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Distribution of niche spaces over different homogeneous river sections at seasonal resolution

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Abstract:

Planktic algae have an essential role in the food web as primary producers; the determination of the ecological niche space occupied by them is thus essential in strategies aimed at sustaining the biodiversity of surface waters. In the present study, principal component analysis combined with the outlying mean index was applied to 14 water quality time series (1993-2005) derived from three previously determined homogeneous sections of the Hungarian part of the River Tisza. As a result, the seasonal distribution of the ecological n-dimensional hypervolumes was determined for the different river sections. In the first upper section, the seasonal niches overlay each other, and no clear separation could be detected. In the middle- and lower reaches, however, a clear separation between the seasons was observed. The identification of these separate niches of the various seasons as the main indicators/drivers of certain ecological communities (e.g. phytoplankton) proved possible.

Keywords: combined cluster and discriminant analysis, homogeneous groups, hydrochemical seasons, niche space, principal component analysis

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1. Introduction

The role of planktic algae as primary producers in the aquatic food webs is well-established; they have a clear and substantial role *in shaping the composition of biota of aquatic ecosystems* (Wehr and Descy, 1998) with chemical-, physical-, and biological factors defining the structure of phytoplankton communities (Reynolds, 1984; 1996; 2006). These factors may be considered as those determining an n-dimensional hypervolume within which a species can persist, i.e. an ecological niche (Dolédec et al., 2000; Blonder et al., 2014). The precise determination of such niches, and thus their indicators, is essential in phytoplankton ecology, as it demonstrates the environmental position of the community. One of the first steps in defining a niche is the definition of this n-dimensional hypervolume, and this may be achieved using a set of multivariate data analysis techniques, e.g. correspondence analysis (Hill, 1974), canonical correspondence analysis (Pappas and Stoermer, 1997), redundancy analysis (Ter Braak, 1987), or the outlying mean index (Dolédec et al., 2000; Karasiewicz et al., 2017).

The concept of ecological niches has attracted great interest with the growing awareness of environmental change, especially in terms of the study of the impacts of niche shifts within a community (Karasiewicz et al., 2017) in aquatic environments (Peterson, 2011). It is generally accepted that water quality sampling units displaying similar behaviors may be expected to support similar communities. So changes in environmental gradients (Dolédec et al., 2000) will therefore indicate, and drive the change in the communities. By exploring the niche spaces in sets of sampling sites rather than unique ones, the number of data assessed can be increased. Therefore, the n-dimensional hypervolume determination of homogeneous groups of sampling sites could enhance the robustness and significance of the obtained ecological models.

Finding an optimal classification of sampling sites, for e.g. monitoring network optimization, is a common task in the fields of biology, ecology, geology, geography, and related disciplines. However, a classification which is “simply” optimal does not necessarily ensure homogeneity (Kovács et al., 2014). The increasing number of studies setting as their aim the determination of not only similar, but homogeneous groups of sampling sites in lakes (Kovács et al., 2014), rivers (Tanos et al., 2015; Kovács et al., 2015) or subsurface water systems (Kovács et al., 2015) provides an opportunity to explore n-dimensional hypervolumes in subsets of multiple sampling sites in which the members/elements share equal underlying processes (Kovács et al., 2014). The assessment of variables measured in homogeneous groups therefore provides a good opportunity to increase the amount of data obtained from domains with the same environmental conditions (global niche; Karasiewicz et al., 2017).

The determination of n-dimensional hypervolumes is frequently performed spatially to assess the degree of phylogenetic relatedness between e.g. various amphibian taxa (Hof, 2010), instream invertebrates (Heino, 2015; Heino and Grönroos, 2014) within a geographical region. The other most frequently considered aspect is seasonal shifts in the niche of taxa (Mérigoux and Dolédec, 2004).

The aim of the present study was therefore, to explore how changes in the n-dimensional hypervolumes along the River Tisza (Central Europe’s second largest potamal river), between the river’s homogeneous sub-regions in space and time may indicate changes in the composition of phytoplankton communities. It is expected that the position and breadth of the niche spaces of the seasons will change in space, delineating those seasons. A clear separation would enable the development of strategies for sustaining different communities in the different sections of the riverine ecosystems.

2. Materials and methods

The River Tisza gathers the waters of the Carpathian Basin's Eastern region. It is a highly important ecological corridor (Zsuga et al., 2004), stretching through 5 countries (966 river km, 594.5 in Hungary) from its spring in the Eastern Carpathians in the Ukraine to its confluence with the Danube at Titel in Serbia. Its watershed is 157,186 km^2 (Lászlóffy, 1982), of which approx. 47,000 km^2 is located in Hungary. The average annual runoff of the Tisza is 25.4×10^6 m^3 (Pécsi, 1969). In Hungary, the river's water quality directly affects the lives of approx. 1.5 m inhabitants.

Heading downstream along the river's Hungarian section, the following tributaries are worth mentioning: the Szamos, Bodrog, Sajó, Zagyva, Kőrös, and Maros rivers (Fig. 1). Based on the runoff of these tributaries, the Szamos might be expected to have the strongest effect on the main flow (at its mouth its average runoff exceeds half of the average runoff of the Tisza; Tanos, 2017). Moreover, a considerable "changing effect" is to be expected from the Bodrog, Sajó, Zagyva, Kőrös, and Maros Rivers in relation to the periodic behavior of the river.

Besides these tributaries, other, mostly anthropogenic factors, such as water barrage systems (WBS; e.g. Tiszalök WBS, Fig. 1), or lakes (e.g. Kisköre Reservoir; Fig. 1) affect the water quality of river sections (Kentel and Alp, 2013; Moreira and Poole, 1993). Even ice regime changes may occur on rivers due to the installation of WBSs as seen on other Central European rivers (Takács et al., 2013; Takács and Kern, 2015; Takács et al., 2018).

An artificial lake exists on the river, Kisköre Reservoir (also known as Lake Tisza; length: 27 km, mean depth: 1.3 m, total area: 127 km^2), constructed in 1973, and planned to function as a part of a future WBS. Nowadays, rather than an "industrial" installation it functions as a much-frequented recreation zone and nature reserve. In addition, non-point source nutrient loads arriving from agricultural areas have to be accounted for as well (Mander and Forsberg, 2000); there are several large cities along the river (e.g. Szeged at T13) which also have an environmental impact on the river's water quality (Fig.1).

The previously mentioned factors (tributaries, WBS etc.), together with the fact that downstream the River Tisza is increasingly becoming a lower section river, have caused the sampling sites of the river (Fig. 1) to form homogeneous groups, characterizing sub-sections with essentially different water quality (Tanos et al., 2015). The uppermost group of homogeneous sampling sites (T3 & T4) represents the transition zone between the hydrologically upper and middle sections of the River Tisza (Várbíró et al., 2007). Here, the water is still transparent, but after the Szamos River, the amount of nutrients increases, dissolved oxygen decreases and the sediment is mainly coarse grained sand. The middle homogeneous group of sampling sites (T7 & T8) is located just upstream of the WBS. The water quality is affected mainly by the damming of the WBS and nutrient input from the Bodrog and Sajó rivers. The lowest group (T12 & T13) mirrors a clearly formed middle-section type of river. It is characterized by a decreased flow velocity and elevated nutrient content brought by the River Kőrös to the main channel (Tanos et al., 2015; Tanos, 2017)..

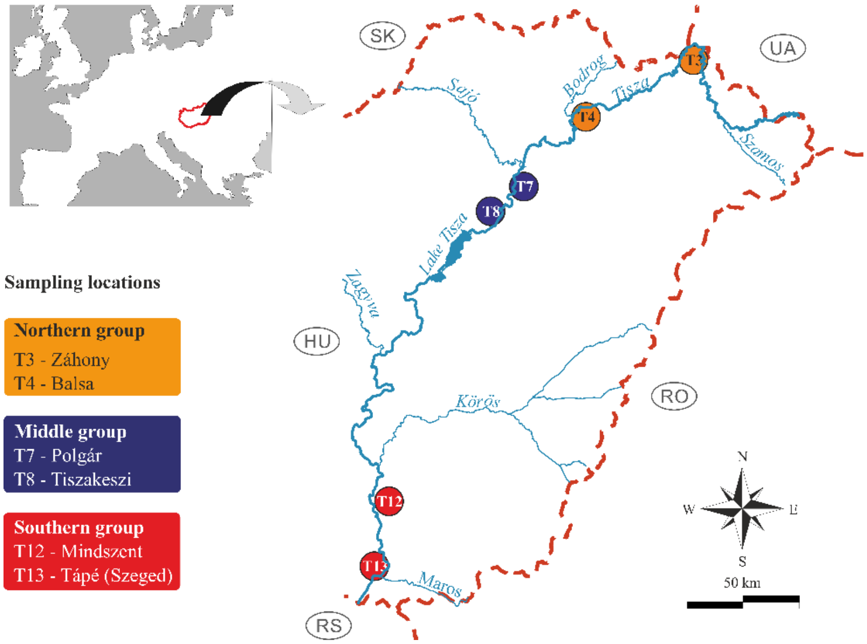


Fig. 1. Hungarian section of the River Tisza and its explored sampling sites. The similar color circles around the codes of the sampling sites indicate that those belong to the same homogeneous group defined in Tanos et al. (2015).

In the course of the analyses, the time series of 14 water quality variables (Table 1) for the years 1993-2005 from 6 sampling sites (Fig. 1) were examined. The parameters were sampled by various water inspectorates weekly and biweekly. Due to the large area monitored, these samples were not taken on the same day. Thus, after 2005, the sampling frequency was rarefied and the set of parameters changed. The number of data analyzed was ~50,000 in total.

Table 1. Variable groups of response and explanatory water quality variables measured in the Hungarian section of the River Tisza (1993-2005).

Response variables	Explanatory Variables
Dissolved oxygen (DO; mg L^{-1})	Runoff (m^3 s^{-1})
Biological oxygen demand (BOD-5; mg L^{-1})	Water temperature (T_W; °C)
Ca^{2+} (mg L^{-1})	
Mg^{2+} (mg L^{-1})	
Na^{+} (mg L^{-1})	
K^{+} (mg L^{-1})	
Cl^{-} (mg L^{-1})	
SO_4^{2-} (mg L^{-1})	
HCO_3^{-} (mg L^{-1})	
NH_4-N (mg L^{-1})	
NO_3-N (mg L^{-1})	
PO_4-P (SRP-P; μg L^{-1})	
Chlorophyll-a (Chl-a; μg L^{-1})	

To be able to interpret the results in light of the seasonality of phytoplankton assemblages, phytoplankton composition data was used available for2007-2010. The related investigations were carried out by regional water authorities and research institutions. The original database contained the relative abundance of the species. These species were then sorted into different algal functional groups (codons) according to Reynolds et al. (2002) and Padisák et al. (2009) and their abundance was determined (Table 2) for the homogeneous sections of the River Tisza (Tanos et al., 2015). For details see Fig. 1 and Section 2.1.2.

Table 2. Phytoplankton codon group's average relative abundance in the homogeneous river sections (Tanos et al., 2015) of the River Tisza (2007-2010). Abundances > 5 % are highlighted in bold.

Codon group	Northern	Middle	Southern
A	1%	0%	1%
B	**23%**	**9%**	**13%**
C	**17%**	**31%**	**11%**

D	**21%**	**27%**	**17%**
E	1%	0%	0%
F	0%	0%	0%
G	0%	0%	0%
H1	1%	0%	**16%**
J	**5%**	**7%**	**10%**
K	1%	0%	0%
LM	0%	0%	0%
LO	0%	0%	2%
M	0%	0%	0%
P	3%	1%	8%
S1	3%	0%	5%
S2	0%	0%	0%
SN	0%	0%	0%
T	0%	0%	0%
TIB	**24%**	**9%**	**11%**
TIC	0%	1%	0%
TID	0%	0%	1%
U	0%	0%	0%
V	3%	0%	0%
W0	**9%**	**8%**	1%
W1	1%	2%	**9%**
W2	1%	0%	4%
WS	1%	0%	0%
X1	**5%**	**9%**	**7%**
X2	**5%**	**8%**	0%
X3	5%	4%	3%
Y	**6%**	4%	**14%**
YPh	0%	0%	0%

2.1. Methodology

2.1.1. Principal component analysis and niche characterization

The backbone of the present study was principal component analysis (PCA), a frequently used multidimensional data analysis technique (Tabachnik and Fidell, 1996), mainly applied for dimension reduction. In the present study, the PCs were considered based on their scree plots (Catell, 1966) takin only those into account which had an eigenvalue >1 (Kaiser (1960), thus the

13 dimensional dataset at hand was reduced to 3 dimensional vectors with uncorrelated coordinates using the first three principal components. It should be noted that in the study the observations' principal components are referred to as PC scores, while the elements of the eigenvectors of the empirical correlation matrix will be referred to as loadings. These measure the relationship of the coordinates and the PCs with Pearson correlation coefficient. Only those loadings falling outside the ±0.6 interval are considered meaningful.

Niche position and niche breadth were determined using the Outlying Mean Index (OMI) analysis (Dolédec et al., 2000). OMI usually measures the marginality of species' habitat distribution across a given study area (Heino and Soininen, 2006), with the correlation matrix of environmental variables and the occurrence of different species as inputs in the different geographical regions. In the present case, the input correlation matrix was derived from the response water quality variables (Table 1), while in the place of the occurrence of species, hydrochemical seasons are the subject of the niches. In practical terms, this means that the occurrence of the season is the target variable. Thus the niche position, marginality and tolerance of each season and its characteristics are tested along the watercourse.

2.1.2. Steps in the analysis

The homogeneous sections of the Hungarian part of the River Tisza were considered in order to explore the stochastic relationship of its water quality variables and determine its niche space. First, the time series of the response variables (Table 1) of the homogeneous groups of sampling sites (two sites per group, as previously determined by CCDA - Tanos et al., 2015), were taken into account. Briefly, CCDA compares all combinations of hierarchical cluster groups to random groupings and suggests the further division of the obtained cluster groups using linear discriminant analysis (Kovács et al., 2014).

The time series of the homogeneous groups were then assessed using exploratory principal component analysis (Rogerson, 2001). It is presumed that this will afford an insight into the linear relationship of the water quality variables in the homogeneous groups and lead to a better understanding of the given river sub-section (Tanos et al., 2011). Moreover, by assigning a seasonal (e.g. winter, spring) tag to the data and visualizing the PCA results on bi-plots, the importance of a given response variable in a given season can be determined.

As a next step, the obtained PCs were correlated with the explanatory variables' (Table 1) time series measured in the homogeneous groups themselves, providing information on how water temperature and runoff affect the stochastic relations (background factors).

As final step, the n-dimensional hypervolumes (Blonder et al., 2014) were determined for the three homogeneous sections of the River Tisza, taking hydrochemical seasonality (Tanos et al., 2015) into account as well.

All computations were performed using `R` 3.2.3 (R Core Team, 2015), `Vegan` (Oksanen et al., 2018) and `ade4` (Dray et al., 2007) packages and MS Excel 2016.

3. Results

The research was conducted on the homogeneous groups of sampling sites: Northern, Middle, and Southern groups (Fig. 1) previously objectively determined by Tanos et al. (2015)

using Combined Cluster and Discriminant Analysis (CCDA) (Kovács et al., 2014) on a set of water quality variables similar to that assessed in the present study.

3.1. General overview

In the assessed river sections, the concentration of ions did not vary to a high degree between the homogeneous groups of sampling sites However, DO content and BOD displayed a clear decreasing trend. While Chl-a and runoff indicated a continuous increase in absolute values, SRP slightly decreased in the Middle group.By the time the nutrients (Chl-a and SRP-P) had reached the Southern group, they had increased by ~20 and ~35% respectively in mean concentration compared to the values found in the Northern Group (Table 3).

In general, the variability – based on the coefficients of variation (CV; Table 3) - of the observed water quality variables decreased downstream, with e.g. the N forms, BOD displaying a decreasing and then slightly increasing trend downstream. Still, the CVs of the N forms or e.g. BOD in the Southern Group do no exceed those in the Northern Group. It should be noted that the largest decrease in CV was witnessed in the case of Chl-a, where it dropped from ~500% to ~110% between the Northern and Southern Groups (Table 3).

Table 3. Descriptive statistics of water quality variables for each of the homogeneous groups on the River Tisza.

		Runoff	T_W	DO	BOD	Ca^{2+}	Mg^{2+}	Na^+	K^+	Cl^-	SO_4^{2-}	HCO_3^-	NH_4-N	NO_3-N	SRP-P	Chl-a
Northern group	● Mean	434	12.0	11.95	3.56	40.64	8.29	27.82	3.38	34.18	33.8	138.4	0.12	0.82	65.28	4.88
	SD	471	8.2	2.97	2.53	9.74	3.67	14.64	1.72	18.33	14.85	43.66	0.16	0.46	91.06	24.69
	CV	1.09	0.68	0.25	0.71	0.24	0.44	0.53	0.51	0.54	0.44	0.32	1.33	0.56	1.39	5.06
	Range	3391	27.1	20.85	34.9	63.3	26.1	99.5	18.4	116.4	116.6	341.7	1.31	2.07	1214	87.9
Middle group	● Mean	541	13.0	9.61	3.75	48.27	10.12	22.66	3.63	29.21	50.22	154.5	0.25	1.31	56.06	5.3
	SD	462	8.4	2.02	1.54	8.28	2.8	8.68	0.81	11.8	10.53	27.6	0.27	0.45	37.57	7.314
	CV	0.85	0.64	0.21	0.41	0.17	0.28	0.38	0.22	0.4	0.21	0.18	1.08	0.34	0.67	1.38
	Range	2935	29.5	10.6	7.4	40.7	22	43.6	5.5	66	52.5	133.6	2.07	3.37	440	80.6
Southern group	● Mean	645	12.5	9.37	1.88	45.95	9.42	24.27	3.4	27.09	46.09	158.3	0.21	1.29	87.9	5.8
	SD	479	8.8	2.08	0.88	8.21	2.84	8.94	0.85	10.4	11.59	32.89	0.26	0.57	49.75	6.728
	CV	0.74	0.71	0.22	0.47	0.18	0.3	0.37	0.25	0.38	0.25	0.21	1.24	0.44	0.57	1.16
	Range	2668	29.1	8.5	5	65	31.4	58.2	6.2	48	87.4	197.7	1.71	3.59	649	90.8

3.2. Stochastic relationship of water quality variables in the sub-sections (homogeneous groups) of the River Tisza

The cumulative explanatory power of the first three PCs is > 46% in each group, and the percentage of explained variance increases monotonically downstream (Table 4). Between the Northern and Southern groups the explanatory power of PCs almost doubles in the first two PCs, while the third PC explains ~10% of the total variance in every group, regardless of its location. According to the Kaiser-Meyer Olkin criterion, the measure of sampling adequacy (MSA; Kaiser and Rice, 1974) in the Middle and Southern groups is appropriate and very good respectively, while in the Northern group caution has to be taken, since it is <0.5. This is most probably due to the higher variability of water quality in the Northern groups sampling sites compared to the other two groups (Table 3).

Table 4. Percentage and cumulative percentage of explained variance in the PCs. with Measure of sampling adequacy (MSA) indicated for the correlation matrices of the different groups.

Homogeneous Group	**PC1**	**PC2**	**PC3**	**sum (PC1, PC2, PC3)**	**MSA**
🟠 Northern	25.29%	10.88%	10%	46.17%	0.42
🟣 Middle	40.42%	16.99%	10.94%	68.35%	0.75
🔴 Southern	41.22%	20.09%	10.23%	72.54%	0.79

From the perspective of dependent variables, in all of the homogeneous group of sampling sites, in the first PC the ions are the most determining (Table 5a). In the 2nd PC, the degree to which variance is explained is mostly determined by DO; this is true of all three groups, what is more, with an increasing degree of importance downstream (increased loadings in absolute value). Furthermore, downstream of the Northern group, DO changes its sign relative to the ions (Table 5a). In the Northern group, neither nitrate-nitrogen nor Chl-a plays an important role in any of the PCs, unlike in the other two groups downstream. It should be noted that in the Middle group Chl-a has a high loading (-0.61) in the 2nd PC, while in the Southern group this was with the 3rd PC (loading: 0.87; Table 5a). In the Middle- and Southern groups, BOD also takes on an importance with a PC loading >0.7. Regarding the 3rd PC, in the Northern group, there is no variable which can be considered as a main factor.I In the Middle group's 3rd PC BOD and, as previously stated, in the Southern group's 3rd PC, Chl-a becomes the most important factor (Table 5a).

With regard to the independent variables, over the whole river section, in every group runoff displays a significant negative correlation only with the first PC (i.e. that which is determined to the greatest extent by ions) (Table 5b). This indicates that when runoff increases, the amount of ions decreases.. The other available explanatory variable, water temperature (T_w), showed a significant linear relationship with only the second PC of the Middle and Southern groups (r<-0.8; Table 5b). Since, DO has a positive relationship with the 2nd PC while T_W has a negative relationship with it, this reflects the notion that with the increase of T_W, the amount of DO decreases in the Middle- and Southern groups. In the case of nitrate-nitrogen a similar relationship is also to be observed in the Middle group, where with the increase of T_W, Chl-a is expected to increase as well (Table 5). The conclusion may therefore be drawn that in the Middle- and Southern groups, of the available independent variables, T_W plays the most determining role in relation to the biological processes represented by the 2nd PC (Table 5b).

Table 5. Loadings of the assessed (response) water quality variables in the first three principal components A) and the correlation coefficients of the explanatory variables and the obtained PCs B). Loadings in red are outside the chosen ±0.6 interval (A) and the significant (p<0.05) correlation coefficients (r) are marked with an asterisk (*) in paned (B).

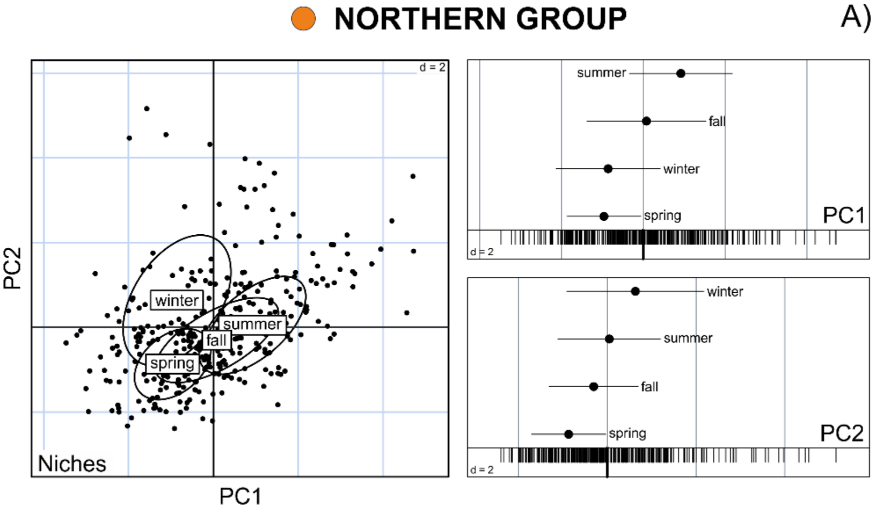
A)		● **Northern group**			● **Middle group**			● **Southern group**		
		Dim1	**Dim2**	**Dim3**	**Dim1**	**Dim2**	**Dim3**	**Dim1**	**Dim2**	**Dim3**
Principal Component Analysis	DO	-0.03	**-0.62**	0.1	-0.07	**0.71**	0.38	-0.06	**0.84**	-0.06
	BOD	-0.43	0.22	0.34	0.17	0.16	**0.82**	0.07	**0.7**	0.57
	Ca^{2+}	**0.77**	0.15	-0.08	**0.9**	0.05	-0.13	**0.83**	-0.05	-0.38
	Mg^{2+}	0.48	0.16	-0.32	**0.72**	0.18	-0.07	**0.73**	-0.01	0.08
	Na^+	**0.81**	-0.11	0.04	**0.89**	-0.15	0.08	**0.94**	-0.01	0.1
	K^+	0.48	0.32	0.37	**0.72**	-0.15	0.08	**0.8**	-0.01	-0.04
	Cl^-	**0.7**	0.09	0.21	**0.89**	-0.19	0.04	**0.88**	-0.14	0.16
	SO_4^{2-}	0.38	-0.29	0.54	**0.89**	0.21	0	**0.79**	0.21	-0.07
	HCO_3^-	**0.69**	0.14	-0.53	**0.9**	0.01	-0.18	**0.92**	-0.06	-0.17
	NH_4-N	0.21	0.41	0.48	0.31	0.58	-0.01	0.31	**0.73**	0.08
	NO_3-N	-0.37	0.48	0.04	-0.04	**0.8**	0.21	-0.12	**0.85**	-0.14
	SRP-P	-0.24	0.55	-0.11	0.16	0.42	-0.43	0.48	0.02	0.05
	Chl-a	0.2	-0.02	0.27	0.25	**-0.61**	0.55	0.17	-0.33	**0.87**
B)										
r	Runoff	-0.58*	0.21	0.06	-0.69*	0.2	0.03	-0.59*	0.19	-0.14

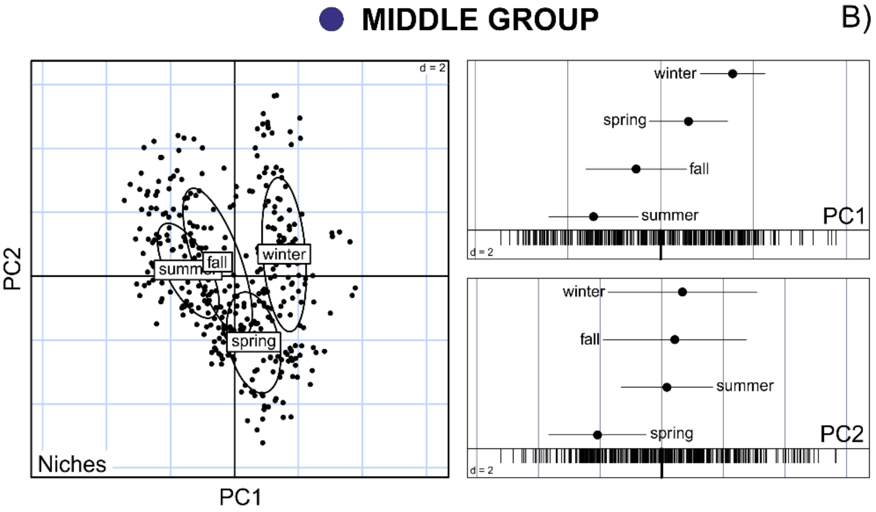
T_W	0.19	-0.13	-0.08	0.068	-0.82*	-0.12	0.11	-0.83*	0.25

3.3. Determination of seasonal n-dimensional hypervolume

The n-dimensional hypervolumes of the three homogeneous sections of the river (Fig. 1) made it clear that in the Northern group there is just a marginal difference between the positions and breadth of the niches in relation to the seasons, especially in the 1st PC (Fig. 2a). This was reflected in the power of the linear relationship between the variables, as also with the PCs. These, in turn, were relatively evenly distributed between PC1 and PC2 (Fig. 2a left panel). A slight differentiation is to be seen in the niche space of PC2, detemined primarily by dissolved oxygen (Table 5a). In this niche space only spring occupies a slightly marginal position.

In the Middle and Southern groups, separation of the niches of the various seasons, is mostly characteristic in PC1, where winter and summer take the furthermost position from one-another. In the 1st PC the ions were the most determining, and in which spring bore a greater similarity to winter, and fall to summer (Fig. 2b). In PC2, only spring separated from the other seasons, which is mostly determined by the nutrients. This however, is less characteristic in PC2 of the Southern group. The only substantial difference between the Middle and Southern groups compared to the Northern group was to be observed in the closer position of the overlapping niche spaces of the seasons, rendering winter almost totally separate from the other seasons in PC1 (Fig. 2b,c). In PC2, only spring separated (Fig. 2b,c)


NORTHERN GROUP
A)
d = 2
winter
summer
fall
spring
Niches
PC2
PC1
summer
fall
winter
spring
PC1
d = 2
winter
summer
fall
spring
PC2
d = 2


MIDDLE GROUP
B)
d = 2
winter
summer
fall
spring
Niches
PC2
PC1
winter
spring
fall
summer
PC1
d = 2
winter
fall
summer
spring
PC2
d = 2

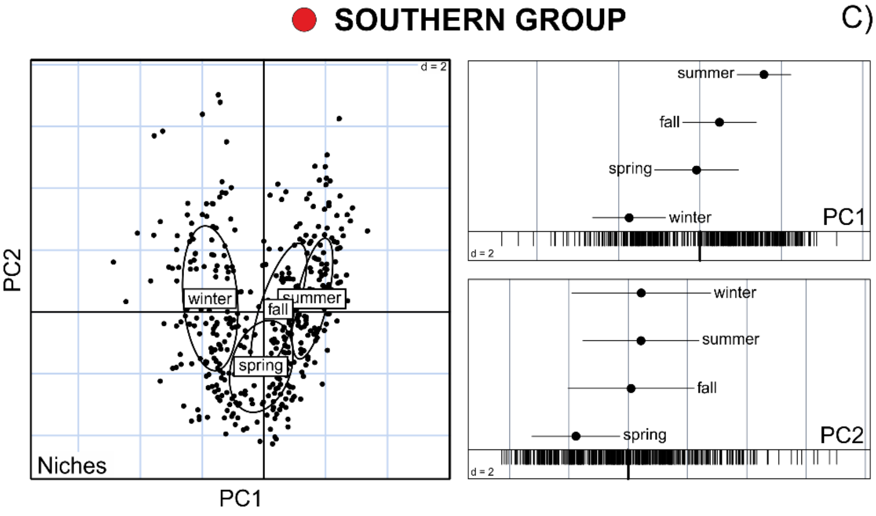

SOUTHERN GROUP
C)
d = 2
winter
summer
fall
spring
Niches
PC2
PC1
summer
fall
spring
winter
PC1
d = 2
winter
summer
fall
spring
PC2
d = 2

Fig. 2. Niche position of water quality observations in an n-dimensional hyperspace across the Hungarian section of the River Tisza. Left column: biplots of the first and second PCs, where black dots represent the observations, rings correspond to the 70% confidence ellipses estimated using the mean niche position for each season in the Northern A), Middle B) and Southern C) groups.

Right column: one axis presentation of outlying mean index results for the Northern A), Middle B) and Southern C) groups for PCs 1 and 2 (upper and lower sub-panels, respectively). Species distribution arranged according to site scores (black ticks); mean distribution indicated by a black dot.

4. Discussion

4.1. Stochastic relationships and absolute values of water quality parameters

The concentration of the ions in the homogeneous groups of the Hungarian section of the River Tisza did not vary to a significant high degree with the increase of runoff downstream (Tanos et al., 2015), and accounted for most of the variance over the whole river section (Table 5). This was reflected in the significant negative correlation between runoff and the first PC (Table 5b), in which ions played the most important role (Table 5a). However, along with flow velocity, the amount of dissolved oxygen also decreased downstream (Cox, 2003), while its importance increased. This, in turn, was reflected in its increased loading of DO in the 2nd PC (Table 5a). Interestingly, BOD did not behave as expected; instead of displaying an increase (Cox, 2003; Huang et al., 2010), BOD decreased. This may be the result of a combination of effects. Due to its macrophyte cover (Lukács et al. 2015)the Kisköre Reservoir is capable of retaining compounds that could lead to an elevated BOD in the lower sections of the river. A similar phenomenon is to be observed in wetlands particularly created for such a purpose (Hatvani et al., 2014, 2017). . Additionally, the River Kőrös does not bring an elevated level of inorganic nutrients (-20-30% compared to the River Tisza;Tanos, 2017). In the meanwhile due to the decreased flow velocity the dissolution of oxygen decreases as well; even the elevated levels of Chl-a content (+ ~20%) (Table 3) cannot compensate for the effects of these processes.

The decrease in SRP-P concentration in the Middle group may be related to the damming effect of the water barrage system (Tanos, 2017). This slows the water down, causing increased transparency, thus making a limiting factor of the light and temperature conditions for phytoplankton rather than nutrients (Vukovic et al., 2014). This was also reflected in the significant ($p<0.05$) and strong ($r<-0.82$) relationship between T_W and the 2nd PC of the Middle and Southern groups. In addition, it should be noted that with the characteristics of the river increasingly resembling those of a lower section river (sediment deposition, low turbidity, high transparency (Vukovic et al., 2014)), a continuous increase was seen in the absolute values of phytoplankton biomass (Kovács et al., 2017) and in their degree of importance as well (Tables 3 &5a).

4.2. Ecological covariances taking seasonality into account

Describing the habitat pattern of phytoplankton communities is crucial in determining the range of driving environmental variables (or constraints) in space and time (Vannotte et al., 1980). This habitat pattern could then serve as a revitalized niche of the community. There is a clear change in the niche space downstream in terms of both seasons and the parameters driving water quality. This change refers not only to the composition, but also to the position and breadth of the niche spaces (Table 2). The narrower the breadth, the more specific the niche spaces, and this occurred mostly in spring and summer on the River Tisza (Fig. 2).

In the Northern group, ions are the most determining factor, while phytoplankton and water temperature have only a marginal role, as along with DO, on account of the higher turbidity and low transparency of this river sub-section (Table 5). Here the river system is driven mainly by the concentration of ions and not nutrients, thus, the system does not “suffer” from the limitation of inorganic nutrients. This results directly in the uncharacteristic separation of any one of the seasons (with the slight exception of spring) from the others in the niche space (Fig. 2a). In fact, this finding is in accordance with the previously-existing knowledge that aquatic systems dominated by planktic- and benthic diatoms (TIB 1codon) are present in all seasons in upstream rhithral river sections (Vannotte et al., 1980; Wang et al., 2018; Table 2.). In general, the main factor most probably causing the change in diatom presence is sedimentation, but due to the relatively short residence time upstream, this does not happen either. Downstream, however, the impact of the changes in physical environment becomes more dominant (Bolgovics et al., 2017; Abonyi, 2012). The positive loading of chloride in the first PCs (loading=0.7; Table 5a) indicate that one of the most dominant diatom species is a halophilic centric diatom (codon C), but this characteristic is also true of other planktic diatoms in the River Tisza and other watercourses as well (B-Béres et al., 2017; Table 2.). The greater the distance from the source, the greater the degree to which seasonality became the main driving force in the structuring of river phytoplankton community composition, with lower TIB- codon and higher J and Y codon ratio (Table 2).

The Middle- and Southern groups of the River Tisza behave like the lower part of a potamal river and can be compared to a shallow, but disturbed, lake in which the inorganic nutrient input is a highly limiting factor on phytoplankton communities (Abonyi et al., 2012; Wang et al., 2018). This is reflected in the determining role of the N forms (Table 5a) and the mean niche positions of the seasons. This shift in niche also occurs as a functional shift in phytoplankton (Table 2), as is also the case in the Pearl River system (Wang et al. 2018). These observations are consonant with the fact that the primary nutrients (C, N, P,) in rivers are generally non-limiting factors in phytoplankton biomass (Minaudo et al., 2015). In the case of the River Tisza, this finds reflection in the non-determining role of primary nutrients in relation to the determined niche spaces of the river sections. With regard to seasons, both summer and winter separate in the first PC, while in the second PC, where N forms are dominant, this does not happen. In PC2spring separates from the other seasons (Fig. 2). In similar settings, it has been documented (Salmaso, 2003) that in general three types of the phytoplankton occur in a river. The first group includes large late winter/spring tychoplanktic diatoms (Varbiro et al. 2007), which develop in periods of high water turbulence and strong physical control, with high nutrient concentrations. This is clearly mirrored by the large TIB codon abundance in the northern part of the river. These diatoms, however are able to occupy the separate spring niche space determined in PC2 of the Middle- and Southern groups, where the quantity of nutrients and runoff is higher (both N and P increased), concentration of DO is lower than in the North (Table 3).

The second group of phytoplankton characterized by codons B, C and D is tolerant to grazing and sinking in stratified, stable conditions, and also of the nutrient-deficient conditions characteristic of the lower reaches of the river. Moreover, since these have different types of nutrient substrates, they are able to tolerate nutrient deficiency, even if this is not their preferred environment.

A third group of species (e.g. coenobial chlorococcoid green algae) develop in environmental conditions falling between those preferred by the two preceding types, and are mostly characteristic of the summer season (Salmaso, 2003).

Therefore, due to the abrupt spring/early summer change decreasing the degree of physical disturbance, mirrored in the relationship between the time series of the water quality parameters and the PCs (Table 5) and the seasonal separation of the niche spaces (Fig. 2), as summer progresses, the stabilization of environmental factors offers a window to a new group of species. However, in late summer/fall, thanks to increasing rainfall and falling temperature, species characterizing the winter/spring season reenter the community in accordance with typical plankton dynamics.

4. Conclusions

By conducting stochastic analyses of the three homogeneous river sections of the Hungarian part of the River Tisza (consisting of multiple sampling sites), it proved possible to look at an increased number of observations, thus enhancing the effectiveness of the predictive models and the robustness of the results.

The principal component- and outlying mean index analyses conducted on these datasets indicated that (i) in the upper section of the river, the separation of the ecological niche spaces is not characteristic, while (ii) downstream a seasonal separation of the n-dimensional hypervolumes is to be observed, and (iii) the downstream change in the composition of the driving parameters of water quality (e.g. increased influence of ions and organic components) was responsible for the differentiation of the phytoplankton communities in their reaction to the niche separation.

The study provides an example on how the combination of state-of-the-art multivariate statistical methods is able to (i) increase data density without information loss, thus (ii) enhance the robustness of the models and (iii) effectively determine hydrochemical seasons and (iv) indicate both the background factors and also the ecological niches of a riverine ecosystem.

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