, Attica, Greece

“The ability of open-ended systems, subject to persistent unidirectional flow, to support plankton is paradoxical ... On the other hand, the wax and wane of specific populations in given rivers seem fully reproducible; they are scarcely stochastic events”. Colin S. Reynolds, *Ecology of phytoplankton* (2006)

Historical backgrounds of river phytoplankton studies

In contrast with common assumptions that can be found in the scientific literature, river phytoplankton has extensively been studied for a long time. The first reports on “potamoplankton” can be found as early as the end of the nineteenth century, even though these papers were essentially descriptive. The authors mentioned the presence of algae suspended in the water of lowland rivers, sometimes in considerable quantity (see, e.g. Zacharias, 1898; Welch, 1952; Whitton, 1975). The ecological understanding of potamoplankton dynamics that time was scarce. Nevertheless, from the first half of the twentieth century, potamoplankton was mentioned to be found in large and in lowland rivers with slow flow, where phytoplankton may vary considerably both in terms of quantity and quality. According to these early studies, species composition did not differ from that of other freshwater bodies (e.g. Kofoid, 1908).

As early as the 1920s, scientists could relate the variation of potamoplankton abundance with river water discharge and current velocity. des Cilleuls (1928), for instance, presented a remarkable synthesis on potamoplankton studies in Europe, Asia and America, referring to former ideas developed by Kofoid (1908). As a particular example, the role of current velocity understood as a major factor determining the time allowed to planktic algae for developing populations, was recognised already:

L’influence notable qu’exerce le courant sur le plancton réside ... dans le fait qu’il est un facteur important dans la détermination du temps pendant lequel le plancton peut naître et s’accroître des Cilleuls, *Le phytoplancton de la Loire et de ses affluents dans la région Saumuroise* (1928)

In other words, the importance of water residence time was understood clearly, even with the simple mathematical assumption that residence time should be long enough to allow a sufficient number of generations to build up a cell population of detectable size.

The origin of the plankton, in particular the role of backwaters, has been recognised as another key topic. That is, there must be a permanent source of plankton to the mainstem as potamoplankton is transported downstream. The origin of river phytoplankton has been addressed early by Kofoid (1908), Butcher (1932) and Talling and Rzóška (1967). Interestingly, Butcher insisted on the origin from the benthos, whereas Talling and Rzóška argued for recruitment from lentic habitats connected to the mainstem of the River Nile. Besides this emphasis on hydrology, Reinhard (1931) noted the influence of temperature and light on potamoplankton growth. By contrast, nutrient supply did not seem to be a key factor controlling planktic algal growth since most of the systems studied were eutrophic, with DIN, SRP and SRSi levels well above cells’ requirements for growth (see, e.g. Kowalczewski & Lack, 1971 on the River Thames). In a remarkable paper “Ideas for a synthetic approach to the ecology of running waters”, Margalef (1960) added mathematical reasoning on planktic river algae based on the analogy between a fully mixed river compartment and a chemostat. He concluded that “in a watercourse with laminar flow, no population could maintain itself. It is necessary to a certain amount on turbulent mixing” (Margalef, 1960). This may have inspired subsequent studies on the role of flow heterogeneity in rivers, notably by Colin Reynolds et al.

Major inputs of Colin S. Reynolds into river phytoplankton ecology

Colin S. Reynolds synthesised and drew conclusions early from knowledge acquired previously in potamoplankton ecology in a book chapter edited by F.E. Round, another specialist of algal ecology (Reynolds, in Round, 1988). Among others, he insisted on the control by fluvial discharge, which is the major constraint on phytoplankton development and maintenance in a unidirectional flow. This was not new, of course, but C.S. Reynolds added further mathematical reasoning about growth rates and variation in water discharge affecting the travel times of algal populations in rivers. Building also on Margalef’s thoughts about the role of turbulence and incomplete mixing in successive river compartments, he addressed then the paradox of maintenance of potamoplankton

populations. Considering the effects of water turbidity on growth and channel depth on settling losses, he assumed a role of “retention zones” in the maintenance of river plankton, still from reasoning on hydrodynamics in river channels developed by modellers. This paved the way for further research that provided evidence of such “dead zones” in rivers, as in the study of the River Severn (see Reynolds et al., 1991; Reynolds & Glaister, 1993). These works contributed largely to recognise the co-existence of potamoplankton populations with contrasting adaptations, and the mechanism of the survival of “seeding” from previously settled cells or colonies (Reynolds & Descy, 1996).

Such studies, as well as thoughts of C.S. Reynolds (1984) on phytoplankton assemblages, led naturally to understand species selection by environmental factors in a more mechanistic way, that is, according to species functional traits like eco-physiological properties. Following mathematical considerations on turbulent flow affecting the transport of algae (Reynolds, 1994a), Reynolds demonstrated how vertical mixing in a (more or less) turbid and turbulent water column selects for phytoplankters with appropriate traits (Reynolds, 1994b). These functional characteristics were photosynthetic efficiency, accessory pigments, specific settling rate, specific growth rate and morphology, by which he could explain the usual dominance of centric diatoms and coccal green algae in lowland rivers. Obviously, the functional group concept of phytoplankton (Reynolds et al., 2002) was inherent to these reflections.

From taxonomic towards the functional classification of river phytoplankton sensu Reynolds

Characteristic patterns in the composition of river phytoplankton have mainly been recognised at a larger spatial scale. Critical environmental factors that shape river phytoplankton composition are downstream travel time (i.e. the opportunity for growth), river depth and turbulence, all affecting both the entrainment of algae in the water column and the corresponding underwater light climate (Reynolds, 1994b). These “master variables” alter along large rivers in a predictable way, partly gradually as synthesised in the River Continuum Concept (Vannote et al., 1980),

partly stepwise due to major shifts in hydrogeomorphology and climate (i.e. functional river zonation, Thorp et al., 2006). River phytoplankton composition can follow changes of these variables and indicate both gradual and river zone-related alterations of the environment (Abonyi et al., 2014).

Upstream river sections are fast-flowing, where true planktic phytoplankton is rare due to the short water residence time. However, benthic taxa, especially diatoms, can detach from the substrates and occur frequently in the plankton (Reynolds & Glaister, 1993; Piirsoo, 2001; Soyulu and Gönülol, 2003; Farahani et al., 2006). Further downstream, the increase of water residence time allows the growth of true planktic elements. In these river sections, higher nutrient availability, turbulent and turbid flow conditions often favour fast-growing algae with low-light tolerance, e.g. centric diatoms (Reynolds, 1994b; Reynolds & Descy, 1996). The dominance of centric diatoms, where it occurs, is a characteristic and recurring phenomenon in the middle sections of large rivers (see Gosselain et al., 1994; Garnier et al., 1995; Kiss, 1996). However, shallowness, lower water discharge, higher water temperature and corresponding enhanced underwater light availability favour the dominance, or co-dominance of chlorococcalean greens in the middle and downstream river sections (see Reynolds & Descy, 1996 and references therein). Similar to centric diatoms, fast growth and high surface-to-volume ratio characterise these taxa, and as they are exposed to lower settling velocity, their dominance is favoured over large and heavy diatoms (Reynolds et al., 1994). Accordingly, when turbulent and turbid environmental conditions in the middle river section shift to shallowness and increased light availability further downstream, phytoplankton community may shift in dominance from centric diatoms to coccal green algae. Excellent examples are the River Loire (Descy et al., 2011; Abonyi et al., 2012) and the lower section of the River Danube (Stoyneva, 1994). On the other hand, deep, well-mixed, and therefore turbid downstream river sections might constrain planktic algal production, or select for the dominance of centric diatoms due to their low-light adaptation in a turbulent and turbid environment (Reynolds & Descy, 1996).

Mechanisms that generate selective forcing on river phytoplankton composition are similar among seasons. Downstream travel time, turbulence, water temperature and underwater light climate are season

specific due to seasonal variation in water discharge and insolation. Accordingly, characteristic community compositions, e.g. centric or coccal green algal dominance may “move” upstream or downstream seasonally. From the middle to downstream river sections, the seasonal shift—either from coccal greens to centric, or centrics to greens—occur in a rather gradual way (Reynolds & Descy, 1996). Shift in selection-forcing acts on river phytoplankton composition both in time (Descy & Mouvet, 1984) and space (Abonyi et al., 2014), depending on water depth, turbulence and the corresponding light regime (op. cit.). Rivers are, therefore, highly selective environments, where only a relatively small number of phytoplankton genera can achieve dominance (Rojo et al., 1994; Reynolds, 1994b). Whenever the high selective pressure alleviates, i.e. higher water retention time, moderate turbulence and enhanced light availability, slow-growing taxa may occur and enrich the diversity of river phytoplankton (Reynolds & Descy, 1996).

Non-taxonomic “functional” classifications of phytoplankton have long been existing. Margalef (1958) described first that phytoplankton was directed towards two possible ends in selectivity: r-selection (small cell size, fast growth, e.g. centric diatoms) and K selection (large cell size, slow growth, special abilities like motility, e.g. dinoflagellates, Fig. 1). Seasonal succession is primarily affected by the shift from enhanced mixing to stable conditions and high towards low nutrient availability in the water column, where phytoplankton may develop from the dominance of r-selected towards K-selected taxa. In unimpounded temperate rivers, one may expect that under non-limiting nutrient conditions and continuous mixing, succession is set back constantly that selects for fast-growing (r-type) taxa, while bloom-forming cyanobacteria and large dinoflagellates are virtually excluded (Reynolds & Descy, 1996). On the other hand, temporally extended slow flow conditions, when they occur, may allow the occurrence of K-strategists in lotic systems (e.g. dinoflagellates, Gosselain et al. 1994), especially in calm summer periods at river sections following impoundments (see, e.g. Köhler, 1994).

A significant next step was the adaptation of the ‘CSR’ classification of plant strategies sensu Grime (1977) to phytoplankton ecology by Colin S. Reynolds (Reynolds, 1987). In the context of mixing and

nutrient availability, phytoplankton taxa can also be classified as C-strategists (good Competitors by rapid exploitation of available resources), S-strategists (Stress tolerance in resource limitations), and R-strategists (Ruderals with resistance to disturbances) (Reynolds, 2006; Fig. 1b). The CSR concept is the simplest approach that may handle river phytoplankton successfully, being exposed to continuous mixing (R-selection force) and limited time frame for growth (C-selection). Fast-growing opportunists (C-strategists, e.g. centrics) and process-constrained ruderals (CR-strategists, e.g. coccal greens) have a clear advantage in river phytoplankton (Gosselain & Descy, 2002; Reynolds, 2006). The continuous recognition of characteristic co-occurrence of phytoplankton taxa under specific set of environmental conditions led Reynolds to his well-recognised phytoplankton functional group concept (Reynolds, 1984, 1997; Reynolds et al., 2002), also applied later on rivers.

Functional groups comprise taxa that process any ecological component (e.g. resource use) in a similar way, and therefore, provide similar ecosystem services or functions (Blondel, 2003). In phytoplankton ecology, multiple ‘functional group’ concepts have been developed (Salmaso et al., 2015), among which the Functional Group Concept sensu Reynolds (FG approach) had its own old roots (see also Reynolds, 1988). The first 14 lake phytoplankton assemblage types (also known as functional groups or coda) were based on co-occurring taxa with similar seasonality (Reynolds, 1984). Recently, the term ‘FG’ refers to species with similar morphological and physiological traits, as well as ecological features (Reynolds et al., 2002; Salmaso et al., 2015). Compared with other classifications, the FG concept describes habitat properties in a relatively well-defined way (Padišák et al., 2009). FGs reflect on the physical environment (i.e. preference in mixing, Reynolds, 1994b; Naselli-Flores & Barone, 2011), disturbance frequency (e.g. tolerance to alterations in mixing, Lindenschmidt & Chorus, 1998; Hambright & Zohary, 2000), trophic state and seasonality (Padišák et al., 2009; Salmaso et al., 2015; Fig. 1c, d).

The number of described FGs has increased up to 40 (Padišák et al., 2009), including also specific ones for river algae. These were epiphytic cyanobacteria (codon T_C), epi- and metaphytic desmids, filamentous greens and sediment-dwelling diatoms (codon T_D) that occur in slow-flowing rivers with emergent

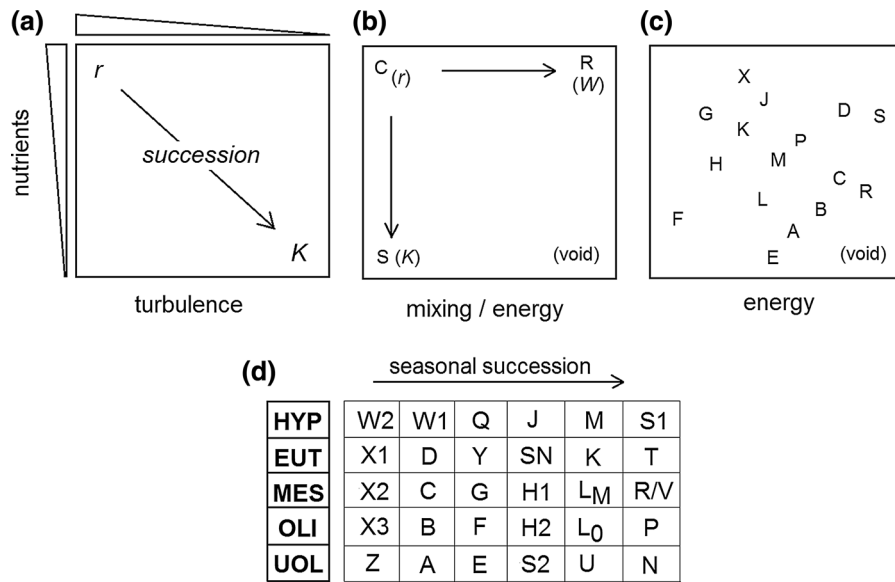


Fig. 1 **a** Two possible ends of selectivity in phytoplankton: r- and K-selected taxa along the environmental gradients of turbulence and nutrient content (Margalef, 1958), **b** the r-K selection completed by R-selected species sensu Reynolds (Reynolds, 1997) following Grime (1977), **c** habitat templates of characteristic phytoplankton associations (coda) along the

gradients of energy and nutrient content (Reynolds 1987, 1997), **d** coda classification sensu Reynolds along with temporal succession and trophic status (Reynolds, 2005). Redrawn and modified from Margalef (1958) and Reynolds (1997, 2005), appeared first in Abonyi (2015)

macrophytes, as well as epilithic pennate diatoms, being characteristic in highly lotic environments (Borics et al., 2007). Although the FG approach classified limnetic phytoplankton first, it also appeared to be relevant in rivers (Reynolds, 2003), partly due to the close resemblance between shallow lake and large river phytoplankton (Reynolds et al., 1994). High inorganic turbidity and corresponding steep underwater light gradient characterise both systems, selecting for phytoplankton taxa adapted to low irradiance and its high-frequency fluctuation during continuous mixing (Reynolds et al., 1994, Table 1).

Best-adapted river phytoplankton taxa are efficient light harvesters, and can tolerate and persist in low irradiance environments (coda C and D, Table 1). Coccal green algae better adapted to moderate turbulence (even to meroplankty), higher water temperature and higher light availability are classified into coda J, X1 and F; still being characteristic in shallow, mixed, highly enriched systems. Phytoplankton taxa that occur typically in eutrophic stratifying and shallow lakes with low nitrogen content (codon H1), eutrophic to hypertrophic stratifying lakes (codon L_M), continuous or semi-continuous mixed layers of 2–3 m in thickness under eutrophic state (codon P) are excellent

indicators of eutrophic impoundments in rivers (Table 1). Taxa that grow under reduced turbulence (e.g. codon X2), and are rather characteristic in oligotrophic conditions (e.g. codon X3), may successfully indicate long-term changes in hydrology and the trophic state (Abonyi et al., 2018a).

The application of the FG approach in river phytoplankton ecology and ecological status indication

Since the first applications of the FG approach in river systems (Devercelli, 2006; Soares et al., 2007), more than fifty river phytoplankton studies described and used the approach to explain changes in potamoplankton composition. These studies reported that the FG approach could reflect alterations in hydrology at diverse spatial and temporal scales (Várbíró et al., 2007; Abonyi et al., 2012, 2014; Stankovic et al., 2012; Bolgovics et al., 2017). Also, it enhanced the understanding of compositional changes of phytoplankton along the gradient of lateral connectivity in river floodplains (Nabout et al., 2006; Mihaljević et al., 2009; Stević et al., 2013; Bortolini et al., 2014).

Table 1 Habitat templates and the Functional Group (FG) classification of characteristic river phytoplankton taxa sensu Reynolds (see, Reynolds et al., 2002; Borics et al., 2007; Padišák et al., 2009)

Codon	Habitat template	Characteristic taxa in rivers	Comment
C	Eutrophic small- and medium-sized lakes with species sensitive to the onset of stratification	<i>Asterionella formosa</i> , <i>Cyclotella meneghiniana</i>	Typical in the middle river section of large eutrophic rivers; mixing conditions have to meet the habitat template
D	Shallow turbid waters including rivers	<i>Stephanodiscus hantzschii</i> , <i>Skeletonema potamos</i> , <i>Nitzschia acicularis</i> , <i>Nitzschia fruticosa</i> , <i>Actinocyclus normanii</i>	Typical in the middle river sections of large eutrophic rivers
F	Clear, deeply mixed meso-eutrophic lakes	<i>Dictyosphaerium</i> spp., <i>Oocystis</i> spp.	Middle and lower sections of large rivers indicating enhanced water residence time, moderate turbulence and enhanced underwater light availability. Often in co-dominance with taxa from codon J
H1	Eutrophic, both stratified and shallow lakes with low nitrogen content	<i>Dolichospermum</i> spp., <i>Aphanizomenon</i> spp.	Characteristic taxa of eutrophic reservoirs if mixing conditions and the trophic status meet the habitat template
J	Shallow, mixed, highly enriched systems, including low-gradient rivers	<i>Pediastrum</i> spp. <i>Scenedesmus</i> spp.	Middle and lower sections of large rivers, often in co-dominance with taxa from codon D
L_M	Eutrophic to hypertrophic, small- to medium-sized lake	<i>Ceratium</i> co-occurring with <i>Microcystis</i> spp.	Typical association in eutrophic stratifying reservoirs
P	Continuous or semi-continuous mixed layer of 2–3 m in thickness under eutrophic status	<i>Fragilaria crotonensis</i> , <i>Aulacoseira</i> spp. planktic <i>Closterium</i> such as <i>C. acutum</i> , <i>C. aciculare</i>	Typical taxa of eutrophic reservoirs when mixing conditions meet the habitat template
S1	Turbid mixed environments	<i>Planktothrix agardhii</i> , <i>Limnithrix redekei</i> , <i>Pseudanabaena limnetica</i> , <i>Planktolyngbya</i> spp.	Potential taxa of eutrophic rivers when turbulence and turbidity suffice the habitat template
T_B	Highly lotic environments, streams and rivulets	Large benthic Pennales such as <i>Navicula</i> spp. <i>Gomphonema</i> spp. <i>Melosira</i> spp. <i>Fragilaria</i> type <i>construens</i>	Benthic diatoms detached from the substrates—characteristic in rhithral and highly turbulent rivers
T_C	Eutrophic standing waters, or slow-flowing rivers with emergent macrophytes	<i>Anabaena</i> spp. <i>Lynngbya</i> spp. <i>Phormidium</i> spp. <i>Oscillatoria</i> spp.	All benthic and epiphytic cyanobacteria that occur in rivers should be classified into T_C
T_D	Mesotrophic standing waters, or slow-flowing rivers with emergent macrophytes	<i>Cosmarium</i> spp., benthic <i>Closterium</i> spp. filamentous green algae like <i>Hydrodictyon</i> spp.	All benthic, epi- and metaphytic desmids and filamentous greens that occur in rivers should be classified into T_D
X1	Shallow, eu-hypertrophic environments	<i>Chlorella</i> spp. <i>Monoraphidium</i> spp.	Middle and lower sections of large rivers, often in co-dominance with taxa from codon J
X2	Shallow, meso-eutrophic environment	<i>Plagioselmis</i> spp. <i>Chlamydomonas</i> spp. small-sized <i>Cryptomonas</i> spp.	Middle and lower sections of large rivers with enhanced water residence time and moderate turbulence
X3	Shallow, well-mixed oligotrophic environments	<i>Chrysococcus</i> spp. <i>Koliella</i> spp., <i>Schroederia</i> spp.	Middle and lower sections of large rivers indicating oligotrophication potentially. Often in co-occurrence with taxa from codon X2

The characteristic occurrence of FGs is summarised based on Devercelli et al. (2006, 2010), Borics et al. (2007), Soares et al. (2007); Padišák et al. (2009), Abonyi et al. (2012, 2018a); Kruk et al. (2017), Wang et al. (2018); and Frau et al. (2019)

The FG system also helped recognise how phytoplankton of floodplain lakes could shape the composition of river phytoplankton in the main channel (Townsend, 2006; Devercelli & O'Farrell, 2013). In the case of channel-reservoirs, structural alterations of phytoplankton assemblages could also be described and explained well by FGs (Nogueira et al., 2010; Bovo-Scomparin et al., 2013; Zhu et al., 2013; Tian, et al., 2014). Temporal shifts in the dominance of FGs could help highlight constraints that affect phytoplankton assemblages of reservoirs (Li et al., 2011; Wang et al., 2011; Yang et al., 2011; Moura et al., 2013).

A practical application of Reynolds' FG system was the evaluation of tolerances of each FG in rivers to specific natural *versus* anthropogenic impacts, which enabled to assess the ecological state of rivers (Borics et al. 2007). Specific F quality factors were given to each FG according to

- (i) nutrient status (0—hypertrophic to 5—oligotrophic),
- (ii) turbulence (0—standing waters to 5—lotic environment),
- (iii) water residence time for development (0—climax to 5—pioneer community members), and
- (iv) level of risk (0—high risk indicating pollution or potential toxicity to 5—low risk).

The calculation of the $Q_{(r)}$ quality index based on the composition of river phytoplankton assemblages is $Q_{(r)} = \sum_{i=1}^s (p_i \times F)$, where $p_i = n_i/N$, n_i is the biomass of the i th FG, while N is the total biomass. The F factor number allows the $Q_{(r)}$ quality index to range between 0 (the worst) and 5 (the best).

The $Q_{(r)}$ approach has successfully been applied multiple times in European rivers (Piirsoo et al., 2010; Abonyi et al., 2012; Çelik & Sevindik, 2015). Based on a large-scale survey along the River Loire, seasonal minima of the $Q_{(r)}$ index values were synchronised to late summer, but the longer was the distance from the source, the earlier was the seasonal decrease of $Q_{(r)}$ (Abonyi et al., 2012). The index has been implemented as one of the reference measures for ecological status assessments of rivers across Europe (Mischke et al., 2016).

The importance of benthic diatoms in river plankton

Planktic and benthic assemblages of microalgae are not completely separated in rivers, with benthic species found suspended in the river plankton (tychoplankton), and planktic species found in the benthos (see, e.g. the planktic ecological group in Rimet & Bouchez, 2012). The latter case has also been observed in a high-frequency phytoplankton data set from middle- to large-sized rivers, and it was described as the benthic retention hypothesis (Istvánovics & Honti, 2011). According to this hypothesis, algae that sediment fast, especially diatoms, may take advantage of prolonged benthic residence time, in circumstances when it is sufficient to compensate for light-supported growth (op. cit.). The contribution of benthic algae to river algal assemblages has long been recognised (Margalef, 1960), with benthic diatoms, reported constituting as much as half of the plankton community (Rojo et al., 1994). The contribution of benthic taxa to the river plankton is more pronounced in small streams and headwater river sections of large rivers (Leitão & Leprêtre, 1998; Leland, 2003), as well as in shallow parts of large rivers (Stoyneva, 1994). In small rhithral rivers, benthic diatoms can even dominate the plankton (Bolgovics et al., 2017) and thus contribute to the functioning of the river system substantially. In extreme cases, such as found at the lowermost section of the River Danube, benthic species can be dispersed in a continuous way, enriching the potamoplankton constantly (Stoyneva 1994). While the original FG classification sensu Reynolds made no attempt to deal with tychoplanktic taxa within phytoplankton assemblages (Reynolds et al., 2002), they emphasised already the importance of developing such a scheme in the future. Accordingly, functional groups have later been described, including meroplanktic taxa for lake (codon **MP**, Padišák et al., 2006) and tychoplanktic taxa for river phytoplankton (codon **TB**, Borics et al., 2007, see also above).

Similar to Reynolds' phytoplankton functional classification that has been built on Grime's CSR system and connected growth strategies to cell size, functional classifications for phytobenthos have also been developed. McCormick (1996) classified benthic algae along with the same concept: competitors (C) with maximum resource capture and growth rates,

ruderals (R) adapted to colonise disturbed sites with high nutrient supply, and stress-tolerant species (S) adapted to low resource availability including species able to withstand disturbance (D) caused by scouring or herbivory. Biggs et al. (1998) proposed a habitat classification, where functional units of species were linked to the trophic level of the system. Therein, competitors (C) are found in eutrophic, steady systems, ruderals (R) in mesotrophic systems with frequent disturbances, stress-tolerant species (S) in oligotrophic, steady systems and a newly described group of CS species found in mesotrophic, steady systems. Law et al. (2014) linked further the CSR classification to cell size suggesting that C-species have a large surface-to-volume ratio (s/v) but small maximum linear dimension (mld); R species have large s/v and large mld, while S-type species have low s/v and small mld, a characteristic that is opposite to the known lentic definition of S-type species. Law's benthic diatom classification may be the one most directly related to the phytoplankton functional classification scheme sensu Reynolds.

As diatoms constitute a large proportion of phyto-benthos, they have received further attention in the context of functional classifications. A frequently used functional classification of benthic diatoms, the 'diatom ecological guild concept', has been developed to predict nutrient status and disturbance regime of running waters (Passy, 2007). The classification has later been modified to include both life forms (i.e. solitary cells, colonies) and ecological characteristics (i.e. low and high profiles, motile and planktic taxa) as relevant traits (Rimet & Bouchez 2012). Relevant morphological traits can represent the abilities in how benthic diatoms attach to the substrate, and thus, functional differences in how they withstand changes in water flow conditions (Tapolczai et al., 2016). Nevertheless, incorporating the ecological guild concept to the cell size approach was the most reliable for benthic diatoms (Law et al. 2014; B-Béres et al., 2017). The diatom ecological guild concept was also found to be directly related to biomass production of benthic diatoms, outperforming taxonomic classification in explaining biomass variations (Passy & Larson, 2019).

The combination of Reynolds' FG approach and trait-based functional classifications of benthic diatoms enabled better predictions for the community composition from the local environment than the

taxonomic or the FG system alone in a temporally extensive potamoplankton data set (Pearl River, China; Wang et al., 2018). Therefore, the occurrence of benthic diatoms in large river plankton is mostly not random, and can be assessed ecologically in a meaningful way based on combined planktic and benthic algal functional classifications (op. cit.).

Potential future merits of the FG approach in river phytoplankton ecology

The short overview presented above summarises the evolution of river phytoplankton studies from a taxonomic towards a functional perspective, with a special focus on Reynolds' FG system. While the FG scheme represents already a more mechanistic and therefore more predictive approach than taxonomy, it certainly needs improvements. As ecology moves towards mechanistic approaches, the FG system should also follow. A critical improvement was the trait-based FG classification of phytoplankton taxa instead of expert judgement (Kruk et al., 2017), which effort should still be continued and further extended to large taxonomic lists, including also river phytoplankton taxa.

Existing phytoplankton functional group approaches (see also Salmaso & Padisák, 2007; Kruk et al., 2011; Kruk & Segura, 2012) including the FG system, have mainly been advocated in the functional community composition-environment relationship (i.e. how the environment shapes the functional composition of phytoplankton). According to Violle et al. (2007), such classifications summarise taxa by "response traits" to a specific set of environmental conditions, and are rather functional response groups than functional groups (Abonyi et al., 2018b). Future improvements of phytoplankton functional group classifications should enhance our ability to quantify and predict how these ecological groups affect ecosystem functioning (i.e. functional groups according to Blondel 2003, or, functional effect groups according to Hooper et al., 2005).

Recently, the Reynolds FG system has successfully been applied to understand long-term compositional changes in the potamoplankton of the middle Danube River (Abonyi et al., 2018a). The FG approach was especially helpful to recognise a potential long-term gradual regime shift from planktic to benthic

production (op. cit.). While such recognition is necessary for tracking and proving effects of global warming and human impacts on river ecosystems, future merits of the FG system will depend upon whether we can identify and quantify the effects of FGs on ecosystem functioning. In other words, whether we can develop Reynolds's functional response groups further into functional effect groups. Such exact functional information will be necessary to apply the FG concept in resolving timely challenges in river ecology. Primarily, we need to develop the FG concept into quantitative parameters to enable modelling the effects of global warming and human impacts on the functional composition of river phytoplankton and to quantify the corresponding alterations in ecosystem functioning.

Acknowledgements Our manuscript is dedicated to Colin S. Reynolds for his outstanding contribution to phytoplankton ecology. Thousands of future articles will still use his thoughts and show that those thoughts stand the test of time. We thank the Editors, Martin Dokulil, Alex Elliott, Luigi Naselli-Flores and Judit Padisák for inviting us to review the contribution of Colin S. Reynolds to river phytoplankton ecology. Helpful comments from two anonymous reviewers improved our manuscript substantially. AA was supported by the National Research, Development and Innovation Office, Hungary (NKFIH, PD 124681) and by the Austrian Science Fund (FWF Project P 30419-B29). GB was supported by the GINOP-2.3.2-15-2016-00019 project and by National Research, Development and Innovation Office, Hungary (NKFIH, K 132150). ES was supported by the State Scholarships Foundation, Greece (MIS 5033021). Open access funding was provided by Centre for Ecological Research, Hungary.

Authors contributions JPD wrote 'Historical backgrounds of river phytoplankton studies' and 'Major inputs of Colin S. Reynolds into river phytoplankton ecology', AA wrote 'From taxonomic towards the functional classification of river phytoplankton sensu Reynolds', GB wrote 'The application of the FG approach in river phytoplankton ecology and ecological status indication', ES wrote 'The importance of benthic diatoms in river plankton'. AA & ES summarised 'Potential future merits of the FG approach in river phytoplankton ecology' with substantial contributions from JPD and GB.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative

Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abonyi, A., 2015. Phytoplankton functional group composition along the River Loire (France): A limnological approach towards an understanding of phytoplankton longitudinal processes and ecological status indication [PhD Dissertation]. University of Pannonia.
- Abonyi, A., M. Leitão, A. M. Lançon & J. Padisák, 2012. Phytoplankton functional groups as indicators of human impacts along the River Loire (France). *Hydrobiologia* 698(1): 233–249.
- Abonyi, A., M. Leitão, I. Stanković, G. Borics, G. Várbíró & J. Padisák, 2014. A large river (River Loire, France) survey to compare phytoplankton functional approaches: do they display river zones in similar ways? *Ecological Indicators* 46: 11–22.
- Abonyi, A., É. Ács, A. Hidas, I. Grigorszky, G. Várbíró, G. Borics & K. T. Kiss, 2018a. Functional diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the Danube River due to global warming, human impacts and oligotrophication. *Freshwater Biology* 63(5): 456–472.
- Abonyi, A., Z. Horváth & R. Ptacnik, 2018b. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. *Freshwater Biology* 63(2): 178–186.
- B-Béres, V., V. Török, Z. Z. Kókai, Á. Lukács, E. T-Krasznai, B. Tóthmérész & I. Bácsi, 2017. Ecological background of diatom functional groups: comparability of classification systems. *Ecological Indicators* 82: 183–188.
- Biggs, B. J. F., R. J. Stevenson & R. L. Lowe, 1998. A habitat matrix conceptual model for stream periphyton. *Archiv fur Hydrobiologie* 143(1): 25–56.
- Blondel, J., 2003. Guilds or functional groups: does it matter? *Oikos* 100(2): 223–231.
- Bolgovics, Á., G. Várbíró, É. Ács, Z. Trábert, K. T. Kiss, V. Pozderka, J. Görgényi, P. Boda, B. A. Lukács, Z. Nagy-László, A. Abonyi & G. Borics, 2017. Phytoplankton of rhithral rivers: its origin, diversity and possible use for quality-assessment. *Ecological Indicators* 81: 587–596.
- Borics, G., G. Várbíró, I. Grigorszky, E. Krasznai, S. Szabó & T. Kiss Keve, 2007. A new evaluation technique of potamoplankton for the assessment of the ecological status of rivers. *Archiv für Hydrobiologie, Supplementband Large rivers* 17(3–4): 466–486.
- Bortolini, J. C., L. C. Rodrigues, S. Jati & S. Train, 2014. Phytoplankton functional and morphological groups as indicators of environmental variability in a lateral channel

- of the Upper Paraná River floodplain. *Acta Limnologica Brasiliensia* 26: 98–108.
- Bovo-Scomparin, V. M., S. Train & L. C. Rodrigues, 2013. Influence of reservoirs on phytoplankton dispersion and functional traits: a case study in the Upper Paraná River, Brazil. *Hydrobiologia* 702: 115–127.
- Butcher, R. W., 1932. Studies on the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river bed. *Annals of Botany* 46(4): 813–861.
- Çelik, K. & T. O. Sevindik, 2015. The phytoplankton functional group concept provides a reliable basis for ecological status estimation in the Çaygören Reservoir (Turkey). *Turkish Journal of Botany* 39(4): 588–598.
- des Cilleuls, J. L. 1928. Le phytoplancton de la Loire et de ses affluents dans la région Saumuroise. Thèse de doctorat.
- Descy, J. P. & C. Mouvet, 1984. Impact of the Tihange nuclear power plant on the periphyton and the phytoplankton of the Meuse River (Belgium). *Hydrobiologia* 119(2): 119–128.
- Descy, J.-P., M. Leitao, E. Everbecq, J. S. Smits & J.-F. Delière, 2011. Phytoplankton of the River Loire, France: a biodiversity and modelling study. *Journal of Plankton Research* 34: 120–135.
- Devercelli, M., 2006. Phytoplankton of the middle Paraná river during an anomalous hydrological period: a morphological and functional approach. *Hydrobiologia* 563(1): 465–478.
- Devercelli, M., 2010. Changes in phytoplankton morpho-functional groups induced by extreme hydroclimatic events in the Middle Paraná River (Argentina). *Hydrobiologia* 639(1): 5–19.
- Devercelli, M. & I. O'Farrell, 2013. Factors affecting the structure and maintenance of phytoplankton functional groups in a nutrient rich lowland river. *Limnologica* 43(2): 67–78.
- Farahani, F., H. Korehi, S. Mollakarami & S. Skandari, 2006. Phytoplankton diversity and nutrients at the Jajerood River in Iran. *Pakistan Journal of Biological Sciences* 9(9): 1787–1790.
- Frau, D., J. Medrano, C. Calvi & A. Giorgi, 2019. Water quality assessment of a neotropical pampean lowland stream using a phytoplankton functional trait approach. *Environmental Monitoring and Assessment* 191(11): 681. <https://doi.org/10.1007/s10661-019-7849-6>.
- Garnier, J., G. Billen & M. Coste, 1995. Seasonal succession of diatoms and Chlorophyceae in the drainage network of the Seine River: observations and modeling. *Limnology and Oceanography* 40(4): 750–765.
- Gosselain, V. & J.-P. Descy, 2000. Phytoplankton of the River Meuse (1994–1996): form and size structure analysis. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 27(2): 1031.
- Gosselain, V., J.-P. Descy & E. Everbecq, 1994. The phytoplankton community of the River Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. *Hydrobiologia* 289(1): 179–191.
- Grime, J. P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Hambright, K. D. & T. Zohary, 2000. Phytoplankton species diversity control through competitive exclusion and physical disturbances. *Limnology & Oceanography* 45(1): 110–122.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75(1): 3–35.
- Istvánovics, V. & M. Honti, 2011. Phytoplankton growth in three rivers: the role of meroplankton and the benthic retention hypothesis. *Limnology & Oceanography* 56(4): 1439–1452.
- Kiss, K. T., 1996. Diurnal change of planktonic diatoms in the River Danube near Budapest (Hungary). *Algalogical Studies, Archiv für Hydrobiologie, Supplement Volumes* 80: 113–122.
- Kofoid, C. A., 1908. The plankton of the Illinois River, 1894–1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part II. Constituent organisms and their seasonal distribution. *Bulletin of the Illinois State Laboratory of Natural History* 6(2): 1–361.
- Köhler, J., 1994. Origin and succession of phytoplankton in a river-lake system (Spree, Germany). *Hydrobiologia* 289(1–3): 73–83.
- Kowalczewski, A. & T. J. Lack, 1971. Primary production and respiration of the phytoplankton of the Rivers Thames and Kennet at Reading. *Freshwater Biology* 1(2): 197–212.
- Kruk, C., E. T. H. M. Peeters, E. H. Van Nes, V. L. M. Huszar, L. S. Costa & M. Scheffer, 2011. Phytoplankton community composition can be predicted best in terms of morphological groups. *Limnology & Oceanography* 56(1): 110–118.
- Kruk, C. & A. Segura, 2012. The habitat template of phytoplankton morphology-based functional groups. *Hydrobiologia* 698(1): 191–202.
- Kruk, C., M. Devercelli, V. L. M. Huszar, E. Hernández, G. Beamud, M. Diaz, L. H. S. Silva & A. M. Segura, 2017. Classification of Reynolds phytoplankton functional groups using individual traits and machine learning techniques. *Freshwater Biology* 62(10): 1681–1692.
- Law, R. J., J. A. Elliott & S. J. Thackeray, 2014. Do functional or morphological classifications explain stream phyto-benthic community assemblages? *Diatom Research* 29(4): 309–324.
- Leland, H. V., 2003. The influence of water depth and flow regime on phytoplankton biomass and community structure in a shallow, lowland river. *Hydrobiologia* 506–509(1–3): 247–255.
- Leitão, M. & A. Lepretre, 1998. The phytoplankton of the River Loire, France: a typological approach. *Verhandlungen des Internationalen Verein Limnologie* 26: 1050–1056.
- Li, Z., F. Fang, J. S. Guo, Z. Y. Sun, Y. B. Chen & M. Long, 2011. Seasonal succession of phytoplankton function groups in the Xiaojiang (Pengxi) River backwater area, Three Gorges Reservoir. *Huan jing ke xue Huanjing kexue* 32(2): 392–400.
- Lindenschmidt, K.-E. & I. Chorus, 1998. The effect of water column mixing on phytoplankton succession, diversity and similarity. *Journal of Plankton Research* 20(10): 1927–1951.
- Margalef, R., 1960. Ideas for a synthetic approach to the ecology of running waters. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 45(1): 133–153.

- Margalef, R., 1958. Temporal succession and spatial heterogeneity in phytoplankton. In Buzzati-Traverso, A. A. (ed.), *Perspectives in marine biology*. University of California Press, Berkeley: 323–349.
- McCormick, P. V., 1996. Resource competition and species coexistence in freshwater benthic algal assemblages. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, San Diego: 229–252.
- Mihaljević, M., F. Stević, J. Horvatić & B. Hackenberger Kutuzović, 2009. Dual impact of the flood pulses on the phytoplankton assemblages in a Danubian floodplain lake (Kopački Rit Nature Park, Croatia). *Hydrobiologia* 618(1): 77–88.
- Mischke, U., G. Wolfram, J. VanWichelen, D. Hlubíková, D. Belkinova, L. Opatrilova, S. Birk, K. Piirsoo, I. Stanković, G. Várbió, G. Borics, J. Jekabsone, J. Stankeviciene, T. Virbickas, J. Picińska-Fattynowicz, P. Panek, N. Rotaru, R. Garbea, M. Placha, 2016. XGIG Large River Intercalibration Exercise-Milestone 6 Report Intercalibrating the national classifications of ecological status for very large rivers in Europe Biological Quality Element: Phytoplankton 2. Version. pp. 157.
- Moura, A., J. Severiano, N. Tavares & E. Dantas, 2013. The role of a cascade of reservoirs and seasonal variation in the phytoplankton structure in a tropical river. *Brazilian Journal of Biology* 73: 291–298.
- Nabout, J. C., I. S. Nogueira & L. G. Oliveira, 2006. Phytoplankton community of floodplain lakes of the Araguaia River, Brazil, in the rainy and dry seasons. *Journal of Plankton Research* 28(2): 181–193.
- Naselli-Flores, L. & R. Barone, 2011. Fight on plankton! or, phytoplankton shape and size as adaptive tools to get ahead in the struggle for life. *Cryptogamie, Algologie* 32(2): 157–204.
- Nogueira, M., M. Ferrareze, M. Moreira & R. Gouvêa, 2010. Phytoplankton assemblages in a reservoir cascade of a large tropical-subtropical river (SE, Brazil). *Brazilian Journal of Biology* 70(3): 781–793.
- Padisák, J., G. Borics, I. Grigorszky & É. Soróczki-Pintér, 2006. Use of phytoplankton assemblages for monitoring ecological status of lakes within the Water Framework Directive: the assemblage index. *Hydrobiologia* 553(1): 1–14.
- Padisák, J., L. Crossetti & L. Naselli-Flores, 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia* 621(1): 1–19.
- Passy, S. I., 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. *Aquatic Botany* 86(2): 171–178.
- Passy, S. I. & C. A. Larson, 2019. Niche dimensionality and herbivory control stream algal biomass via shifts in guild composition, richness, and evenness. *Ecology* 100(11): e02831. <https://doi.org/10.1002/ecy.2831>.
- Piirsoo, K., 2001. Phytoplankton of Estonian rivers in mid-summer. *Hydrobiologia* 444(1–3): 135–146.
- Piirsoo, K., P. Pall, A. Tuvikene, M. Viik & S. Vilbaste, 2010. Assessment of water quality in a large lowland river (Narva, Estonia/Russia) using a new Hungarian potamoplanktic method. *Estonian Journal of Ecology* 59(4): 243–258.
- Reinhard, E. G., 1931. *The Plankton Ecology of the Upper Mississippi, Minneapolis to Winona*. Ecological Monographs 1(4): 395–464.
- Reynolds, C. S., 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. *Freshwater Biology* 14(2): 111–142.
- Reynolds, C. S., 1994a. The role of fluid motion in the dynamics of phytoplankton in lakes and rivers. In Giller, P. S., A. G. Hildrew & D. Raffaelli (eds), *Ecology of Aquatic Organisms: Scale, Pattern, Process*. Blackwell Scientific Publications, Oxford: 141–187.
- Reynolds, C. S., 1994b. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia* 289(1–3): 9–21.
- Reynolds, C. S. & J. P. Descy, 1996. The production, biomass and structure of phytoplankton in large rivers. *Archiv für Hydrobiologie, Supplementband Large Rivers* 10(1–4): 161–187.
- Reynolds, C. S. & M. S. Glaister, 1993. Spatial and temporal changes in phytoplankton abundance in the upper and middle reaches of the River Severn. *Large Rivers* 9(1): 1–22.
- Reynolds, C. S., 1987. Community organization in the freshwater plankton. In Gee, J. H. R. & P. S. Giller (eds), *Organization of Communities, Past and Present*. Blackwell Scientific Publications, Oxford: 297–325.
- Reynolds, C. S., 1988. Potamoplankton: paradigms, paradoxes and prognoses. In Round, F. E. (ed.), *Algae and the Aquatic Environment*. Biopress Ltd, Bristol: 285–311.
- Reynolds, C. S., 1997. *Vegetation Processes in the Pelagic: A Model for Ecosystem Theory*. Ecology Institute, Oldendorf/Luhe.
- Reynolds, C. S., 2003. Planktic community assembly in flowing water and the ecosystem health of rivers. *Ecological Modelling* 160(3): 191–203.
- Reynolds, C. S., 2005. Expert judgement of phytoplankton composition-functional groups. In Solheim, A. L. (ed) *Reference conditions of European lakes: Indicators and methods for the Water Framework Directive assessment of reference conditions*. REBECCA, version 5: 2005/30/12, pp. 90–104.
- Reynolds, C. S., 2006. *Ecology of Phytoplankton*. Cambridge Univ. Press, Cambridge.
- Reynolds, C. S., P. A. Carling & K. J. Beven, 1991. Flow in river channels: new insights into hydraulic retention. *Archiv für Hydrobiologie* 121(2): 171–179.
- Reynolds, C. S., J. P. Descy & J. Padisák, 1994. Are phytoplankton dynamics in rivers so different from those in shallow lakes? *Hydrobiologia* 289(1): 1–7.
- Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research* 24(5): 417–428.
- Rimet, F. & A. Bouchez, 2012. Life-forms, cell-sizes and ecological guilds of diatoms in European rivers. *Knowledge and Management of Aquatic Ecosystems* 406: 1–14.
- Rojo, C., M. A. Cobelas & M. Arauzo, 1994. An elementary, structural analysis of river phytoplankton. *Hydrobiologia* 289(1): 43–55.

- Salmaso, N. & J. Padisák, 2007. Morpho-Functional Groups and phytoplankton development in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). *Hydrobiologia* 578(1): 97–112.
- Salmaso, N., L. Naselli-Flores, & J. Padisák, 2015. Functional classifications and their application in phytoplankton ecology. *Freshwater Biology* 60(4): 603–619.
- Soares, M. C. S., V. L. M. Huszar & F. Roland, 2007. Phytoplankton dynamics in two tropical rivers with different degrees of human impact (southeast Brazil). *River Research and Applications* 23(7): 698–714.
- Soylu, E. N. & A. Gönülol, 2003. Phytoplankton and seasonal variations of the River Yeşihrmak, Amasya, Turkey. *Turkish Journal of Fisheries and Aquatic Sciences* 3: 17–24.
- Stanković, I., T. Vlahović, M. Gligora Udovič, G. Várbíró & G. Borics, 2012. Phytoplankton functional and morpho-functional approach in large floodplain rivers. *Hydrobiologia* 698(1): 217–231.
- Stević, F., M. Mihaljević & D. Špoljarić, 2013. Changes of phytoplankton functional groups in a floodplain lake associated with hydrological perturbations. *Hydrobiologia* 709(1): 143–158.
- Stoyneva, M. P., 1994. Shallows of the lower Danube as additional sources of potamoplankton. *Hydrobiologia* 289(1): 171–178.
- Talling, J. F. & J. Ržóska, 1967. The development of plankton in relation to hydrological regime in the Blue Nile. *The Journal of Ecology* 55(3): 637–662.
- Tapolczai, K., A. Bouchez, C. Stenger-Kovács, J. Padisák & F. Rimet, 2016. Trait-based ecological classifications for benthic algae: review and perspectives. *Hydrobiologia* 776(1): 1–17.
- Thorp, J. H., M. C. Thoms & M. D. DeLong, 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22(2): 123–147.
- Tian, Y., B. Huang, C. Yu, N. Chen & H. Hong, 2014. Dynamics of phytoplankton communities in the Jiangdong Reservoir of Jiulong River, Fujian, South China. *Chinese Journal of Oceanology and Limnology* 32(2): 255–265.
- Townsend, S. A., 2006. Hydraulic phases, persistent stratification, and phytoplankton in a Tropical Floodplain Lake (Mary River, Northern Australia). *Hydrobiologia* 556(1): 163–179.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37(1): 130–137.
- Várbíró, G., É. Ács, G. Borics, K. Érces, G. Fehér, I. Grigorszky, T. Jappott, G. Kocsis, E. Krasznai, K. Nagy, Z. Nagy-László, Z. Pilinszky & K. T. Kiss, 2007. Use of self organizing maps (SOM) for characterization of riverine phytoplankton associations in Hungary. *Archiv für Hydrobiologie, Supplementband Large rivers* 17(3–4): 383–394.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier, 2007. Let the concept of trait be functional! *Oikos* 116(5): 882–892.
- Wang, C., V. B-Béres, C. Stenger-Kovács, X. Li & A. Abonyi, 2018. Enhanced ecological indication based on combined planktic and benthic functional approaches in large river phytoplankton ecology. *Hydrobiologia* 818(1): 163–175.
- Wang, L., Q. Cai, Y. Xu, L. Kong, L. Tan & M. Zhang, 2011. Weekly dynamics of phytoplankton functional groups under high water level fluctuations in a subtropical reservoir-bay. *Aquatic Ecology* 45(2): 197–212.
- Welch, P. S., 1952. *Limnology*. McGraw-Hill Book Company, New York.
- Whitton, B. A., 1975. *Algae. River Ecology*. B. A. Whitton. Oxford, Blackwell Scientific Publications. vol. 2: 81–105.
- Yang, M., Y. Bi, J. Hu, K. Zhu, G. Zhou & Z. Hu, 2011. Seasonal variation in functional phytoplankton groups in Xiangxi Bay, Three Gorges Reservoir. *Chinese Journal of Oceanology and Limnology* 29(5): 1057–1064.
- Zacharias, O., 1898. *Das Potamoplankton*. *Zoologischer Anzeiger* 21(550): 41–48.
- Zhu, K., Y. Bi & Z. Hu, 2013. Responses of phytoplankton functional groups to the hydrologic regime in the Daning River, a tributary of Three Gorges Reservoir, China. *Science of the Total Environment* 450–451: 169–177.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.