Diatom composition of the rheoplankton in a rhithral river system

Ágnes Bolgovics¹*, Éva Ács², Gábor Várbíró³, Keve Tihamér Kiss², Balázs A. Lukács³, Gábor Borics³

- ¹ University of Eötvös Loránd, 1/A, Pázmány Péter str. H-1117 Budapest, Hungary
- ² MTA Centre for Ecological Research, Danube Research Institute, Jávorka S. U. 14, H-2131 Göd, Hungary
- ³ MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, 18/c., Bem square, H-4026 Debrecen, Hungary

Abstract – Diatom composition of the rheoplankton (phytoplankton) in the Sajó-Hernád river system (Slovakia and Hungary) was studied. Forty two sample sites were designated on the watershed from source to mouth of the two rivers and their tributaries. Samples were taken in July 2012. Altogether, 258 diatom taxa were identified. The microflora was dominated by tychoplanktonic elements. According to the relative abundance of the occurring taxa, four groups could be distinguished. Differentiation of these groups was confirmed by differences in the habitat characteristics, viz. altitude, width of watercourse, macrophyte coverage and river bed material. Diversity of diatom taxa in the phytoplankton was also studied. A positive relationship was found between the macrophyte coverage and the Shannon indices. In contrast, a negative relationship was shown between the macrophyte coverage and Berger-Parker diversity, in which metric the role of the dominant taxa is emphasized. Although the phytoplankton in rhithral rivers is influenced by stochastic events, our results reveal that geographical and hydromorphological characteristics of the rivers and coverage of macrophytes can also play role in shaping the composition and diversity of the phytoplankton.

Keywords: diversity, hydromorphological variables, rhithroplankton

Introduction

In parallel with the physical constraints, structural and functional characteristics of a stream, communities show considerable changes in rivers moving from source to mouth. The biota of the upper sections consists primarily of benthic elements and their survival is essentially based on non-native matter and energy input (VANNOTE et al. 1980). In the lower,

^{*} Corresponding author, e-mail: bolgovics.agnes@okologia.mta.hu

potamal sections of the rivers the native primary production of phytoplankton communities becomes dominant and provides carbon sources for the decomposers (TAMÁS-DVIHALLY 1993, Vörös et al. 2000, THORP and DELONG 2002). The composition of phytoplankton communities shows continuous changes from headwaters to alluvial sections, which can be demonstrated by the ratio of tycho- and euplanktonic algae (VANNOTE et al. 1980). Investigating the phytoplankton of the Tisza River (Hungary) UHERKOVICH (1966 a, b) identified three algal-based river regions: rheon, rheoplankton and plankton. The rheon section is free of algae, in the rheoplankton section tychoplanktonic elements dominate, while in the plankton section euplanktic algae prevail. It has been also demonstrated that the longitudinal variation of the algal assemblages strongly depends on current hydrological conditions (UHERKOVICH 1971). During floods the regions shift downward, and the planktonic region may disappear. This concept is not restricted to the Tisza river catchment, but can be applied to other river systems (STANKOVIĆ et al. 2012, ABONYI et al. 2014). In middle and low discharge periods in the lower sections of alluvial rivers high biomass phytoplankton assemblages might develop, dominated mostly by chlorococcaleans and centric diatoms (SCHMIDT 1994, SCHMIDT et al. 1994, KISS and GENKAL 1996, KISS and SCHMIDT 1998, VÁR-BÍRÓ et al. 2007, KISS et al. 2012). It has been also shown that concerning the dominant algae, the phytoplankton of large potamal rivers is similar to that of shallow turbid lakes (REYNOLDS et al. 1994). The potamoplankton of large rivers has been extensively studied (KISS 1987, KISS and GENKAL 1996, REYNOLDS and DESCY 1996, KISS et al. 2002, KISS and Acs 2009), but the phytoplankton of the upper river segments has received much less attention. What we know from the sporadic studies on stream phytoplankton is that it is dominated by benthic elements, mostly by diatoms (SZEMES 1948, 1967a, 1967b, VÁNCSA 1974, 1976, 1977). The low number of studies dealing with stream phytoplankton can be explained by the fact that most algological investigations are aimed at assessing the ecological state of water bodies, and since quality assessment in the upper sections of the rivers is based on benthic communities, phytoplankton is generally not considered. However, phytoplankton composition in the lower river segments should be strongly influenced by the inocula conveyed by the upper tributaries, which necessitates the investigation of the phytoplankton of these less studied systems.

In previous studies (UHERKOVICH 1971, ROJO et al. 1994) only the basic types of river phytoplankton assemblages were described; viz. rheoplankton dominated by tychoplanktonic taxa and potamoplankton in which euplanktonic elements prevail. Investigating the diversity of phytoplankton in these two river types BORICS et al. (2014) demonstrated that diversity trends are determined by different underlying mechanisms. In rhithral river systems stochastic processes shape the diversity patterns, while in potamal rivers the role of competition seems to be of great importance. Diversity trends were also dependent on the metrics used for diversity calculations.

Much less attention has been paid to the detailed description of the phytoplankton in rhithral rivers (BLUM 1954, 1957) than to the potamoplankton of the lower river segments. Therefore, the aim of the present study was to explore the composition and diversity of the phytoplankton in a rhithral river system. Since previous results (VÁNCSA 1976, POZDERKA et al. 2014) suggested that diatoms are major components of the rheoplankton, we focused exclusively on this group.

We hypothesized that (i) planktonic diatom assemblages are not just stochastic mixtures of species, but are tightly coupled to stream types; (ii) diversity of the planktonic assem-

blages is influenced by the hydro-morphological types of the rivers, and (iii) increases with the size of the water bodies.

Material and methods

Study area

All rivers sampled in this study belong to the Sajó River watershed (Central Europe, Slovakia and Hungary). Sajó is the second largest right-side tributary of the Tisza River containing streams of 1st to 6th orders (STENGER-KOVÁCS et al. 2014). The river rises at Stolické vrchy 1,280 m a.s.l. (Slovakia), and enters the Tisza at 95 m a.s.l. in Hungary, where the Hungarian Great Plain meets the foothills of the Bükk Mountains. The river's catchment area is 12,708 km², its length 223 km, average discharge at the river mouth is 60 m³ s⁻¹. The mean water residence time according to LEOPOLD et al. (1995) and SOBALLE and KIMMEL (1987) is 14.9 days. Annual mean precipitation in the watershed is 600–1,250 mm, annual mean temperature is 4.5–11.0 °C. The upper sections of the River Sajó and its tributaries are typical mountain rivers and although the lower river enters the northern part of the Hungarian Lowland the river keeps its rhithral character, with prevailing coarse substrates (macro and mezolithal).

Sampling

Samples were collected from 42 sampling sites, which covered the whole watershed (Fig. 1) in July 2012. The sampling points were selected to include the main sections of the Sajó and Hernád rivers and the relevant tributaries. Twenty liters of water was filtered through plankton net (mesh size 10 μ m) and concentrated to 50 cm³. Samples were taken from the thalweg. The samples were fixed with formaldehyde (applying 4% final concentration) and stored in plastic containers (CEN 2003). Environmental variables (water temperature, pH, dissolved oxygen, electrical conductivity) were measured on the spot with a



Fig.1. Watershed of the Sajó River and the sampling sites designated. Dashed line marks the Hungarian-Slovakian border. Identical symbols indicate sampling sites which belong to the same cluster. H – Hungary, S – Slovakia.

Hach-Lange HQ40D water quality field kit. Other variables (water depth, width of the river bank, relative frequency of dominant substrates and percentage cover of the main life forms of macrophytes (euhydrophytes and helophytes) were also estimated in parallel with the samplings. For these parameters depending on the size of the rivers 500–1,000 m long river sections were surveyed. The relative abundance of the various sediment types provide useful information on the velocity of water currents, and help in characterising the various types of rhithral river systems.

Sample processing

To study the diatom components of the microflora we prepared permanent slides. For the removal of organic matter the samples were digested using H_2O_2 in a water bath (60 °C), and a drop of HCl was also added to the samples to remove calcium carbonate (CEN 2003). After finishing digestion the frustules were washed in distilled water and mounted in Cargille Meltmount mounting medium (KELLY et al. 1998) (refracting index = 1.704). Cleaned diatoms were identified and counted under oil immersion at a magnification of 1000× with the application of differential interference contrast (DIC). To equalize the counting effort 400 valves were counted in each sample. Identification of diatom species was performed according to KRAMMER and LANGE-BERTALOT (1986–1991), KRAMMER (2003) and HOFMANN et al. (2011).

Data analysis

A cluster analysis based on Euclidean distance and using WARD's (1963) agglomeration algorithm was applied to phytoplankton data with a view to identifying distinct, empirical clusters.

A Kruskal-Wallis Anova was used to test the significance of the relationship between environmental variables and diversity indices.

Indicator value analysis (IndVal) (DUFRENE and LEGENDRE 1997) was used to identify those species that can be considered to be indicators of the groups identified by the cluster analysis. The value of the IndVal index reaches its maximum (1.0) if all individuals of a species are found in one definite group of sites (specificity), and if the species can be found in all sites of that group (fidelity) (DUFRENE and LEGENDRE 1997).

We used a sample-based species accumulation curve (COLWELL et al. 2004) for the prediction of species richness which implements the analytical solution known as »Mao tau«, with standard deviation. The species accumulation curve and the cluster analysis were made with the PAST software package (HAMMER 2001).

In the various metrics used for characterizing diversity of biotic communities different weights are given to the dominant taxa, and thus, the metrics capture different aspects of diversity. To describe all relevant aspects of diversity TOTHMERESZ (1998) proposed the application of special cases of Rényi's entropy (eq. 1). The higher the value of the scale parameter (α) the higher weighting the given to the most abundant taxa. HR₀ is the logarithm of species richness; HR₁ is the Shannon diversity (eq. 3); HR₂ is the Simpson diversity; HR_x is the Berger-Parker index (eq. 5).

eq. 1 HR_{$$\alpha$$} = $\frac{1}{1-\alpha} \log \sum_{i=1}^{s} p_i^{\alpha}$ where $\alpha \ge 0$ and $\alpha \ne 1$

eq. 2
$$HR_0 = \log S$$

eq. 3 $\lim_{\alpha \to 1} HR_\alpha \equiv HR_1 = -\sum_{i=1}^{S} p_i \log p_i$
eq. 4 $HR_2 = -\log \sum_{i=1}^{S} p_i^2$

eq. 5 $HR_{\infty} = -\log(\max p_i)$

PEARSON's (1897) correlation coefficient was applied to explore the relationship between environmental variables and diversity metrics. Family-wise Bonferroni corrections were used to decrease the risk for a Type I error in pairwise comparisons.

Results

Phytoplankton associations

Based on diatom composition four distinct groups could be distinguished (Fig. 2). The results of the IndVal also supported the presence of the four groups identified by the cluster analysis. The IndVal analysis showed that several species had significant (p < 0.05) specificity for and fidelity to the groups (Tab. 1). *Tryblionella levidensis, Cocconeis neodiminu-ta, Didymosphaenia geminata, Hannaea arcus, Navicula splendicula, Placoneis elginensis* were characteristic for the first group. In the second group *Cymatopleura elliptica, Fallacia*



Fig. 2. Dendrogram of sampling sites based on diatom composition of the rhithroplankton.

	Groups	Ind.val.	р
Tryblionella levidensis	1 36.7		0.074
Cocconeis neodiminuta	1	36.4	0.045
Didymosphaenia geminata	1	27.3	0.052
Hannaea arcus	1	28.2	0.137
Navicula splendicula	1	22.1	0.104
Placoneis elginensis	1	36.4	0.054
Amphora veneta	2	37.1	0.056
Cymatopleura elliptica	2	49.4	0.008
Fallacia subhamulata	2	41.7	0.035
Navicula antonii	2	41.8	0.033
Rhopalodia gibba	2	23.7	0.119
Nitzschia dissipata	3	32.9	0.129
Sellaphora bacillum	3	30.4	0.118
Tryblionella constricta	3	34.8	0.100
Gyrosigma acumium	3	40.2	0.065
Gyrosigma attenuatum	3	58.5	0.012
Fragilaria ulna v. acus	3	38.3	0.066
Gomphonema parvulum	3	42.1	0.022
Nitzschia gracilis	3	31.8	0.098
Nitzschia inconspicua	3	37.3	0.106
Nitzschia intermedia	3	37.7	0.040
Aulacoseira granulata	3	53.5	0.012
Handmannia balatonis	3	22.8	0.122
Fragilaria delicatissima	4	23.1	0.117
Gomphonema angustatum	4	36.8	0.061
Navicula erifuga	4	21.9	0.117
Nitzschia capitellata	4	57.8	0.015
Surirella bifrons	4	21.6	0.118
Thalassiosira lacustris	4	49.3	0.011

Tab. 1. Species considered as indicators of the river clusters (1–4) by the IndVal Analysis. Indicatorvalues (Ind.val.) and p-values are shown.

subhamulata, Navicula antonii had the highest fidelity values. *Gyrosigma attenuatum, Aula-coseira granulata* and *Gomphonema parvulum* had high indicator and low p values in the third group. In the fourth cluster *Nitzschia capitellata* and *Thalassiosira lacustris* were the most characteristic elements.

The relationship between the groups identified by the cluster analysis and the relevant physicochemical and hydromorphological variables and macrophyte coverage was also studied (Fig. 3). High-altitude rivers were characteristic of the first group. Small middle



Fig. 3. The distribution of the relevant environmental variables in the four river clusters (1–4). The line graphs indicate mean values \pm standard errors; same letters indicate homogenous groups according to Kruskall–Wallis Anova (p < 0.05).

altitude rivers with coarse substrates constituted the second river cluster. In the third group middle altitude rivers (200–300 m) with relatively high macrophyte abundances were found. Large lowland rivers with fine sediments constituted the fourth cluster.

Diversity

The calculated species diversity metrics showed a very poor relationship with the measured environmental variables (Tab. 2). The value of the Pearson correlation coefficient was low in the cases of all the indices. Relatively high values (> 0.3) were found between the macrophyte coverage and Shannon and Simpson indices. A negative relationship was found between the macrophyte coverage and the Berger-Parker index of dominance (-0.31). Regarding their diversity, the four river clusters showed remarkable differences. In the case of the high altitude rivers the species richness was high. However, occasionally some species occurred in high relative abundance in the samples, which is reflected in the high values of the Berger-Parker dominance index. In the second river group the low species numbers were associated with high dominance index values. A high species number could be observed in the third river group. However the occurrence of species was well balanced in this group, which was clearly illustrated by the low value of the Berger-Parker dominance index. Similarly to the first group, in the fourth river group both richness and dominance values were high (Fig. 4).

Tab. 2. Correlation matrix of the river's attributes and diversity indices. Bolded values indicate significant relationships. CPOM – coarse particulate organic matter, FPOM – fine particulate organic matter.

River's attributes	Taxa	Simpson	Shannon	Berger-Parker
Width of floodplain (m)	-0.18	-0.05	-0.07	0.06
Maximal width of watercourse (m)	-0.05	0.07	0.07	-0.03
Maximal water depth (m)	-0.10	0.03	0.03	0.03
Width of watercourse (actual) (m)	-0.07	0.03	0.05	0.01
Average water depth (actual) (m)	-0.24	-0.23	-0.17	0.24
Temperature (°C)	0.08	0.02	0.11	0.00
pH	-0.12	0.04	0.05	0.05
Conductivity (µS cm ⁻¹)	0.24	0.28	0.29	-0.21
Megalithal > 40 cm	0.01	-0.16	-0.09	0.24
Natural macrolithal > 20-40 cm	-0.07	-0.05	-0.08	0.07
Artificial macrolithal > 20-40 cm	0.00	0.11	0.07	-0.14
Mezolithal $> 6-20$ cm	-0.03	-0.15	-0.15	0.23
Microlithal $> 2-6$ cm	-0.11	-0.02	-0.10	-0.11
Akal > 2 mm-2 cm	0.01	0.13	0.11	-0.15
Psammal > 6 μ m–2 mm	0.21	0.21	0.26	-0.25
Argyllal < 6 μm	-0.16	-0.27	-0.25	0.25
Macro-algae (%)	0.23	0.04	0.07	-0.05
Micro-algae (%)	-0.15	0.11	0.04	-0.15
Submerged macrophytes (%)	0.25	0.22	0.30	-0.24
Emerged macrophytes (%)	0.23	0.31	0.36	-0.35
Living terrestrial macrophytes (%)	0.21	0.15	0.19	-0.17
Xylal (%)	-0.08	-0.17	-0.19	0.15
CPOM (%)	0.15	0.16	0.15	-0.22
FPOM (%)	-0.05	0.21	0.16	-0.28

The observed number of species was related to the very high species diversity of the watershed. However, we also wanted to know how large the potential species pool of the Sajó River's watershed is; therefore, a species accumulation curve was used to characterize the relationship between the sample number and species richness (Fig. 5). The relationship could be described by a power function: $Y = 52.816 \times X^{0.4326}$; where X is the sample number and Y is the species richness of the watershed. The lack of asymptote means that in case of additional samplings increase in the number of taxa is expected.

Discussion

Algae suspended in lotic systems are commonly referred to as potamoplankton (KALFF 2002). However in recent studies this term has been applied to the plankton of large potamal rivers (Stoyneva 1994, Gosselain et al. 1998). Since the potamoplankton consists pri-



Fig. 4. The distribution of the diversity indices in the four river clusters (1–4). The line graphs indicate mean values \pm standard errors; same letters indicate homogenous groups according to Kruskall–Wallis Anova (p < 0.05).



Fig. 5. Species accumulation curve: relationship between the number of collected samples and the predicted number of diatom taxa in the Sajó River watershed. Dashed lines indicate 95% confidence interval.

marily of euplanktonic elements, using this term for the plankton of the upper river segments where tychoplanktonic elements prevail seems ambiguous. Therefore, we propose to use the term rhithroplankton for the planktonic communities of the upper, rhithral rivers.

Phytoplankton associations

Várbíró et al. (2007) differentiated 8 riverine phytoplankton assemblages including one benthic type and seven others, mostly transitional and typical potamal assemblages, and impacted ones. In this study the so called »benthic type« was investigated in high spatial resolution. The presence of the four well delineated phytoplankton groups shown in this study clearly demonstrates that rhithroplankton assemblages cannot be considered as a simple stochastic co-occurrence of benthic species. The first bifurcation in the dendrogram was strongly supported by the altitudinal differences of the rivers in the two groups. Although the additional bifurcations in the group of middle and low altitude rivers were also supported by some hydrological and/or biological variables, in these groups spatial effects occasionally overcame the environmental effects. This was evidenced by the fact that spatial proximity of sampling sites sometimes was associated with similarity in species composition. This kind of spatial autocorrelation was also demonstrated for other microscopic systems (HEINO et al. 2010). The spatial effect was not characteristic of the fourth group. The three sampling points belonging to this group were situated far from each other. However, the hydromorphological characteristics of the groups were similar. The fine substrate (argillaceous) indicates low relief of the river valleys. Two points were at the lowest part of the tributary, while the third point can be found in the upper, impounded stretch of the Hernád River. In these sampling sites as well as the planktonic forms (Aulacoseira granulata, Thalassiosira lacustris) several benthic taxa (Cymatopleura elliptica, Gyrosigma attenuatum, Nitzschia capitellata) had high IndVal values. This can be explained by the fact, that these species frequently occur in lentic environments (SZABÓ et al. 2005), which are more characteristic of the lower parts of the rivers' watershed.

Diversity

Although the values of diversity metrics are exposed to disturbances entering the systems (BORICS et al. 2013), these indices are the most frequently used quantitative descriptors of community properties (HACKER and GAINES 1997). High diversity values might refer to complexity, stability, or to the ecological state of the systems. However, phytoplankton of the rhithral rivers is not a community in the traditional sense of the term. It can be considered an eclectic mixture of benthic and euplanktonic species, which are entrained into the suspension from various habitats. Thus, the plankton integrates the species arriving from benthic substrates, ponds, impoundments, pools and shallows of the rivers (STOYNEVA et al. 1994, BORICS et al. 2007). Since the rhithroplankton diversity reflects the habitat diversity of the river catchment (BORICS et al. 2014), artificial modification of the watershed contributes to the increase of the phytoplankton diversity. The high number of the euplanktonic species observed in the samples is partly attributed to this impact. Occurrence of the species Cyclotella meneghiniana, Aulacoseira granulata or Aulacoseira muzzanensis can be considered natural in rivers' phytoplankton (VÁRBÍRÓ et al. 2007). These taxa can flourish even in benthic environments (ISTVÁNOVICS et al. 2011). However, occurrence of other centrics (Thalassiosira lacustris) refers to the presence of large lentic habitats, or a slightly saline environment, which was not characteristic for the natural catchment of the Sajó River. In the middle sections of the Sajó watershed main channel impoundments and several offriver reservoirs were established which might serve as potential sources of algal inocula.

As to the diversity, our expectation was that diversity would increase in parallel towards the larger rivers, thus, variables like water depth, width of the water-course should correlate with the increase of diversity metrics. In contrast, we found that the only variable that showed significant relationship with diversity metrics was the abundance of macrophytes. Emergent and submerged macrophytes provide prominent substrate for benthic diatoms (PASSY 2007), therefore the presence of macrophytes largely determines the species composition of rhithroplankton. This suggests that the local increase in benthic habitat diversity can play important role in shaping rhithroplankton species diversity.

Phytoplankton diversity is highly sensitive to environmental disturbances (SOMMER et al. 1993) and thus shows considerable spatial and temporal variability both in rivers and lakes. It is indisputable that detailed description of diversity needs long-term monitoring data for the phytoplankton. These kinds of data have been restricted to the potamal sections of the rivers; for the rhithral sections only sporadic data are available. In conclusion, the high spatial resolution snapshot survey performed on the Sajó-Hernád river system provided information on the phytoplankton diversity in rhithral rivers. Our result demonstrated the importance of both environmental and spatial effects on the composition and diversity of rhithroplankton assemblages.

Acknowledgements

This work was funded by the OTKA Grant K104279 and by the Bolyai János fellowship of the Hungarian Academy of Sciences.

References

- ABONYI, A., LEITAO, M., STANKOVIC, I., BORICS, G., VARBIRO, G., PADISAK, J., 2014: A large river (River Loire, France) survey to compare phytoplankton functional approaches: Do they display river zones in similar ways? Ecological Indicators 46,11–22.
- BLUM, J. L., 1954: Evidence for a diurnal pulse in stream phytoplankton. Science 119, 732–734.
- BLUM, J. L., 1957: An ecological study of the algae of the Saline river, Michigan. Hydrobiologia 9, 361–408.
- BORICS, G., VÁRBÍRÓ, G., GRIGORSZKY, I., KRASZNAI, E., SZABÓ, S. and KISS, K. T., 2007: A new evaluation technique of potamo–plankton for the assessment of the ecological status of rivers. Archiv für Hidrobiologie, Large Rivers 17, 465–486.
- BORICS, G., GÖRGÉNYI, J., GRIGORSZKY, I., NAGY, Z. L., TÓTHMÉRÉSZ, B., VÁRBÍRÓ, G., 2014: The role of phytoplankton diversity metrics in shallow lake and river quality assessment. Ecological Indicators, http://dx.doi.org/10.1016/j.ecolind.
- BORICS, G., VÁRBÍRÓ, G., PADISÁK, J., 2013: Disturbance and stress different meanings in ecological dynamics? Hydrobiologia 711, 1–7.
- CEN 2003: Water quality guidance standard for the routine sampling and pretreatment of benthic diatoms from rivers. EN 13946: 2003. Comité Européen de Normalisation, Geneva, 14.

- COLWELL, R. K., MAO, C. X., CHANG, J., 2004: Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85, 2717–2727.
- DUFRENE, M., LEGENDRE, P., 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.
- GOSSELAIN, V., DESCY, J. P., VIROUX, L., JOAQUIM-JUSTO, C., HAMMER, A., METENS, A. SCH-WEITZER, S., 1998: Grazing by large river zooplankton: a key to summer potamoplankton decline? The case of the Meuse and Moselle rivers in 1994 and 1995. Hydrobiologia 370, 199–216.
- HACKER, S. D., GAINES, S. D., 1997: Some implications of direct positive interactions for community species diversity. Ecology 78, 1990–2003.
- HAMMER, Ø., HARPER, D. A. T., RYAN, P. D., 2001: PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 9.
- HEINO, J., BINI, L. M., KARJALAINEN, S. M., MYKRA, H., SOININEN, J., VIEIRA, L. C. G. et al., 2010: Geographical patterns of micro–organismal community structure: are diatoms ubiquitously distributed across boreal streams? Oikos 119, 129–137.
- HOFMANN, G., WERMUN, M., LANGE–BERTALOT, H., 2011: Diatomeen in Süßwasser–Benthos von Mitteleuropa. A. R. G. Gantner Verlag/ Koeltz Scientific Books, Königstein, Germany.
- ISTVÁNOVICS, V., HONTI, M., 2011: Phytoplankton growth in three rivers: the role of meroplankton and the benthic retention hypothesis. Limnology and Oceanography 56,1439– 1452.
- KALFF, J., 2002: Limnology. Inland water ecosystems. Prentice Hall.
- KELLY, M. G., A. CAZAUBON, E. CORING, A. DELL'UOMO, L. ECTOR, B. GOLDSMITH, H. GUASCH, J. HÜRLIMANN, A. JARLMAN, B. KAWECKA, J. KWANDRANS, R. LAUGASTE, E.-A. LINDSTRØM, M. LEITAO, P. MARVAN, J. PADISÁK, E. PIPP, J. PRYGIEL, E. ROTT, S. SABATER, H. VAN DAM & J. VIZINET, 1998: Recommendations for the routine sampling of diatoms for water quality assessments in Europe. Journal of Applied Phycology 10, 215–224.
- Kiss, K. T., 1987: Phytoplankton studies in the Szigetköz section of the Danube during 1981– 1982. Archiv für Hydrobiologie, Algological Studies 47, 247–273.
- Kiss, K. T., Ács, É., 2009: The algal flora of the River Bodrog. Thaiszia Journal of Botany, Kosice 19, Suppl. 1, 99–124.
- KISS, K. T., GENKAL, S. I., 1996: Phytoplankton of the Danube's reservoirs in September 1995 from Germany to Hungary. Limnologische Berichte Donau 1, 143–148.
- KISS, K. T., ÁCS, É., BARKÁCS, K., BORICS, G., BÖDDI, B., ECTOR, L., SOLYMOS, G. K., SZABÓ, K., VARGA, A., VARGA, I., 2002: Qualitative short-term effects of cyanide and heavy metal pollution on phytoplankton and periphyton in the rivers Tisza and Szamos (Hungary). Archiv für Hidrobiologie, Large Rivers 13, 47–72.
- KISS, K. T., KLEE, R., ECTOR, L., ÁCS, É., 2012: Centric diatoms of large rivers and tributaries in Hungary: morphology and biogeographic distribution. Acta Botanica Croatica 71, 311–363.
- KISS, K. T., SCHMIDT, A., 1998: Changes of the Chlorophyta species in the phytoplankton of the Hungarian Section of the Danube river during the last decades (1961–1997). Biologia, Bratislava 53, 509–518.

- KRAMMER, K., 2003: Cymbopleura, Delicata, Navicymbula, Gomphocymbellopsis, Afrocymbella. In: LANGE-BERTALOT, H. (ed.), Diatoms of the European Inland Waters and Comparable Habitats, vol. 4. A. R. Gantner Verlag.
- KRAMMER, H., LANGE-BERTALOT, H., 1986–1991: Bacillariophyceae. In ETTL, H., GÄRTNER G., GERLOFF J., HEYNIG, H., MOLLENHAUER, D., (eds): Süßwasserflora von Mitteleuropa 2 (1–4). Gustav Fischer, Stuttgart.
- LEOPOLD, L. B., WOLMAN, M. G., MILLER, J. P., 1995: Fluvial processes in geomorphology.
- PASSY, I. S., 2007: Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. Aquatic Botany 86, 171–178.
- PEARSON, K., 1897: On a form of spurious correlation which may arise when indices are used in the measurement of organs. Proceedings of the Royal Society of London 60, 487–498.
- POZDERKA, V., BOLGOVICS, Á., BORICS, G., GÖRGÉNYI, J., 2014: What is the relationship between the phytoplankton of the rhithral rivers and the benthic communities? Hidrológiai Közlöny (Journal of the Hungarian Hydrological Society) 94, 77–78.
- REYNOLDS, C. S., DESCY, P. P., 1996: The production, biomass and structure of phytoplankton in large rivers. Archiv für Hidrobiologie, Large Rivers 10, 161–187.
- REYNOLDS, C. S., DESCY, J.-P., PADISÁK, J., 1994: Are phytoplankton dynamics in rivers so different from those in shallow lakes? Hydrobiologia 289, 1–7.
- ROJO, C., ALVAREZ, COBELAS, M., ARAUZO, M., 1994: An elementary, structural analysis of river phytoplankton. Hydrobiologia 289, 43–55.
- SCHMIDT, A., 1994: Main characteristics of phytoplankton of the southern Hungarian section of the River Danube. Hydrobiologia 289, 97–108.
- SCHMIDT, A., KISS, K. T., BARTALIS. É., 1994: Chlorococcal algae in the phytoplankton of the Hungarian section of the River Danube in the early nineties. Biologia, Bratislava 49, 553–562.
- SOBALLE, D. M., KIMMEL, B. L., 1987: A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology 68, 1943–1954.
- SOMMER, U., PADISÁK, J., REYNOLDS, C. S., JUHÁSZNAGY, P., 1993: Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. Hydrobiologia 249, 1–7.
- STANKOVIĆ, I., VLAHOVIĆ, T., GLIGORA, U. M., VÁRBÍRÓ G., BORICS G., 2012: Phytoplankton functional and morpho-functional approach in large floodplain rivers. Hydrobiologia 698, 217–231.
- STENGER-KOVÁCS, C., TÓTH, L., TÓTH, F., HAJNAL, É., PADISÁK, J., 2014: Stream order-dependent diversity metrics of epilithic diatom assemblages. Hydrobiologia 721, 65–71.
- STOYNEVA, M. P., 1994: Shallows of the Lowed Danube as additional sources of potamoplankton. Hydrobiologia 289, 171–178.
- SZABÓ, K., KISS, K. T., TABA, G., ÁCS, É., 2005: Epiphytic diatoms of the Tisza River, Kisköre Reservoir and some oxbows of the Tisza River after the cyanide and heavy metal pollution in 2000. Acta Botanica Croatica 64, 1–46.
- SZEMES, G., 1948: A Zagyva-folyó kovamoszatainak elterjedése a forrástól a torkolatig. Borbásia 8, 89–112.

- SZEMES, G., 1967a: Systematisches Verzeichnis der Pflanzenwelt der Donau mit einer zusammenfassenden Erläuterung. In: LIEPOLD, R. (ed.), Limnologie der Donau, 70–131. Schweizer-Bartsche Verlag, Stuttgart.
- SZEMES, G., 1967b: Das Phytoplankton der Donau. In: LIEPOLD, R. (ed.), Limnologie der Donau, 158–179. Schweizer-Bartsche Verlag, Stuttgart.
- TAMÁS-DVIHALLY, S., 1993: Zum Stoffhaushalt der mittleren Donau. *Archiv für Hydrobiologie*, Large Rivers 9, 53–72.
- THORP, J. H., DELONG, M. D., 2002: Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers? Oikos 96, 543–550.
- Tóthmérész, B., 1998: On the characterization of scale-dependent diversity. Abstracta Botanica 22, 149–156.
- UHERKOVICH, G., 1966a: Das Leben der Tisza. XXVII. Zur Frage der Potamolimnologie und des Potamoplanktons. Acta Biologica Szeged 12, 55–66.
- UHERKOVICH, G., 1966b: Übersicht über das Potamophytoplankton der Tisza (Theiss) in Ungarn. Hydrobiologia 28, 252 – 280.
- UHERKOVICH, G., 1971: Phytoplankton of Tisza River. Szolnok Megyei Múzeumi Adattár 20–22, 1–282.
- VáNCSA, A. L., 1974: Additional data to algae composition of rivers in Northern Hungary considering especially the assessment of water quality conditions. Hidrológiai Közlöny 9, 419–415.
- VÁNCSA, A. L., 1976: Additional data to algae composition of rivers in Northern Hungary considering especially the assessment of water quality. Hidrológiai Közlöny 9, 422– 428.
- VÁNCSA, A. L., 1977: Tychoplanktonical algal associations of the Sajó. Tiscia (Szeged) XII, 57–64.
- VANNOTE, R. L., MINSHALL, W. G., CUMMINS, K.W., SEDELL, J. R., CUSHING, C.E., 1980: The river continuum concept. Candian Journal of Fisheries and Aquatic Sciences 37, 130– 37.
- VÁRBÍRÓ, G., ÁCS, É., BORICS, G., ÉRCES, K., FEHÉR, G., GRIGORSZKY, I. et al., 2007: Use of self–organising maps SOM for characterization of riverine phytoplankton associations in Hungary. *Archiv für Hydrobiologie* 161, 383–394.
- VÁRBÍRÓ, G., BORICS, G., CSÁNYI, B., FEHÉR, G., GRIGORSZKY, I., KISS, K. T., TÓTH, A., ÁCS, É., 2012: Improvement of the ecological water qualification system of rivers based on the first results of the Hungarian phytobenthos surveillance monitoring. Hydrobiologia 695, 125–135.
- Vörös, L., V.–BALOGH, K., HERODEK, S., KISS, K.T., 2000: Underwater light conditions, phytoplankton photosynthesis and bacterioplankton production in the Hungarian section of the River Danube. Archiv für Hydrobiologie, Large Rivers 11, 511–532.
- WARD, J. H., 1963: Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58, 236–244.