

Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary

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ABSTRACT

In this research, indicator properties of the three recently described diatom ecological guilds (low profile, high profile and motile) and their responses to different stressors and disturbances were tested along a temporal gradient. Experiments were run at a standard sampling site in the Torna-stream (Hungary) between 2008 and 2010 using standardized substrata. The low profile guild was dominant during periods with low nutrient (SRP and TN) availability. In contrast, the high profile guild was dominant in resource rich (SRP and SRSi) periods. The motile ecological guild was the most sensitive to the nutrients (TN and SRSi) and some other factors (e.g. temperature, Cl⁻). Increasing irradiance in spring and summer favored the growth of the high and the low profile guild. Higher resistance to floods favored the adhesion type of the low profile guild enabling their summer peak in terms of relative abundance. During high flood periods, incident light availability apparently sufficed the needs of this guild. Seasonal changes of the diatom ecological guilds and guild diversity were robust and predictable. This study supported that the ecological responses of diatom ecological guilds, despite the apparent simplicity of the grouping method, is strong enough to indicate the temporally changing environmental conditions.

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1. Introduction

Nutrient availability, light and other physical and chemical properties (e.g. temperature, pH, ionic composition) of the water are essential variables in aquatic ecosystems and their extent and/or availability change both in space and time, consequently affecting diatom communities (Lavoie et al., 2008; Smucker and Vis, 2011). Their variability is influenced both by natural and anthropogenic impacts and evolutionary adaptation to their extremes (stress) is possible at species level (e.g. evolution of heat or salt tolerant taxa). Disturbances act at a different way. According to definition by Reynolds et al. (1993) "disturbances are primarily non-biotic, stochastic events that result in distinct and abrupt changes in the composition and which interfere with internally driven progress toward self organization and ecological equilibrium; such events are understood to operate through the medium of (e.g.) weather and at the frequency scale of algal generation times". Thus, disturbances (typical examples are floods or intermittent pollution events in rivers) appear unexpectedly, suddenly, they

are short lasting and organisms cannot avoid or prevent them. However, adaptation is possible at community level; in other words, the response can be traced as community change.

Recent research of diatoms is focusing largely on tolerance limits of individual diatom species and aims to search for the relationships between species occurrence and environmental parameters (e.g. Gómez and Licursi, 2001; Potapova, 2011). Ecological importance of the growth forms and life strategies were recognized for phytoplankton, macroalgae and diatoms in the 1970s–1980s (Margalef, 1978; Littler and Littler, 1980; Hudon, 1983). Types of benthic algal growth forms (may involve taxonomically loosely related taxa which use similar habitats and compete for the same resources) based on the shape, posture, type of the adhesion and motility of the species is of basic importance for the ecological success of the species (Hudon and Bourget, 1981; Hudon and Legendre, 1987). After a long time, ecological importance of growth forms was re-recognized (Steinman et al., 1992; Carrick and Steinmann, 2001) and Passy (2007) defined three ecological guilds (low profile, high profile and motile) characterizing them by resource utilization and stress adaptation. She drew the attention to their use as informative indicators in the ecological assessment of running waters. Morphological guilds and physical structure of the diatom assemblages was studied in response to different environmental parameters (Wang et al., 2005) expecting different response of these guilds along nutrient and current velocity gradients (Smucker and Vis, 2010). Recently, experiments were carried out to study functional group

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Table 1
SWOT analysis of the three diatom ecological guilds.

	Strength (S)	Weakness (W)	Opportunity (O)	Threat (T)
High profile	Position allows for superior access of light and nutrients	Exposition to grazing and shear forces	Utilization of small substrate surfaces; access to light/nutrients in case of scarcity	Sudden disturbances
Low profile	Resistance to high flow velocity and floods	Substrate surface (population increase is space limited)	Re-development after disturbance events	Developing canopy by high profile spp. results in shading and nutrient limitation
Motile	Ability to change position	Lack of stabilizing aid	Ability to change position	Any increase in flood velocity

structure of the benthic community along pesticide contamination gradients (Rimet and Bouchez, 2011) and under different grazing pressures (Lange et al., 2011) in rivers.

There has been an ongoing debate on the minimum necessary taxonomic level in recent diatom ecology. Some studies, like Kociolek and Witkowski (2005) emphasize the importance of the species level taxonomy to preserve all the information, while others (e.g. Wunsam et al., 2002; Rimet and Bouchez, 2012) argue that genus level taxonomy is also adequate. Solution of this perpetual struggle is that the taxonomic resolution should meet the study's aim (Ellis, 1985). In biomonitoring programs the most time-, labor- and cost effective methods are needed, without compromising the reliability and interpretability of results, to maximize gaining knowledge of ecological response of the biotic community (Lavoie et al., 2009).

1.1. Research concept

If applying a simple SWOT analysis on the phytobenthos ecological guilds described by Passy (2007), each ecological guild can be characterized by Strengths (the guild has advantage over others), Weaknesses (the guild has disadvantage relative to others), Opportunities (chance to improve performance) and Threats (external elements in the environment that may endanger performance of the guild) corresponding to their position in the biofilm. According to the SWOT analysis (Table 1), the *low profile* guild (situated on the base of the benthic layer) experiences resource stress (by nutrient limitation and shading by algal canopy). They withstand depletion of resources (S) furthermore, they are resistant to the disturbances, like floods (S). They are limited by nutrients and shade (T). In contrast, the *high profile* guild building the upper layer of the phytobenthos is threatened by disturbance (like grazing or flushing) (W, T) but the resource limitation is not characteristic (S) especially if colonies are composed of small cells (O). The *motile* guild is not sensitive either to resource limitation or to disturbance (S) and they can move (O) on short scale according their immediate requirements. However, because of the lack of attachment (W) they are exposed to disturbances and can be easily washed out by flood pulses (T). Their resistance to the disturbance may depend on the canopy of the benthic layer.

In this study, we aimed to explore how the aforementioned three diatom ecological guilds respond to the different stressors and disturbances. In Passy's (2007) study this relationship was analyzed along a spatial gradient, and our study focused on the temporal gradient with a standardized method (standard substrata at standard sampling site). Our hypotheses were the following:

- (i) Guild level ecological analyses of the benthic diatoms can be appropriate for the indication of the changing environmental conditions on temporal gradient.
- (ii) Expected response to temporal and seasonal changes in nutrient (Si, N and P forms) availability: the proportion of the high profile guild will increase with increasing nutrient availability in contrast to the low profile guild which will proportionally

increase in response to decreasing nutrient availability. For the motile guild we do not expect any obvious relationship.

- (iii) Expected response to other stress factors (temperature, conductivity, Cl⁻, pH, COD, DO, oxygen saturation): the low and high profile guilds are more sensitive to these temporally and seasonally changing stressors than the motile guild. The sensitivity sequence is: high profile, low profile and motile ecological guilds.
- (iv) Expected response to rainfalls and floods as disturbances: floods caused by rainfalls decrease the light availability which will favor to the low profile guild. The most sensitive groups to the increased water discharge will be the motile and the high profile guilds, their relative abundance will decrease under high discharge conditions. The low profile guild will tolerate this condition resulting in a higher proportional abundance in the ecological guilds.

2. Material and methods

Torna-stream (length: 51 km) and its catchment area (498 km²) are located on an oval field along an east–west axis in the western part of Hungary. According to the Hungarian national typology system, Torna is a hilly stream with calcareous hydrogeochemistry and coarse bedrock (Type 5) (www1). The climate is temperate humid. The mean annual temperature of the water basin is 10.3 °C, the average temperature of the warm period of the year (from April to September) is 17 °C, while in the cold period (from October to March) is 3.7 °C (www2). The average temperature variation is 21.5 °C in a year. The rainfall is 670–700 mm per year (Gergely et al., 2001). The sampling site was located at the urban section of the stream, in the town Devecser, Hungary (N 47° 06' 63", E 17° 26' 11"; Fig. 1). At the sampling site the riverbed is linear, trapezoid and it is straightened by concrete blocks. The vegetation of the littoral zone is mown, trees are absent. The experiments in the Torna-stream were running between February 2008 and April 2010.

Manufactured (100 mm × 100 mm × 30 mm) and sterilized (H₂O₂ treatment + UV + high temperature) freshwater limestone-bricks from the mines of Süttő (Hungary) were deployed as substrata; they correspond to the calcareous characteristic of the stream. The bricks were exposed (and fixed) in the riffle of Torna-stream (annually 120 bricks) and were used as semi-natural substrata for the sampling. The first deployment started in April 2008 and the second in April 2009. At the beginning of the experiments one randomly chosen brick was removed on every third or fourth day, and after one month sampling was weekly. Between 2008 and 2010, altogether 112 benthic diatom samples were collected. Diatoms were removed from the bricks by tooth-brushing. Digestion of diatoms followed the hot hydrogen-peroxide method (Ács and Kiss, 2004), valves were embedded in Zrax[®]. To determine the relative abundance of the species and diatom ecological guilds, 400 valves per slide were counted at minimum in light microscope (Zeiss Axio Imager A1, Planapochromat DIC lens). Additionally, SEM investigations were applied to identify small, difficult taxa. Classification of the

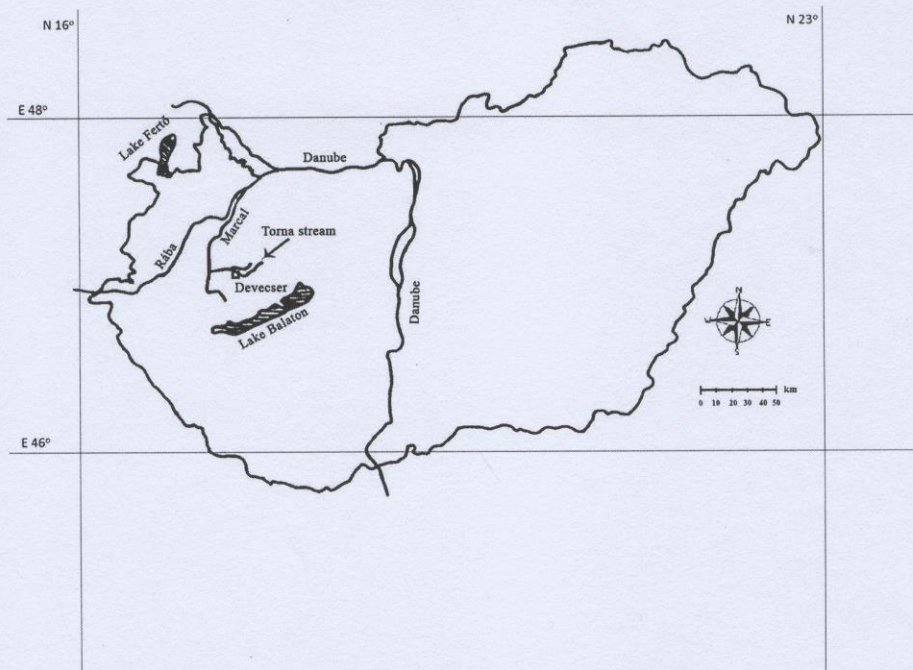


Fig. 1. Sampling site on the Torna-stream, Hungary.

species to high-, low- and motile guilds followed the description by Passy (2007) and Rimet and Bouchez (2011); and further 11 genera were classified into diatom ecological guilds (Cox, 1996): *Delicata* and *Rhoicosphenia* as the members of the high profile guild; *Caloneis*, *Cymatopleura*, *Epithemia*, *Frustulia*, *Hantzschia*, *Hippodonta*, *Pinnularia*, *Stauroneis*, *Surirella* as elements of the motile guild.

Water chemical analyses started earlier (February 2008) than the phytobenthos sampling to get knowledge on the physical and chemical characteristics of the stream water and rate of the changes in the environmental variables. Altogether 123 water samples were collected. Dissolved oxygen, oxygen saturation, conductivity, pH and temperature were measured *in situ* with a portable multi-parameter digital meter (HQ40d – Hach Lange, Düsseldorf, Germany). Water samples were collected for further laboratory analyses to measure the concentrations of N and P forms (spectrophotometric method; APHA, 1998), soluble reactive silica (SRSi) (spectrophotometric method; Wetzel and Likens, 2000), chloride and chemical oxygen demand (COD) (titrimetric method; APHA, 1998).

The light field at the sampling location was measured with US-SQS/L spherical quantum micro sensor (Heinz Walz GmbH) connected to a data logger (LI-1400, Licor, USA). Light attenuation coefficient, k (m^{-1}), of the water column was calculated from simultaneous measurements of irradiances in the field at time of samplings at both the substrate and water surface with the Lambert–Beer function (Kirk, 1994). A continuous record of total

daily global radiation recorded at a nearby site (Szentkirályszabadja) was provided by the Meteorological Service of Hungary. Knowing the global radiation data and vertical attenuation coefficient, values the irradiance level reaching the stream bed was estimated. Daily irradiance ($\mu mol\ m^{-2}\ d^{-1}$) at the surface of the substrates was calculated as the sum of the hourly irradiances from sunrise to sunset. One week average irradiances and water discharge values (daily water discharge data were provided by the regional Water Authority) were used to calculate correlations with different diatom ecological guilds.

Principal component analysis (PCA) was performed to (i) verify the main tendencies in the environmental variables of the Torna-stream, with data transformed by 'ranging' and (ii) to access the variability of biological data (diatom species), with data transformed by ' $\log(x+1)$ '. Integrated analysis of the main abiotic variables and the diatom species were accessed by canonical correspondence analysis (CCA), with abiotic and biological data transformed by 'ranging' and ' $\log(x+1)$ '. The software used was PCOrd version 4.1 (McCune and Mefford, 1999). Statistical analyses were performed on a data set involving only sampling occasions (82 parallel samples) when layered benthic assemblages were developed (thus avoiding the initial colonization phase). Species and guild diversities were calculated by the Shannon function. Spearman's rank correlations were calculated using the R computing environment (R 2.11.0, R Development Core Team, 2010). Adjustment of the significance levels followed the sequential Bonferroni method (Motulsky, 1995).

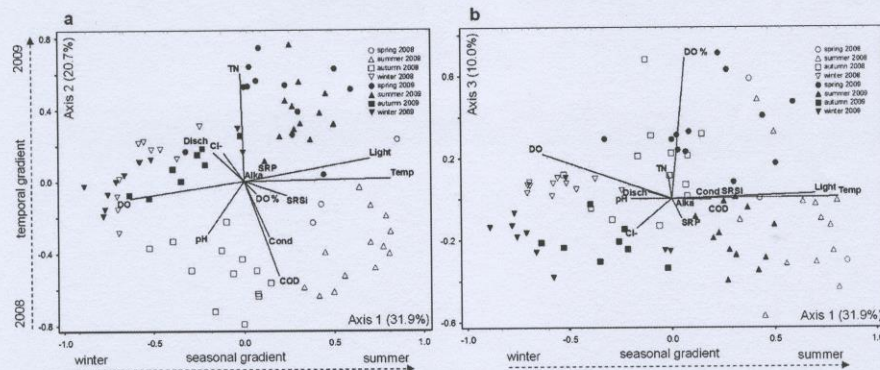


Fig. 2. Principal component analysis diagram with ordination of axis 1 and 2 (a) and axis 1 and 3 (b) of environmental variables of the Torna-stream from May 2008 until April 2010. Legends: DO = dissolved oxygen, DO % = oxygen saturation; Cond = conductivity; Temp = water temperature; Alka = alkalinity; COD = chemical oxygen demand; SRP = soluble reactive silica; pH = pH; SRP = soluble reactive phosphorus; TN = total nitrogen; Cl⁻ = chloride; Light = average irradiance; Disch = discharge.

3. Results

3.1. Environmental scenario

Principal component analysis (PCA) performed with environmental variables explained 62.6% of data variability in three axes. The most important variables to axis one ordination were: temperature ($r=0.901$) irradiance level ($r=0.836$) and dissolved oxygen ($r=-0.794$). For axis two, total nitrogen (TN) ($r=0.772$), COD ($r=-0.724$) and conductivity ($r=-0.553$) were the most important variables and for axis three ordination oxygen saturation (DO%) ($r=0.828$) was most important (Fig. 2).

Axis one represented the seasonal (summer–winter) gradient. Along the second ordination axis an annual gradient was observed in the PCA diagram, the sample units from 2008 being on the negative side of axis two. On its positive side, the sample units from 2009 were associated with higher values of TN, Cl⁻ and discharge. The third axis showed a pattern especially oriented by the higher values of oxygen saturation especially in spring 2009. The seasonal mean values and standard deviations of the environmental parameters are given in Table 2.

3.2. Integrated analysis

The canonical correspondence analysis (CCA) performed with seven abiotic variables (the ones representing the highest correlation with the first two axes of the PCA, thus avoiding redundant variables and maintaining ecological importance for diatom guilds) and all the diatom species accounted to eigenvalues of 0.155 and 0.077 for the first two axes, respectively (Fig. 3). The Pearson correlation of environment–species was high for both axes ($r=0.889$ and $r=0.753$), and indicated a strong correlation between abiotic variables and species distribution. The Monte Carlo test (99 permutations; $p < 0.05$) demonstrated that the ordination of axes 1 and 2 was statistically significant ($p = 0.01$), and did not occur at random.

Canonical coefficient pointed out that Cl⁻ (-1.0086) and irradiance (-0.250) were the most important variables to axis one ordination and temperature (0.582) and discharge (-0.486) to axis two. Retaining the dependence of environmental variables and the diatom species to the axes ordinations, the intraset correlations selected Cl⁻ (-0.989) and TN (-0.426) as the most important variables to axis one and temperature (0.810) and dissolved oxygen (-0.733) to axis two.

The CCA diagram showed that species responded first to the annual gradient (2008 → 2009) as demonstrated by the first axis and after that to the seasonal pattern (summer → winter) as demonstrated by axis two (Fig. 3).

Some representatives of high profile guild, such as *Gomphonema vibrio* Ehrenberg (GVIB), *Gomphonema truncatum* Ehrenberg (GTRU), *Melosira varians* C. Agardh (MVAR), *Fragilaria fasciculata* (C. Agardh) Lange-Bertalot (FFAS), *Ulnaria ulna* (Nitzsch) P. Compère (FULN), *Diatoma tenuis* Agardh (DITE), *Gomphonema parvulum* (Kützinger) Kützinger var. *parvulum* (GPAR) *Fragilaria capucina* var. *vaucheriae* (Kützinger) Lange-Bertalot (FCVA) and *Gomphonema pumilum* (Grunow) Reichard & Lange-Bertalot (GPUM) were ordinated in the positive side of axis one, under low values of chloride and TN, from sampling units in 2008. Other representatives of this guild were positively associated with SRP, temperature and light intensity, associated mainly with sampling units from summer 2009 (*Fragilaria nanana* Lange-Bertalot (FNAN), *Aulacoseira granulata* (Ehrenberg) Simonsen (AUGR), *Staurosirella*

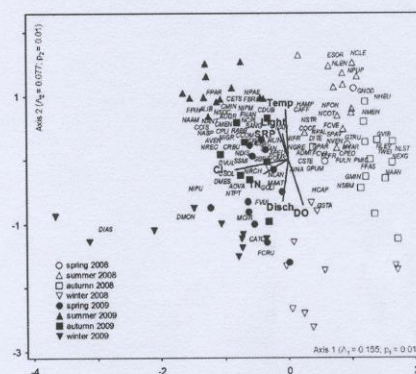


Fig. 3. Canonical correspondence analysis diagram of environmental variables and diatoms species of Torna-stream from May 2008 until April 2010. Legends: DO = dissolved oxygen, Temp = water temperature; SRP = soluble reactive phosphorus; TN = total nitrogen; Cl⁻ = chloride; Light = average irradiance; Disch = discharge; species abbreviation follows OMNIDIA codes.

Table 2
The measured physical and chemical parameters of the Torna-stream between 2008 and 2010.

year, season	DO (mg l ⁻¹)	O ₂ sat- uration (%)	Temperature (°C)	pH	Irradiance (μmol m ⁻² d ⁻¹)	Discharge (m ³ s ⁻¹)	TN (mg l ⁻¹)	COD (mg l ⁻¹ O ₂)	SRP (μg l ⁻¹)	SRSi (mg l ⁻¹)	Cl ⁻ (mg l ⁻¹)	Conductivity (μS cm ⁻¹)
2008 Spring	Mean	109.3	13.4	8.1	9137	0.48	1.49	5.54	23.93	2.95	6.91	1536
	SD	1.2	3.2	0.2	1459	0.07	0.80	3.66	33.50	1.23	1.10	108
2008 Summer	Mean	8.3	21.6	8.0	7391	0.44	1.50	13.40	23.71	5.11	7.21	1669
	SD	0.7	6.1	0.1	1642	0.08	0.60	5.60	13.41	1.42	2.14	217
2008 Autumn	Mean	10.8	14.3	8.0	2704	0.39	3.43	14.27	13.83	6.11	8.69	1309
	SD	0.7	2.8	0.2	1174	0.05	0.38	4.61	13.87	0.88	2.24	260
2008–2009 Winter	Mean	11.5	92.7	5.1	8.0	1174	32.47	1.81	21.71	4.24	12.15	1332
	SD	0.5	2.1	1.8	0.1	664	2.93	1.83	14.26	0.96	3.67	172
2009 Spring	Mean	10.0	98.3	13.2	7.8	6944	77.05	2.01	19.12	4.50	14.63	1135
	SD	0.5	4.7	2.9	0.1	2619	1.44	2.24	9.72	0.38	1.50	112
2009 Summer	Mean	8.7	19.5	7.7	6845	0.49	34.75	1.73	32.45	4.83	20.27	1075
	SD	0.7	6.1	1.9	1817	0.1	0.04	0.66	21.80	0.53	6.01	84
2009 Autumn	Mean	9.8	12.9	7.9	2262	0.39	20.24	1.66	3.90	4.12	25.24	1041
	SD	0.6	3.5	0.1	1139	0.04	0.05	0.28	15.99	0.72	2.39	46
2009–2010 Winter	Mean	11.5	90.3	4.2	995	0.52	17.58	2.86	4.49	2.86	28.27	1054
	SD	0.8	2.2	0.1	613	0.08	0.15	0.65	4.49	0.99	1.87	30
2010 Spring	Mean	10.3	94.0	10.3	8.0	1.09	21.05	4.46	14.53	3.65	37.97	1017
	SD	1.1	4.0	0.1	–	0.75	0.06	1.93	3.58	0.50	6.10	64

pinnata Ehrenberg (FPIN), *Pseudostaurosira parasitica* (W. Smith) Morale (FPAR), *Diatoma vulgaris* Bory (DVUL), *Diatoma mesodon* (Ehrenberg) Kützing (DMES) and *D. moniliformis* Kützing (DMON) (high profile guild) were ordinated to the higher values of Cl⁻ and TN.

Considering the low profile guild, certain species were associated to the higher values of temperature, light and SRP [especially *Cymbella affinis* Kützing (CAFF), *Cyclotella ocellata* Pantocsek (COCE), *Cyclotella dubius* (Fricke) Round (CDUB), *Cyclotella comta* Kützing (CCOM)] and others were negatively associated to SRP, occurring under higher concentration of TN, discharge and Cl⁻, such as *Amphora ovalis* (Kützing) Kützing (AOVA), *Meridion circulare* (Gréville) C. Agardh (MCIR), *Amphora inariensis* Krammer (AINA) and *Cyclotella stelligera* Cleve & Grunow (CSTE), ordinated in the negative side of axis 2 with winter sampling units.

Representatives of motile guild did not exhibit clear distribution patterns that would outline a consequent abiotic scenario.

According to Spearman's rank correlation and the Bonferroni–Holmes correction the low profile ecological guild was sensitive for four, the high profile guild altogether for three parameters. Their response to the changes of temperature and oxygen saturation was similar. The proportion of the high profile guild was closer connected with the conductivity, however the correlation was not significant after sequential Bonferroni correction (Table 3). The motile ecological guild correlated significantly with eight different physical and chemical parameters (Table 3) and this guild showed stronger correlation with the environmental variables (Table 3) than the other two, except COD. This guild was very sensitive to the changes of the Cl⁻ ion and water temperature (Table 3). Each guild responded to the changes of oxygen saturation, the low and the high profile guild preferred highly saturated periods in contrast to the motile guild (Table 3). Using the sequential Bonferroni method water, discharge did not influence the amount of the diatom ecological guilds; however, it is noticeable (without the correction) that the increasing water discharge reduced the proportion of the high profile guild ($r = -0.23$) in favour of the motile guild (Table 3). Among the nutrients the TN had negative, the SRSi had positive effect on the abundance of motile guild. The high profile guild may increase in abundance under higher nutrient (SRP and SRSi) concentration in contrast to the low profile guild (under higher SRP and TN content). The higher irradiance level favoured the low profile guild, the motile guild benefited in shaded periods (Table 3). The sunny periods could also further enhance the proportion of the low profile guild.

The guild diversity showed significant correlations with nine environmental parameters, while the species diversity with only five. The guild diversity was best related to the TN and the Cl⁻ ion, while the species diversity to the water temperature and discharge (Table 3). The enhanced irradiance level favoured primarily the guild diversity, while the higher water discharge reduced both diversities (Table 3).

Changes in relative abundance of the three guilds were rather clear from season to season in both years. From spring to summer the proportion of the high ecological guild decreased, while the low and motile guilds increased. From summer to autumn the low and high guilds decreased and the relative abundance of the species in the motile guild increased. This pattern continued from autumn to winter; however in 2008 the high profile guild did not show characteristic changes. From winter to spring the high profile guild started to increase and the abundance of low and motile guilds decreased (Fig. 4). The dominance of the high profile guild was the highest in spring, and the low profile guild dominated in summer. In autumn and mostly in winter the dominance of the motile guild was apparent (Fig. 4).

Table 3

Significant Spearman's rank correlations between diatom guilds, guild diversity, species diversity and the environmental variables (cursive letter marked by star = significant correlation, $p < 0.5$; bold letter = significant correlation according to sequential Bonferroni method).

Variables	Low profile	High profile	Motile	Guild diversity	Species diversity
Water temperature	0.35	0.43	-0.55	0.55	0.52
Dissolved oxygen	-0.16	-0.25 [*]	0.32 [*]	-0.25 [*]	-0.25 [*]
Oxygen saturation	0.36	0.35	-0.45	0.52	0.46
COD	0.40	0.12	-0.36	0.36	0.22 [*]
Conductivity	0.25 [*]	0.34 [*]	-0.41	0.39	0.12
pH	-0.05	-0.06	0.05	-0.08	-0.13
SRP	-0.25 [*]	0.27 [*]	-0.15	0.03	0.29 [*]
TN	-0.27 [*]	0.12	0.41	-0.58	-0.23
SRSi	0.02	0.33 [*]	-0.39	0.42	0.47
Cl ⁻	0.28 [*]	-0.53	0.6	-0.56	-0.37
Irradiance	0.43	0.27 [*]	-0.44	0.40	0.23 [*]
Water discharge	-0.05	-0.23 [*]	0.25 [*]	-0.38	-0.50

In general, the average guild diversity was the highest in summer (1.07 [2008] and 0.99 [2009]), while it was the smallest in spring (0.85 [2008] and 0.67 [2009]) and in winter (0.96 [2008] and 0.66 [2009]). The average species diversity and species number showed similar results: the highest species diversity and species number were observed in summer (diversity: 3.7 [2008]–3.9 [2009] and species number: 27 [2008]–36 [2009]) or autumn (diversity: 3.9 [2008] and species number: 32 [2008–2009]). The seasonal changes in the guild and species diversity as well as changes in the species number exhibited a rather clear pattern: from spring to summer the guild diversity increased and reached the peak in summer. From this season through autumn to winter the guild diversity decreased continuously. Between winter and spring the changes were different in the two consecutive years. In case of the species

diversity and species number similar trends were observed with one outlier: the changes in these variables were opposite from summer to autumn in 2008 and 2009 (Fig. 5).

4. Discussion

The Torna-stream is exposed to different natural and anthropogenic impacts. Latter includes contaminants (e.g. nutrients, salts) and habitat alteration (current alteration, channel simplification, reduction of the flow variability). Among the environmental parameters, temperature, irradiance level, DO, TN, COD and conductivity were the most important physical and chemical variables with seasonal and annual changes in the Torna-stream. Based on the seasonal and annual fluctuation of these factors, composition of benthic community varies (Hameed, 2003). According to the CCA, Cl⁻, irradiance level, temperature, discharge, TN and DO were most important environmental factors affecting the diatom species composition of the Torna-stream following an annual and a seasonal gradient in importance order.

Cl⁻ is a key factor for diatom assemblages as shown in earlier studies (Napolitano et al., 1994; Potapova and Charles, 2003; Smucker and Vis, 2010; Bere and Tundisi, 2011). Increased Cl⁻ concentrations have negative effect not only on the growth and development of the individual diatom species (Videau et al., 1980), but also on the biomass and production. In ecophysiological sense, Cl⁻ inhibits the hydration of carbon-dioxide in the photosynthesis (Dionisio-Sese and Miyachi, 1992). The chlorine-tolerant organisms are also tolerant to other environmental stressors (Dickson et al., 1977). The Cl⁻ concentration was very high in the studied section of the Torna-stream (the seasonal mean 6.9–38 mg l⁻¹) compared to its upstream sections where the annual average Cl⁻ concentration < 2.4 mg l⁻¹ (unpublished data) or to other Hungarian streams (e.g. Koloska, Pécsely) classified as natural streams with Cl⁻ concentrations of 4–8 mg l⁻¹ in the upstream section (Kiss et al., 2004). The conductivity of the stream was also high indicating the high ionic concentrations e.g. of Cl⁻ (seasonal mean: 1017–1669 $\mu\text{S cm}^{-1}$) whereas seasonal mean of the conductivity in one of its tributary streams was only 774–935 $\mu\text{S cm}^{-1}$ (unpublished data), and in upstream section of the Torna this annual average value was < 726 $\mu\text{S cm}^{-1}$ (Kovács et al., 2011). Concentration of ions increases along the agricultural to urban areas (Bere and Tundisi, 2011). The conductivity/salinity is one of the most important factors influencing diatom assemblages in rivers (Pan et al., 1996; Kovács et al., 2006; Frankovich et al., 2006; Bere and Tundisi, 2011), as observed in the Torna-stream, too. Diatom community is sensitive to the conductivity (Lane and Brown, 2007; Potapova and Charles, 2003) which reflects the geology of the catchment area, the closeness of the sea (Rimet et al., 2007; Chaib et al., 2011) or the anthropogenic stresses like industrial sewage, agro-fertilizers or winter de-icing (Fore and Grafe, 2002; Smucker and Vis, 2009). Soil

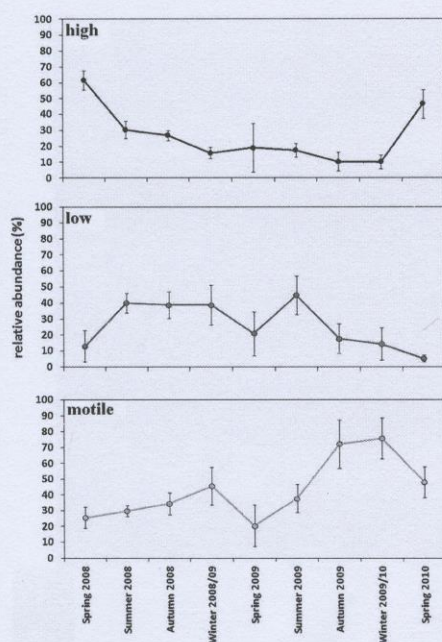


Fig. 4. Relative abundance (mean and standard deviation) of the three diatom ecological guilds from season to season in two consecutive years.

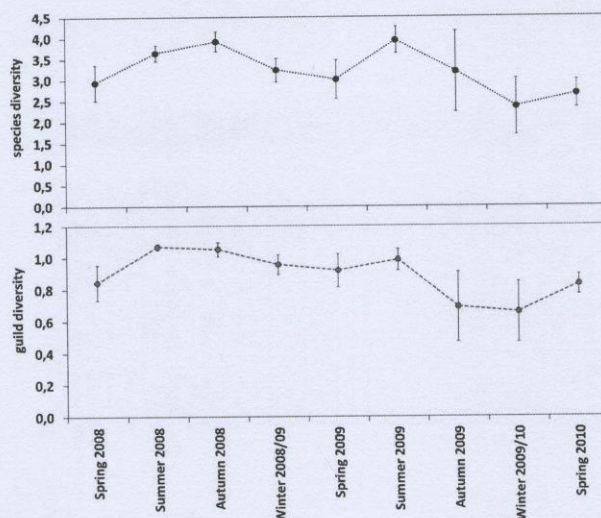


Fig. 5. Shannon diversity on guild and species level (mean and standard deviation) from season to season in two consecutive years.

erosion, municipal and agricultural wastewaters can also increase the conductivity of rivers (Leland, 1995). The secondary salinization is due to human activities like certain industries, irrigation and road salting. Nowadays, this secondary salinization qualifies as one of the most important surface water contaminations (Williams, 1999; Ziemann and Schulz, 2011.). The geology of the bedrock in the area of the Torna-stream does not justify the high conductivity of the stream therefore it can be attributed to human influences. The diatom ecological guilds were more sensitive to Cl^- than to conductivity. The high profile guild was negative while the motile guild was positive indicator of the high Cl^- content of the Torna-stream. From the motile guild e.g. *Nitzschia recta* and *N. gracilis* appeared as Cl^- tolerant taxa, while *G. parvulum*, *U. ulna* as high motile species were sensitive to this ion and indicate the lower Cl^- concentration. *Nitzschia palea* (motile species) was already published (Dickson et al., 1977) as a dominant taxon in strongly polluted sites with high Cl^- . However, in this study this species was only subdominant (average relative abundance 1–3%). Motile growth forms increase with higher sewage level while erect and stalked species representing the high profile guild decrease (Smucker and Vis, 2010). The guild and species diversity of the diatom community were also reduced by higher Cl^- content of the water as well as species diversity of Amphibians (www3). This result parallels the results of phytoplankton research in Hungarian small lakes where species number was in a strong negative correlation with conductivity (Padisák et al., 2003).

The species distribution is affected by the concentration of the different nutrients (Stevenson et al., 2008). In the Torna-stream diatom ecological guilds also changed along SRP, TN and SRSi gradients. The nitrate tolerant taxa were the same as for low temperature e.g. *Frustulia vulgaris* (Thwaites) De Toni, *Navicula tripunctata* (O.F. Müller) Bory, *Nitzschia pusilla* Grunow representing the motile ecological guild. This guild showed the strongest correlations with TN and SRSi, but not with SRP. The reason could be that only stone substratum was sampled, and motile diatoms exhibit stronger relationships with N and P in case of multi-habitat sampling (Smucker and Vis, 2010). In winter and spring, the increased TN concentration

and N tolerant diatom communities are characteristic which can be attributed to the decreased the terrestrial biotic retaining due to the flushing effect of the snowmelts or floods (Smucker and Vis, 2011). In this study, the proportion of the low profile guild increased with the decreasing TN and SRP concentration, which coincides with the other observation showing that low profile guild is dominant at sites with low nutrients and resources scarcity (Passy, 2007; Lange et al., 2011). The low profile guild was not sensitive to the SRSi content, however e.g. the included *Achnanthes minutissimum* was a positive indicator of Si content in an earlier study (Stenger-Kovács et al., 2006). Contrary to this group, the high profile guild was dominant in resource rich (Lange et al., 2011), eutrophic sites of the downstream sections (Passy, 2007). Our study supported this result since the high profile guild was higher in samples with high SRP and SRSi content. Furthermore, the current reduces the nutrient-poor boundary layers above the epilithon community (Borchardt, 1996; Stevenson et al., 2006), that affect auspiciously the growth of high profile diatoms in spring. Because of the thick epiphyton, the nearby cells could overlap, and nutrient poor regions may occur within the epilithon (Borchardt, 1996; Stevenson et al., 2006; Tuchman, 1996). These habitat properties may favor low-profile diatoms.

Seasonal changes of the biotic and abiotic factors affected annual dynamics of the periphyton. Light intensity and temperatures differences of spring and winter are responsible for these seasonal changes (Chen et al., 2010). Grazing can limit oscillation of the seasonal variability in the benthic community (Abe et al., 2007). The invertebrate activity is typically low in spring in the cold water (Power, 1992; Pék et al., 2010) and represents a seasonally recurrent pattern upon diatom communities (Shamsudin and Sleight, 1994). Seasonality played a key role in the diatom community of the Torna-stream. The ecological guilds and guild diversity responded to the changes from season to season. The seasonally changing temperature and related changes in dissolved oxygen determined the species composition and the proportion of the different diatom ecological guilds. At higher temperatures generalist and eurythermic species are more abundant (Perkins et al., 2010) and temperature sensitive organisms disappear. The indicators of the higher

temperature and low dissolved oxygen concentration were the high profile (e.g. *F. nanana*) and the low profile guild (e.g. *C. affinis*). The high profile guild became dominant in spring in the colonization phase indicating increasing water temperature. The appearance and higher relative abundance of stalked taxa (*Fragilaria*, *Gomphonema*) included in the high profile guild, and the motile taxa (*Navicula*) in the first phases of the succession were supported in other observations (Ács, 1998; Hameed, 2003). However, stalked diatoms included in the high ecological guild have greater affinity to epilithic habitats (Smucker and Vis, 2010) like the applied stone substratum, while motile and unattached diatoms are more abundant in multi-habitat samples (Smucker and Vis, 2010). All the three diatom ecological guilds were sensitive to the temperature, especially the motile ecological guild which was associated to the cold water temperature. The response of the low profile guild was positive, while the motile guild's negative to the COD, which means that these guilds can be a good indicators of oxygen levels changing in relation to the intensity of decomposition.

The seasonal and annual fluctuation of environmental factors and disturbances can determine the diatom assemblages not only in arid (Gastith and Resh, 1999) but also in other regions of the Earth, especially in regions where the effect caused by the global climate change intensifies. In 2008 and 2009 the weather in Hungary was unusual. Heavy rainfalls occurred in summer, autumn and winter when the precipitation was twice but in some months three or four times higher than in spring. In the summer–winter period the proportion of the high profile guild decreased due to recurrent floods, in accordance with the expected vulnerability to increased shear forces (Biggs and Thomsen, 1995; Yang et al., 2009). By summer, the low profile ecological guild (dominated by prostrate taxa) became dominant. The shear stress of high discharge during flooding may restrict the thickness of the epilithon. In these periods the communities are often dominated by low-profile diatoms like *Cocconeis* or *Cymbella* (Poff et al., 1990). The dominance of low guild in summer indicated increased daily irradiances and the decreased shading since the high profile group was removed by floods. The higher irradiance level can penetrate the algal matrix and can reach the deeper layers of the epilithon (Dodds, 1992). Additionally, the prostrate forms may have physiological mechanisms which allow them to survive and maintain under low light conditions in the lower layer of epilithon (Hill, 1996; Lange et al., 2011). This group, due its location in the benthic layer, may utilize weaker irradiance better than the high profile guild; furthermore it is resistant to the flood disturbances (Francoeur and Biggs, 2006). The lower temperature enabled the motile guild to develop peaks in relative abundances in winter periods. Motile guild might include species which are cold adapted, the cooler water temperature and lower light intensity may favour to their growth and metabolism. More investigations, especially ecophysiological studies are needed to verify this question. Furthermore, these taxa could regulate their position through phototaxis. In late autumn and winter motile guild could maximize their light exposure through moving to the surface layer of the epilithon and minimize the relative abundance loss during high flow velocities. Diurnal vertical movements have not been reported on stone substrates, but such migrations in thick epilithic communities would clearly favour motile diatoms (Hill, 1996).

In the Torna-stream the most important strength of the low profile guild was its resistance to high discharge (S) and its independence from the DO and SRSi (S). Under high discharge conditions, they had the opportunity to utilize irradiance more effectively (O). This guild was threatened by the high SRP and TN content of the water (T). The direct access of the high profile guild to some important resources (SRP, SRSi, irradiance) (S) enabled the guild to be a better indicator of resource availability in stream water than the other guilds. This guild was sensitive to the high Cl^- concentration and to the discharge (W, T) in contrast to the motile guild which was

Cl^- tolerant (S). The motile guild was positively associated to the water discharge, which indicated their ability to change position in the biofilms (S, O). Among the resources, increasing SRSi and the irradiance basically reduced relative abundance of this guild (T).

Diversity is an important indicator tool to follow ecosystem processes in streams (Biggs and Smith, 2002). The species diversity based on the Shannon formula is the most frequently calculated and used diversity. However, a number of elements of the ecological diversity can be better characterized if we use well defined and coded features like e.g. ecological strategies (Standovár and Primack, 2001) as base instead of taxonomic species. The guild diversity may satisfy this desire. In this study, the seasonal changes in the ecological guild diversity and in the species diversity were similar except the period from summer to autumn when they provided contradictory results in the two consecutive years. Between the guild and species diversity, the former correlated with nine the latter with five environmental parameters, but only the guild diversity was strongly indicative for the elevated TN and conductivity originating from urban and industrial sewage of an upstream town, Ajka. For this reason, monitoring of the ecological guild diversity may represent a potential alternative in the ecological status assessment of streams. Using standard substratum (e.g. stone) data for diversity assessment are comparable (Potapova and Charles, 2005) not only within but also among the streams (Burkholder, 1996). Comparing the data of more rivers the presence or absence of hydromorphological modifications (Strayer, 2006) or the substratum type (a given substratum or multi-habitat samples) can modify the observed diversity (Smucker and Vis, 2010) which always have to be taken into account.

5. Conclusions

Despite the apparent simplicity of diatom ecological guilds, their ecological meaning is strong enough to be good indicator of environmental changes. The guild diversity showed significant correlation with a number of environmental parameters, therefore guild diversity may serve as another metric to assess biodiversity.

The low profile guild was dominant during the periods with low nutrient (SRP, TN) availability. In contrast, the high profile guild was dominant in resource rich (SRP and SRSi) periods. Among the guilds, the motile guild did show the strongest correlations with inorganic TN or SRSi but not with SRP.

The motile ecological guild was more sensitive to temperature, conductivity, Cl^- , DO, oxygen saturation than the high profile (less sensitive) and low profile guilds (the least sensitive). The number of the significant correlations with the environmental parameters was higher and stronger than that of the two other guilds, unlike expectations.

Response of the low profile group which dominated in the summers was complex to the disturbance events: the increasing light intensity in spring and summer favored the growth of the low guild. Although during the high flood periods increasing turbidity decreased incident light, its availability was still better for the low profile guild due to relative abundance loss of high profile guild during the floods. The adhesion type of the low profile guild enabled the summer peak in relative abundance because of the higher resistance to this disturbance. In contrast to our hypothesis the proportion of the motile guild was not reduced by floods, their amount was higher during the higher discharge periods of this study.

In summary, seasonal patterns and trends could be well defined for the different ecological guilds and the guild diversity. Seasonal changes of the diatom ecological guilds were robust and predictable. The high profile guild is characteristic in spring, the low profile in summer, while the motile group reached its

maximum contribution in winter. The guild diversity was the highest in summer and the lowest in winter and during the colonization phase.

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