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The role of some abiotic factors in shaping the phytoplankton biomass and niche characteristics of the phytoplankton functional groups in rivers of the Carpathian Basin

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”In dealing with any aspect of limnology, as perhaps any other branch of science, it is impossible to avoid the thought that no work is perfect and that the greater proportion of published investigations are very imperfect indeed. Every one of us is at fault in some way or another, every one of us must attempt to achieve progressively higher standards in accuracy, scope and imagination.” G. E. Hutchinson”
[The Prospect Before Us (1963)]

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Abbreviations

Codon/Coda: letters referring to the given functional groups of phytoplankton proposed by Reynolds et al. (2002)
BOD5: Biological oxygen demand of 5 days
Chl-a: Chlorophyll-*a*
CDSR: Cumulative daily solar radiation values for 1-60 days
COD_{Cr}: Chemical oxygen demand using dichromate method for determination
COND: Water conductivity
DLE: Days of light exposure
DSR: Sum of daily solar radiation
FG: Functional group of phytoplankton (Reynolds et al., 2002)
FGs: Functional groups of phytoplankton (Reynolds et al., 2002)
NH_4-N: Ammonium nitrogen **(**dissolved**)**
NO_2-N: Nitrite nitrogen (dissolved)
NO_3-N: Nitrate- nitrogen (dissolved)
nMDS: Non-metric multidimensional scaling
Inertia: Variability of species niches
OMI: Outlying Main Index
ORTOP: Orto-phosphate phosphorus (dissolved)
PAR: Photosynthetically Active Radiation (spectral range of 400-700 nm)
PCA: Principal Component Analysis
Q: Water discharge
RTOL: Residual tolerance referring to tolerance of phytoplankton functional groups
Si: **S**ilica (dissolved)
TN: Total nitrogen (dissolved)
TOL: Tolerance of the phytoplankton functional groups
TP: Total Phosphorus (dissolved)
TSM: Total Suspended Solids-Total-Suspended Materials
TW: Water temperature
WRT: Theoretical water residence time
Z_{eu}/Z_{mix}: Euphotic layer/ mixed layer ratio

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Abstract

Niche concept *sensu* Hutchinson and phytoplankton functional group (FG) concept *sensu* Reynolds can be considered as cornerstones of phytoplankton ecology. An increasing number of papers use these concepts to better understand the processes that govern diversity and the functioning of phytoplankton assemblages, both in rivers and lakes. The importance of underwater light on phytoplankton biomass has been also studied intensively by using a wide array of methodological approaches. One of the main objectives of my studies was to assess the effects of cumulative daily solar radiation (CDSR) on spatiotemporal dynamics of phytoplankton biomass in the rhithral and potamal rivers of the Carpathian Basin. Moreover, the influence of theoretical water residence time (WRT) on this relationship has also been investigated. The other main objective of the study was to define by using the Outlying Main Index (OMI) method, the niche space characteristics, breadth and position of phytoplankton FGs for rivers of the same area. Furthermore, I aimed to investigate the role of niche space characteristics in the regional occupancy of FGs. OMI method proved to be suitable for identifying riverine FGs niche position and tolerance ranges in the niche space defined by the considered environmental variables. For both studies, large datasets were used, including data on daily solar radiation for a 1–60-day period, theoretical water residence time, chlorophyll-*a* concentration (Chl-*a* ,i.e. used as a proxy of biomass), relative biomass of FGs, trophic, hydrological, and physico-chemical variables respectively. A priory to analyses some main hypothesises were formulated.

The major findings of the Thesis are the followings:

- CDSR-Chl-*a* relationships were found to be significant for the majority of rivers with different order numbers (except rivers with short residence time), and two main shapes of CDSR- Chl-*a* relationship were described;
    i. CDSR-Chl-*a* relationship was found as unimodal for rhithral rivers (i.e. with coarse substrate);
    ii. CDSR-Chl-*a* relationship showed a steady increase for larger, potamal rivers (with fine substrate).
- CDSR-Chl-*a* relationship was significantly influenced by longer WRT, even when residence time was shorter than the cumulative solar radiation period.
- The niche space of the FGs in rivers could be defined by the numerical characterisation of FGs niche position and breadth and are influenced primarily by trophic and hydrological variables.

- Phytoplankton FGs could be clustered in six Niche Groups in rivers.
- Regional distribution of FGs was similarly influenced by their niche position and niche breadth and their role in regional distribution of FGs can be separated.
- The hypothesis, that FGs with central positions will have a wide breadth niche, while those with marginal positions will have a narrow niche breadth was not supported by the results.
- OMI analysis reveals that the niche position of several FGs differed from that suggested their habitat templates defined in lakes.

In summary, my present study leads to two conclusions:

1. first, the residence time of water and the incoming solar radiation has a pronounced impact on the spatio-temporal changes of phytoplankton biomass in rivers,
2. second, several FGs *sensu* Reynolds have well-defined but slightly different positions in the riverine niche space than their suggested habitat templates in lakes, and both characteristics play a similarly important role in the regional distribution of the FGs.

Összegzés

Hutchinson niche elmélete, valamint Reynolds fitoplankton funkcionális csoport koncepciója a fitoplankton ökológia sarokköveinek tekinthetők. Folyamatosan bővül azon tanulmányok száma, melyek ezen elméleti alapokra támaszkodva igyekeznek feltárni azon folyamatokat, amelyek tavi és a folyóvízi fitoplankton közösségek működésének dinamikáját és sokféleségét szabályozzák.

Számos, különböző módszertani megközelítéssel tanulmányozták a vízalatti fényviszonyok fitoplankton biomasszára kifejtett hatását is. Kutatásaim egyik fő célkitűzésként a kumulatív napsugárzás (KNS) folyóvízi fitoplankton biomassza tér- és időbeli dinamikára kifejtett hatását vizsgáltam a Kárpát-medence ritrális és potamális folyóiban. Továbbá célkitűzésem volt annak a meghatározása, hogy a víz tartózkodási idejének változása (VTI) hogyan befolyásolja a fitoplankton biomassza KNS függvényében történő változását. Kutatásom másik fő célkitűzéseként fogalmaztam meg, hogy az Outlying Main Index (OMI) módszert használva meghatározzam ugyanazon vizsgálati területre vonatkozóan a folyóvízi fitoplankton funkcionális csoportok (FCs-k) niche terének a fő jellegzetességet, a niche tér szélességét és a niche pozícióját. További célkitűzésem volt annak vizsgálata, hogy milyen szerepet töltenek be a niche tér jellemzők a FCs-k regionális elterjedésében. Az OMI-módszer alkalmasnak bizonyult a folyami FCs-k niche tér pozíciójának és tolerancia tartományának azonosítására a vizsgált környezeti tényezők által meghatározott niche térben.

A kutatások nagy méretű adatbázisok felhasználásával történtek és az elsőre vonatkozóan tartalmazták a VTI, az 1-60 nap időszakra vonatkozó KNS, a klorofill-a (Kl-*a*) koncentráció (biomassza proxyként használva) adatokat. A második kutatás tekintetében tartalmazták a FCs-k relatív biomassza adatait, valamint a tápanyagokra, a hidrológiai viszonyokra, és a fizikai és a kémiai változókra vonatkozó adatokat. A vizsgálatokat megelőzően hipotéziseket is megfogalmaztunk.

Az értekezés főbb megállapításai a következők:

- A különböző rendűségű folyóvizek többségénél a KNS-Chl-*a* közötti összefüggés szignifikánsnak bizonyult (kivéve a rövid tartózkodási idejű folyókat) és két fő jelleggörbével jellemezhető:
    i. A ritrális köves aljzatú folyóknál a KNS-Kl-*a* összefüggés unimodális jellegű,
    ii. a potamális, finom mederanyaggal jellemezhető nagy folyóknál a KNS-Kl-*a* összefüggés fokozatosan emelkedő jelleget mutatott.

- KNS-Chl-*a* közötti összefüggést a hosszabb tartózkodási idő (VTI) szignifikánsan befolyásolta még a KNS <VTI esetekben is.
- A folyókban a FCs-k niche terét a niche tér pozíció és szélesség (toleranciatartomány) számszerű jellemzésével lehetett meghatározni, és a niche tér jellemzőket elsősorban trofikus és hidrológiai változók befolyásolták.
- A fitoplankton FCs-k a folyókra vonatkozóan hat fő niche csoportba lehetett besorolni.
- A funkcionális csoportok regionális elterjedését a niche tér helyzete és szélessége (toleranciatartománya) szignifikánsan befolyásolta, azonban regionális elterjedésükben betöltött szerepük szétválaszható.
- A hipotézist, mely szerint a centrális helyzetű FCs-k széles, míg a marginális helyzetűek keskeny toleranciájú niche térrel rendelkeznek nem lehetett igazolni.
- Az OMI elemzés rámutatott arra, hogy számos FCs-k niche terének helyzete eltér attól a helyzettől amelyre a tavakra meghatározott élőhely mintázatuk alapján következtetni lehetett.

Eredményeimet összefoglalva az alábbi két következtetés vonható le a vizsgálataimból:

1. elsősorban, a folyókban a víz tartózkodási ideje és a beérkező napsugárzás jelentős hatást gyakorol a fitoplankton biomassza tér-időbeli változásaira,
2. másodsorban, a folyóvízi niche térben a Reynolds-féle FCs-k jól meghatározott pozícióval rendelkeznek amely kissé eltér attól a helyzettől melyekre a tavakra leírt habitát mintázat alapján számítani lehetett, valamint mindkét niche jellegzetesség hasonlóan szignifikáns szerepet játszik a funkcionális csoportok regionális eloszlásában.

Rezumat

Conceptul de nișă, așa cum îl definește Hutchinson și, cel al grupului funcțional de fitoplancton, așa cum îl definește Reynolds, se pot considera puncte de cotitură în ecologia fitoplanctonului. Un număr tot mai mare de publicații se bazează pe aceste concepte pentru o mai bună înțelegere a proceselor care guvernează diversitatea și funcționarea comunităților fitoplanctonice, atât în râuri, cât și în lacuri. De asemenea, s-au efectuat studii utilizându-se o mare varietate de metode studiind efectul luminii din columna apei asupra biomasei fitoplanctonului. Unul dintre principalele obiective ale studiilor a fost evaluarea efectelor radiației solare zilnice cumulate (RSZC) asupra dinamicii spațio-temporale a biomasei phytoplanctonului din râurile de tip rhitrhal si potamal al Bazinului Carpatic. Mai mult decât atât, am investigat influența timpului teoretic de retenție a apei (TRA) asupra acestei relații. Celălalt obiectiv principal al studiilor a fost acela de a defini, prin utilizarea metodei Outlying Main Index (OMI), caracteristicile spațiului de nișă, lățimea și poziția al grupurilor functionale fitoplanctonice (GFe) pentru râurile din aceeași zonă. Metoda OMI s-a dovedit a fi potrivită pentru identificarea poziției nișelor GFe și a intervalelor de toleranță în spațiul nișei, determinate de variabilele de mediu luate în considerare. Pentru ambele studii au fost folosite baze mari de date. Prima basa de date a inclus date despre radiațiile solare zilnice cumulate pe o perioadă de 1-60 zile, timpul teoretic de retenție a apei și a concentrației de Chl-*a* (mod de estimare a biomasei), iar a doua date despre biomasa relativă a GFe, variabile de troficitate, hidrologice și fizico-chimice. Unele scopuri principale și ipoteze au fost formulate înaintea analizelor.

Cele mai importante concluzii ale acestei teze de doctorat sunt următoarele;

- Relația RSZC-Chl-*a* este semnificativă pentru majoritatea diferitelor tipuri de râuri (excepție fiind râurile cu timp scurt de retenție), și au fost descrise două forme principale a relației RSZC-Chl-*a*:

i. Relația RSZC-Chl-*a* a arătat o formă unimodală pentru râurile rhithrale cu substrat grosier.

ii. Relația RSZC-Chl-*a* a arătat o creștere treptată în cazul râurilor mai mari potamale, avînd în general un substrat fin.

- Relația RSZC-Chl-*a* a fost influențată semnificativ de TRA mai lung, chiar și atunci când timpul de rezidență a fost mai scurt decât perioada cumulativă a radiației solare.

- Spațiul de nișă al GFe fluviale putea fi determinată prin caracterizarea numerică a poziției și lățimi a nisei grupurilor funcționale fiind delimitate în primul rând de variabilele trofice și hidrologice.
- GFe fitoplanctonului din râuri pot fi impărțite în șase grupuri de nișe.
- Rezultatele obținute nu au confirmat ipoteza conform căreia GF cu poziție centrală ar avea o nișă de lățime mare iar cele cu poziție marginală una de lățime ingustă.
- Distribuția regională a GFe fost influențată în mod similar de poziția lor de nișă și de lățimea nișei, iar rolul lor în distribuția regională a GFe poate fi separat.
- Analiza OMI a arătat că poziția nișelor GFe a fost diferită față de ce au sugerat modelele lor de habitat pentru lacuri.

Rezumând , studiul meu de față conduce la două concluzii:

1. în primul rând, timpul de retenție a apei și radiațiile solare au un impact semnificativ asupra schimbărilor spațio-temporale ale biomasei fitoplanctonice din râuri,
2. și al doilea rând, multe GFe sensu Reynolds au poziții bine definite în spațiul de nișă fluvial dar puțin diferite față de cele sugerate de characteristicile habitatelor descrise pentru lacuri, și ambele caractere de nisă au un rol significant in distribuția regională al grupurilor funcționale.

1 Introduction

1.1 Motivation

I have been working for almost twenty years in a Regional Environmental Laboratory, where my task was to assess the quality of surface waters in the lower Tisza valley (Hungary). During my work, I studied thousands of river phytoplankton samples (collected mainly from River Tisza, Hármas-Körös and Maros) and encountered interesting questions related to the composition and development of the planktic assemblages. Although earlier I have been involved in several scientific projects, I had the opportunity to immerse myself in scientific research, when I joined the Doctoral School of Chemistry and Environmental Science of the University of Pannonia in 2015 as a PhD student. During my PhD studies, I focused my attention on understanding the relevant drivers that shape river phytoplankton assemblages, both in terms of their composition and biomass. I was especially interested in the possible extension of the niche concept to the higher organisation levels such as the FGs *sensu* Reynolds.

1.2 Structure of the thesis

My dissertation is based on two papers. In the first study, I describe the impact of direct solar radiation and water residence time on riverine phytoplankton biomass. In the second part, I summarize the results of the study in which I defined the habitat template of the phytoplankton functional groups *sensu* Reynolds, using a niche-based approach and the influence of niche characteristics on the regional distribution of the phytoplankton functional groups (FGs).

1.3 Literature review

1.3.1 Types and terminology of phytoplankton

Phytoplankton includes all microscopic algae and cyanobacteria that spend a considerable (or the entire) part of their lifecycle floating in the water column. Albeit some groups are motile because they have special organelles or mechanisms to control their buoyancy, the position of algae in the water is primarily controlled by water currents, especially in a lotic environment (Reynolds, 2006). Phytoplankton is usually divided into subgroups according to their size and their habitat preferences (Sieburth et al., 1978).

Based on the size of the algae the following groups can be distinguished:

- picophytoplankton (0.2-2 µm) - unicellular cyanobacteria and eukaryotic algae,
- nanophytoplankton (2-20 µm) - most freshwater algal taxa,
- microphytoplankton (20-200 µm) – many freshwater unicellular, or colonial, coenobium-forming eukaryotic algae,
- mezophytoplankton (200-2000 µm) -larger colonial, coenobial or filamentous taxa,
- macrophytoplankton (> 2000 µm) largest filamentous cyanobacteria and algal taxa.

Based on their life history strategy “phytoplankton” can be separated into two categories:

- euplanktic algae spend their entire life cycle in the water column,
- tychoplanktic forms spend most of their life cycle attached to different substrates, but due to mechanical constraints can be entrained into the water column, switching to planktic life.

The term meroplankton has been used for the group of algae that spend most of their life on the sediment surface but due to wind actions and turbulent mixing, they can be easily resuspended (Stoyneva, 1994; Reynolds, 2006; Istvánovics and Honti, 2011). This term is almost identical to the tychoplankton, but in shallow lakes, the benthic and planktic life strategies can periodically change, and the lakes have also, so-called meroplanktic dynamics (Padisák and Dokulil, 1994).

In terms of their habitat preferences phytoplankton of rivers can also be separated into subgroups:

- Zacharias (1898) who was one of the first pioneers of riverine phytoplankton research, showed that the largest rivers can support the development of specific riverine phytoplankton, and proposed the name “potamoplankton” for these assemblages,

- The term rheoplankton has been also used as a synonym of potamoplankton (Eddy, 1934; Lackey, 1941; Borics et al., 2007),
- During the last decades, the expression rhithroplankton appeared in the literature, referring to the planktic assemblages' characteristic for the detached algal communities of the upper river segments (Bolgovics et al., 2017).

Overviewing the terminology shown above, I propose to use rheoplankton as a general term for the phytoplankton of watercourses, rhithroplankton for the plankton in the upper, and potamoplankton for that of the lower river segments.

1.3.2 Source of the riverine phytoplankton

An important field of riverine phytoplankton research is related to the question of what the possible sources of planktic elements are. Even in the early stages of riverine phytoplankton research, it was demonstrated that the primary sources of phytoplankton are the upstream stretches of rivers and the bordering lakes and oxbows (Zacharias, 1898; Eddy, 1934). Wawrik (1968) investigated the origin of phytoplankton species in the Danube and found that the phytoplankton of the river is mostly of autochthonous origin. According to other authors (Czernin-Chudenitz, 1966; Istvánovics et al., 2012), adjacent backwaters and dead arms that are permanently or temporarily connected with the main channel are important allochthonous sources of the riverine phytoplankton. On the other hand, the other "inner" source of potamoplankton is the phytobenthos, characteristic of the rhithral (i.e. upper) rivers or river sections (Butcher, 1940; Blum, 1956; Istvánovics and Honti, 2011; Bolgovics et al., 2017). Benthic algae detached from rhithral substrates are usually the dominant elements of phytoplankton of the upper river segments (Rojo et al., 1994; Reynolds and Descy, 1996). According to the meroplankton hypothesis (Istvánovics and Honti, 2011), benthic diatoms settled earlier in shallows of rivers, (and where the favourable light condition support an enhanced growth rate) can be easily resuspended in the water column due to the gas bubbles released by bentic algae during their photosynthesis and by small flood pulses (Istvánovics and Honti, 2011). Stoyneva (1994) also concluded that retention zones (shallows or stagnant water sections, bays) formed in natural rivers serve as significant sources of potamoplankton. The proportion of these retention zones can reach as much as 10-20% of the whole river surface in case of some rivers (Reynolds, 2000).

1.3.3 Main abiotic factors shaping the spatio-temporal structure and biomass of the riverine phytoplankton

The role of planktic algae as primary producers is unquestionable as phytoplankton from the Global Ocean produces about half of the organic matter and oxygen of the Earth (Field et al., 1998) and is responsible for more than the half of the global dinitrogen fixation (Naselli-Flores and Padisák, 2022). They have a key role in shaping the composition of the biota of aquatic ecosystems, not only by producing organic carbon and providing a primary food source for herbivorous grazers (Wehr and Descy, 1998) but also by creating complex interactions with the environment. Therefore, there is an obvious need to understand the driving constraints of phytoplankton dynamics both in lakes and rivers. A significant amount of knowledge has been accumulated concerning phytoplankton dynamics and ecology in lacustrine environments. Several models were published on the phytoplankton succession (Sommer et al., 1986; Sommer, 1989), on the development of phytoplankton biomass (reviewed in Phillips et al., 2008), or on the mechanisms that drive phytoplankton diversity (Hutchinson, 1961; Roy and Chattopadhyay, 2007). This focused the attention of ecologists on the research of the lacustrine ecosystems, not surprisingly at a time when Limnology was a leading science branch of Ecology. During the early phase of the limnological research history, lakes were considered as almost closed ecosystems with rapid changes in their biota that made them ideal for ecological studies (Rigler and Peters, 1995).

Compared to lakes, much less information is available about the ecology of phytoplankton in riverine ecosystems (Reynolds, 2000). The earliest papers dealing with riverine phytoplankton focused mostly on taxonomic composition and seasonal changes of potamoplankton of some rivers in North America and Europe (Egerton, 2014). It has been recognized that the seasonal distribution of phytoplankton in rivers changes cyclically (Fritsch 1902, 1903, 1905; Kofoid, 1903, 1908; Coffing 1937). Eddy (1934) published a monograph summarising the most important results of the previous studies on the riverine rheoplankton, and describing the seasonal patterns and dynamics of riverine phytoplankton assemblages. He argued that most of the river’s diatom taxa dominate during winter which is followed by diatom-chrysophyte assemblages in spring. In summer, besides diatoms, the number of green algal taxa increases and by the end of summer green algae, euglenophytes and blue-green algal taxa reach their maximum diversity. Diatom dominance appears again, and by the end of autumn, the overall biomass of phytoplankton decreases. The first efforts to clarify the role of some abiotic variables in the seasonal compositional changes of riverine assemblages also appeared in this study. Some authors highlighted the importance of seasonal changes in water temperature (Allen, 1920; Roach, 1932) as a crucial factor influencing the taxonomical and biomass dynamics of rheoplankton. Eddy (1934) in his monograph highlighted the complex effect of temperature, underlining that the variation in temperature and some physical properties of water influences the reproduction rate of algae. Other limnologists demonstrated that nutrients (Pearsall, 1923, 1932), and light climate (Whipple, 1896; Purdy, 1922) are also crucial in the annual cycle of potamoplankton. Wiebe (1931) concluded that increments in algal numbers were related to dissolved phosphorus (P) concentrations. Hupp (1943) argued that increments in diatom cell numbers are accompanied by the higher level of dissolved oxygen (O_2), pH, and temperature, and lower concentrations of dissolved nutrients (nitrogen and phosphorus forms), silicon (Si) and carbon dioxide (CO_2). Some important conclusions were also made in this study regarding the relationship between the hydrological and morphological characteristics of rivers and the composition and abundance of phytoplankton biomass.

It was also highlighted that some hydrological factors, like, current velocity and water discharge (Q) are among the most important environmental constraints of potamoplankton biomass (Allen, 1920). The maximum phytoplankton biomass is reached in summer when usually the lowest discharge prevails (Coffing, 1937; Hupp, 1943). In turn, Kofoid (1903) concluded that at least 7-9 days of riverine water residence time (WRT) is required for the formation of a permanent potamoplankton community. Water residence time is the time frame (expressed in days) that is needed for a water parcel to travel the distance between the river source and a given point of the river. Eddy found that rivers with a WRT shorter than 20 days can hardly support a permanent phytoplankton assemblage (Eddy, 1934). Dam construction and river bed regulations also changed the taxonomic composition and spatial distribution of phytoplankton (Galtsoff, 1921). In summary, it can be stated that by the middle of the twentieth century, the most important abiotic constraints shaping the composition and biomass of riverine phytoplankton (i.e. rheoplankton) were identified and some important roles of those factors were already clarified.

Since the end of the 19th century, rivers have been the subject of significant industrial, communal and agricultural pollution worldwide. Accordingly, several researchers focused on the effects of anthropogenic pollution (Kolkwitz and Marsson, 1902, 1908; Kolkwitz, 1912; Blum, 1956). The overall conclusion of the research was that each kind of pollution mentioned above change the natural composition and biomass of riverine phytoplankton. While the most severe industrial pollution could dramatically decrease the diversity and biomass of algal communities, agricultural and domestic pollutants could have even a contrary effect on algal biomass and taxonomical diversity (Brinley, 1942; Butcher, 1947; Blum, 1956). The first phytoplankton-based water quality assessment system had been based on the observations in longitudinal changes of riverine phytoplankton communities affected by different kinds and levels of pollution (Kolkwitz and Marsson, 1908; Pantle and Buck, 1955; Zelinka and Marvan, 1961). Moreover, it was demonstrated that in the middle and lower sections of temperate rivers algal growth could not deplete the nutrient pools of the rivers (Blum 1956; Reynolds, 1994). This is understandable because rivers are open systems, whose lower sections receive regular nutrient supplies from the upper catchment areas and the accompanying floodplains. Nutrient concentrations in these rivers are orders of magnitude higher than those considered limiting for algal growth (Borics, 2015). Finally, it is important to mention that anthropogenic activities (e.g.: channelization, dam construction etc.) heavily impacted the natural riverscapes by altering hydro- and geomorphological characteristics of rivers with severe consequences on their ecosystems, biotic composition and functional properties (Dynesius and Nilsson, 1994). Recent studies highlighted that two third of the Earth largest rivers were affected moderately or severely by such activities (Grill et al., 2019).

1.3.4 Watershed-based models to explain the composition of the biotic communities

During the last decades, several frameworks were developed to conceptualise the functioning of riverine ecosystems both at river channel and catchment scale. The Stream Zonation Concept (Illies and Botoseanu 1963; Hawkes, 1975), River Continuum Concept (Vannote et al., 1980), Nutrient Spiralling Concept (Newbold et al., 1981), Flood Pulse Concept (Junk and Wantzen, 2004), or Riverine Productivity Model (Thorp and Delong, 1994), Inshore Retention Model (Schiemer et al., 2001) are the most relevant conceptual models that aim to outline a framework within which the main processes of the riverine ecosystems (i.e.: details of the acquisition of energy and nutrient sources, production of organic matter, the role of the floodplain, etc.) can be understood. Some other concepts like the Serial Discontinuity Concept elaborated by Ward and Stanford (1983) or the Cascading Reservoir Continuum Concept (Barbosa et al., 1999) have been developed to meet the unique circumstances generated by the artificial modifications of the hydrology of riverine systems. In their “Riverine Ecosystem Synthesis” Thorp et al. (2006) aimed to combine the above theories to describe the structure and functioning of running freshwater ecosystems.

Besides the above-mentioned large frameworks, several specific models have been developed for predicting temporal and spatial changes of riverine algal associations. Some of these models accurately simulated spatio-temporal variations in the composition and biomass of the potamoplankton of the Thames (Whitehead and Hornberger, 1984), the Seine (Billen et al., 1994; Garnier et al., 1995), and the Meuse (Everbecq et al., 2001). These results are very important steps to refine the role of environmental background variables influencing rheoplankton dynamics in rivers and for evaluating the complex relationships among them (Whitehead et al., 2015). However the results of these models are highly dependent on the range of considered factors and the used statistical methods. Some of them need biotic background variables (Riversthaler model; Billen et al., 1994) that are usually not available for most of the monitored rivers, therefore their applicability is limited.

In my thesis, I focused on two important variables, that are crucial in shaping rheoplankton biomass and have not been addressed in the previous works. These are the water residence time and cumulative solar radiation. Cumulative daily solar radiation(CDSR) is the global daily solar radiation cumulated in a given time period expressed in days and can be calculated by summing up the daily global solar radiation energy characteristic for the given period and location.

1.3.5 The role of water residence time and flow characteristics in shaping riverine phytoplankton

Water movements are characteristic for both lakes and rivers, but the distinctive characteristic between these two realms is the unidirectional flow of water in the river beds which is generated by gravitational forces (Reynolds et al., 1994; Padisák, 2005). This unidirectional flow creates huge differences between the lentic and lotic systems in their basic environmental variables (details are discussed in the classical limnology book of Welch, 1952). One of the essential differences between lakes and rivers is that lentic ecosystems generally have much longer water residence time (Padisák, 2005). This means that lakes in general, provide a more stable environment than even the large potamal rivers having much shorter residence times and share great stochasticity regarding the fluctuation of hydrological constraints (Descy, 1993). Water residence time in lakes is the time frame needed for replacement of the entire water volume of a lake, while in rivers in the time frame (i.e. expressed in days) needed for travelling the water parcel from the river source to the mouth of the river.

Compositional changes and the net increase in phytoplankton biomass depend not only on the local physical and chemical properties of water (e.g., water temperature, light climate, nutrients) but on hydrological factors like turbulence, water velocity and residence time, as well (Reynolds and Descy, 1996). Since time does matter in the development of rheoplankton, it is crucial to know how WRT relates to the doubling time of the elements of phytoplankton. Despite difficulties in measuring the *in vivo* growth rate of different algal species, there are some promising attempts in the literature. Van Steveninck et al. (1992), determined the rate of increase of the algal biomass by monitoring the changes in chlorophyll-*a* (Chl-*a*) concentration in a representative section of the Rhine. Based on their measurements, the amount of planktic chlorophyll-*a* (a proxy measure of algal biomass) increased from 13.8 μg l^{-1} to 132 μg l^{-1} while the water mass travelled 233 km. Based on this, the number of algae per day almost doubled, and this required an average of five hours of sunshine per day. For medium-sized rivers in England (Wye, Bure) and large rivers in Belgium (Meuse), the time required to double the number of algae was estimated to be 2.7–3 days (Jones, 1984; Moss and Balls 1989; Descy and Gosselain, 1994). Studying the effect of water velocity on the growth of the Thames' phytoplankton community, it has been shown that a positive growth rate is typical at water velocities less than 0.3 m s^{-1} (Bowles and Quennel, 1971). Later, regarding phytoplankton dynamics of the Tisza river and some tributaries, it was proved (Istvánovics et al., 2012) that for some planktic diatom, and cryptophyte species, a positive growth rate can occur at even higher 0.5-0.7 m s^{-1} velocities. Nevertheless, increments in the number of some Crysophyta, Euglenophya and tychoplanktic diatom taxa were observed at lower velocities (0,1-0,4 m s^{-1}). Köhler (1997) studied the changes in algae number of the Severn River (using dialysis chambers) as a function of changes in water depth, light, and turbulence conditions. He found a strong positive correlation between turbulence conditions and algal growth rate. It was found that elongated diatoms (i.e. Pennales) settled in an average of three times shorter than unicellular green algae (i.e. Chlorococcales) species. Furthermore, the growth rate of diatom taxa was faster in the turbulent main channel (i.e. there was less sedimentation loss) than in the retention zones. Regarding the relationships between the species-specific sedimentation rate and growth rate of algae and water depth, the lower the water depth, the higher the growth rate required for a given species to remain in suspension (Reynolds et al., 1991; Reynolds, 1994).

WRT can affect either positively or negatively the growth of planktic assemblages (Lucas et al., 2009). In upper river segments, WRT is not sufficient for the development of phytoplankton (Borics et al., 2007; Lucas et al., 2009) since planktic assemblages consist primarily of suspended benthic elements (mostly pennate diatoms) entrained from various surfaces of the riverbed (Várbíró et al., 2007; Abonyi et al., 2014; Bolgovics et al., 2015, 2017).

Bolgovics et al. (2017) demonstrated that in the upper river segment where the small WRT does not enable the development of large biomass phytoplankton assemblages a so-called rhithroplankton prevails. This benthic diatom-dominated assemblage is continuously enriched with euplanktic species further downstream. As a result, the middle and lower sections of large rivers are characterised by high-biomass of euplanktic phytoplankton assemblages (Borics et al., 2007; Várbíró et al., 2007). The stochastic changes of these elements can be described by characteristic meroplankton dynamics (Istvánovics and Honti, 2011).

High levels of nutrients and long WRT, however, provide necessary but not sufficient conditions for the development of phytoplankton in water courses as underwater light is a crucial impacting factor of the potamoplankton (Lucas et al., 2009).

1.3.6 The role of light in shaping riverine phytoplankton

In the second part of the 20th century, more and more research aimed at elucidating the more subtle role of abiotic factors on phytoplankton growth (using *in vitro* conditions). Several papers were published on the growth of algae concerning the light intensity, temperature and nutrient concentrations. It was demonstrated that algal species with a higher surface/volume ratio have a competitive advantage at low light intensity (Sorokin and Krauss, 1958; Reynolds and Descy, 1996). A positive correlation was demonstrated between temperature and algal growth and it was also highlighted that this relationship has a species-, and even, a clone-specific nature (Goldman and Carpenter, 1974). The relationship between reproduction rates and light intensity variation for the major algal groups was published by Richardson et al. (1983). In this study, they concluded that planktic green algae achieve maximum growth rate at a higher light intensity, while cyanobacterial taxa grow better at low irradiances. Moreover, species of the latter group developed some adaptive mechanisms (e.g. regulating buoyancy, and protecting photosynthetic apparatus) against inappropriate underwater light climate (Walsby, 1969). However, Richardson et al. (1983) concluded that regardless of their taxonomic position almost all species can grow at their maximum rate at relatively low intensity of solar radiation (PAR < 250 μE m^{-2} s^{-1}), much lower than the maximum available light intensity (1500-2000 μE·m^{-2} s^{-1}) that can be measured at the surface of waters. Rivers are highly variable systems, where the environmental characteristics are subjected to extreme fluctuations (Bukaveckas et al., 2011). From these environmental features, light conditions are among the most important regulatory factors of phytoplankton in rivers (Cole et al., 1992; Bukaveckas et al., 2011; Ochs et al., 2013).

1.3.7 Functional concept *sensu* Reynolds in phytoplankton ecology

One of the most remarkable advances in phytoplankton ecology during the recent two decades was the recognition that phytoplankton taxa sharing similar morphological and physiological traits, can prefer similar habitats, and therefore can be merged into so-called functional groups (for details see e.g. Reynolds et al., 2002; Padisák et al., 2009; Kruk et al., 2010; Kruk and Segura, 2012; Salmaso et al., 2015, Derot et al., 2020). This approach, by reducing the number of functional units (from species level to higher functional ones), and equipping them with a habitat template helps to understand the processes that shape the diversity and functioning of planktic assemblages.

These functional groups (FGs) have mainly been identified by field observations, using data from lakes (Reynolds et al., 2002; Padisák et al., 2003; Salmaso and Padisák, 2007). Habitat templates of the FGs have been characterised by their specific tolerances and preferences, mixing regime, grazing, nutrients, and light availability (Reynolds et al., 2002), but it has not been described in a mechanistic and quantitative way. Based on recent opinions, Reynolds's FGs can be considered as functional response groups, because the elements might have differences in their individual traits, but their response to the constraints of the environment is identical (Violle et al., 2007; Abonyi et al., 2018a, 2020). Reynolds et al. (2002) merged the phytoplankton species into 31 functional groups (FGs) labelled with the different alphanumerical coda from **A** to **Z**. The number of described FGs has increased to 34 groups (Padisák et al., 2009), including some specific ones. Later, Borics et al. (2007) introduced some functional groups, characteristic of rivers. These were: epiphytic cyanobacteria taxa (coda **TIC**), epiphytic and metaphytic desmids and filamentous green algae taxa (coda **TID**), that occur in slow-flowing rivers with emergent macrophytes. Another specific riverine group is the benthic habitat preferring, mostly pennate diatom taxa (**TIB**) of smaller highly lotic rivers and rivulets (Borics, 2015; Bolgovics et al., 2017). Thus, despite the obvious differences between limnetic and lotic ecosystems, Reynolds' concept could be successfully extended and applied to river phytoplankton (Várbíró et al., 2007, Stanković et al., 2012; Abonyi et al., 2012, 2014, 2018a, 2018b). The most characteristic phytoplankton taxa of rivers are some centric and pennate diatoms merged in functional groups **A, B**, **C D**, which are adapted to poor underwater light climate possessing efficient light-harvesting capacities, that is high surface/volume ratio (Reynolds et al., 2002). Taxa merged in groups **J** and **F** are mostly coccoid, unicellular, or colonial green algae preferring moderate turbulence, higher water temperature and light availability. These groups are most characteristic of the lower segments of large rivers (Borics et al., 2007). Members of group **X1** (i.e. unicellular green algae taxa) indicate high nutrient content in rivers, while the occurrence of group **X2** and **X3** (e.g. small flagellated Chrysophyta and Cryptophyta taxa) indicate low turbulence, relatively nutrient poor conditions and long term changes in hydrological characteristics (Abonyi et al., 2018b). Elements of group **Y** (Cryptophyta taxa), **W0** (i.e. *Chlamydomonas* taxa) are medium unicellular flagellated taxa, while larger flagellate taxa (e.g. Euglenophyta, Dinophyta, taxa) are included in the group **W1** and **W2**. All these groups indicate low turbulence and velocity and high organic content (dammed stretches, sewage inflows (Várbíró et al., 2007). Taxa merged in the groups **H1**, **H2** (i.e. filamentous cyanobacteria taxa), codon **P** (e.g. some centric diatom and desmid taxa) and **L_O**, **LM**, **M** (e.g. some dinoflagellate and colonial cyanobacteria taxa) are indicators of similar riverine conditions (Borics et al, 2007; Borics, 2015). All the latter groups albeit can be subdominant elements of the (mostly) summer-autumn potamoplankton assemblages, they are not fully adapted to riverine conditions (Padisák et al., 2009). Moreover, almost all the elements of the previously described FGs for lakes (not discussed herein), can appear everywhere in rivers if the connections with adjacent lentic habitats are provided. However, they are quickly filtered out by inappropriate environmental conditions. Functional group concept *sensu* Reynolds was successfully applied to reveal productivity–diversity (Borics et al., 2012, 2014; Török et al., 2016), diversity–functioning (Stanković et al., 2012; Abonyi et al., 2018b), composition–water quality (Abonyi et al., 2012; Bolgovics et al., 2017; Wang et al., 2014) relationships. Nevertheless, habitat templates of this widely applied phytoplankton functional approach have not been assessed quantitatively for riverine ecosystems.

1.3.8 The niche concept in community ecology

Recognition of the fact that species require a certain range of environmental parameters for their survival and reproduction already appeared in publications by the 19th century naturalists (Pocheville, 2015). The term itself appeared first in R.H. Johnson's (1910) monography on the evolution of the colour pattern of lady beetles: "*One expects the different species in a region to occupy different niches in the environment*". However, Grinnell (1917) and Elton

(1927) were those who developed the scientific basis of the niche concept, although they followed different aims and approaches. Grinnell (1917) described the niche of a bird species (California thrasher; *Toxostoma redivivum* Gambel 1945) focusing on so-called “zonal, associational and faunal factors”. This niche concept appeared as a habitat niche later in the literature (Wuenscher, 1974).

In contrast, in Elton’s niche concept the emphasis was given to functionality, i.e. relations of animals to food and enemies, in other words, the niche represents the position of the species in the trophic chain (Elton, 1927). Despite differences in habitat and functional niches, theoretically, both concepts enabled vacant niches, and species equivalences i.e. species in different regions can play equal roles.

One of the most prominent steps toward the development of an operative niche concept was made by Hutchinson (1957) who provided a geometric formalization of the niche. He defined the niche as an n-dimensional hypervolume, in which all environmental variables (biotic and abiotic) necessary for the species for its survival are represented by axes. This concept amalgamates both habitat and functional niches because habitat characteristics and nutritional relations can be considered subsets of the hypervolume. The fundamental difference between Hutchinson’s niche and other previous concepts is, that Hutchinson’s niche belongs to the species and not to the habitat or the position in a food chain. With his model, Hutchinson aimed to explain species coexistence, which became a central issue in community ecology, especially after the publication of his famous Paradox of the Plankton (Hutchinson, 1961). Due to the geometric formalization, the fact that “species having identical niche position in the niche space cannot coexist” could be easily conceived. Despite its elegance, in the sixties, Hutchinson’s niche concept was not considered as a milestone. From the late sixties, many papers were published in ecology in which the authors formulated their niche definitions. Hurlbert (1981) called this period as “Hundred Flowers” phase. Interestingly, among the several contributors, some argued against the concept, because they found that it was so loosely defined, that it precluded empirical validation. In the seventies, two ecological textbooks were published (Collier, et al., 1973; Ricklefs, 1976) in which the term “niche” had not been mentioned at all. Emphasising the role of resource utilization MacArthur and Levin (1967) improved further the concept in the late sixties. The axes that represented the ranges of environmental variables in Hutchinson’s model have been replaced by resource utilization distributions, which can be visualized as histograms. Although this model has been applied first to pre-existing datasets, later it triggered many empirical studies, especially in the field of species competitions and coexistence (Schoener, 1989). The notion that not only the environmental variables but the response of communities to the environment somehow should be involved in the niche concept appeared in the seventies (Wuenscher, 1974; Colwell and Fuentes, 1975). *"The set of all environmental variables (essentially the habitat) and all organism responses, and both the habitat and total response are subsets of the niche*" (Wuenscher, 1974). "*The response of organisms to different environments (different points in niche space) is an essential component of the niche*" (Colwell and Fuentes, 1975). However, the present, hopefully, a consolidated version of the concept has been constructed by Chase and Leibold (2003). In their proposed framework, the niche has been defined as the union of the impacts of the ecological factors on the organism and the impacts of the organism on these factors. They also highlighted, how this concept can help us to understand the drivers and impacts of current environmental challenges like habitat degradation, extinctions, invasions (Chase and Leibold, 2003). Although, in general, the niche has been assigned to species or populations of species, the concept was applied to other organizational levels, such as supra-specific taxa (Van Valen, 1971), and multi-specific assemblages (Root, 1967). This explicitly implies that the sum of the specific niches will give the niche of the higher organisational unit.

It is worth to mention the Ecostatus concept of the Hungarian ecologist Pál Juhász-Nagy because his theory could help us to understand the theoretical uncertainties regarding niche definitions proposed previously by several ecologists. In his concept, he proposed the introduction of two new niche-related notions: eco-status and milieu. The milieu can be interpreted as an abstract space that is defined by environmental constraints with some possible effect on an organism population, or on a supra individual unit. etc. The Ecostatus or Ecological state is that part of the milieu that corresponds to presumably limiting constraints of a biological object, therefore the analogy between the definition of niche space and eco-status is obvious. The main difference between these two definitions is that while Hutchinson's niche space is a hyperspace defined by the limiting environmental constraints, the Ecostatus is the space where the biological object can be found and influenced by potentially limiting factors and is distributed accordingly (Gallé, 2013).

1.3.9 Main characteristics of the niche space

Theoretical niche definitions consider species under a defined set of environmental conditions (i.e. abiotic factors) and represent a so-called fundamental niche. However, because of different biological interactions, a species hardly ever realizes the full size of its fundamental niche and the typically reduced n-dimensional hypervolume that is occupied by a species is called the realised niche (Whittaker et al., 1973; Grüner et al., 2011). I must note here that there are some opinions suggesting that positive biotic interactions (facilitation) might result in a situation when realised niche can be larger than the fundamental niche (Bruno et al., 2003), or the two niche spaces can completely overlap (Rodriguez-Cabal et al., 2012).

The main characteristics of the realized niche space are niche breadth (the range of constraints belonging to the given species within the hypervolume) and niche position (the most probable position of the species in the hypervolume (Dolédec et al., 2000). Defining these two niche characteristics is an important step towards the quantitative characterisation of the niche space.

1.3.10 Niche characteristics and regional occupancy relationship

Niche characteristics of species have been proposed to explain their distributions (Heino, 2005). The niche breadth hypothesis (i.e. tolerance range) supposes a positive correlation between niche breadth and the regional distribution of species. Thus, species with higher tolerances to environmental factors and with multiple resource utilization capacities are widely distributed. In contrast, species with a narrow niche breadth should have limited distribution (Brown, 1984). This model also states that there is a unimodal species frequency distribution, where most species are rare and only a few species are widely distributed (Heino, 2005). Niche breadth, including tolerance to abiotic factors, is a body size-dependent measure (Cattaneo et al., 1998; Passy, 2012). According to the metacommunity theory, body size and niche breadth control species distributions both directly and indirectly through population density. In small and passively dispersing organisms, abundance and distribution respond negatively to body size, but positively to niche breadth, whereas in larger and actively dispersing animals, both distribution and body size correlate positively with niche breadth (Passy, 2012).

Nevertheless, several authors argue that there is no consistent support for the theory that niche breadth determines species' regional distribution (Tales et al., 2004; Heino, 2005; Heino and Soininen, 2006, Lengyel et al., 2020).

Another fundamental characteristic of the niche space is the position of species, which defines the marginality of species distribution in the niche space. Species with rather central (i.e. non-marginal) distribution can use a wide range of resources and tolerate general habitat conditions, while those with marginal distribution are characteristic for more extreme habitat conditions with narrower resource preferences (Venier and Fahrig, 1996; Tales et al., 2004). This explicitly assumes that non-marginal species with low values of niche positions should be more widely distributed at a regional scale than marginal ones with high values for niche positions (Dolédec et al., 2000). Further studies support the aforementioned negative relationship between niche position and regional distribution of species (Gregory and Gaston, 2000; Tales et al., 2004; Heino, 2005). Both concepts can provide plausible explanations for the regional occupancy of species, however, without any consensus on which one provides better insight into mechanisms shaping the observed patterns of species distributions. Indeed, the two concepts may highlight complementary aspects of the niche concept and can be considered simultaneous rather than competing approaches (Gaston et al., 1997; Heino and Soininen, 2006).

1.3.11 Statistical methods used for the determination of the niche space

During the past decades, several statistical methods and models have been developed to describe and characterise the ecological niche of species. Colwell and Futuyma (1971) calculated niche breath by measuring the uniformity of individual species distribution among a set of resources. Another method for quantifying the niche breadth of species is using a proportional similarity index by measuring the similarity between the frequency distribution of available resources used by individuals of a population (Dolédec et al., 2000). Furthermore, ordination techniques are among the most frequently used tools for the investigation of the hyperspace (Austin, 1985; Grossman et al, 1991) and species-environmental gradients relationship (Dolédec and Chessel, 1994). Correspondence Analysis (CA; Hill, 1973) is a multivariate ordination technique that is used for the investigation of niche separation of species (Thioulouse and Chessel, 1992) Furthermore, Canonical Correspondence Analysis (CCA; ter Braak, 1986) was explicitly designed to analyse how species niches are separated along environmental gradients. This method best suits the examination of unimodal responses of species to environmental conditions and implies that the importance of environmental variables can be considered proportional to the abundance of species per site (Palmer, 1993; ter Braak and Verdonschot, 1995). If a linear response of species is expected (or probable) the use of redundancy analysis (RDA) may be suggested (Dolédec et al, 2000). However principal component analysis (PCA) has also been proposed as a method for niche determination of species (Sabatier et al., 1989; Lebreton et al., 1991). To help the visualisation and numerical characterization of the niche space Dolédec et al. (2000)

developed the Outlying Main Index (OMI) method. The OMI index measures the marginality of species distribution along environmental gradients. It also calculates the niche breadth (i.e. tolerance ranges) of species. This ordination method has been successfully used for the characterization and quantification of species' niches of both terrestrial (Thuiller et al., 2004; Randa and Yunger, 2006; Treier et al., 2009; Pironon et al., 2018) and aquatic organisms (Heino and Soininen, 2006; Soininen and Heino, 2007; Buisson et al., 2008; Hof et al., 2010; Heino and Mendoza, 2016).

2 The role of cumulative daily solar radiation in shaping phytoplankton biomass[1]

2.1 Aims and hypotheses

While several field and laboratory studies focused on the relationship between the underwater light climate and phytoplankton growth (Talling, 1971; Dokulil, 1994; Reynolds, 1994; Vörös et al., 2000; Ochs et al., 2013), much less attention has been devoted to the role of light intensity and duration of the radiation entering the water surface. The upper surface of a continuous sheet of deep clouds can reflect ~70% of the total solar radiation and can absorb an additional ~20% (Kirk, 1985). Thus, it is possible that due to the weather conditions, nearly tenfold differences in the daily incident solar irradiance might occur (Várbíró et al., 2018). This should have a pronounced effect on the biomass production of phytoplankton. Moreover, the water residence time is another important regulating factor of the riverine phytoplankton biomass spatio-temporal dynamics.

Long-term monitoring of surface waters related to WFD of EU, and meteorological stations from Hungary, produced a huge amount of data on water discharge, chlorophyll-*a* (Chl-*a*), and the number of sunny hours (i.e. DSR). The coupling of these databases provides a potentially powerful method to study the relationship between light exposure and phytoplankton biomass, which is one of the main aims of the present dissertation. Therefore, I aimed to investigate the combined impact of the cumulative daily solar radiation (CDSR) and the water residence time on the biomass of the riverine phytoplankton in hydro-geomorphologically different river types. Moreover, the effect of cumulative daily solar radiation (entering the surface of rivers) on the dynamics of phytoplankton biomass has not been studied before.

Concerning this topic I tested two main hypotheses:

1. cumulative solar irradiance has a significant effect on river phytoplankton biomass,
2. river hydro- and geomorphological characteristics have a pronounced influence on the relationship between phytoplankton biomass and light exposure.

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[1] This chapter is based on the following publication: Várbíró, G., Padisák, J., Nagy-László Z., Abonyi, A., Stanković, I., Gligora Udovič, M., B-Béres, V. and Borics, G. (2018). How length of light exposure shapes the development of riverine algal biomass in temperate rivers. Hydrobiologia, 809, 53-63. https://doi.org/10.1007/s10750-017-3447-1

2.2 Materials and Methods

2.2.1 Study area

The study area is common for both research topics of the dissertation and is located in the central part of the Carpathian Basin, which corresponds to the Middle Danube watershed in Hungary. The renewing water budget of Hungary is determined primarily by the yearly 108,89 km^3 (i.e. multiannual average) water transported by the rivers entering into the central part of the Carpathian Basin (Varga et al. 2018). The water budget of Hungary is determined primarily by the annual 55,9 km^3 mean precipitation which is around half of the volume of water transported by the rivers entering into the Carpathian Basin. However most of the precipitation is lost during evapotranspiration processes of the vegetation and therefore only 8,2 % is received by the rivers, while 5,8 % of the precipitation contributing to the supply of the underground water budget (Varga et al., 2018). Furthermore, as the Basin is covered mainly by porous sediments there is also significant (i.e. 20-30 %) underground inflow and outflow (Mezősi, 2017). Hungary has a lowland-dominated territory (93,030 km^2), rich in rivers. Approximately 2/3 of this area is occupied by two large plains, and the ratio of hilly and mountainous areas with an altitude above 400m is less than 2 % (Matyasovszky et al., 1999). Therefore, the climate of this region is relatively uniform and can be characterised as mainly humid continental with warm and dry summers and cold and wet winters (Mezősi, 2017). The average annual air temperature is ~11 ºC, while the summer average temperature varies between 19 and 21ºC. Annual mean precipitation fluctuates between 500 and 800 mm (Mezősi, 2017).

All the rivers involved in the studies except the potamal Zala River (catchment area (ca) ~ 5500 km^2) are tributaries of the Middle-Danube with a catchment area of more than 200,000 km^2. Based on hydro-geomorphological characteristics 19 rivers included in this study can be grouped in rhithral type with a coarse substrate (e.g. gravel, pebble) and 17 rivers in potamal types with fine (e.g. sand) substrate. The uppermost stretch of the River Tisza is rhithral, while the middle and lower stretches are potamal.

Zala River with five sampling sites (Fig. 1, No 84-88) is the main tributary of Lake Balaton, and during the past two centuries faced strong hydro- and geomorphological modifications (Hatvani et al., 2014).

The Hungarian Danube is a regulated river but it largely preserved its natural hydro- and geomorphological characteristics because most of the regulation works were done on its side arms (e.g. sluice), or smaller alterations within the river bed (e.g. dragging's, groynes). River embankments were not built on the Hungarian river section, but on the lower Hungarian river stretch some meanders have been cut off (Ihrig, 1973). The sampling locations on the Danube covered the whole Hungarian stretch of the river (Fig. 1, No 13-25).

The largest regulated rhithral tributaries of the Danube River in Hungary are the River Rába (ca. 10,000 km^2) and the Ipoly (ca. 5000 km^2), both were sampled in one site (Fig. 1, No 52 and 37). I must note herein that the Rába River is the tributary of the Mosoni Danube (Fig. 1, No 49-50) which is the longest side branch of the Middle Danube (121 river km). On both rivers, several dams were constructed and several meandering segments were cut off (Ihrig, 1973; Weipert, 2014).

The Dráva River is another large tributary of the Danube, with a catchment area (ca. 40,000 km^2). River regulation works (i.e. upstream dam construction, meandering sections cut off on lower segments) changed the natural geomorphology of the Dráva riverbed. The Hungarian section of the Dráva River was sampled at three locations (Fig. 1, No 10-12), while its largest affluent Mura River was at one site (Fig. 1, No 51). However, the Hungarian stretch of the river preserves almost a pristine riverscape (Kiss and Andrási, 2015).

The potamal Tisza River is the largest regulated tributary of the Danube and has an individual watershed of 157,000 km^2. The original 1492 km natural length of the river was shortened to 962 km (Vágás, 1982). During the regulation of the river in the 19th century several meanders were cut off, drastically reducing the natural floodplain of the river (Pálfai, 2003). Moreover, two hydro electrical power plants were constructed at Tiszalök (i.e. river km 518) and at Kisköre river km 402).

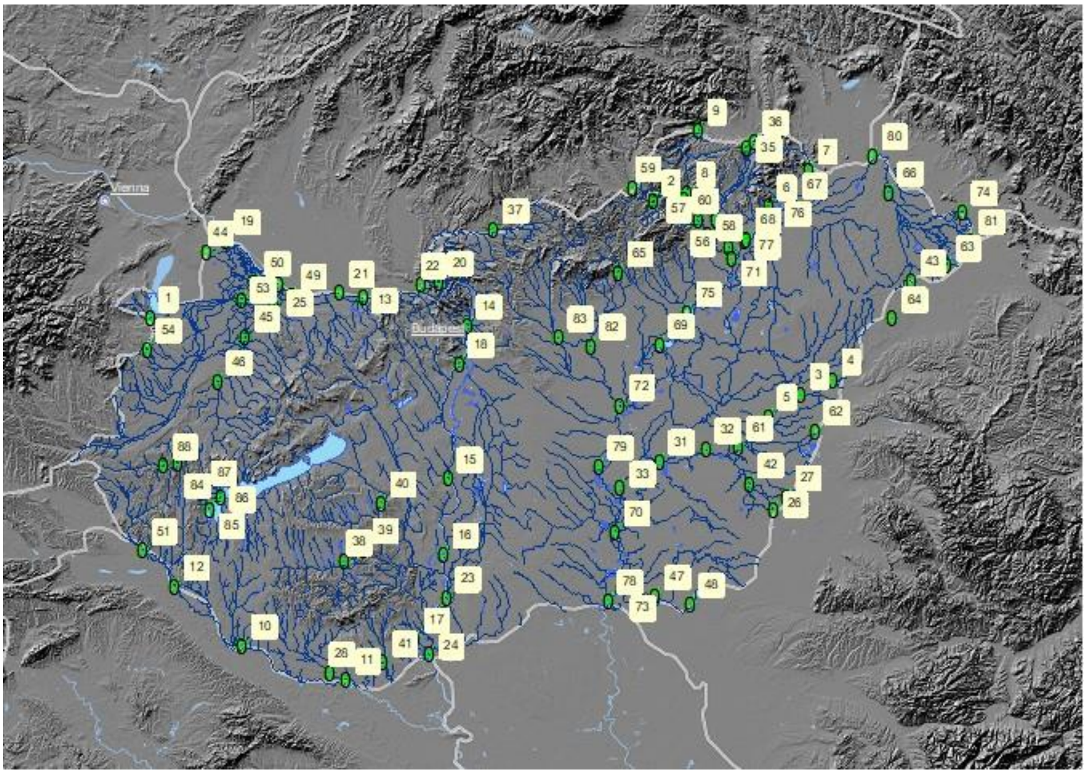

Figure 1. Map of the studied rivers and sampling locations within the Carpathian Basin. Site numbers refer to sampling locations. Appendix 1., Table 1.

In this way, in the Hungarian Tisza three hydro-geomorphologically distinct sections can be distinguished; two meandering (with sampling sites Fig. 1, No 74, 66, 80, 67, 68 and No 72, 79, 70, 73, 78 respectively), and the middle section impacted by damming situated between sites No 77, 71, 76, 75, 69 (Istvánovics et al, 2012).

The main and largest left bank potamal tributaries of the Tisza are the Szamos River with two sampling site (Fig. 1, No 63-64, catchment area ~15,500 km^2)·, Hármas–Körös River with three (Fig. 1, No 31-33, ca. 27,500 km^2) and Maros River with two sites (Fig 1, No 47- 48, ca. 30,000 km^2) respectively. The main potamal tributaries of the Hármas Körös included in the study are the rhithral Sebes Körös (Fig. 1, No 61-62), the potamal Fehér-, Fekete- and Kettős Körös (Fig. 1 No 26, 27 and 42) rivers. All these tributaries have been regulated (embankments, channelization, dam construction). On the right side of the Tisza watershed, the potamal Bodrog (Fig. 1, No 6-7, ca ~13,000 km^2), the rhitral Sajó (Fig. 1, No 55-60, ca. 13,500 km^2) and the domestic potamal Zagyva (Fig. 1, No 82-83, ca~4500 km^2) rivers are the largest tributaries of the Tisza. The flow regime of Bodrog River is strongly influenced by the upstream, dammed-up section of the River Tisza, giving the Bodrog potamal almost lake-like characteristics (Istvánovics et al., 2012). The other rivers and rivulets (Strahler order >5) not detailed herein, have relatively small catchment areas in the range of 100-7000 km^2 and mainly channelized riverbeds.

2.2.2 Database and data handling

Growing season (May-September) sestonic Chl-*a* data for the period of 1992-2010 of the rivers in the Carpathian Basin were used as proxies of phytoplankton biomass.

Water discharge (Q) and Chl-*a* data were provided by the Hungarian Water Quality Monitoring Database, maintained by the General Directorate of Water Management. The initial database contained Chl-*a* and daily water discharge (Q) data from 52 rivers from 103 sampling sites (Fig. 1., Appendix 1.).

Since time is a crucial factor necessary for phytoplankton development, we calculated the water residence time (WRT) for each sampling point. This variable can be calculated if the size of the catchment area and the actual water discharge data are known (Soballe and Kimmel, 1987; Reynolds, 2000). Theoretical water residence time (WRT) was calculated as a function of the drainage area (Ad, km^2) and water discharge (Q, m^3 s^{-1}) using the equation proposed by Soballe and Kimmel (1987):

$$\mathrm{WRT} = 0.08 \times \mathrm{Ad}^{0.6} \times Q^{-0.1}$$

where;

WRT: water residence time (day)

Ad: area of the catchment above the sampling site (km^2)

Q: discharge (Q, m^3 s^{-1})

Water discharge data were measured on daily basis at each sampling location by Water Directorates. Catchment areas above the sampling sites were also available in the database of the Water Directorates.

Water samples were taken from the talweg of the rivers on a weekly, biweekly or monthly basis (Kiss et al., 1996). Chl-*a* measurements were performed by the Regional Environmental Laboratories according to the hot-ethanol extraction method (MSZ ISO 10260:1993).

Before the analyses, several screening steps were performed to exclude all those rivers or sites where obvious anthropogenic impacts were present. First, the small lowland macrophyte-dominated streams were excluded from the matrix. In the second step, all rivers, where sporadic extremely high Chl-*a* values indicated the obvious impact of in-stream or off-river reservoirs, were ruled out. Moreover, data were screened to exclude those sites, where short water residence time (WRT <5 days) was coupled with high mean phytoplankton biomass (Chl-a > 30 µg l^{-1}) which indicated again the presence of the off-river reservoirs or ponds. Thus, the dataset contained 13,044 sampling events (for Chl-a) at 88 sites of 35 rivers The relevant average hydrological (i.e. WRT), morphological (i.e. rhithral/potamal) and chemical (Chl-a, nutrients) parameters average and minimum-maximum values of the studied rivers are shown in Appendix 1, Table 1.

As a surrogate measure of light exposure, the sum of daily solar radiation (DSR) values was used. The dataset of the Hungarian Meteorological Service included sunshine hours for Budapest. The regional differences in global radiation in Hungary are smaller than 10% (Szász, 1997). Since this value is much smaller than the value of the possible daily variation, this simplification hardly affects the results to be obtained.

DSR was derived from sunshine hours in each day, applying Angstrom's (1924) formula with coefficients applicable to Hungary (Szász, 1997):

$$\mathrm{DSR} = (0.28 + 0.72\frac{S}{S_m})$$

where;

DSR: daily solar radiation (MJ m^{-2})

DSR_0: Monthly theoretically possible global radiation on a horizontal surface in Hungary (MJ m^{-2})

S: measured daily values of the bright sunshine hours for the given day

S_m: maximum possible sunshine hours for the given date (monthly mean values were applied)

2.2.3 Statistical analyses

Analyses of the cumulative energy of the daily solar radiation (CDSR) and chlorophyll-a relationship.

Log transformed Chl-a values were plotted against the log CDSR values cumulated for each of the exposure periods and at each sampling site. The period ranged from one day to sixty days, and the building of the model matrix is described in Table 1. General linear regression model (Montgomery et al., 2012) was used with the following equation to assess the effect of cumulated DSR values on Chl-a.

$$\log(\mathrm{Chl} - a) = \propto + \beta \log(\mathrm{CDSR}_i) + e$$

where;

Chl-a : Chlorophyll-a content in µg l^{-1}

CDSR $_i$: the cumulative energy on the i^{th} day

β: slope

α: intercept

e: residuals

The coefficients of determination (R^2), the slope (β) and level of significance ($P<0.05$) were used to determine the overall fit of the models. Solar radiation values were cumulated for 1, 2, 3, ….to 60 days prior to the sampling dates each sampling site. Thus sixty Chl-a = f(CDSR) linear models were constructed for each sampling site. Altogether 5280 (60×88) model results were evaluated. However, slope values of the regression lines significantly different from zero does not necessarily mean that phytoplankton biomass is considerably determined by the cumulated light exposure. Therefore, the slopes of regressions were also plotted against the days of light exposure (DLE). The maxima of these curves indicate the length of light exposure having the highest explained variance of phytoplankton biomass. Furthermore for the analyses of water residence time on the cumulative daily light exposure-chlorophyll-a relationship, water residence time for each sample was plotted against the slope values of CDSR-Chl-a relationship. Furthermore, for the analyses of water residence time on the cumulative daily light exposure -chlorophyll-a relationship, WRT for each sample was plotted against the slope values of CDSR-Chl-a relationship.

These investigations were performed for the the rhithral and potamal rivers and for the two largest rivers Danube and Tisza respectively. All statistical analyses were performed by using Rstudio (R Core Team, 2023).

Table 1. Building of the site level matrix used for studying the cumulative daily solar radiation (CDSR) – Chl-a relationships

Site A

	Y axis for Plot 1-60^{th}		X axis for Plot 1^{st}	X axis for Plot 2^{nd}	••••••	X axis for Plot 60^{th}
Coda of measurements from 1 to N	Chl-a (µg l^{-1})	Date of sampling	DSR 1 day earlier (MJ m^{-2})	Sum of DSR 1 +2 days earlier (MJ m^{-2})	••••••	Sum of DSR 1+2+3 ……. +60 days earlier (MJ m^{-2})
1	17	05.07.2001	27	50	••••••	1115
2	23	06.08.2001	7	22	••••••	1225
3	60	07.09.2001	18	33	••••••	890
•	•	•	•	•	••••••	•
•	•	•	•	•	••••••	•
•	•	•	•	•	••••••	•
N	63	09.09.2007	21	43	••••••	1370

2.3 Results

2.3.1 Cumulative solar radiation -riverine phytoplankton biomass relationship

Phytoplankton biomass (i.e., Chl-*a* concentration) varied considerably at each sampling site (Appendix 1., Table. 1). Differences were mostly moderate (i.e. one order) in small rhithral streams but exceeded two orders of magnitude in large lowland rivers. DSR values varied between 1.6 and 32 MJ m^{-2} day^{-1}. CDSR values showed approximately 10 times differences across the whole range of light exposure days (Fig. 2).

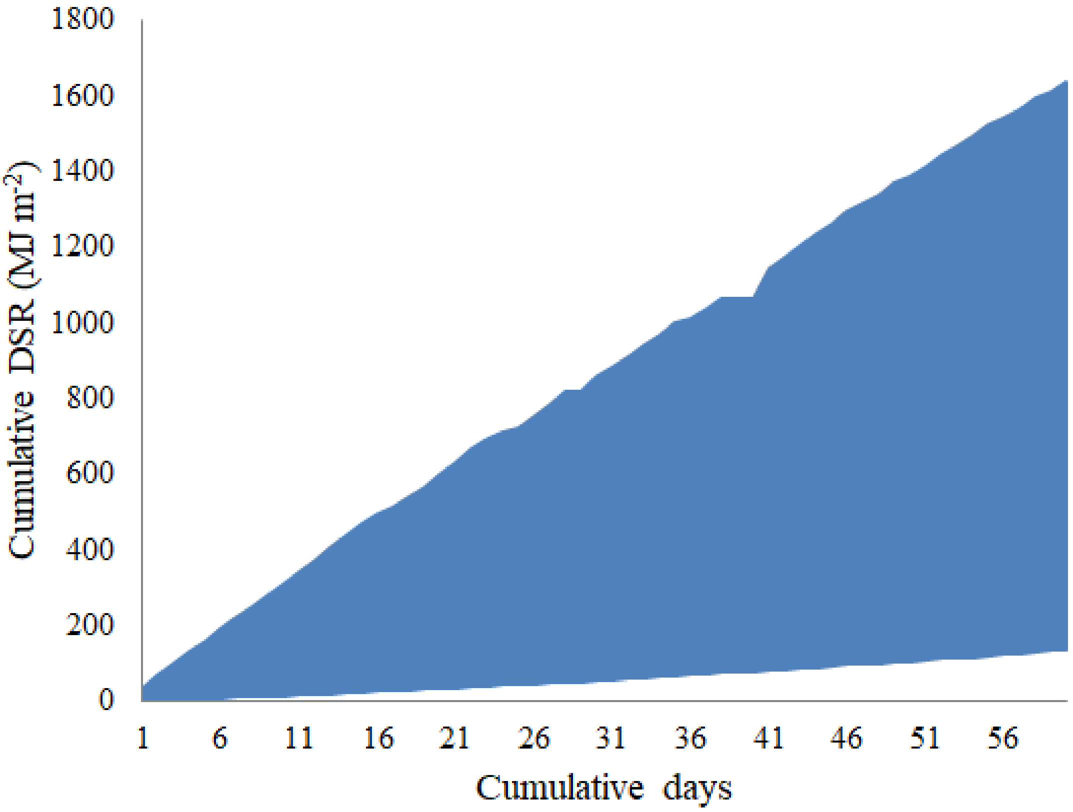

Figure 2. The range of cumulative daily solar radiation (CDSR in MJ m-2) in the range of time periods studied (1-60 days). The blue areas represent the minimum to maximum values that occurred in the database for a given day.

In most rivers, Chl-*a*-CDSR relationships were significant and could be described by linear regression models. Exceptions were mostly those few watercourses where the WRT was less than 6-8 days.

Based on the shapes of the curves two distinct patterns could be distinguished; monotonously increasing and hump-shaped (Fig. 3 a-d). In case of lower potamal sections of the rivers (Fig. 3 b,c), the observed steady increase in slope values indicates that a pronounced increment of phytoplankton biomass needs longer light exposure (~30-60 days). In contrast, a mostly hump-shaped relationship (Fig. 3 d) occurred in the rhithral and upper rhithral sections of the rivers, which implies that a significant increase in phytoplankton biomass could be expected generally at shorter light exposure (~10-30 days). In the River Danube shape of the curves explaining higher biomass increment was unimodal similar to that of rhithral rivers. However the upper stretch of the Hungarian section of the Danube (Fig. 3. a), similarly to rhithral rivers, a shorter light exposure period (7-12~days) is needed for the substantial increment of the phytoplankton biomass.

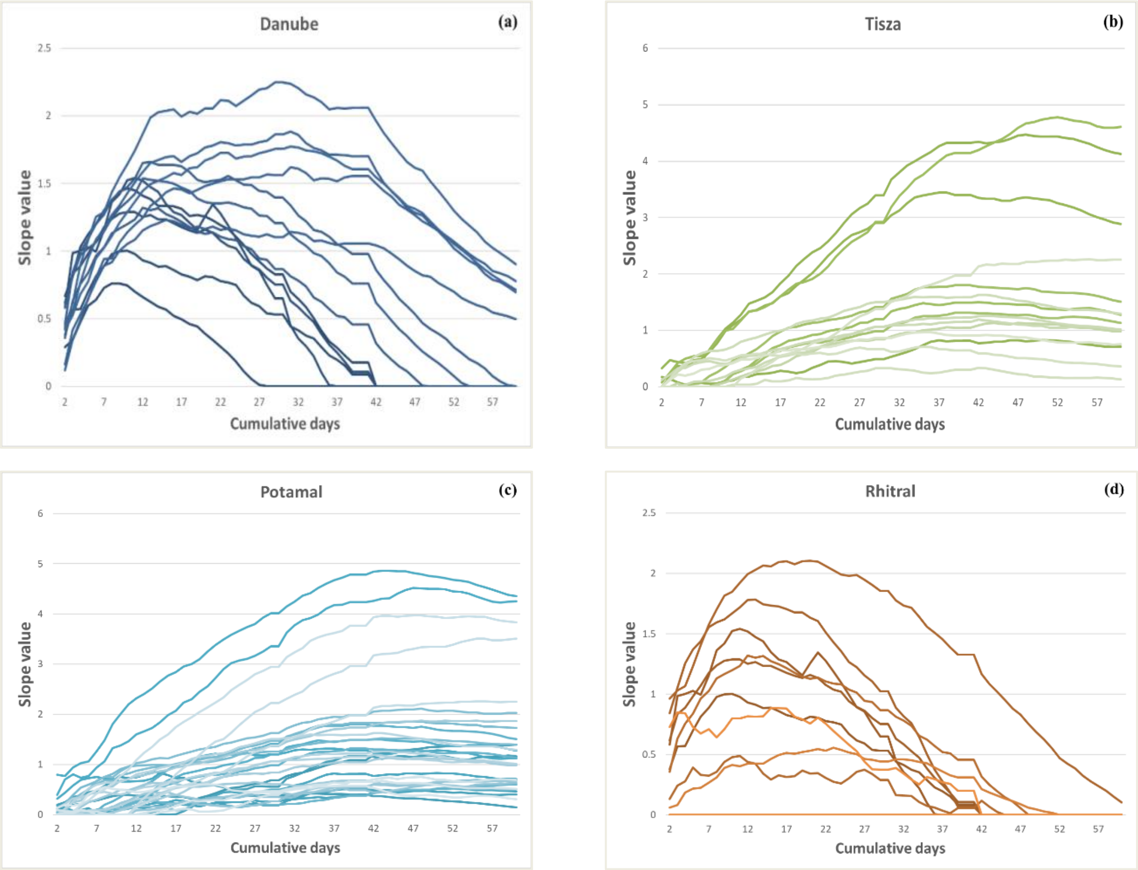

Figure 3. Line plots illustrating the relationship between the estimated slopes of linear regression lines of Chl-*a* - CDSR relationships and the number of days contributing to the CDSR: (a) Danube, (b) Tisza, (c) Potamal, and (d) Rhihtral. The lines refer to different sampling sites.

2.3.2 Impact of the water residence time on the cumulative solar radiation-phytoplankton biomass relationship

The slope *(β)* of the regressions i.e., the dependence of phytoplankton biomass on solar radiation was also influenced by water residence time (Fig. 4 a-d).

In case of the River Danube, the water residence periods were longer (48-58 days) than the corresponding (~15-40 days) CDSR periods explaining the highest biomass increments (Fig.

4a). In the Danube the, the peak of the hump-shaped curve shifted towards the longer light exposure range (30-40 days), slightly flattened in the lower river sections (higher values of WRT) and had a maximum slope value of $\beta = 1.8$ (Fig. 4a).

In River Tisza, the steady increase of slope values with DLE could also be observed, but it showed a bimodal character along the WRT with peaks reaching the slope value of $\beta \sim 3,2$ (Fig. 4b).

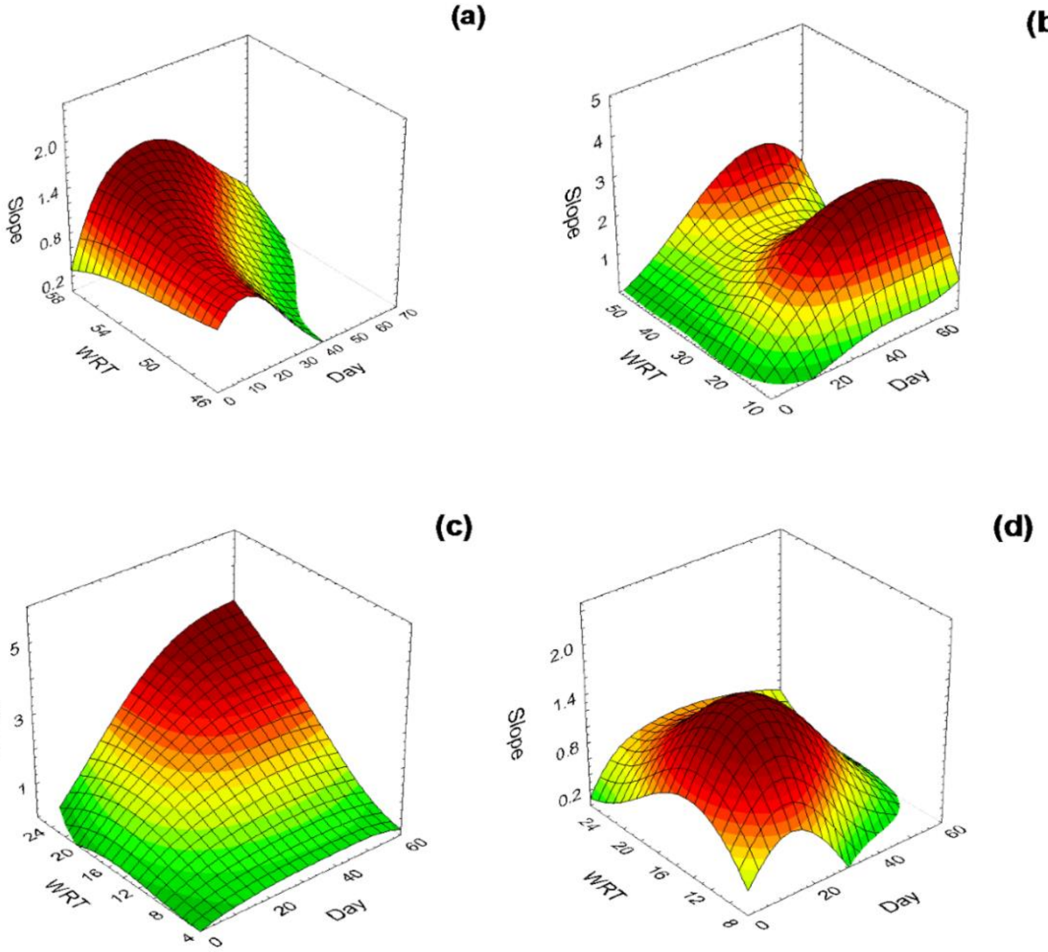

Figure 4. Three-dimensional plots of the slope for Chl-a regressed against CDSR in the light of the cumulative time period studied and the water residence time (WRT) in the different river types: (a) Danube, (b) Tisza, (c) Potamal, and (d) Rhithral

The highest slope values characterised the lowland, potamal rivers with fine (e.g. sandy, muddy) substrate. In this river group, the values showed a steady increase both with the DLE and WRT increasing and attained the $\beta = 5$ values (Fig. 4c).

The increment of phytoplankton biomass in rhithral rivers with the coarse substrate was less pronounced. The slope values showed a unimodal relationship both with light exposure range and WRT. Maximum slope values were only ~1.5 and fell in the range of 10-30 DLE and 12-20 days of WRT (Fig. 4d).

However, in both river types (with the exception of the Danube), the WRT periods were significantly shorter than the corresponding CDSR periods required for the significant biomass increment.(Fig. 4 a-c). The explained variances of the applied linear regression models were closely related to the slope values (Fig. 5 a-d). Non-significant results were mostly characteristic for a couple of rivers, or for river segments with residence time < 6-8 days.(red dots Fig. 5) The highest R^2 values characterised the lowland streams with a fine substrate. In this potamal river group, the explained variance attained the 0.32 value (Fig. 5c). The River Tisza (R^2max.~ 0,28) and the lower sections of the Hungarian Danube (R^2max.~ 0,22) also belong to this category (Fig.5 a,b). Although the explained variances of the models were smaller in the case of rhithral rivers with coarse substrates, these values were reasonably high (R^2~ 0.18) for several sites (Fig. 5d).

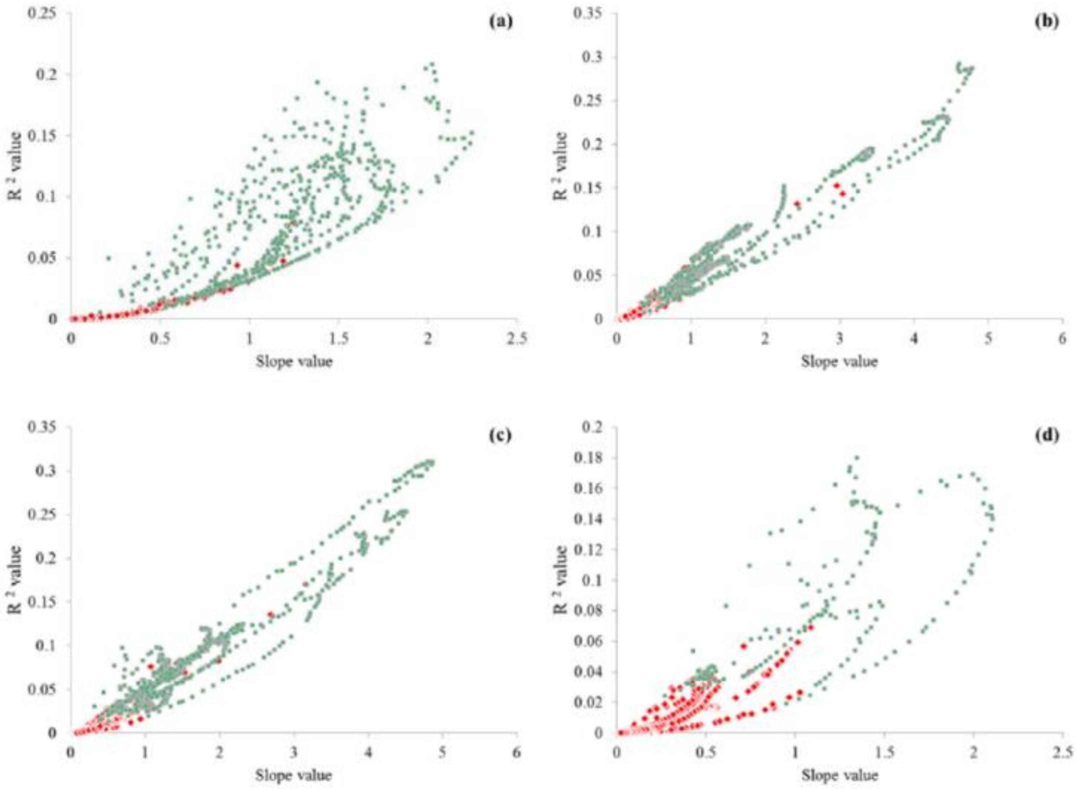

Figure 5. The scatterplot between R^2 and slope values in the different river types from Chl-a regressed against CDSR for each cumulative day. (a) Danube, (b) Tisza, (c) Potamal, and (d) Rhithral. Dots refer to individual models, red dots indicate non-significant models.

2.4 Discussion

2.4.1 The role of river characteristics and light exposure in shaping riverine phytoplankton

Solar radiation appeared to be a strong predictor of phytoplankton biomass in most rivers. However, depending on the type of water body solar radiation accounted for about 10–95% of the heat input into surface waters (Birge, 1916; Platts, 1983). Water temperature has a profound influence on the photosynthetic activity of algae and by studying the processes on a longer time scale (i.e. from January to July in the temperate region) it could be very difficult to distinguish the impacts of temperature on the phytoplankton biomass from that of the solar radiation. The five-month time frame applied in this study covered the warmest period of the years when the water temperature is relatively constant (range of changes ~5-7 °C at site level), while the daily variation of DSR values occasionally reached 20-fold differences (1.6 – 32 MJ m^{-2} day^{-1}) and variation of DSR values cumulated for the maximal 60-day long period still attained a 10-fold difference (Fig. 2).

In several watercourses or river segments, no significant relationships between DSR and Chl-*a* were found. In these cases, however, short water residence time (< 6-8 days) explained the non-significant relationships. Interestingly, for several rivers, it could be observed that the highest slope and R^2 values fell in a range of the light exposure gradient (DLE) where the number of light exposure days exceeded the WRT of the given watercourse (Fig.4 b-d). This contradiction in rhithral rivers can be explained by considering the composition and recruitment of phytoplankton in these river type. Phytoplankton of rhithral rivers (rivers with low WRT values and coarse substrates) consists primarily of tychoplanktic elements, i.e. benthic taxa that entrained to the plankton after detached from the substrates (Bolgovics et al., 2015, 2017). Thus, the phytoplankton of rhithral rivers strongly depends on the composition and biomass of the benthic algae (i.e. diatoms) living in the various habitats of the riverbed, and the current velocity has to be sufficient (~0,1-0,3 m s^{-1}) to keep benthic organisms in suspension (Bowles and Quennel 1971; Istvánovics et al., 2010). Since the development of mature phytobenthos needs a longer time to build its canopy, typically more than four weeks (Lengyel et al., 2015; Tapolczai et al., 2016), it is not surprising that the number of light exposure days belonging to the highest slope values is higher than WRT of the given rhithral river (Fig. 4d).

In the lowland, potamal rivers where both the slopes and R^2 values showed a steady increase with the days of DSR, the number of days belonging to the highest slope and R^2

values (60 days) also exceeded the WRT of the rivers (~16-23 days; Fig. 4c). In these rivers, high-biomass/low-diversity phytoplankton prevails (Borics et al., 2014) and is dominated by medium-sized centric diatoms like *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal & Kociolek (Várbíró et al., 2007). These taxa are considered euplanktic elements, i.e. species that live mostly in the pelagial. However, Istvánovics and Honti (2011) demonstrated that in slow-flowing rivers centric diatoms with high sedimentation rates at flow velocities below 0,4 m s^{-1} (Istvánovics et al., 2010) settle to the bottom and can have a prolonged benthic residence. This practically means that these taxa can exhibit meroplanktic life histories in this kind of river. Due to sufficiently strong hydraulic forces (e.g. smaller floods) or oxygen bubbles produced by photosynthesis, they can entrain into the suspension again. This so-called benthic retention hypothesis argues that the residence time of large-celled diatoms exceeds that of the advecting, truly planktic algae. This explicitly explains the "days of CDSR > WRT" controversy.

Istvánovics and Honti (2011) described this meroplankton dynamics for the river Szamos (Hungary), which was also part of our study and had the highest slope and R^2 values. These meroplankton dynamics enable the development of high phytoplankton biomass (the maximum value of Chl-*a* in the River Szamos was 520 µg l^{-1} in our database), which, considering an approximately 1 meter mean depth for the river in the summer period, is very close to the theoretical maximum of the depth-integrated Chl-*a* content of surface waters (600 µg·L^{-1}) estimated by Reynolds (2006) and measured occasionally in hypereutrophic ponds (Borics et al., 2000).

The impact of the two large tributaries (Szamos and Maros) on the phytoplankton of the Tisza can be seen in Fig. 4b. The bimodal character of the slope values of the Tisza was unequivocally due to these large eutrophic inflows (i.e. biomass increment) and dammed middle river section (i.e. high sedimentation loss). The curves of slope values showed unimodal distribution in case of the Danube. Phytoplankton biomass increment shoved shifting peak towards the longer light exposure range and characterised with longer WRT periods than the corresponding CDSR periods explaining highest biomass increment (Fig. 4a). This pattern is consistent with the typological differences that can be observed along the 417 km Hungarian section of the river. In the upper rithral-like river segment, the channel bed is composed of coarse sediment (e.g. cobbles and gravel) while the lower river segment is covered with sand. Parallel with this shift in river type, biological elements including macroinvertebrates (Graf et al., 2008), fish (Erős et al., 2016) and planktic algae (Dokulil and Donabaum, 2014) also showed compositional and/or quantitative changes. The position of the peaks in the upper river segment of the Danube fall between 7-12 days (Fig. 3a.), which is surprisingly shorter than the range that characterised the small streams and rhithral rivers (12-25 days) (Fig. 3d.). Sedimentation of diatoms and increment of truly planktic taxa in the reservoirs might have a pronounced influence on the composition and biomass of the phytoplankton, which modifies its response to the CDSR. Profiles of the curves belonging to the lower sections of the Danube became similar to that of the lowland potamal rivers (Fig. 3a, 3c.). However, declines of the curves in the CDSR > 42 days range (Fig. 3a) indicates that the meroplankton dynamics, which must be responsible for the high slope values in lowland rivers with fine sediment (Fig. 3c) even in case of long light exposure does not play a significant role in the river Danube.

Modelling the river phytoplankton biomass is a challenging task. Nutrients, suspended particles, turbidity, residence time and catchment area, are the most frequently used variables in empirical models to predict the biomass of algae or its proxy, the sestonic Chl-*a* (Bum and Pick, 1996).

Fluctuation of discharge, the impacts of impoundments and the various river influents result in the low explanatory power of the models. Moreover, the correlation between environmental factors and Chl-*a* concentration is blurred by the contradictory results regarding the importance of the considered variables (e.g. TP concentration by Bum and Pick, 1996 *versus* discharge and WRT by Soballe and Kimmel, 1987; Bowes et al., 2012) in the increment of sestonic algal biomass. What we have learned from the majority of studies dealing with eutrophication is that nutrients are essential for algal growth and the nutrient–Chl-*a* relationship is nonlinear (Phillips et al., 2008). This relationship can be highly significant not only for lakes but also for rivers (Van Nieuwenhuyse and Jones, 1996). Nevertheless, as was shown by the aforementioned authors who studied the relationship in the 5-1000 $\mu g\ l^{-1}$ TP range, the strong relationship can only be demonstrated if the TP gradient is large. In the eutrophic range where TP highly exceeds 100 $\mu g\ l^{-1}$, the TP– Chl-*a* relationship is almost asymptotic both for lakes (Borics et al., 2014; Phillips et al., 2008) and rivers (Van Nieuwenhuyse and Jones, 1996), which makes the adequate modelling of phytoplankton growth difficult. Some studies emphasised the role of light in the growth of river phytoplankton and proposed to use it in predictive models (Descy et al., 1987; Descy and Gosselain, 1994; Reynolds et al., 2004). There are many ways of using solar radiation in the models. The fact that occasionally a negative relationship was found between solar radiation and river phytoplankton biomass (Whitehead et al., 1997) highlights the need for a more thorough examination of this issue. The importance of our results is that they are the first to show that CDSR has a great influence on the riverine phytoplankton biomass, and this influence strongly depends on the type of the watercourse and the length of light exposure. Moreover a recent study with similar topic and significant result, support the usefulness of the global and cumulative solar radiation inclusion in phytoplankton biomass predictive models (Kamjunke et al., 2021). It could be important to mention that even if the Zeu/Zmix ratio is low, phytoplankton might not disappear from the water, and might even accumulate if there are external sources of phytoplankton to the system (e.g. supplements from wetlands or lakes).

In cases when the CDSR–Chl-*a* relationship was significant, the explained variance (R^2) of the regression models varied between 0.03 and 0.32. The highest R^2 values were obtained for the large highly eutrophic lowland rivers with fine sediments. Since phytoplankton is constrained by several regulatory factors among which many are difficult to measure, or not measured routinely at all, solar radiation could be the most relevant explanatory variable that cannot be neglected in future predictive modelling of riverine phytoplankton biomass.

The other important message of our study is that in the future, changes in river phytoplankton biomass can be affected by global warming. One of the important consequences of global warming for the mid-latitude continents is the decline in the average summer rainfall (Rowell and Jones, 2006; Rowell, 2009). This potentially means increased aridity, lower cloudiness (Dai, 2011) and higher air temperature (Desortová and Punčochář, 2011). These altered conditions, therefore, are expected to contribute to the development of high phytoplankton biomass in rivers and increase the risk of critical water quality changes.

3 Niche characteristics of phytoplankton functional groups in temperate rivers and their role in regional distribution[2]

3.1 Aims and hypotheses

Phytoplankton species inhabit various habitat types having a characteristic set of environmental conditions. This set of conditions can be considered as niches, or habitat templates of specific groups of species (ter Braak and Verdonschot, 1995). As was discussed in the literature overview of this thesis niche space has been generally assigned to species or populations of species. Nevertheless, the concept was applied to higher organizational levels, such as supra-specific taxa (Van Valen 1971), and multi-specific assemblages (Root, 1967). Functional groups of phytoplankton (Reynolds et al., 2002) are one of these higher organisational levels. Some niche (i.e. habitat) characteristics of phytoplankton species have been characterised when indicator taxa lists were created, levels there have not been attempts to define and numerically characterise the niche space for phytoplankton of higher organisational level. Although the application of functional approaches has become widespread in phytoplankton ecology, studies aiming to link functional units of river phytoplankton assemblages to characteristic habitat templates (or niches) have been missing. Therefore as a second topic of my dissertation, using the OMI approach, I aim to implement the niche concept into river phytoplankton ecology and define the niche characteristics of Reynolds' FGs quantitatively by their niche breadth and niche position. To reach this research goal I formulated two main hypotheses;

1. following the concept of McNaughton and Wolf (1970), niche position and niche breadth are related to each other; in other words, FGs with central niche positions have wide, while those with marginal niche positions have narrow niche breadth,
2. niche characteristics predict the regional occupancy of FGs, accordingly, OMI enables us to identify roles that FGs may play in riverine phytoplankton.

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[2] This chanter is based in the following publication: Nagy-László, Z., Padisák, J., Borics, G., Abonyi, A., B-Béres, V. and Várbíró, G. (2020). Analysis of niche characteristics of phytoplankton functional groups in fluvial ecosystems. Journal of Plankton Research, 42, 355-367. https://doi.org/10.1093/plankt/fbaa020

3.2 Materials and methods

3.2.1 Study area

The study area covers the Hungarian part of the Carpathian Basin. The sampling sites are indicated in Fig. 6. A detailed geomorphological description of the investigated rivers could be found in Chapter 2.2.1 (Appendix 2, Table 2.).

The same study area of the Middle Danube watershed was used for the determination of niche characteristics of phytoplankton functional groups and to analyse their role in regional distribution. The main geomorphological characteristics of the rivers involved in the study have been discussed in Chapter 2.2.1.; therefore herein will not be detailed. 18 rivers with 39 sampling locations were included in this study (Fig. 6). All the rivers (regarding the territory of Hungary) are tributaries of the independent Danube, Tisza and Dráva catchment area.

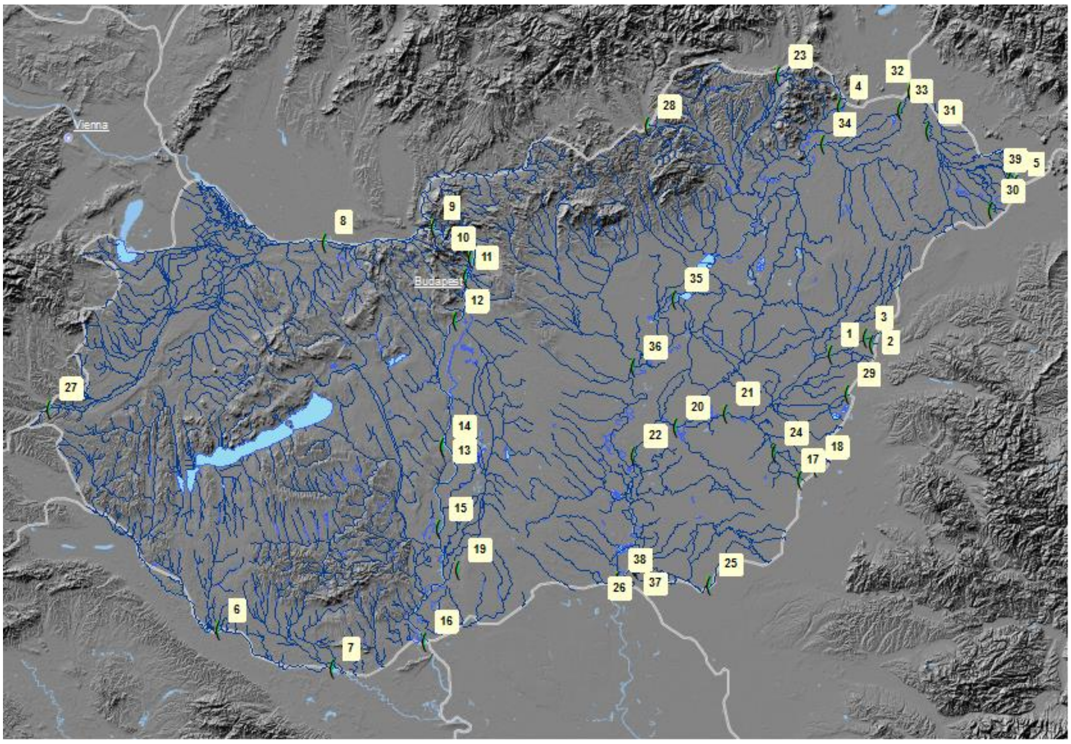


Figure 6. Map of the studied rivers and sampling locations within the Carpathian Basin. Site numbers refers to sampling locations (Appendix 2, Table 2.)

The largest tributaries of the River Tisza (Fig. 6, No 31-38) are the Szamos River (Fig. 6, No 30), Hármas Körös River (Fig. 6, No 20-22) and Maros River (Fig. 6, No 25-26) joining the river in the upper, middle and lower sections. Some other larger direct tributaries of the Tisza are River Túr (Fig. 6, No 39), Sajó (Fig. 6, No 28), and Bodrog (Fig. 6, No 4). The two main tributaries of the Sajó are River Hernád (Fig. 6, No 23) and Bodva (Fig. 6, No 5), while the main tributary of the River Hármas Körös is, Sebes Körös (Fig.6 ,No 29) with Berettyó (Fig. 6, No 1-3), Fehér- (Fig. 6, No 17), Fekete- (Fig. 6 ,No 18) and Kettős Körös (Fig. 6, No 24) rivers.

Sampling sites (Fig. 6, No 8-16) of the Danube, covering the whole middle section of the river with one tributary the River Rába No (27), while Dráva River (Fig. 6, No 6-7) with smaller tributary Fekete Víz rivulet (Fig. 6, No 19) were also included in the study.

3.2.2 Database and data handling

For the niche space characterization of riverine phytoplankton FGs *sensu* Reynolds, phytoplankton data of the Hungarian National Water Quality Database was used. As a first step, the database was pre-screened to exclude all those sampling events where some of the considered environmental variables data were missing. Therefore the final dataset covers 809 sampling events of 18 rivers (Strahler orders above six) and 39 sampling sites from the years 2005 to 2014. Investigated rivers (Fig. 6.) are part of the Hungarian Water Quality Monitoring Network that tracks the ecological status according to the EU Water Framework Directive (EU/2000).

The environmental data matrix used in this study covered various elementary physical and chemical parameters. These were: water discharge (Q), theoretical water residence time (WRT), pH, conductivity (COND), water temperature (WT), total suspended solids (TSM), chemical and biochemical oxygen demand (COD_{Cr}, BOD_5), dissolved phosphorous (ORTOP, total-P) and nitrogen forms (NH_4-N, NO_2-N, NO_3-N, total-N). All of these parameters were measured on a biweekly or monthly basis from samples collected from the thalweg of the rivers (Kiss et al., 1996). For phytoplankton analyses, samples were collected 3-4 times in a year between April and October covering the so-called vegetation period of phytoplankton assemblage.

Daily measured water discharge (Q) data were provided by the Hydrographic Monitoring Network database maintained by the General Directorate of Water Management. Additional water discharge data was also used from the Middle and Lower Tisza Regional Water Directorates.

Theoretical water residence time (WRT) was calculated as it was shown in the previous chapter (2.2.2.) of the thesis.

The phytoplankton taxonomical dataset included 1359 algal taxa that were assigned into 33 Functional groups (FGs) according to Reynolds et al. (2002), Padisák et al. (2009), and Borics et al. (2007). This database contained the relative biomass of each phytoplankton taxa. Biovolume calculations were based on the method proposed by Hillebrand et al. (1999). Taxonomic identification of algae was performed at the species or genus level by using relevant national and international specialized literature.

For further analyses, we calculated the relative biomass of FGs in each sample by summing up the relative biovolume of taxa identified within each FG.

Phytoplankton counting, taxonomical identification and measurements of the environmental variables were performed by the Regional Environmental Laboratories according to Hungarian Standards (MSZ EN ISO - that all correspond to the reference European standards - EN ISO, referred in the references).

Since present-day habitat conditions are matched by present-day traits in the organisms (Townsend and Hildrew, 1994), the samples were considered independent observational units. Based on the original databases, two consolidated data matrices were created for statistical analyses. These contained the measured and average values of the considered environmental variables for all sampling sites, and the relative and mean biomass values of the FGs for all study sites and the whole study period (Appendix 2., Table 2.; Appendix 3., Table 3.). The number of samples in which FGs occurred was considered as the regional occupancy of FGs.

3.2.3 Statistical analysis

Outlying Main Index (OMI) a multivariate method proposed by Dolédec et al. (2000) was used for the analyses of riverine phytoplankton FGs' niche space. Although the method was originally designed for the determination of the main niche characteristics (position–marginality, and breadth–tolerance) of species, here we consider the approach suitable for the characterization of phytoplankton FGs' niche space.

Marginality was calculated by measuring the distance between the average habitat conditions of the considered environmental variables used by each FG and the mean habitat conditions being characteristic (i.e. for a theoretically defined ubiquitous species) of the entire area studied. Therefore species, or phytoplankton functional groups (FGs) having high values of OMI index can be considered marginal species with low habitat availability and those with low OMI values as non-marginal (i.e. centroid) species with high habitat availability. Niche breadth calculation allows the estimation of tolerance ranges of individual FGs. OMI provides a useful tool for the assessment of the species-environment relationship, considering that the response of species to habitat characteristics can either be unimodal or almost linear. This technique also assures an even weight to sample units with contrasting species and abundance values (for more details see Dolédec et al., 2000).

As a first step of OMI analyses a Principal Component Analysis (PCA; Hotelling, 1933) was performed for evaluation of the relationships between environmental variables by using the data matrix containing dataset of the considered environmental variables. In the second step niche parameters (Inertia, OMI, Tolerance and Residual tolerance (Rtol) values of individual FGs were calculated with niche parameter function of the ade4 and witomi R package (Thioulouse et al., 1997, Karasiewicz et al., 2017). Finally (by using the same statistical packages) FGs were plotted in the space delimited by PCA axes of the environmental parameters (Fig. 9.). To test the level of significance between the observed FGs' marginality (i.e. niche position) and its simulated values, 10,000 permutations were run under the null hypothesis that all FGs are identical in terms of their environmental preferences and tolerances (Heino and Soininen, 2006). To avoid the arbitrary characterization of niche Group by using discrete OMI or tolerance (Tol) values as boundaries, a Bray-Curtis (Bray and Curtis, 1957) dissimilarity matrix was compiled containing niche characteristics of individual phytoplankton functional groups. Then based on dissimilarity matrix Non-metric multidimensional scaling (Kruskal, 1964) was performed for the visualisation of similarities of niche characteristics among FGs.

Using three discrete categories for niche position (central, intermediate, marginal) and two for niche breadth (narrow, wide) theoretically six phytoplankton functional niche groups can be created. Therefore K-means clustering (i.e.with six predefined niche groups) was applied to identify niche groups, clustering FGs with similar niche characteristics (Lloyd, 1982). Multiple linear regressions were applied to assess the separated and aggregated impact of niche position and niche breadth on regional occupancy of the functional groups (Montgomery et al., 2012). All statistical analyses were performed by using Rstudio (R Core Team, 2023).

3.3 Results

3.3.1 Phytoplankton assemblage functional composition and abundance in the studied rivers

The phytoplankton dataset contained 1359 algal taxa that could be assigned into 33 Functional groups (FGs). Therefore almost all the FGs described in former literature were represented in this study. FGs **TIB**, **D**, **J**, **C, Y, X1, W$_0$** and **X3** occurred in >50% of samples and merged merely taxa adapted to riverine habitats (Fig. 7., Appendix 3, Table 3.). FGs exceeding 10% in occurrence frequency were, **B, X2, P, W1, L$_O$, W$_S$**, **S1, W2, E and H1** characteristic mostly for meso-eutrophic mixed lakes or lake layers.

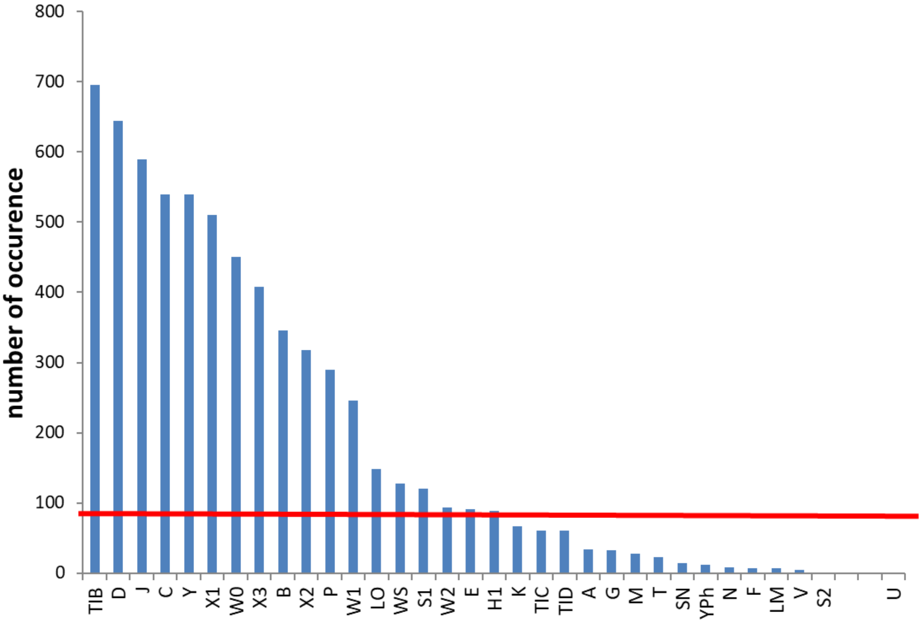


Figure 7. Distribution of the phytoplankton functional groups in samples in relation to the total number of samples (809). The bold line represents a 10 % threshold of FG occurrences.

All the other groups with the lowest occurrences in samples are characteristic for certain types of lacustrine habitats (e.g. **AG**, **M**, **V, U**), or rithral rivers segments with aquatic macrophytes (e.g. **TIC**, **TID**).

3.3.2 Phytoplankton functional groups niche space characteristics

PCA analyses reveal that related to the first axes of PCA, conductivity (COND), biological (BOD5) and chemical oxygen demand (CODcr) were negatively correlated with some dissolved nutrient forms (e.g. NO$_3$-N, TN, ORTOP) and positively with other form (e.g. NH$_4$). Moreover based on the second axes of PCA, hydrological variables (Q, WRT) showed a negative correlation with the majority (e.g. COD, TSM, COND, NH_4, TP) of the physical and chemical variables (Figure 8a).

The most important environmental predictors affecting the functional group composition were, COD_{Cr}, (i.e. proxy of organic material content) and nutrients (Axes 1.; Fig. 8a). Moreover, hydrological habitat variables like water residence time (WRT) and water discharge (Q) appeared to be also relevant (Axes 2; Fig. 8a). The first axes of the OMI's PCA explained 87 % in the variance of functional groups, while the second one explained 6.4 % (Table 2).

Table 2. Explained variance of the functional groups related to the PCA of the environmental variables.

	Axes 1	Axes 2	Axes 3	Axes 4	Axes 5
Eigenvalues:	3.3761	0.24816	0.12881	0.03979	0.02642
Projected inertia (%):	87.009	6.395	3.32	1.026	0.681
Cumulative projected inertia (%):	87.01	93.4	96.72	97.75	98.43

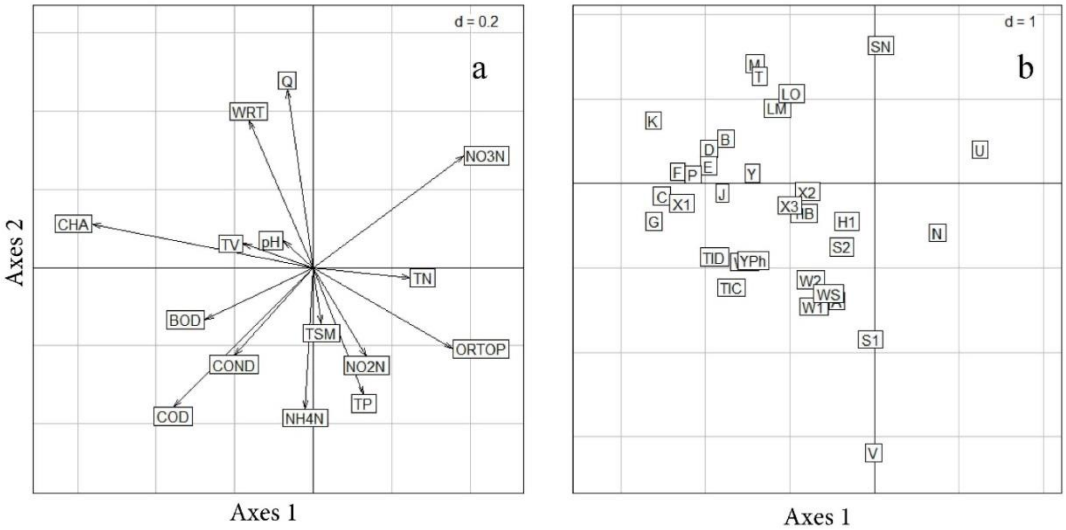


Figure 8. PCA of (a) environmental variables and the position of FGs (b) in the PCA plane.

The main niche parameters of each FG calculated with OMI analysis are summarised in Table 3. Niche position of most FGs differed significantly from a random distribution, represented by their *P*-values ≤0,05 (i.e. significance of marginality).

Table 3. Relevant metrics calculated during the OMI analysis**.** Inertia: quantification of the influence of environmental variables on niche separation of the phytoplankton FGs. OMI: marginality (i.e. position), Tol: niche breadth, Rtol: residual tolerance, OMI %; Tol %; Rtol %: represent the corresponding percentage of variability; p: significance of marginality. FGs with significant OMI values are highlighted in bold.

FG	**Inertia**	**OMI**	**Tol**	**Rtol**	**OMI %**	**Tol %**	**Rtol %**	**p**
A	19.97	5.72	7.67	6.58	28.7	38.4	32.9	0.098
B	16.15	3.64	2.12	10.39	22.5	13.1	64.3	0.000
C	19.57	6.37	2.33	10.87	32.6	11.9	55.6	0.000
D	16.29	4.03	2.53	9.73	24.7	15.5	59.8	0.000
E	19.97	4.3	2.34	13.34	21.5	11.7	66.8	0.004
F	15.76	9.36	1.58	4.82	59.4	10	30.6	0.022
G	22.71	7.47	2.71	12.53	32.9	11.9	55.2	0.000
H1	18.16	0.96	2	15.2	5.3	11	83.7	0.258
J	18.5	3.31	3.07	12.12	17.9	16.6	65.5	0.000
K	15.66	8.11	1.87	5.68	51.8	11.9	36.3	0.005
L_M	17.57	3.83	2.19	11.55	21.8	12.5	65.7	0.577
L_O	16.49	2.66	2.36	11.48	16.1	14.3	69.6	0.000
M	11.52	6.1	1.21	4.2	53	10.5	36.5	0.032
N	14.19	3.96	0.24	9.99	27.9	1.7	70.4	0.828
P	19.44	5.2	3.41	10.84	26.7	17.5	55.7	0.000
S1	17.5	7.5	3.6	6.41	42.8	20.5	36.6	0.123
S2	4.28	4.28	0	0	100	0	0	0.981
S_N	7.01	4.67	0.01	2.34	66.5	0.1	33.4	0.140
T	12.47	4.12	2.66	5.68	33	21.4	45.6	0.094
TIB	16.36	0.93	2.33	13.11	5.7	14.2	80.1	0.000
TIC	28.22	6.13	7.77	14.31	21.7	27.5	50.7	0.002
TID	18.48	5.66	1.59	11.23	30.6	8.6	60.8	0.024
U	26.89	26.89	0	0	100	0	0	0.100
W_0	21.26	3.25	3.31	14.7	15.3	15.6	69.1	0.000
V	31.11	30.94	0.04	0.13	99.4	0.1	0.4	0.062
W1	29.34	3.52	3.6	22.23	12	12.3	75.7	0.000
W2	21.06	2.32	2.91	15.83	11	13.8	75.2	0.011
W_S	18.8	3.24	4.02	11.55	17.2	21.4	61.4	0.011
X1	18.13	5.32	2.4	10.41	29.4	13.2	57.4	0.000
X2	18.5	1.41	1.47	15.62	7.6	8	84.4	0.052
X3	16.01	1.25	1.95	12.81	7.8	12.2	80	0.000
Y	20.72	3	2.93	14.8	14.5	14.1	71.4	0.000
Y_{Ph}	9.91	4.06	1.51	4.35	40.9	15.2	43.9	0.433

The K-means clustering separated the FGs into six niche groups on the nMDS ordination plot (Fig. 9, Table 4).

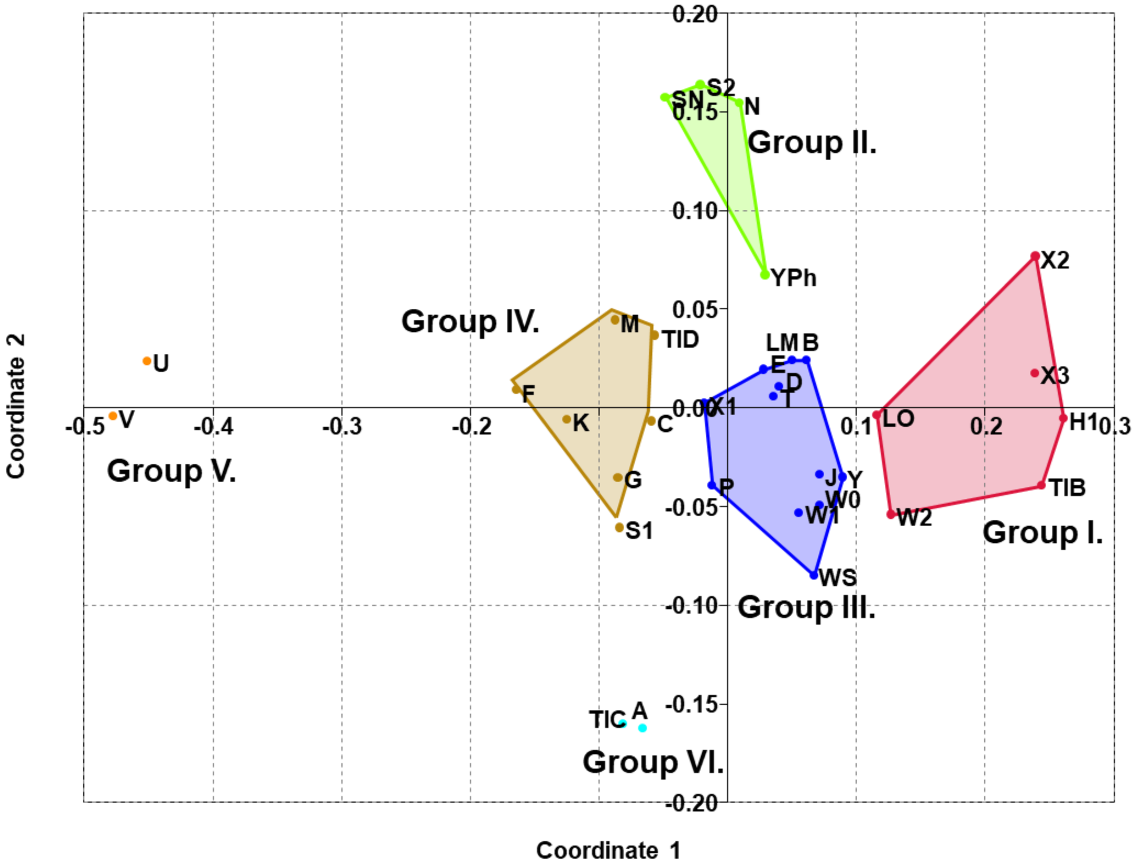
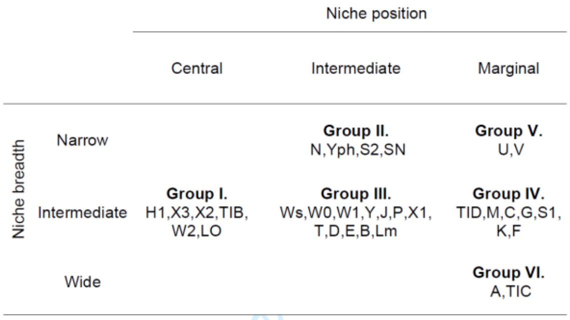


Figure 9. NMDS ordination of niche position and niche breadth with the position of the FGs and Niche Groups.

FGs following the initial theoretical consideration (i.e. regarding niche space grouping) with central niche position and narrow or wide niche breadth and with intermediate position and wide niche breadth were not found. Instead based on K-means clustering three of the niche groups realised niche space could be characterised with intermediate niche breadth. (Table 4).

Group I contains FGs that have a central niche position and intermediate niche breadth. **Group II** with an intermediate niche position and narrow niche breadth included FGs that rarely occur in our dataset and show non-significant results regarding their niche position. **Group III** includes most of the identified FGs with intermediate niche positions and intermediate niche breadth. FGs with narrow niche breadth had intermediate (i.e. **Group II**) or marginal (i.e. **Group V**) niche positions. Niche **Groups IV, V,** and **VI** with marginal niche positions showed the largest variation in niche breadth since narrow, intermediate and wide niche breadth occurred among them (Table 4). Distribution of functional groups with relevant taxa among the six niche groups is summarised in Table 5. Non-significant results were obtained for FGs that only scarcely occurred in the dataset (Table 3, Table 5).

Table 4. Possible combination of theoretical and realised niche types with the relevant functional groups (FGs).



		Niche position		
		Central	Intermediate	Marginal
Niche breadth	Narrow		**Group II.** N,Yph,S2,SN	**Group V.** U,V
	Intermediate	**Group I.** H1,X3,X2,TIB, W2,LO	**Group III.** Ws,W0,W1,Y,J,P,X1, T,D,E,B,Lm	**Group IV.** TID,M,C,G,S1, K,F
	Wide			**Group VI.** A,TIC

Table 5. Different Niche types with the relevant functional groups (FGs) and characteristic taxa and species. Bold alphanumerical coda denote significant niche position, non bold alphanumerical coda denote non-significant position in the niche space.

Type coda	Type description	Coda of FGs	Characteristic species
Group I.	Central position and intermediate niche breadth	H1, **X2, X3, TIB, W2, L_O**	H1: *Dolichospermum flos-aquae* (Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek; **X2**: *Plagioselmis, Rhodomonas*; **X3**: *Chrysococcus;* **TIB**: *Nitzschia, Navicula, Achnanthes; Achnathidium* **W2**: *Trachelomonas*, small dinoflagellates; **L_O**: *Peridinium, Merismopedia*
Group II.	Intermediate niche position and narrow niche breadth	N, Y_{ph}, S2, S_N	N: *Cosmarium*, *Tabellaria***;** Y_{ph}: *Phacotus lenticularis* (Ehrenberg) Diesing; S2: *Spirulina*, *Raphidiopsis*; S_N:*Raphidiopsis raciborskii* (Woloszynska) Aguilera & al.
Group III.	Intermediate niche position and intermediate niche breadth.	**W_S, W0, W1, Y, J, P, X1**, T, **D, E, B**, L_M	**W_S**: *Synura*; **W0**: *Chlamydomonas*, *Chlorella*, *Beggiatoa alba* Trevisan*;* **W1**: *Euglena*, *Phacus*; **Y**: *Cryptomonas;* **J**: *Scenedesmus*, *Actinastrum*, *Crucigenia*; **P**: *Aulacoseira granulata* (Ehrenberg) Simonsen, *Pediastrum*; **X1**: *Monoraphidium*, *Ankistrodesmus;* T: *Planctonema*, *Closterium aciculare* T. West*;* **D**: *Ulnaria acus* (Kützing) Aboal, *Stephanodiscus hantzschii* Grunow, *Discostella pseudostelligera* (Hustedt) Houk & Klee*;* **E**: *Dinobryon*, *Mallomonas*; **B**: *Lindavia comta* (Kützing) Nakov, Guillory, Julius, Theriot& Alverson; L_M: *Ceratium, Microcystis*
Group IV.	marginal niche position and intermediate niche breadth.	**TID, M, C, G**, S1, **F, K,**	**TID**: benthic diatoms, desmids, filamentous green algal taxa; **M**: *Microcystis*, *Sphaerococcum*; **C**: *Asterionella formosa* Hassall, *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal & Kociolek, *Discostella stelligera* **(**Cleve & Grunow) Houk & Klee**;** **G**: *Volvox*, *Eudorina*; S1: *Planktothrix*, *Limnothrix redekei* (Goor) Meffert, *Pseudanabaena limnetica* (Lemmermann) Komárek **F**: *Oocystis*, *Elakathotrix*; **K**: *Aphanothece*, *Aphanocapsa*
Group V.	Marginal niche position and narrow niche breadth	U, V	U: *Uroglena*; V: *Chromatium, Chlorobium*
Group VI.	Marginal niche position and wide niche breadth	A**, TIC**	A: *Lindavia glomerata* (H.Bachmann) Adesalu & Julius, *Urosolenia longiseta* (O.Zacharias) Edlund & Stoermer*;* **TIC**: benthic cyanobacteria taxa, *Oscillatoria, Phormidium, Lyngbya*

By using linear graph illustrations, the position and breadth of each functional group were visualized along the first two axes of the factorial plane of OMI (Fig. 10).

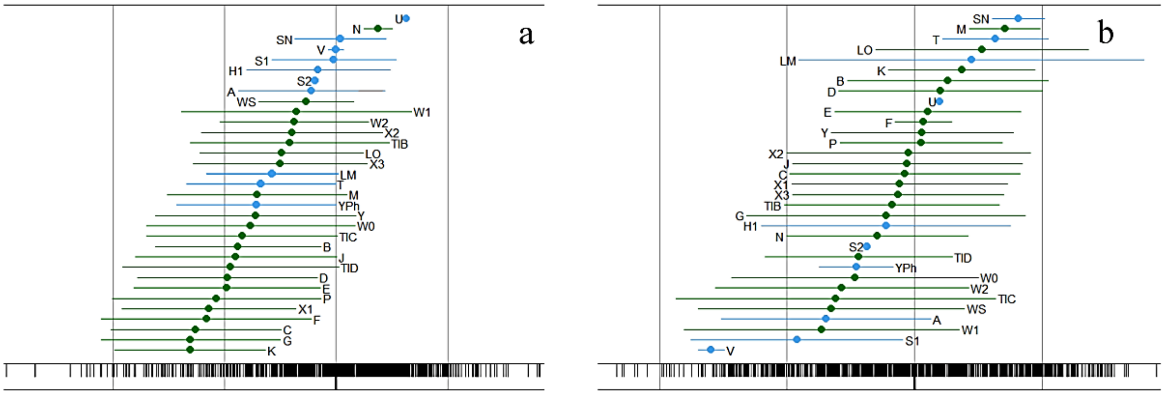


Figure 10 . Linear graphs illustrating the niche position of the identified functional groups along the first (a) and second axes (b) of the OMI analysis (green dots indicate significant, while blue ones non-significant results). Thin horizontal lines denote FGs niche breadth.

Niche **Group I** includes FGs (e.g. **X2**, **X3**, **TIB**,) positioned merely in the middle third of the first axis of the OMI plain, which corresponded to habitat conditions close to the average environmental characteristics of the studied area (Fig. 10a).

The members of **Group IV** (e.g. **K, G**, **C**, **F**), and **Group III** (e.g., **X1**, **P**, **J**) placed left along the first axis of the OMI plain parallel lower nutrients ranges.

The niche position of **Group V** (**U**, **V**) and **Group II** (e.g. **S_N**, **N**, **S2**) appeared right towards higher nutrient ranges. The other FGs positioned themselves merely in the middle third of the first axis. **Group VI** represents a niche space characteristic for both higher (e.g. **A**) and lower (e.g. **TIC**) nutrient conditions (Fig. 10a).

Along the second axis of the OMI plain some members of **Group I** (e.g. **Lo**), **Group II** (e.g. **S_N**) **, Group III** (e.g. **B**, **D**, **E**) and **Group IV** (e.g. **M**, **K**), showed an upright position in the OMI plane, together with longer WRT and Q that are characteristic for larger rivers. Other elements of **Group I** (e.g., **X2**, **X3, TIB**), **Group III** (e.g.**, J**, **X1, Y**, **P**) and **Group IV** (e.g., **C, G**) are located merely in the middle third of the second axis of the OMI factorial plane closer to average hydrological conditions (Fig. 10b). Functional groups merged in niche group **II** (**N**, **S2**, **Y_{ph}**) were positioned mostly toward lower ranges of hydrological variables. Nevertheless, some other members of **Group I** (e.g. **W2**), **Group III** (**Ws, Wo**, **W1**) and **Group VI** (e.g. **A**, **TIC**) were positioned in the lower discharge and WRT range. Functional elements of **Group V** (**U**, **V)** showed occurrence at extreme ranges of hydrological variables, but their position was non-significant according to OMI analysis (Fig. 10b).

3.3.3 Niche characteristics and phytoplankton FGs regional distribution relationship

Linear regression revealed that niche position (OMI) was related to niche breadth (Tol) weakly and non-significantly (R^2=0.115, P=0.053, $F_{[1,\ 31]}$=4.03,). Nevertheless, linear regression showed a positive and significant relationship between regional occupancy and niche breadth (R^2= 0.3847, P <0.001, $F_{[2,\ 30]}$=19.38), that is, FGs of higher tolerance values are widely distributed in the studied rivers (Fig. 11a.). An opposite tendency could be observed between regional occupancy and niche position of the FGs (R^2 = 0.3453, P <0.001, $F_{[1,30]}$ =16.35, Fig. 11b).

Functional groups having central niche positions in the OMI plain occurred more frequently, therefore having wider distribution than those with marginal positions. Applying multiple linear regression we found that the two niche characteristics affected regional occupancy of FGs significantly in a simultaneous way (R^2adj=0.515, P <0.001, $F_{[2,30]}$=17.99).

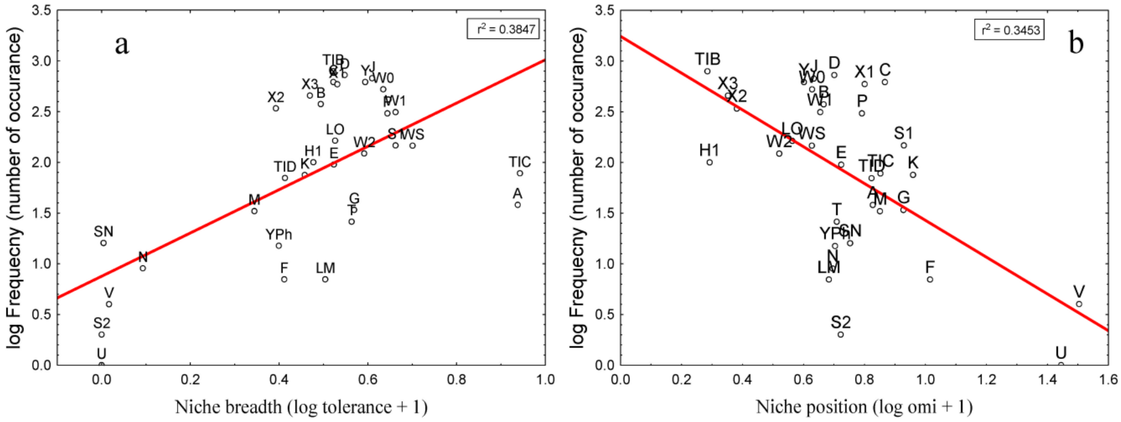


Figure 11. Relationship between regional occupancy and (b) niche position, and (a) niche breadth of phytoplankton functional groups sensu Reynolds. Lines denote linear regressions.

3.4 Discussion

In this study, I used the OMI approach to visualize and numerically characterize the niche space of riverine functional groups of algae. Theoretically, the fundamental niche characterizes the niche space where an organism can survive and multiply in the absence of competitors (grazers, parasites). Because in the real world these conditions cannot be fulfilled, what we can measure and define by the OMI tool is the realised niche of the organism or group of organisms. In our case, the two axes of the OMI plain covered the two most important characteristics of the niche space in the riverine environment, i.e. nutrient supply and hydrological constraints. The first axis of the OMI plain was primarily related to phytoplankton biomass and nutrients. Nevertheless it was also related to COD_{Cr} and BOD5 what can be explained primarly by phytoplankton biomass (Fig. 8a, Fig. 10a). This finding was in good agreement with the results of former studies; i.e. similarly to standing waters, composition and biomass in riverine phytoplankton are strongly influenced by nutrients (Hecky and Kilham, 1988). The second OMI axis correlated well with two size-related hydrological parameters; water residence time (WRT) and discharge (Fig 8a, Fig.10b). Both variables have special importance in aquatic environments. In rivers, these variables determine the time frame necessary for the phytoplankton to multiply, and establish typical riverine assemblages, referred to as potamoplankton (Soballe and Kimmel, 1987; Reynolds and Descy, 1996; Várbíró et al., 2018).

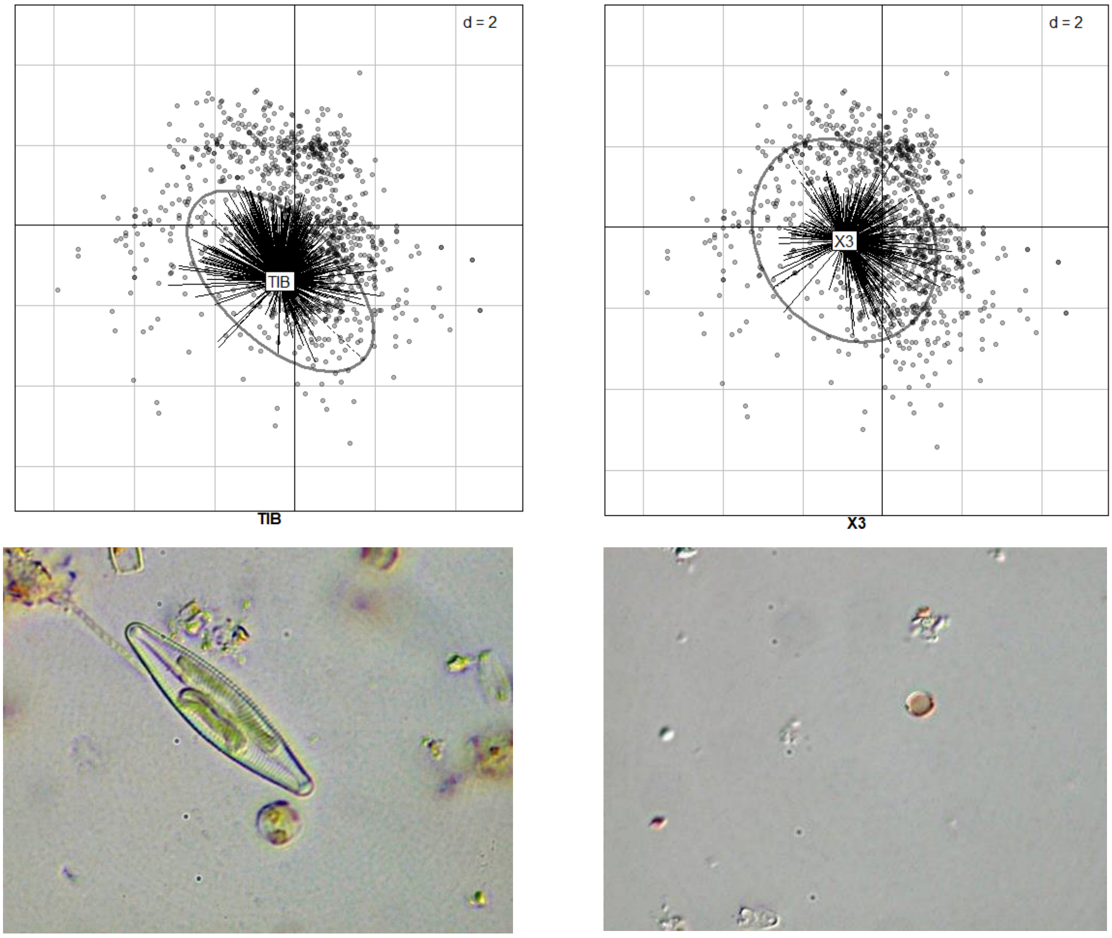
3.4.1 Niche position and niche breadth relationship

Our first hypothesis that there is a relationship between niche position and niche breadth was not supported by the results. The lack of a significant relationship between niche position and niche breadth means that their potential role in the distribution of phytoplankton species can be separated (Gaston et al., 1997). Both niche characteristics have a similarly strong relationship with the regional occupancy of FGs (R^2=0.38 with niche breadth, R^2=0.34 with niche position). During the interpretation of these results, two issues must be considered: a methodological limitation, and the strongly eclectic nature of the riverine phytoplankton (Borics et al., 2014). The first is related to the fact that regional occupancy was measured on presence-absence basis. Although the relative abundance of taxa occasionally can be as low as 0.25% (since ~400 units are counted during the microscopic analyses of phytoplankton samples), its presence has to be recorded and considered when regional occupancy is calculated for the given FG. However, this is usually compensated by the fact that most of the FGs contain more than one taxa. The other issue is that the composition of the riverine phytoplankton is highly stochastic especially in the upper river sections. In the lower potamal sections of rivers, similarly to lakes, the composition and diversity of potamoplankton are governed mostly by internal processes, i.e. competition for light and nutrients and maintaining buoyancy (Borics et al., 2014, Naselli-Flores and Padisák, 2023). However, in the upper sections of the rivers, where an absolute abundance of the phytoplankton is considerably less, impacts of the various inflows entering the rivers can be very important (Istvánovics et al, 2010). Under natural conditions, in the rhithral river segments, the phytoplankton is mostly dominated by tychoplanktic elements (Bolgovics et al., 2017). However, the effluents of constructed standing waters (Dynesius and Nilsson, 1994; Nilsson et al., 2005), especially reservoirs, in the watershed may basically determine the composition of phytoplankton (Barbosa et al., 1999; Sabater et al., 2009; Istvánovics et al., 2010, 2012). From the perspective of metacommunity theory (Leibold and Chase, 2017), phytoplankton in the upper river segment is determined by characteristic source-sink dynamics, where the numerous standing waters (as sources) inoculate the rivers (as sinks) with limnophilic algae. However, many of them not adapted to riverine conditions, and therefore, show negative reproduction rates, leading to disappearance from the plankton further downstream. Such intensive source-sink dynamics could explain why almost all the FGs described in the literature occurred in our dataset, and additionally, can increase the niche breadth of FGs considerably. Despite stochasticity in riverine phytoplankton is relevant, this can also be overridden by deterministic processes, which basically shape the niche position and niche breadth of those FGs that are considered characteristic for riverine assemblages.

3.4.2 Niche characteristics of the functional groups

Group I merges FGs with central niche position and intermediate niche breadth (Fig. 12). **Group II** includes FGs with intermediate niche position and narrow breadth (Fig. 13), **Group III** includes most of the identified FGs with intermediate niche positions and intermediate niche breadth (Fig. 14). Functional groups in **Group IV** have intermediate niche breadth (Fig. 15), in **Group V** have narrow breadth (Fig. 16), and in **Group VI** the FGs have wide breadth (Fig 17). All the later three groups have marginal niche position in the fundamental niche space.

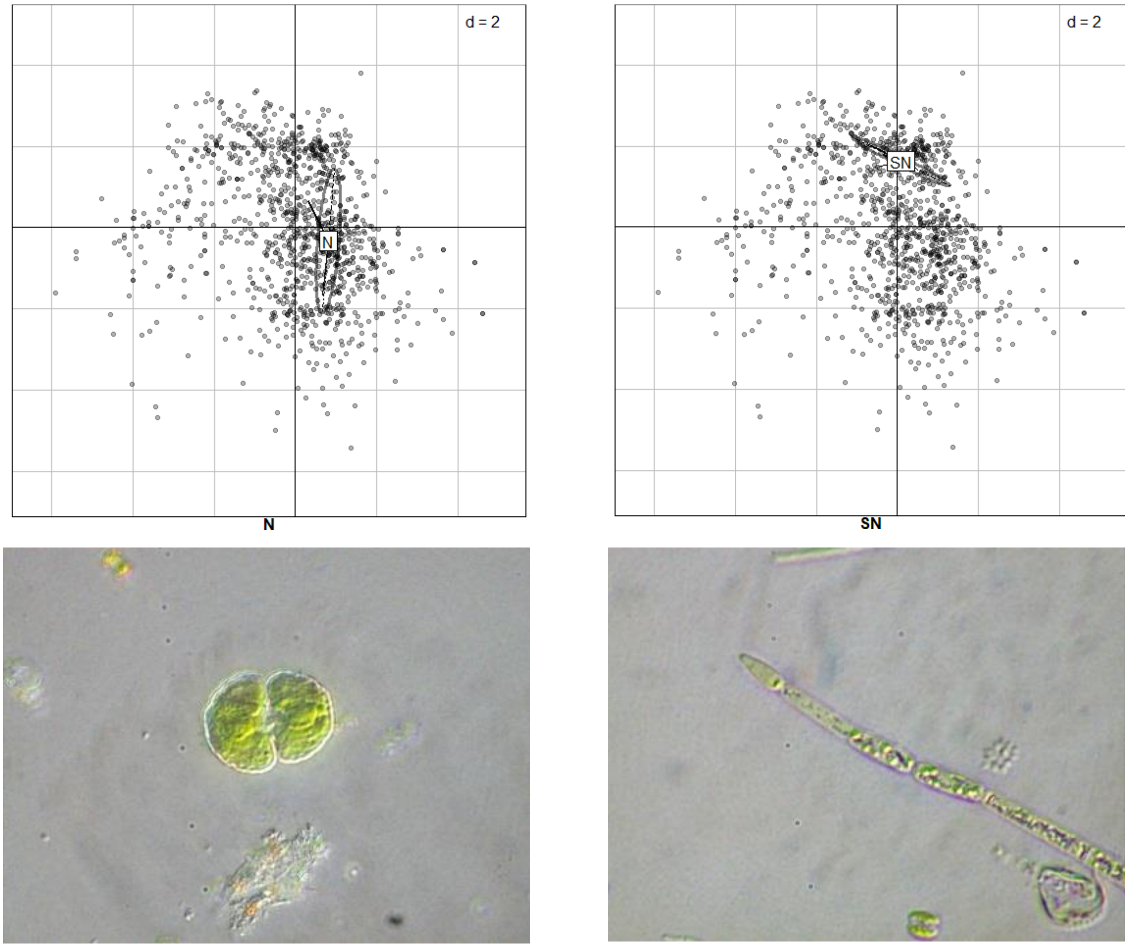
Functional groups with central (i.e. **Group I**, Fig. 12), and intermediate niche positions (**Group III** , Fig. 14.), involve taxa typical for rivers (Rojo et al., 1994; Reynolds and Descy, 1996; Várbíró et al., 2007). Due to their downstream flushing from the benthic habitats, tychoplanktic diatoms (**TIB**) of **Group**, **I** occurred in most samples >85% (Fig. 12). The general occurrence of this group at the sampling locations resulted in its central position and less explained by intermediate niche breadth which supports our first hypothesis partially. On the other hand, tychoplanktic diatom taxa merged in group **TIB**, which showed the highest distribution in rivers that are sensitive to sedimentation (Köhler, 1997; Istvánovics et al., 2012). Therefore, in impounded and low river segments, the impact of lower water velocity and competitive advantage of truly, lake-characteristic euplanktic elements impacted their regional distribution by reducing their tolerance range. The **X2** and **X3** FGs from the same **Group I** include elements (with lower occurrence in the sample units), that are mostly small-sized flagellates (i.e. *Plagioselmis, Chrysococcus*) preferring average conditions both in terms of trophic and hydraulic characteristics but avoid extremities (Fig. 12). Recent results suggest that these algae prefer medium and low discharge events, and due to the frequently occurring arid periods they become dominant elements of the phytoplankton in large rivers like in the River Loir and River Danube (Abonyi et al., 2012, Abonyi et al, 2018b). However, it is reasonable to suppose that in harsher environmental situations (in atypical hydrological conditions: e.g. high floods, elevated TSM) these taxa are suppressed quickly, or outcompeted by other elements of the plankton, which reduces their niche breadth. The results were exactly opposite to our expectations because we supposed that in central position these FGs would have wide instead of intermediate niche breadth.



TIB *Navicula lanceolata* Ehrenberg **X3** *Chrysococcus biporus* Skuja

Figure 12. **Group I.** (e.g.**TIB**, **X3**) -central niche position, intermediate niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche.

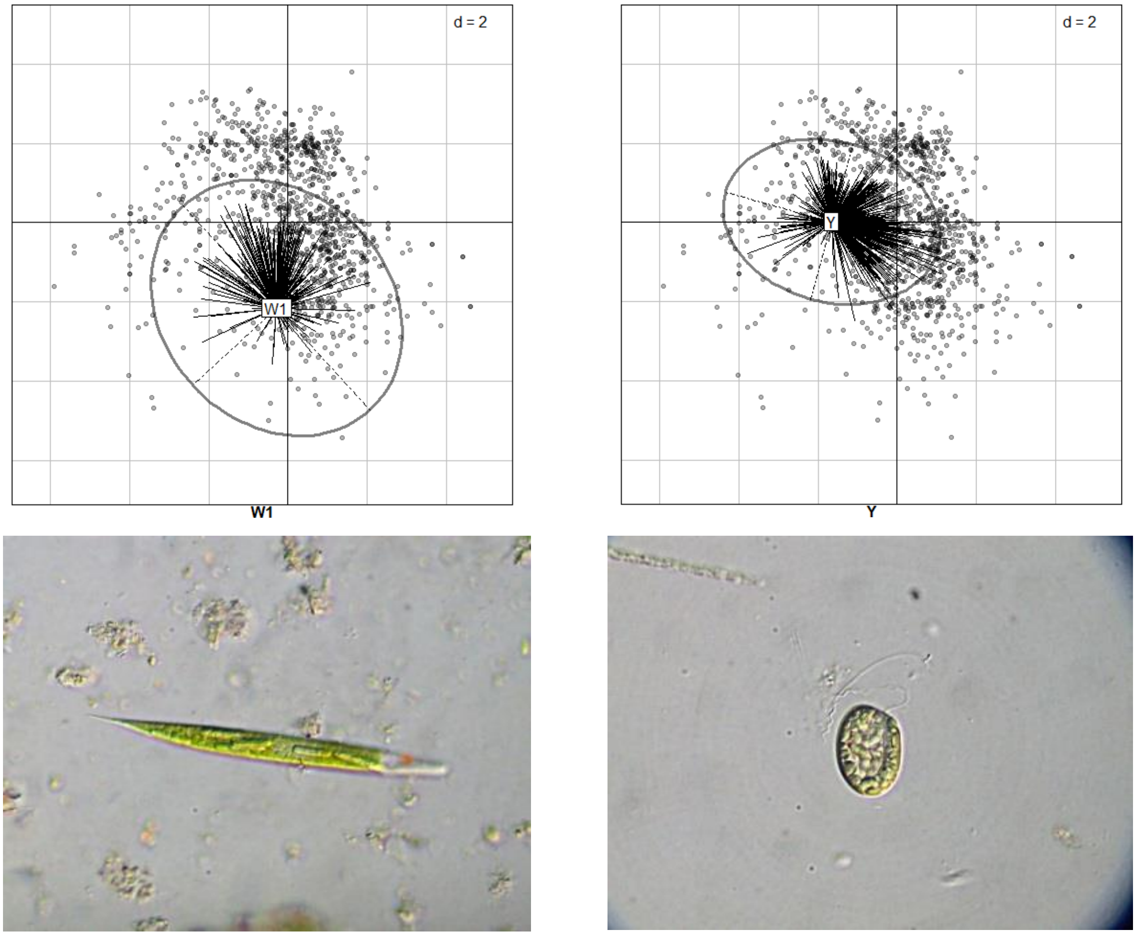
Group II (Fig. 13) merged FGs with intermediate niche position and narrow breadth, compared to **Group V** (Fig. 16.) which had marginal position and narrow breadth. Elements of these latter two cluster groups do not occur frequently in riverine assemblages and merges limnophilic taxa characteristic for lakes (Borics et al, 2007; Várbíró et al., 2007; Padisák et al., 2009). Furthermore, functional elements clustered in these niche groups occurred only at a few sites or rivers (i.e. <2%) with low biomass, therefore showing non significant position in the realised niche space. Here we argue that these niche groups appear in those river segments and in time periods when and where the source-sink dynamics are potentially the most relevant process affecting phytoplankton composition.



N *Cosmarium* spp.

SN *Raphidiopsis raciborskii* (Woloszynska) Aguilera & al.

Figure 13. **Group II.** (e.g. **N, SN**) - intermediate niche position, narrow niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche.

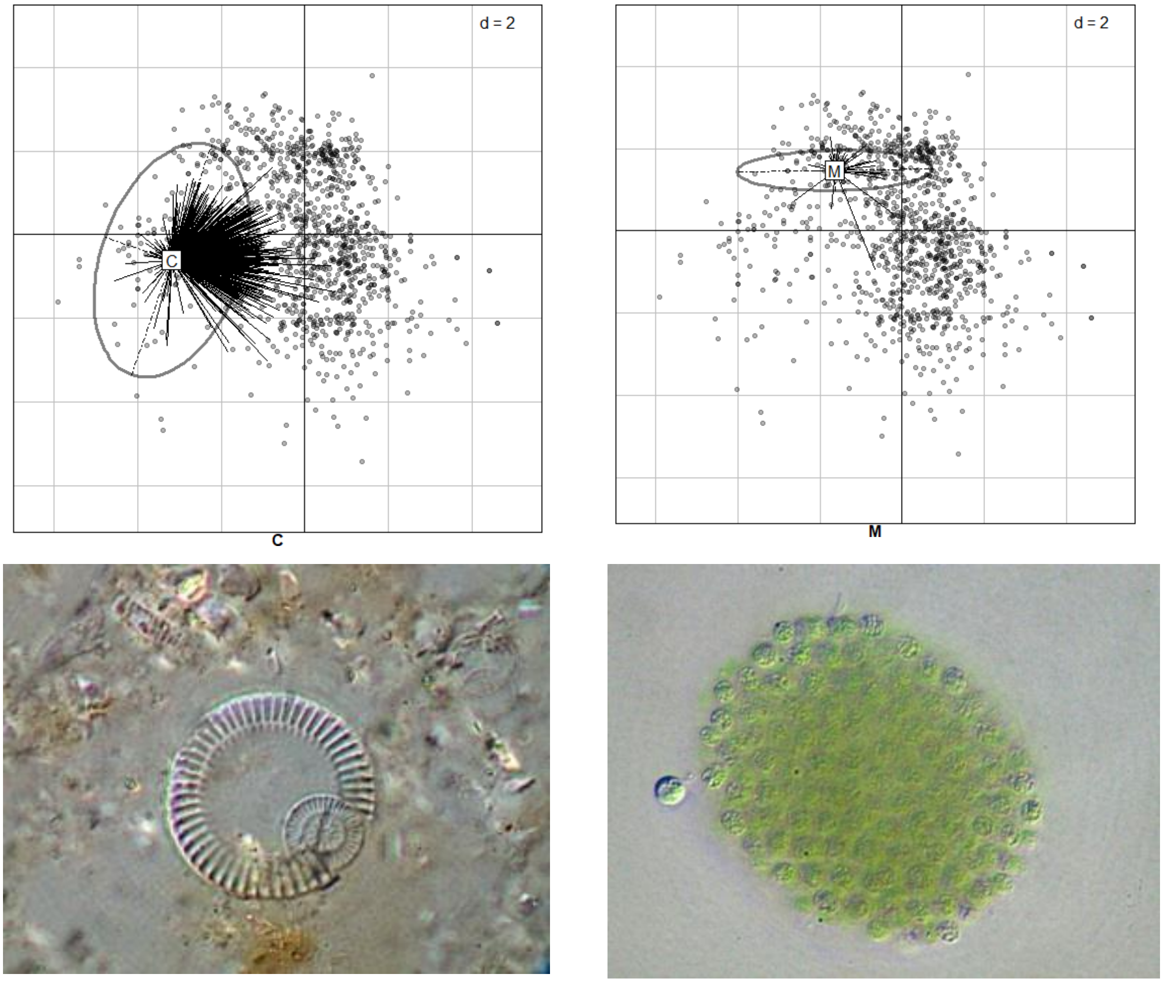


W1 *Lepocinclis acus* (O.F.Müller)& B.Marin Melkonian

Y *Cryptomonas ovata* Ehrenberg

Figure 14. **Group III.** (e.g. **W1**, **Y**) - intermediate niche position, intermediate niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche.

Since we hypothesised that marginal niche position coincides with narrow niche breadth the niche space represented by **Group IV** (Fig. 15) also contradicts our hypothesis. The FGs in this group have marginal niche positions with intermediate niche breadth. The most characteristic member in this group for the studied rivers is codon **C**. Since centric diatoms belonging to this FG (e.g. *Stephanocyclus meneghinianus, Pantocsekiella ocellata* (Pantocsek) K. T. Kiss & Ács, *Discostella stelligera* (Cleve & Grunow) Houk & Klee, *Stephanodiscus* spp.) are highly characteristic in phytoplankton of rivers (Reynolds and Descy, 1996; Kiss et.al., 2012; Stanković et al., 2012; Bolgovics et al., 2017), our finding seems unrealistic.

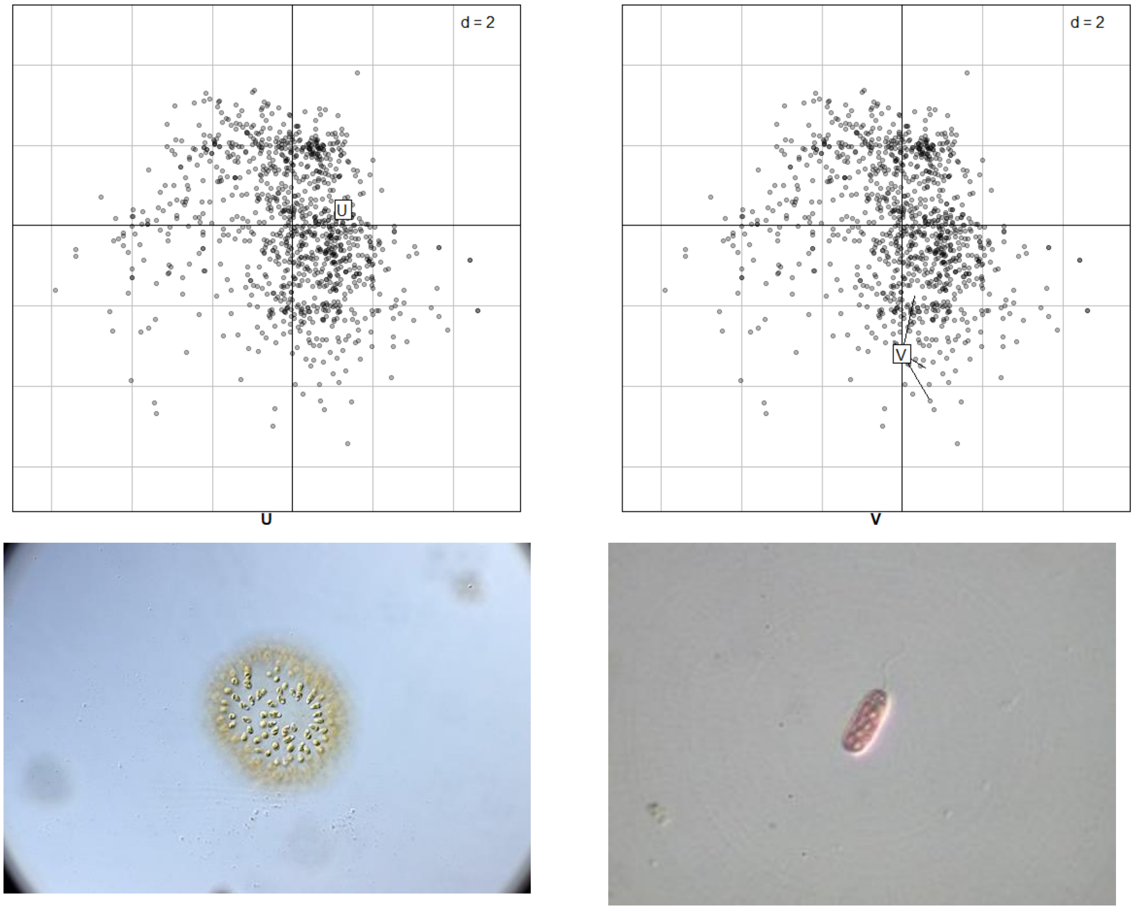


C *Stephanocyclus meneghinianus* vs. smaller *Discostella stelligera*

M *Microcystis flos-aquae* (Wittrock) Kirchner

Figure 15. **Group IV**. (**C**, **M**) **-** marginal niche position, intermediate niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche.

However, considering that functional group **C** is strongly related to high biomass communities, one may expect that bloom conditions potentially shift the position of the **C** group from the central niche position that would otherwise stand for the most characteristic habitat conditions. Furthermore, elements of this cluster group are also present in low biomass assemblages and are sensitive to sedimentation and then (and depending on the actual discharge conditions) may become resuspended again along with other meroplanktic taxa (Istvánovics and Honti, 2011) both in small and large rivers. Therefore, despite its marginal niche position, this group has an intermediate niche breadth.

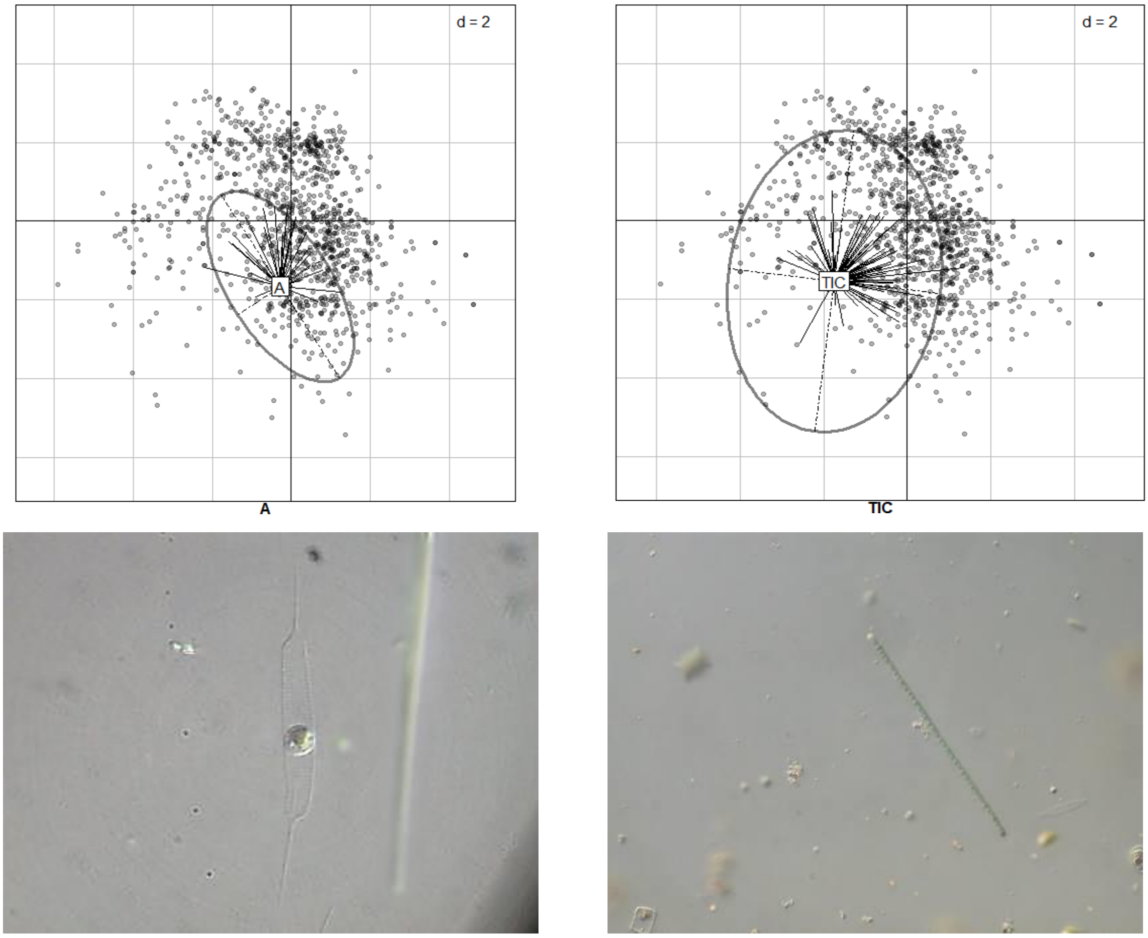


U *Uroglena* sp.

V *Chromatium okenii* (Ehrenberg) Perty

Figure 16. **Group V.**(**U**, **V**) - marginal niche position, narrow niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche. Notice: *Uroglena* sp. photo used with the permission of Dr. Enikő Török Krasznai.

The marginal position of **Group VI** (Fig. 17.) was not surprising, as it consists mainly of benthic filamentous cyanobacteria FG (i.e., **TIC)** characteristic for rhithral or dammed sections of rivers. In this section of the rivers, they are primary components of phytobenthos (i.e., epilithon, epiphyton) and appear in the downstream section as tychoplanktic elements usually in low biomass range. The wide breadth (i.e. tolerance range) of FG belongings to this niche group can be explained rather by contrasting characteristics of the preferred habitats.



A *Urosolenia longiseta* (O. Zacharias) Edlund & Stoermer

TIC *Oscillatoria* sp.

Figure 17. **Group VI. (A**, **TIC)-** marginal niche position, wide niche breadth. Graphical visualisation of relevant FGs realised niche space with characteristic taxa photos. Dots on graphs represent sample distribution in the niche space. Ellipses envelop the FGs' realized niche.

The position of the identified cluster groups in the first, mostly trophic-related axis of the OMI plain clearly shows the differences between lake and river phytoplankton functional composition.(Fig.10a) The high biomass eutrophic phytoplankton in lakes are frequently dominated by bloom-forming cyanobacteria belonging to **Group I** (e.g. **H1**: *Dolichospermum* spp.) **Group II** (e.g. **S_N**: *Raphidiopsis raciborskii*) and **Group IV** (**S1***: Planktothrix* spp., **M**: *Microcystis* spp.). These elements in rivers indicate anthropogenic impacts on the watershed. However, the distribution of these elements was not significantly different from the random distributions in rivers supported otherwise by non-significant P values of their niche positions (e.g. **H1**, **S_N,** and **S1**).

A significant marginal position was characteristic only for the **M** functional group, (**Group IV**) which occurred at mostly the lower biomass range,(Fig. 10a) but reached extremely high biomass in a river segment which explicitly explains its niche space position (Fig. 15).

These FGs are expected to be characteristic merely for hypertrophic dammed-up river sections where lake-like conditions prevail (Fabbro and Duivenvoorden, 1996). These K-strategist functional elements both need long time periods to establish high biomass assemblages (Reynolds, 2006) and are non-adapted to highly turbid riverine conditions (Padisák et al., 1999). Accordingly, these FGs are scattered along the second OMI axis determined primarily by WRT and water discharge, including those functional groups that create the so-called source-sink-populations and cannot be considered as autochthonous elements of the potamoplankton (Fig 10b). Thus, the niche structures of these groups must depend on the characteristics of the watershed and are shaped by stochastic (i.e. merely hydrological) processes.

Although rivers exclusively from the Carpathian Basin were investigated in this study, our conclusions are not restricted to this region but should be considered for riverine planktic assemblages in other geographic areas. Since the rather harsh (turbid) physical constraints that the riverine environments can provide for the elements of the phytoplankton are highly similar everywhere in the world regardless of latitudinal differences, the composition of river phytoplankton also shows considerable similarities (Rojo et al., 1994).

4 Conclusions

Phytoplankton is the basic element of the foodchain of large rivers and smaller rivers and also of the hydromorphologicaly modified ones. Protection and restoration of these systems requires to understand how phytoplankton is recruited, increases or decreases its biomass, and changes its composition. Hundreds of papers addressed these and related issues, but in my thesis I aimed to focus on two important but less studied topics: how phytoplankton biomass depends on the cumulative daily irradiance, and how riverine phytoplankton functional groups are positioned in a multivariate niche space.

In my thesis, I have shown that cumulative daily solar radiation (CDSR) plays a significant role in determining the biomass of phytoplankton in rivers. We found that different types of rivers respond differently to solar radiation, both in terms of the rate of increase and the amount of variance explained. Given the strength of the relationship between CDSR and chlorophyll-*a* (Chl-*a*), it is important to include solar irradiance in empirical models that predict phytoplankton biomass, particularly in light-limited eutrophic rivers.

Global warming affects the Earth’s hydrological processes in many ways. The impact of increased river runoff on catchment phosphorus levels has been well documented. By increasing nutrient loads, global warming indirectly affects riverine phytoplankton. However, our study has shown that Global warming may have a more direct effect on river phytoplankton biomass. The increased solar radiation expected in many regions of the Earth has a direct and significant impact on river phytoplankton biomass. This must be taken into account when developing future predictive models for primary producers in riverine ecosystems, with implications for water quality management.

I applied the Outlying Mean Index (OMI) approach to riverine phytoplankton assemblages and obtained reliable results for the niche characteristics of phytoplankton functional groups (FGs) as defined by Reynolds. Our hypothesis that FGs with a central niche position would have a wide niche breadth while those with a marginal niche position would have a narrow niche breadth was not supported by our results. Contrary to our expectations, we found functional groups with both central niche positions and intermediate niche breadths as well as marginal niche positions with wide niche breadths. The lack of a relationship between these two niche characteristics suggests that the occurrence of FGs in rivers is influenced by both their niche breadth and their niche position. Characterizing these niche variables can enhance our understanding of the factors that determine the distribution of phytoplankton FGs in rivers.

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7 Results in Thesis Points

7.1 The role of cumulative daily solar radiation and water residence time in shaping spatio-temporal variation of phytoplankton biomass in temperate rivers

7.1.1 Cumulative solar irradiance has a significant effect on riverine phytoplankton biomass dynamics in both river types

Based on slope values of the CDSR-Chl-*a* relationship two main shapes of phytoplankton biomass response curves to light exposure periods can be distinguished:

1. unimodal for rhithral rivers with coarse substrate showing a lower value of slopes, β max.~ 2,
2. monotonously increasing for potamal rivers with fine substrate characterised with highest slope values, β max.=5.

The shape of the two characteristic regression slopes lines reveals that in potamal rivers longer (~30-60 days) light exposure period, while in rhithral rivers a shorter one (~10-30 days) is required for pronounced phytoplankton biomass increment. In the River Danube shape of the curves explaining higher biomass increment was unimodal similar to that of rhithral rivers. However, in the upper stretch of the Danube, even a much shorter (7-12 day long) CDSR period is required for the significant increment of the phytoplankton biomass.

This phenomenon can be explained by the large numbers of connected reservoirs, where the altered hydrological and trophic conditions are coupled with compositional and biomass changes of phytoplankton assemblages. The decrease in the slope values in the range of CDSR> 40 days in the Danube might be explained by the minor contribution of meroplankton dynamics (i.e. sedimentation→ high reproduction rate at bottom→ resuspension) to biomass increment inRiver Danube even in case of the longest light exposure. The explained Chl-*a* variances (R^2) of the applied linear regression models were closely related to the slope β values. Non- significant results were characteristic for the rivers (or river-segments) with short water residence time (< 6-8 days).

7.1.2 Hydrological characteristics have a pronounced influence on the relationship between phytoplankton biomass and light exposure

3D plots were used for the visualisation of the impact of water residence time on CDSR-Chl-*a* relationship and based on the plots shape, it was found that changes in WRT periods significantly affected the correlation between cumulative solar radiation periods and biomass changes. Nevertheless, for the River Tisza, the 3D plot shape showed a bimodal character, which can be clearly explained by the inflow of the largest eutrophic River Szamos and Maros (i.e. biomass increment) and dammed middle Tisza section (i.e. sedimentation loss of diatoms). In case of the River Danube the water residence periods were longer than corresponding CDSR periods explaining the highest biomass increments. These findings could be explained by typological differences (i.e. upper rhitrhal like, lower potamal) along the Hungarian stretch of the river. However, in both river types, the WRT periods were significantly shorter than the corresponding CDSR periods required for the significant biomass increment. In rhithral rivers this controversy can be explained by the way of recruitment of phytoplankton. In this river type tychoplanctic diatoms constitute the majority of phytoplankton assemblages, and during their benthic life stage a longer time frame (i.e. at least 30 days) is required for them to develop high biomass assemblages. In the potamal rivers a special meroplankton dynamics (i.e. sedimentation→ high reproduction rate at bottom→ resuspension) of the centric diatoms could serve as an explanation of WRT< CDSR controversy.

7.2 Niche characteristics of phytoplankton functional groups in temperate rivers and their role in regional distribution

7.2.1 Niche space characteristics, position and breadth of the riverine FGs were determined primarily by trophic and hydrological variables

Almost all the FGs described in the former literature were represented in this study. The largest distribution showed FGs adapted to riverine habitat, while those with the lowest distribution were for certain types of lakes or rhithral river segments. OMI analyses reveal that the niche space of phytoplankton FGs was primarily delimited by nutrients (87 % of variance) and by hydrological constraints (6.4 % variance). The results were in good agreement with the concluding remarks of former studies; that composition and biomass in riverine phytoplankton are strongly influenced by nutrients and hydrological variables. Water discharge and residence time have special importance (i. e. strongly related to downstream flow), these variables determine the time frame necessary for the phytoplankton to multiply and establish potamoplankton assemblages. Based on niche position and niche breadth calculated by OMI analysis, the K-mean clustering merged phytoplankton functional groups in six Niche Groups. **Group I** merges FGs with central niche position and intermediate niche breadth; niche **Group II** includes FGs with intermediate niche position and narrow breadth; and **Group III** includes most of the identified FGs with intermediate niche positions and intermediate niche breadth. Functional groups in **Group IV** have intermediate niche breadth, in **Group V** have narrow breadth, and in **Group VI** the FGs have wide breadth. The members of all three groups have marginal positions in the realised niche space. OMI analysis revealed that functional groups that rarely occur in rivers showed mostly non-significant results regarding niche space characteristics.

7.2.2 Niche space characteristics play asignificant role in the regional distribution of the phytoplankton functional groups

Linear regression analyses revealed that phytoplankton functional groups with larger tolerance range, were widely distributed in the studied riverine network (R^2=0.3847, P <0.001, $F_{[2, 30]}$=19.38), while those with central position occurred more frequently, therefore with higher distribution (R^2=0.3453, P <0.001, $F_{[1, 30]}$ =16.35). The position and niche breadth of the functional groups was related weakly and marginally significantly to each other (R^2= 0.115, , P=0.053, $F_{[1, 31]}$=4.03), which means that their role in regional occupancy can be separated. Nevertheless, multiple linear regression (R^2adj=0.515, P <0.001, $F_{[2, 30]}$ =17.99) proved that both niche characteristics have similar significance in the regional distribution of the phytoplankton functional groups.

7.2.3 The hypothesis that FGs with central niche positions have wide, while those with marginal niche positions have narrow niche breadth was not supported by the results

Regarding the niche characteristics of FGs, two aspects must be considered in rivers. First, a methodological limitation, as the regional occupancy was based on presence/absence data and second, the strongly eclectic (variable) nature of the riverine phytoplankton. However, the first is compensated by the fact that FGs merely merge more than one taxon. The second issue is that the composition of phytoplankton in a riverine network is highly stochastic. In the rhithral river sections, the spatio-temporal changes in the composition of low biomass functional assemblages are impacted by source-sink dynamics (i.e. oxbows, tributaries, phytobenthos as sources and the riverine habitat as a sink), and by stochastic hydrological events. Further downstream the composition of functional assemblages (besides the source-sink dynamics) is governed by deterministic processes like possession of adaptive traits that help them in competition for light and resources, or tolerating sedimentation, etc. Furthermore, dam construction and inflowing reservoirs may influence the niche space characteristics of all FGs. All these processes may explain why the niche position of FGs in rivers is different from what we expected knowing their habitat templates in lacustrine environments. It also explains why some of the functional elements characteristic of rivers have niche space position and breadth which contradict our hypothesis (e.g.: **X2**, X3, TIB, C, TIC) and why limnophilic groups characteristic of lakes are scattered along the two main deterministic axes of the OMI planes.

8 List of publications

8.1 Publications related to the dissertation

Várbíró, G., Padisák, J., **Nagy-László**, **Z**., Abonyi, A., Stanković, I., Udovič, M. G. and Borics, G. (2018). How length of light exposure shapes the development of riverine algal biomass in temperate rivers? Hydrobiologia, 809, 53-63. https://doi.org/10.1007/s10750-017-3447-1 **IF**: **2.325**, **SJR: Q1**

Nagy-László, Z., Padisák, J., Borics, G., Abonyi, A., B-Béres, V. and Várbíró, G. (2020). Analysis of niche characteristics of phytoplankton functional groups in fluvial ecosystems. Journal of Plankton Research, 42, 355-367. https://doi.org/10.1093/plankt/fbaa020 **IF: 2.455, SJR: Q1**

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Nagy-László, **Zs**., P, Holló I., Krímer, T (2002). A cianid- és nehézfémszennyezés nyomon követése és hatásuk az Alsó-Tisza planktonikus élővilágára. Acta Biologica Debrecina - Supplementum Oecologica Hungarica 11 117-133.

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Holló, P., I., Petri, A., **Nagy-László**, **Zs**. (2008). Adatok a Dél-Alföld kis vízfolyásainak, valamint kis és közepes állóvizeinek makroszkópikus vízi gerinctelen faunájához. Acta Biologica Debrecina-Supplementum Oecologica Hungarica, 18, 191-201.

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Borics, G., Nagy, L., Miron, S., Grigorszky, I., **László-Nagy**, **Z**., Lukács, B. A., G-Tóth , L. and Várbíró, G. (2013). Which factors affect phytoplankton biomass in shallow eutrophic lakes? Hydrobiologia, 714, 93-104. http://dx.doi.org/10.1007/s10750-013-1525-6 **IF: 2.212, SJR: Q2**

Borics, G., Görgényi, J., Grigorszky, I., **László-Nagy**, **Z**., Tóthmérész, B., Krasznai, E. and Várbíró, G. (2014). The role of phytoplankton diversity metrics in shallow lake and river quality assessment. Ecological Indicators, 45, 28-36. http://dx.doi.org/10.1016/j.ecolind.2014.03.011 **IF: 3.444**, **SJR: Q1**

Borics, G; Lukács, B. A., Grigorszky, I., **László-Nagy**, **Z**., G-Tóth, L., Bolgovics, Á., Szabó, S., Görgényi, J., Várbíró, G. (2014). Phytoplankton-based shallow lake types in the Carpathian basin: steps towards a bottom-up typology. Fundamental and Applied Limnology, 184, 23-34. http://dx.doi.org/10.1127/1863-9135/2014/0518 **IF: 1.077**, **SJR: Q2**

Deli, J., Gonda, S., **Nagy**, **L. Z**., Szabó, I., Gulyás-Fekete, G., Agócs, A., Marton, A. and Vasas, G. (2014). Carotenoid composition of three bloom-forming algae species. Food Research International, 65, 215-223. http://dx.doi.org/10.1016/j.foodres.2014.05.020 **IF: 3.518**, **SJR: Q1**

Ács, É., Borics, G., Boda, P., Csányi, B., Duleba, M., Engloner, A., Erős, T., Földi, A., Grigorszky, I., György, Á. I., Kiss K., T., K.-Szilágyi, E., Lukács, B. A., **Nagy-László**, **Zs**., Pozderka, V., Sály, P., Szalóky, Z., Szekeres, J., Trábert, Zs., Várbíró, G. (2015).

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Nagy-László, **Zs**., Várbíró, G., Abonyi, A., Padisák, J., Borics, G. (2016). A planktonikus növényi biomassza és a trofitás változása a Tisza hazai szakaszán és mellékfolyóiban. Hidrológiai Közlöny, 96, 64-69.

Bolgovics, Á., Ács, É., Várbáró, G., Görgényi, J., Kiss, K. T., Földi, A., **Nagy-László**, **Zs**., Trábert, Zs.,Borics, G., (2017). Benthic diatom-based lake types in Hungary. Fundamental and Applied Limnology, 189, 105-116. http://dx.doi.org/10.1127/fal/2016/0942 **IF: 1.361, SJR: Q2**

Bolgovics, Á., Várbíró, G., Ács, É., Trábert, Z., Kiss, K T., Pozderka, V., Görgényi, J., Boda, P., Lukács, B. A., **Nagy-László**, **Z**., Abonyi, A. and Borics, G. (2017). Phytoplankton of rhithral rivers: its origin, diversity and possible use for quality-assessment. Ecological Indicators, 81, 587-596. https://doi.org/10.1016/j.ecolind.2017.04.052 **IF: 3.983, SJR: Q1**

8.3 Conference attendances related to the dissertation

Nagy-László, **Zs**., Padisák, J., Borics G., Abonyi A., Béres-B. V., Várbíró G.: Fitoplankton funkcionális csoportok niche terének elemzése és tipizálása a Közép-Duna vízgyűjtőn. X. Algológus találkozó és továbbképzés, 9 May 2017, Budapest, Hungary. **oral presentation**

Várbíró G., Padisák, J., **Nagy-László**, **Zs**., Abonyi, A., Stanković, I., Udovič, M. G., Béres-B., V., Borics, G.: Does the length of light exposure matter for algal biomass development in temperate rivers? 10.Symposium for European Freshwater Science, 2-7 July 2017, Olomuc, Czech Republic. **poster presentation**

Nagy-László, **Zs**., Borics, G., Abonyi, A., Padisák, J., Várbíró, G.: Phytoplankton functional niches in fluvial ecosystems. 1st. International Conference on Community Ecology, 28-29 September 2017, Budapest, Hungary. **oral presentation**

Borics G., **Nagy-László**, **Zs**., Várbíró G.: A napfénytartalom és fitoplankton kapcsolata folyókban. LIX. Hidrobiológus Napok, A hidrobiológia helye a víztudományokban, 4-6 October 2017, Tihany, Hungary. **oral presentation**

Nagy-László, **Zs**., Borics, G., Abonyi, A., Padisák, J., Várbíró, G.: Fitoplankton funkcionális niche-ek jellemzése a Közép-Duna Vízgyűjtőn, Kvantitatív Ökológiai Szimpózium, 23 October 2017, Budapest, Hungary. **oral presentation**

Nagy-László, **Zs**., Padisák J., Borics G., Abonyi A., Béres-B., V., Várbíró G.: Fitoplankton funkcionális csoportok niche terének elemzése és tipizálása a Közép-Duna vízgyűjtőn. XII. Algológus találkozó és továbbképzés, 9 May 2019, Budapest, Hungary. **oral presentation**

8.4 Other conference attendances

Nagy-László, **Zs**., Várbíró G., Abonyi A., Padisák J., Borics G.: A planktonikus növényi biomassza és a trofitás változása a Tisza hazai szakaszán és mellékfolyóiban. LVII. Hidrobiológus Napok, Genetikai és molekuláris biológiai kutatások jelentősége a hidrobiológiában, 7-9 October, 2015, Tihany, Hungary. **oral presentation**

B.-Béres, V., **Nagy-László, Zs**., T-Krasznai, E., Stenger-Kovács, Cs., Barreto, S., Kiss, G., Buczkó, K., Abonyi., A.: Hagyományteremtés a mikroszkópikus világ tudományos ismeretterjesztésében: az „év algája” szavazás. LVII Hidrobiológus Napok, Genetikai és molekuláris biológiai kutatások jelentősége a hidrobiológiában, 7-9 October 2015, Tihany, Hungary**. poster presentation**

Nagy-László, **Zs.**, Várbíró, G., Abonyi, A., Padisák, J., Borics, G.: A planktonikus növényi biomassza és a trofitás változása a Tiszában és mellékfolyóiban, VIII. Algológus találkozó és továbbképzés, 3 december 2015, Budapest, Hungary. **oral presentation**

9 Appendix

Appendix 1, Table 1. Database with sampling sites , river types and descriptive statistics of physical and chemical variables characteristic for the studied

	River Name	Sampling site	type	River system	Number of samples	Average WRT (days)	Average Chlorophyll-a (µg l^{-1})	Min-Max Chlorophyll-a (µg l^{-1})	Average Non-organic nitrogen (mg l^{-1})	Min-Max Non-organic nitrogen (mg l^{-1})	Average Orthophosphate-phosphorus (µg l^{-1})	Min-Max Orthophosphate-phosphorus (µg l^{-1})
1	Arany-patak	Nagycenk	rhitral	Danube	99	2.7	4.83	2.2 - 24.7	4.31	1.13 - 8.68	133.56	10 - 724
2	Bán-patak	Bánhorváti	rhitral	Tisza	145	2.7	5.39	1.3 - 327	1.76	0.33 - 5.37	77.43	2 - 587
3	Berettyó	Berettyóújfalu	potamal	Tisza	289	12.9	5.43	1.3 - 348.3	1.84	0.26 - 6.01	249.99	16 - 1738
4	Berettyó	Pocsaj	potamal	Tisza	315	12.8	5.11	1.1 - 166.7	1.75	0.14 - 6.23	82.11	3 - 447
5	Berettyó	Szeghalom	potamal	Tisza	297	12.6	5.17	1.3 - 251	1.26	0.15 - 3.61	122.79	7 - 580
6	Bodrog	Bodrogkeresztúr	potamal	Tisza	250	14.6	4.3	1.2 - 42.8	1.54	0.51 - 3.21	68.16	2 - 284
7	Bodrog	Felsőberecki	potamal	Tisza	333	14.8	5.63	1.2 - 80.9	1.70	0.64 - 4.76	67.35	2 - 192
8	Bódva	Borsodszirák	rhitral	Tisza	303	6.2	7.74	1.3 - 178.2	3.32	0.78 - 7.87	63.75	2 - 287
9	Bódva	Hidvégardó	rhitral	Tisza	322	4.9	8.09	1.1 - 120.2	4.09	1.3 - 9.47	82.12	2 - 316
13	Danube	Almásneszmély	potamal	Danube	991	52.4	22.78	1.6 - 401	2.49	0.45 - 5.31	125.79	7 - 544
14	Danube	Budapest	potamal	Danube	880	53.4	13.34	1.1 - 154	2.19	0.48 - 4.48	50.35	2 - 391
15	Danube	Dunaföldvár	potamal	Danube	893	54.2	18.54	1.2 - 227	2.31	0.49 - 5.28	58.13	2 - 4401
16	Danube	Fajsz	potamal	Danube	425	54.3	22.21	1.1 - 234	2.27	0.59 - 4.8	55.73	2 - 212
17	Danube	Mohács	potamal	Danube	403	57.5	22.99	1.4 - 197	2.26	0.63 - 5.01	58.62	2 - 293
18	Danube	Nagytétény	potamal	Danube	711	53.5	14.46	1.2 - 142	2.33	0.52 - 4.5	58.14	2 - 209
19	Danube	Rajka	potamal	Danube	1121	50.5	15.62	1.2 - 197	2.42	0.31 - 5.27	127.51	3 - 639
20	Danube	Szob	potamal	Danube	1088	53.4	11.54	1.1 - 152	2.26	0.7 - 4.75	61.93	2 - 235
21	Danube	Komárom	potamal	Danube	1492	52.8	14.23	1.6 - 448	2.37	0.64 - 7.99	82.77	2 - 479
22	Danube	Esztergom	potamal	Danube	190	52.9	15.11	2.2 - 151.9	2.23	0.58 - 4.44	68.94	7 - 300

23	Danube	Baja	potamal	Danube	1041	57.5	17.81	1.4 - 270	2.18	0.54 - 4.79	56.36	2 - 391
24	Danube	Hercegszántó,	potamal	Danube	608	57.6	21.09	1.5 - 202	2.21	0.48 - 4.7	54.84	2 - 212
25	Danube	Győrzámoly	potamal	Danube	516	47.8	12.97	1.6 - 134	2.28	0.21 - 4.53	78.28	3 - 466
10	Dráva	Barcs	rhitral	Danube	315	24.2	5.52	1.1 - 38	1.44	0.46 - 3.23	40.59	2 - 179
11	Dráva	Drávaszabolcs	rhitral	Danube	316	24.3	7.05	1.4 - 95	1.47	0.04 - 3.34	49.20	3 - 218
12	Dráva	Őrtilos	rhitral	Danube	292	22.3	5.15	1.1 - 31	1.44	0.72 - 3.26	35.38	3 - 111
26	Fehér-Körös	Gyulavári	potamal	Tisza	323	9.6	4.41	1.3 - 176.8	0.78	0.06 - 1.88	49.73	2 - 453
27	Fekete-Körös	Sarkad	potamal	Tisza	329	8.0	4.62	1.3 - 48	0.95	0.04 - 4.43	54.65	2 - 505
28	Fekete-viz	Cun	rhitral	Tisza	240	6.3	9.18	1.6 - 149	2.33	0.17 - 9.18	135.56	29 - 600
29	Felső-Válicka-patak	Zalaegerszeg	rhitral	Danube	74	1.8	8.83	1.7 - 65	0.94	0.03 - 3.24	64.68	2 - 166
30	Hangony-patak	Center	rhitral	Danube	292	2.6	4.95	1.6 - 43	6.27	1.87 - 21.56	706.12	49 - 2631
31	Hármas-Körös	Békésszentandrás	potamal	Danube	255	22.8	6.62	1.3 - 102.8	1.14	0.07 - 2.88	140.87	33 - 543
32	Hármas-Körös	Gyoma	potamal	Tisza	276	23.2	5.95	1.6 - 55.5	1.12	0.09 - 2.64	87.59	5 - 271
33	Hármas-Körös	Magyartés	potamal	Tisza	262	23.5	5.79	1.2 - 99.5	1.35	0.26 - 4.73	128.42	20 - 401
34	Hernád	Gesztely	rhitral	Tisza	356	10.3	9.69	1.2 - 432.3	3.92	1.47 - 8.02	217.72	2 - 590
35	Hernád	Hernádszurdok	rhitral	Tisza	371	9.5	6.79	1.1 - 74.7	4.33	1.49 - 9.14	267.83	2 - 815
36	Hernád	Tornyosnémeti	rhitral	Tisza	396	9.4	6.55	1.2 - 50.4	4.29	1.61 - 9.73	272.61	2 - 815
37	Ipoly	Balassagyarmat	rhitral	Danube	290	11.6	5.13	1.1 - 313.1	3.08	0.67 - 7.89	239.83	3 - 782
38	Kapos	Dombóvár	rhitral	Danube	226	9.0	21.01	1.6 - 87	4.32	1.8 - 10.64	374.74	68 - 2699
39	Kapos	Kurd	rhitral	Danube	89	8.7	21.66	1.7 - 321	4.31	0.41 - 8.98	316.92	10 - 1454
40	Kapos	Pincehely	rhitral	Danube	122	8.5	28.93	1.7 - 963	4.22	0.86 - 9.11	251.69	68 - 777
41	Karasica	Villány	rhitral	Danube	236	3.0	29.6	3.7 - 214	2.93	0.27 - 7.44	74.32	7 - 326
42	Kettős-Körös	Békés	potamal	Tisza	269	14.9	5.2	1.3 - 71.4	0.83	0.03 - 2.55	47.09	2 - 398
43	Kraszna	Mérk	potamal	Tisza	419	9.0	8.26	1.1 - 239.1	2.77	0.08 - 10.18	457.32	31 - 1858
44	Lajta-főág	Hegyeshalom	potamal	Danube	384	6.5	5.5	1.6 - 160.8	2.84	0.4 - 7.64	92.22	7 - 293
45	Marcal	Mórichida	potamal	Danube	238	8.8	9.16	2 - 224.8	4.08	0.07 - 14.21	356.70	10 - 1829
46	Marcal	Mersevát	potamal	Danube	51	7.4	9.6	2 - 141	1.94	0.28 - 5.78	64.24	3 - 189
47	Maros	Makó	potamal	Tisza	490	24.0	19.51	1.2 - 984	3.12	0.21 - 34.33	72.34	2 - 1839

48	Maros	Nagylak	potamal	Tisza	458	23.9	16.84	1.3 - 549	1.71	0.19 - 5.98	42.58	3 - 186
49	Mosoni-Duna	Győr	potamal	Danube	382	18.6	12.62	2 - 250.8	2.51	0.14 - 8.29	121.04	7 - 440
50	Mosoni-Duna	Mecsér	potamal	Danube	435	12.0	8.44	1.6 - 203.7	2.03	0.1 - 8.63	80.35	7 - 505
51	Mura	Letenye	rhitral	Danube	57	14.9	7.56	2 - 124.5	1.48	0.29 - 2.97	52.70	16 - 95
52	Rába	Győr	rhitral	Danube	551	14.4	18.29	2 - 410	3.00	0.15 - 12.98	121.99	3 - 632
53	Rábca	Lébény	rhitral	Danube	376	10.5	8.82	1.6 - 292.3	2.90	0.21 - 110.66	278.16	16 - 1291
54	Répce	Répcevis	rhitral	Danube	47	4.8	10.37	3 - 70	2.86	1.15 - 4.56	137.28	33 - 1239
55	Sajó	Kesznyéten	rhitral	Tisza	479	17.8	10.42	1.1 - 501	3.64	1.29 - 12.93	258.47	29 - 1434
56	Sajó	Miskolc	rhitral	Tisza	538	18.0	8.51	1.2 - 279.6	3.44	1.05 - 13.62	142.13	10 - 482
57	Sajó	Sajókaza	rhitral	Tisza	365	9.5	6.4	1.1 - 236.3	2.52	0.55 - 7.72	122.17	2 - 310
58	Sajó	Sajólád	rhitral	Tisza	413	17.6	8.35	1.1 - 139.8	3.50	1.16 - 7.4	234.17	36 - 763
59	Sajó	Sajópüspöki	rhitral	Tisza	551	9.6	5.54	1.1 - 179.5	2.37	0.92 - 7.1	105.90	2 - 489
60	Sajó	Sajószentpéter	rhitral	Tisza	501	18.4	7.55	1.2 - 421.6	3.20	1.18 - 12.27	146.53	2 - 554
61	Sebes-Körös	Körösladány	rhitral	Tisza	272	14.6	5.98	1.5 - 68.1	1.45	0.37 - 3.49	103.29	16 - 396
62	Sebes-Körös	Körösszakál	rhitral	Tisza	332	7.3	6.96	1.4 - 91	1.88	0.52 - 4.66	131.79	7 - 746
63	Szamos	Csenger	potamal	Tisza	448	17.0	11.25	1.1 - 519.5	1.31	0.08 - 8.41	68.69	3 - 479
64	Szamos	Tunyogmatolcs	potamal	Tisza	244	16.9	11.13	1.1 - 480.2	1.37	0.07 - 4.28	82.38	2 - 1050
65	Tarna-patak	Verpelét	rhitral	Tisza	285	4.1	6.41	1.2 - 303.3	2.79	0.2 - 6.22	152.00	2 - 3064
66	Tisza	Aranyosapáti	potamal	Tisza	239	24.0	8.18	1.1 - 216.9	0.91	0.06 - 3.61	56.54	3 - 368
67	Tisza	Balsa	potamal	Tisza	268	29.6	8.55	1.1 - 177	0.97	0.02 - 3.37	69.17	3 - 1219
68	Tisza	Tiszalök	potamal	Tisza	312	29.3	5.62	1.1 - 99.3	1.22	0.19 - 4.08	53.86	3 - 244
69	Tisza	Kisköre	potamal	Tisza	256	35.5	5.83	1.7 - 104	1.25	0.32 - 2.58	52.35	7 - 391
70	Tisza	Mindszent	potamal	Tisza	293	45.0	6.28	1.2 - 318.5	1.55	0.37 - 9.3	82.02	13 - 401
71	Tisza	Polgár	potamal	Tisza	382	34.6	7.89	1.1 - 178.6	1.69	0.21 - 5.03	57.98	2 - 440
72	Tisza	Szolnok	potamal	Tisza	503	36.1	8.05	1.4 - 108.9	1.59	0.27 - 5.83	62.32	7 - 310
73	Tisza	Tápé	potamal	Tisza	302	45.1	6.05	1.4 - 270.9	1.59	0.43 - 7.49	80.19	2 - 293
74	Tisza	Tiszabecs	rhitral	Tisza	265	12.9	3.26	1.1 - 188.2	0.81	0.06 - 3.67	37.70	2 - 290
75	Tisza	Tiszafüred	potamal	Tisza	377	34.4	7.1	1.6 - 158	1.52	0.09 - 6.31	64.37	2 - 391

76	Tisza	Tiszakeszi	potamal	Tisza	352	34.5	7.62	1.2 - 81	1.66	0.24 - 4.85	57.83	2 - 205
77	Tisza	Tiszalök	potamal	Tisza	351	34.3	7.2	1.1 - 114.1	1.40	0.16 - 4.6	36.11	2 - 143
78	Tisza	Tiszasziget	potamal	Tisza	1115	50.9	11.01	1.1 - 393	1.81	0.32 - 9.67	70.69	3 - 391
79	Tisza	Tiszaug	potamal	Tisza	372	37.8	7.91	1.7 - 102	1.48	0.21 - 4.12	79.23	7 - 391
80	Tisza	Záhony	potamal	Tisza	275	23.5	8.28	1.1 - 280.9	0.95	0.04 - 3.42	60.81	6 - 525
81	Túr	Kishódos	potamal	Tisza	269	5.9	5.35	1.1 - 68	0.83	0.11 - 2.78	52.74	9 - 287
82	Zagyva	Jásztelek	potamal	Tisza	386	10.4	14.85	1.6 - 300	3.18	0.51 - 7.52	804.42	176 - 2673
83	Zagyva	Szentlőrinckáta	potamal	Tisza	377	7.5	17.83	1.6 - 380	4.24	0.69 - 10.76	752.48	78 - 3260
84	Zala	Alibánfa, vizmérce	potamal	Danube	112	5.3	6.77	1.7 - 36	1.97	0.69 - 4.08	156.99	17 - 1519
85	Zala	Andráshida	potamal	Danube	127	1.3	8.11	2 - 63	1.93	0.69 - 2.99	59.37	16 - 166
86	Zala	Keszthely-Fenékpuszta	potamal	Danube	331	5.7	32.69	2.2 - 416	0.55	0 - 2.97	59.58	2 - 430
87	Zala	Zalaapáti	potamal	Danube	419	6.0	8.51	1.7 - 98.6	2.00	0.25 - 6.94	183.22	10 - 737
88	Zala	Zalavár-Balatonhidvég	potamal	Danube	463	6.1	105.18	2.2 - 824.9	0.48	0 - 3.41	20.47	2 - 450

Appendix 2, Table 2 .Database of the studied rivers with sampling locations, GPS coordinates and mean ± SE values of the considered environmental variables for the analysis of niche characteristics of phytoplankton Reynolds' FGs in fluvial ecosystems. n- refers to the number of samples.

	Sampling location	latitude	longitude	Watershed	n	Q	WRT	BOD_5	CHA	NH4-N	NO3-N	NO2-N	ORTOP PP	COD_{cr}	TP	TN	pH	COND	TV	TSM
				km^2		m^3 s^{-1}	days	mg l^{-1}	µg l^{-1}	mg l^{-1}	mg l^{-1}	mg l^{-1}	µg l^{-1}	mg l^{-1}	µg l^{-1}	µg l^{-1}		µS cm^{-1}	^{0} C	mg l^{-1}
1	Berettyó, Berettyóújfalu	47.21	21.56	7055	15	8.15 ± 1.52	13.6 ± 0.27	3.83 ± 0.74	20.47 ± 9.66	0.1 ± 0.03	0.82 ± 0.08	0.02 ± 0	121.85 ± 21.24	29.29 ± 1.97	329.13 ± 85.08	1920 ± 173.81	8.04 ± 0.07	619.57 ± 37.36	20.02 ± 1.34	38.07 ± 9.57
2	Berettyó, Kismarja	47.25	21.84	7055	41	8.34 ± 1.23	13.74 ± 0.19	4.02 ± 0.31	7.82 ± 2.86	0.14 ± 0.02	1.1 ± 0.05	0.03 ± 0	58.56 ± 5.66	25.95 ± 1.25	255.46 ± 25.17	2317.07 ± 111.47	7.86 ± 0.02	452.32 ± 17.48	11.87 ± 1.16	109.54 ± 23.62
3	Berettyó, Pocsaj	47.28	21.80	7055	3	8.24 ± 3.83	13.6 ± 0.75	3.5 ± 1.57	5.8 ± 0.9	0.16 ± 0.03	0.97 ± 0.03	0.03 ± 0.01	58.24 ± 11.24	21.63 ± 1.74	398.33 ± 241.05	2600 ± 793.73	7.89 ± 0.08	507 ± 84.06	12.07 ± 2.96	62.33 ± 35.96
4	Bodrog, Sátoraljaújhely	48.35	21.68	12337	27	114.32 ± 15.91	14.56 ± 0.2	3 ± 0.39	3.71 ± 0.47	0.12 ± 0.01	0.97 ± 0.03	0.04 ± 0	60.88 ± 5.81	13 ± 0.73	100.74 ± 6.01	1501.11 ± 74.29	7.89 ± 0.03	346.33 ± 10.93	18.89 ± 0.91	24.93 ± 6.08
5	Bódva, Sajószentpéter	47.96	22.88	1770	8	4.81 ± 2.14	6.41 ± 0.21	4.36 ± 0.57	16.16 ± 6.02	0.07 ± 0.01	2.74 ± 0.16	0.03 ± 0	58.59 ± 14.22	17 ± 1.91	137.5 ± 19.89	3918.75 ± 326.25	7.98 ± 0.04	550.5 ± 27.27	17.46 ± 1.61	31 ± 7.05
6	Dráva, Barcs	45.95	17.44	37490	22	557.98 ± 37.31	23.71 ± 0.15	1.73 ± 0.12	5.38 ± 0.73	0.04 ± 0	0.97 ± 0.07	0.01 ± 0	18.37 ± 2.46	8.91 ± 0.63	58.53 ± 6.48	1334.84 ± 92.08	8.11 ± 0.04	293.92 ± 7.59	16.56 ± 1.17	21.32 ± 3.97
7	Dráva, Drávaszabolcs	45.78	18.20	37490	15	622.8 ± 61.08	23.5 ± 0.23	1.6 ± 0.12	7.47 ± 1.3	0.06 ± 0.01	0.79 ± 0.03	0.01 ± 0	29.09 ± 8.63	7.95 ± 0.65	80.33 ± 13.21	1203.17 ± 112.49	8.14 ± 0.03	300.37 ± 8.56	18.12 ± 1.02	20.07 ± 5.62
8	Duna, Komárom	47.75	18.12	175718	28	2185 ± 161.01	52.35 ± 0.34	3.39 ± 0.34	12.42 ± 2.63	0.03 ± 0	1.62 ± 0.09	0.01 ± 0	33.93 ± 3.48	9.67 ± 0.42	177.14 ± 67.98	2415 ± 180.26	8.08 ± 0.07	362.18 ± 9.64	16.84 ± 0.73	30.64 ± 3.23
9	Duna, Szob	47.82	18.86	181811	27	2395.56 ± 201.13	53.09 ± 0.43	3.2 ± 0.25	15.66 ± 3.37	0.04 ± 0	1.49 ± 0.06	0.01 ± 0	56.6 ± 6.05	12.41 ± 0.57	104.81 ± 9.45	1678.52 ± 84.19	8.24 ± 0.05	405.93 ± 9.16	18.46 ± 1.11	27.67 ± 4.75
10	Duna, Göd	47.68	19.12	181811	14	1627.86 ± 112.55	54.83 ± 0.35	3.53 ± 0.36	23.61 ± 8.1	0.04 ± 0.01	1.83 ± 0.37	0.01 ± 0	37.5 ± 7.63	13.57 ± 0.78	96.43 ± 14.4	2024.29 ± 373.27	8.4 ± 0.08	388.57 ± 18.09	18.76 ± 1.85	35 ± 18.55
11	Duna, Budapest upper	47.59	19.08	182638	14	2166.43 ± 175.86	53.53 ± 0.45	2.95 ± 0.33	18.39 ± 5.68	0.04 ± 0.01	1.32 ± 0.12	0.01 ± 0	34.15 ± 6.07	11.71 ± 0.76	77.14 ± 10.61	1425.71 ± 123.7	8.36 ± 0.06	367.86 ± 13.59	18.09 ± 1.57	14.93 ± 1.89
12	Duna, Budapest lower	47.39	19.01	182638	21	2435.71 ± 198.72	53.03 ± 0.43	2.92 ± 0.27	17.03 ± 5.15	0.04 ± 0.01	1.48 ± 0.15	0.01 ± 0	39.29 ± 4.74	11.9 ± 0.59	79.05 ± 8.51	1607.14 ± 159.05	8.31 ± 0.04	372.38 ± 10.3	17.87 ± 1.36	23.76 ± 4.03
13	Duna, Solt	46.81	18.93	185388	26	2308.17 ± 119.13	53.58 ± 0.26	2.49 ± 0.23	31.67 ± 6.73	0.04 ± 0	1.47 ± 0.1	0.01 ± 0	39.42 ± 4.37	11.87 ± 0.63	99.62 ± 4.21	2001.35 ± 119.89	8.32 ± 0.06	398.12 ± 8.71	17.4 ± 1.01	26.92 ± 2.1
14	Duna, Dunaföldvár	46.81	18.93	185531	19	2323.68 ± 121.91	53.53 ± 0.27	2.57 ± 0.29	36.72 ± 7.8	0.04 ± 0.01	1.54 ± 0.13	0.01 ± 0	40.05 ± 4.15	12.45 ± 0.61	104.21 ± 4.53	2116.32 ± 146.48	8.34 ± 0.06	397.29 ± 11.74	16.52 ± 1.29	26.21 ± 2.04

15	Duna, Fajsz	46.43	18.90	186745	4	2205 ± 156.98	53.93 ± 0.38	3.5 ± 0.94	78 ± 6.98	0.03 ± 0.01	1.64 ± 0.23	0.01 ± 0	16.42 ± 4.49	13.75 ± 0.48	92.5 ± 11.09	2362.5 ± 403.43	8.67 ± 0.12	398.75 ± 26.8	19.85 ± 2.69	26 ± 4.18
16	Duna, Hercegszántó	45.91	18.81	206745	38	2493.82 ± 162.07	57.01 ± 0.34	2.27 ± 0.19	20.72 ± 4.42	0.05 ± 0	1.52 ± 0.08	0.01 ± 0	49.55 ± 3.34	10.76 ± 0.39	110.88 ± 4.54	1999.11 ± 95.1	8.28 ± 0.04	401.45 ± 7.81	16.41 ± 0.91	32.3 ± 2.59
17	Fehér-Körös, Gyulavári	46.63	21.33	4498	55	138.45 ± 9.78	7.87 ± 0.11	2.46 ± 0.18	3.65 ± 0.6	0.08 ± 0.01	0.65 ± 0.04	0.01 ± 0	49.09 ± 4.74	13.34 ± 0.78	137.53 ± 9.87	1347.29 ± 96.52	7.09 ± 0.34	315.67 ± 9.28	12.39 ± 1.13	38.39 ± 8.08
18	Fekete-Körös, Sarkad	46.69	21.43	3438	53	35.86 ± 4.37	7.7 ± 0.09	1.89 ± 0.12	2.67 ± 0.3	0.06 ± 0.01	0.63 ± 0.04	0.01 ± 0	38.09 ± 4.93	10.73 ± 0.72	110.31 ± 9.46	1229.06 ± 90.9	7.07 ± 0.35	288.26 ± 5.1	12.67 ± 1.18	27.56 ± 4.93
19	Fekete-víz, Cun	46.24	19.03	1763	7	7.5 ± 4.67	6.42 ± 0.34	2.66 ± 1.36	14.66 ± 6.76	0.09 ± 0.02	0.83 ± 0.25	0.05 ± 0.02	172.32 ± 15.45	18.86 ± 1.74	244.29 ± 37.85	1547.14 ± 314.81	8.03 ± 0.09	783.57 ± 58.05	20.37 ± 0.84	21.29 ± 7.73
20	Hármas-Körös, Békésszentandrás	46.89	20.50	25464	13	146.24 ± 26.55	21.8 ± 0.36	2.18 ± 0.23	2.13 ± 0.49	0.14 ± 0.02	1.19 ± 0.14	0.02 ± 0	43.28 ± 2.18	15.65 ± 1.12	214.15 ± 15.72	2033.85 ± 191.76	7.85 ± 0.04	424.58 ± 19.9	9.56 ± 2.6	20.85 ± 4.21
21	Hármas-Körös, Gyoma	46.95	20.84	25464	11	73.9 ± 18.84	23.93 ± 0.71	2.85 ± 0.61	2.6 ± 0.35	0.09 ± 0.01	0.69 ± 0.05	0.02 ± 0	167.2 ± 58.68	16.87 ± 1.34	360.31 ± 185.74	2354.55 ± 1021.88	8.01 ± 0.03	341.35 ± 18.05	20.74 ± 1.49	30.86 ± 11.86
22	Hármas-Körös, Szentes	46.76	20.21	27464	7	66.34 ± 18.51	24.75 ± 0.59	1.34 ± 0.23	4.14 ± 1.01	0.06 ± 0.01	0.69 ± 0.09	0.01 ± 0	63.48 ± 10.98	15.06 ± 2.31	161.43 ± 10.56	1140 ± 98	7.85 ± 0.12	459.29 ± 35.27	15.89 ± 1.91	19.71 ± 7.02
23	Hernád felső Zsujta	48.50	21.26	4705	12	47.36 ± 9.76	8.96 ± 0.22	2.93 ± 0.45	6.78 ± 2.5	0.09 ± 0.01	1.99 ± 0.06	0.04 ± 0.01	90.63 ± 11.68	15.75 ± 2	166.67 ± 23.62	2657.5 ± 82.29	8.15 ± 0.04	476.58 ± 17.64	16.17 ± 1.22	50.67 ± 14.04
24	Kettős-Körös, Békés	46.76	21.16	10474	17	77.94 ± 18.31	13.84 ± 0.25	1.54 ± 0.11	2.11 ± 0.39	0.06 ± 0.01	0.78 ± 0.05	0.01 ± 0	16.14 ± 1.94	11.24 ± 1.08	110.82 ± 10.98	1335.29 ± 92.82	7.95 ± 0.04	311 ± 12.04	10.97 ± 2.21	24.24 ± 13.99
25	Maros, Nagylak	46.16	20.70	30309	50	186.92 ± 22.69	23.87 ± 0.25	3.02 ± 0.3	55.61 ± 9.44	0.05 ± 0.01	0.89 ± 0.09	0.01 ± 0	17.47 ± 1.82	27.31 ± 1.68	198.95 ± 19.63	1528.4 ± 124.22	8.19 ± 0.06	453.03 ± 15.7	19.03 ± 0.92	121.43 ± 16.49
26	Maros, Szeged	46.24	20.22	30641	6	100 ± 17.31	25.15 ± 0.63	3.35 ± 0.99	93.83 ± 29.99	0.02 ± 0	0.89 ± 0.24	0.01 ± 0	11.59 ± 2.93	21.78 ± 4.69	106.67 ± 24.99	1253.33 ± 195.07	8.44 ± 0.18	479 ± 29.72	16.32 ± 1.07	43.5 ± 7.43
27	Rába, Szentgotthárd	46.95	16.27	5274	13	8.02 ± 2.18	4.42 ± 0.07	4.39 ± 0.33	18.16 ± 4.13	0.06 ± 0.01	2.26 ± 0.16	0.03 ± 0	53.27 ± 7.48	16.1 ± 2.46	248.46 ± 52.52	3586.15 ± 349.02	8.05 ± 0.05	554.19 ± 26.89	17.19 ± 1.1	78.23 ± 37.03
28	Sajó felső Sajópüspöki	48.28	20.34	4379	12	27.49 ± 6.18	9.09 ± 0.23	3.26 ± 0.44	3.51 ± 0.51	0.08 ± 0.01	1.71 ± 0.06	0.03 ± 0	54.17 ± 7.5	15.17 ± 3	118.33 ± 29.56	2248.33 ± 129	8.01 ± 0.04	380.25 ± 18	14.82 ± 1.01	44.25 ± 17.72
29	Sebes-Körös, Körösszakál	47.02	21.66	2896	44	23.74 ± 2.59	7.14 ± 0.07	2.17 ± 0.15	2.71 ± 0.37	0.11 ± 0.01	1.29 ± 0.09	0.03 ± 0	88.85 ± 8.38	9.86 ± 0.56	150.5 ± 13.99	1946.14 ± 122.84	5.99 ± 0.53	253.77 ± 8.41	14.82 ± 1.14	15.42 ± 1.94
30	Szamos, Csenger	47.84	22.69	15857	39	159.36 ± 14.79	16.29 ± 0.17	4.5 ± 0.33	13.82 ± 3.75	0.18 ± 0.02	0.88 ± 0.06	0.03 ± 0	42.91 ± 7.99	32.73 ± 2.13	282.96 ± 52.72	2164.1 ± 149.83	7.98 ± 0.02	532.54 ± 22.25	11.46 ± 1.27	80.54 ± 17.43
31	Tisza, Aranyosapáti	48.22	22.28	33723	11	277.18 ± 59.24	24.23 ± 0.44	3.16 ± 0.58	33.09 ± 12.2	0.08 ± 0.02	0.58 ± 0.08	0.01 ± 0	17.41 ± 3.19	23.42 ± 2.12	129.31 ± 25.96	1536.36 ± 152.12	8.06 ± 0.04	409.35 ± 34.33	19.81 ± 1.31	36.36 ± 10.07
32	Tisza, Záhony	48.41	22.17	33723	44	464.49 ± 43.26	23.02 ± 0.23	3.63 ± 0.3	16.95 ± 3.72	0.11 ± 0.02	0.7 ± 0.05	0.02 ± 0	25.33 ± 2.21	23.26 ± 1.19	189.55 ± 52.89	1366.91 ± 86.33	7.94 ± 0.03	372.84 ± 15.68	12.11 ± 1.2	86.8 ± 13.69
33	Tisza, Tuzsér	48.32	22.09	33723	5	209.6 ± 37.67	24.6 ± 0.45	5.86 ± 1.47	41.42 ± 23.92	0.2 ± 0.09	0.32 ± 0.12	0.02 ± 0.01	36.91 ± 18.17	31.86 ± 4.63	127.6 ± 43.84	2500 ± 1415.98	8.18 ± 0.16	478.4 ± 46.36	21.12 ± 1.4	23.2 ± 9.97

34	Tisza, Balsa	48.18	21.55	49503	12	410.91 ± 84.02	33.33 ± 2.81	3.1 ± 0.43	18.82 ± 8.17	0.08 ± 0.01	0.71 ± 0.1	0.02 ± 0	25.48 ± 3.7	23.89 ± 1.83	108.52 ± 15.89	1470.83 ± 131.64	7.94 ± 0.05	404.53 ± 28.75	16.89 ± 1.67	44 ± 10.54
35	Tisza, Kisköre	47.48	20.51	75763	12	448.25 ± 72.28	37.22 ± 0.49	3.38 ± 0.38	15.02 ± 3.46	0.07 ± 0.01	0.75 ± 0.06	0.02 ± 0	36.72 ± 6.86	14.75 ± 1.67	88.75 ± 10.23	970.42 ± 104.57	8.07 ± 0.05	509.38 ± 59.95	18.38 ± 1.32	58.08 ± 16.51
36	Tisza, Szolnok	47.17	20.22	75763	5	478.8 ± 92.05	36.93 ± 0.87	2.42 ± 0.38	11.76 ± 3.62	0.19 ± 0.14	0.88 ± 0.09	0.02 ± 0	35.63 ± 8.54	13.2 ± 1.2	118 ± 13.19	1176 ± 204.27	7.95 ± 0.06	405.6 ± 31.19	18.88 ± 2.25	42 ± 12.28
37	Tisza, Szeged	46.25	20.20	139271	6	368.1 ± 81.06	54.95 ± 1.46	1.25 ± 0.32	9.12 ± 3.4	0.05 ± 0.01	0.7 ± 0.09	0.01 ± 0	37.49 ± 9.74	13.07 ± 1.25	113.33 ± 7.15	1128.33 ± 116.23	8.16 ± 0.1	477.67 ± 26.9	16.33 ± 1.15	13.83 ± 2.97
38	Tisza, Tiszasziget	46.19	20.10	169271	39	766.44 ± 97.78	51.69 ± 0.6	1.54 ± 0.12	21.29 ± 3.27	0.05 ± 0.01	0.76 ± 0.06	0.01 ± 0	20.66 ± 2.5	16.78 ± 0.89	138.57 ± 10.82	1314 ± 81.45	7.89 ± 0.05	393.18 ± 11.19	19.56 ± 1.01	45.65 ± 9.02
39	Túr, Kishódos	47.98	22.83	1703	14	983 ± 151.01	3.54 ± 0.05	2.61 ± 0.33	5.96 ± 1.57	0.08 ± 0.01	0.63 ± 0.07	0.01 ± 0	33.83 ± 3.56	14.45 ± 1.62	105.25 ± 12.54	1142.86 ± 118.47	7.67 ± 0.08	176.09 ± 13.87	9.89 ± 1.88	41.86 ± 16.18

Appendix 3.Table 3. List of the studied rivers with the sampling locations and mean values of the total and of considered functional groups biomass in mg l^{-1}.

	Sampling location	total avgbiom	A	B	C	D	E	F	G	H1	J	K	LM	LO	M	N	P	S1	S2
1	Berettyó, Berettyóújfalu	4.18	0.00	0.84	1.37	0.27	0.00	0.00	0.07	0.00	0.99	0.00	0.00	0.05	0.00	0.00	0.06	0.01	0.00
	Berettyó, Kismarja	14.76	0.00	0.04	0.29	0.18	0.00	0.00	0.02	0.02	0.52	0.00	0.00	0.00	0.00	0.00	0.03	0.14	0.00
3	Berettyó, Pocsaj	2.74	0.00	0.04	0.16	0.14	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
4	Bodrog, Sátoraljaújhely	0.95	0.00	0.00	0.09	0.34	0.00	0.00	0.01	0.04	0.05	0.00	0.01	0.02	0.00	0.00	0.07	0.00	0.00
5	Bódva, Sajószentpéter	3.49	0.00	0.03	0.34	0.67	0.00	0.00	0.01	0.17	0.70	0.00	0.00	0.00	0.00	0.00	0.21	0.02	0.00
6	Dráva, Barcs	0.65	0.00	0.03	0.01	0.04	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
7	Dráva, Drávaszabolcs	0.7	0.00	0.06	0.03	0.13	0.00	0.00	0.03	0.01	0.06	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
8	Duna, Komárom	4.96	0.00	0.00	0.50	1.23	0.01	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
9	Duna, Szob	5.15	0.00	0.00	5.09	1.49	0.00	0.00	0.00	0.01	0.53	0.00	0.00	0.05	1.87	0.00	0.04	0.00	0.00
10	Duna, Göd	9.71	0.00	0.00	7.43	2.46	0.00	0.00	0.00	0.00	0.62	0.00	0.00	0.00	15.22	0.00	0.11	0.00	0.00
11	Duna, Budapest upstream	7.77	0.00	0.23	5.38	1.63	0.00	0.00	0.11	0.00	0.93	0.00	0.01	0.12	0.91	0.00	0.21	0.00	0.00
12	Duna, Budapest downstream	4.33	0.00	0.00	10.02	2.45	0.00	0.00	0.09	0.00	0.63	0.00	0.29	0.20	6.71	0.00	0.16	0.00	0.00
13	Duna, Solt	3.99	0.00	0.47	0.19	2.16	0.00	0.00	0.00	0.02	0.27	0.01	0.00	0.28	0.01	0.00	0.12	0.00	0.00

Sampling location	total avgbiom	A	B	C	D	E	F	G	H1	J	K	LM	LO	M	N	P	S1	S2
Duna, Dunaföldvár	4.03	0.00	0.63	0.21	1.91	0.01	0.00	0.00	0.04	0.31	0.01	0.00	0.29	0.01	0.00	0.01	0.01	0.00
Duna, Fajsz	8.9	0.00	0.76	0.33	3.58	0.00	0.00	0.00	0.02	0.62	0.01	0.00	0.22	0.01	0.00	0.00	0.00	0.00
Duna, Hercegszántó	2.67	0.00	0.46	0.12	1.17	0.00	0.00	0.06	0.01	0.13	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00
Fehér-Körös, Gyulavári	1.7	0.00	0.03	0.11	0.08	0.00	0.00	0.00	0.02	0.19	0.00	0.01	0.00	0.00	0.00	0.31	0.00	0.00
Fekete-Körös, Sarkad	0.8	0.00	0.02	0.07	0.06	0.00	0.00	0.01	0.00	0.11	0.00	0.00	0.01	0.00	0.00	0.09	0.00	0.00
Fekete-víz, Cun	2.23	0.00	0.07	0.04	0.11	0.00	0.00	0.00	0.07	0.29	0.01	0.05	0.31	0.01	0.00	0.01	0.00	0.00
Hármas-Körös, Békésszentandrás	0.14	0.00	0.08	0.17	0.15	0.00	0.00	0.01	0.00	0.07	0.00	0.00	0.10	0.00	0.00	0.20	0.00	0.00
Hármas-Körös, Gyoma	0.52	0.00	0.03	0.13	0.06	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00
Hármas-Körös, Szentes	0.31	0.00	0.01	0.06	0.02	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
Hernád felső Zsujta	1.51	0.00	0.05	0.20	0.27	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00
Kettős-Körös, Békés	3.57	0.00	0.36	0.10	0.28	0.01	0.00	0.24	0.00	0.15	0.00	0.00	0.15	0.00	0.00	0.12	0.00	0.00
Maros, Nagylak	18.81	0.00	0.15	2.42	1.51	0.00	0.00	0.01	0.00	1.27	0.00	0.00	0.00	0.00	0.00	0.52	0.00	0.00
Maros, Szeged	15.21	0.02	0.15	3.45	1.29	0.00	0.00	0.00	0.01	1.28	0.00	0.01	0.07	0.00	0.00	0.93	0.00	0.00
Rába, Szentgotthárd	2.28	0.65	0.30	0.47	0.36	0.00	0.00	0.00	0.00	0.81	0.00	0.00	0.00	0.00	0.40	1.19	0.00	0.00
Sajó felső Sajópüspöki	0.5	0.5	0.00	0.00	0.04	0.17	0.00	0.00	0.00	0.02	0.06	0.00	0.00	0.01	0.00	0.00	0.06	0.00
Sebes-Körös, Körösszakál	1.29	0.00	0.07	0.03	0.15	0.00	0.00	0.00	0.02	0.06	0.00	0.00	0.03	0.00	0.00	0.03	0.00	0.00
Szamos, Csenger	11.53	0.01	0.25	5.98	1.59	0.01	0.00	0.18	0.00	0.76	0.00	0.00	0.10	0.00	0.00	0.07	0.01	0.00
Tisza, Aranyosapáti	13.13	0.00	0.46	7.51	1.60	0.01	0.00	0.01	0.00	0.67	0.00	0.00	0.10	0.00	0.00	0.07	0.00	0.00
Tisza, Záhony	5.36	0.00	0.46	3.02	1.40	0.01	0.00	0.06	0.00	0.58	0.00	0.00	0.01	0.00	0.00	0.04	0.00	0.00
Tisza, Tuzsér	46.86	0.00	0.29	16.55	3.74	0.01	0.00	0.15	0.00	3.46	0.00	0.00	0.00	0.00	0.00	0.12	0.01	0.00
Tisza, Balsa	5.36	0.01	0.27	5.43	2.39	0.03	0.00	0.05	0.01	1.55	0.00	0.00	0.13	0.00	0.00	0.06	0.00	0.00
Tisza, Kisköre	5.67	0.01	0.06	1.92	1.84	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.27	0.00	0.00	0.08	0.00	0.00
Tisza, Szolnok	2.3	0.05	0.00	0.28	1.27	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.04	0.00	0.00	0.02	0.00	0.00
Tisza, Szeged	0.68	0.00	0.00	0.23	0.04	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00
Tisza, Tiszasziget	3.55	0.00	0.02	0.84	0.39	0.00	0.00	0.00	0.01	0.31	0.00	0.00	0.04	0.00	0.00	0.21	0.02	0.00
Túr, Kishódos	2.21	0.00	0.05	0.21	0.18	0.00	0.00	0.00	0.01	0.75	0.00	0.08	0.02	0.00	0.00	0.28	0.00	0.00

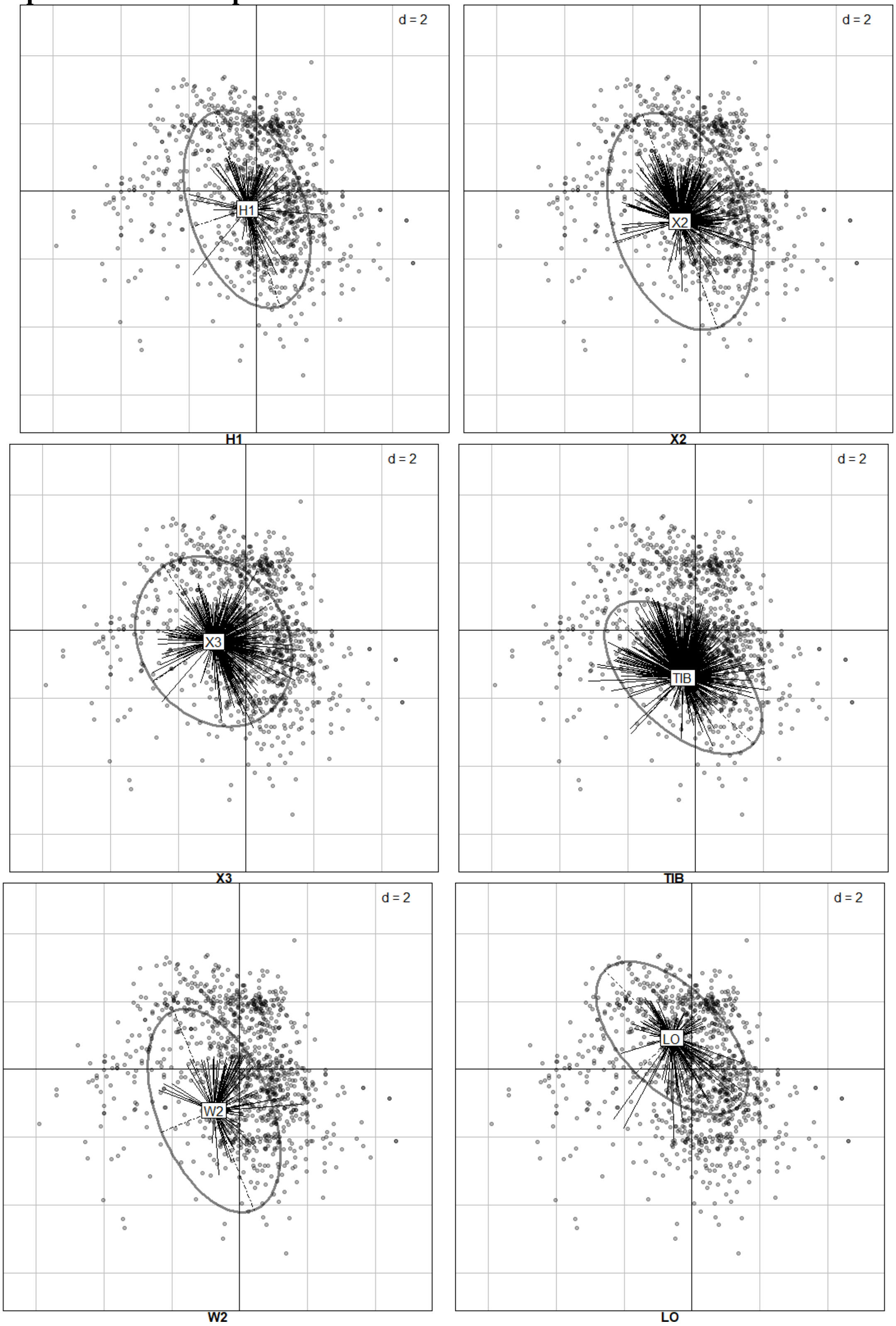
	Sampling location	total avgbiom	SN	T	TIB	TIC	TID	U	V	W0	W1	W2	WS	X1	X2	X3	Y	Yph
1	Berettyó, Berettyóújfalu	4.18	0.00	0.00	0.42	0.00	0.02	0.00	0.00	0.70	0.13	0.02	0.04	0.06	0.01	0.01	0.09	0.00
2	Berettyó, Kismarja	14.76	0.00	0.00	8.25	0.00	0.00	0.00	0.00	0.67	0.19	0.01	0.02	0.02	0.00	0.02	0.03	0.00
3	Berettyó, Pocsaj	2.74	0.00	0.0.0	1.17	0.01	0.01	0.00	0.00	0.15	0.03	0.00	0.02	0.02	0.00	0.01	0.02	0.00
4	Bodrog, Sátoraljaújhely	0.95	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.01	0.00	0.02	0.01	0.07	0.00
5	Bódva, Sajószentpéter	3.49	0.00	0.00	0.94	0.00	0.10	0.00	0.00	0.01	0.06	0.01	0.00	0.06	0.01	0.01	0.14	0.00
6	Dráva, Barcs	0.65	0.00	0.0.0	0.24	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.01	0.00	0.03	0.01	0.02	0.00
7	Dráva, Drávaszabolcs	0.7	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.05	0.02	0.00	0.01	0.00	0.05	0.01	0.03	0.00
8	Duna, Komárom	4.96	0.00	0.0.4	1.21	0.05	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.03	1.21	0.05
9	Duna, Szob	5.15	0.00	0.01	3.37	0.02	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.02	0.00	0.00	0.10	0.00
10	Duna, Göd	9.71	0.00	0.00	1.10	0.04	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.05	0.01	0.00	0.10	0.00
11	Duna, Budapest upstream	7.77	0.00	0.00	1.25	0.04	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.11	0.18	0.00	0.20	0.00
12	Duna, Budapest downstream	4.33	0.00	0.01	0.37	0.00	0.00	0.00	0.00	0.13	0.02	0.00	0.00	0.10	0.02	0.00	0.05	0.00
13	Duna, Solt	3.99	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.11	0.01	0.00	0.01	0.02	0.02	0.01	0.22	0.00
14	Duna, Dunaföldvár	4.03	0.01	0.00	0.36	0.00	0.00	0.00	0.00	0.07	0.01	0.00	0.01	0.01	0.03	0.02	0.07	0.00
15	Duna, Fajsz	8.9	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.13	0.03	0.00	0.03	0.02	0.03	0.01	0.10	0.00
16	Duna, Hercegszántó	2.67	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.01	0.01	0.03	0.02	0.08	0.00
17	Fehér-Körös, Gyulavári	1.7	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.08	0.03	0.01	0.00	0.02	0.07	0.01	0.18	0.00
18	Fekete-Körös, Sarkad	0.8	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.12	0.07	0.00	0.01	0.02	0.02	0.00	0.20	0.00
19	Fekete-víz, Cun	2.23	0.00	0.00	0.28	0.05	0.15	0.00	0.00	0.13	0.13	0.03	0.04	0.01	0.01	0.01	0.25	0.00
20	Hármas-Körös, Békésszentandrás	0.14	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.17	0.07	0.00	0.03	0.02	0.10	0.01	0.73	0.00
21	Hármas-Körös, Gyoma	0.52	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.06	0.10	0.00	0.01	0.01	0.05	0.00	0.30	0.00
22	Hármas-Körös, Szentes	0.31	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.07	0.08	0.00	0.00	0.00	0.00	0.00	0.23	0.01
23	Hernád felső Zsujta	1.51	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.11	0.06	0.02	0.03	0.03	0.03	0.01	0.13	0.00
24	Kettős-Körös, Békés	3.57	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.37	0.08	0.01	0.01	0.04	0.07	0.02	0.60	0.00

25	Maros, Nagylak	18.81	0.00	0.00	2.75	0.00	0.00	0.00	0.00	0.22	0.06	0.00	0.00	0.14	0.00	0.02	0.36	0.00
26	Maros, Szeged	15.21	0.00	0.00	2.18	0.01	0.00	0.00	0.00	0.07	0.03	0.01	0.00	0.11	0.00	0.01	0.42	0.00
27	Rába, Szentgotthárd	2.28	0.00	0.00	9.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
28	Sajó felső Sajópüspöki	0.5	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.1	0.00
29	Sebes-Körös, Körösszakál	1.29	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.04	0.08	0.00	0.00	0.00	0.01	0.01	0.02	0.00
30	Szamos, Csenger	11.53	0.00	0.00	0.82	0.00	0.01	0.00	0.00	0.59	0.07	0.01	0.03	0.09	0.14	0.02	0.11	0.00
31	Tisza, Aranyosapáti	13.13	0.00	0.00	0.36	0.00	0.02	0.00	0.00	0.18	0.05	0.00	0.00	0.08	0.02	0.02	0.04	0.00
32	Tisza, Záhony	5.36	0.00	0.00	0.39	0.00	0.02	0.00	0.00	0.16	0.01	0.01	0.01	0.06	0.03	0.03	0.06	0.00
33	Tisza, Tuzsér	46.86	0.00	0.00	0.19	0.09	0.00	0.00	0.00	0.77	0.01	0.00	0.00	0.14	0.00	0.01	0.00	0.00
34	Tisza, Balsa	5.36	0.00	0.00	0.29	0.00	0.01	0.00	0.00	0.52	0.06	0.00	0.00	0.12	0.04	0.02	0.12	0.00
35	Tisza, Kisköre	5.67	0.00	0.00	0.30	0.02	0.00	0.00	0.00	0.05	0.02	0.05	0.00	0.06	0.10	0.04	0.35	0.00
36	Tisza, Szolnok	2.3	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.17	0.01	0.00	0.00	0.03	0.02	0.02	0.02	0.00
37	Tisza, Szeged	0.68	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.06	0.00
38	Tisza, Tiszasziget	3.55	0.00	0.00	0.20	0.00	0.01	0.00	0.00	0.02	0.01	0.01	0.00	0.02	0.00	0.01	0.21	0.00
39	Túr, Kishódos	2.21	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.12	0.23	0.04	0.06	0.04	0.05	0.10	0.36	0.00

Appendix, Table 4. Visualisation of phytoplankton functional group niche space clustered in a distinct niche group. Dots denote samples, while thin lines show occurrences of the FG at sampling sites.

Intersection of the perpendicular thicker lines shows theoretical central position of the theoretical ubiquitous species.

Group I. Central niche position and intermediate niche breadth



H1

X2

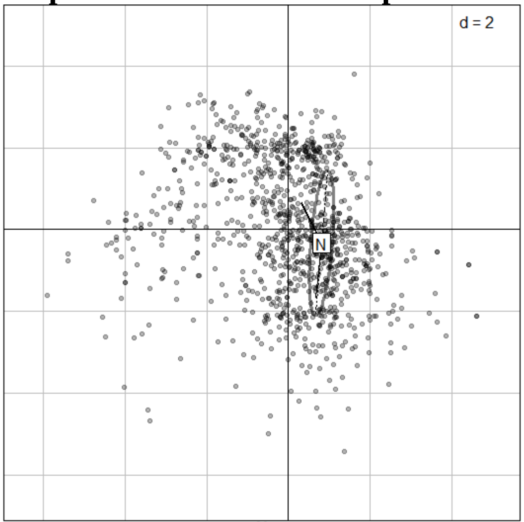
X3

TIB

W2

LO

Group II. Intermediate niche position and narrow niche breadth



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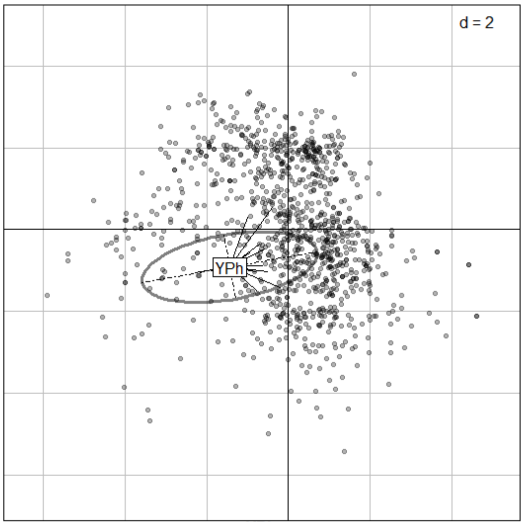
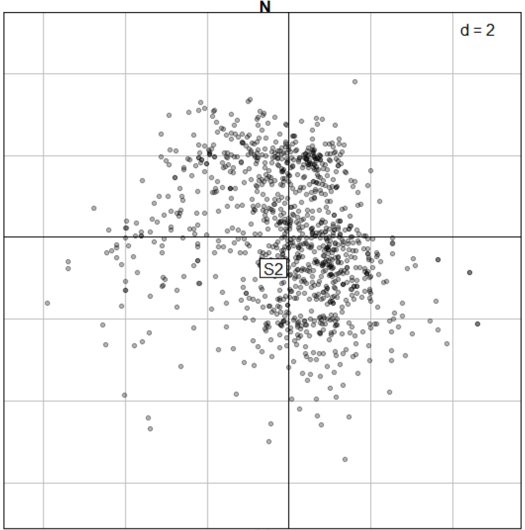
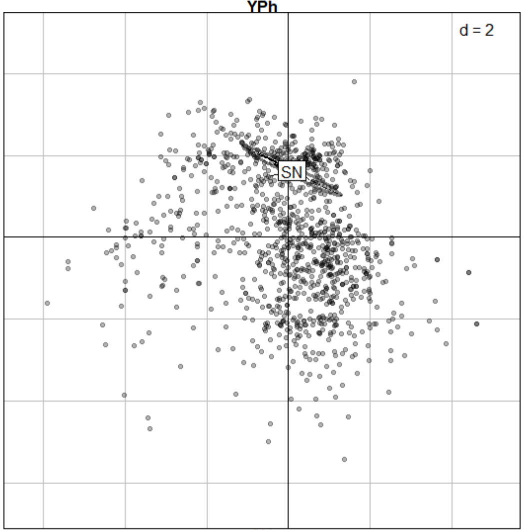


YPh

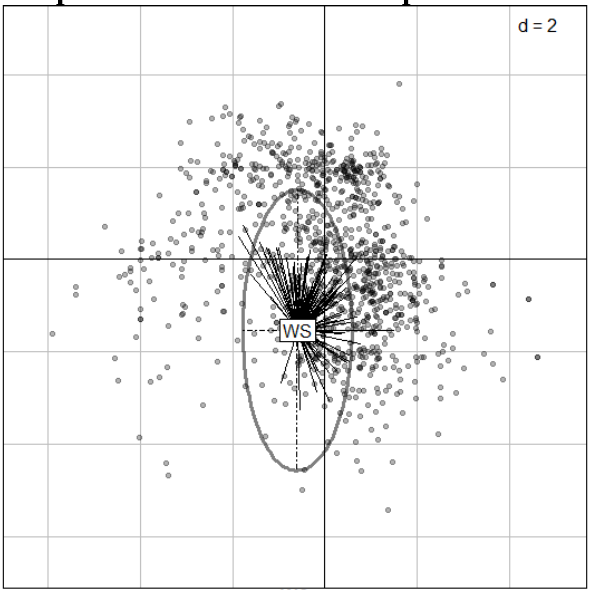


S2

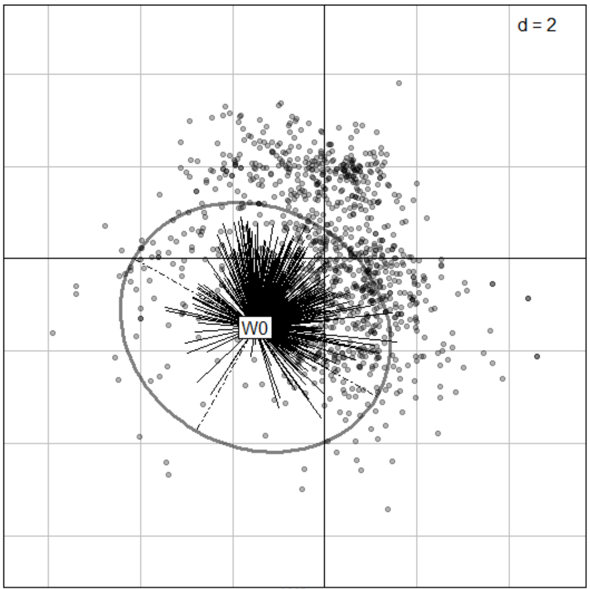


SN

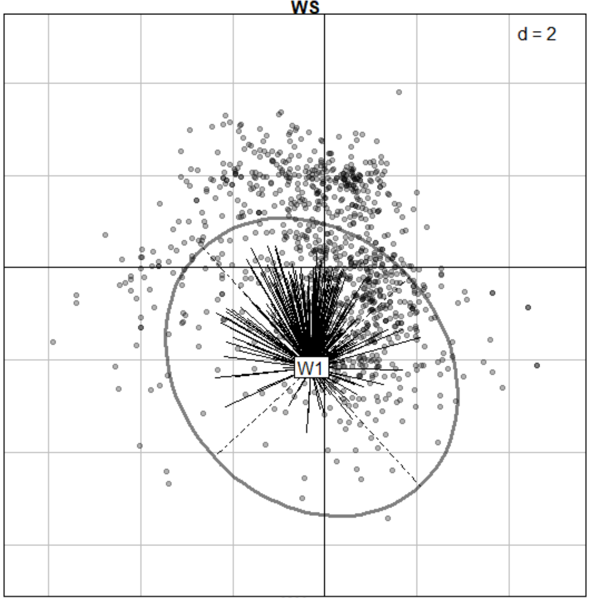
Group III. Intermedaite niche position and intermediate niche breadth



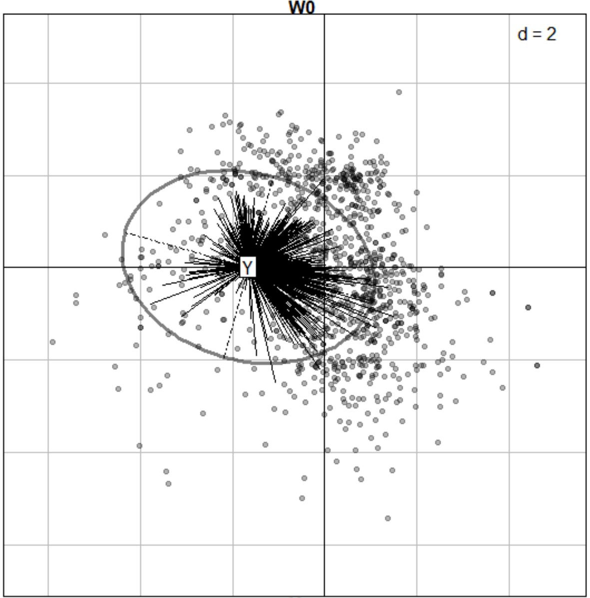
WS



W0



W1



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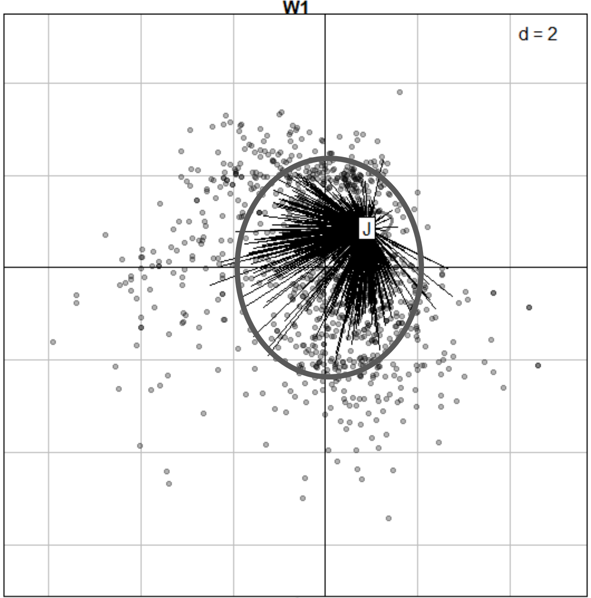
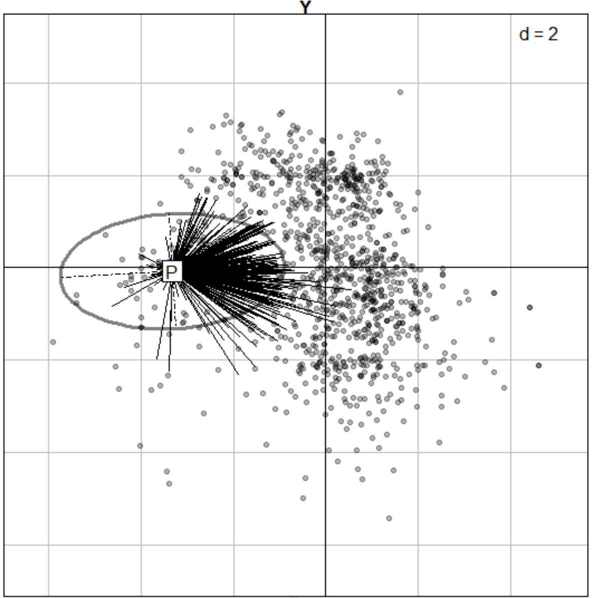


J



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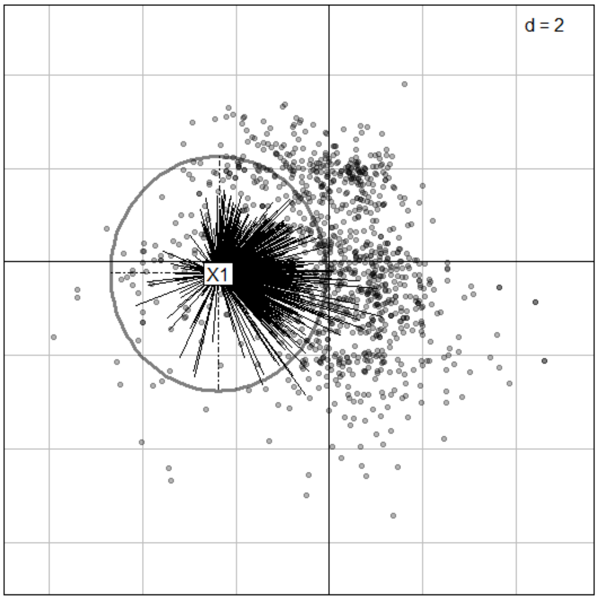
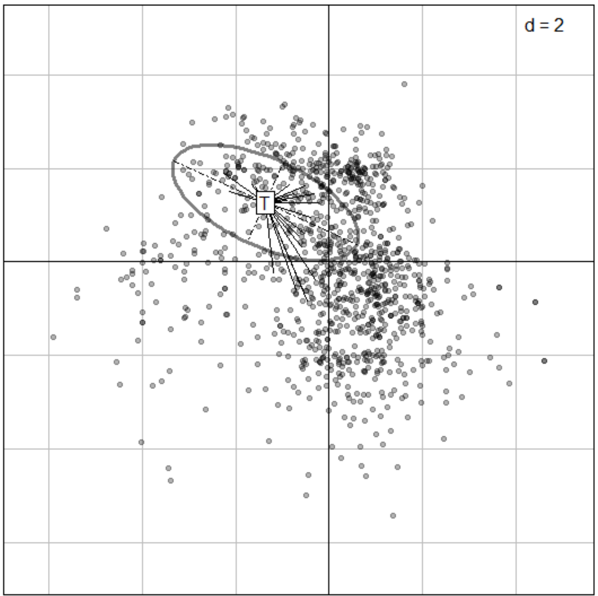
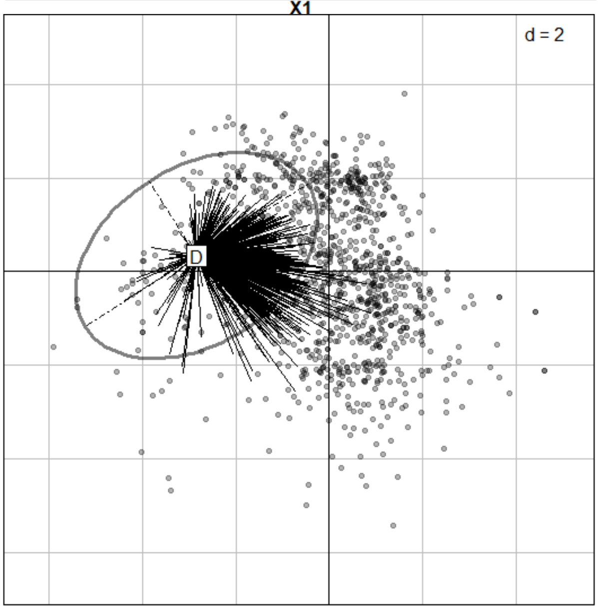


X1



T



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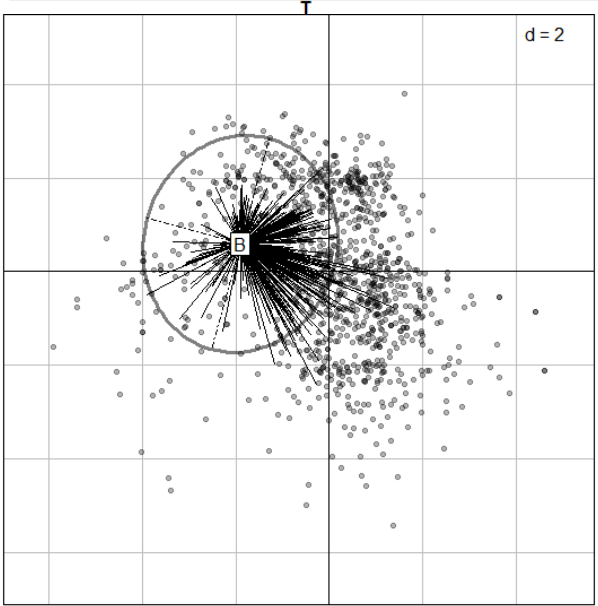

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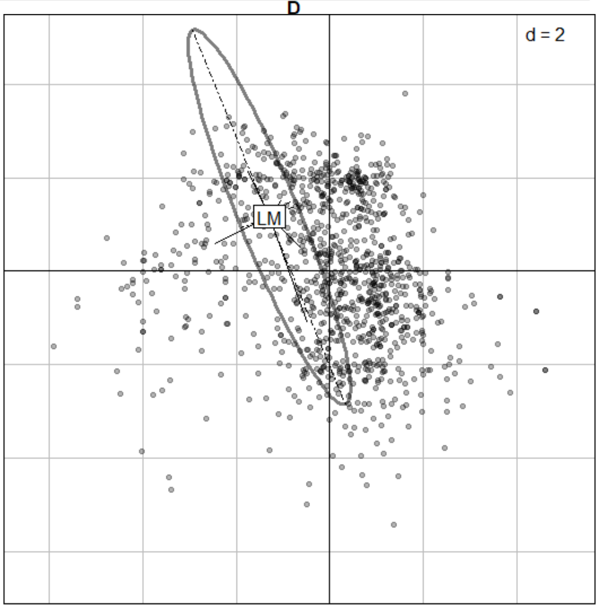
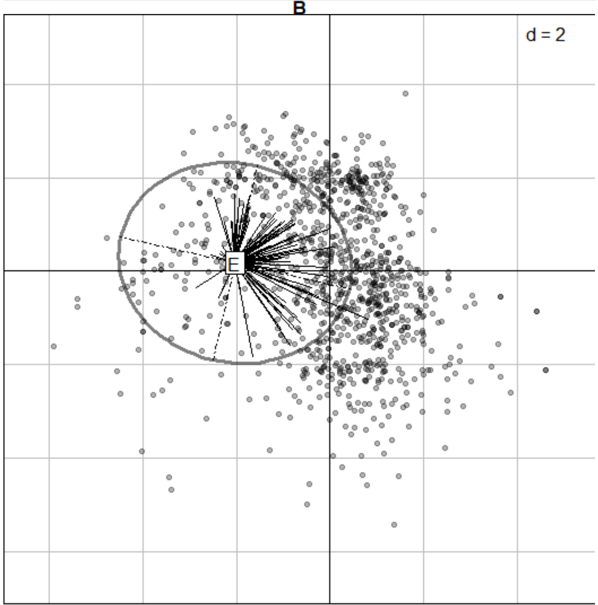
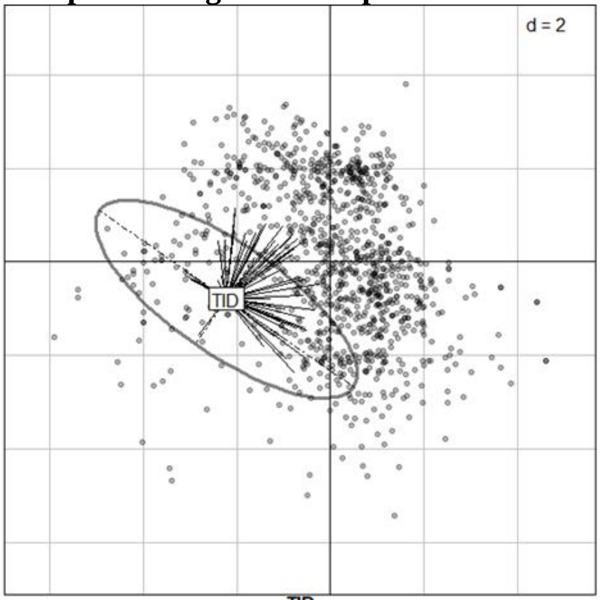


LM

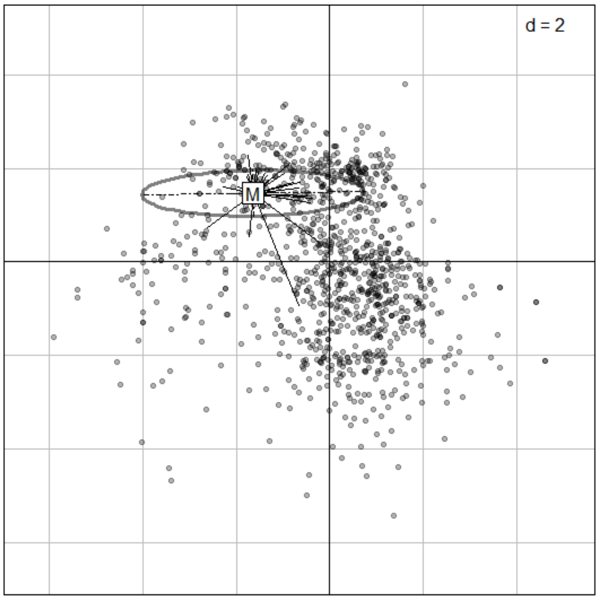


E

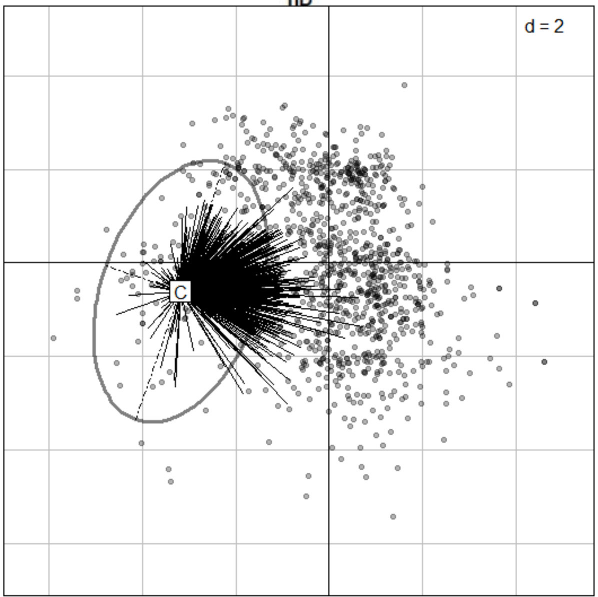
Group IV. Marginal niche position and intermediate niche breadth



TID



M



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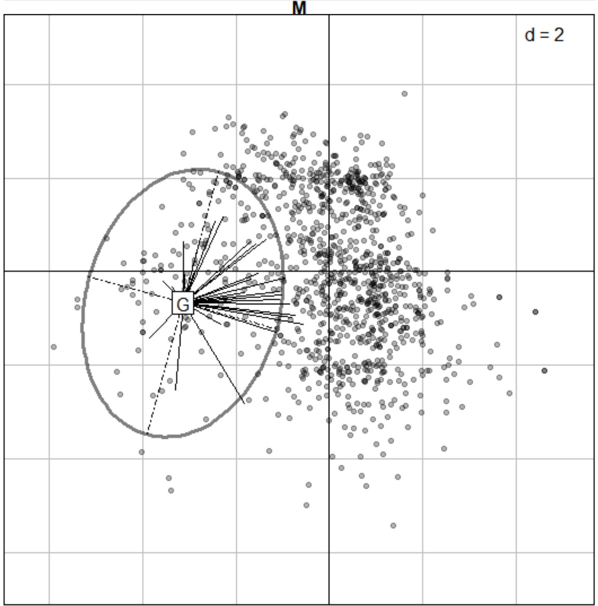
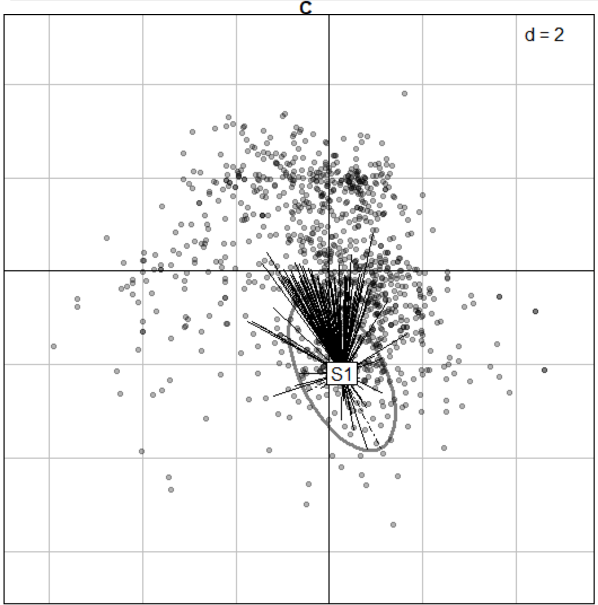
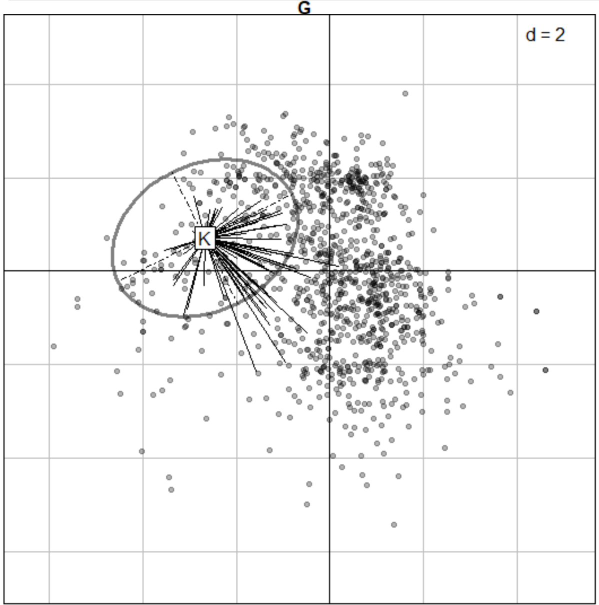


G



S1



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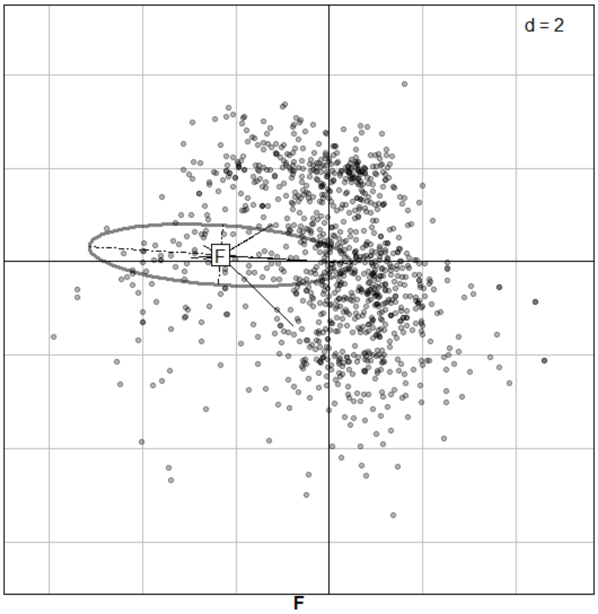
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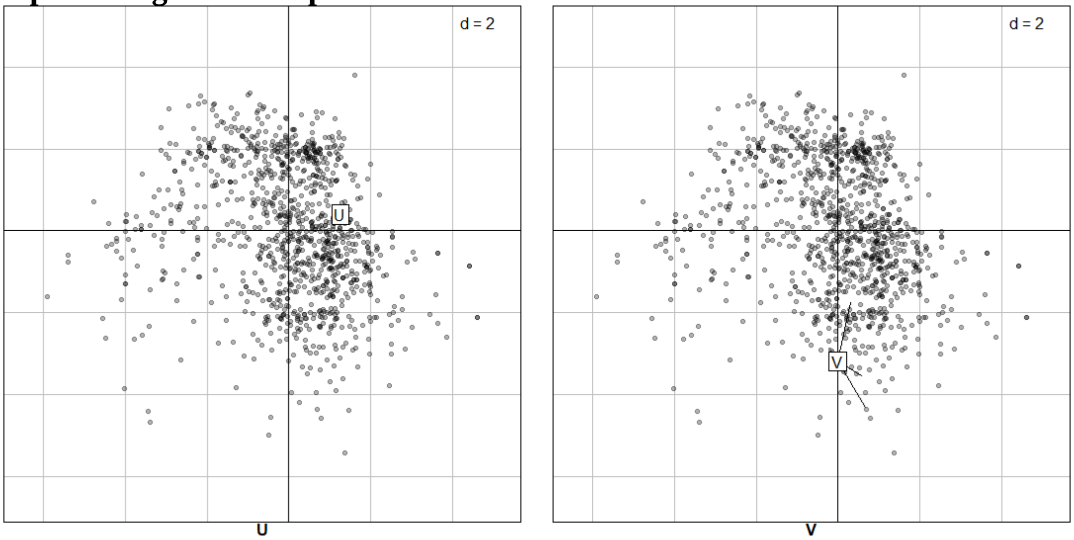
F
F

Group V. marginal niche position and narrow niche breadth



Group VI. Marginal niche position and wide niche breadth