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The influence of river functionality on habitat selection by Ephemeroptera in spatially and temporally diverse lowland rivers, with particular reference to the River Bug

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Abstract

The purpose of this work is the designation of changes in the environmental preferences of mayflies in the prevailing conditions in a large lowland river little changed by human activity. During the study, the occurrence of the following species were recorded: *Cercobrachys minutus* (54.2%); *Procloeon nana* (24.5%); *Pseudocentroptiloides shadini* (7.6%); *Ametropus fragilis* (2.9%), which were numerously represented and formed a permanent element of the fauna, and *Baetopus wartensis* (0.1%) and *Oligoneurisca borysthenica* which were noted very rarely and were accidental species. The differences and similarities in the functionality of the psammophilous and other mayfly assemblages were assessed. The data from the last fifteen years of study was investigated and compared with those from other rivers which were more managed. PCA was used to distinguish the main factors influencing habitat selection at particular stages of life history and the tendency for drifting.

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INTRODUCTION

Due to difficulties with their localization, psammophilous mayflies are not easy to study ecologically (McCafferty 1991), which is why knowledge about the environmental demands of particular species from this group is not extensive. However, mayflies are important links in the trophic chains of water organisms and so there is a need to understand their requirements.

In recent years, changes in the species composition of their assemblages have been observed as expressed by the loss of some species and structural alterations in communities based on the strong domination of a few species (Sowa 1990).

It was decided, therefore, to investigate the little known changes in habitat preferences which occur during the life cycles of mayflies inhabiting the River Bug. The investigations of these habitat preferences and adaptability to environmental changes are valuable for their protection and, in turn, for the protection of the whole assemblage of psammophilous species.

THE AREA OF THE STUDY

The River Bug does not show strong erosional activity. Therefore, the diameter of the particles does not exceed 20 mm, which corresponds with the size class defined as gravel. The speed of the water is very changeable. In the slow reaches the bottom debris stabilizes, and the lack of turbulent movement allows suspended inorganic and organic particles to settle on the river bed. The speed of the water current also determines the shape of the river bed. It changes from a uniformly flat form, which is maintained during slow flow, through surface rippling, to dune forms with large asymmetric humps.

The wide, shallow, unstable bed of the River Bug creates good conditions for the formation of sand bars shaped in asymmetric dunes with gentle proximal and steep distal slopes. They are formed in the winter and spring when high water levels are prevalent and large amounts of sand are moved. In the summer, when the flow is at its lowest, they become exposed and alluvial islands are gradually eroded, washed away, and metamorphosed. Depending on water velocity, the deposited material is segregated or moved en masse from one place to another. Shifting sandy beds are fixed and a considerable area can be covered by silt.

According to the classification proposed by Church (1992), the channel of the River Bug is described as irregular, wandering, and with frequent, irregular channel islands. The mean width of the river is 130 m with a gradient of 0.1 per thousand and a discharge of 127 m^3 s^{-1}, and fluctuations in water level reach

5 m (Swenson 2000). The current survey showed that the mean depth in the summer is 1 m and current velocity is 0.7 m s^{-1}.

The low stability of the substratum results in the failure of vegetation becoming established and forming dense stands. In the backwaters there are species from the phytocenoses *Potamogetum perfoliati* and *Elodeetum canadensis*, while the banks of the river are overgrown by grasses from the *Phalaridetum arundinacea* association. These grasses only develop on some parts of the river bank and form a narrow strip about 1 m wide. More often the banks are overgrown by willow scrub that enter deeper into the channel and slow the water current in this 2-3 m zone causing the sedimentation of marginal silts. Lentic still waters and stony substrata are rare, and only where there is human activity do they have an impact. Together, all these environments cover about 5% of the river bed, the rest is comprised by sands.

The water of the River Bug was monitored by the Provincial Inspectorates for Environmental Protection in Siedlce and Biała Podlaska. Their negative assessments were influenced only by some indicators; the water contained too much suspended matter and had a high concentration of chlorophyll *a*. Periodically, it had increased BOD and a high concentration of total phosphorus. The most important feature of the water was the high level of dissolved oxygen, which has the greatest impact on mayfly fauna (Table 1).

Table 1

Selected parameters that characterize waters of the River Bug in Kózki and Brok. Values which indicate poor water quality are circled

Localities	Kózki (52°21’ N 22°52’ E)						Brok (52°41’ N 21°50’ E)					
	1989			1994			1989			1994		
Indices	Min	Max	Average	Min	Max	Average	Min	Max	Average	Min	Max	Average
pH	7.3	8.7	8.2	7.2	9	8.1	7.2	8.2	7.8	7.9	9	8.4
dissolved oxygen [mg 0_2 l^{-1}]	7.4	18.4	12.6	6.6	14.2	10.5	7	12.8	9.7	5.2	12.7	9.7
% oxygen saturation	62	202	115	62	148	94	60	110	79	43	121	88
BOD_5 [mg 0_2 l^{-1}]	2	19	5	2.1	7.3	3.9	2.4	13.3	7.3	2.3	15.3	5.8
dissolved matter [mg l^{-1}]	-	-	-	333	458	401.5	208	464	332.4	154	481	375.1
conductivity [μS cm^{-1}]	110	480	296	336	791	662	-	-	-	282	884	556
total suspension [mg l^{-1}]	9	85	28	3	61	24	3	86	38	8	70	28
ammonium [mg N NH_4 l^{-1}]	0.2	2	0.93	0.21	1.3	0.52	0.01	0.32	0.11	0.05	1.5	0.32
nitrates [mg N NO_3 l^{-1}]	0.1	6	1.6	0.04	4.3	1.4	0.02	2	0.74	0.04	2.5	1
total nitrogen [mg N l^{-1}]	-	-	-	1.6	6.2	3.3	-	-	-	1.57	3.97	2.74
phosphates [mg PO_4 l^{-1}]	0.9	7.3	2.9	0.26	1	0.5	0.1	1.63	0.51	0.14	0.67	0.39
total phosphorus [mg P l^{-1}]	-	-	-	0.13	0.86	0.3	-	-	-	0.08	0.44	0.22
chlorophyll *a* [μg l^{-1}]	-	-	-	4	212	71	-	-	-	60	238	112

SUBJECT OF INVESTIGATION

Psammophilous mayflies show adaptations for partial or complete burial in the sand or living on its surface (Edmunds and McCafferty 1996). Burrowing species, whose nymphs can sometimes exist in sand, inhabit more compact substrata. One of the main adaptations, which is characteristic of most of them, is their very long claws, which are unparalleled in other species. Such structures enable nymphs to anchor themselves among the grains of sand or hold themselves over a thin layer of fine silt. Furthermore, they are good swimmers and this enables them to move very quickly from one place to another. The streamlined shape of the body makes such behaviour easier. Other species, which cover their bodies with sand, have very short claws (or no claws at all), but they are all filter feeders. Shifting sand prevents the establishment of algae and water turbulences resist the sedimentation of suspended matter. Nymphs of species, which stay partially covered by sand with the aid of rows of bristles located on the forelegs and some mouth parts, strain organic matter. In *Oligoneurisca borysthenica*, there are tufts of additional gills near the base of the forelegs and the mouth parts for increased oxygen exchange when abdomen is covered by sand.

All nymphs that inhabit sand have brightly coloured bodies; most often they are light brown with a faintly marked pattern of darker pigmentation. Generally, the brown spots appear on the middle tergites of the abdomen and imitate darker grains of sand. The background of the rest of the body merges with the colour of the lighter fractions of the sand, so coloured nymphs are noticeable only when they move. *Cercobrachys minutus* nymphs, which are among the smallest mayflies, are more intensely pigmented and mimic darker lumps of substratum to which they most often attach.

MATERIALS AND METHODS

Preliminary investigations, which were undertaken in the early 1980s (Głazaczow 1998), indicated that the River Bug is inhabited by psammophilous mayflies. This prompted undertaking systematic studies that began a few years later and concluded in 2001. Winter time was omitted from the current study. Nymph locations were established with the kicking technique, and the disturbed animals were gathered into a hand net. Standardized samples were collected with a Surber sampler that extracted mayflies from 0.05 m^2 of substratum. In total, 365 such samples were analyzed in groups of fives from each location (73×0.25 m^2). A drift net was deployed to complete the collection. In order to establish the life cycle stages, changes in nymph body length over the following months were investigated.

Statistical analysis

Ordination techniques (Jongman et al. 1995), specifically principal component analysis, were applied to identify environmental gradients that could influence the quantitative composition of the assemblages. The comparison of community species composition was calculated with the between-group linkage Euclidean distance method. The confidence limits for density were calculated with the bootstrap method, and the confidence limits for frequency with the method proposed by Krebs (1989). Kruskall–Wallis nonparametric ANOVA was used to test for differences in dependent variables among groups. In lieu of post-hoc multiple comparisons procedures, Dunn's test was applied with Alpha set at 0.05. All statistical analyses were performed using Statistica version 6.0 for Windows and analizaTOR version 2.0.

RESULTS

The assemblage of psammophilous mayflies in the River Bug was composed of almost all the European species (except *Beninghia ulmeri*), but only four, *Cercobrachys minutus, Ametropus fragilis, Procloeon nana,* and *Pseudocentroptiloides shadini,* were abundant and form the permanent element of the fauna. The remaining two species, *Baetopus wartensis* and *Oligoneurisca borysthenica,* were noted very rarely and were accidental species.

Cercobrachys minutus was the most numerous species, although its nymphs did not exhibit special adaptations for maintaining themselves on a shifting substratum. They occupied the largest area of the river bed, but were dominant (D=45%) in the shallows with silty-sand substratum. They were not adapted to rapid dislocation and so preferred more stable parts of the river bed. In addition to compact sand, they were found occasionally on shifting substratum where they were attached to particles of gravel. Observations indicated that their distribution was grouped. The highest average density was in July (28 nymphs/0.25 m^2) with a frequency of 70%.

Procloeon nana was also an abundant species (D=24%). It occurred in different parts of the river-bed and was more numerous in places where depth did not exceed 50 cm. It dwelt on silty and compact sands, where the substratum formed a varied structure and silty sections were covered by thin layers of sand, and it avoided mud in places without a current. The largest density (92 nymphs/0.25 m^2) was noted in June and was the highest of all psammophilous mayflies. However, their average values from June (14 nymphs) were nearly the same as in July (13 nymphs) with frequencies of 70% and 60%, respectively.

Pseudocentroptiloides shadini occupied similar habitats to the species mentioned above, but it was considerably less abundant (D=8%). It occurred occasionally on silty-sand substratum, but more numerously on the compact sand near the transitional zone between these two substrata. Consequently, it was quite frequently gathered in slightly deeper places (40 - 70 cm). The maximum density (34 nymphs/0.25 m^2) occurred at the end of June, with an average of 8 nymphs and a frequency of 40% and similarly in the following month (7 nymphs and 38% frequency).

Ametropus fragilis preferred compact sand substratum, which enabled the nymphs to cover themselves with sand, and therefore they avoided the silty bed. It was found in the samples collected deeper (30 - 60 cm) and not numerously in the shifting sand. On average, 3 nymphs (max. 10) were noted on 0.25 m^2. The low density was matched by low frequency (28%).

From the scarcity of data concerning other species (*Baetopus wartensis, Oligoneurisca borysthenica* noted in the early 1980s), it can be surmised that they occur on the compact sand substratum. The examples of the distribution of psammophilous mayflies in the cross-section profile of the river bed, depending on substratum and depth, are presented in the Fig. 1.

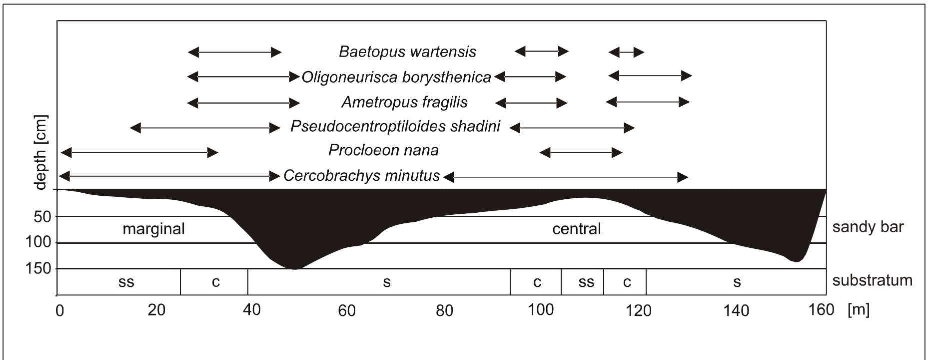

Fig. 1. Distribution of psammophilous mayfly nymphs on a cross profile of the River Bug channel in the place where two sandy bars were formed; c- compact sand, s – shifting sand, ss –silty-sand, substrata.

Thirteen species not included in the psammophilous group were found on the silty-sand substratum. Only two species, *Caenis pseudorivulorum* and *Procloeon bifidum*, were more abundant there. Their densities were significantly lower than most of psammophilous species and did not reach 10 specimens on 0.25 m^2 with a frequency of 15-45%. The next three species, *Brachycercus harrisella, Caenis macrura*, and *Ephoron virgo*, were considerably less abundant. On 0.25 m^2, only a few nymphs of these species were noted at a frequency of about 10%. The remaining species, *Procloeon pulchrum, Labiobaetis tricolor, Baetis buceratus, Seratella ignita, Heptagenia flava, Ephemera danica, Ephemera vulgata*, and *Oligoneuriella pallida*, occurred on the silty-sand substratum occasionally and were noted only in the qualitative samples. The numerical characteristics of the mayfly nymph assemblages are presented in Table 2.

Table 2

Numerical characteristics of the mayfly nymph assemblages populating substrata in the River Bug (73 samples); psammophilous species are distinguished by bold type. The mean intensity of density is given for species represented by more than one specimen.

Species	Mean density	95% confidence interval	Mean intensity of density	95% confidence interval	Frequency [%]	95% confidence interval	Domination [%]
C. minutus	**11.92**	**7.72-18.11**	**19.9**	**12.9-30.2**	**60.0**	**46.5-72.4**	**45.2**
P. nana	**6.46**	**3.51-12.26**	**12.9**	**7.0-24.5**	**50.0**	**36.8-63.2**	**24.5**
P. shadini	**2.01**	**1.09-4.04**	**5.7**	**3.1-11.5**	**35.0**	**23.1-48.4**	**7.6**
C. pseudorivulorum	1.53	0.96-2.40	3.7	2.3-5.8	41.7	29.1-55.1	5.8
P. bifidum	1.39	0.18-6.46	13.9	1.8-64.6	10.0	3.8-20.5	5.3
C. macrura	0.90	0.16-3.83	6.0	1.0-25.5	15.0	7.1-26.6	3.4
A. fragilis	**0.77**	**0.44-1.37**	**2.7**	**1.6-4.8**	**28.3**	**17.5-41.4**	**2.9**
E. virgo	0.42	0.12-1.16	4.2	1.2-11.6	10.0	3.8-20.5	1.6
B. fuscatus	0.32	0.08-0.97	3.2	0.8-9.7	10.0	3.8-20.5	1.2
B. harrisella	0.25	0.04-1.03	3.8	0.6-15.4	6.7	1.8-16.2	1.0
Baetis sp.	0.15	0.06-0.28	1.3	0.5-2.4	11.7	4.8-22.6	0.6
B. buceratus	0.05	0.00-0.15			1.7	0.0-8.9	0.2
B. wartensis	**0.04**	**0.00-0.11**	**1.1**	**0.0-3.4**	**3.3**	**0.4-11.5**	**0.1**
H. flava	0.03	0.00-0.08	1.0	0.0-2.5	3.3	0.4-11.5	0.1
H. fuscogrisea	0.03	0.00-0.08	1.0	0.0-2.5	3.3	0.4-11.5	0.1
O. pallida	0.03	0.00-0.08	1.0	0.0-2.5	3.3	0.4-11.5	0.1
Labiobaetis sp.	0.02	0.00-0.01			1.7	0.0-8.9	0.1
E. notata	0.02	0.00-0.01			1.7	0.0-8.9	0.1
P. pulchrum	0.02	0.00-0.01			1.7	0.0-8.9	0.1

An attempt to explain the influences of environmental factors on the distribution of mayfly nymphs is presented in the ordination diagram (Fig. 2). Isolines show the number of species in a particular sample. Most of the species are grouped into the shallow places with fast moving water. *C. minutus* is the only species which chooses the coarse particle substratum, which is the result of its tendency to hold on to particles of gravel. Similarly, *Oligoneuriella pallida* lives on the stable parts of the substratum, and *Ephoron virgo*, a burrowing species, prefers non-eroded parts of the bed. The shallow, swift water with substratum of compact sand is occupied by *P. shadini* and similarly *Baetis fuscatus* and *Caenis pseudorivulorum*, which periodically colonize compact sand from other substrata such as plants, wood, etc. *P. nana* preferred fine sand and slow currents, while *A. fragilis* and *Caenis macrura*, which live on stones or muddy beds and also enter quiet pools, preferred deeper water.

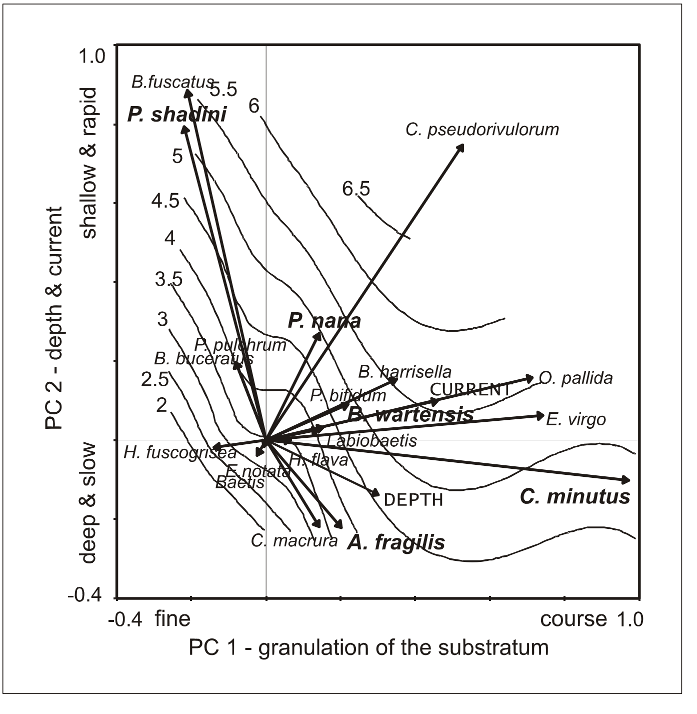

Fig. 2. Ordination diagram (PCA) of the mayfly nymph assemblage occurring on the substratum in the River Bug. Isolines show the number of species recorded in particular samples. Additional variables (current and depth) facilitate the interpretation of the axis. Psammophilous species are distinguished by bold type.

Changes in water level caused variations in the quality of particles which bind the river bed. The adaptation for this is the rapid displacement expressed by the tendency to drift. These dependencies are presented in an ordination diagram (PCA) of the mayfly nymph assemblage drifting with the current (Fig. 3). Psammophilous mayflies living on the less stable substrata were frequent elements of drift. The species that made up the greatest proportion of this drift element was *P. nana,* which occupied the most changeable bed. Pieces of dead wood inhabited by *Heptagenia flava* and *Caenis pseudorivulorum* are included on the list of unstable substrata. Wood transported by the river becomes stranded in the shallows and partially dries out, so mayflies living on it have to drift and find other suitable substrata. *Procloeon bifidum* nymphs were also frequently noted in the drift nets. This is one of the most abundant species in the River Bug and, therefore, was numerously transported by the water.

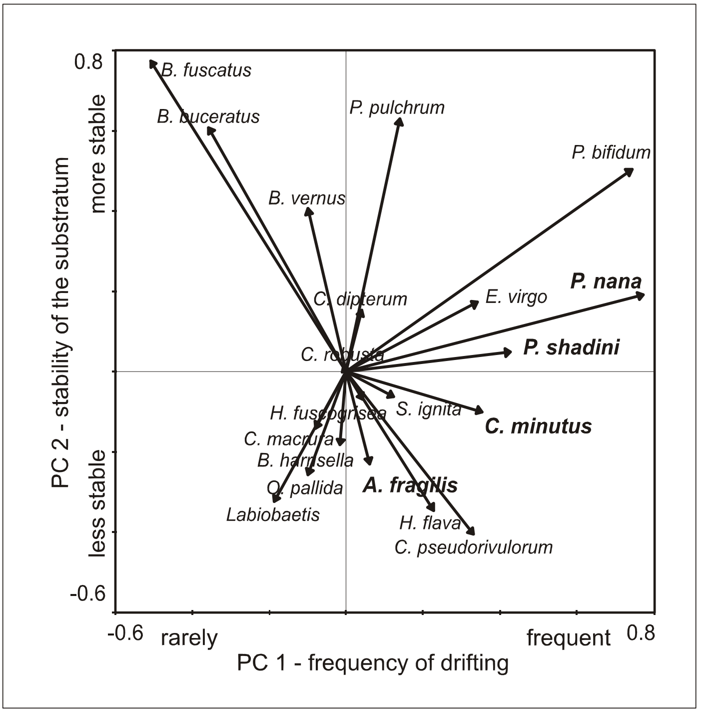

Fig. 3. Ordination diagram (PCA) of the mayfly nymph assemblage drifting with the current. Stability of the substratum refers to the environment of the nymphs. Psammophilous species are distinguished by bold type.

Similarly, *Ephoron virgo* nymphs that were completing their life cycle swam with the water just before their synchronized emergence.

Most of the mayfly species occurring in this area were characterized by development in the summer period. All psammophilous species have one generation during the year, and except for *A. fragilis*, development of their nymphs is weakly synchronized so they are noted in all summer months. They appear at the beginning of June, their numbers gradually increase to a maximum in July, and in the following months their numbers decrease. The period of the colonization of sandy substratum finishes in September. This scheme of colonization of sandy substratum is typical for the more numerous species of *C. minutus* and *P. nana*. *P. shadini* is characterized by a somewhat different intensity of colonization. Their nymphs were observed in the greatest numbers in June and the following months showed a gradual decrease in numbers. It was difficult to determine the maximum point of population development for rare species (*B. wartensis*, *O. borysthenica*), but it was inferred from the scarce data that they also occurred between June and September. The growth of *A. fragilis* nymphs lasted longer; it began in June and July reaching the greatest abundance in August when there was a decrease in the numbers of other species, and it finished in the spring with emergence in May (Fig. 4).

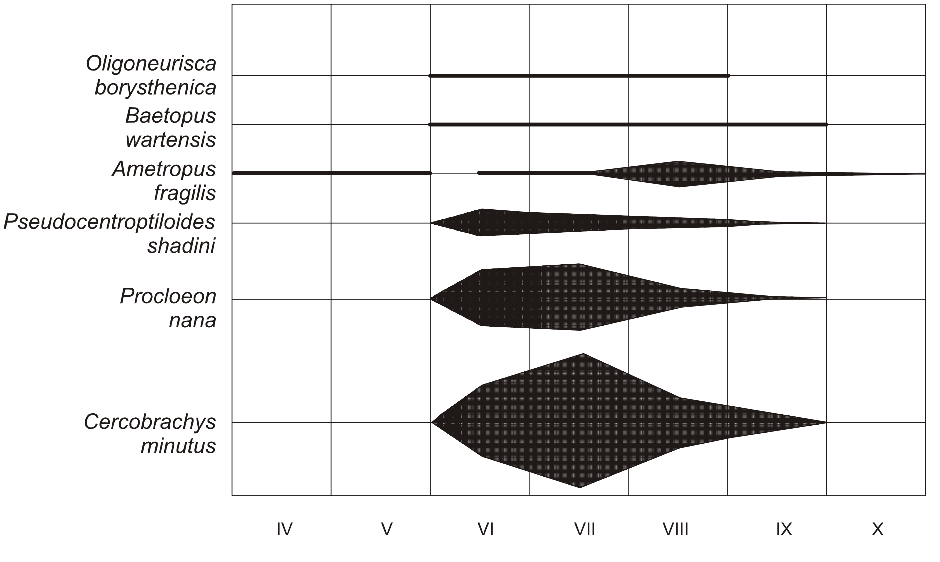

Fig. 4. Periods of colonization of the sandy substratum by psammophilous species; the widths of the figures show the proportional participation of each species in the assemblage.

A series of disadvantageous changes has taken place in the mayfly fauna of the River Bug since the 1980s. In recent years *Oligoneurisca borysthenica*, *Isnonychia ignota*, and *Heptagenia coerulans* have become extinct. At the present time, *Potamanthus luteus* and *Ephemera lineata* are also not noted; however, previously only single specimens were noted so it is difficult to conclude if they are extinct or are still very rare. *Oligoneuriella pallida*, which was dominant in the early 1980s, and the numbers of *Seratella ignita*, *Baetis fuscatus*, and *Heptagenia sulphurea* have decreased greatly. The numbers of other species, despite some changes, have remained at a stable level.

The mayfly species composition in the River Bug was compared to those that occur in other larger Polish rivers (Fig. 5). All of the psammophilous species were only noted in the Warta River (Keffermüller 1960), and the assemblage from the Bug mostly corresponded with it. The only psammophilous species which occurred in all rivers was *A. fragilis*, and this was the only species found in the Pilica River (Jażdżewska 1979). The next species that was noted very often was *C. minutus*, which, except in the Pilica River, was found in all the other rivers. Mayfly fauna from the River San (Sowa 1975) was most distinguished, and, due to its proximity to the piedmont, species from the family Heptageniidae were represented numerously.

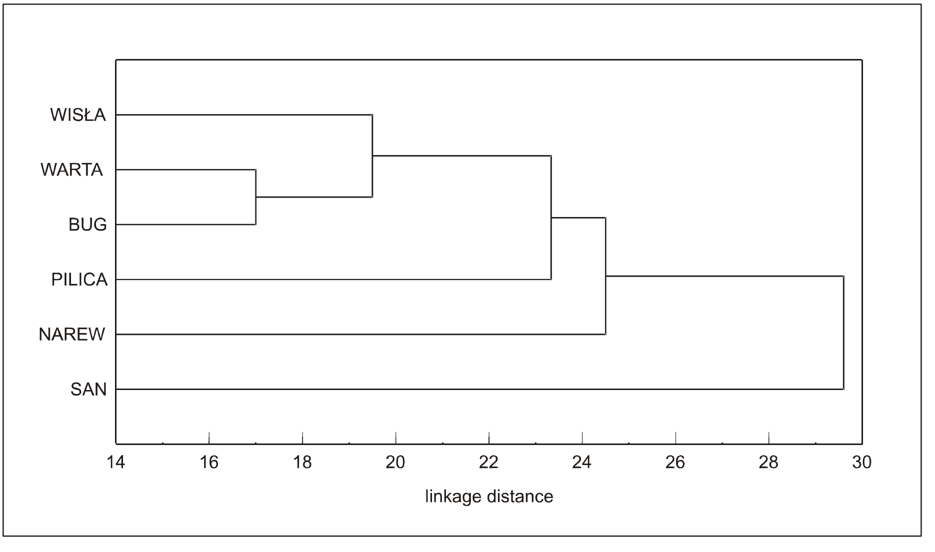

Fig. 5. Similarity of the mayfly fauna from larger Polish rivers calculated by the between-group linkage Euclidean distance method.

DISCUSSION

It is difficult to discuss the environmental preferences of psammopilous mayflies in the context of the literature, because most earlier investigations either refer to species composition (Sowa 1980) or they addressed a single group, the Ephemeroptera. Where they were analyzed in more detail, no psammophilous mayflies were recorded (Bazzanti 1991), and this was partly caused by pollution.

Psammophilous mayflies can inhabit river beds comprised of compact substratum which, in the zone with slower flow, is covered by silt (described as silty-sand substratum), and they may only partially enter the shifting sand. However, compact sand devoid of silty sediments is inhabited by all psammophilous species. It is also the most appropriate habitat for nymphs of the species which cover their bodies with sand (*A. fragilis* and *O. borysthenica*). Silty-sand substratum is colonized more numerously by *Procloeon nana* nymphs. Although they enter the compact sand without silt, they are not as numerous there. The less specialized nymphs of *Cercobrachys minutus* can be found on silty-sand river beds, where they are most abundant, but also on compact, shifting sand. They exploit nearly the entire river bed and are the only psammophilous species that are also found on gravel. This feature distinguishes this species from the other psammophilous mayflies.

Depending on the bed structure, the different settlement zones represent varying percentages of the river bed. When only one bar is formed, it may cover 20-30% of the river bed surface, but at a site where a few bars are heaped, these areas could increase to 50%. In the parts of the river where there are no bars, suitable places for inhabitation occur only along the banks in a belt a few meters wide that comprises 5% of the bed. Since the mean width of the River Bug is 130 m, psammophilous mayflies therefore occupy a 10-70 m zone across the river. Their mean density on 0.25 m^2 is 26 nymphs (max. 101).

Their tendency to drift makes easier the rapid colonization of suitable substrata as they change with the water current. Similarly, unstable fragments of dead wood are relocated by the water and uncovered when they become stuck in the shallows. Species living on plants have a lower propensity for drifting.

Most of the mayfly species occurring in this area are characterized by a summer period of development. Although living in the same season intensifies food competition, the time of their occurrence coincides with that when the river is at its most fecund and the largest amount of suspended matter is present. Psammophilous mayflies tailor their life cycles to the most profitable food conditions. Except for *Ametropus fragilis*, the development of their nymphs is weakly synchronized, and so they are noted in all summer months.

Species that are not included in the psammophilous group appear periodically in the sandy substratum because their main habitats are different types of substratum. Their eggs develop on sand which is why very young nymphs, which are in the first stages of the life cycle, are found there. Their favored substratum is colonized by later stages. The highest number of individuals of these species were noted on the silty-sand bed, they were considerably less numerous on the compact sand, and they did not occur at all on shifting sand.

Sandy substrata do not provide a suitable environment for animals. Only psammophilous species that are adapted to live and feed on this unstable substratum can survive there. Apart from mayflies, numerous oligochaetes, chironomids, and bivalves are found. These animals gather in the shallow parts of the river where hydraulic stress is at its lowest (Remple et al. 2000). Such places appear on the ridges of the sand bars and after the water level drops on the margins of instream islands or in the canals dividing them. This results in the localized distribution of psammophilous fauna and in changes in the character of the substratum. The latter are caused by even small fluctuations in water level that result in the rapid displacement of fauna and the colonization of new, more suitable, environments.

Although they do not reach very large abundances or high densities, psammophilous mayflies are very important in the great lowland rivers because sands comprise more than 90% of the substratum (Mikulski and Tarwid 1951). This is a very large area which can only be populated by especially adapted invertebrates of which mayflies are a significant element. The non-psammophilous mayflies inhabit the marginal environments only, but when their densities are very high, they periodically try to colonize the nearby sandy substratum.

Opportunities for comparing the data obtained in the current study with the results of earlier investigations are limited additionally by the quality of earlier studies, which report lists of species only, without taking into consideration the quantitative structures of their assemblages. That is why the cladogram presented in Fig. 2 reflects only the resemblance of the mayfly species composition from the large Polish lowland rivers and could be an incomplete assessment. Determining the real view of the assemblages, together with their dominance structure, enables constructing a more natural picture of resemblance. This is particularly important now when changes connected with the transformation of the psammophilous mayfly environment concern just changes in their dominance structure. Further rigorous studies involving more quantitative analyses of this group of mayflies are required.

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