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Interaction of Ciliate Communities with Cyanobacterial Water Bloom in a Shallow, Hypertrophic Reservoir

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Abstract. The response of ciliate communities to cyanobacterial bloom was investigated in a shallow, hypertrophic reservoir in Slovakia, Central Europe. Seasonal dynamics of ciliate communities corresponded negatively with course of water bloom formation. The highest numbers and abundances of ciliate species occurred during the spring season when cyanobacterial bloom was not fully developed, while there was an abrupt decrease in both numbers and abundances at the beginning of summer when water bloom culminated. Cyanobacterial blooming thus significantly lowered diversity and equitability of ciliate communities: many rare and sporadic species disappeared and few common taxa flourished and dominated. Nonetheless, these leading ciliates formed a functionally diverse assemblage whose members showed mostly positive contemporaneous and only rarely time-shifted interactions. There were fine filter feeders (*Cinetochilum margaritaceum*, *Dexiotricha granulosa*, *Paramecium caudatum* and *Spirostomum teres*) grazing heterotrophic bacteria and picocyanobacteria, omnivorous fine to coarse filter feeders (*Frontonia leucas*) as well as hunters (*Coleps hirtus*, *Holophrya teres* and *Loxophyllum helus*) looking for an individual prey. Also a comparatively rich, anaerobic coenosis comprising various bacterivorous armophoreans and plagiopyleans, developed at the bottom of the reservoir. Our study documents that ciliates form functionally diverse communities with potential to control cyanobacterial blooms in hypertrophic reservoirs.

Key words: association networks, benthos, Ciliophora, feeding groups, plankton, seasonal dynamics

INTRODUCTION

Eutrophication of surface waters is currently considered to be one of the most serious problems in water ecosystems. The high content of nutrients in water, especially of phosphorus and nitrogen, causes disruption of biological equilibrium and often leads to the development of harmful water blooms (e.g., Heisler *et al.* 2008, Yang *et al.* 2008, Krevš *et al.* 2010, Paerl and Otten 2013). The large amounts of cyanobacterial and algal biomass distort the oxygen regime in water reservoirs, which negatively influences water organisms and might even lead to their death. Subsequently, the cyanobacterial and algal biomass settles down, causing the phosphorus reserves in the sediment to be more than hundred times higher than in the water column. The content of soluble reactive phosphorus depends on the interaction of water with sediments and in turn affects the formation of water bloom (Søndergaard *et al.* 2003, Xie *et al.* 2003, Xie 2006).

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Another problem connected with cyanobacterial blooms is their toxicity. This is caused by lipopolysaccharides, which are components of the cyanobacterial cell wall, and/or by the so-called cyanotoxins that are by-products of the cyanobacterial metabolism (e.g., Moustaka-Gouni *et al.* 2006, Adamovský *et al.* 2007, Bláha *et al.* 2009). Microcystins are among the most widespread cyanotoxins (Maršálek *et al.* 2000, Bláha *et al.* 2009, Song *et al.* 2009, Liu *et al.* 2011) and as much as 75% of water reservoirs may harbour cyanobacteria producing these dangerous poisons (Bláhová *et al.* 2008). A further serious problem concerns infiltration of cyanobacteria and/or their toxins into sources of drinking water, which may cause health issues in humans (Bláha *et al.* 2009, Jayatissa *et al.* 2006, Song *et al.* 2009) and animals (Gugger *et al.* 2005, Adamovský *et al.* 2007).

Because of the impact of cyanobacterial blooms on human and animal health as well as on the stability of natural ecosystems, various approaches have been proposed to eliminate cyanobacterial toxins (Rositano *et al*. 1998, Qiao *et al*. 2005). Application of environmental-friendly techniques based on ecological principles is another good perspective to control or eliminate water blooms (Song *et al.* 2009). From this standpoint, some ciliate species might be a useful natural tool for regulation of cyanobacterial blooming. Therefore, in the present study, we investigated the response of ciliate communities to cyanobacterial bloom and attempted to recognize ciliate taxa that flourish during cyanobacterial blooming and hence could be good candidates for its control.

MATERIALS AND METHODS

Study site

The investigated water reservoir is situated in the outlying area of the town of Modra, West Slovakia (48°18'55.28" N, 17°19'2.4" E) at an altitude of 144 m a. s. l. Originally it was built as a fire fighting water reservoir for the needs of the town, as evidenced by the concrete banks along the whole circumference of the basin and by the drive-way for fire truck machinery. However, in the last decades, the reservoir has served only as a fishpond. The surface of the water basin covers 0.55 hectares and its maximum depth is ca. 2 m at high-level water conditions. Since there is no direct inflow or outflow, the reservoir is supplied only by water from snowmelt during the winter and spring seasons and from rainfall throughout the year. Some nutrients are supplied also from local people by feeding the fish. In June 2010, three tons of composite sorbent, which is a natural substance able to absorb phosphorus from the water, were deposited in the basin to reduce the mass development of cyanobacterial water bloom.

Sampling and sample processing

Both planktonic and benthic samples were taken in monthly intervals over a period between September 2013 and October 2014. The following physical and chemical parameters were measured *in situ* by a multi-functional instrument HANNA Multimeter HI 9828 in morning hours (8:30–9:30 a.m.): pH, dissolved oxygen (mg/L), oxygen saturation (%), conductivity (µS/cm), TDS (mg/L), and water temperature (ºC). The content of dissolved reactive phosphorus (DRP) and nitrate (NO_3^-) were determined using a Spectroquant® Multy Colorimeter (Merck). Water bloom cyanobacteria were counted in the chamber Cyrus and the obtained data were recalculated to 1 mL. Consequently, the state of water bloom development was estimated on the basis of abundances of cyanobacteria and was expressed on the following five-degree scale: 1 for samples with less than 1×10^5 cells/mL; 2 for $1–5\times10^5$ cells/mL; 3 for 5×10^5–1×10^6 cells/mL; 4 for $1–3\times10^6$ cells/mL; and 5 for samples with more than 3×10^6 cells/mL.

Plankton samples were collected from a single spot in the centre of the reservoir, while benthic samples were taken from four spots localized on the north, south, east and west side of the basin. Material was obtained using a take-off apparatus with a volume of 1 L. Samples were analyzed for ciliates within a maximum of 8 hours after collection by means of a light microscope Leica DM2500 equipped with differential interference contrast. Sampled ciliates were first carefully examined *in vivo* and then processed by the protargol and the dry silver nitrate impregnation method (Foissner 2014). Species identification followed Curds (1985), Foissner *et al.* (1991, 1992, 1994, 1995), Foissner and Berger (1996), Dovgal (2013) and references cited therein. Quantitative analyses included enumerating of active ciliates in 20 subsamples, each with a volume of 50 µL (Madoni 1984).

Analysis of ciliate feeding patterns

Ciliates were assigned to the trophic groups based on the food vacuole analysis and according to Foissner *et al.* (1995) and Macek *et al.* (2006). The following feeding pattern categories were recognized: (i) fine filter feeders, (ii) fine to coarse filter feeders, (iii) hunters of flagellates, other ciliates and algae including diatom scrapers, and (iv) suckers of other ciliates. Because vacuole contents were analyzed by means of bright field microscopy, it was not possible to unambiguously decide whether chlorophyll-bearing particles were ingested as a prey or were used as kleptoplasts. Therefore, mixotrophy was not delimited as a distinct (sub)category, but putative mixotrophs were assigned to one of the aforementioned groups. For further details and classification of taxa into categories, see Supplementary Table S1.

Coenological, saprobiological and statistical analyses

Species diversity of ciliate communities was measured by Shannon-Wiener's index *H* using natural logarithms (Poole 1974, Spellerberg and Fedor 2003):

$$H = -\sum_{i=1}^{S} P_i \ln P_i$$

where P_i is the abundance proportion of individuals of the i-th species and S is the total number of species in a community. Equitability E_H of communities was calculated according to the equation proposed by Sheldon (1969):

$$E_H = \frac{H}{H_{\max}} = \frac{-\sum_{i=1}^{S} P_i \ln P_i}{\ln S}$$

where H is the Shannon-Wiener's index and $H_{\max}$ is the maximum possible diversity for a community of S equally abundant species. Equitability assumes values between 0 and 1, with 1 being complete evenness.

Similarity of communities was assessed by hierarchical cluster analyses (completed linkage in a combination with Wishart's similarity ratio index) in the computer program NCLAS from the package Syn-Tax (Podani 1993). Principal component analysis of study spots was performed in the computer program Canoco (ter Braak and Šmilauer 1998).

Saprobiological characterization of the water reservoir was based on saprobic values from Sládeček's list of ciliates revised by Foissner *et al.* (1995). Saprobic index was calculated according to the formulae proposed by Pantle and Buck (1955):

$$SIPB = \frac{\sum A \times SI_i}{\sum A}$$

where A is the abundance of each species and SI_i is the saprobity index of the i-th species. Saprobity was also expressed separately for each saprobic class (oligosaprobity, β-mesosaprobity, α-mesosaprobity and polysaprobity) following the approach of Zelinka and Marvan (1961):

$$SIZM = \frac{\sum A \times I \times r_i}{\sum A \times I}$$

where A is the abundance of each species, I is the indicative weight of a species, and r_i is the relative proportion of a species in a saprobic class.

Relation between degree of development of cyanobacterial water bloom and various parameters was evaluated by Spearman's rank correlation coefficient. These non-parametric analyses were conducted in the program Statistica. All taxonomy and environmental data were also subjected to correlation analyses using the eLSA python package (Xia *et al.* 2013). Raw data were first F-transformed and normalized, then local similarity scores as well as contemporaneous and time-shifted Pearson and Spearman correlation coefficients, their signs (positive or negative) and levels of significance (p-values) were calculated. A maximal time lag of one step was set. Significant results were filtered by p-values < 0.05 and used to construct an association network in Cytoscape v. 3.1.1 (Shannon *et al.* 2003).

RESULTS

Physical and chemical parameters, development of water bloom

Physical and chemical variables were measured at all study spots. Since the differences were negligible, average values were calculated for the whole water reservoir at each sampling date (Table 1). It is notable that the water basin was generally characterized by high pH values (7.79–10.42), with a maximum at the period of culmination of water bloom. Similarly, contents of dissolved oxygen reached peaks during June and July water blooms. Contents of dissolved reactive phosphorus and nitrate were usually very low, sometimes even below detection limit, during the whole sampling period, indicating their high consumption by bloom-forming cyanobacteria. Comparatively high phosphorus and nitrogen values were noted in March and April 2014, respectively, which caused a massive development of water bloom in the following months.

Development of cyanobacterial water bloom in the reservoir was assessed by a categorical scale with five degrees (see Materials and methods). Formation of water bloom started in the spring season (from April to May 2014) and culminated in the summer months. *Aphanocapsa delicatissima*, *Microcystis ichtyoblabe* and *Sphaerospermum aphanizomenoides* were dominant bloom-forming cyanobacteria in the basin studied. The course of seasonal changes in cyanobacterial bloom is shown in Fig. 1a.

Community structure and seasonal dynamics

In total, 86 ciliate taxa were identified during the study period from October 2013 to November 2014 (Supplementary Table S1). Only three species (*Cinetochilum margaritaceum*, *Frontonia leucas* and *Holophrya teres*) were recorded at a frequency of 100%. On the contrary, 37.2% of species were sporadic and were observed only once. Comparatively large differences in the composition of the species spectrum were revealed between planktonic and benthic communities. All 86 taxa were found in the benthos, while only 32 of them were reported also from the plankton. The most frequent species in the plankton were *Cinetochilum margaritaceum*, *Dexiotricha granulosa* and *Rimostrombidium humile*. On the other hand, typical planktonobionts, such as *Askenasia volvox*, *Limnostrombidium pelagicum* and *Pseudovorticella natans*, were recorded comparatively rarely.

Table 1. Selected parameters of the Modra water reservoir during the period between September 2013 and September 2014.

Parameter	Month/Year												
	IX/13	X/13	XI/13	XII/13	I/14	II/14	III/14	IV/14	V/14	VI/14	VII/14	VIII/14	IX/14
Water temperature (°C)	16.7	11.4	6.4	3.1	5.7	3.7	8.7	8.5	12.7	21.1	21.5	19.2	18.2
pH value	9.18	7.80	7.79	8.04	8.57	8.26	8.77	9.59	9.34	10.21	10.42	8.09	8.16
Dissolved O_2 (mg/L)	6.98	6.40	8.53	1.97	5.88	11.45	10.28	10.64	7.89	14.52	10.31	2.87	9.37
O_2 saturation (%)	74.7	59.6	78.8	14.9	50.2	102.6	89.2	92.8	76.0	164.5	120.0	31.8	99.9
NO_3 (mg/L)	na	na	na	0.03	0.03	bdl	0.03	0.80	bdl	bdl	0.05	bdl	bdl
Total nitrogen (mg/L)	na	na	na	0.13	0.13	bdl	0.13	3.54	bdl	bdl	0.22	bdl	bdl
DRP (mg/L)	na	na	na	bdl	0.02	0.07	0.38	0.04	0.03	0.01	0.05	0.07	0.04
Total phosphorus (mg/L)	na	na	na	bdl	0.06	0.21	1.17	0.12	0.09	0.03	0.15	0.21	0.12
Conductivity (µS/cm)	441	552	571	602	579	560	577	494	497	462	415	520	473
TDS (mg/L)	221	276	285	301	290	282	321	247	249	232	208	264	238
Degree of water bloom	5	4	2	2	2	2	3	4	5	4	5	5	4

na – data not available; bdl – below detection limit.

According to statistical analyses, the plankton community was detached at a high level of dissimilarity from all benthic study spots that were clustered together. The most similar benthic communities developed at the west, east and north sides of the reservoir, while the most dissimilar coenosis was formed at the south study spot (Fig. 2a). This is very likely caused by slightly different environmental conditions on the south side of the reservoir, where organic material tends to accumulate due to the prevailing winds. A similar picture was also obtained by principal component analysis. Communities from the north, west and east benthic study spots were grouped together, while the coenosis from the south benthic study spot and the plankton assemblage were distinctly separated from these three benthic communities as well as from each other (Fig. 2b).

The course of seasonal dynamics was affected by development of water bloom. The highest number of ciliate species was noted during the spring season, with an abrupt decrease at the beginning of summer when mass cyanobacterial bloom culminated. Lower numbers of species were then recorded until October 2014. There was a gradual increase in species number from late autumn 2013 to the spring season 2014 (Table 2). Thus, with respect to the number of species and their abundances, there were basically two maxima: a pronounced one in spring and an inconspicuous one during autumn. Benthic communities followed this pattern and displayed a very conspicuous spring and a rather indistinct autumn maximum (Fig. 1c). Specifically, 34 species reaching a total abundance of about 1722 ind/mL were noted in April 2014 and 17 taxa with about 1415 ind/mL were recorded in September 2014. By contrast, there was a distinct depression in June 2014, when only 11 species accounting for 310 ind/mL were found. As concerns plankton communities, some deviations from this general pattern were observed in that there were three maxima (Fig. 1d): in October 2013 (12 taxa, 755 ind/mL), January 2014 (10 taxa, 320 ind/mL) and May 2014 (12 taxa, 360 ind/mL). Because of this variation, there was only a very weak negative and statistically insignificant relation between the number of ciliate species and the degree of development of cyanobacterial bloom (Spearman rank correlation, $r_s = -0.38$, $p > 0.05$).

Shannon-Wiener's index oscillated between 1.80 in August 2014 and 2.80 in February 2014 (Table 2; Fig. 1b). Generally, the lowest values were noted during summer months that are characterized by culmination of water bloom, causing disappearance of most rare

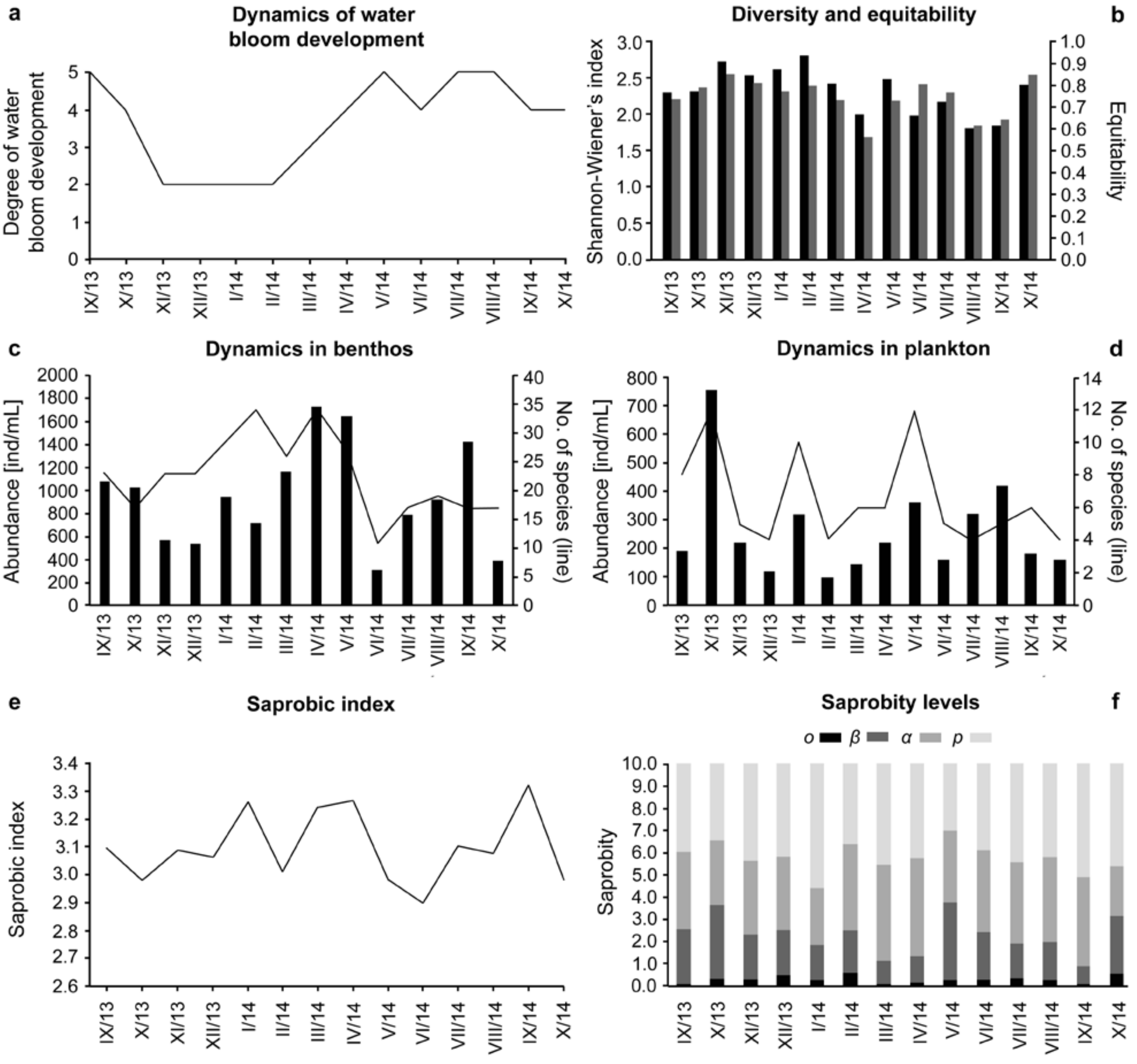

Fig. 1. Changes of selected parameters in the Modra water reservoir during the period between September 2013 and October 2014. **a**. Course of water bloom development. **b**. Changes in diversity and equitability of ciliate communities. **c**. Changes in abundances and numbers of ciliate species in the benthos. **d**. Changes in abundances and numbers of ciliate species in the plankton. **e**. Changes in saprobic index as indicated by ciliate communities. **f.** Changes in proportions of saprobity levels as indicated by ciliate communities.

species. Also correlation analyses confirmed a statistically significant negative relation between diversity index and the degree of cyanobacterial water bloom ($r_s = -0.69$, $p < 0.05$). Likewise, the equitability of communities negatively followed development of water bloom, although this was not proven to be statistically significant ($r_s = -0.53$, $p > 0.05$). The least equitable community ($E_H = 0.56$) was recognized in April 2014, which was characterized by an onset of mass water bloom, while the most even community ($E_H = 0.85$) was observed in October 2014 when cyanobacterial bloom declined (Table 2; Fig. 1b).

Table 2. Characterization of ciliate communities in the Modra water reservoir during the period between September 2013 and October 2014.

Collection date	Abundance (ind/mL)[a]					Diversity characteristics[b]				Saprobity characteristics[c]			
	Total	FFF	FCFF	HU	SU	H	E_H	n	SI	o	β	α	p
September 2013	897	594	89	214	0	2.30	0.73	23	3.09	0.10	2.46	3.48	3.94
October 2013	964	454	130	380	0	2.31	0.79	19	2.98	0.33	3.32	2.95	3.37
November 2013	496	324	40	128	4	2.72	0.85	25	3.08	0.30	2.01	3.38	4.30
December 2013	452	316	36	100	0	2.54	0.81	23	3.06	0.50	2.02	3.33	4.13
January 2014	816	672	48	96	0	2.62	0.77	30	3.25	0.27	1.58	2.55	5.59
February 2014	592	444	76	72	0	2.80	0.80	34	3.01	0.58	1.93	3.87	3.59
March 2014	956	711	97	148	0	2.43	0.73	28	3.24	0.09	1.03	4.35	4.51
April 2014	1422	1161	59	194	8	1.99	0.56	35	3.26	0.15	1.18	4.43	4.22
May 2014	1384	956	216	208	4	2.48	0.73	30	2.98	0.27	3.48	3.24	2.99
June 2014	280	172	64	44	0	1.99	0.80	12	2.89	0.30	2.11	3.73	3.84
July 2014	692	416	88	188	0	2.17	0.77	17	3.10	0.35	1.54	3.69	4.40
August 2014	818	665	68	81	4	1.80	0.61	19	3.07	0.28	1.69	3.84	4.17
September 2014	1168	868	76	212	12	1.85	0.64	18	3.31	0.09	0.79	4.04	5.06
October 2014	340	240	52	48	0	2.40	0.85	17	2.98	0.56	2.55	2.26	4.60

[a] FFF – fine filter feeders; FCFF – fine to coarse filter feeders; HU – hunters; SU – suckers.

[b] H – Shannon-Wiener's species diversity index; E_H – equitability; n – number of taxa.

[c] SI – saprobic index; o – oligosaprobity; β – beta-mesosaprobity; α – alpha-mesosaprobity; p – polysaprobity.

As concerns feeding groups, 50% of the recorded species were fine filter feeders, 21% fine to coarse filter feeders, 26.7% hunters of flagellates, other ciliates and algae, and only 2.3% were sucking feeders. The apparent over-dominance of filter feeders in the reservoir indicates that there is an intense bacterial decomposition of organic matter including sedimented and decaying picocyanobacteria (Table 2; Fig. 3). Abundances of fine filter feeders and hunters were very weakly positively correlated with the degree of water bloom development, but these relations were statistically insignificant ($r_s = 0.28$ and 0.43, $p > 0.05$). However, the numbers of fine to coarse filter feeders were positively and statistically significantly correlated with water bloom ($r_s = 0.59, p < 0.05$).

We recognized several species that flourish during cyanobacterial blooming and thus could be considered to be rather tolerant to its side effects: *Cinetochilum margaritaceum*, *Coleps hirtus*, *Dexiotricha granulosa*, *Frontonia leucas*, *Holophrya teres*, *Paramecium caudatum* and *Spirostomum teres*. Some of them were able to reach mass abundances even during culmination of water bloom. Moreover, *F. leucas*, *H. teres*, *P. caudatum* and *S. teres* are comparatively large species and hence could play an important role in the community structure with respect to their biomass.

Species-specific and environmental associations in the water reservoir

Correlation analysis resulted in 25 positive and 10 negative associations. The majority of relations were contemporaneous and only five were time-shifted. Network analysis of significant correlations generated five comparatively small and independent association clusters (Fig. 4). Abundances of most ciliate taxa did not correlate with the environmental parameters measured, indicating their low overall variation and/or high versatility of ciliate taxa. Only numbers of *Frontonia leucas* were positively correlated with temperature (Pearson correlation, $r = 0.63$, $p = 0.020$) and those of *Pelagovorticella natans* were positively correlated with conductivity ($r = 0.65, p = 0.017$) and TDS ($r = 0.57, p = 0.043$), while negatively with temperature ($r = -0.63$, $p = 0.020$), oxygen saturation ($r = -0.55$, $p = 0.049$) and degree of water bloom development ($r = -0.68, p = 0.011$).

The second cluster contained a comparatively diverse group of five species. They were linked by positive correlations, indicating a non-competitive nature of their interrelationships. This is corroborated also

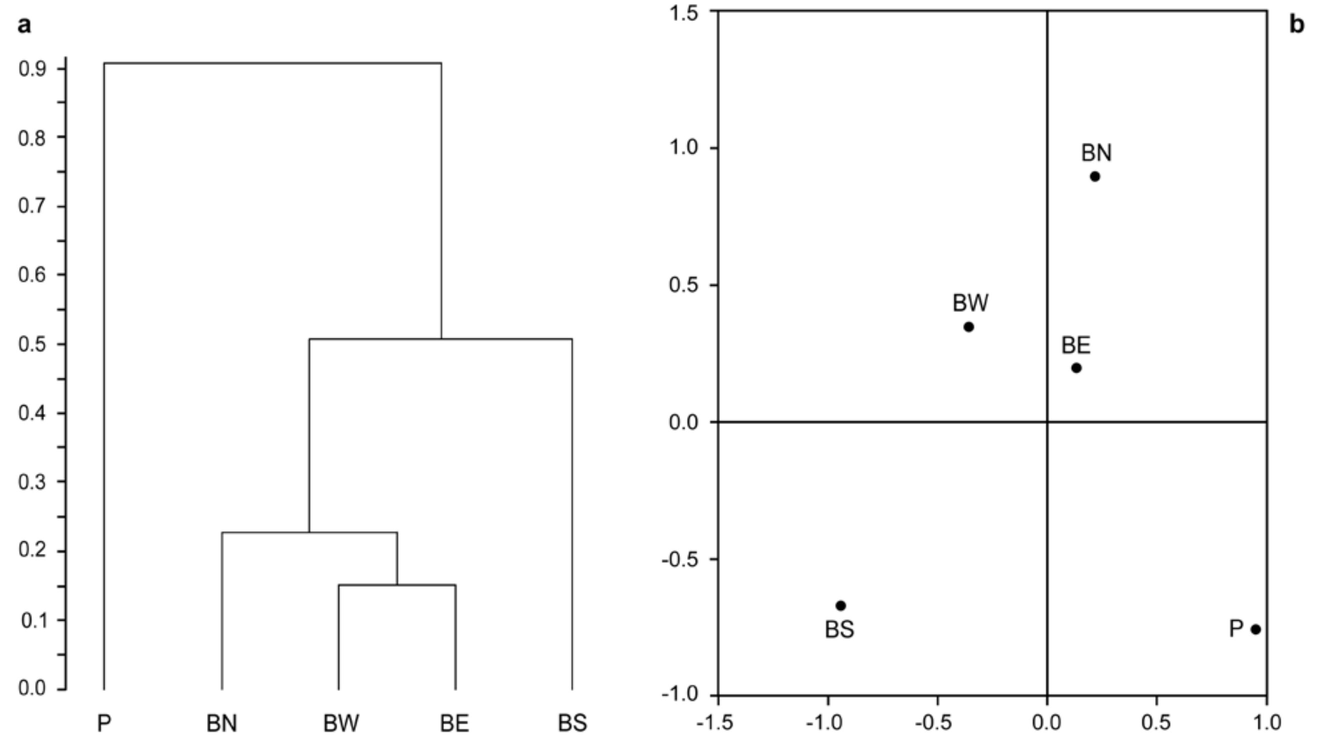

Fig. 2. Similarity of ciliate communities at five study spots from the Modra reservoir. **a.** Hierarchical cluster analysis (complete linkage method and Wishart's index). Vertical axis represents the scale of dissimilarity. **b.** PCA ordination diagram. Eigenvalues of two first axes are $\lambda_1 = 0.759$ and $\lambda_2 = 0.193$, accounting for 95.1% of the total variation. BE – benthic east study spot; BN – benthic north study spot; BS – benthic south study spot; BW – benthic west study spot; P – plankton.

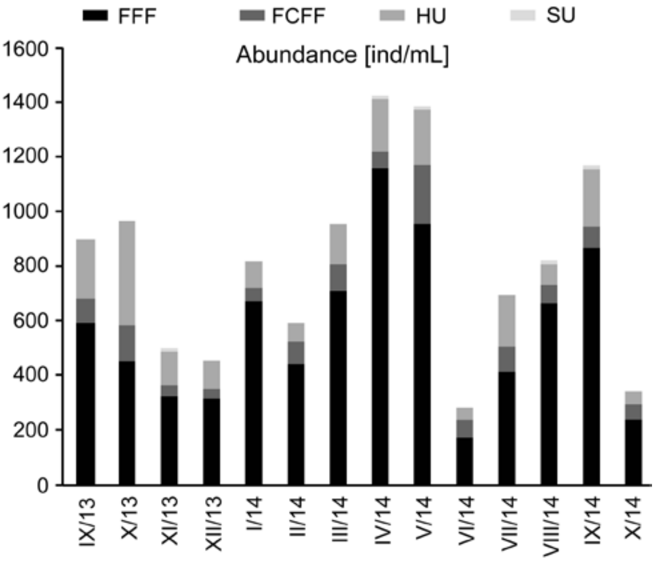

Fig. 3. Changes in abundances of ciliate feeding groups in the Modra water reservoir during the period between September 2013 and October 2014. FFF – fine filter feeders; FCFF – fine to coarse filter feeders; HU – hunters; SU – suckers.

by their different ecological preferences: *Trithigmostoma cucullus* is a diatom scraper, *Rimostrombidium humile* a planktonobiont feeding on pico(cyano)bacteria, *Spirostomum teres* a benthic, picobacterial grazer, *Euplotes patella* an agile omnivore, and *Ctedoctema acanthocryptum* is a fine filter feeder.

The third cluster contained only three fine filter feeders: two sessile peritrichs (*Vorticella microstoma* and *Epistylis chrysemydis*) and a single anaerobic armophorean (*Caenomorpha uniserialis*). Abundances of *V. microstoma* showed time-shifted associations with both *E. chrysemydis* ($r = 0.73$, $p = 0.004$) and *C. uniserialis* ($r = 0.71$, $p = 0.007$), which is suggestive of some temporal constraints in their ecological preferences.

The fourth cluster comprised two anaerobic armophoreans (*Brachonella spiralis* and *C. medusula*) feeding on heterotrophic bacteria in the benthos of the reservoir. Changes in their abundances were linked by a contemporaneous, positive correlation ($r = 0.63$, $p = 0.020$), indicating their cross-feeding activities under anoxic conditions.

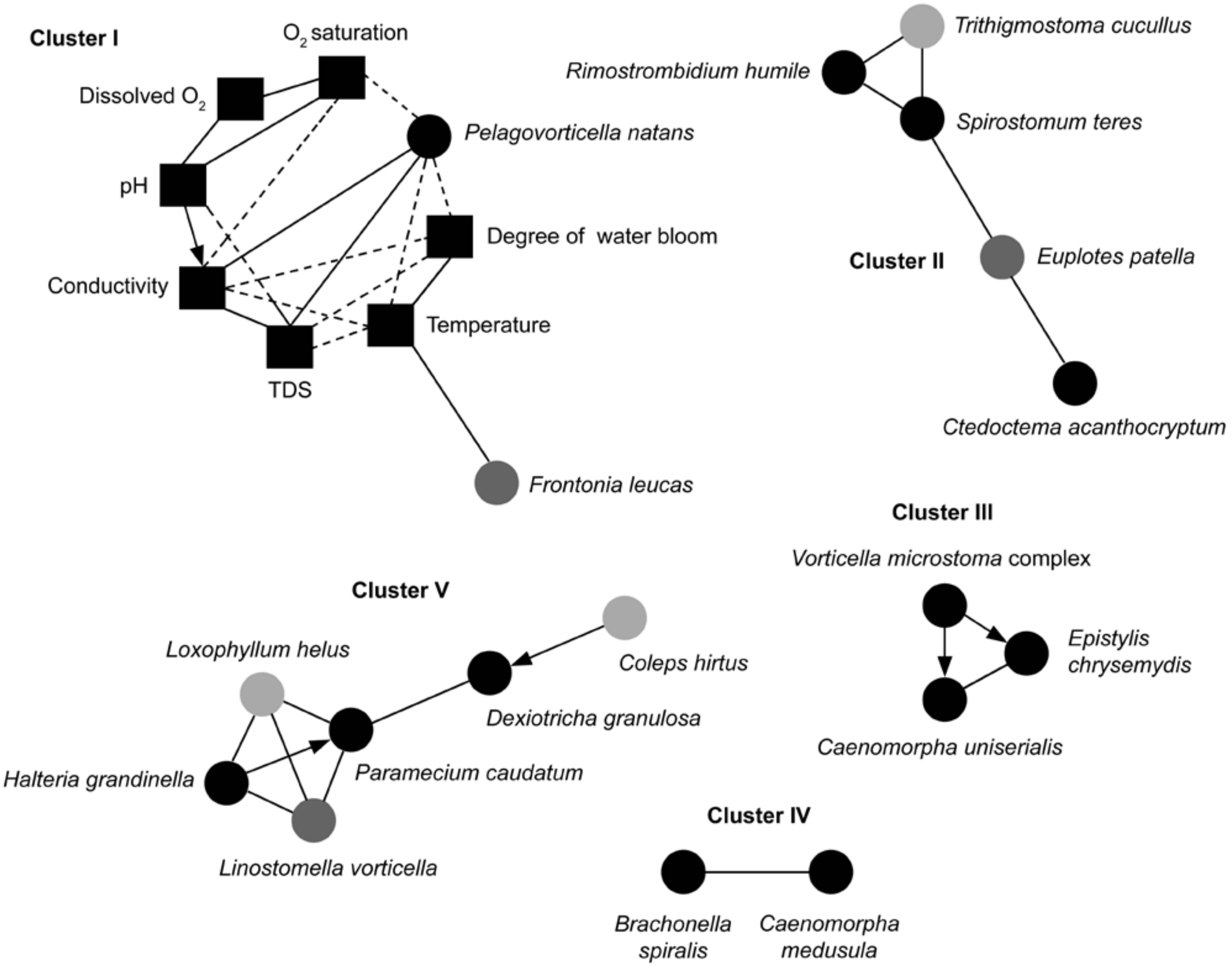

Fig. 4. Association networks based on time-shifted local similarity analysis (eLSA). Edges denote statistically significant connections ($p < 0.05$). Solid lines represent positive correlations, while dashed lines negative associations. Arrows point to the parameters that were delayed.

The last cluster included six taxa interconnected by complex associations. The voracious prostome hunter *Coleps hirtus* was linked with the bacterivorous *Dexiotricha granulosa* by a time-shifted correlation ($r = 0.65$, $p = 0.017$). The haptorian hunter *Loxophyllum helus*, the fine filter feeding *Halteria grandinella* and the bacterivorous *Paramecium caudatum* as well as the omnivorous *Linostomella vorticella* were united by six edges, only one of them representing a time-shifted association (*H. grandinella–P. caudatum*; $r = 0.63$, $p = 0.022$).

Saprobiological characterization of the water reservoir

During the whole sampling period, saprobic index reached high values ranging from 2.89 to 3.31 (Table 2). This indicates α-mesosaprobity to polysaprobity and corresponds to the water quality class III. The most distinct changes in saprobic index were detected between June 2014 and September 2014 (Fig. 1e). Specifically, in June 2014, saprobic index had the lowest value due to the lowest ciliate abundances, as a response to the strongly developed water bloom. In September 2014, water bloom declined and sedimented to the bottom where it was decomposed by bacteria that serve as a food source for fine and fine to coarse filter feeders which are typically characterized by high values of saprobic index.

The high organic load in the water reservoir was documented also by the prevalence of the polysaprobic level during the whole sampling period. Only a few exceptions were detected: the α-mesosaprobic level dominated in February 2014 and April 2014, while the β-mesosaprobic level prevailed over the α-mesosaprobic level in May 2014 (Table 2; Fig. 1f).

According to correlation analyses, there is no relation between saprobic index and state of water bloom ($r_s = –0.09, p > 0.05$). This very likely reflects the small overall variation in saprobity of the reservoir throughout the whole sampling period.

DISCUSSION

Cyanobacterial bloom and N/P cycling

Increased eutrophication usually occurs in small and shallow water reservoirs and fishponds that have no macrovegetation as well as no permanent inflow and outflow. Often nutrients have a tendency to accumulate in sediments of such water bodies, which in turn causes formation of water blooms. However, cyanobacterial blooms are not restricted to hypertrophic reservoirs, but occur also in lakes with low nutrient concentrations. This is possible because of substantial effects of bloom-forming cyanobacteria on nutrient cycling (Cottingham *et al.* 2015). Some pelagic cyanobacteria are able to transform dissolved, atmospherically-derived N_2 into biologically active forms (Schindler 2012, Beversdorf *et al.* 2013, Scott and Grantz 2013) or access pools of phosphorus in sediments and transport it to surface waters (Xie *et al.* 2003, Xie 2006). N-fixing cyanobacteria thus can help to reduce N limitation and maintain relatively high primary productivity also when N:P ratio is well below phytoplankton demand (Schindler *et al.* 2008). However, cyanobacteria not able to fix atmospheric N_2 (e.g., *Microcystis* and *Aphanocapsa*) dominated in the Modra reservoir, indicating that it is a hypertrophic water body (cf. Xu *et al.* 2010, Paerl and Otten 2013). This is also corroborated by the present saprobiological analyses, showing that a-mesosaprobic and polysaprobic levels prevail in the Modra reservoir (Table 2; Fig. 1f).

Xie *et al.* (2003) found that internal P loading by *Microcystis* during bloom formation could be two to four times as high as the average external loading. This observation is also indirectly supported by our hydrochemistry analyses (Table 1). The highest P concentrations were noted in March 2014, but these significantly decreased in the following months as P very likely became bounded in cells of bloom-forming cyanobacteria. Likewise, N concentrations were low in the Modra reservoir, indicating that it was also trapped in the organic matter of cyanobacteria and available to other organisms through grazing or when a bloom decays and bacterial growth occurs (Engström-Öst *et al.* 2013).

Ciliate diversity and cyanobacterial bloom

The Modra reservoir maintains a comparatively stable number of taxa over a period from 2008 to 2015. Specifically, the recorded numbers varied only from 74 to 87 species in a span of seven years (Tirjaková 2010, Illyová *et al.* 2013, present study). We find these numbers to be, however, relatively low in comparison with other stagnant and eutrophized running waters, where well over hundred species use to occur (e.g., Foissner and Moog 1992, Matis and Tirjaková 1992, Tirjaková and Vďačný 2013). This difference might be caused by water bloom that acts as a stress factor for ciliate communities. Indeed, the highest numbers of species in the Modra reservoir were recorded in spring, when water bloom was not well formed (Tirjaková 2010, present study). Further, only 32 out of the 86 recorded species were found also in the plankton. Other authors reported poor species diversities in the plankton of water bodies with cyanobacterial water bloom as well (e.g., Araújo and Costa 2007, Mayer *et al.* 1997, Velho *et al.* 2013,Esquivel *et al.* 2016).

Over years also phytoplankton communities have changed in the Modra reservoir. Specifically, the green alga *Golenkiniopsis longispina* was dominant until year 2010 (Hindák and Hindáková 2010). However, it was replaced by *Aphanocapsa delicatissima*, *Microcystis ichtyoblabe* and *Sphaerospermum aphanizomenoides*, when three tons of composite sorbent were deposited in the Modra basin (Illyová *et al.* 2013). We also noticed some changes in ciliate communities after application of the sorbent. Specifically, Tirjaková (2010) observed dominancy of sessile ciliates from the subclasses Suctoria and especially Peritrichia in the Modra reservoir from 2008 to 2010. Most of those ciliates were recorded also during the course of this study from 2013 to 2014, but they reached only low abundances. Although the total number of ciliate taxa has almost not changed (86 vs. 87), the species identity reached only about 40% between the present study and that of Tirjaková (2010). We speculate that this might have been caused by the application of the sorbent along with the change of bloom-forming species.

Anaerobic and microaerophilic ciliates

Cyanobacterial over-production may lead to anoxia at the bottom of water reservoirs (e.g., Søndergaard *et al.* 2003, Yang *et al.* 2008, Molot *et al.* 2014). This was well documented also in the Modra basin by the presence of a comparatively diverse assemblage of anaerobic ciliates in the benthos: *Brachonella spiralis*, *Bothrostoma undulans*, *Caenomorpha uniserialis*, *C. medusula*, *Epalxella* spp., *Plagiopyla nasuta* and members of the genus *Metopus*. Moreover, we recorded the large, microaerophilic *Spirostomum teres* not only in the benthos but also in the plankton where its abundances varied from 5 ind/mL (October 2013; 59.6% O_2 saturation) to 40 ind/mL (March 2014; 89.2% O_2 saturation). This is an interesting observation, because species larger than 150 µm are not supposed to migrate from benthos into the water column (Finlay 1981). However, Hayward *et al.* (2003) documented that the huge, anaerobic *Geleia* and *Tracheloraphis* species could switch from a benthic to a planktonic lifestyle as appropriate conditions (seasonal anoxia) develop in the water column. Fenchel and Bernard (1996) showed that microaerophilic ciliates have a more or less distinct and species-specific preference for an oxygen saturation, though some species are rather versatile. This seems to be also the case of *S. teres* which was recorded under a wide range of O_2 conditions, i.e., in the oxic/anoxic interface (Bark and Watts 1984), at O_2 content < 1mg/L (Goulder 1973) and 0.4–3.2 mg/L (Neidl 1989). We detected *S. teres* even under much higher O_2 concentrations (6.40–10.28 mg/L). Therefore, we speculate that the presence of *S. teres* in the plankton may not be accidental, but could reflect its ample ecological valence.

Control of cyanobacterial bloom by ciliates

The most natural means of elimination of over-production of cyanobacteria and algae are plankton filtrators. Although many studies hint that crustaceans are important consumers of phytoplankton (e.g., Mayer *et al.* 1997, Stibor *et al.* 2004), they were recorded at comparatively low abundances in the hypertrophic Modra reservoir (Illyová *et al.* 2013). This was explained by adverse oxygen conditions and toxicity of cyanobacterial bloom. In this case, ciliates may have the potential to play a pivotal role in regulation or elimination of harmful cyanobacterial blooms (Zingel *et al.* 2007, Davis *et al.* 2012, Esquivel *et al.* 2016). There is also experimental evidence that toxin-producing cyanobacteria can sustain ciliate growth (Fabbro *et al.* 2001, Combes *et al.* 2013). We also observed potentially toxigenic cyanobacteria in food vacuoles of various ciliates (*Cinetochilum margaritaceum*, *Coleps hirtus*, *Frontonia leucas*, *Halteria grandinella* and *Holophrya teres*). Likewise, Dias and D'Agosto (2006) and Šimek *et al.* (1995) pointed out that *F. leucas* and *H. grandinella* are able to graze cyanobacteria and Esquivel *et al.* (2016) could not exclude ingestion of the toxin-producing filamentous cyanobacterium *Cylindrospermopsis* by ciliates in the tropical Catemaco lake. Nevertheless, there was still a distinct prevalence of ciliates feeding on heterotrophic bacteria in the Modra basin. This clear over-dominance of bacterivorous fine filter feeders is due to the ongoing intense decomposition processes (Blatterer 2008, Mieczan *et al.* 2012), including the decay of died water bloom cyanobacteria. These produce layers of sediments that are degraded by heterotrophic bacteria which, in turn, serve as a food source for ciliates (Engström-Öst *et al.* 2013, Kalinowska *et al.* 2013). In this way, ciliates channel pico(cyano)bacterial production to the uppermost trophic levels (Sherr and Sherr 2002).

We have detected several ciliate species (*Cinetochilum margaritaceum*, *Coleps hirtus*, *Dexiotricha granulosa*, *Frontonia leucas*, *Holophrya teres*, *Paramecium caudatum* and *Spirostomum teres*) that flourished during culmination of water bloom. Three of them, *Cinetochilum margaritaceum*, *Frontonia leucas* and *Holophrya teres*, were also present permanently in the Modra reservoir, which documents their high versatility and ample ecological valencies. Since *F. leucas* and *H. teres* are comparatively large and voracious species, they might be potentially utilized in controlling cyanobacterial water bloom or in elimination of intense vegetation colouration of water. Similarly, Song *et al.* (2009) stated that some protists (e.g., *Aspidisca* spp. and *Vorticella* spp.) and microscopic animals (e.g., *Philodina* spp. and *Lecane* spp.) that live in the rhizosphere of water macrovegetation, could help to remove cyanobacteria and their toxins (microcystins) from the environment.

CONCLUSIONS

Cyanobacterial water blooms generally affect ciliate communities by lowering their diversity and equitability. Only relatively few versatile ciliate species flourish during culmination of cyanobacterial bloom. These ciliates, however, occupy a variety of ecological niches, ranging from fine trough coarse filter feeders to voracious hunters. Also comparatively rich coenoses form under anoxic conditions at the bottom of water bodies with harmful cyanobacterial blooms. Armophoreans and plagiopyleans graze there heterotrophic bacteria which, in turn, decompose the sedimented, died water bloom cyanobacteria. Ciliates thus form functionally diverse assemblages that have the capacity to control cyanobacterial blooming in hypertrophic water reservoirs.

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SUPPLEMENTARY

Table S1. List of ciliates recorded in the Modra water reservoir during the period between September 2013 and October 2014.

No.	Taxon	Feeding group	Collection date													
			2013				2014									
			IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X
1	*Acineria uncinata* Tucolesco, 1962	Hunter			+					+			+			
2	*Acinetides lacustris* (Stokes, 1886)	Sucker													+	
3	*Actinobolina vorax* (Wenrich, 1929)	Hunter								+						
4	*Actinobolina weinrichii* Wang & Nie, 1933	Hunter					+				+					
5	*Amphileptus pleurosigma* (Stokes, 1884)	Hunter	+											+		
6	*Askenasia volvox* (Eichwald, 1852)	Mixotrophic (?) hunter			+								+			
7	*Aspidisca cicada* (Müller, 1786)	Fine filter feeder									+					
8	*Aspidisca lynceus* (Müller, 1773)	Fine filter feeder											+			
9	*Balantidion pellucidum* Eberhard, 1862	Hunter					+									
10	*Bothrostoma undulans* Stokes, 1887	Fine filter feeder													+	
11	*Brachonella spiralis* (Smith, 1897)	Fine filter feeder		+		+			+		+	+			+	
12	*Bursaria truncatella* Müller, 1773	Fine to coarse filter feeder								+						
13	*Caenomorpha medusula (*Perty, 1852)	Fine filter feeder	+	+		+		+	+	+	+	+	+		+	+
14	*Caenomorpha uniserialis* Levander, 1894	Fine filter feeder			+			+	+	+						+
15	*Cinetochilum margaritaceum* (Ehrenberg, 1831)	Fine filter feeder	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	*Coleps hirtus* (Müller, 1786)	Hunter	+	+	+	+	+		+	+		+	+	+	+	+
17	*Colpoda* sp.	Fine filter feeder														+
18	*Ctedoctema acanthocryptum* Stokes, 1884	Fine filter feeder	+		+		+	+	+							
19	*Cyclidium glaucoma* Müller, 1773	Fine filter feeder	+		+	+	+			+	+					
20	*Dexiotricha granulosa* (Kent, 1881)	Fine filter feeder	+	+	+	+	+	+	+	+	+		+	+	+	+
21	*Dexiotrichides centralis* (Stokes, 1885)	Fine filter feeder					+									
22	*Discophrya crassipes* (Rieder, 1936)	Sucker			+					+	+			+		
23	*Epalxella mirabilis* (Roux, 1899)	Fine filter feeder											+			
24	*Epalxella striata* (Kahl, 1926)	Fine filter feeder							+							
25	*Epistylis entzii* Stiller, 1935	Fine filter feeder					+	+					+		+	
26	*Epistylis chrysemydis* Bishop & Jahn, 1941	Fine filter feeder	+	+	+	+	+		+	+				+		
27	*Epistylis plicatilis* Ehrenberg, 1831	Fine filter feeder	+					+				+		+		
28	*Euplotes patella* (Müller, 1773)	Fine to coarse filter feeder	+	+	+	+	+				+					

29	*Frontonia leucas* (Ehrenberg, 1833)	Fine to coarse filter feeder	+	+	+	+	+	+	+	+	+	+	+	+	+	+
30	*Glaucoma scintillans* Ehrenberg, 1830	Fine filter feeder					+									
31	*Halteria grandinella* (Müller, 1773)	Fine filter feeder				+	+	+	+		+	+	+	+		
32	*Holophrya teres* (Ehrenberg, 1833)	Hunter	+	+	+	+	+	+	+	+	+	+	+	+	+	+
33	*Holosticha kessleri* (Wrześniowski, 1877)	Fine to coarse filter feeder						+	+							
34	*Homalozoon vermiculare* (Stokes, 1887)	Hunter				+	+		+							+
35	*Chilodonella uncinata* (Ehrenberg, 1838)	Fine filter feeder	+		+	+		+		+				+		
36	*Lagynophrya acuminata* Kahl, 1953	Hunter						+		+	+		+			
37	*Lagynus elegans* (Engelmann, 1862)	Hunter		+	+			+				+			+	
38	*Limnostrombidium pelagicum* (Kahl, 1932)	Fine filter feeder								+						
39	*Linostomella vorticella* (Ehrenberg, 1833)	Fine to coarse filter feeder		+	+		+	+		+	+					
40	*Litonotus crystallinus* (Vuxanovici, 1960)	Hunter			+	+				+			+			
41	*Litonotus cygnus* (Müller, 1773)	Hunter							+							
42	*Litonotus lamella* (Müller, 1773)	Hunter		+	+	+		+								
43	*Litonotus varsaviensis* (Wrześniowski, 1866)	Hunter	+													
44	*Loxocephalus elipticus* Kahl, 1931	Fine filter feeder		+												
45	*Loxophyllum helus* (Stokes, 1884)	Hunter	+	+						+	+			+	+	+
46	*Mesodinium acarus* Stein, 1867	Mixotrophic (?) hunter	+	+												
47	*Metopus es* (Müller, 1776)	Fine filter feeder	+		+	+	+	+		+		+	+	+	+	+
48	*Metopus ovalis* Kahl, 1927	Fine filter feeder				+										
49	*Metopus striatus* McMurrich, 1884	Fine filter feeder							+							
50	*Monodinium balbianii* Fabré-Domergue, 1888	Mixotrophic (?) hunter				+	+			+						
51	*Oxytricha chlorelligera* Kahl, 1932	Mixotrophic fine to coarse filter feeder						+								
52	*Oxytricha saprobia* Kahl, 1932	Fine to coarse filter feeder	+						+							
53	*Oxytricha setigera* Stokes, 1891	Fine to coarse filter feeder					+	+	+					+		
54	*Paramecium aurelia* complex	Fine filter feeder	+													
55	*Paramecium bursaria* (Ehrenberg, 1831)	Mixotrophic fine filter feeder								+	+					
56	*Paramecium caudatum* Ehrenberg, 1833	Fine filter feeder		+	+	+	+	+	+	+	+			+	+	
57	*Pelagovorticella mayeri* (Fauré-Fremiet, 1920)	Fine filter feeder								+						
58	*Pelagovorticella natans* (Fauré-Fremiet, 1924)	Fine filter feeder			+	+	+	+	+							
59	*Phialina* spp.	Hunter						+								
60	*Plagiopyla nasuta* Stein, 1860	Fine filter feeder							+							+
61	*Pleuronema coronatum* Kent, 1881	Fine to coarse filter feeder								+	+					
62	*Prorodon niveus* Ehrenberg, 1933	Hunter									+					

No.	Taxon	Feeding group	Collection date													
			2013				2014									
			IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X
63	*Pseudoblepharisma tenue* (Kahl, 1926)	Fine filter feeder								+				+		
64	*Pseudostrombidium planctonicum* Horváth, 1933	Fine filter feeder							+		+					
65	*Rimostrombidium humile* (Penard, 1922)	Mixotrophic (?) fine filter feeder		+	+	+	+	+			+			+	+	+
66	*Saprodinium dentatum* (Lauterborn, 1901)	Fine filter feeder	+					+								+
67	*Spirostomum teres* Claparède & Lachmann, 1858	Fine filter feeder	+	+	+	+	+	+	+	+	+		+	+		
68	*Stentor coeruleus* (Pallas, 1766)	Fine to coarse filter feeder							+	+	+				+	
69	*Stentor muelleri* Ehrenberg, 1831	Fine to coarse filter feeder									+					
70	*Stylonychia mytilus* complex	Fine to coarse filter feeder					+	+		+		+				
71	*Stylonychia stylomuscorum* (Foissner, Blatterer, Berger & Kohmann, 1991)	Fine to coarse filter feeder						+								
72	*Tachysoma pellionellum* (Müller, 1773)	Fine to coarse filter feeder					+	+	+						+	+
73	*Tetmemena pustulata* (Müller, 1786)	Fine to coarse filter feeder									+					
74	*Tintinnidium pusillum* Entz, 1909	Fine filter feeder								+	+					
75	*Trithigmostoma cucullus* (Müller, 1786)	Hunter	+	+	+		+	+	+	+	+					
76	*Trochilia minuta* (Roux, 1899)	Fine filter feeder	+													
77	*Urocentrum turbo* (Müller, 1786)	Fine to coarse filter feeder					+	+	+	+						
78	*Urostyla grandis* Ehrenberg, 1830	Fine to coarse filter feeder								+	+					+
79	*Urostyla viridis* Stein, 1859	Fine to coarse filter feeder													+	
80	*Urotricha farcta* Claparède & Lachmann, 1859	Hunter					+	+								
81	*Urotricha globosa* Schewiakoff, 1892	Hunter						+								
82	*Vorticella aquadulcis* complex	Fine filter feeder			+											
83	*Vorticella campanula* Ehrenberg, 1831	Fine filter feeder								+	+					+
84	*Vorticella convallaria* complex	Fine filter feeder						+								
85	*Vorticella chlorellata* Stiller, 1940	Mixotrophic fine filter feeder				+										
86	*Vorticella microstoma* complex	Fine filter feeder					+	+	+	+	+	+	+	+		