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Structure of epiphyton communities on Lake Baikal submerged macrophytes

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Abstract: We carried out a first study of Lake Baikal epiphyton on six species of submerged macrophytes: *Myriophyllum spicatum* L., *Potamogeton perfoliatus* L., *Potamogeton* sp., *Sparganium gramineum* Georgi, *Ceratophyllum demersum* L., and *Elodea canadensis* Michaux. We identified 70 epiphyton species and intraspecific taxa belonging to 3 phyla, viz. Ochrophyta, Cyanobacteria, and Chlorophyta. Nine species of Cyanobacteria were new records for Lake Baikal. Epiphyton communities differing in species composition and quantitative characteristics grew on diverse species of submerged macrophytes. High levels of species richness were recorded on *Sparganium gramineum* and *Potamogeton* sp., whereas low diversity of epiphyton was observed on *Myriophyllum spicatum* and *Elodea canadensis.* A monodominant community was revealed on the invasive *Elodea canadensis* represented by *Cocconeis placentula* var. *placentula*. Specific characteristics of morphology of submerged macrophytes influenced the structural organization and quantitative development of epiphyton. Epiphyton abundance and biomass were higher on upper sections of most plants than on lower sections, probably because of canopy shading of macrophyte lower portions.

Key words: submerged macrophytes, epiphyton, Lake Baikal

Introduction

Submerged macrophytes are spread throughout continental freshwater bodies and seas. They are very important components of diverse ecosystems as many ecological processes are closely interrelated with their development (Winter and Duthie 2000; Madsen et al. 2001; Leu et al. 2002; Kiss et al. 2003; Potapova and Charles 2005; Albay and Akçaalan 2008). Submerged macrophytes serving as a substratum contribute to the formation of epiphyton and play a great role in production processes of the littoral zone and in self-purification of water bodies (Votyakova 2007; Chernysheva 2007; Tarashchuk 2008). Epiphyton composition of submerged macrophytes is diverse in different water bodies (Gons 1982; Caput and Plenkovia-Moraj 2000; Comte and Cazaubon 2002). Of special interest is epiphyton of submerged macrophytes of Lake Baikal, one of the oldest and deepest lakes in the world, which houses over 86 species (Azovsky and Chepinoga 2007). With such a large diversity of submerged macrophytes, a study of their epiphyton would be of considerable ecosystem relevance, and yet the structure and function of Lake Baikal's potentially important autotrophic link are largely unknown.

The aim of our work was to characterize species diversity and specific characteristics of vertical microdistribution of abundance and biomass of algal epiphyton on Lake Baikal submerged macrophytes.

Material and methods

Study sites and sampling. The material was collected in Lake Baikal in August 2008-2009: Kurkutskaya Bay (N 53°01'427, E 106°52'407), Posolsk Sor (N 51°55'149, E 106°09'419), Bolshiye Koty Bay (N 51°54'047, E 105°04'083) at 3 m during the vegetative activity of submerged macrophytes. The water temperature was 16°C in Bolshiye Koty Bay and 17-20 °C at other sampling sites. The water was transparent to the bottom (Secchi disk) in Kurkutskaya Bay, Bolshiye Koty Bay and to 2 m in Posolsk Sor. Water transparency was measured from the boat.

Divers lowered a bell-like gauze net (No. 35) to the lake bottom covered by stands of submerged macrophytes. Macrophytes were cut at their base with a knife, the bell net was tightened with a rope and then delivered to the shore. Macrophytes were placed into a large cuvette, sorted by species and fixed with 4% formalin in 500 ml glass containers. Forty-five samples were collected for quantitative analysis of phytoepiphyton species composition from different bays of Lake Baikal.

Qualitative samples collected in Kurkutskaya Bay were used for analysis of vertical distribution of phytoepiphyton on submerged macrophytes. We measured the height in cm of specimens, cut them into three sections (1 – upper, 2 – middle and 3 – lower), then fixed them separately in 15 ml bottles containing 4% formalin. Six specimens of the invasive *Elodea canadensis* were also collected. Since the height of this plant did not exceed 8 cm, it was not cut into sections. We collected 51 samples for quantitative analysis of phytoepiphyton. We analysed 96 quantitative and qualitative samples of plants.

Laboratory methods. Phytoepiphyton in qualitative samples was brushed off into a large cuvette, then concentrated and treated according to Kozhova and Melnik (1978).

For quantitative analysis of phytoepiphyton we fixed parts of the macrophytes together with the solution and placed them into Petri dishes. Epiphyton was thoroughly brushed off and rinsed with the fixative. The volume of suspension was measured and poured into bottles. The bottle content was shaken. Then 0.1 ml of suspension (3 replications) was placed into a chamber. Microalgae were counted under a light microscope Axiovert-200. The final abundance of each species was considered to be the average from three replications. In order to identify the diatom frustules, the diatom valves were cleaned using hydrogen peroxide to eliminate organic matter (Krammer and Lange-Bertalot 1986). A scanning electron microscope Philips SEM 525M was used for more precise identification of diatom species. Biovolume of each algal species was determined from the average size of cells measured on microscope images (Programme Video-TestT-Size 5.0, Russia). Abundance and biomass of epiphyton were standardized on the basis of the dry weight (DW) of macrophytes. Air-wet and dry weights were measured for cleaned macrophyte sections. To determine dry weight, macrophytes were pre-dried in an oven at 105°C for 3 days, and weighed on electronic scales (AND, Japan) to the nearest 0.1 mg at 20-22°C air temperature.

Data analysis. Frequency of species occurrence (P, %) was determined from the ratio between the number of samples in which a species was present and the total number of the samples analysed.

A cluster analysis of floristic similarity in epiphyton samples collected from macrophytes was constructed by the paired group average value using the Jaccard similarity coefficient as a measure (Jaccard 1901).

Communities of epiphyton microalgae (<200 µm) were isolated according to prevalence in species abundance (cell g^{-1} DW). Species diversity of epiphyton was calculated using the Shannon diversity index in bits per individual:

$$H = -\Sigma n_i/N\log2(n_i/N),$$

where: n_i is the abundance of species (cell g^{-1} DW macrophyte), N is the total number of all individuals (cell g^{-1} DW macrophyte), and H is species diversity (Odum 1971).

Species were identified according to Azovsky and Chepinoga (2007) for submerged macrophytes; Izhboldina (2007) for Chlorophyta; Skvortzow (1937), Krammer and Lange-Bertalot (1986, 1988), Foged et al. (1993), Hartley (1996), Lange-Bertalot (2001), Lange-Bertalot and Metzeltin (2008) for Ochrophyta; Komárek and Anagnostidis (1999, 2005) for Cyanobacteria. All taxa were named according to AlgaeBase (www.algaebase.org).

Results and discussion

Epiphyton of submerged macrophytes was very diverse. There were 3 phyla present: Ochrophyta, Cyanobacteria and Chlorophyta, including 38 genera, and 67 species and intraspecific taxa (Table 1).

Diatoms made up the majority of epiphyton biomass (99.3% of total), whereas Cyanobacteria dominated in numerical abundance. The highest values of biomass were recorded for the following diatom genera: *Cocconeis*, *Rhopalodia*, *Epithemia*, *Gomphonema*, and *Navicula*. Although Cyanobacteria made up only 0.6% of total epiphyton biomass, their percentage contribution to total numerical abundance (68.5%) of microalgae was much higher than that of diatoms (31.1%). Cyanobacteria *Leibleinia* sp., *Anabaena inaequalis*, *Clastidium setigerum,* and *Heteroleibleinia rigidula* formed the largest species proportions of epiphyton numerical abundance. Among Cyanobacteria, 9 species were recorded for the first time in Lake Baikal, and three of these species were dominant (Table 1, Fig. 1).

Large numerous (> 2000 µm) colonies of *Gloeotrichia pisum* were often observed (40 %) on the genus

Table 1. Taxonomic spectrum and frequency (P,%) of epiphyton species

Taxa	P	Taxa	P
Cyanobacteria		*Achnanthidium affine* (Grun.) Czarn.	3
Aphanocapsa parasitica (Kütz.) Kom. et An. *	3	*Achnanthidium minutissimum* (Kütz.) Czarn.	7
Chroococcus minutus (Kütz.) Näg.*	17	*Planothidium delicatulum* (Kütz.) Round et Bukht.	3
Clastidium setigerum Kirchn.*	10	*P. rostratum* (Østr.) Lang.-Bert.	10
Pseudanabaena catenata Lauterb.*	3	*Craticula cuspidata* (Kütz.) D.G. Mann	20
Leibleinia sp. *	50	*Cymbella lanceolata* (C. Ag.) C. Ag.	7
Leptolyngbya pseudovalderiana (Woronich.) An. et Kom.*	3	*Navicula cryptocephala* Kütz.	40
Leptolyngbya sp.*	4	*N. radiosa* Kütz.	57
Heteroleibleinia rigidula (Hansg. et Hansg.) Hoff.*	17	*N. tripunctata* (O. Müll.) Bory	37
Phormidium sp.	3	*Neidium iridis* (Ehr.) Cl.	3
Stratonostoc sp.	2	*Gyrosigma acuminatum* (Kütz.) Rabenh.	13
Anabaena inaequalis (Kütz.) Born. et Flah.*	70	*G. baicalensis* Skv.	10
Calothrix sp.	3	*Nitzschia amphibia* Grun.	10
Gloeotrichia pisum (C. Agar.) Thur.ex Born. et Flhaul.	40	*N. dissipata* (Kütz.) Grun.	13
Ochrophyta		*N. intermedia* Hant. ex Cl. et Grun.	7
Fragilaria crotonensis Kitt.	3	*N. recta* Hant. ex Rabenh.	17
F. capucina var. *acuta* (Ehr.) Rabenh.	13	*Rhopalodia gibba* (Ehr.) O. Müll.	67
Ulnaria acus (Kütz.) M.Aboal	3	*Epithemia sorex* Kütz.	35
U. ulna var. *acus* (Kütz.) Lang.-Bert.	3	*E. sorex* var. *gracilis* Hust.	35
Meridion circulare (Grevil.) C.Agardh.	3	*E. turgida* var. *turgida* (Ehr.) Kütz.	63
Diatoma vulgaris var. *vulgaris* Bory de Sain.-Vin.	3	*E. adnata* (Kütz.) Bréb.	23
Rhoicosphenia curvata (Kütz.) Grun.	27	*E. zebra* var. *saxonica* (Kütz.) Grun.	43
Cymbella aspera (Ehr.) Cl.	10	*E. intermedia* Fricke.	13
C. tumida var. *tumida* (Brėb. et Kütz.) Grun.	60	*Eunotia clevei* var. *hispida* Skv.	20
C. turgidula Grun.	23	*E. pectinalis* (Kütz.) Rabenh.	10
Encyonema ventricosum (C.Agardh.) Grun.	50	*E. polydentula* Brun.	17
Gomphonema acuminatum Ehr.	3	*E. diodon* Ehr.	10
G. intricatum Kütz.	3	*Cymatopleura elliptica* (Brėb.) W. Sm.	2
G. olivaceum (Horn.) Kütz.	17	*C. solea* (Brėb.) W. Sm.	2
G. quadripunctatum (Østr.) Wisl.	37	**Chlorophyta**	
G. ventricosum Greg.	50	*Pseudopediastrum boryanum* (Turp.) E. Hegew.	10
G. tergestinum (Grun.) Fricke	5	*Monoraphidium contortum* (Thur.) Kom.-Legn.	7
Cocconeis placentula var. *placentula* Ehr.	100	*Actinastrum hantzschii* var. *gracile* V.K. Tshern.	3
C. placentula var. *lineata* (Ehr.) van Heur.	100	*Scenedesmus quadricauda* (Turp.) Bréb.	33
C. pediculus Ehr.	47	*Spirogyra* sp.	7

* – new species for Lake Baikal

Potamogeton (Table 1). The quantity of Chlorophyta in epiphyton was low, comprising 0.4% of total epiphyton numerical abundance and 0.1% of total biomass.

Cluster analysis showed that the species composition of epiphyton on different macrophytes varied (Fig. 2). *Potamogeton* sp., *P. perfoliatus, Sparganium gramineum,* and *Ceratophyllum demersum* had similar composition of epiphyton, whereas the species composition on *Myriophyllum spicatum* and *Elodea canadensis* was diverse.

General characteristics of the quantitative distribution of epiphyton on macrophytes and on their separate sections are given in Table 2 and Fig. 3.

The structure of epiphyton communities on *Elodea canadensis* differed from that in the communities on the lower section of indigenous submerged macrophytes (Fig. 4).

In Lake Baikal, the most diverse species composition of submerged macrophytes is recorded in Maloye More (Small Sea), Chivyrkuy Bay, Posolsk and Verkhneangarsk Sors (Azovsky and Chepinoga 2007). Kurkutskaya Bay, where we carried out sampling, adjoins the shore of the Strait of Olkhon Gate connecting Maloye More with the open waters of Lake Baikal. The water temperature in the bay is 17°C, O_2 concentration – 9.2-10.3 mg l^{-1}, NO_3^- – 0.00-0.19 mg l^{-1}, PO_4^{3-} – 0.003 mg l^{-1}, SiO_2 – 2.4-8.4 mg l^{-1}, and CO_2 – 2.2-1.0 mg l^{-1}. This bay is characterized by the same temperature regime, hydrological and chemical characteristics of water, shallow depths (not deeper than

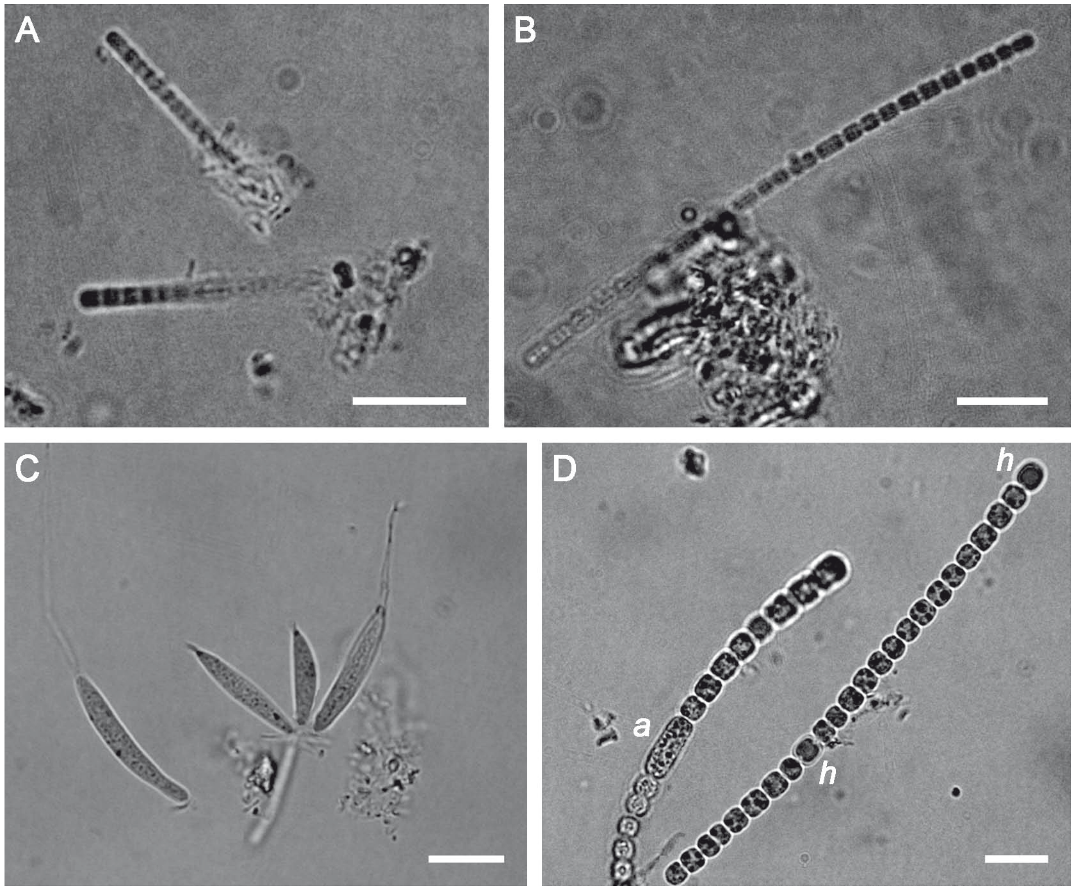

Fig. 1. Epiphytic cyanobacteria species recorded for the first time in Lake Baikal. (A) *Heteroleibleinia rigidula*. (B) *Pseudanabaena catenata*. (C) *Clastidium setigerum*. (D) *Anabaena inaequalis (a* – akinete, *h* – heterocyst*)*. Bar (A-D) = 10 μm

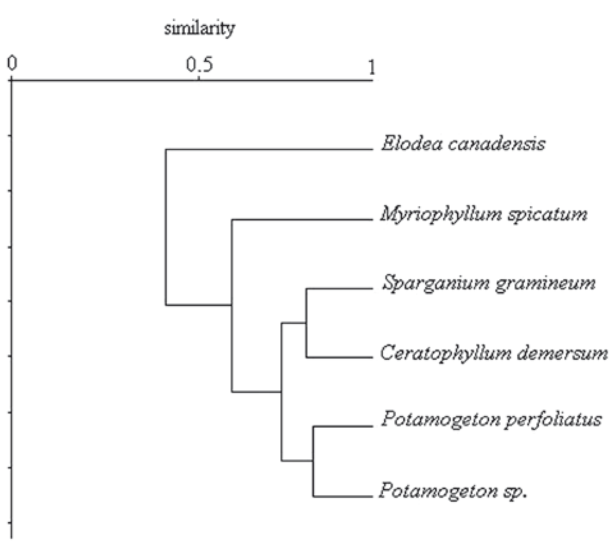

Fig. 2. A dendrogram of floristic similarity in epiphyton samples collected from macrophytes (Jaccard coefficient)

5 m) and the prevalence of silt and sand in bottom sediments of different levels of silting like the littoralsor zone of Lake Baikal (Kozhov 1962). This area of studies is referred to as a mesotrophic type due to the value of gross primary production (90 g C_{org} m^{-2}) and intensity of phytoplankton photosynthesis (Kulagin and Pomazkina 1977). Favourable temperatures and high concentrations of organic matter (5.27%) play an important role in structuring of vegetation communities (Kozhov 1962; Vykhristyuk 1978). During our survey in Kurkutskaya Bay, 11 species of submerged macrophytes were recorded in phytocoenosis, with a dominant *Myriophyllum spicatum*, and with subdominant species: *Potamogeton* sp., *Sparganium gramineum*, *Ceratophyllum demersum*, *Elodea canadensis, Potamogeton perfoliatus*, and others. Thus, the epiphyton in Kurkutskaya Bay inhabits diverse submerged macrophytes and develops under environmental conditions that differ from those of Lake Baikal's open waters.

Table 2. General characteristic of submerged macrophyte epiphyton in Lake Baikal

Macrophytes	h [cm]	S	H, bit	N×10⁶ (cell g⁻¹ DW) / B (mg g⁻¹ DW)	σ_N / σ_B	D
M. spicatum	35-40	19	1.2	29.9 / 6.0	30.5 / 1.8	*Heteroleibleinia rigidula, Clastidium setigerum*, *Leibleinia sp., Cocconeis placentula* var. *placentula*, *C. placentula* var. *lineata*
P. perfoliatus	42-50	34	1.4	11.5 / 6.2	9.1 / 5.7	*Anabaena inaequalis*, *Leibleinia* sp., *Cocconeis placentula* var. *lineata*, *C. placentula* var. *placentula*, *Epithemia zebra* var. *saxonica*, *E. turgida* var. *turgida*
Potamogeton sp.	19-28	41	1.3	25.8 / 20.0	17.7 / 7.9	*Anabaena inaequalis*, *Cocconeis placentula* var. *lineata, C. placentula* var. *placentula, Epithemia turgida* var. *turgida, E. sorex*, *E. zebra* var. *saxonica*, *Rhopalodia gibba*
S. gramineum	36-56	37	1.5	19.4 / 23.9	19.1 / 29.7	*Anabaena inaequalis*, *Leibleinia* sp., *Cocconeis placentula* var. *placentula*, *C. placentula* var. *lineata, Rhopalodia gibba*, *Epithemia sorex*
C. demersum	8-12	31	1.3	2.8 / 3.7	3.3 / 3.3	*Leibleinia* sp., *Cocconeis placentula* var. *placentula*, *C. placentula* var. *lineata*, *Chroococcus minutus*
E. canadensis	3-8	19	0.1	27.9 / 84.6	16.9 / 51.0	*Cocconeis placentula* var. *placentula*

h – species height; S – number of epiphyton species; H – Index of species diversity according to the Shannon index; N×10⁶ – average and σ_N – standard deviation of epiphyton abundance; B – average and σ_B – standard deviation of epiphyton biomass; D – abundant species of microalgae

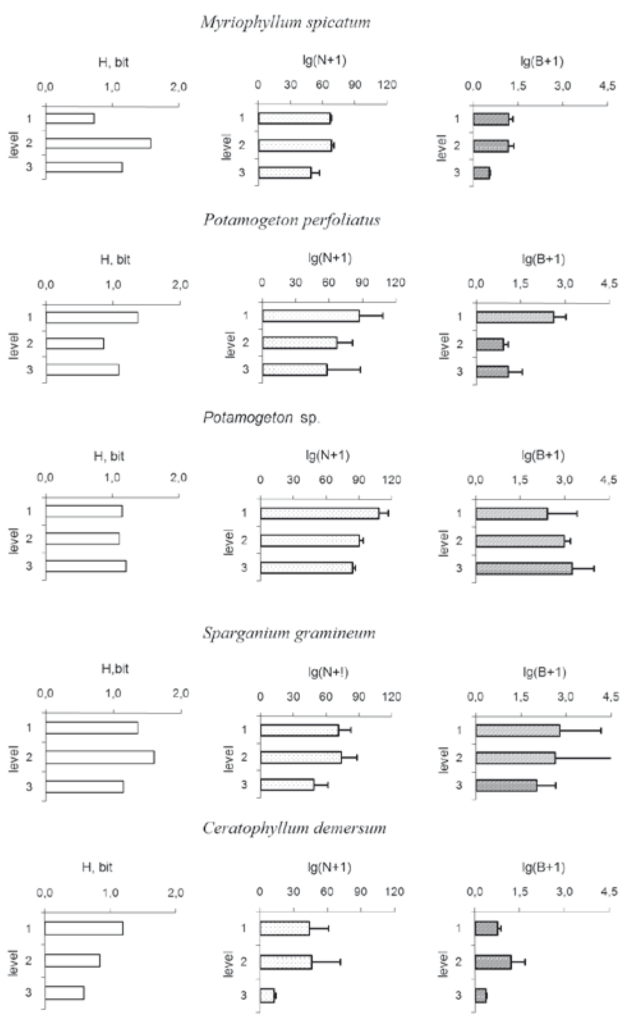

Fig. 3. Diversity, biomasses, and abundances of microalgae in macrophyte sections. Ordinate axis – sections: 1 – upper, 2 – middle, 3 – lower. Abscissa axis: (A) H, bit – Shannon diversity index; (B) lg (B + 1) – biomass logarithm (mg g⁻¹ DW) of phytoepiphyton; (C) lg (N + 1) – abundance logarithm (N × 10⁶ cell g⁻¹ DW) of phytoepiphyton

Among epiphyton of macrophytes, the most common (100% frequency) and the most numerically abundant in Kurkutskaya Bay are *Cocconeis* specimens, especially *C. placentula* var. *placentula* and *C. placentula* var. *lineata*. These diatoms attach their valves to the substratum; when the host macrophyte was *Elodea canadensis*, taxa of *Cocconeis* had very high biomasses and numerical abundances, forming solid mat monoculture on leaves of Canadian pondweed (Fig. 4, Fig. 5).

Specimens of *Cocconeis* are typical of epiphyton in other water bodies (Eminson and Moss 1980; Birkett and Gardiner 2005; Lebreton et al. 2009; Potapova and Charles 2005; etc.). Epipsammon, epipelon, and epilithon of Lake Baikal's open waters have been extensively studied (Meyer 1930; Kozhov 1962; Pomazkina and Rodionova 2004; Kravtsova et al. 2006; Izhboldina 2007). *Cocconeis* specimens are widely spread in the littoral zone of Lake Baikal. However, we for the first time recorded such high density of representatives of

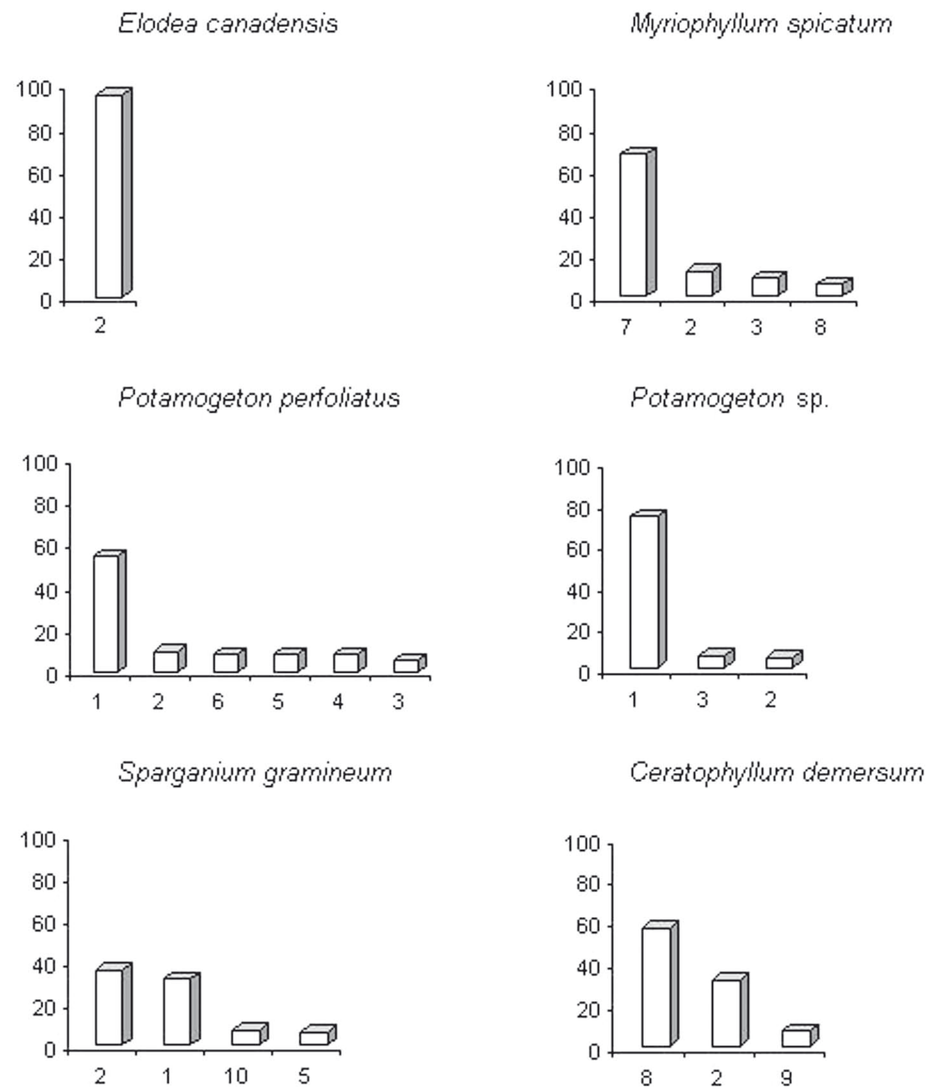

Fig. 4. Structure of phytoepiphyton communities in the lower section of aquatic plants. Ordinate axis – percentage (%) of dominant species in total abundance of phytoepiphyton; abscissa axis – numbers of species of the dominant complex: 1 – *Anabaena inaequalis*, 2 – *Cocconeis placentula* var. *placentula*, 3 – *C. placentula* var. *lineata*, 4 – *Epithemia sorex*, 5 – *E. turgida* var. *turgida*, 6 – *E. zebra* var. *saxonica*, 7 – *Heteroleibleinia rigidula*, 8 – *Leibleinia* sp., 9 – *Navicula radiosa*, 10 – *Rhopalodia gibba*

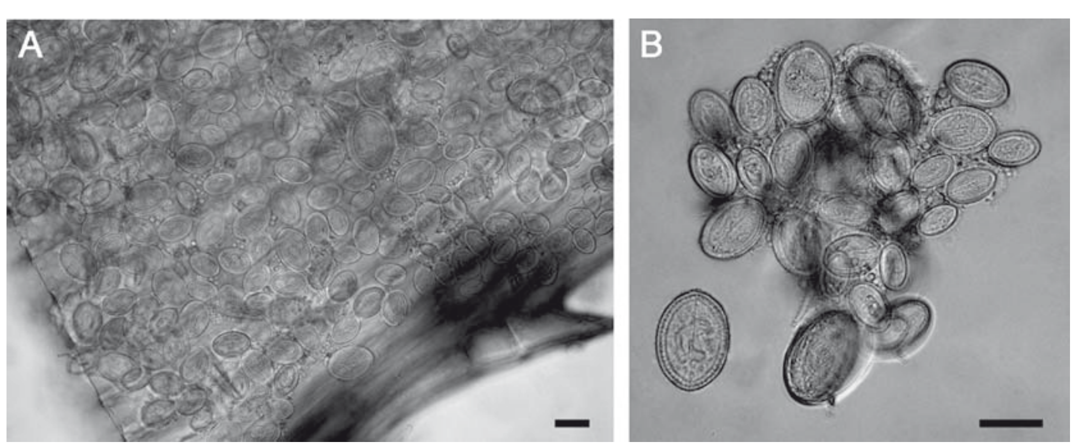

Fig. 5. Monoculture of the *Cocconeis* specimens on leaves of *Elodea canadensis*. (A) leaf surface of *E. canadensis* covered with *Cocconeis* spp.; (B) cells of *Cocconeis* spp. brushed from the leaf. Bar (A-B) = 20 µm

this genus on host macrophyte *Elodea canadensis* (Fig. 5). In addition to light and temperature conditions, wind waves may favourably affect the growth of *Cocconeis*. Sabater et al. (1998) showed that shaded conditions were relevant for the occurrence of *Cocconeis*. Specimens of genera *Cocconeis* and *Navicula* are more dependent on water currents than attached colony-forming species (Tanaka 1984; Ryabushko et al. 2003). Active wave mixing caused by northwesterly winds sometimes reaching hurricane strength of up to 40 m s^{-1} (Kozhov 1962) creates conditions for rapid growth of diatoms, in particular the genus *Cocconeis*.

In addition to *Cocconeis*, the dominant epiphyton complex consists of abundant and diverse species of *Epithemia* and *Rhopalodia*, which are characteristic of epiphyton in many water bodies (Barinova and Medvedeva 1996). However, *Epithemia* and *Rhopalodia* have not been found in the phytoepiphyton of the Selenga River which flows to the lake (Baldanova 1998).

The vertical microdistribution of epiphyton on macrophytes was quantitatively uneven. The highest numbers were more frequently observed on the upper sections of plants than on lower ones (Fig. 3). This is probably due to light attenuation by the thick surface canopy of macrophytes. Quantities of algal abundance decrease at low light levels (Gons 1982; Ryabushko et al. 2003).

Variability in epiphytic diatom communities may be attributed rather to the sampling site than to environmental habitat conditions (Eminson and Moss 1980; Winter and Duthie 2000). Diatom associations differ among macrophyte species, indicating substratum preferences (Table 2, Fig. 2). In Kurkutskaya Bay, epiphyton species diversity (according to the Shannon index) on *Sparganium gramineum* and *Potamogeton perfoliatus*, which have large "contact" surfaces due to their sizes and forms of leaves, are higher than on other species studied. Both epiphyton diversity and abundance are closely related to particular morphological characteristics of submerged macrophytes. It is clear that the form and size of *Ceratophyllum demersum* leaves are unfavourable for epiphyton colonization; we recorded the lowest quantitative abundance on this species. The development of epiphyton is likely to be affected not only by morphological specific characteristics of plants but also by allelopathic interactions. It is known that allelopathic interactions also influence the composition and abundance of epiphyton (Leu et al. 2002; Gross 2003). Mass growth of the genus *Cocconeis* on leaf surfaces of *Elodea canadensis* is probably attributable to the diatoms' resistance to elevated peroxidase activity in this pondweed (Kozhova et al. 1985).

Lake Baikal epiphyton are largely similar to those of other European water bodies. Average values of epiphyton numerical abundance and biomass on all submerged macrophytes studied vary within the range between 3×10^6 cell g^{-1} DW macrophyte and 30×10^6 cell g^{-1} DW macrophyte, and within the range of 4 mg g^{-1} DW macrophyte to 85 mg g^{-1} DW macrophyte, respectively. These values are comparable to those from other water bodies (Oksiyuk et al. 1999; Tarashchuk 2008).

Conclusion

In conclusion, the differences in the species composition, numerical abundances and biomasses of epiphyton are determined by ecological and morphological (shape) characteristics of host macrophytes as substrata. The phytoepiphyton community on Canadian pondweed differs in structural characteristics from that on the indigenous macrophytes of Lake Baikal. It is characterized by low species diversity and high concentrations of one dominant species. Intensive development of *E. canadensis* in the lake may cause the development of an epiphyton community with low species diversity and high biomass, thus increasing total productivity of autotrophs in the littoral-sor zone of Lake Baikal.

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