

Establishment of equilibrium states and effect of disturbances on benthic diatom assemblages of the Torna-stream, Hungary

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Abstract This paper analyses the establishment of equilibrium states in relation to natural disturbances in epilithic diatom assemblages. Sterilized limestone bricks were exposed between April 2008 and 2009 in the Torna-stream and were removed one by one on every third day in the first month and then weekly until May 2010. Physical and chemical parameters were measured on the field and in laboratory. Equilibrium states were restricted to three separate months: July 2008, May and January 2009 taking the consistence of biomass (chlorophyll-*a*) into consideration. *Cocconeis placentula* sensu lato, *Fragilaria vaucheriae*, *Gomphonema parvulum*, *G. olivaceum*, *Navicula gregaria*, *N. lanceolata*, *Nitzschia linearis*, and *Surirella brebissonii* took part in the equilibrium assemblages, two of which dominated by a single species. Analyses of environmental constancy during equilibrium phases

allowed concluding that resilience of a developed equilibrium phase may ensure biotic constancy even though the underpinning environmental background fluctuates at higher amplitude. The conclusions of our study on attached stream diatom assemblages are similar to those found for temperate lakes: equilibrium states are rare, unpredictable, ephemeral, may occur both in relatively stable and strongly fluctuating environments, and are mostly characterized by monodominance, but contrary to phytoplankton, their establishment requires a longer time to develop corresponding to differences in generation times.

Keywords Benthic diatom assemblages · Equilibrium state · Disturbance · Environmental constancy

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Introduction

Implementation of the Water Framework Directive (WFD, 2000) initiated a number of phytobenthos surveys in European countries (e.g. King et al., 2006; Kelly et al., 2008, 2009; Várbíró et al., 2012). One of the most robust arguments for using diatoms in ecological status assessment is their high species number. Although methods of status assessment from sampling to data analyses, including the applied indices, improved markedly, the underlying ecological knowledge has remained incomplete (Kelly,

2013). Until now, process-based research on relationships between environmental factors, population dynamics, and community attributes has been largely missing. For example, except for a very early study (Ács & Kiss, 1993) the effect of disturbances is poorly understood, especially in relation to the opportunity of development equilibrium states. In phytoplankton, prevalence of equilibrium states is authoritative and basically determines the sampling period (Padisák et al., 2006) for WFD status assessment.

Hardin's (1960) Competitive Exclusion Principle (only as many species may co-exist as the number of limiting resources) predicts equilibrium plant communities with low species number. However, plant communities typically consist of many species in Nature. This contradiction is well known as the Paradox of Plankton (Hutchinson, 1961). For its explanation, a number of equilibrium and non-equilibrium theories were proposed (Hutchinson, 1961; Richerson et al., 1970; Wilson, 1990). The non-equilibrium theories attribute basic role to disturbances (e.g. current velocity) preventing competitive exclusion. According to Connell's (1978) intermediate disturbance hypothesis (IDH), in absence of disturbance diversity will be reduced by competitive exclusion. When disturbance is very frequent, only pioneer species can establish resulting also in low diversity. This hypothesis predicts that the communities reach maximal diversity at disturbances with intermediate frequency and intensity. Considering the relatively high number of diatom species in phyto-benthos samples, logic suggests that we monitor disturbed, non-equilibrium diatom communities where separation of causes and consequences is doubtful (Reynolds et al., 1993).

Disturbance can be measured as response of the association to alternating forces (Juhász-Nagy, 1993). It is a complex variable: the origin of the disturbance is less important than its presence, frequency, and intensity (Sommer et al., 1993). After any kind of disturbance, the recovery of community is strongly controlled by the succession processes (Odum, 1969, 1971).

Case studies evidenced that in natural phytoplankton communities it is very difficult to delimit equilibrium phases mostly because of the insufficient sampling frequency and absence of physical and chemical background data. As recommended for phytoplankton communities by Sommer et al. (1993), in the equilibrium phase (i) a maximum of three species contribute more than 80% of the total

biomass, (ii) for at least 2 weeks, (iii) without significant variation in total biomass. These conditions were widely tested by the scientists, but as these criteria proved to be too strict, some modifications were allowed. Based on several studies (Morabito et al., 2003; Naselli-Flores et al., 2003; Nixdorf et al., 2003), increasing the number of co-dominating species to 4–5 was necessary. Furthermore, the generation time of the species in a phytoplankton and in a periphyton community is different. For this reason, the 2 weeks constancy required for phytoplankton have to be increased to 4–5 weeks for attached diatoms. Mischke & Nixdorf (2003) allowed $\pm 15\%$ variation in constancy of the total biomass.

Investigations of the equilibrium phases of stream diatoms are not to be found. Since environmental parameters of a stream ecosystem often change suddenly and significantly, we hypothesize that the equilibrium communities cannot develop or occur only very rarely.

Materials and methods

The sampling site for this study was the midland Torna-stream, in the area of the town Devecser, Hungary (N47°06,612', E17°26,154', altitude 170 m; Stenger-Kovács et al., 2013). Semi-natural limestone bricks were used as substratum. The size of the bricks is 10 × 10 × 3 cm, the surface is flat with minimal roughness. The measured roughness was 1.019 (Látos, 2012) according to Shelly (1979). Prior to the experiments, the stones were sterilized by cc. hydrogen peroxide, heat treatment (120°C) and UV light.

From April 2008 to May 2009, 62 phyto-benthos samples were taken (first period), and further 50 samples were collected between April 2009 and May 2010 (second period). The limestone bricks were collected randomly one by one every third day in the first month, and then weekly. Diatom valves were cleaned by hot hydrogen peroxide method, and embedded in Zrax[®] resin. At least 400 valves per slide were counted with Nixon light microscope (1,000× magnification). The species were identified according to the *Süßwasserflora von Mitteleuropa* (Krammer & Lange-Bertalot, 1991, 1997, 1999a, b), *Iconographia Diatomologica* (Lange-Bertalot, 2000a, b, 2004, 2008), *Diatoms of Europe* (Lange-Bertalot, 2000a, b, 2001, 2002), and *Diatomeen im Süßwasser-*

Benthos von Mitteleuropa (Hofmann et al., 2011). Three parameters (length, breadth, and girdle) of ten specimens were measured, and their volumes were calculated following the formulas in the NAWQA program (2001). Biomass data were obtained as the product of relative individual numbers among the 400 valves and biovolume data. Establishment of equilibrium phases was based on data expressing relative contribution to total biomass, and these data were used to separate dominants (>5%), frequent species (1–5%), and rare species (<1%). The net growth rates of the species were calculated based on the exponential equation of population growth described by Malthus (1873) and Turchin (2001).

Water temperature (°C), pH, dissolved oxygen (DO, mg l⁻¹), oxygen saturation (DO%) and conductivity (μS cm⁻¹) were measured on the field by HQd 40 Field Case mobile set. NO₂⁻, NO₃⁻, SRP, TP, SRSi, and NH₄⁺ were quantified with spectrophotometry (APHA, 1998; Wetzel & Likens, 2000), and Cl⁻, SO₄²⁻, COD, and alkalinity with titrimetry (APHA, 1998). The regional Water Authority provided daily discharge data. The chlorophyll-*a* content of the epilithon was extracted directly from the substratum surface with 90% acetone (Üveges & Padisák, 2011), and was measured according to Wetzel and Likens (2000 using a Metertech UV/VIS Spektrophotometer, SP8001). To avoid the impact of pheopigments, the acid method was applied (Lorenzen, 1967; Tett et al., 1975).

Principal component analysis (PCA) was carried out by Minitab[®] Statistical Software program free version 15 (Minitab, Inc., State College, PA), the detailed results of which can be read in Stenger-Kovács et al. (2013).

Results

Altogether 100 diatom species were identified. The average number of the species was 25 ± 5 in the first year, while it was 28 ± 9 in the second year. In the first year, arithmetic mean of Shannon–Weaver diversity was 3.41 ± 0.5 , while in the second year it was 2.99 ± 1.05 .

Fulfilment of the first and second conditions of equilibrium state

The following species contributed equilibria: (Fig. 1): *Gomphonema olivaceum* (GOLI), *Gomphonema*

parvulum (GPAR), *Diatoma tenuis* (DITE), *Fragilaria vaucheriae* (FCVA), *Navicula cryptotenella* (NCRY), *Navicula gregaria* (NGRE), *Navicula lanceolata* (NLAN), *Surirella brebissonii* (SBRE), *Cocconeis placentula sensu lato* (CPLI), *Planothidium frequentissimum* (PLFR), *Ulnaria ulna* (FULN), and *Nitzschia linearis* (NLIN). CPLI, FCVA, and NLAN were most frequently the dominant species during almost the whole first year (Fig. 1). In January, *Gomphonema parvulum* was replaced by *Gomphonema olivaceum*. *Ulnaria ulna*, *Diatoma tenuis*, and *Planothidium frequentissimum* were abundant only occasionally.

In the second year, *Diatoma tenuis*, *Ulnaria ulna*, and *Planothidium frequentissimum* did not appear among the dominant species; *Navicula cryptotenella* and *Nitzschia linearis* appeared as new members in the assemblage. *Gomphonema olivaceum* showed a similar seasonal dynamics as in the first period (Fig. 1).

According to the first assumption, $80 \pm 10\%$ of the biomass should consist of no more than 5 species (Fig. 2). In 2008, the cumulative values of the 5 dominant species usually reached 72% of the biomass, except in October and February. Diversity did not change significantly (its variation did not exceed 10%) from June to December: It varied commonly between 3.46 and 3.96. In the first month, and from January to April, the diversity was lower (average 2.95). Next year, there was a long period (from June to October 2009) when this cumulative contribution did not reach this limit value (<72%). The diversity was high (more than 3.28) during this period. When the cumulative biomass of the five species reached 72% of the total biomass, the diversity significantly decreased ($r = -0.81$); it was lower than 2.72.

Third condition of equilibrium state

Chlorophyll-*a* content increased during the vegetation period in both years (Fig. 3). Annual average chlorophyll-*a* was higher in the second year. In the first period, there were two significant peaks: one in late summer ($94 \mu\text{g cm}^{-2}$), and the other in the next April ($69 \mu\text{g cm}^{-2}$). In the second year, the chlorophyll-*a* content reached its maximum amounts in November ($42 \mu\text{g cm}^{-2}$) and in January ($37 \mu\text{g cm}^{-2}$).

In the first year (Fig. 3A), monthly biomass was constant (biomass variation <15%) only in July, when the average value of chlorophyll-*a* was $7 \mu\text{g cm}^{-2}$. In the second year (Fig. 3B), monthly biomass did not

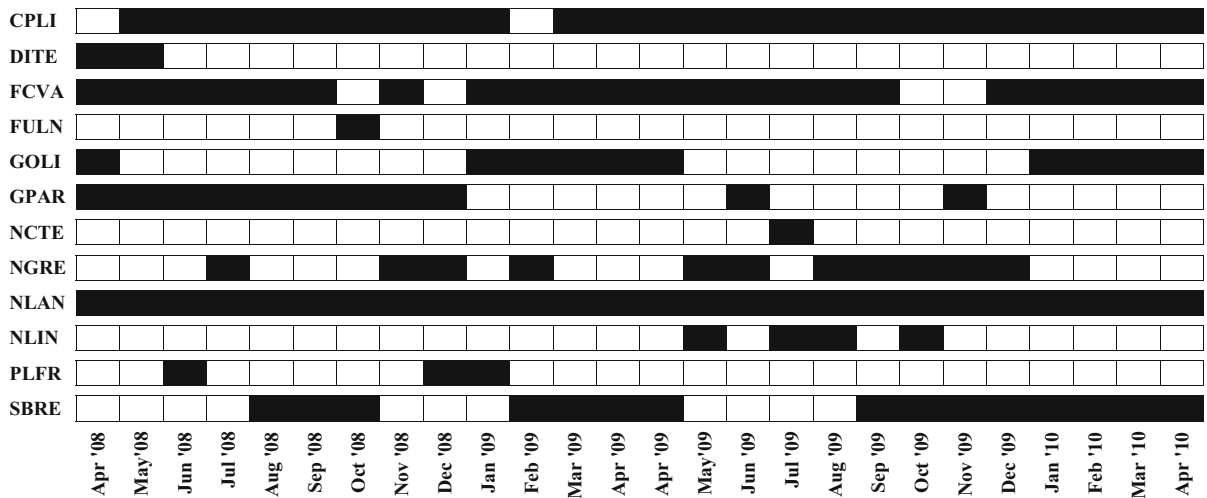


Fig. 1 Species compositions of the diatom community considering no more than five species (cumulative contribution to total biomass >80%)

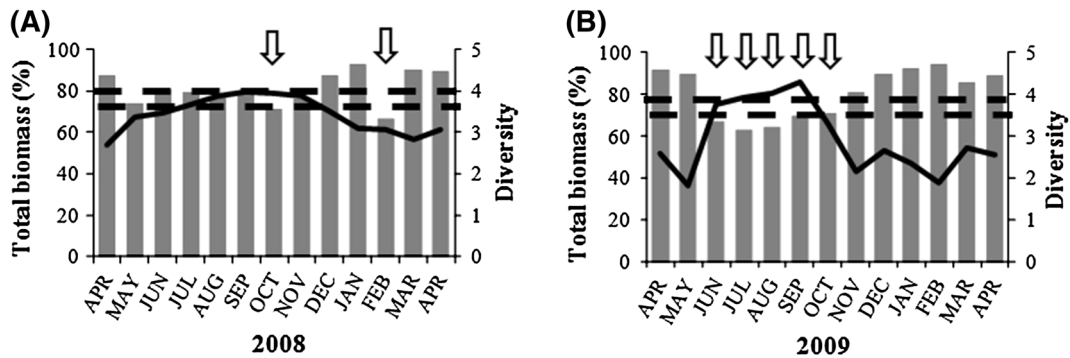


Fig. 2 Contribution of the five most dominant species to the total biomass (grey bars), and Shannon diversity (black line) during the first (A) and second (B) year (line 80%, broken line 72%, arrow month where the first condition did not occur)

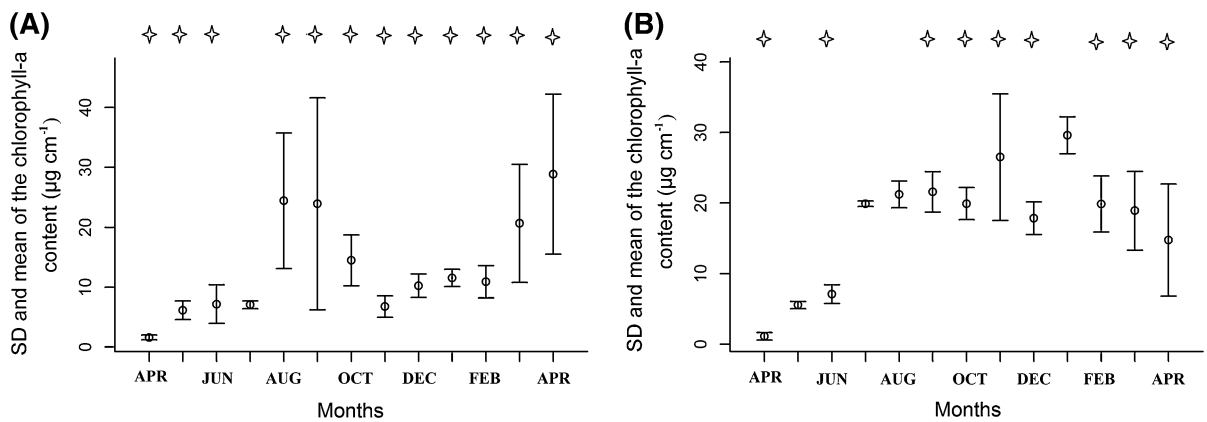


Fig. 3 Mean and the SD of chlorophyll-a content in the first (A) and the second period (B) (star month when the biomass changed significantly)

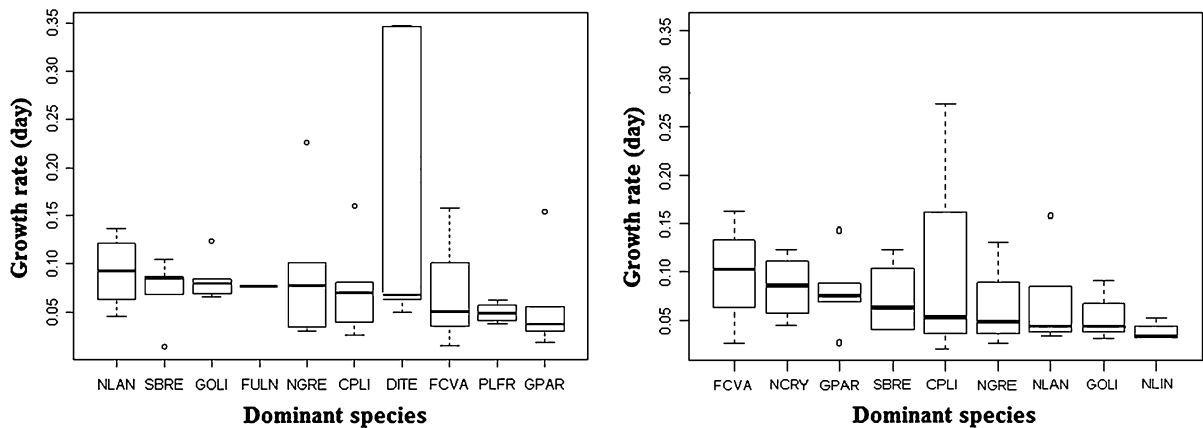


Fig. 4 The net growth rates (k) of the dominant species in the first and the second year in descending order

change significantly in May (average chlorophyll- a : $6 \mu\text{g cm}^{-2}$), July ($20 \mu\text{g cm}^{-2}$), August ($21 \mu\text{g cm}^{-2}$), and January ($30 \mu\text{g cm}^{-2}$).

Figure 4 shows the net growth rates (k) of the dominant species participating in the equilibrium assemblages during the two periods. In the first year, *Navicula lanceolata* ($k = 0.09$) and *Surirella brebissoni* ($k = 0.07$) had high net growth rates. *Planothidium frequentissimum* ($k = 0.04$) and *Gomphonema parvulum* ($k = 0.05$) exhibited lower net growth rates. This situation was different in the second year: *Fragilaria vaucheriae* ($k = 0.10$) had the highest, while *Nitzschia linearis* had the lowest ($k = 0.03$) net growth rate. *Navicula lanceolata* and *Gomphonema olivaceum* had similar net growth rates ($k = 0.04$). In this year, the net growth rates of *Navicula cryptotenella* and *Gomphonema parvulum* were higher ($k_{\text{NCRY}} = 0.08$, $k_{\text{GPAR}} = 0.07$) than *Navicula gregaria* or *Gomphonema olivaceum* ($k_{\text{NGREG}} = 0.05$, $k_{\text{GOLI}} = 0.04$). In the second year, *Navicula lanceolata* and *Gomphonema olivaceum* ($k = 0.04$) showed lower net growth rates, while *Fragilaria vaucheriae* ($k = 0.10$) and *Gomphonema parvulum* ($k = 0.07$) had higher net growth rates than in the first year. *Cocconeis placentula* sensu lato had medium net growth rate in both years.

Chemical and physical parameters

Table 1 summarizes the coefficients of variation (CV) of the parameters. The most balanced factors ($<20\%$) were the DO, DO% and pH. Temperature, conductivity, alkalinity, Cl^- concentration, and discharge were

also mainly homogeneous except some shorter intervals. The measured phosphorus and nitrogen forms, SO_4^{2-} , SRSi concentration, and COD were extremely variable ($>20\%$) during the entire period.

In the first year (2008–2009), the DO, conductivity, discharge, and SRP fluctuated (compared to the equilibrium state) in most cases (7–9 out of 13), but the changes of NO_3^- ion and TP were also important (5–6 out of 13). The CV of NH_4^+ , SRSi, SO_4^{2-} and alkalinity did not exceed the values measured in the supposed equilibrium states. If we consider each month, most of the parameters fluctuated at the same time in September (8 variables out of 16), in April, August, December, and January (5–6 out of 16). In most cases, three or four variables fluctuated at the same time. In the second year, DO (8 months out of 13) fluctuated in most of the cases, while the other environmental parameters did not change or not significantly (1–3 out of 13) compared to the steady states. Contrary to the previous year, commonly 1–3 parameters fluctuated a lot together in the month and the highest number of variables (4 out of 16) changed together in December.

Taking all the three conditions of establishment of the equilibrium status into consideration (Tables 2, 3), in most cases (10 times out of 13) only two conditions, while in October and February none of the conditions was fulfilled at the same time. Equilibrium state (when all of the conditions were realized) was found only in July. In the second year, three times (June, September, October) none of the conditions was fulfilled. In July and August just one condition, while in 6 further months two conditions were fulfilled. The three

Table 1 Percentage coefficient of variation of the parameters (italicized cells indicate higher variations of the given environmental parameter than in the equilibrium phase, bold numbers indicate the strong and extreme variabilities)

	2008												2010												
	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
DO	12.6	8.1	8.7	2.1	13.3	11.7	4.2	4.4	5.9	6.0	1.0	3.0	4.1	4.6	12.2	4.5	2.4	5.8	9.5	9.7	7.8	4.2	14.3	9.8	7.1
DO%	10.8	10.2	6.1	8.4	7.9	9.2	7.3	7.9	1.6	2.3	1.2	4.3	4.0	9.6	11.7	7.0	1.9	6.0	3.2	3.0	1.5	2.1	6.1	7.3	2.5
Temperature (°C)	17.5	14.5	12.5	14.5	15.2	19.5	13.8	41.3	28.2	80.1	23.2	17.5	9.1	18.9	11.9	6.4	9.8	7.5	21.6	27.1	54.4	43.1	82.7	45.0	29.7
pH	9.6	0.4	1.6	3.2	1.4	4.5	2.4	1.2	2.5	2.1	2.2	0.7	0.7	3.1	3.2	3.9	2.4	2.0	2.3	1.5	2.0	1.3	3.0	0.7	2.3
Conductivity ($\mu\text{S cm}^{-1}$)	12.5	3.2	28.1	5.0	15.0	27.2	2.5	25.9	18.0	5.4	9.4	11.5	13.9	11.1	10.5	11.5	4.0	2.5	6.5	10.2	4.1	1.1	4.4	2.9	14.0
NO ₂ ⁻ (mg l ⁻¹)	24.9	32.7	48.6	66.4	60.9	67.4	64.2	54.8	61.1	28.2	14.3	11.9	15.2	50.7	42.0	38.5	66.5	31.6	53.3	49.1	41.6	21.6	19.4	28.0	68.1
NO ₃ ⁻ (mg l ⁻¹)	40.0	52.3	48.5	36.3	29.9	38.8	47.9	8.9	29.5	20.7	34.9	8.7	12.1	29.6	21.4	8.1	2.7	8.0	6.9	13.3	8.0	4.8	2.2	3.0	8.8
NH ₄ ⁺ (mg l ⁻¹)	63.3	103.5	96.7	151.6	61.9	25.5	158.2	127.5	84.3	69.1	40.9	32.1	148.5	90.1	115.0	77.2	98.3	13.5	68.3	74.1	118.9	39.7	33.6	74.8	21.0
COD (mg O ₂ l ⁻¹)	70.9	117.1	61.1	51.5	7.5	11.6	96.3	12.2	198.4	28.6	135.4	111.2	101.8	196.4	18.6	10.2	48.8	16.6	31.6	4.0	37.1	17.7	5.5	34.7	65.0
SRP ($\mu\text{g l}^{-1}$)	72.4	170.4	34.3	26.0	41.1	22.7	129.3	115.5	136.9	68.2	40.3	100.6	21.1	38.4	60.8	33.0	11.7	11.2	11.3	26.7	19.6	38.9	13.1	36.7	33.7
TP ($\mu\text{g l}^{-1}$)	90.3	80.3	51.4	102.4	180.6	129.8	69.6	138.5	146.0	113.8	49.7	64.9	16.1	75.6	17.3	26.9	50.2	41.7	72.1	73.1	18.3	24.6	22.0	31.0	82.1
SRSi (mg l ⁻¹)	10.2	50.6	44.6	51.2	29.9	17.1	3.5	20.7	47.8	5.8	16.5	6.6	11.9	8.7	11.1	7.5	7.3	12.3	20.9	23.0	7.9	45.1	45.8	22.2	12.7
SO ₄ ²⁻ (mg l ⁻¹)	16.9	14.5	34.1	107.6	6.1	96.6	56.7	26.0	27.2	13.7	10.7	12.1	19.1	33.8	19.1	32.5	9.8	19.0	31.6	25.9	17.2	5.4	30.3	18.0	37.2
HCO ₃ ⁻ (mg l ⁻¹)	17.1	14.4	24.0	24.3	8.8	15.9	21.7	9.5	14.2	16.0	11.0	12.6	7.3	12.1	2.0	14.2	3.9	6.2	3.1	11.7	42.8	8.5	11.2	81.5	8.6
Cl ⁻ (mg l ⁻¹)	24.1	20.3	40.6	35.0	48.7	37.9	31.7	18.3	10.9	17.6	6.0	8.8	9.7	19.1	10.3	20.1	3.3	14.0	9.1	4.6	6.7	7.9	2.2	25.4	12.6
Discharge (m ³ s ⁻¹)	6.2	6.8	6.8	7.1	9.6	15.2	14.9	13.4	20.9	20.3	17.0	16.4	8.0	4.8	5.8	10.1	11.1	10.5	6.8	14.8	14.9	14.0	14.0	13.9	11.3

Table 2 Equilibrium conditions in the first year (+ fulfilled, – not fulfilled)

	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
1st Condition (max. 5 species contribute more than 80% of total biomass)	+	+	+	+	+	+	–	+	+	+	–	+	+
2nd Condition (for at least 4 weeks)	+	+	+	+	+	+	–	+	+	+	–	+	+
3rd Condition (without significant variation in total biomass)	–	–	–	+	–	–	–	–	–	–	–	–	–

Table 3 Equilibrium conditions in the second year (+ fulfilled, – not fulfilled)

	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
1st Condition (max. 5 species contribute more than 80% of total biomass)	+	+	–	–	–	–	–	+	+	+	+	+	+
2nd Condition (for at least 4 weeks)	+	+	–	–	–	–	–	+	+	+	+	+	+
3rd Condition (without significant variation in total biomass)	–	+	–	+	+	–	–	–	–	+	–	–	–

Table 4 The species composition in the equilibrium states (and its contribution to the total biomass)

	1st Equilibrium phase	2nd Equilibrium phase	3rd Equilibrium phase
Sp 1	<i>Cocconeis placentula</i> sensu lato (45.2%)	<i>Cocconeis placentula</i> sensu lato (79.4%)	<i>Navicula lanceolata</i> (78.4%)
Sp 2	<i>Fragilaria vauchariae</i> (13.7%)		
Sp 3	<i>Navicula lanceolata</i> (10.1%)		
Sp 4	<i>Gomphonema parvulum</i> (6.8%)		
Sp 5	<i>Navicula gregaria</i> (3.3%)		

equilibrium conditions were realized at the same time only in May and January. Species composition in the equilibrium phases is given in Table 4.

Discussion

Heraclitus's evergreen wisdom “*One cannot step into the same river twice*” goes to philosophical depths, but even in its most immediate meaning it expresses the continuously changing nature of running waters. Here the word “river”, small to large, cannot be replaced by the word “lake”. Variability of running waters can be observed by naked eyes especially through changes in discharge, flow velocity, and suspended solids.

Many diatom species were identified early as good indicators of some major variables (for example salinity or conductivity) or the entire habitat (Hustedt, 1930). After recognizing a number of important

properties of diatoms useful for monitoring water quality (like occurrence in almost all inland waters, high species number, relatively standard taxonomy, easy-to-archive slides, etc.), development of diatom indices started blossoming (see Whitton, 2012 for a summary), and this kind of research has been accelerating since issuing of the Water Framework Directive (WFD, 2000) that designated benthic microalgae as one of the five major biological quality elements. During the last 25 years, most studies on river diatoms were directly or indirectly related to application of the WFD including elaboration of national metrics, selection of relevant indices, improving assessments by intercalibration exercises, etc. (e.g. Kelly et al., 2009 and references cited therein). As case and comparative studies accumulated, doubts started to emerge about the overall applied methods and their appropriateness in assessing real ecological status. In his seminal paper, Kelly (2013) concluded that more

Table 5 The main environmental variables determining the attached diatom assemblages according to the literature

Study site	Species number	Sample number	Main environmental variables	Statistical methods	Reference
1 Mid-altitude streams in Italy	174	72	N-NO ₃ , TP, Cl ⁻ , conductivity, pH	CCA (Canonical Correspondence Analyses)	Bona et al. (2007)
2 Boreal streams in Finland	448	223	Catchment area, colour, altitude, TP, TN, pH	RDA (Redundancy Analysis)	Heino et al. (2010)
3 Mid-Appalachian stream in USA	522	199	Conductivity, pH, TP, TN, Cl ⁻	CCA	Hill et al. (2001)
4 Schwartzbaach, Consdorferbaach, Sauerbaach and Hemeschbaach streams in Luxembourg	65	20	Conductivity, SO ₄ ²⁻ , NH ₄ ⁺ , potassium, TOC, pH, temperature, Mg ²⁺ , slope	PCA (Principal Component Analysis), CCA	Hlúbiková et al. (2014)
5 Streams in Hungary and Sweden	246	102	Ca ²⁺ , alkalinity, Mg ²⁺ , pH, conductivity, NH ₄ ⁺	CCA	Kovács et al. (2006)
6 Muga, Fluvia, Ter, Tordera, Besos, Llobregat, Segre, Foix, Gaia, Francolí streams in Spain	195	57	Temperature, conductivity, altitude, NO ₃ ⁻ , BOD, stream order	CCA	Leira & Sabater (2005)
7 Rodríguez Stream in Argentina	66	24	Temperature, conductivity, BOD, COD, NH ₄ ⁺ , NO ₃ ⁻ , NO ₂ ⁻ , SRP	PCA, t-test	Licursi & Gómez (2009)
8 Corona stream in Portugal	133	28	Conductivity, pH, HCO ₃ ⁻ , SO ₄ ²⁻ , Ca ²⁺ , Cl ⁻ , Cu ²⁺ , Li ⁺ , Mg ²⁺ , Na ⁺ , B, Mn, Ni, Zn, Co, Fe	CCA	Luís et al. (2011)
9 Nairobi River in Kenya	190	50	Altitude, DO, pH, NO ₃ ⁻ , NO ₂ ⁻ , Conductivity, PO ₄ ³⁻ , COD, alkalinity	CCA	Ndiritu et al. (2006)
10 Cozine creek in Oregon	159	25	SiO ₂ , NH ₄ ⁺ , ANC, pH, TN	CCA	Pan et al. (2004)
11 Buck Creek in the Adirondacks, USA	27	69	Water level, Cl ⁻ , SO ₄ ²⁻ , Mg ²⁺ , organic and inorganic monomeric Al, DOC, pH, NO ₃ ⁻	RDA, MANOVA (Multivariate Analysis of Variance)	Passy (2006)
12 Mesta River in Bulgaria	47	99	Current velocity, phosphates, nitrates	ANOVA (Analysis of Variance)	Passy (2007)
13 Streams in Ontario	231	41	Watershed area, wetland and urban area, conductivity, TP, Cl ⁻ , DOC, TDN, TSS	RDA	Porter-Goff et al. (2013)
14 USA rivers and streams	1548	2735	Temperature, pH, water mineral content	CCA	Potapova & Charles (2002)
15 Headwater streams in Luxembourg	411	289	NO ₂ ⁻ , DO, TP, Carbonate hardness, NO ₃ ⁻ , pH	CCA, forward selection	Rimet et al. (2004)
16 Boreal stream in Finland	212	141	Conductivity, TP, pH, latitude, colour, turbidity	CCA, PCA	Soininen et al. (2004)
17 Felent creek in Turkey	117	41	Temperature, conductivity, pH	CCA	Solak et al. (2012)
18 Torna stream, Hungary			Temperature, irradiance level, DO, TN, COD, conductivity, DO%, Cl ⁻ , discharge	PCA, CCA	Stenger-Kovács et al. (2013)

Table 5 continued

Study site	Species number	Sample number	Main environmental variables	Statistical methods	Reference
19 46 rivers, brooks, and ditches in the islands of Hiiumaa and Saaremaa and in West Estonia	205	75	Temperature, BOD, SRP, NO ₂ ⁻ , NO ₃ ⁻ , pH, NH ₄ ⁺ , N:P	RDA	Vilbaste & Truu (2003)
20 Clear Creek, Deep Creek, Johnson Creek in Oregon, USA	84	45	Conductivity, SRP, NO ₃ ⁻ , NO ₂ ⁻ , temperature, turbidity	CCA	Walker & Pan (2006)
21 Grand River, Ontario, in Canada	148	186	Alkalinity, BOD, TP, conductivity, suspended solids, NO ₅	CCA	Winter & Duthie (2000)

knowledge is needed about traits of phyto-benthos, with deep roots in functional ecology to achieve a better coupling of cause and effect, similarly as has been done for benthic macroinvertebrates.

During the last 25 years, phytoplankton ecologists focused rather on coupling habitat properties with morphological and/or physiological traits of phytoplankton that resulted in three functional classifications (Reynolds et al., 2002; Salmaso & Padišák, 2007; Kruk et al., 2010). Two of them are applied for the ecological status assessment according to the WFD (Padišák et al., 2006; Phillips et al., 2011). Additionally, much effort was dedicated to the understanding of the diversity–disturbance relationship (Reynolds et al., 1993; Sommer et al., 1993), and the closely related emergence of equilibrium states (Naselli-Flores et al., 2003).

According to the original assumptions (Sommer et al., 1993), progress towards an equilibrium state requires environmental constancy during a sufficiently long time for allowing selection of the best-fit species or species complexes (up to 5 according to reasons and considerations detailed in the introduction). In statistical models elaborated for explaining relationships between compositions of attached diatom assemblages and environmental variables, the following determinant groups were selected repeatedly (Table 5; and also see references therein):

- Variables describing a temporal scale (season), like temperature, DO, oxygen saturation
- Nutrient conditions (nitrate, nitrite, ammonium, SRP, SRSi) or trophic state (TN, TP) and nutrient ratios
- Variables describing ionic composition (conductivity, chloride, sulphate, some other elements)
- Acidity–alkalinity (pH, alkalinity, calcium concentration)
- Organic content (BOD, COD, colour, TOC, PON... etc.)
- Light conditions (turbidity, suspended solids)
- Spatial and land use descriptors (catchment, altitude, slope, urban areas, etc.) and in some special cases
- Toxic agents
- Interestingly, the probably most important physical variable (measured as discharge or flow velocity) is largely neglected.

Therefore, it seems reasonable to analyse constancy of such variables during the equilibrium phases found

in this study. During the first equilibrium state (July, 2008), the most important variables determined by the PCA and CCA (Stenger-Kovács et al., 2013) changed significantly (>20%): Nitrogen forms showed approximately 36–152%, COD 50%, while Cl^- exhibited 35% CV. Furthermore, extremely variable concentrations of phosphorus forms were recorded (SRP: 26%, TP: 102.5%). In the second one, similar trends were observed, but instead of Cl^- , the SO_4^{2-} concentration had higher CV. A decreasing fluctuation of these variables were detected in the third equilibrium phase (January, 2010), but the correlations of variation of these factors were still significant (20–40%). Additionally in this month, the temperature, as another main environmental parameter, determined by PCA and CCA showed higher CV (43%). Analyses of environmental constancy during equilibrium phases are not available in the literature; however, these data allow concluding that resilience of a developed equilibrium phase may ensure biotic constancy even though the underpinning environmental background fluctuates at higher amplitude.

The number of coexisting species varied between one and five (1st equilibrium state: *Cocconeis placentula* sensu lato, *Fragilaria vaucheriae*, *Gomphonema parvulum*, *Navicula gregaria*, and *Navicula lanceolata*; 2nd: *Cocconeis placentula* sensu lato; 3rd: *Navicula lanceolata*). This observation is similar to findings for phytoplankton: monodominance is more likely in such phases than coexistence of more than one species (Padisák et al., 2003). However, mechanisms resulting in equilibrium are more diverse than competitive exclusion (Rojo & Álvarez-Cobelas, 2003). For example, during the second equilibrium phase disturbance intensities were rather high. *Cocconeis placentula* sensu lato is a fresh-brackish water diatom. It is a non-motile species, attaching by the valve face and mucilage to the substratum. *Cocconeis placentula* sensu lato is associated with low organic-matter content (Lange-Bertalot, 1979; Gómez, 1998; Kelly, 1998), and it is favoured by moderate or high nutrient concentrations (Yallop et al., 2009; Gómez & Licursi, 2001). This is confirmed also by the IPS (Specific Pollution Index) indicator values (1.0) and taxon sensitivities (4.0), which mean that *Cocconeis placentula* sensu lato tolerates elevated concentrations of organically bound nitrogen. According to its autecological features, the high relative contribution to total biomass of this pioneer species (Hofmann et al., 2011)

might be the result of its stress tolerance (sensu Borics et al., 2013) rather than of competitive exclusion.

During the 3rd equilibrium phase *Navicula lanceolata* built up 78.4% of the total biomass (Table 4), and this period was characterized by highest environmental constancy. According to the slow net growth rates of the species, *Navicula lanceolata* can be characterized as a climax species. It is also a fresh-brackish species but typically occurs in cold waters, and it is motile (Hofmann et al., 2011). Its belonging to the motile guild (Stenger-Kovács et al., 2013) allows the species to resist against moderate water discharge. According to Kelly (1998) *Navicula lanceolata* is an organic-matter-pollution-tolerant species. As indicated in many works (e.g. Lange-Bertalot, 1979; Krammer & Lange-Bertalot, 1999a), this species is more abundant at lower temperatures (the end of autumn, winter, and early spring). The IPS indicator value is 1.0, the taxon sensitivity is 3.8, and in this month the concentration of the nutrients were moderate or high, which also contributed to the increase of this species. In the absence of nutrient limitation, temperature was the primary factor allowing emergence of *Navicula lanceolata*. The species found in equilibrium states in this study are either stress-tolerant or K-selected ones with low net growth rates in agreement with observations on phytoplankton (Padisák et al., 2003; Stoyneva, 2003). In our study, steady state did not occur during the colonization periods (when the diversity was low) in contrast of Hameed's (2003) study, where, paradoxically, the equilibrium state was suggested during the colonization period.

Overall, non-equilibrium states of the diatom assemblage were characteristic during this study. The Torna-stream is a fast-changing ecosystem like non-stratified lakes, with discharge as the major regulating environmental factor by affecting nutrient supplies and the light regime (Descy, 1993). Although there was no nitrogen or phosphorus limitation during the entire study, in the non-equilibrium phases 3 or more environmental parameters (mainly the conductivity, SRP, DO, discharge) changed significantly or the amplitudes of variation of fewer parameters were high at the same time.

Contrary to Reynolds' (1984, 1988) theoretical presumptions (river phytoplankton should be dominated by r, fast-growing species which are able to develop in a strongly disturbed and light-limited

environment), Shannon diversity remained high during almost the entire first year, because disturbance reached intermediate intensities and frequencies, allowing smaller, fast-growing species to co-occur with the K-strategist species as described in the IDH. In the second period after the steady state in May, the diversity was high due to intensive disturbances which excluded the equilibrium phase. This maximal diversity collapsed in September, probably due to Si depletion. After it, despite that the environmental conditions were sufficient for the developing of the steady state, there was no sufficiently long undisturbed period which is necessary to reach it. Naselli-Flores et al. (2003) also concluded that, in the absence of disturbance, there should be enough time to progress towards the equilibrium state. For phytoplankton, 35–60 days were required to achieve equilibrium (Sommer, 1985, 1989; Reynolds, 1993; Padišák, 1994), but it appears reasonable that it should be longer for the periphyton because of the different (longer) generation times.

In most of the cases, changes in biomass prevented detection of the equilibrium phases. In both years, chlorophyll-*a* concentrations continued increasing until autumn (September in the first year and November) and then restarted again in approximately February in both years, which could hardly be explained by Si utilization.

Similar to lakes in temperate regions, equilibrium phases in the diatom assemblage occurred only occasionally and were ephemeral but could develop both in relatively permanent and in highly variable environments (Mischke & Nixdorf, 2003; Naselli-Flores et al., 2003; O'Farrell et al., 2003; Rojo & Álvarez-Cobelas, 2003; Stoyneva, 2003). In the case of some water chemical parameters, threshold values could be defined: if the CV of conductivity >14%, pH > 4%, NO₂⁻ > 66.5% and DO > 5.8%, equilibrium state could not develop. The degree of change in these parameters alone was enough to prevent the development of an equilibrium phase. However, in other cases lower amplitude of variance was observed for two–three variables and their combined effect led to the non-equilibrium phase. Experiences on phytoplankton assemblages report on the climate determination of the probability of development of equilibrium states: they are more likely to occur and last longer in warmer climates (Komárková & Tavera,

2003; Becker et al., 2008; Li et al., 2011). Such relationship is to be explored for stream diatoms.

As to the ecological status according to the WFD, there were no significant differences between the equilibrium and non-equilibrium phases since the IPS values varied between 3 and 4 independently from the equilibrium status.

The conclusions of our study on attached stream diatom assemblages are similar to those found in temperate lakes: equilibrium states are rare, unpredictable, ephemeral, may occur both in relatively stable and strongly fluctuating environments, and are mostly characterized by monodominance but, contrary to the phytoplankton, their establishment requires a longer time to develop corresponding to difference in generation times.

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