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Research article

Phytoperiphyton on the shells of *Dreissena polymorpha* (Pallas) in Lake Naroch♣

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Abstract

The aim of this study was to reveal the taxonomic diversity of algae that colonize the shells of zebra mussels, *Dreissena polymorpha*, in mesotrophic Lake Naroch (Belarus). In total, 155 algal species have been identified in collected samples, with Bacillariophyta, Chlorophyta and Cyanophyta being the most common divisions. The species richness of phytoperiphyton from *Dreissena* shells appeared to be much higher than that of phytoplankton (30 species found). Taxonomic diversity of the phytoperiphyton was found to significantly decline with depth, which we explain by decreasing sun irradiance. In contrast to depth, the length of *Dreissena* shells did not demonstrate any relationships with the composition of algal communities.

Key words: Belarus, *Dreissena*, Lake Naroch, phytoperiphyton, shells, taxonomic diversity

Introduction

In the early 19th century, soon after the construction in Europe of several shipping canals connecting the rivers of the Black and Baltic Sea basins, the bivalve mollusc *Dreissena polymorpha* (Pallas) (zebra mussel) began its spread outside its native Ponto-Caspian region. To date, zebra mussels have colonised all major river basins of Europe and, to a somewhat lesser extent, those in North America (reviewed in Kinzelbach 1992; Starobogatov and Andreeva 1994; Karatayev et al. 2003; 2007).

Dreissena polymorpha is a typical 'ecological engineer', i.e. species that '*directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials*' (Jones et al. 1994). One of the ecological impacts caused by zebra mussels is due to the formation of complex 3D-structures composed of their shells, which creates a new type of benthic habitat. Clumps of mussels attract various types of aquatic organisms,

♣ This paper was presented at the special session "Dreissenology" of the 15th International Conference on Aquatic Invasive Species – ICAIS 2007, September 23-27, 2007, Nijmegen especially detritophagous species, which are provided with a shell-based shelter as well as abundant food resources in the form of *D.polymorpha* faeces and pseudofaeces. In addition, the filtration activity of zebra mussels improves the oxygen regime for benthic invertebrates. All these environmental effects caused by aggregations of *D. polymorpha* are well researched (reviewed in Karatayev et al. 1997; 2002). At the same time, aquatic ecologists have actually overlooked the potential that zebra mussel shells are likely to substantially increase the amount of hard substrate available for occupation by sessile organisms. Taking into account that *D. polymorpha* may reach extremely high densities, we have hypothesized that periphyton growing on the mussels' shells make a considerable contribution to transformation of matter and energy in invaded ecosystems (Mastitsky and Makarevich 2007).

In 2006, we initiated a research project, the main goals of which were to reveal the structure and functional parameters of periphyton that grows on shells of *D. polymorpha* in Lake Naroch (Belarus). As this lake has a wide littoral zone (Ostapenya 1985), periphyton plays an important role in the functioning of its ecosystem (Zhukova et al. 2007a). Submerged macrophytes, mainly *Chara* spp., served as the main substrate for periphyton communities in Lake Naroch before the invasion of *D. polymorpha* in the mid-1980s (Makarevich 1983, 1995). After invasion, shells of zebra mussels provided periphyton with an additional surface to grow on. Using data on density and size structure of the *D. polymorpha* population obtained in 2005 (Mastitsky et al. 2006), and by using the empirical relationship between shell length and surface area ($S=0.017*L^{1.942}$), we estimated that the total area of hard substrate presented by *Dreissena* shells in Lake Naroch is currently about 8 km^2 (11% of the lake surface area). The amount of periphyton present on this 'additional substrate' in August 2006 was estimated to be 100 tons of organic matter, i.e. ca. 14% of the amount that was present on *Chara* spp. in August 1981 (Makarevich et al. 2007).

The set of functional groups of periphyton growing on zebra mussel shells was found to be very similar to that growing on other substrates in Lake Naroch; about 60% of periphyton dry weight is composed of a mineral fraction, with the biotic component dominated by autotrophs (up to 25% of total dry weight) (Makarevich et al. 2007). In this paper we present a deeper insight into the structure of *D. polymorpha* periphyton in Lake Naroch. Our goal was to reveal the taxonomic diversity of algae that colonize *Dreissena* surface in relation to the shell size and the lake depth that mussels inhabit. Algal diversity in phytoperiphyton from zebra mussels was also compared with that present in phytoplankton.

Material and Methods

Study area

Lake Naroch is a mesotrophic polymictic waterbody located in the north-western part of Belarus (54°51'N, 26°46'E). In combination with two other interconnected lakes (Myastro and Batorino), it constitutes the so called 'Narochanskaya Lake System'. The main morphometric parameters of Lake Naroch are as follows: surface area – 79.6 km^2; mean depth – 8.9 m; maximal depth – 24.8 m. The lake is divided by a peninsula into small (north-western) and large (south-eastern) stretches. Lake bathymetry is composed of a complex relief represented by interchangeable depressions, ridges and plateaus. A considerable part of the waterbody is shallow, e.g., a depth of 2 m bounds ca. 14% of the entire lake's surface area (Ostapenya 1985). Wide littoral zone and high water transparency (6.7 ± 0.6 m in 2005, mean ± standard deviation; Zhukova et al. 2007b) determine an ample development of submerged macrophytes (Gigevich 1985; Zhukova et al. 2005). The main substrate in the littoral zone is sand; however, rocky areas are also present in northern part of the lake.

Dreissena polymorpha was first recorded in Lake Naroch in 1989 (Ostapenya et al. 1993). Most likely, it entered this waterbody from the upstream Lake Myastro, where zebra mussels were found somewhat earlier, i.e. in 1984 (Ostapenya et al. 1993). Burlakova (1998) suggests that adult individuals of *D. polymorpha* were introduced into Lake Myastro on fishing tackle from commercial fisheries. The first extensive sampling conducted in Lake Naroch in 1990 showed that average density of *D. polymorpha* was only 7.4 ind./m^2, and the biomass was 1.5 g/m^2. Further observations revealed an exponential growth of *Dreissena* population, typical of many invasive species. In 1995, for example, the average density and biomass of the mussels across the whole area of the lake were about 1500 ind./m^2 and 110 g/m^2, respectively (Burlakova et al. 2006). Afterwards, the abundance of *D. polymorpha* in Lake Naroch did not demonstrate any significant oscillations. For instance, the most recent sampling conducted in 2005 (Mastitsky et al. 2006) resulted in estimations of the density and biomass identical to those obtained in 1995 (Karatayev et al. 2006). Currently, *D. polymorpha* is distributed in the lake as deep as to 8 m, with the maximal abundance observed at 2 to 4 m (Mastitsky et al. 2006). The main substrate for attachment of zebra mussels are submerged macrophytes (Karatayev et al. 2006; Mastitsky et al. 2006).

Sampling protocols

On 12 July 2006, zebra mussels were collected with a Petersen grab (0.025 m^2) from depths of 0.8, 4 and 6 m along 3 transects located in the northern stretch of Lake Naroch (coordinates of the shore points of transects: 54°54'13"N, 26°44'49"E; 54°54'18"N, 26°43'46"E; 54°54'57" N, 26°41'25"E). The chosen transects embraced all major types of habitats present in this part of the lake. To compare the species composition of algae from the periphyton of *D. polymorpha* shells with that of phytoplankton, 1 L samples of phytoplankton were simultaneously taken at the same sites and depths and preserved with Utermöhl fixative (n = 9).

Zebra mussels collected from identical depths were pooled together into integral samples. Whenever possible, the shell length of 100-200 mussels was measured with callipers to the nearest millimeter to reveal the size structure of *D. polymorpha* colonies at different depths and to estimate the mean shell length. All manipulations with mussels were conducted in the laboratory immediately after sampling and in a very gentle way to avoid disturbing the periphyton on shells. Based on measurements, the mussels were sorted out into size classes using 5-mm interval (e.g., 5.0 – 9.9 mm; 10.0 – 14.9 mm, 15.0 – 19.9 mm, and so on).

The periphyton was carefully removed from *D. polymorpha* shells with a scalpel into filtered (1.5 µm, Nucleopor) lake water (100-800 ml) (Figure 1). The number of mussels from a given size class involved to obtain such samples of periphyton was proportional to abundance of that class in the entire size structure at a given depth. Typically, this number ranged from 20-100 mussels. The samples of periphyton were preserved with Utermöhl fixative.

Taxonomic identification of algae from the samples of periphyton and phytoplankton was performed to the lowest possible level using standard methods and popular keys. In this paper we use the system of taxonomy accepted in the catalogue of algal flora of Belarus (Mikheeva 1999).

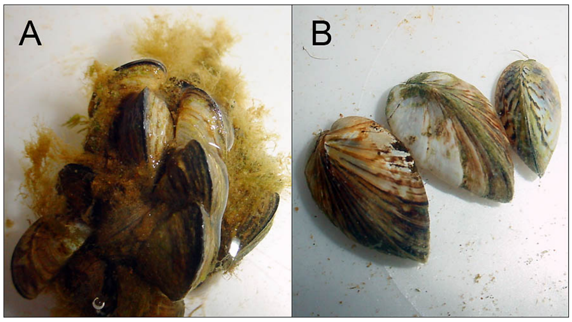

Figure 1. Before (A) and after (B) removal of phytoperiphyton from the shells of zebra mussels (Photograph by Dr. Alexander P. Ostapenya, Belarusian State University)

Statistical analysis

Multidimensional scaling (MDS; 100 iterations, minimum stress 0.001) based on Sorensen coefficient of similarity was performed using PRIMER 6 software to reveal if the algal communities from different samples form any clusters. When such clusters were found, the ANOSIM routine of PRIMER was used to test if the dissimilarity between them was statistically significant at the significance level of $\alpha = 0.05$ (Clarke and Warwick 2001).

Results and Discussion

Diversity of algae in periphyton of D. polymorpha shells

The algal component of the periphyton of *D. polymorpha* shells appeared to be highly diverse taxonomically (Annex 1; Table 1). In total, 155 species (166 intraspecies taxa) were identified in collected samples. This included the first record in Belarus of the cyanobacteria *Calothrix ramenskii* Elenk (Mikheeva 1999). This typical epiphytic species was abundant on the shells of zebra mussels from almost all size classes but only at the sample depth of 0.8 m.

The identified species belonged to 7 divisions – Bacillariophyta, Chlorophyta, Cyanophyta, Cryptophyta, Dinophyta, Chrysophyta and

Euglenophyta, which were not proportionately present in the samples (Figure 2). The highest taxonomic diversity was characteristic of Bacillariophyta (23 genera, 65 species, 73 intra-species taxa), with the genera *Navicula*, *Cymbella* and *Gomphonema* presented by the largest number of species (Annex 1).

Table 1. Taxonomic diversity of algae in the periphyton of *D. polymorpha* shells

Parameter	Estimate
Number of intraspecies taxa (IT)	166
Number of species (S)	155
Number of genera (G)	72
Number of families (F)	48
S/G index	2.15
IT/G index	2.31
S/F index	3.23
G/F index	1.5
Number of genera presented by the only species	40
Number of genera presented by ≥5 species	7

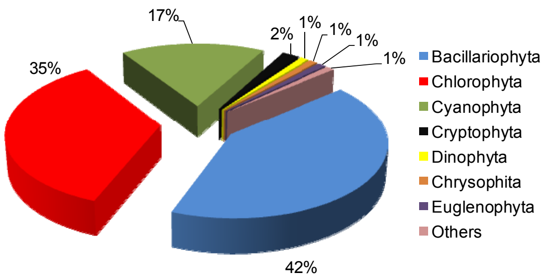

Figure 2. Contribution of different algal divisions to species richness of phytoperiphyton collected from *D. polymorpha* shells

Chlorophyta were at the second position in terms of taxonomic diversity (28 genera, 55 species, 58 intraspecies taxa). The most common green algae were those from the genera *Cosmarium* and *Scenedesmus*. The third position belonged to Cyanophyta, which were represented by 14 genera and 27 species. *Gleocapsa* spp. were the most frequently observed cyanobacteria (Annex 1). Representatives of other divisions had a minor role in contributing to the diversity of periphyton on *D. polymorpha* shells (Figure 2; Annex 1).

About 35% of all species were typical benthic inhabitants, 22% were plankton-benthic forms, and 14% were typical planktonic species (based on classification by Barinova et al. 2006). Biotope preferences of the other 29% species are unknown.

Our data are the first to characterise the taxonomic diversity of algae growing on *D. polymorpha* shells. The diversity of these algae appears to be comparable with that of fouling communities from other hard substrates present in Lake Naroch. For example, Sysova (2008) has studied the algal component of periphyton from the surfaces of 4 species of vascular aquatic plants common in the lake and found 212 species within 86 genera. As in our study (Figure 2), the most common divisions in her samples were Bacillariophyta (45% of total species richness), Chlorophyta (36%) and Cyanophyta (7%).

Diversity of phytoperiphyton in relation to depth and size of zebra mussels

MDS-analysis has shown that algal communities of the periphyton of *D. polymorpha* shells form three clusters in close relation to the depth that mussels inhabit (Figure 3). The dissimilarity of species composition between these clusters was statistically significant (P < 0.001, ANOSIM).

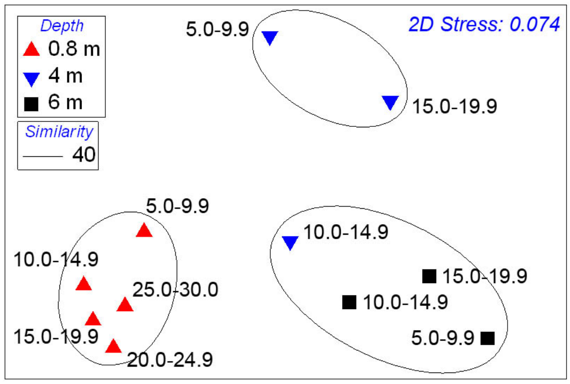

Figure 3. MDS ordination of the samples of phytoperiphyton collected from zebra mussels of different size and from different depths. Each point corresponds to a sample from a 5-mm size class based on the mussels' shell length

The most pronounced differences were observed between samples from the depth of 0.8 m and those from two other depth zones (P = 0.018 for both comparisons, ANOSIM pairwise tests). However, the dissimilarity between samples from 4 m and 6 m was not statistically significant (P=0.10, ANOSIM pairwise test), indicative of similar ecological conditions that determine the species composition of algae in the periphyton of *D. polymorpha* shells at these depths. In contrast to depth, the length of zebra mussel shells did not influence the composition of algal communities, i.e. the samples representing different size classes of *Dreissena* did not form any clusters (Figure 3).

We suppose that the revealed bathymetric pattern in composition of algal communities of the periphyton of *D. polymorpha* is primarily determined by light. The highest taxonomic diversity of algae was observed in the samples collected from well illuminated depth of 0.8 m. In respect to decreasing sun irradiance in deeper habitats, the number of species was regularly declining (Table 2). The fraction of particular divisions in total species richness of algae also changed with depth (Table 2; Figure 4). For instance, representatives of the Cryptophyta, Dinophyta and Chrysophyta groups occurred exclusively in shallows (Table 2; Figure 4). The fraction of Chlorophyta was gradually declining with depth (from 34% at 0.8 m to 12.5% at 6 m), while the fraction of Bacillariophyta demonstrated the opposite pattern (42% at 0.8 m vs. 67.5% at 6 m). It appears, thus, that diatom algae present in the periphyton of *D. polymorpha* shells are most tolerant of decreased sun irradiance.

Table 2. Diversity of algal taxa in periphyton collected from zebra mussels at different depths

Number of species	Depth (m)		
	0.8	4	6
Total number	146	50	40
Bacillariophyta	61	25	27
Chlorophyta	50	13	5
Cyanophyta	27	11	7
Cryptophyta	3	0	0
Dinophyta	1	0	0
Chrysophyta	3	0	0
Euglenophyta	1	1	1

The important role of light in determining the structure of phytoperiphyton communities is also confirmed by the strong negative correlation observed between depth and concentration of chlorophyll a in samples of periphyton collected from the same molluscs that were used in this study (T. A. Makarevich and S. E. Mastitsky, unpublished).

Comparison of algal communities between periphyton and phytoplankton

Only 30 species were found in samples of phytoplankton taken at the same sites where zebra mussels had been collected. Such low species richness resulted in a clearly separate clustering of the phytoplankton and periphyton samples on the MDS ordination plot (Figure 5; P < 0.001, ANOSIM). Just a few species appeared to be common in both communities, e.g., *Microcystis aeruginosa* (Kütz.), *Aphanothece clathrata* W. et G. S. West, *Navicula* sp., and some others.

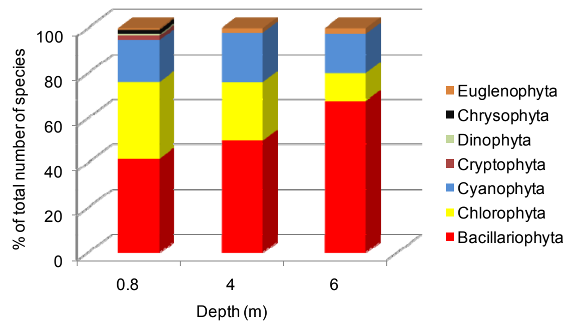

Figure 4. Contribution of different algal divisions to species richness of the phytoperiphyton of *D. polymorpha* shells at sampled depths

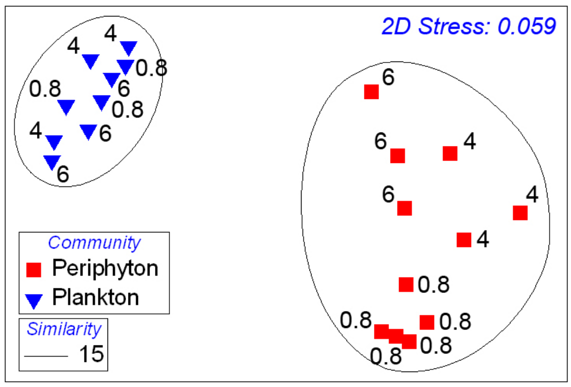

Figure 5. MDS ordination of the samples of phytoplankton and phytoperiphyton from *D. polymorpha* shells. Numbers indicate sampling depths

Presence of lower taxonomic diversity in phytoplankton than in periphyton is a well known phenomenon. As of 2005, total species richness of phytoplankton uncovered in Lake Naroch was 170 algal species (Lukyanova and Mikheeva 2008), while in periphyton from macrophytes it was 212 species (Sysova 2008). High biodiversity of periphyton communities is likely a consequence of their existence on the border between two phases – hard surface and water, where life is 'concentrated' due to more favorable conditions for mineral nutrition. In addition, the filtration activity of *D. polymorpha* often results in a considerable shift in the direction of energy flow from the pelagic zone to the benthic one ('benthification') (Karatayev et al. 2002; Mills et al. 2003) and this may also favor the development of periphyton communities, which grow on mussel shells. On the other hand, re-allocation of such nutrients as phosphorus and nitrogen from the water column to the bottom leads to decrease of the phytoplankton biodiversity. There were 337 species in the phytoplankton of Lake Naroch before the invasion of *D. polymorpha* in mid-1980s (Mikheeva 1985). Lukyanova and Mikheeva (2008) think that decline of the phytoplankton diversity to 170 species might be directly related to benthification caused by zebra mussels. However, intensive grazing of *D. polymorpha* on phytoplankton is also a likely cause for dramatic decrease of phytoplankton diversity (Karatayev et al. 2002).

Acknowledgements

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Annex 1

Species composition of phytoperiphyton collected from *Dreissena polymorpha* shells in Lake Naroch

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Division Cyanophyta												
Anabaena Bory sp.	un	+	+	+	+	+	+	–	+	–	–	–
Aphanothece clathrata W. et G. S. West f. clathrata	p	+	+	+	+	+	+	+	+	–	–	+
Aphanothece stagnina (Spreng.) B.-Peters. et Geitl. f. *stagnina*	pb	–	–	+	–	–	–	–	–	–	–	–
Calothrix (Ag.) V. Poljansk. sp.	e	+	+	+	–	+	+	+	–	–	+	–
Calothrix ramenskii Elenk.	e	–	+	+	+	+	–	–	–	–	–	–
Coelosphaerium dubium Grun.	p	–	–	+	–	–	–	–	–	–	–	–
Gloeocapsa limnetica (Lemm.) Hollerb. f. *limnetica*	p	–	+	–	+	–	–	–	–	–	–	–
Gloeocapsa minima (Keissl.) Hollerb. ampl. f. *minima*	p	+	+	+	+	+	–	–	–	–	–	–
Gloeocapsa minor (Kütz.) Hollerb. ampl. f. *minor*	p	+	+	+	+	–	–	+	–	–	–	–
Gloeocapsa minuta (Kütz.) Hollerb. f. *minuta*	p	–	–	+	–	–	–	–	–	–	–	–
Gloeocapsa turgida (Kütz.) Hollerb. f. *turgida*	pb	–	+	+	+	+	–	+	+	–	–	–
Gloeotrichia pisum (Ag.) Thur.	b	–	–	–	–	+	–	–	–	–	–	–
Gomphosphaeria lacustris Chod. f. *lacustris*	p	+	+	+	–	–	–	–	–	–	–	–
Lyngbya Ag. sp.1	un	+	+	+	+	+	+	+	+	+	+	+
Lyngbya Ag. sp.2	un	–	–	+	+	+	–	–	–	–	+	+
Lyngbya kuetzingiana f. *ucrainica* (Schirsch.) Elenk.	b	–	+	+	+	+	–	+	–	+	+	–
Lyngbya limnetica Lemm. f. *limnetica*	p, s	+	+	–	–	–	–	+	–	–	–	–
Microcystis aeruginosa (Kütz.) Elenk. f. *aeruginosa*	p	+	+	+	+	+	–	–	–	–	–	–
Microcystis pulverea (Wood.) Elenk. f. *pulverea*	pb	+	+	–	–	–	–	–	–	–	–	–
Nostoc Adanson sp.	un	+	+	+	+	+	–	–	–	–	–	–
Nostoc linckia (Roth) Born. et Flah. in sensu Elenk. f. *linckia*	un	+	+	+	+	+	–	–	–	–	–	–
Oscillatoria limnetica Lemm. f. *limnetica*	pb	–	–	–	–	+	–	–	–	–	–	–
Oscillatoria Vauch. sp.	un	+	+	+	+	+	–	–	–	–	–	–
Oscillatoria woronichinii Anissim.	e	–	–	+	–	–	–	–	–	–	–	–
Phormidium Kütz. sp.	un	+	–	–	+	+	–	+	+	–	+	+
Pseudanabaena bipes Böcher	b	–	–	+	+	+	–	+	–	+	+	+
Schizothrix (Kütz.) Gom. sp.	un	+	–	–	+	+	–	+	–	–	–	–

Annex 1 (continued)

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Division Cryptophyta												
Cryptomonas Ehr.sp.	un	–	–	–	+	+	–	–	–	–	–	–
Cryptomonas gracilis Skuja	p	+	+	–	–	–	–	–	–	–	–	–
Rhodomonas pusilla (Bachm.) Javor. var. *pusilla*	un	–	+	+	–	–	–	–	–	–	–	–
Division Dinophyta												
Peridinium Ehr. sp.	un	+	+	+	+	+	–	–	–	–	–	–
Division Chrysophyta												
Kephyrion mastigophorum Schmid	un	–	+	–	–	–	–	–	–	–	–	–
Mallomonas Perty sp.	un	+	+	–	–	–	–	–	–	–	–	–
Pseudokephyrion entzii Conr.	un	+	–	–	–	–	–	–	–	–	–	–
Division Bacillariophyta												
Achnanthes Bory sp. 1,	un	+	+	+	+	+	–	+	+	+	+	+
Achnanthes Bory sp. 2	un	+	+	+	+	+	–	+	–	+	+	–
Achnanthes minutissima Kütz. var. *minutissima*	b	+	+	+	+	+	+	+	+	+	+	+
Amphora ovalis (Kütz.) Kütz. var. *ovalis*	b	–	+	+	+	+	–	–	–	–	+	–
Amphora ovalis var. *constricta* Skv.	b	–	–	–	+	–	–	–	–	–	–	–
Amphora pediculus (Kütz.) Grun.	b	–	–	+	+	+	+	–	+	–	+	–
Asterionella formosa Hass.	p	–	–	–	+	–	–	–	–	–	–	–
Caloneis amphisbaena (Bory) Cl. var. *amphisbaena*	b	+	–	–	–	–	–	–	–	–	–	–
Caloneis bacillum (Grun.) Mert. var. *bacillum*	b	–	–	–	+	–	–	–	–	–	–	–
Caloneis silicula (Ehr.) Cl. var. *silicula*	b	–	–	–	–	–	–	–	–	–	+	–
Cocconeis placentula Ehr. var. *placentula*	pb	–	+	+	+	+	–	+	+	–	+	+
Cocconeis placentula var. *euglypta* (Ehr.) Grun.	pb	+	+	+	+	+	+	+	+	+	+	+
Cyclotella (Kütz.) Bréb. sp.	un	+	+	+	+	+	–	–	+	+	+	+
Cyclotella comta (Ehr.) Kütz. var. *comta*	p	+	+	+	+	+	+	+	–	–	+	+
Cyclotella meneghiniana Kütz. var. *meneghiniana*	pb	+	+	+	+	+	–	–	+	+	+	+
Cymatopleura solea (Bréb.) W. Sm. var. *solea*	pb	–	–	–	+	+	–	–	–	–	+	–
Cymbella affinis Kütz.	b	+	–	+	+	+	–	–	+	–	–	–
Cymbella cistula (Hemp.) Grun. var. *cistula*	b	–	+	+	+	–	–	–	–	–	–	–
Cymbella cymbiformis Agardh var. *cymbiformis*	b	+	+	+	+	+	–	–	–	–	–	+
Cymbella elginensis Krammer	b	+	+	+	+	+	+	–	–	–	+	–

Annex 1 (continued)

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Cymbella helvetica Kütz. var. *helvetica*	b	–	–	+	+	+	–	–	–	–	–	–
Cymbella lanceolata (Ehr.) Kirchn. var. *lanceolata*	b	+	–	–	–	–	–	–	–	–	–	–
Cymbella lata Grun. var. *lata*	b	–	+	–	+	–	–	–	–	–	–	–
Cymbella naviculiformis Auersw.	b	–	–	+	–	+	–	–	–	–	–	–
Cymbella parva (W. Sm.) Cl.	b	–	–	+	+	+	–	–	–	–	–	–
Cymbella silesiaca Breisch. in Rabenh.	b	+	+	+	+	+	–	+	–	+	+	+
Diatoma tenuis Agardh	pb	+	+	+	+	+	–	–	–	–	–	–
Epithemia adnata (Kütz.) Bréb.	b	+	+	+	+	+	+	+	+	+	+	+
Epithemia sorex Kütz. var. *sorex*	b	+	+	+	+	+	+	+	+	–	–	+
Epithemia turgida (Ehr.) Kütz. var. *turgida*	b	–	+	+	–	+	+	+	–	–	–	–
Eunotia fallax var. *groenlandica* (Grun.) Lange-Bertalot et Nörpel	b	–	–	+	–	+	–	–	–	–	–	–
Eunotia pectinalis (Dillw. O. F. Müll. Kütz.) Rabenh. var. *pectinalis*	b	–	–	–	+	–	–	–	–	–	–	–
Fragilaria constricta Ehr. f. *constricta*	b	–	–	+	–	–	–	–	–	–	–	–
Fragilaria construens (Ehr.) Grun. var. *construens*	pb	+	+	+	+	+	–	–	–	–	–	–
Fragilaria construens f. *venter* (Ehr.) Hust.	pb	–	–	+	–	–	–	–	–	–	–	–
Fragilaria leptostauron var. *martyi* (Herib.) Lange-Bertalot	b	–	–	+	–	–	–	–	–	–	–	–
Fragilaria pinnata Ehr. var. *pinnata*	b	–	+	+	–	+	–	–	–	–	+	–
Gomphocymbella ancylis Jousé	b	–	–	–	+	–	–	–	–	–	–	–
Gomphonema acuminatum Ehr. var. *acuminatum*	pb	–	+	+	+	+	–	–	–	–	–	–
Gomphonema acuminatum var. *coronatum* (Ehr.) W. Sm.	b	–	+	+	+	+	–	–	–	–	–	–
Gomphonema Agardh sp.	un	+	+	+	–	–	–	–	–	+	–	–
Gomphonema longiceps Ehr. var. *longiceps*	b	–	–	–	+	+	+	+	–	–	+	–
Gomphonema longiceps var. *montanum* (Schum.) Cl.	b	+	–	+	+	+	–	+	–	–	–	–
Gomphonema longiceps var. *montanum* f. *suecium* Grun.	b	–	–	+	+	–	–	–	–	–	–	–
Gomphonema longiceps var. *subclavatum* Grun.	b	–	–	+	–	–	–	–	–	–	+	–
Gomphonema olivaceum (Lyngb.) Kütz. var. *olivaceum*	b	+	–	+	+	+	–	+	–	–	–	+
Gomphonema parvulum (Kütz.) var. *parvulum*	b	–	–	–	+	–	–	+	–	+	+	+
Gomphonema truncatum Ehr.	b	+	+	+	+	+	–	+	–	+	–	–

Annex 1 (continued)

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Hantzschia amphioxys (Ehr.) Grun. var. *amphioxys*	b	+	–	–	–	–	–	–	–	–	–	–
Mastogloia elliptica var. *dansei* (Thw.) Grun.	b	–	+	+	–	+	–	–	–	–	–	–
Mastogloia smithii var. *lacustris* Grun.	b	–	–	–	–	–	+	–	–	–	–	–
Navicula Bory sp.	un	–	–	+	+	+	–	–	–	–	+	–
Navicula capitata Ehr. var. *capitata*	b	+	–	–	+	+	–	–	–	–	–	–
Navicula cocconeiformis Greg.	b	–	+	–	–	–	–	–	–	–	–	–
Navicula cryptocephala Kütz. var. *cryptocephala*	pb	+	+	+	+	+	–	–	+	–	–	–
Navicula peregrina (Ehr.) Kütz. var. *peregrina*	b	–	+	–	+	+	–	–	–	–	–	–
Navicula radiosa Kütz. var. *radiosa*	b	–	+	–	–	–	–	–	–	–	+	–
Navicula tripunctata (O. F. Müll.) Bory	b	–	–	+	+	+	–	–	–	–	–	–
Navicula tuscula (Ehr.) Grun. f. *tuscula*	pb	+	+	+	+	+	–	–	–	–	–	+
Neidium dubium (Ehr.) Cl. var. *dubium*	b	–	+	–	+	+	–	–	–	–	–	–
Nitzschia dissipata (Kütz.) Grun. var. *dissipata*	b	–	–	–	–	+	–	–	–	–	–	–
Nitzschia Hass. sp.	un	–	–	–	+	+	–	+	–	–	–	–
Nitzschia palea (Kütz.) W. Sm. var. *palea*	pb	–	+	–	–	–	–	–	–	–	–	–
Nitzschia sigma (Kütz.) W. Sm. var. *sigma*	b	–	–	–	+	–	–	–	–	–	–	–
Pinnularia Ehr. sp.	b	–	–	–	+	–	–	–	–	–	–	–
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	pb	–	+	+	+	+	+	–	–	–	–	–
Rhopalodia gibba (Ehr.) O. Müll. var. *gibba*	b	+	+	+	+	+	+	–	+	–	–	–
Rhopalodia gibba var. *parallela* (Grun.) H. et M. Peragello	b	–	–	+	–	–	–	–	–	–	–	–
Synedra acus Kütz. var. *acus*	p	+	+	+	+	–	–	–	–	–	–	–
Synedra amphicephala Kütz. var. *amphicephala*	b	+	+	+	+	+	+	+	–	–	+	+
Synedra Ehr. sp.	un	+	–	–	–	–	–	–	–	–	–	–
Synedra ulna (Nitzsch.) Ehr. var. *ulna*	pb	+	+	+	+	+	–	–	+	–	–	–
Tabellaria fenestrata (Lyngb.) Kütz. var. *fenestrata*	pb	+	+	–	–	–	–	–	–	–	+	–
Division Euglenophyta												
Trachelomonas volvocina Ehr. var. *volvocina*	b	–	+	+	+	–	–	+	–	–	+	–

Annex 1 (continued)

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Division Chlorophyta												
Ankistrodesmus acicularis (A. Br.) Korschik. var. *acicularis*	p	–	–	+	–	+	–	–	–	–	–	–
Ankistrodesmus minutissimus Korschik.	p	–	–	+	+	+	–	+	–	–	–	–
Ankistrodesmus pseudomirabilis Korschik. var. *pseudomirabilis*	p	–	+	+	+	–	–	–	–	–	–	–
Ankistrodesmus pseudomirabilis var. *spiralis* Korschik.	p	–	–	+	–	–	–	–	–	–	–	–
Bicuspidellopsis triangularis Korschik.	e	–	–	–	+	–	–	–	–	–	–	–
Bulbochaete Agardh sp.	e	+	+	+	+	+	–	+	+	–	–	–
Characium A. Braun et Kütz. sp.	e	–	–	–	+	+	–	–	–	–	–	–
Characium obtusum A. Br.	e	–	–	–	–	–	–	+	–	–	–	–
Characium ornithocephalum A. Br.	e	–	–	–	–	–	–	+	–	–	–	–
Chlamydomonas Ehr. sp.	un	–	+	–	+	–	–	–	–	–	–	–
Cladophora Kütz. sp.	un	–	–	–	+	+	–	+	–	–	–	–
Coelastrum sphaericum Näg.	pb	–	–	–	+	–	–	–	–	–	–	–
Coenocystis Korschik. sp.	un	–	–	–	+	–	–	–	–	–	–	–
Coleochaete Bréb. sp.	e	+	+	+	+	+	+	+	–	–	+	–
Coleochaete scutata Bréb. f. *scutata*	b	–	–	+	–	–	–	–	–	–	–	–
Cosmarium Corda sp.	un	–	+	–	–	–	–	–	–	–	–	–
Cosmarium granatum Bréb. var. granatum	b	–	+	+	+	+	–	–	–	–	–	–
Cosmarium humile (Gay) Nordst. var. *humile*	b	+	+	+	+	+	–	–	–	–	–	–
Cosmarium impressulum Elfv. var *impressulum*	pb	–	+	–	–	+	–	–	–	–	–	–
Cosmarium meneghinii Bréb. var. *meneghinii*	un	–	+	+	–	+	–	+	–	–	–	–
Cosmarium pygmaeum Arch. var. *pygmaeum*	pb	–	–	–	+	–	–	–	–	–	–	–
Cosmarium trilobulatum Reinsch var. *trilobulatum*	un	–	–	+	–	–	–	–	–	–	–	–
Cosmarium umbilicatum Lütkem	b	–	–	+	+	+	–	–	–	–	–	–
Cosmarium venustum (Bréb.) Arch. var. *venustum*	pb	–	–	+	–	+	–	–	–	–	–	–
Crucigenia apiculata (Lemm.) Schmidle	p	–	–	–	+	–	–	–	–	–	–	–
Dictyosphaerium pulchellum Wood var. *pulchellum*	pb	+	+	+	+	–	+	+	–	–	–	–
Didymocystis planctonica Korschik.	un	–	–	+	+	+	–	–	–	–	–	+
Elakatothrix Wille sp.	un	–	–	–	+	–	–	–	–	–	–	–
Geminella Turp. sp.	pb	+	+	+	+	+	+	+	–	–	+	–
Gonatozygon De Bary sp.	e	–	+	–	–	–	–	–	–	–	–	–

Annex 1 (continued)

Taxa	Typical habitat	Depth (m)										
		0.8					4.0			6.0		
		Size class of zebra mussels (based on shell length)**										
		I	II	III	IV	V	I	II	III	I	II	III
Hyaloraphidium rectum Korschik.	un	–	–	+	–	–	–	–	–	–	–	–
Hydrianum viride (Scherff.) Ettl.	e	–	–	–	–	–	–	+	–	+	+	+
Leptosira Borzi sp.	e	–	–	–	–	–	+	+	+	–	–	–
Mougeotia Agardh sp.	pb	+	+	–	–	–	–	–	–	–	–	–
Oedogonium Link. sp.	e	+	+	+	+	–	–	–	–	–	–	–
Oocystis crassa Wittr. var. *crassa*	p	+	–	+	–	–	–	–	–	–	–	–
Oocystis marssonii Lemm.	p	–	–	–	+	–	–	–	–	–	–	–
Oocystis parva W. et W.	p	–	–	–	+	–	–	–	–	–	–	–
Oocystis solitaria Wittr. var. *solitaria*	p	–	–	+	+	+	–	–	+	–	–	–
Pediasrum tetras (Ehr.) Ralfs var. *tetras*	pb	–	+	+	+	+	–	–	–	–	–	–
Pediastrum boryanum (Turp.) Menegh. var. *boryanum*	pb	+	+	+	+	+	–	+	–	–	–	–
Pediastrum boryanum var. *longicorne* Reinsch.	pb	–	+	+	–	+	+	–	–	–	–	–
Scenedesmus acuminatus (Lagerh.) Chod. var. *acuminatus*	pb	–	+	–	+	+	–	–	–	–	–	–
Scenedesmus acutiformis Schröd. var. *acutiformis*	pb	–	+	–	–	–	–	–	–	–	–	–
Scenedesmus apiculatus (G. et G. S. West) Chod. var. *apiculatus*	p	–	–	+	–	–	–	–	–	–	–	–
Scenedesmus bijugatus (Turp.) Kütz. var. *bijugatus*	p	+	+	+	+	+	–	–	–	–	–	–
Scenedesmus denticulatus Lagerh. var. *denticulatus*	pb	–	+	+	+	–	–	–	–	–	–	–
Scenedesmus obliquus (Turp.) Kütz. var. *obliquus*	pb	–	+	+	+	+	–	–	–	–	–	–
Scenedesmus quadricauda (Turp.) Bréb. var. *quadricauda*	p	–	+	–	+	+	–	–	–	–	–	–
Scenedesmus quadricauda var. *longispina* (Chod.) G. M. Smith	un	–	+	–	–	–	–	–	–	–	–	–
Scenedesmus spinosus (R.Chod.) Hegew.	pb	–	–	+	+	+	–	–	–	–	–	–
Spirogyra Link. sp.	pb	+	+	+	–	–	–	–	–	–	–	–
Staurastrum Meyen sp.	un	–	+	–	–	+	–	–	–	–	–	–
Stigeoclonium farctum Berth. var. *farctum*	e	–	+	–	–	–	–	–	–	–	–	–
Stigeoclonium Kütz. sp.	e	–	–	–	–	–	–	–	–	+	–	+
Tetraëdron caudatum (Corda) Hansg. var. *caudatum*	pb	–	–	+	–	–	–	–	–	–	–	–
Tetraëdron minimum (A. Br.) Hansg. var. *minimum*	pb	–	+	+	+	+	–	–	–	–	–	–
Tetraëdron triangulare Korschik.	pb	–	–	–	+	–	–	–	–	–	–	–
Geminella Turp. sp.	pb	+	+	+	+	+	+	+	–	–	+	–

* Typical habitats are classified in accordance with Barinova et al. 2006: ‘p’ – plankton; ‘b’ – benthos in a wide sense; ‘pb’ – plankton-benthos; ‘e’ – epiphytic; ‘s’ – soil; ‘un’ – typical habitat is unknown.
** I – 5.0-9.9 mm; II – 10.0-14.9 mm; III – 15.0-19.9 mm; IV – 20.0-24.9 mm;V – 25.0-35.0 mm.