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Vegetation of Estonian watercourses; the drainage basin of the southern coast of the Gulf of Finland

Jaanus Paal[1] & Tiiu Trei[2]

[1)] *Institute of Botany and Ecology, University of Tartu, Lai St. 40, 51005 Tartu, Estonia (e-mail: jpaal@ut.ee)*
[2)] *Institute of Zoology and Botany, Estonian Agricultural University, Riia St. 181, 51014 Tartu, Estonia (e-mail: treit@zbi.ee)*

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The general aims of the current study were (i) to develop a classification of the aquatic macrophyte communities of the Estonian watercourses flowing into the Gulf of Finland, (ii) to distinguish the main ecological variables which determine the occurrence of the dominating species and discriminate between the community types and, (iii) to establish a classification of river reaches (habitats) and to identify the parameters distinguishing them. The data were clustered into 23 vegetation types of which 18 were dominated by vascular plant species, while five clusters included communities of cryptogams. Water BOD_5, current velocity and riverbed material proved to be the variables separating the clusters most reliably. The occurrence of single species is affected by different environmental variables; from this point of view the most important physical environmental variables are extent of bottom coverage with fine sediments and water turbidity; among the chemical variables content of O_2, NH_4-N and PO_4-P, as well as N/P ratio are of considerable importance. As the species dominating in the clusters are mostly characterised by a very large geographical distribution and a wide ecological amplitude, the established community types are well known from other regions of Europe as well. However, comparison of the ecological parameters of the established community types with those obtained by other researchers revealed marked discrepancies in many cases. The river reaches clustered into four habitat types were significantly separated by water depth and turbidity as well as by riverbed substrate. In this way, in every habitat type there occur plant communities of different types; also, communities of a certain type can grow in different type habitats.

Key words: aquatic vegetation, cluster analysis, discriminant analysis, ecology, environmental variables, generalised linear model analysis, habitat types, water chemistry

Introduction

The current study is part of the larger project *Biota of the Estonian Rivers*, which was carried out by the River Biology Group of the Institute of Zoology and Botany of the Estonian Agricultural University under the supervision of Dr. A. Järvekülg. The purpose of the project was to

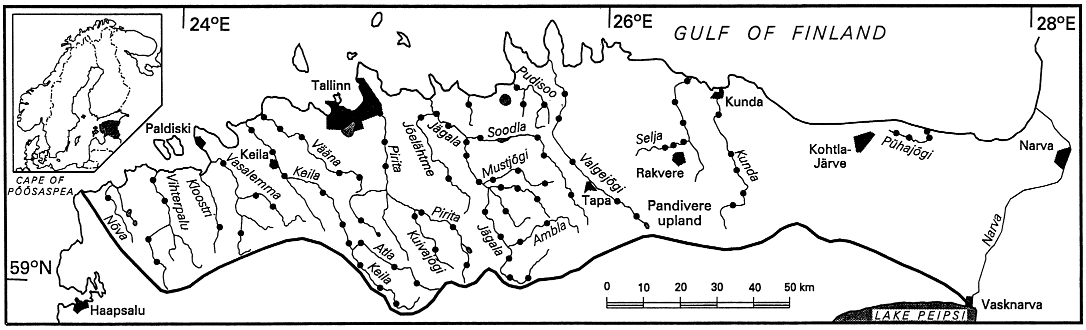

Fig. 1. Rivers of the drainage basin of the southern coast of the Gulf of Finland (except the Narva River) and location of the studied reaches.

obtain a complete overview of the structure and state of the ecosystems of the Estonian flowing waters. All main components of the river biota (phytoplankton, bakterioplankton, microphytobenthos, macrophytobenthos, zoobenthos and ichthyofauna) were studied and a complex of ecological variables (cf. below), characterising the living conditions of water organisms, was determined (Järvekülg 2001).

The aim of the present paper was (i) to use the data collected within the project for elaborating a classification of the macrophyte communities of the Estonian watercourses, (ii) to identify the factors determining the structure of the vegetation types, (iii) to distinguish the main environmental factors determining the occurrence of the most prominent plant species, (iv) to establish a classification of river reaches (habitats) and to test which parameters separate them and, (v) to compare how well the vegetation types correspond to the habitat types. The paper deals with the watercourses of the drainage basin of the Gulf of Finland. The results are discussed in the context of the other studies of the riverine vegetation undertaken elsewhere in Europe.

Material and methods

Study area

The study area (10 319 km^2) comprises the watercourses and their tributaries discharging into the Gulf of Finland (excl. the Narva River system; Fig. 1). In the west, it borders with the Cape of Põõsaspea and in the east with Vasknarva village; the southern boundary is the Pandivere Upland watershed. The average density of the network of the watercourses is 0.78 km km^{-2} (Loopmann 1979). The watercourses are comparatively short, only two rivers (Keila and Pirita) are longer than 100 km, and the length of 6 rivers exceeds 50 km (Table 1), while 13 (43%) of the studied watercourses are shorter

Table 1. Morphometric parameters of the larger rivers in the drainage basin of the Gulf of Finland (after Loopmann 1979).

River	Length (km)	Catchment area (km^2)	Average width (m)		Average depth (m)	
			Medium course	Lower course	Medium course	Lower course
Keila	116	682	20	25	1.8	2.0
Pirita	105	799	25	35	1.8	1.0
Jägala	97	1570	20	40	2.0	2.5
Valge	85	453	20	15	2.0	0.5
Soodla	75	236	15	8	1.5	1.0
Kunda	64	532	10	15	1.0	0.6
Vääna	64	316	8	15	1.0	1.5
Vasalemma	50	403	6	15	0.6	1.0

than 30 km (Loopmann 1979, Arukaevu 1986). Almost all rivers were dredged and straightened to some extent in the 20th century.

Usually, the riverbeds are engraved in the limestone bedrock. In the eastern part they rise from the Pandivere and Jõhvi Uplands having an absolute altitude of about 75–80 m; in the western part they issue from the edge formations of the glacier sheet or from mires. In their upper and medium courses, the rivers and streams flow on a relatively flat Ordovician limestone plateau. Of the watercourses studied, 34% have low current velocity (0.1–0.25 m s^{-1}), while the current velocity of 32% of the watercourses is moderate (0.25–0.5 m s^{-1}). In the lower course the stream gradient is relatively large and the rivers pass through the north Estonian limestone escarpment (klint), forming several rapids, terraces and waterfalls, where current velocity may reach 1.5–2 m s^{-1} (Järvekülg 2001).

Groundwater is the main contributor to discharge, besides snow melt and rain (Loopmann 1979). Groundwater flows out of karst springs, mainly on the Pandivere Upland. As a result, 51% of the reaches have cool water (13.1–17.0 °C) and 18% have cold water (< 13 °C) in midsummer. In 83% of the studied sites water in the drainage basin was slightly alkaline with pH 7.3–8.0, maximum 8.4. Due to the high concentration of mineral compounds, especially $Ca(HCO_3)_2$, the seasonal changes of pH are small (Järvekülg 2001).

The content of dissolved oxygen in water ranges mostly between 7.0–11.0 mg O_2 l^{-1}. The content of nutrients in water varies widely but is rather high at most sites. At 67 sites (70.5%) the concentration of total N exceeds 1500 mg m^{-3} and in seven reaches it is about 5000 mg m^{-3} (max 7238 mg m^{-3}). The Pandivere Upland and its outskirts as well as the Kõrvemaa area, situated to the SW, are the main districts where the concentration of nitrogen compounds in the water of the spring-fed rivers is high. This is a consequence of the misuse of fertilisers on arable land in the period 1960–1990, which led to the contamination of the upper aquifers of groundwater, especially in the areas of karsted carbonate rocks (Järvekülg & Viik 1994).

High phosphorus concentration is mainly caused by point source pollution with wastewaters from towns and settlements (Rakvere, Jõhvi, Toila, Kukruse, etc.) and from big complexes of seasonal holiday cottages, e.g. the area between Paldiski and Kuusalu. The content of total P exceeded 50 mg m^{-3} in the water of 43 sites (45%); at 19 sites the content of total P was 100–300 mg m^{-3} and at six sites it exceeded 300 mg m^{-3} (max 1560 mg m^{-3}).

Sampling

Data were sampled from 50–100-m-long river reaches where the physical conditions of the river appeared visually homogeneous. As the choice of the reaches for field analysis depended on their accessibility, the studied reaches were usually located near bridges. The number of reaches varied from three to ten for the bigger rivers and from one to three for the tributaries.

For every reach, the following morphometric and hydrological characteristics were estimated (Järvekülg 2001): (i) river width (m); (ii) river depth (m); (iii) current velocity in the main stream (m s^{-1}); (iv) water turbidity (1 = clear, 2 = slightly turbid, 3 = turbid); (v) bottom substrate, i.e. prevailing bed-forming material (1 = silt or clay, 2 = sand, 3 = gravel, shingle, 4 = stones, limestone blocks), (vi) extent of fine sediment coverage (1 = none, 2 = partial, 3 = extensive). The number of points at which measurements were made differed among the reaches; if the conditions were more or less uniform, three points were considered sufficient for averaging, in the case of varying conditions additional points were included.

Water for hydrochemical analyses for every reach was collected without replicates from a depth of 0.1–0.5 m in the main stream (Järvekülg 2001). We evaluated: (i) pH, *in situ* with the colorimetric scale GM-58; (ii) dissolved oxygen content (mg l^{-1}), *in situ* with the calibrated portable oxygen meter "Marvet Junior 95"; (iii) saturation with O_2 (%) for standard water temperature; (iv) biological oxygen demand (BOD_5, mg O_2 l^{-1}) obtained from the difference between two measurements of dissolved oxygen before and after the incubation period (5 days at 20 °C in the dark); (v) content of total N, total P, nitrogen and phosphorus compounds (mg m^{-3}) determined in accordance with Grasshoff *et al.* (1982); (vi) N/P ratio calculated as the ratio of the amount of inorganic nitrogen (NO_3-N + NO_2-N + NH_4-N) to the amount of inorganic phosphorus (PO_4-P).

Data on the macrophyte vegetation was gathered from 109 reaches of 37 watercourses during June and July 1991, 1993 and 1995. In most reaches (61%) one or two plant communities (stands, assemblages) were distinguished, while in four reaches up to five communities were identified. As the communities were regarded as vegetation patches having a relatively homogeneous floristic composition and physiognomy, both features were mainly determined by the dominating species; the area for communities was at least 4–5 m^2 on gravel and finer bed material, or 1 m^2 on stones and limestone blocks. Every community was analysed separately ignoring the transitional areas between them. Species abundance in the community was estimated using the following scale: 1 = species occurring with a relatively low abundance, 3 = species growing in small aggregations, 5 = species forming large aggregations or occurring in communities as co-dominants, 10 = dominating species. Occurrence of floating mats of filamentous macroalgae was evaluated using a three-step scale: 1 = scarce, 2 = moderate, 3 = abundant. Bryophytes and macroalgae were sampled and identified in the laboratory. The riverbank vegetation was excluded from analysis. For every community, the predominant bottom substrate material was specified using the same scale as for the whole reaches.

The taxonomic nomenclature of vascular plants is based on *Flora Europaea* vols. 1–5 (1964–1980). The guides by Mäemets (1984) and Leht (1999) were used for the identification of vascular plants, and the guide by Ingerpuu and Vellak (1998) was used for bryophytes. For the identification of algae the following literature sources were used: van den Hoek (1963), Vinogradova *et al.* (1980), Gollerbakh and Krasavina (1983), Topachevski and Masyuk (1984), Moshkova and Gollerbakh (1986).

Data processing

Taking into consideration that at a number of sites the aquatic vegetation was very scarce due to poor light conditions, the data for 85 reaches, including 210 plant communities of 25 rivers, were selected for statistical analysis.

For the cluster analysis of the plant communities, the unweighted average linkage method (Podani 2000) with the Euclidean distance as the similarity measure was employed. The method shows good concordance with the vegetation structure of watercourses, where usually only one or two species are clearly dominating. On the basis of the obtained dendrogram, at first small clusters, including at least three communities, were separated.

In order to measure the statistical reliability of the clusters, the α-criterion (Duda & Hart 1976) was used:

$$\alpha = \frac{\left(1 - \frac{2}{\pi d} - \frac{I_2}{I_1}\right)}{\sqrt{\frac{2\left(1 - \frac{8}{\pi^2 d}\right)}{nd}}} \tag{1}$$

where

$$I_2 = \sum_{\vec{x} \in X} \left\| \vec{x} - \vec{m} \right\|^2 \tag{2}$$

$$I_1 = \sum_{i=1}^{2} \sum_{\vec{x} \in X} \left\| \vec{x} - \vec{m}_i \right\|^2 \tag{3}$$

I_1 is the sum of the square distances between the centroid of the merged complex of two clusters and the objects (descriptions of the vegetation), I_2 is the sum of the square distances between the objects and the centroids of their clusters after dividing the complex into two suboptimal parts, $\vec{x}$ is the vector of an object, $\vec{m}$ is the vector of the centroid of the merged complex, $\vec{m}_i$ is the vector of the centroid of cluster x_i, d = dimensionality of the merged complex, d = min (q, n – 1), where q and n are the number of species and the number of sample plots in the merged complex, respectively. To obtain a better interpretation of the estimates, it is more convenient to use the corresponding probabilities as the coefficients of indistinctness (CI) instead of the direct values (Paal & Kolodyazhnyi 1983, Paal 1987):

$$\mathrm{CI} = \frac{100}{\sqrt{2\pi}} \int_{\alpha}^{\infty} \exp\left(\frac{-x^2}{2}\right) dx \tag{4}$$

If the value of CI for the clusters neighbouring in the dendrogram was larger than 5.0, the clusters were merged and analysis was repeated until a reliable classification structure was established.

To test which environmental variables discriminate between the vegetation clusters, discriminant analysis was carried out. As the data of water chemistry and the physical environment in the current study were measured only as the average values for the whole reach, the same environmental data were set to correspond to all communities recorded from one reach. Prior to analysis, the chemical data of water, except for pH, were $\log_{10}$ transformed, which enabled a closer approximation of the distribution of their residuals to a normal distribution.

The probable occurrence of the most abundant species in the watercourse reaches as the function of the $\log_{10}$-transformed variables of water chemistry and the variables of physical environment was tested by the analysis of a generalised linear model (GLZ). For this, the dominating species of the established vegetation clusters were selected and their abundance values were rescaled to presence–absence for every reach. The analysis was carried out assuming that a dependent variable follows the binomial distribution; logit regression and the maximum likelihood criterion were used, and the type III sums of squares test was applied.

The river reaches were clustered using 6 physical environmental parameters (river width and depth, current velocity, water turbidity, extent of fine sediment coverage and prevailing bed-forming material). Cluster analysis was performed employing the minimal incremental sum of squares method, similarity matrix was calculated by the distance for mixed data (Podani 2000). Discriminant function analysis was carried out as in the case of vegetation clusters. The reaches were ordinated on a scatterplot of canonical scores.

Cluster analysis was performed with the program package SYN-TAX 2000 (Podani 2001); the indistinctness coefficients were calculated using the original program SYNCONT 3.0 developed by S. Kolodyazhnyi, J. Paal and A. Kink (in possession of the authors); the computation of the basic statistics, as well as discriminant analysis, canonical analysis and GLZ analysis was carried out with the program package STATISTICA 6.0 (Statistica 2001).

Results

After merging several small indistinct clusters and following the established limit that a cluster must comprise as a minimum of three samples, cluster analysis resulted in 23 clusters (Table 2). Almost all clusters (vegetation types) are significantly distinct, only cluster 23 has a slight continuum with three other clusters, $CI_{9,23} = 5.2$, $CI_{17,23} = 7.1$ and $CI_{21,23} = 5.9$. The value of the cophenetic correlation of the dendrogram is 0.788, indicating its good correspondence to the structure of the similarity matrix. The most frequent are the plant communities dominated by *Sparganium erectum* (cluster 1), *Potamogeton perfoliatus* (cluster 17) and *Schoenoplectus lacustris* and *Sium latifolium* (cluster 15).

The results of discriminant function analysis show (Table 3) that in terms of the environmental variables the obtained vegetation clusters are significantly separated by BOD_5, current velocity, and bottom substrate. Still, the average values of the environmental parameters, calculated for the vegetation clusters (Table 4), should be interpreted with some precaution, as these parameters were not estimated for every single community but only as an average for the whole river reach. For this reason, these results are to some extent 'overaveraged' and are not strictly specific. Nevertheless, as small clusters including less than three samples were excluded, the statistical means here are not senseless and will enable the characterisation of the clusters.

For the occurrence of the dominating species, the most important water chemistry parameters appear to be the content of NH_4-N and PO_4-P, as well as O_2 content and the N/P ratio, affecting the occurrence of five, four and three studied species, respectively (Table 5). Of the parameters of the physical environment, extent of bottom coverage with fine sediments is important for seven species and water turbidity for six species. Among the analysed species the most sensitive to changes in the environmental variables are *Hippuris vulgaris*, *Equisetum fluviatile, Phalaris arundinacea* and *Potamogeton alpinus*. At the

Table 2A. Centroids of clusters 1 to 9. The cluster number is followed by the number of communities in the cluster (in brackets). Med = species median value, Fr = species frequency in communities (%); if the median is expressed as an average of two values, both were taken into account in the calculation of frequency.

Species	Cluster																	
	1 (19)		2 (4)		3 (10)		4 (11)		5 (11)		6 (4)		7 (11)		8 (3)		9 (3)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Acorus calamus	0	5	–	–	0	20	0	9	0	9	–	–	–	–	–	–	–	–
Agrostis stolonifera var. *prorepens*	0	16	–	–	–	–	0	18	–	–	–	–	–	–	–	–	0	33
Alisma plantago-aquatica	0	42	0.5	50	0	30	0	9	0	45	–	–	0	36	–	–	0	33
Alopecurus aequalis	0	5	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Berula erecta	–	–	–	–	–	–	–	–	–	–	–	–	0	9	–	–	–	–
Bidens tripartita	0	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Butomus umbellatus	0	11	–	–	10	100	0	9	0	9	0	25	0	27	–	–	–	–
Calla palustris	–	–	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Callitriche spp.	0	11	–	–	–	–	0	9	–	–	–	–	–	–	–	–	–	–
Caltha palustris	0	5	–	–	0	10	0	9	–	–	–	–	0	9	–	–	–	–
Cardamine amara	–	–	–	–	0	10	–	–	–	–	–	–	–	–	0	33	–	–
Cardamine pratensis	0	5	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Carex acuta	0	11	–	–	0	10	–	–	0	27	0	25	–	–	–	–	–	–
Carex rostrata	0	11	–	–	–	–	–	–	0	9	–	–	–	–	–	–	–	–
Carex spp.	–	–	0	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Catabrosa aquatica	0	21	–	–	0	10	–	–	0	9	–	–	–	–	–	–	–	–
Ceratophyllum demersum	0	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Comarum palustre	0	11	–	–	0	20	–	–	–	–	–	–	0	9	–	–	–	–
Elodea canadensis	0	26	–	–	–	–	0	18	–	–	0.5	50	0	27	–	–	–	–
Epilobium hirsutum	0	26	0	25	0	20	0	–	–	9	0	–	–	–	–	–	–	–
Epilobium tetragonum	–	–	–	–	–	–	–	–	0	9	–	–	–	–	–	–	–	–
Equisetum fluviatile	0	32	–	–	0	20	1	64	10	100	0.5	50	1	64	1	100	1	67
Eupatorium cannabinum	0	11	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Galium palustre	0	5	–	–	–	–	–	–	0	9	–	–	–	–	–	–	–	–
Glyceria fluitans	0	26	0	25	0	10	–	–	0	18	0	25	–	–	–	–	1	67
Glyceria maxima	–	–	0	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hippuris vulgaris	–	–	–	–	0	20	10	100	0	18	0.5	50	0	18	–	–	0	33
Iris pseudacorus	0	11	–	–	–	–	0	9	0	18	0	25	–	–	–	–	–	–
Lemna minor	0	42	0	25	0	40	–	–	0	27	–	–	1	64	–	–	1	67
Lemna trisulca	0	26	–	–	0	20	–	–	0	9	–	–	0	27	–	–	0	33
Lycopus europaeus	–	–	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Lysimachia thyrsiflora	0	21	1	75	0	20	0	36	0	45	0	25	0	36	–	–	–	–
Lythrum salicaria	0	–	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Mentha aquatica	0	37	–	–	0	20	0	18	1	55	10	100	0	27	0	33	–	–
Mentha × verticillata	0	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Menyanthes trifoliata	–	–	–	–	–	–	–	–	0	9	0	25	0	9	–	–	–	–
Myosotis scorpioides	0	47	–	–	0.5	50	0	36	0	36	1	75	0	18	0	33	0	33
Myriophyllum spicatum	0	5	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Myriophyllum verticillatum	–	–	–	–	–	–	–	–	–	–	0	25	0	9	0	33	–	–
Nuphar lutea	0	16	–	–	0	20	0	45	0	9	–	–	10	100	10	100	0	33
Oenanthe aquatica	0	5	–	–	–	–	0	9	–	–	–	–	–	–	–	–	–	–
Phalaris arundinacea	0	21	0	25	0	20	–	–	0	18	–	–	–	–	–	–	–	–
Phragmites australis	0	11	10	100	–	–	–	–	0	36	0	25	–	–	0	33	1	67
Potamogeton alpinus	–	–	–	–	0	10	0	18	–	–	–	–	0	18	–	–	–	–
Potamogeton natans	–	–	–	–	–	–	–	–	0	18	–	–	0	9	–	–	–	–
Potamogeton pectinatus	0	11	–	–	–	–	–	–	–	–	–	–	0	9	–	–	–	–
Potamogeton perfoliatus	–	–	–	–	0	10	–	–	–	–	–	–	0	9	–	–	–	–
Potamogeton spp.	0	5	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–

continues

Table 2A. Continued.

Species	Cluster 1 (19)		2 (4)		3 (10)		4 (11)		5 (11)		6 (4)		7 (11)		8 (3)		9 (3)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Potamogeton × *meinshausenii*	–	–	–	–	–	–	9	0	–	–	–	–	–	–	–	–	–	–
Ranunculus circinatus	–	–	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Ranunculus lingua	–	–	–	–	0	10	0	18	0	36	0.5	50	0	18	0	33	–	–
Ranunculus trichophyllus	–	–	–	–	0	10	0	9	–	–	–	–	0	9	–	–	–	–
Rorippa amphibia	0	11	0.5	50	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Rumex aquaticus	0	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rumex obtusifolius	0	5	–	–	0	10	–	–	0	9	–	–	–	–	–	–	–	–
Rumex spp.	–	–	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Sagittaria sagittifolia	0	5	–	–	0	20	0	9	0	9	–	–	0	45	10	100	10	100
Schoenoplectus lacustris	0	16	1	75	0	40	0	36	0	27	0	25	0	18	–	–	0	33
Scirpus sylvaticus	0	32	–	–	0	10	–	–	0	9	–	–	–	–	–	–	0	33
Sium latifolium	0	16	0	25	1	60	–	–	0	27	0	25	0	9	–	–	0	33
Solanum dulcamara	0	11	–	–	0	10	–	–	0	18	–	–	0	9	–	–	–	–
Sparganium emersum	0	11	–	–	–	–	–	–	0	9	–	–	–	–	–	–	–	–
Sparganium erectum	10	100	–	–	0.5	50	0	18	0	45	–	–	0	9	–	–	1	67
Sparganium spp.	0	32	–	–	0	20	0	36	0	9	–	–	0	36	0	33	0	33
Spirodela polyrhiza	0	11	0	25	0	20	–	–	–	–	–	–	0	9	–	–	1	67
Stellaria palustris	–	–	–	–	0	10	–	–	–	–	–	–	–	–	–	–	–	–
Stratiotes aloides	–	–	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Typha latifolia	0	5	0	25	0	30	–	–	0	18	–	–	0	9	–	–	–	–
Veronica anagallis-aquatica	0	37	–	–	0	10	0	36	0	45	0	25	0	27	–	–	0	33
Veronica beccabunga	0	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Filamentous macroalgae	0	26	0	25	0	20	–	–	–	–	–	–	0	27	–	–	0	33
Total number of species in cluster		49		14		41		25		35		23		32		10		18
Number of species in community		5–14		5–7		5–12		4–8		4–13		5–14		4–13		4–7		5–11
Mean number of species per community		8		6		9		6		9		8		8		5		9

Table 2B. Centroids of clusters 10 to 18.

Species	Cluster 10 (4)		11 (12)		12 (4)		13 (4)		14 (19)		15 (4)		16 (4)		17 (4)		18 (5)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Acorus calamus	–	–	0	8	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Agrostis stolonifera var. *prorepens*	–	–	0	8	–	–	–	–	–	–	–	–	–	–	–	–	0	20
Alisma plantago-aquatica	1	75	0	42	0	25	0	25	0	37	0	25	0	25	–	–	0	40
Alopecurus aequalis	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Butomus umbellatus	–	–	0	17	–	–	0	25	0	26	–	–	–	–	0.5	50	–	–
Calla palustris	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Callitriche spp.	–	–	0	17	–	–	–	–	0	5	–	–	–	–	–	–	0	20
Caltha palustris	–	–	0	17	–	–	0	25	0	5	–	–	–	–	–	–	–	–

continues

Table 2B. Continued.

Species	Cluster																	
	10 (4)		11 (12)		12 (4)		13 (4)		14 (19)		15 (4)		16 (4)		17 (4)		18 (5)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Cardamine amara	–	–	0	8	–	–	–	–	0	5	–	–	–	–	–	–	0	40
Carex acuta	–	–	0	8	–	–	–	–	0	26	0.5	50	–	–	–	–	–	–
Carex rostrata	–	–	0	8	–	–	–	–	0	5	0	25	–	–	–	–	–	–
Carex vesicaria	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Catabrosa aquatica	–	–	0	8	–	–	–	–	0	5	1	75	5	75	–	–	–	–
Comarum palustre	–	–	–	–	–	–	–	–	0	16	1	75	0	25	–	–	–	–
Elodea canadensis	0	25	0	17	0.5	50	–	–	0	5	–	–	0	25	0	25	0	20
Epilobium hirsutum	–	–	–	–	–	–	–	–	0	11	0	25	0	25	–	–	–	–
Equisetum fluviatile	0	25	0	42	0.5	50	0.5	50	0	47	1	75	–	–	–	–	0	20
Eupatorium cannabinum	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	0	20
Glyceria fluitans	–	–	0	25	–	–	–	–	0	21	0.5	50	–	–	–	–	–	–
Glyceria maxima	–	–	0	8	–	–	–	–	0	11	–	–	–	–	–	–	0	20
Glyceria spp.	–	–	0	8	–	–	–	–	0	5	–	–	–	–	–	–	0	40
Hippuris vulgaris	0	25	0	25	0.5	50	–	–	0	5	2.5	50	–	–	–	–	0	40
Iris pseudacorus	–	–	0	25	–	–	–	–	0	21	–	–	–	–	–	–	0	20
Juncus nodulosus	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Lemna minor	0.5	50	0	33	0.5	50	–	–	0	32	1	75	–	–	0	25	–	–
Lemna trisulca	0	25	0	25	–	–	–	–	0	11	0	25	–	–	–	–	–	–
Lysimachia thyrsiflora	–	–	0	42	–	–	–	–	0	42	1	75	–	–	–	–	–	–
Lysimachia vulgaris	–	–	–	–	–	–	–	–	0	11	1	75	–	–	–	–	–	–
Mentha aquatica	0	25	0	8	–	–	0	25	0	32	0	25	–	–	–	–	0	20
Menyanthes trifoliata	–	–	–	–	–	–	–	–	0	11	–	–	–	–	–	–	–	–
Myosotis scorpioides	–	–	1	58	–	–	0	25	0	47	0	25	0	25	–	–	0	40
Nuphar lutea	1	75	0.5	50	–	–	1	75	0	26	0.5	50	–	–	1	75	0	20
Oenanthe aquatica	–	–	0	17	–	–	–	–	0	11	–	–	–	–	–	–	–	–
Phalaris arundinacea	–	–	0	8	–	–	–	–	0	16	3	75	10	100	–	–	–	–
Phragmites australis	–	–	0	8	–	–	–	–	0	32	–	–	–	–	–	–	0	20
Potamogeton alpinus	0	25	–	–	–	–	10	100	–	–	–	–	–	–	–	–	–	–
Potamogeton crispus	–	–	–	–	–	–	0	25	–	–	–	–	–	–	–	–	–	–
Potamogeton zizii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	25	–	–
Potamogeton lucens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	25	–	–
Potamogeton natans	–	–	0	8	10	100	0.5	50	–	–	0	25	–	–	–	–	–	–
Potamogeton pectinatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	25	–	–
Potamogeton perfoliatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	100	–	–
Potamogeton spp.	–	–	–	–	–	–	0	25	0	5	–	–	–	–	–	–	–	–
Potamogeton × *meinshausenii*	10	100	–	–	–	–	0	25	–	–	–	–	–	–	–	–	–	–
Ranunculus lingua	–	–	0	17	–	–	–	–	0	21	1	75	–	–	–	–	0	20
Ranunculus trichophyllus	–	–	0	8	–	–	0	25	–	–	–	–	–	–	–	–	10	100
Rorippa amphibia	–	–	0	17	–	–	–	–	0	21	–	–	–	–	–	–	0	20
Rorippa palustris	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Rorippa × *anceps*	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Rumex aquaticus	–	–	0	17	–	–	–	–	–	–	–	–	0	25	–	–	0	20
Rumex obtusifolius	–	–	0	8	–	–	–	–	0	11	–	–	–	–	–	–	–	–
Sagittaria sagittifolia	0	25	0	25	–	–	0	25	0	21	–	–	–	–	0	25	0	20
Schoenoplectus lacustris	–	–	0	25	–	–	–	–	10	100	5	100	–	–	0	25	0	20
Scirpus radicans	–	–	0	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scirpus sylvaticus	–	–	0	8	–	–	–	–	0	5	–	–	–	–	–	–	0	20
Scolochloa festucacea	–	–	0	8	–	–	0	25	–	–	–	–	–	–	–	–	–	–
Sium latifolium	–	–	0	17	–	–	–	–	0	47	10	100	–	–	0	25	–	–
Solanum dulcamara	–	–	0	25	–	–	–	–	0	5	–	–	0	25	–	–	–	–

continues

Table 2B. Continued.

Species	Cluster																	
	10 (4)		11 (12)		12 (4)		13 (4)		14 (19)		15 (4)		16 (4)		17 (4)		18 (5)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Sparganium emersum	–	–	–	–	–	–	–	–	–	–	–	–	0	25	–	–	–	–
Sparganium erectum	–	–	0	33	–	–	–	–	0	37	0.5	50	1	75	–	–	0	20
Sparganium spp.	0.5	50	10	100	0.5	50	0	75	0	26	–	–	–	–	0	25	0	20
Spirodela polyrhiza	–	–	0	25	0	25	–	–	0	11	1	75	–	–	0	25	–	–
Stellaria palustris	–	–	–	–	–	–	–	–	–	–	0	25	–	–	–	–	–	–
Stratiotes aloides	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Typha angustifolia	–	–	–	–	–	–	–	–	0	5	–	–	–	–	–	–	–	–
Typha latifolia	–	–	0	8	–	–	–	–	0	5	0	25	0	25	–	–	–	–
Veronica anagallis-aquatica	0.5	50	0	42	0	25	–	–	0	16	–	–	–	–	–	–	5	80
Veronica beccabunga	–	–	0	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Filamentous macroalgae	–	–	0	8	–	–	–	–	0	16	1	50	1	75	1.5	75	–	–
Total number of species in cluster		13		45		10		17		51		25		12		13		23
Number of species in community		3–8		4–18		1–72		4–11		5–17		6–18		2–9		4–6		3–13
Mean number of species per community		6		9		5		7		9		14		5		5		7

Table 2C. Centroids of clusters 19 to 23.

Species	Cluster									
	19 (16)		20 (9)		21 (8)		22 (5)		23 (7)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Amblystegium riparium	0	13	0	11	0	13	–	–	10	100
Amblystegium tenax	–	–	–	–	–	–	–	–	0	14
Amblystegium varium	–	–	–	–	–	–	–	–	0	14
Brachythecium rivulare	–	–	–	–	–	–	–	–	0	14
Brachythecium rutabulum	–	–	–	–	–	–	–	–	0	14
Cratoneuron filicinum	–	–	–	–	–	–	–	–	0	14
Fontinalis antipyretica	0	44	10	100	0.5	50	10	100	10	86
Schistidium apocarpum	–	–	–	–	–	–	–	–	0	14
Batrachospermum moniliforme	0	6	0	33	0	13	0	20	0	14
Batrachospermum spp.	0	6	0	11	0	13	0	40	0	14
Chaetophora spp.	0	6	–	–	–	–	–	–	0	14
Chantransia chalybea	0	13	0	11	0	13	–	–	0	29
Chara spp.	–	–	–	–	0	13	–	–	10	86
Cladophora glomerata	10	100	10	100	0	38	–	–	–	–
Cladophora spp.	–	–	–	–	0	13	–	–	–	–
Enteromorpha spp.	–	–	–	–	0	25	–	–	–	–
Lemanea spp.	0	6	–	–	–	–	–	–	0	14
Microspora spp.	0	6	–	–	0	13	0	20	0	14
Oscillatoria spp. (as film)	0	13	–	–	0	13	–	–	0	14
Oscillatoria spp. (as filaments)	0	6	–	–	–	–	–	–	–	–
Rhizoclonium hieroglyphicum	–	–	0	11	–	–	–	–	–	–
Spirogyra spp.	0	19	–	–	–	–	–	–	0	14

continues

Table 2C. Continued.

Species	Cluster									
	19 (16)		20 (9)		21 (8)		22 (5)		23 (7)	
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
Stigeoclonium spp.	0	13	0	11	–	–	–	–	–	–
Tetraspora spp.	–	–	–	–	0	13	–	–	–	–
Ulothrix zonata	0	25	0	11	–	–	–	–	–	–
Vaucheria spp.	5	81	1	77	10	100	1	60	0	29
Filamentous algae	–	–	–	–	0	25	–	–	–	–
Total number of species in cluster		18		10		14		6		18
Number of species in community		2–6		2–6		1–7		2–3		4–10
Mean number of species per community		5		4		3		3		5

Table 3. Separation of the vegetation types and habitat types (river stretches) by environmental parameters, summary of the discriminant function analyses. *F*-remove = the *F*-criterion value associated with Partial Wilks' λ criterion, *P* = significance level; pH = pH estimated *in situ*, O_2 = content of dissolved oxygen (mg l^{-1}), O_2-sat = O_2 saturation (%), BOD_5 = biological oxygen demand (mg O_2 l^{-1}), Tot-N = content of total nitrogen, NO_3-N = content of NO_3 nitrogen (mg m^{-3}), NO_2-N = content of NO_2 nitrogen (mg m^{-3}), NH_4-N = content of NH_4 nitrogen (mg m^{-3}), Tot-P = content of total phosphorus, PO_4-P = content of PO_4 phosphorus (mg m^{-3}), N/P = ratio of N to P calculated from the ratio of the amount of inorganic nitrogen (NO_3-N + NO_2-N + NH_4-N) to the amount of inorganic phosphate (PO_4-P), Wid = river width (m), Dep = river depth (m), Vel = current velocity (m s^{-1}), WTur = water turbidity, FSed = extent of bottom coverage with fine sediments, BSub = bottom substrate.

Variable	Vegetation types		Habitat types	
	F-remove	*P*	*F*-remove	*P*
pH	1.017	0.447	0.946	0.424
O_2	1.001	0.467	0.892	0.450
O_2-sat	0.996	0.473	1.020	0.390
BOD_5	1.775	0.025	1.351	0.266
Tot-N	1.090	0.364	0.425	0.736
NO_3-N	1.137	0.316	0.454	0.715
NO_2-N	1.136	0.316	0.296	0.828
NH_4-N	1.147	0.306	0.825	0.485
Tot-P	0.558	0.944	0.314	0.815
PO_4-P	0.632	0.895	2.041	0.117
N/P	0.991	0.479	0.998	0.400
Wid	1.250	0.217	0.514	0.674
Dep	0.773	0.754	2.819	0.046
Vel	1.778	0.024	1.191	0.321
WTur	0.787	0.737	26.040	< 0.000
FSed	0.772	0.755	1.312	0.279
BSub	6.417	< 0.000	44.030	< 0.000

same time, considering the analysed data set, such species as *Mentha aquatica*, *Nuphar lutea*, *Potamogeton* × *meinshausenii*, *P. natans*, *P. perfoliatus* and *Sagittaria sagittifolia* do not display any response to the environmental parameters.

The studied watercourse reaches form four big groups which can be interpreted as habitat types (Table 6). All types form clearly separate, only slightly overlapping clusters on the ordination plot (Fig. 2). The 1st habitat type includes the widest and deepest reaches; the water is somewhat turbid or turbid, bottom is at least partly covered by fine sediments, the riverbed substrate is mostly sand or gravel. To the 2nd habitat type belong also comparatively wide stretches of medium depth but with the highest velocity; the water is clear or slightly turbid, fine sediments on bottom are lacking, the substrate is formed by boulders or limestone blocks. The 3rd habitat type represents narrow but rather deep reaches of rivers or rivulets with clear water; sandy bottom is without fine sediments. The last habitat type is characterised by reaches of medium width, depth and velocity; the water is clear, gravelly bottom is partly covered with mud. The 2nd habitat type was encountered relatively more frequently and the 4th type relatively more seldom than the other two types. According to discriminant analysis, the habitat types are significantly separated by water depth and turbidity as well as by riverbed substrate (Table 3).

Cross tabulation of the vegetation types and habitat types (Table 7) clearly demonstrates that

Table 4A. Average values of the environmental variables for vegetation clusters 1 to 9. Mean = mean value, Error = error of mean, other denotations as in Tables 2 and 3.

Variable	Cluster																	
	1		2		3		4		5		6		7		8		9	
	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error
pH	7.8	0.1	7.8	0.2	7.7	0.1	7.8	0.1	7.8	0.1	7.9	0.2	7.8	0.1	7.7	0.2	8.0	0.0
O_2	8.0	0.6	8.4	0.7	8.2	0.9	8.8	0.8	8.3	0.8	9.2	1.7	9.5	0.7	10.1	0.1	8.6	0.7
O_2-sat	79.2	6.0	78.8	6.0	78.5	8.9	81.9	7.1	79.1	6.7	92.3	19.6	93.0	6.0	94.3	3.2	85.0	8.0
BOD_5	3.7	0.5	1.9	0.1	3.3	0.5	2.8	0.4	3.1	0.5	3.6	0.6	3.4	0.4	6.3	1.3	3.4	0.9
Tot-N	2505.4	427.8	2286.8	751.0	2729.7	696.8	2095.0	290.2	2518.3	573.5	2093.5	484.6	2182.2	435.5	3529.7	359.6	1924.3	112.6
NO_3-N	1395.9	298.5	1915.8	863.0	1828.0	483.0	1660.5	354.1	1673.9	388.3	1152.8	630.3	1591.0	437.4	3073.3	507.8	1562.3	125.3
NO_2-N	248.4	121.7	125.0	28.4	376.0	234.1	227.3	77.5	389.1	209.3	82.5	22.9	198.2	62.8	146.7	29.1	346.7	220.4
NH_4-N	566.9	320.2	14.8	6.8	420.4	405.5	120.2	104.3	388.0	368.2	296.8	288.4	63.5	39.9	4.0	1.2	23.3	13.2
Tot-P	249.1	93.3	35.0	5.4	118.3	42.6	65.9	10.9	57.4	10.6	81.3	27.7	83.0	23.7	26.3	4.1	48.3	15.5
PO_4-P	198.8	84.1	12.8	1.7	85.9	38.2	39.4	9.8	31.0	8.6	54.3	21.5	57.7	22.1	10.7	4.2	14.7	4.6
N/P	28.8	7.7	183.7	87.9	67.3	26.9	99.1	27.6	91.0	25.6	134.8	119.4	115.2	44.9	343.4	79.9	132.3	35.8
Wid	12.7	2.2	9.5	3.7	13.1	2.5	15.8	4.8	10.0	3.2	13.0	4.4	10.7	2.3	7.0	1.0	26.3	17.1
Dep	0.6	0.1	0.9	0.4	0.6	0.1	0.7	0.2	0.5	0.1	0.5	0.2	0.5	0.1	0.9	0.1	1.1	0.5
Vel	0.5	0.1	0.2	0.0	0.5	0.1	0.4	0.1	0.3	0.1	0.5	0.2	0.4	0.1	0.3	0.1	0.3	0.1
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
WTur	1	52.6	1.5	100	1.5	80.0	1	72.7	1	100	1	75.0	2	36.4	1	100	1	66.7
FSed	2	47.4	2	50.0	2	20.0	1	54.5	2	36.4	2	50.0	1	54.5	1	66.7	1	66.7
BSub	3	52.6	2.5	100	3	70.0	3	72.7	3	63.6	3	50.0	3	36.4	2	100	3	33.3

Table 4B. Average environmental variables of the vegetation clusters 10 to18.

Variable	Cluster																	
	10		11		12		13		14		15		16		17		18	
	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error
pH	7.8	0.1	7.9	0.1	7.9	0.1	7.8	0.2	7.9	0.1	8.0	0.0	7.9	0.1	7.8	0.1	7.9	0.1
O_2	11.3	0.4	9.5	0.8	10.1	1.7	9.2	1.6	8.6	0.5	9.8	1.1	10.4	1.5	7.5	0.2	10.2	1.1
O_2-sat	108.0	1.8	91.5	7.5	95.3	15.4	91.5	19.6	84.2	5.5	95.3	12.2	101.0	12.8	72.0	2.3	97.2	9.2
BOD_5	4.9	0.6	2.7	0.3	2.1	0.1	3.8	0.6	2.8	0.3	3.4	0.5	2.0	0.2	1.8	0.3	2.1	0.2
Tot-N	2327.8	510.8	2489.0	365.7	3215.3	81.6	1469.0	162.6	2470.5	356.5	2907.8	909.9	2304.0	990.4	2534.0	454.3	2610.6	735.3
NO_3-N	1927.5	434.3	2070.3	378.6	2949.5	91.6	919.0	219.1	1715.3	274.5	2286.8	963.1	1919.8	973.1	1904.8	686.9	2242.0	702.1
NO_2-N	350.0	35.6	128.8	42.0	162.5	34.7	250.0	179.0	267.4	121.8	367.5	63.7	102.5	46.6	77.5	16.5	224.0	105.4
NH_4-N	31.5	6.4	21.8	12.0	13.3	8.4	17.3	11.1	288.5	218.6	49.5	35.1	18.0	7.5	16.0	7.5	30.0	10.3
Tot-P	44.8	5.9	68.2	14.4	47.5	14.4	93.3	26.9	84.6	18.5	93.5	22.1	81.8	29.9	66.8	32.5	108.6	61.1
PO_4-P	13.8	2.8	46.3	13.5	26.5	10.3	56.5	26.9	50.4	12.1	50.0	15.9	57.5	25.7	46.0	28.6	88.0	58.0
N/P	176.6	57.4	75.0	19.0	174.8	94.7	57.4	29.0	120.4	41.4	82.6	51.1	42.4	21.1	118.9	78.8	121.1	54.7
Wid	15.3	6.7	18.3	3.8	11.3	3.6	31.0	10.0	11.3	1.6	6.3	0.8	13.0	5.6	12.8	4.1	18.0	8.2
Dep	0.5	0.0	0.8	0.1	0.6	0.1	0.9	0.4	0.6	0.1	0.6	0.1	0.6	0.2	0.8	0.1	0.9	0.1
Vel	0.4	0.1	0.4	0.1	0.4	0.1	0.5	0.2	0.4	0.1	0.2	0.1	0.1	0.0	0.7	0.2	0.5	0.2
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fr
WTur	1.5	100	1	58.3	1	75.0	1.5	75.0	1	63.2	3	75.0	1.5	100	1.5	100	2	40.0
FSed	1	100	1	58.3	1	75.0	2	75.0	2	31.6	3	75.0	1.5	100	2.5	75.0	2	40.0
BSub	3	0.0	3	66.7	3	75.0	3	75.0	3	52.6	1	75.0	3	75.0	3	100	2	60.0

Table 4C. Average environmental variables of the vegetation clusters 19 to 23.

Variable	Cluster									
	19		20		21		22		23	
	Mean	Error	Mean	Error	Mean	Error	Mean	Error	Mean	Error
pH	7.8	0.1	7.8	0.1	7.8	0.1	7.9	0.1	7.6	0.1
O2	10.1	0.5	10.4	0.6	9.5	0.6	9.5	0.6	9.2	1.1
O2-sat	96.2	5.2	96.9	4.4	88.9	5.7	90.4	6.1	85.3	10.4
BOD_5	3.2	0.4	3.3	0.7	2.4	0.4	3.1	0.9	3.2	0.2
Tot-N	2954.0	454.1	2671.4	526.3	2504.8	510.0	2200.0	372.4	2195.3	383.5
NO_3-N	2476.3	441.9	2285.2	485.0	2074.8	553.3	1570.4	343.2	1587.9	495.1
NO_2-N	220.0	43.5	120.0	35.7	117.5	58.1	244.0	67.0	104.3	30.4
NH_4-N	109.4	83.9	40.1	26.8	11.9	6.3	18.4	6.9	168.4	165.6
Tot-P	128.4	54.2	175.0	102.5	91.3	37.0	65.0	20.8	54.0	16.2
PO_4-P	98.4	48.8	122.0	84.3	61.9	36.0	33.2	13.0	33.0	14.5
N/P	150.8	58.5	123.9	33.9	107.7	47.2	181.0	134.5	261.4	126.4
Wid	12.2	1.8	11.9	2.7	11.6	1.8	10.8	1.9	17.1	6.0
Dep	0.7	0.1	0.8	0.2	0.9	0.1	0.6	0.1	0.7	0.1
Vel	0.6	0.1	0.3	0.1	0.7	0.1	0.4	0.1	0.2	0.1
	Med	Fr	Med	Fr	Med	Fr	Med	Fr	Med	Fre
WTur	1	62.5	1	55.6	1	62.5	1	80.0	1	57.1
FSed	2	56.3	2	22.2	1.5	75.0	1	80.0	2	28.6
BSub	4	100	4	100	4	100	4	100	4	100

plant communities of different types can grow in every habitat type; also, communities of a certain type can occur in different type habitats. Only the distribution of the communities of cluster 8, dominated by *Nuphar lutea* and *Sagittaria sagittifolia*, is limited to one (3rd) habitat type.

Discussion

As all Estonian rivers and streams are situated at an altitude of 0–200 m from sea level, their vegetation communities fit rather well the eutrophic lowland community group which is one of the four floral river groups established in Great Britain (Holmes *et al.* 1998). The same conclusion was made by Riis *et al.* (2000) concerning the Danish rivers.

According to the prevailing life form of the dominating species, the distinguished community types (clusters) can be arranged into the following four groups (the species are presented in alphabetical order):

1. Communites of helophytes: *Equisetum fluviatile* (cluster 5), *Mentha aquatica* (cluster 6), *Phalaris arundinacea* (cluster 16), *Phragmites australis* (cluster 2), *Sium latifolium* (cluster 15), *Sparganium erectum* (cluster 1);
2. Communities of the rooted vegetation with floating leaves (*Nymphoidea*): *Nuphar lutea* (cluster 7), *Nuphar lutea–Sagittaria sagittifolia* (cluster 8), *Potamogeton natans* (cluster 12);
3. Communities of submerged vegetation: *Butomus umbellatus* (cluster 3), *Hippuris vulgaris* (cluster 4), *Potamogeton alpinus* (cluster 13), *P.* × *meinshausenii* (cluster 10), *P. perfoliatus* (cluster 17), *Ranunculus trichophyllus* (cluster 18), *Sagittaria sagittifolia* (cluster 9), *Schoenoplectus lacustris* (cluster 14), *Sparganium* spp. (cluster 11);
4. Communities of mosses and macroalgae on stones: *Amblystegium riparium–Fontinalis antipyretica* (cluster 23), *F. antipyretica* (cluster 22), *F. antipyretica–Cladophora glomerata* (cluster 20), *C. glomerata* (cluster 19), *Vaucheria* spp. (cluster 21).

Thus the submerged vegetation, dominating altogether in 72 communities and nine com-

Table 5. Significance level of the effect of the environmental variables on the occurrence of the dominating species according to generalised linear model logit link analyses (type III sums of squares test); only values $P \leq 0.050$ are presented. Denotations as in Table 3.

Species	Environmental parameter																
	pH	O_2	O_2-sat	BOD_5	Tot-N	NO_3-N	NO_2-N	NH_4-N	Tot-P	PO_4-P	N/P	Wid	Dep	Vel	WTur	FSed	BSub
Butomus umbellatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.011	–	–
Equisetum fluviatile	–	–	0.043	0.034	–	–	–	–	–	–	–	–	–	0.002	–	0.039	–
Hippuris vulgaris	–	–	–	–	–	0.026	0.001	0.012	0.042	0.001	0.012	–	–	–	–	–	–
Mentha aquatica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nuphar lutea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phalaris arundinacea	–	–	–	–	–	–	–	0.021	–	0.031	0.004	–	–	–	–	0.016	–
Phragmites australis	–	–	–	–	–	–	–	–	–	–	–	–	–	0.003	–	–	–
Potamogeton x *meinshausenii*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potamogeton alpinus	–	–	–	0.030	–	–	–	–	–	–	–	0.001	–	–	0.001	0.025	–
Potamogeton natans	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potamogeton perfoliatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ranunculus trichophyllus	–	–	–	0.012	–	–	–	–	–	–	–	–	–	–	0.015	0.001	–
Sagittaria sagittifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Schoenoplectus lacustris	0.003	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.022	–
Sium latifolium	0.004	–	–	–	–	–	–	–	–	–	–	–	–	–	0.001	–	0.014
Sparganium erectum s.l.	–	–	–	–	–	–	–	0.002	–	0.008	0.006	–	–	–	–	–	–
Sparganium spp. (*S. emersum*)	–	–	–	–	–	–	–	–	–	–	–	0.017	–	–	–	–	–
Veronica anagallis-aquatica	–	–	–	–	–	–	–	0.049	–	–	–	–	–	–	–	–	–
Amblystegium riparium	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.039	–	–
Cladophora glomerata	–	0.031	–	–	–	–	–	0.038	–	–	–	–	–	–	–	0.047	–
Fontinalis antipyretica	–	0.042	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vaucheria spp.	–	0.003	0.008	–	–	–	–	–	–	0.038	–	–	–	–	0.046	0.043	0.032

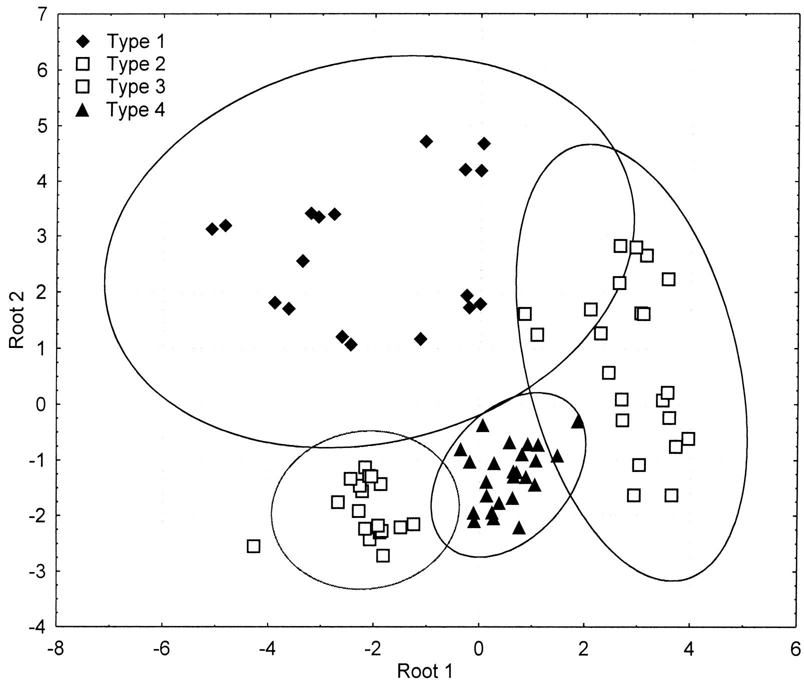

Fig. 2. Scatterplot of the habitats (river reaches) canonical scores, root 1 *vs.* root 2. The marks of every species-cluster are surrounded by the prediction interval ellipse (probability $\alpha = 0.95$).

munity types, is by far the most prominent in sample. The helophytes and cryptogams have an almost equal representation, prevailing in 46 communities and six community types, and in 45 communities and five community types, respectively. The *Nymphoidea*, dominating in only 18 communities and three community types, have a rather limited distribution.

The most frequent community types were dominated by *Sparganium erectum s. lato* and

Table 6. Centroids of the habitat types (reach clusters) established by 6 physical environmental parameters. Mean = arithmetical mean, E_m = error of mean, Med = median, Fr = frequency (%). The last four parameters presented here were not included in the analysis. Denotations as in Table 3.

Parameter	Cluster							
	1 (18)		2 (22)		3 (18)		4 (15)	
	Mean	E_m	Mean	E_m	Mean	E_m	Mean	E_m
Wid	16.1	3.5	14.8	1.6	8.1	0.9	11.3	1.5
Dep	0.9	0.1	0.6	< 0.0	0.8	0.1	0.6	0.1
Vel	0.2	< 0.0	0.7	0.1	0.3	< 0.0	0.4	0.1
	Med	Fr	Med	Fr	Med	Fr	Med	Fr
WTur	2.5	100	1.5	95.5	1.0	100	1.0	100
FSed	2.5	77.7	1.0	68.2	1.0	61.1	2.0	36.0
BSub	2.0	38.9	4.0	90.9	2.0	94.4	3.0	100
Stones		5.6		90.9		0.0		4.0
Gravel		33.3		9.1		0.0		96.0
Sand		38.9		0.0		94.4		0.0
Clay + silt		22.2		0.0		5.6		0.0

Schoenoplectus lacustris (n = 19), followed by *Cladophora glomerata* (n = 16) and *Sparganium* spp. (n = 12). Besides the communities recorded from at least three reaches, stands with dominating *Catabrosa aquatica, Glyceria maxima, Menyanthes trifoliata* and *Typha latifolia* were described from two reaches and stands with dominating *Berula erecta, Potamogeton crispus* and *P. lucens* from one reach. Many of these communities, rare in the drainage basins of the southern coast of the Gulf of Finland are, according to the preliminary data, more common in the other drainage basins of Estonia. In addition, the small assemblages of the macroscopic red algae *Batrachospermum moniliforme, Chantransia chalybea, Lemanea*, the green alga *Chaetophora* and macroscopic films of blue-green algae (*Phormidium* spp.) were sometimes found in various combinations on stones.

We failed to discover any geographical regularity in the distribution of the established community types within the studied drainage basin. This is obviously related to the comparatively low variation of the ecological features of the studied reaches.

Table 7. Representation of vegetation types in habitat types.

Vegetation type	Habitat type				
	1	2	3	4	Total
1	3	9	1	6	19
2	2	–	1	1	4
3	2	3	–	5	10
4	2	3	2	4	11
5	–	3	1	7	11
6	1	1	1	1	4
7	3	3	3	2	11
8	–	–	3	–	3
9	1	–	1	1	3
10	–	2	2	–	4
11	4	1	1	6	12
12	–	2	1	1	4
13	1	2	–	1	4
14	5	3	3	8	19
15	3	–	–	1	4
16	–	3	1	–	4
17	1	1	–	2	4
18	2	1	1	1	5
19	1	6	2	7	16
20	2	4	3	–	9
21	2	3	2	1	8
22	1	–	1	3	5
23	2	1	1	3	7
Total	38	51	31	61	181

Almost all established clusters (community types) have a single dominant (Tables 2). Two dominants are characteristic of the communities of cluster 8 (*Nuphar lutea*, *Sagittaria sagittifolia*), cluster 15 (*Schoenoplectus lacustris*, *Sium latifolium*) and cluster 20 (*Fontinalis antipyretica, Cladophora glomerata*). The most species-rich are the communities dominated by *Schoenoplectus lacustris* (cluster 14, 51 taxa) and *Sparganium erectum* (cluster 1, 49 taxa), to a lesser extent also the communities of *Sparganium* spp. (presumably *S. emersum*, cluster 11, 45 taxa) and *Butomus umbellatus* (cluster 3, 41 taxa). Remarkably species-poor, in comparison with the vascular species dominated communities, are all assemblages of cryptogams (clusters 19–23, 6–18 taxa altogether).

Low species number, frequent monodominance and a comparatively simple structure of the plant communities of flowing waters have been recognised by numerous authors for different countries and climatic zones (e.g. Butcher 1933, Gessner 1955, den Hartog & Segal 1964, Wiegleb 1981a, 1981b, Feoli & Gerdol 1982, Chernaya 1987, Muotka & Virtanen 1995). Development of such dominance controlled communities (*sensu* Yodzis 1986) can be largely explained by the vegetative multiplication of water plants, but also with the ability of the propagules to attach to a suitable substrate (Gessner 1955, Shilov 1975, Ellenberg 1988, Sinkevichiene 1992, Willby 2002). The floristic composition of the studied watercourses is not affected by the cutting of aquatic weeds which is a common practice in many West European countries (e.g. Best 1994, Baattrup-Pedersen & Riis 1999, Riis *et al*. 2001).

Most of the community types established in the current study are, with certain geographical variations, well-known and widely represented in Europe; only the communities dominated by bryophytes and/or algae have been less described. Nevertheless, comparison of the ecological optima or amplitude limits estimated by different researchers for the same species clearly shows that these values are often rather inconsistent.

For example, Kohler *et al.* (1971) have argued that the communities of *Sparganium erectum* (cluster 1) have a relatively small ecological amplitude and are usually distributed in river sections where the content of PO_4 and NH_4 ions is low. According to Newbold and Holmes (1987), this species is the most common in mesotrophic to eutrophic waters, while according to Ellenberg (1988) it can grow in rather heavily polluted rivers. More recently, Grasmück *et al.* (1995) found that *S. erectum* dominated communities are ecologically ubiquitous. The data of the current analysis show that in comparison with the other community types, communities of this type are characterised by the highest NH_4-N, total P and PO_4-P content in water, while the N/P ratio is minimal and water is relatively poor in oxygen (Table 4A). GLZ analysis confirms that the occurrence of *S. erectum* is significantly associated with the NH_4-N and PO_4-P content in water as well as with the N/P ratio (Table 5).

We usually found the communities dominated by *Mentha aquatica* (cluster 6) in reaches where the content of NO_2-N and NO_3-N in water was comparatively low (Table 4A). Our results are consistent with those of Carbiener *et al.* (1990) who estimated that *M. aquatica* is confined to highly oligotrophic water, however, according to Newbold and Holmes (1987), this species is present more often in oligo-mesotrophic to eutrophic rivers. Ellenberg (1988) has noted the high tolerance range of this species, which is able to grow in clean to rather heavily polluted waters.

The species-poor communities with the dominating *Potamogeton natans* (cluster 12) were recorded from reaches with O_2-rich water, where also the content of total N and NO_3-N was high, while content of NH_4-N and BOD_5 were relatively low (Table 4B). A low content of PO_4-P and NH_4-N was estimated in the water of such communities also by Kohler *et al.* (1971). Still, Newbold and Holmes (1967) argued that *P. natans* grows mainly in meso-eutrophic to eutrophic rivers. Rodwell *et al.* (1995) noted that in Great Britain these communities are tolerant of nutrient poor conditions and turbulent waters. According to Oberdorfer (1992), in southern Germany similar communities are encountered in bog pools with a low degree of trophy and acidic water.

Communities with the dominating *Fontinalis antipyretica* (cluster 22) or *Amblystegium riparium* (cluster 23) were identified from reaches where the water is relatively poor in chemical compounds (Table 4C). According to GLZ analysis, *F. antipyretica* responds significantly to water O_2 content, while *A. riparium* is affected by water turbidity (Table 5). Numerous authors (Sirjola 1969, Kohler *et al.* 1971, Rautava 1972, Newbold & Holmes 1987, Ellenberg 1988, Virtanen 1995, Muotka & Virtanen 1995) have noted the wide ecological tolerance of *F. antipyretica*; according to Carbiener *et al.* (1990) it can grow in oligo-mesotrophic to eutrophic waters. Therefore, the communities dominated by *F. antipyretica* can thrive in different kinds of flowing waters in an extensive geographical area (cf. also Backhaus 1967, Rautava 1972, Arendt 1982, Bogachev 1986, Vitt *et al.* 1986, Vuori *et al.* 1999). In England, communities of *A. riparium* are closely associated with organic pollution growing, for example, in brewery effluent channels (Kelly & Huntley 1987, Birch *et al.* 1989); Newbold and Holmes (1987) identified *A. riparium* as a mesotrophic to a eutrophic species.

Based on these four examples (*Sparganium erectum*, *Mentha aquatica*, *Potamogeton natans*, and the mosses *Fontinalis antipyretica* and *Amblystegium riparium*), we agree with Barendregt and Bio (2003) that there is no one explicitly prevailing environment variable explaining the structure or distribution of macrophyte communities; each individual species displays its specific preference by setting of variables. Different opinions about the ecological optima or amplitude limits for one and the same species evidently arise from the much higher ecological tolerance of the concerned species than a researcher can usually grasp for a certain geographical region. The dominants in all discussed community types (except for *Potamogeton* × *meinshausenii*) have a large ecological amplitude (Shilov 1975, Ellenberg 1988) and a very extensive distribution area. According to Hultén and Fries (1986) and Kuz'michev (1992), species such as *Butomus umbellatus*, *Nuphar lutea* and *Sparganium emersum* occur widely in whole Eurasia, *Potamogeton alpinus* in Europe and in western and central Siberia, *Sium latifolium* in

Europe and in western Asia, and *Schoenoplectus lacustris* in Eurasia and in northern Africa. *Phragmites australis* is considered a nearly cosmopolitan species, and the remaining ten dominating species have a circumpolar distribution, occurring in Eurasia and in northern America. All this supports the intrazonal character (Grigor'ev & Solomeshch 1987) of aquatic vegetation communities.

Discrepancies between the results of different authors are largely connected also with the methods employed in data sampling, first of all, with the scale followed in establishment of sample units. For example, while Shilov (1975), Sinkevichiene (1992) or Rodwell *et al.* (1995) used sample plots of 4 m^2 for description of aquatic plant communities, Golub and Losev (1990a) used plots of 4–100 m^2, Backhaus (1967), Thièbaut and Muller (1999) sampled river stretches of 50 m, Wiegleb (1981a, 1981b, 1983, 1984), Wegener (1982), Grasmück *et al.* (1995) sampled stretches of 50–100 m, and Raven *et al.* (1997) and Demars and Harper (1998) sampled stretches of 500 m, then it is certainly difficult to reach an agreement of results. Obviously, more efforts should be directed towards unification of the research methods for aquatic vegetation as well as towards specification of the scale and use of 'plant community', 'habitat' and other related terms.

Floristic remarks

A characteristic feature of the studied communities is the predominance of submerged life forms. For example, *Butomus umbellatus, Hippuris vulgaris* and *Sagittaria sagittifolia* occurred almost exclusively as submerged forms; also *Sparganium* spp. and *Schoenoplectus lacustris* were mostly represented by submerged forms, though in several reaches they were also growing as emergents. *Sparganium erectum s. lato* was represented mainly by the subsp. *microcarpum*. Submerged plants or vegetative plants of *Sparganium* with floating leaves and without reproductive organs were determined as *Sparganium* spp. Presumably, the majority of them belong to *S. emersum*; however, submerged vegetative specimens of *S. erectum* and *S. emersum* are similar and difficult to distinguish.

The poorly known hybridogenous species *Potamogeton* × *meinshausenii* was described by Juzepchuk in 1955 and was considered an ancient hybrid of *P. pectinatus* × *P. vaginatus*. It was proved by herbarium material that this species was rather widely distributed in northwestern and northern Russia (Mäemets 1984). A similar taxon, *P. bottnica* occurring nowadays in the coastal regions of the Gulf of Bothnia, can be regarded as the synonym of *P.* × *meinshausenii*. Mäemets (1984) was of the opinion that the species under discussion may represent an ancient hybrid of *P. vaginatus* with *P. filiformis*, as some of its important anatomic and morphological features (e.g. obtuse leaves, partially closed leaf sheaths) are not characteristic of *P. pectinatus* but of *P. filiformis*. Sharing this standpoint, we did not use the name *P. bottnica* in the current study. *Potamogeton* × *meinshausenii* formed communities in four reaches of one tributary of the Jägala River. A similar community type has been described from some other drainage basins in Estonia (Trei 2001). In rivers of Lithuania *P.* × *meinshausenii* forms dense monodominant assemblages (Sinkevichiene 1992).

Callitriche spp. was found with low abundance altogether in seven reaches; as a dominating species it was recorded from only one reach in 1995 but not later. According to Tabaka *et al.* (1996), *C. cophocarpa* is considered frequent in Estonia. In our material, collected from several Estonian watercourses, *C. hermaphroditica* seems to be quite frequent, occurring always in small quantities.

The genus *Ranunculus* is represented by three species in Estonian watercourses: *R. circinatus, R. lingua* and *R. trichophyllus*. The first of them was registered from two reaches as small assemblages; *R. lingua* was rather frequent, occurring in 26 reaches and forming smaller or larger stands or growing as single specimens; *R. trichophyllus* occurred altogether in 12 reaches and was dominating in five communities (Table 2B).

Myriophyllum spicatum and *M. verticillatum* were both recorded from two reaches, *M. spicatum* dominated in one reach.

Hippuris vulgaris occurred as f. *submersa* in 23 reaches and formed large monodominant communities in 11 reaches (Table 2B).

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