Biologia 63/6: 859—865, 2008
Section Botany
DOI: 10.2478/s11756-008-0113-0

Green algae as a structural element of phytoperiphyton[1] communities in streams of NW Russia*

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Abstract: Observations were made on the development and distribution of phytoperiphyton communities in 66 lake-river systems in NW Russia from Lake Ladoga to the Barents Sea. In total, 130 genera and 648 species were identified from different substrates, belonging to *Cyanophyta* (19.1%), *Bacillariophyta* (59.6%), *Chlorophyta* (18.7%), and algae from other orders (2.6%). In all streams diatoms dominated by species richness, but they were surpassed by green algae in terms of biomass. The green algae ranged from small planktonic forms to large filamentous species and produced easily visible algal communities. Among the planktonic forms the desmids were the most diverse group. They occurred in attached communities of all rivers and, while never abundant, were widespread. The attached community's biomass was dominated by green algae. Among these, the filamentous algae *Mougeotia* sp., *Oedogonium* sp., *Zygnema* sp., *Spirogyra* sp. and *Ulothrix zonata* exhibited mass development in streams. Their distribution was patchy in the basin, with a total cover varying from less than 1% to 90% of the stream bottom. In some river stretches the diversity and predominance of green algae could be due, in part, to poorly developed riparian canopies.

Key words: green algae; phytoperiphyton; rivers

Introduction

Success, achieved in many aspects of modern hydrobiology, does not mean that algological studies are not needed any more. On the contrary, they become more sophisticated and often provide a basis for correct interpretation of available evidence. Such is the study of regional floras that requires the knowledge of local physico-geographic characteristics. However, although the scope of floristic studies in Russia is steadily expanding, the structure and dynamics of algal flora in many areas are still poorly understood. Due to this lack of knowledge only an approximate assessment of the species diversity of many taxa is possible at present. Floristic studies are particularly significant for North European Russia because algae start to play a far more important role in ecosystems than higher plants as the natural environment becomes more extreme (Whitton 1984).

In fast flowing, oligotrophic lotic habitats, attached algal communities (phytoperiphyton) are often the only primary producers and play an important role in the energy transformation of the ecosystem (Biggs 1996). Phytoperiphyton, which has a highly distinctive species composition and time and space dynamics, has been studied far less thoroughly than phytoplankton. In small rivers of North European Russia, the algal coenoses of encrusting organisms had not been studied regularly at all until our research was launched.

In the present paper, the structural pattern of phytoperiphyton and its functioning in the rivers of North European Russia is analyzed. Special attention is given to the distribution of green algae that are widespread in the periphyton. The studies were carried out under the Russian Academy of Sciences Biodiversity Programme, which focuses on the study of the present status of lake-river systems in Northwest Russia.

Material and methods

The present paper reports the results of periphyton studies carried out during 1997–2006 in 66 rivers located in various parts of NW Russia between Lake Ladoga and the Barents Sea (Fig. 1). All rivers have many lakes along their course and the stream sections act as connections between a mosaic of lakes, peatbogs and wetlands, and as a result, complex lake-river systems are formed. The percentage of lakes in the drainage basin area ranges from 5 to 30%. Bogs account for 70–90 %, and drainage areas cover 200 to 10267 km^2.

[1] The term periphyton adopted here follows the definition of Odum (1971): "Assemblages which include both plant and animal organisms growing attached to submerged objects". The prefix phyto- is added to indicate that of the whole biocoenoses only phototrophs are considered in this study.

* Presented at the International Symposium *Biology and Taxonomy of Green Algae V*, Smolenice, June 26–29, 2007, Slovakia.

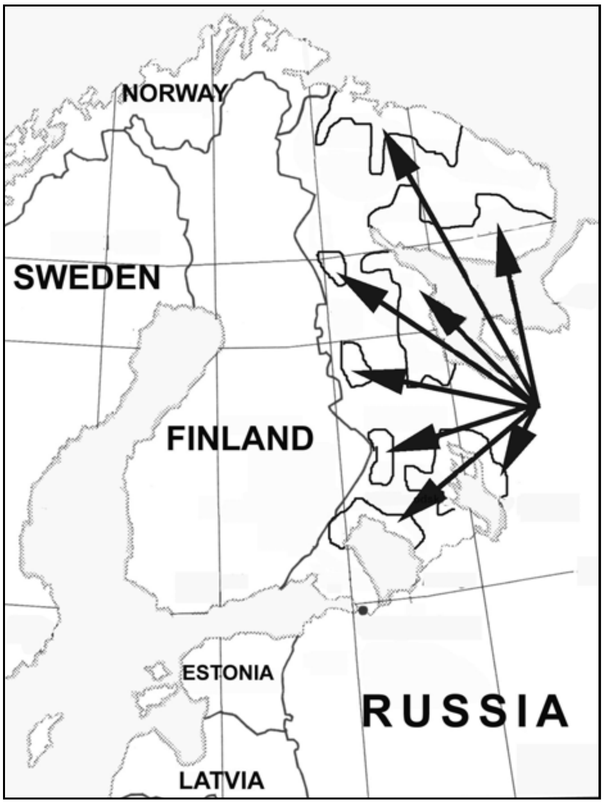

Fig. 1. The study area with arrows indicating the catchments of the investigated rivers.

The rivers consist predominantly of numerous rapids and have a high gradient ranging from 0.31 to 6.03mineralization values less than 50 mg L^{-1}, low levels of most nutrients, and often dark-brown water (50–400 mg L^{-1} Pt). The pH is near neutral, and ranges from 6.30 to 7.80 and can reach up to 5.0 in upstream river stretches.

Depending on the size of the river between five and ten sampling sites were chosen. Throughout the investigation standard sampling techniques were employed. Approximately ten samples were collected at each site. Wherever possible this was done by scraping the surface of rocks, stones and pebbles. In other cases it was performed by squeezing mosses (*Fontinalis* spp.), macroscopic algae (*Chara* spp.) or by scraping the surface of stems and leaves of vascular plants [*Equisetum fluviatile* E., *Phragmites australis* (Cav.) Trin. ex Steud., and *Myriophyllum* spp.]. The amount of periphyton material sampled from each substrate was proportional to the surface area covered by the substrate types on the sampling location. To assess anthropogenic impact, to minimize the effects of shading by riparian vegetation and to eliminate the influence of the substrate and variations in depth and hydrological regime, all location samples were collected in an open-canopy area from a rock sized 20–30 cm. The methods used are generally comparable to the CEN standard (CEN 2005) and followed the methodology previously described by Wetzel (1979) and Jarlman et al. (1996).

The periphyton algae were collected in tubes of equal volume and preserved in formaldehyde. In the laboratory the samples were studied in two steps. Firstly, filamentous algae were analyzed using the counting chamber technique at a magnification of 150×. At the same time the cells of filamentous algae were measured and their ratio to diatoms was estimated. The biovolume was calculated using the table of Kuzmin (1984), and 10^{12} μm^3 were understood as equal to 1g of biomass (Guseva 1956). At least 200 valves per slide were identified and counted. The contribution of individual taxa to the formation of phytoperiphyton biomass was thus assessed.

Secondly, diatoms were purified by gently boiling in a 2:1 mixture of concentrated nitric and sulphuric acid for 2–4 h). Diatom slides were mounted in Hyrax. Identifications and calculations were made by microscopy at 1000ń upon oil immersion.

The rest of the sample was used to estimate phytoperiphyton biomass on each rock from chlorophyll-a (mg m^{-2}). Chlorophyll-a was determined spectrophotometrically (Strickland & Parsons 1972), and the percentage of chlorophyll a was calculated as the ratio of chlorophyll a concentration to ash-free dry weight of organic matter. Results on algal abundance and biomass were also presented as the number of cells and as fresh biomass (mg) per square cm of the substrate. Surface areas were estimated according to Graham et al. (1988). Cell counts were used to calculate the Shannon-Weaver diversity index (Shannon & Weaver 1963).

Cluster analysis was based upon relative abundance of algal species in the periphyton and carried out using the Statistica software (Ward's method, Euclidean distance).

For diatoms we followed the taxonomy proposed by Gleser et al. (1988, 1992) and for other groups we followed Gollerbakh (1951–1983). Data on the geographic distribution of algae were obtained from floristic guides (Raspopov 1971; Getsen 1985; Levadnaya 1986; Jakovlev 2000). Ecological characteristics of algae were determined with Omnidia 2 software (Lecointe et al. 1993).

Results and discussion

A total of 648 species of algae belonging to 130 genera, 66 families, 24 orders and 9 divisions was identified in the periphyton of 66 rivers (Komulaynen 2004a, b). The most diverse group was diatoms (59.6% of total the number of taxa).

Green algae are in third place with respect to the number of species (Table 1), being only surpassed by diatoms and blue-green algae: 121 species (18.7% of the total number of species) representing 6 orders, 16 families and 37 genera. A more detailed description of the periphyton diversity can be found in Komulaynen et al. (2006).

Most of the dominant filamentous green algae may be classified as "ubiquitous" taxa that are typical of oligotrophic water bodies of the boreal zone. Their dominance in the periphyton of the investigated rivers points to a similarity of the conditions for the development of the algal flora, whereas the differences are probably due to some variations in the sampling time. The low mineral content of the rivers accounts for a high diversity of species indifferent to salinity. Indifferent species predominate, as is usually the case in humic water, and acidophilic form a fairly large group. In the rivers studied, the periphyton clearly shows the characteristics of a cryophilic flora, and a great length of the area from south to north is responsible for a difference in the ratio of boreal, arctalpine and widespread species in the algal flora of some rivers.

Table 1. Diversity statistics of divisions of algae present in the periphyton. Legend: a – number of species, b — number of species as a percentage of all species, c – position of the order with respect to the number of species, d – number of dominant species in an order, e – number of dominant species in an order as a percentage of all dominant species, f – position of the order with respect to the number of dominant species.

Divisions	a	b	c	d	e	f
Raphidophyta	1	0.2	7–9	1	0.7	5–6
Euglenophyta	1	0.2	7–9	0	0.0	7–8
Cyanophyta	124	19.1	2	35	23.5	2
Chrysophyta	5	0.8	5	0	0.7	5–6
Dinophyta	2	0.3	6	0	0.0	7–8
Bacillariophyta	386	59.6	1	85	57.0	1
Chlorophyta	121	18.7	3	21	14.1	3
Xanthophyta	1	0.2	7–9	0	0.0	7–8
Rhodophyta	7	1.1	4	6	7.7	4
Total algal flora	648	100		149	100	

Table 3. Frequency of occurrence (pF), frequency of dominance (DF) and order of dominance (Dt = DF/pF 100) for the species dominating by abundance (N% > 10) and biomass (B% > 10).

Species	pF	N		B	
		DF	Dt	DF	Dt
Microspora amoena	10.6	–	–	7.6	71.5
Ulothrix zonata	37.9	–	–	25.8	68.0
Draparnaldia glomerata	18.2	–	–	1.5	8.3
D. plumose	13.6	1.5	11.1	3.0	22.3
Coleochaete divergens	1.5	–	–	1.5	100.0
C. scutata	4.5	–	–	1.5	33.7
Bulbochaete sp.	60.6	1.5	2.5	10.6	17.5
Oedogonium sp.	51.5	7.6	14.7	9.1	17.7
Cladophora glomerata	16.7	1.5	9.1	3.0	18.1
Percursaria percursa	3.0	1.5	50.5	–	–
Spirogyra sp.	45.5	6.1	13.3	10.6	23.3
Zygnema sp.	51.5	15.2	29.4	34.8	67.7
Mougeotia sp.	72.7	6.1	8.3	43.9	60.4

Table 2. Statistics of families of algae with respect to the number of taxa in the periphyton.
Legend: a – number of species, b – number of species as a percentage of all species, c – position of the family with respect to the number of species, d – number of dominant species in a family, e – number of dominant species in a family as a percentage of all dominant species, f – position of the family with respect to the number of dominant species.

Families	a	b	c	d	e	f
Oscillatoriaceae	33	5.1	7–8	5	3.4	7–12
Fragilariaceae	47	7.3	3	12	8.1	2
Eunotiaceae	34	5.3	5	14	9.4	1
Achnanthaceae	38	5.9	6	5	3.4	7–12
Naviculaceae	101	15.7	1	11	7.4	3
Cymbellaceae	39	6.0	4	9	6.0	5–6
Gomphonemataceae	29	4.5	7–8	10	6.7	4
Desmidiaceae	83	12.9	2	0	0.0	44–66
Number of species in leading families	244	37.4		83	55.7	
Total algal flora	648	100		149	100	

The green algal species richness is attributed mainly to representatives of one family, Desmidiaceae, which occupies the second position among all identified families in terms of the number of taxa (Table 2).

The taxonomic diversity of Desmidiaceae is due to an indirect impact of the climate acting through mire formation and a reduced effect of calcareous rocks. Many of the species are confined or chiefly occur in the arctic zone, and avoid high-humic watercourses. The highest species numbers are found in the genera *Cosmarium* (22), *Euastrum* (7) and *Closterium* (11). However, all the species contribute only single specimens to the algal coenoses and play no significant part in the formation of their structure; their contribution to the biomass of the communities is certainly insignificant, too.

Chlorococcales are more diverse in the periphyton of the tributaries to Lakes Onego and Ladoga. Here too, however, *Sphaerocystis schroeteri* is the only species of the 13 identified which is present relatively constantly in the attached algal communities. However, the relative abundance of planktonic species was in excess of 20% only in the periphyton of the rivers Lizhma and Syapsya that have lake percentages of 20.4 and 19.4% in the drainage basin area and in some river sectors located downstream from flowing lakes. Green planktonic forms were also encountered among them.

The majority of green algal species identified in attached algal communities (46.5%) are euperiphytonic, filamentous forms. They are most constantly present in the algal coenoses and often dominate in terms of biomass. Special mention deserve *Ulothrix zonata*, *Bulbochaete* sp., *Oedogonium* sp., *Spirogyra* sp., *Zygnema* sp., *Mougeotia* sp. whose frequency of occurrence is 11–37%.

Phytoperiphyton is formed of species that vary in cell length from 1–2 to several hundred microns, and the cell volume of filamentous green algae (*Mougeotia, Zygnema, Ulothrix*) is at least 1000 times that of some species of the genera *Sphaerocystis* and *Achnanthes*. Therefore, the dominant complexes, consisting of species that dominate in abundance and biomass, differ markedly in structure. In the rivers studied, 149 species taxa that make up 28.0% dominate in abundance and 96 species (14.8%) in biomass. In fact, however, the structure of phytoperiphyton is formed by just 24 species that make up over 10% of total biomass. Thirteen of them are green algae (Table 3). A significant factor is their capacity to form aggregations both on and above the substratum, thus extending the substratum surface area and enhancing the formation of secondary epiflora. It is not surprising therefore that it is the abundance of green algae that is used as the criterion for clustering rivers by biomass. Therefore, it is their abundance that is responsible for the integration of rivers when clusterization is carried out using biomass data (Fig. 2). It is *Ulothrix*

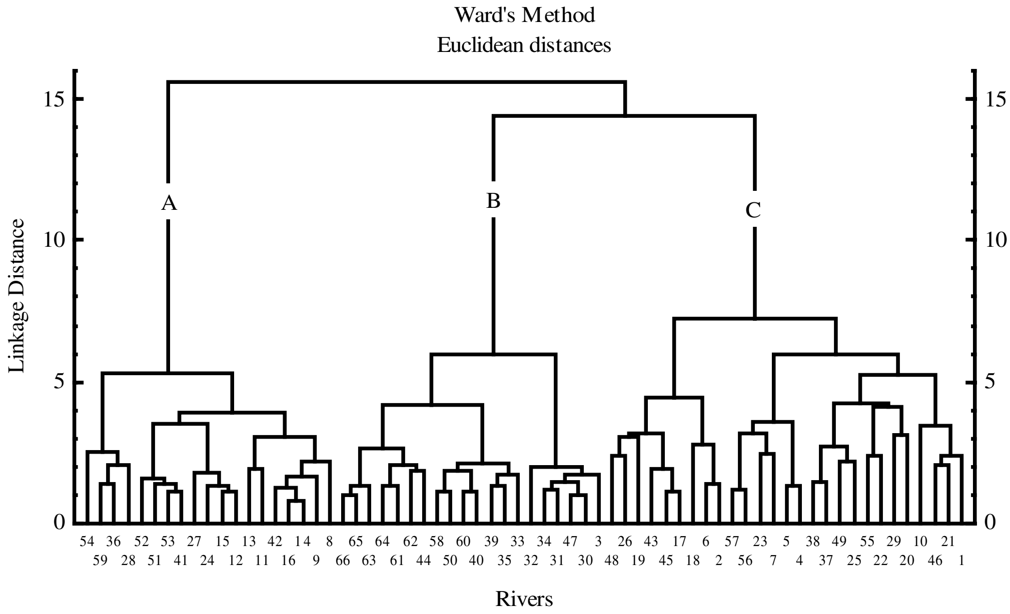

Fig. 2. Dendrogram showing river grouping according to the species composition (relative biomass) of periphyton.

zonata in group A and *Zygnema* spp. and *Mougeotia* spp in group B. Group C includes rivers, where phytoperiphyton biomass structure is not so uniform. Here, the species complex that dominates in biomass comprises both filamentous algae (in addition to the aforementioned species, it is formed by *Oedogonium* spp., *Cladophora glomerata*, *Draparnaldia plumosa* and *Microspora amoena*) and diatoms (*Didymosphenia geminata, Tabellaria flocculosa, Achnanthes minutissima* and *Eunotia* spp.). Furthermore, for the rivers of North Karelia and the Kola Peninsula the biomass of groups of phytoperiphyton is formed by blue-green algae, such as *Stigonema mamillosum*, *Nostoc* spp. and *Tolypothrix* spp., and in the rivers of the Pribelomorian Lowland by *Goniostomum semen* (Raphidophyta).

The territory, in which the basins of the rivers studied are located, extends from south to north over 1000 km. Owing to the presence of large water bodies, such as the White Sea and Lakes Ladoga and Onega, climatic differences are not so conspicuous as in E. Russia, but variations in the structure of phytoperiphyton from north to south are quite distinct. Diatoms generally dominate, and the species diversity increases gradually southwards. The algal flora of the periphyton in the South Karelian rivers comprises algae of the divisions Euglenophyta, Dinophyta and Charophyta that do not occur in rivers on the Kola Peninsula. In algal coenoses, filamentous algae of the order Zygnematales are replaced by algae of the orders Cladophorales, Chaetophorales and Oedogoniales. As a result, *Cladophora glomerata* is constantly present in the periphyton, and *Zygnema* and *Mougeotia*, the species characteristic of rivers with soft water and a high colour index, become less abundant.

In northern rivers blue-green algae are generally less diverse than are green algae (Getsen 1985). The Cyanophyta/Chlorophyta ratio estimated for periphyton varies between 0.13 and 2.00 with an average of 0.62 (Fig. 3). This seems to reflect the specific pattern of the attached algal communities. Thus, *Cyanophyta* are even more prolific and diverse in northern Karelian and Kolsky Peninsulas rivers than are *Chlorophyta.*

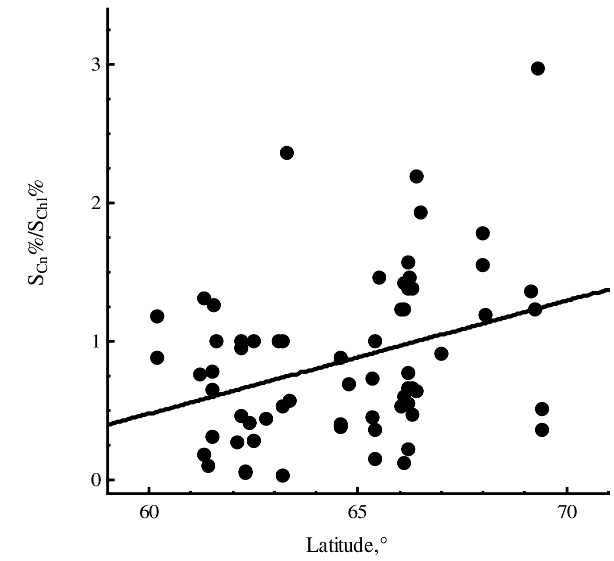

Fig. 3. The change of the relation Cyanophyta-Chlorophyta (relative number of species) with latitude in the phytoperiphyton of the studied rivers.

The beds of the rivers studied are a combination of various habitats formed by substrate-current interactions. The maximum species diversity and biomass are observed on large stable rocks at a depth of up to 10 cm in the so-called “splash” or “amphibiotic” zone together with blue-green algae, such as *Stigonema* spp., *Nostoc* spp., *Tolypothrix* spp. and *Calothrix* spp., that can resist the erosion and periodical drying-out of the substrate; the green alga *Ulothrix zonata* dominates. Therefore, when analyzing ”biotopic” heterogeneity, one should first focus on the distinctive structural pattern of phy-

Table 4. Principal parameters of phytoperiphyton structure in rapids and pools sections (Lizhma river, 8.10.2003).

Parameters	Pools	Riffles
Biodiversity (H)	2.2 (1.8–3.0)	2.8 (1.2–3.8)
Biomass (g m^{-2})	7.4 (0.9–32.0)	132.0 (4.3–324.0)
Chlorophyll *a* (mg m^{-2})	26.9 (5.9–71.0)	443.1 (21.0–1621.5)

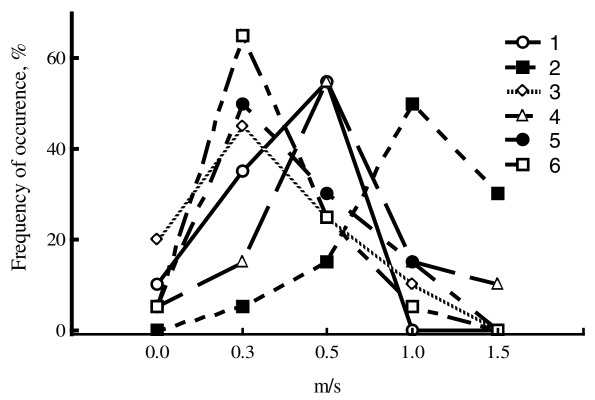

Fig. 4. Frequency of occurrence of some filamentous algae at different current speeds. 1 – *Batrachospermum foeniculaceum,* 2 – *Lemanea* spp., 3 – *Stigonema mamillosum,* 4 – *Zygnema* spp., 5 – *Ulothrix zonata,* 6 – *Calothrix* spp. + *Tolypothrix* spp.

toperiphyton in river rapids and reaches (Table 4).

Examination of ecological conditions associated with the occurrence of attached algal communities suggests that the water current is a major "selecting" factor responsible for the mosaic distribution of phytoperiphyton assemblages. Changes in the current velocity lead to variations in phytoperiphyton biomass and species diversity between individual samples from the same locality.

The positive effect of current was revealed long time ago by the vigorous growth of filamentous algae at river rapids (Fig. 4). The algal coenoses of encrusting organisms at rapids are dominated by nonbranching filamentous forms, such as *Stigeoclonium tenue*, *Ulothrix zonata, Lemanea fluviatilis* etc., and diatoms pressed closely against the substrate, e.g. *Cocconeis* spp.*, Ceratoneis* spp. and *Cymbella* spp. The growth of some species, e.g. *Lemanea* sp., is maximum only at a current velocity over 1 m s^{-1}.

At the same time, in nutrient-enriched streams maximum biomass values were reported from river sectors with slower current velocity, where green filamentous algae, commonly those of the genus *Spirogyra*, also prevail. Algal mats may detach from the substrate and move to the surface in late summer to form so-called metaphyton.

Biotopic characteristics in the structure of periphyton are also due to the fact that the phytoperiphyton in the rivers studied is formed and functions in a highly heterogeneous and often insufficient light regime. Illumination intensity decreases primarily because of a high colour index that is characteristic of the rivers of the

Table 5. The structure of phytoperiphyton communities in the river Lizhma in relation to depth.

	Depth (m)			
	0.0	0.1	0.3	0.7
	Biomass % (mean ± SD)			
Chlorophyta	62.2 ± 10.0	64.3 ± 13.0	1.5 ± 1.1	1.3 ± 0.9
Cyanophyta	21.0 ± 3.7	7.0 ± 2.4	5.7 ± 5.0	1.8 ± 1.3
Bacillariophyta	16.8 ± 10.8	28.7 ± 13.4	92.8 ± 4.6	96.9 ± 1.4

Table 6. The structure of phytoperiphyton communities in the river Ulosetiko in relation to illumination.

	Illumination (lux)		
	30	750	1200
	Biomass %. (Mean ± SD)		
Chlorophyta	1.8 ± 1.2	89.4 ± 6.7	91.0 ± 7.7
Rhodophyta	13.0 ± 2.1	4.5 ± 1.7	1.8 ± 1.0
Bacillariophyta	84.6 ± 2.3	6.1 ± 6.2	7.2 ± 7.9

region. Therefore, at a depth as little as 50–70 cm and at a colour index over 100 degrees phytoperiphyton is absent. Illumination is observed to decline rapidly during high-water periods, when large quantities of mineral and organic matter are washed away from the catchment area.

It should be noted that green filamentous algae that commonly dominated at an illumination in excess of 4500 lx and exhibit distinct zoning are the first to be affected by a decline in illumination (Table 5). In addition to vertical zoning, most rivers also show horizontal zoning, which is due to the shadowing of coastal vegetation that intercepts up to 95% of incident light. This effect is particularly clear in small tributaries were the leaf canopy of adjacent trees can almost completely overhang the streambed (Table 6). It is in these sectors that we have revealed a "back or reverse seasonal succession" of phytoperiphyton, which typically occurs in rivers when a climax community, formed originally in the spring, gradually loses its density.

When analyzing the spatial dynamics of periphyton, of special interest is undoubtedly a zone with both lotic and lentic conditions, and where allochthonous forms become more abundant in the periphyton at the lake-river boundary. The composition of the allochthonous algal flora depends on the morphometry and nutrient content of upstream lotic lakes and the abundance of potential migrants. Allochthonous forms are most commonly dominated by *Aulacosira* spp., *Melosira* spp., *Fragilaria* spp. and *Tabellaria fenestrata.* The most considerable effect on the formation of periphyton is exerted by planktonic green algae (*Palmodictyon viride, Hyalotheca mucosa*) and blue-green algae (*Gloeotrichia echinulata, Microcys-*

tis aeruginosa, Aphanizomenon flos-aquae, Anabaena spp., *Woronichinia naegeliana*), i.e. species that cause water bloom.

Short-term changes in the structure of phytoperiphyton are revealed upon colonization of artificial substrates and restoration of destroyed communities. The rate of initial colonization depends on the abundance of potential settlers, their settling rate and their ability to aggregate. The pioneer algal flora on experimental substrates consists basically of unicellular forms such as *Ceratoneis, Cocconeis*, *Achnanthes* and *Cymbella*. Therefore, the biomass of phytoperiphyton on experimental substrates was much lower than the maximum observed on natural substrates, primarily because of the absence of green filamentous algae.

The long-term dynamics of phytoperiphyton in the rivers is shown by two basic models: 1) a relatively permanent low biomass period, characteristic of fine-pebble grounds, particularly in shadowed sectors, and 2) a seasonal cycle.

The seasonal cycle is characterized by a "*classical*" taxonomic succession, in which diatoms typically dominate before and after spring flood, bluegreen algae prevail in biomass during the summer season and green filamentous algae predominate in the autumn. Variations in the species composition of the phytoperiphyton are paralleled by variations in the density of the communities formed. The maximum biomass in rivers is observed in the spring before the appearance of foliage and at the end of the summer.

Seasonal variations in the species composition and biomass of phytoperiphyton depend largely on the structure of groups of filamentous green algae. As the relative abundance of green algae in the algal coenoses of encrusting organisms rises, the potential productivity of phytoperiphyton increases because of a rise in chlorophyll *a* concentration.

In conclusions, green algae are a significant constituent of periphyton communities in small rivers of North European Russia. They are represented in the periphyton by unicellular, colonial and multicellular, micro- and macroscopic forms that contribute to the formation of the structure of algal coenoses in different ways. The leading role is undoubtedly played by filamentous algae (Ulothrix, Zygnema and Oedogonium) that form the microstructure of the periphyton. They commonly inhabit areas that are inaccessible to, or unfavourable for other groups of macrophytes (bryophytes and vascular plants) such as rapids or piles of boulders. Their phytocoenoses often cover large areas and produce a considerable biomass. Of greater importance is the ability of filamentous algae to form clusters both on substrates and in the water above the substrate. In this environment the boundary layer acquires new properties. A crucial effect on the rate of formation is exerted by the structure of filamentous encrusting organisms, rather than the quality of the rocky substrate surface. The total surface, available for colonization, increases, and a complex structure, used as substrate by secondary encrusting organisms and as a microbiotope by invertebrates, is produced. As bluegreen and red algae begin to dominate, the species diversity increases, and when green filamentous algae grow on a large scale, species diversity decreases. As a result, the taxonomic structure of periphyton generally changes, which should undoubtedly be considered when launching monitoring programmes in small rivers and choosing sampling time and sampling sites.

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Received September 1, 2007
Accepted March 17, 2008