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Diversity of macrobenthos in lowland streams: ecological determinants and taxonomic specificity

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ABSTRACT

The present study contains the results of an investigation of the relationships between the environmental variables and the taxonomic diversity of common and important groups of benthic macrofauna: Chironomidae, Ephemeroptera, Odonata, Hirudinea and Gastropoda, collected from various types of bottom substrate in seven lowland streams of north-eastern Poland. Four metrics were used to express the diversity of the studied taxa in each sample as the examples of its four different aspects: species richness, rarity, Shannon-Weaver's diversity index and Pielou evenness index. The values of total species richness and Shannon-Weaver index were rarified by functional extrapolation with Michaelis-Menten asymptotic function chosen as a richness estimator. There are high differences in taxonomic diversity of benthic animals between the studied streams. The results of estimation of total species richness and total species diversity are mainly affected by the diversity of the taxon richest in species – larval Chironomidae and, to a lesser extent, Hirudinea. The total taxonomic diversity significantly correlates with the status of riparian vegetation and with the isolation of the sampling site, while the relationship with other environmental parameters, i.e. pollution and seasonality, is not significant. The diversity of Gastropoda and Hirudinea is significantly affected by pollution (positively), water depth and seasonality; whereas the diversity of Ephemeroptera and Chironomidae by the state of riparian vegetation, and that of Odonata by stream width and isolation of the site. The study presents and discusses reduced diversity of certain higher taxa as a result of a reduction in pollution loading to a stream with simultaneous unchanged values of the total diversity.

Key words: biological assessment, biological diversity, rarefaction, macrobenthos, stream

1. INTRODUCTION

The sustaining of the so-called biological diversity is a priority of nature conservation in terrestrial, marine and freshwater environments (Brooks *et al*. 2006). Therefore, the assessment of biological diversity and its probably most important element – taxonomic diversity – plays a very significant role as the basis for nature protection. On the other hand, various indices expressing the biological diversity of chosen groups of organisms are used as common metrics in biological assessment of environmental quality. The assumption that habitat degradation results in significant and predictable decrease in taxonomic diversity is an important objective of various methods of biological assessment based on freshwater organisms, especially on benthic invertebrates (e.g., Lenat 1988; Jüttner *et al*. 1996; Carlisle 2008). The decrease in taxonomic diversity due to habitat degradation could be assessed as a reduced species richness (stressors not allowing less tolerant species to colonize or to persist in degraded sites – Townsend & Hildrew 1994) or depletion in the values of any of numerous indices of diversity (stress eliminates sensitive taxa and results in a greater numerical dominance of those able to persist – Jones 2008).

It seems, that there are two very important impediments connected with the assessment of taxonomic diversity for the purposes of stream ecology – taxonomic sufficiency and taxonomic incompleteness of evaluation. The lack of researchers' consensus for the former, defined by Jones (2008) as the level of taxonomic details with which organisms must be identified, results in problems with comparing the datasets from different environments. The latter results in preparing and publishing datasets where higher taxa are identified on unequal level (e.g., Angradi 1996; Adams *et al*. 2005; Statzner *et al*. 2008). Both procedures make the potential meta-analyses extremely difficult. Moreover, diversity indices respond strongly and unpredictably when a taxonomic detail changes (Jones 2008), so it can also make the search for general ecological determinants of stream taxonomic diversity not-achievable. It seems self-evident that datasets arranged for the purposes of biodiversity study should be based on detailed identification on the maximal level (species or species groups) of all higher taxa present in the habitat, at least those ones which are numerous and common. To compare the biological diversity in different habitats (Whittaker's β diversity) suitable indices should be carefully chosen and correctly used, in accordance with Hurlbert's (1971) observation that "diversity per se does not exist".

The values of two diversity indices based on benthic macrofauna are taken into account in two methods of biological assessment of freshwaters implemented in Poland: Margalef index as the supplement of BMWPpl biotic index, in which animals are identified on the family level (Fleituch *et al*. 2002) and Margalef index and Shannon-Weaver index as a complementing metrics in STAR-AQEM procedure, which requires lamily level (Buffagni *et al*. 2006) or mixed level identification (mainly family or genus) of macrobenthos (Buffagni *et al*. 2004, also in Polish version of that method which is being developed - Tończyk 2006).

Typically, the diversity indices used in biological assessment studies are calculated for highly important indicator groups like Chironomidae (Cranston 1995) and EPT (larval Ephemeroptera, Plecoptera and Trichoptera) or for a selected part of macrobenthic taxa (Barbour *et al*. 1996), identified on the level of genus or family (e.g., Fleituch *et al*. 2002), and much more rarely for all macrobenthos (e.g., Johnson & Hering 2009). In numerous papers analyzing the relationships between environmental parameters and the diversity of benthic invertebrates, some groups have been typically omitted or treated as a single taxon (Jones 2008). Unfortunately, those groups, more difficult than others to identify on the species level, are at once extremely rich in species and very important in terms of trophic function, e.g., larval Diptera. Therefore, conclusions from such studies about the reaction of diversity of macrobenthos to changes in environmental parameters seem to be controversial, when the most diverse taxonomic groups are identified on the level of genus or tribe (Statzner *et al*. 2008). The idea that the groups richest in species should be excluded from the biomonitoring protocols to make the procedure easier has also been formulated (Rabeni & Wang 2001). Notwithstanding, the results of biological assessment based on the measurement of taxonomic diversity seem to be erratic when such methodological assumptions are used. And after all, "for comparisons between areas, accurate identifications of the taxa are considered fundamental because the species of each area are treated as having equal weight..." (Humphries *et al*. 1995). In extreme situations, large-scale studies on changes in biological diversity of aquatic organisms are based on data in which neither Insecta nor Oligochaeta are identified (Leppakoski *et al*. 1999). The large, sometimes predominant part of total taxonomic diversity of stream macrobenthos is included within the groups that are difficult to identify, like Chironomidae, Limoniidae, Tipuliidae, Tabanidae and Oligochaeta. An analysis of Zwick's Breitenbach Stream (Germany) complete animal species list (Allan 1995) showed , that larval Diptera composes almost half of total species richness and *ca* 68% of macrofauna species richness, while the family Chironomidae solely represents 15% and 22%, respectively. The so-called "lowest practical taxonomic level" used for identification by certain stream ecologists (Waite *et al*. 2004; Adams *et al.* 2005) as a pragmatic compromise between increasing information content and increasing time and costs along the level of taxonomic detail (Jones 2008) is very insufficient for the needs of biodiversity studies.

Differences in taxonomic diversity of stream fauna due to environmental patterns have been documented in numerous studies, e.g., as the effect of moderate pollution (Barbour *et al*. 1996, Koperski 2005, 2009), oxygen depletion (Jacobsen 2008), climatic differences (Heino 2002), type of bottom substrate (Jähnig *et al*. 2008), type of land-use in catchment area (Utz *et al*. 2009), flow velocity (Strzelec & Królczyk 2004), organic matter accumulation and substratum characteristics (Graça *et al*. 2004). In an exhaustive study by Ribera (2007) the diversity of lotic invertebrates is suggested to be determined by historical, geological and climatic constraints of habitats. Some researchers, however, present results explaining the lack of a significant effect of well-known environmental variables on the species diversity of macrobenthos: reduced discharge (Dewson *et al*. 2007) or land-use type (Sandin *et al*. 2006). A potentially great influence of a certain pattern on the results of diversity assessment, commonly neglected by researchers as diversed "attractiveness" and "accessibility" of sampling sites are presented by Sanchez-Fernandez *et al*. (2008). Wide applicability of methods to assess long- and short-term changes in biodiversity, proposed for instance by Lamb *et al.* (2009), seems to be ambiguous – it can only be applied in some well-studied, regularly and intensively assessed environments.

There are many sharp or subtle differences in response of each higher taxon of stream macrobenthos to important environmental factors. This kind of differences between higher taxa in taxonomic diversity has been presented in numerous studies. The diversity of Odonata seems to be strongly correlated with the local climatic specifics (Eversham & Cooper 1998); furthermore, it is more sensitive than the diversity of other taxonomic groups to the structure of riparian vegetation (Smith *et al*. 2007). Differences between the diversities of higher taxa as a result of divergence in stream bottom have been presented, among others, by Benke *et al*. (1984) and Jähnig *et al*. (2008). The richness of four insect orders studied by Rosemond *et al*. (1992) was affected in different ways by chemical parameters of stream waters.

The main aims of the present study were: (i) looking for the relations between environmental variables in lowland streams and the taxonomic diversity of common and numerous groups of benthic macrofauna identified at the species/species group level; (ii) analyzing the response of the selected groups diversity to changes in environmental variables; (iii) comparing the response of the diversity of each single group to environmental variables with the response of the total diversity of. macrobenthos.

2. METHODS

Fifty nine samples of benthic macrofauna were taken between April 2001 and October 2007 at 14 sites on seven lowland streams localised on the Mazurskie

Fig. 1. Map of the sampling area. Lakes shown as grey figures on the upper plot, sampling sites – as black dots.

Tab. 1. Main characteristics of the sampling sites and mean values of environmental metrics: AIP - Additive index of pollution (6-30), Ext/Int - the type of land use, DeBS - degradation of bottom substrate (%), DeRV - degradation of riparian vegetation (%), DiAH - diversity of aquatic habitats (1-9) DiRV - diversity of riparian vegetation (1-7). See Methods for details.

Stream	Site	Coordinates			Environmental metrics					
		Lat. N	Long. E	# samples	AIP	Ext/Int	DeBS	DeRV	DiAH	DiRV
Lesna	1	53.941	22.277	8	19	0.5	70	40	8	6
Swiecek	1	53.671	22.001	4	15	3	30	25	6	5
	2	53.706	22.081	4	17	1	60	90	8	6
	3	53.709	22.085	3	17	4	50	30	3	5
Konopka	1	53.662	22.004	3	15.5	1	30	40	5	4
	2	53.665	21.985	3	20	0.5	50	40	7	5
Osa	1	53.821	21.649	3	14	5	10	30	3	4
	2	53.819	21.648	3	14	2	10	30	5	5
Orzysza	1	53.809	21.941	6	9	0.2	20	80	7	2
	2	53.806	21.917	3	10	0.1	50	90	8	3
	3	53.809	21.888	3	9	7	0	5	6	7
Wilkus	1	53.712	21.864	3	16.5	0.5	20	40	6	4
	2	53.695	21.886	2	16.5	0.5	30	60	5	3
Elk	1	53.953	22.259	10	11	8	20	0	9	7
	2	53.946	22.257	4	11	5	0	0	7	6

(Masurian) Lakeland in north-eastern Poland (Fig. 1, Tab. 1). Nineteen samples were taken in spring (March–May), 24 in summer (June–August), 16 in Autumn (September–October). Macroinvertebrates were collected using a modified version of Lenat's (1988) qualitative collection method from each type of bottom substrate present at the site and artificial, multiplate structures were placed in the stream for approximately four weeks. Simultaneously, the main physical and chemical parameters of water were measured (pH, conductivity, hardness, concentration of: oxygen, orthophosphates, nitrates, ammonia, chloride, anionic surfactants, sulphide) and main morphometric parameters of the stream (width and depth) were noted. Physical parameters and oxygen concentration were measured using Corning Checkmate equipment, while chemical parameters – using the Merck Nova 600 field spectrophotometer.

Additionally, five environmental metrics were observed up to the distance of 50 m from the sampling site and assessed in arbitral scales (Tab. 1):

1. the type of land use (Ext/Int) – an area of extensive land use (forest, shrubs, meadows) in relation to extensive land use (residentials, agriculture, roads, bridges, pastures) - data based on field observations and the analysis of topographic maps;
2. the degradation of the stream bottom substrate (DeBS, %) - the percentage of the bottom area under man-made reconstruction and covered by concrete, rubbish and trash;
3. the degradation of the riparian vegetation (DeRV, %);
4. the diversity of the aquatic habitat (DiAH, based on maximal number of types of bottom substrate present at the sampling site: sand, mud, stones, logs, debris, emergent plants, submerged plants, artificial substrate, living parts of terrestrial plants, scale 1-9);
5. the diversity of the riparian vegetation (DiRV based on maximal number of the types of riparian vegetation: meadows and pastures, reed-bed, weeds, willow bush, sparse trees, coniferous forest, broadleaf riparian forest, scale 1-7).

Also, the level of isolation of each sampling site, meaning the distance from the sampling site to the nearest standing water-body, was noted.

Six abiotic metrics (conductivity, concentrations of: orto-phosphate, nitrate, ammonia, surfactants, chloride) were used to compose the additive index of pollution (AIP). In accordance with the procedure devised by Barbour et al. (1996), scores (5, 3, or 1, with respect to the quartile ranges) were developed for these metrics to allow for aggregation into an index. The summed up scores for the parameters were treated as the value of AIP (scale 6-30).

The mean values of environmental parameters measured are presented in table 1. The mean values and ranges of the main morphometric parameters of a stream (width and depth) as well as the data on the type of land use, the level of degradation and diversity of the aquatic and riparian vegetation in year 2001 were presented in previous papers (Koperski 2005, 2009) and suggest that part of the studied environment should be considered as almost not-degraded and the rest as moderately degraded.

The analysis of diversity was based on the data on five higher taxa, rich in species, numerous and common in most of samples, treated further as indicators of total diversity of macrobenthos. Invertebrates selected for study: Gastropoda, Hirudinea, and larval stages of Chironomidae, Odonata and Ephemeroptera were identified on the basis of keys by Klink & Moller-Pillot (2003), Wiederholm (1983), Piechocki (1979), Nesemann & Neubert (1999), Eiseler (2005), Heidemann & Seidenbusch (2002). The taxonomic names of each taxa are presented in agreement with the nomenclature in Nesemann & Neubert (1999), Jażdżewska (2007), Tończyk & Mielewczyk (2007), Siciński (2007) and Piechocki (2008). Accurate identification of certain larval Chironomidae on the species level or even recognition between certain species at larval stage was impossible on the basis of morphology – in such situations identification on the level of "species group" was carried out.

Four metrics were used to express the diversity of the studied taxa in each sample as the examples of its four different aspects: species richness (number of species and species groups found in a sample), rare species richness (rarity – the number of species and species groups found in samples with frequency lower than 10%), Shannon-Weaver's diversity index ($\hat{H}$) and Pielou evenness index (J). Species richness in a habitat is the main parameter of taxonomic diversity and is treated as a surrogate for biodiversity (Marshall *et al*. 2006). The number of rare species is a suitable faunistic metric, complementary to the total species richness, as it was documented by Cao *et al*. (1998). Shannon-Weaver index is the most commonly used richness-based index of diversity, while Pielou's evenness index is the measure of equitability. Values of all metrics were calculated for each of five higher taxa and for all taxa in each stream. The values of metrics which were calculated for all studied taxa are called below "total diversity" or "total species richness" but it must be emphasized that those taxa composed at the most half of all the species number present at the studied sites.

The values of total species richness and Shannon-Weaver index were estimated (rarified) by functional extrapolation with EstimateS software (Version 7.5, R.K. Colwell, http://purl.oclc.org.estimate). The most commonly used Michaelis-Menten asymptotic function was chosen as MMMeans richness estimator (Colwell & Coddington 1994). To compare the values of total species richness between streams and between higher taxa, trend lines (best fitted logarithmic regression) were created with Microsoft Excel. To compare the values of the rare species richness between streams and between higher taxa, samples of 1000 individuals were extrapolated using the trend lines (best fitted logarithmic regression, Microsoft Excel) based on rarified values of Shannon-Weaver diversity and original values of evenness and rare species richness.

To determine the strength and direction of the relations between diversity metrics of higher taxa and the analysed environmental parameters the values of Spearman correlation coefficient and probability of its significance were calculated (Statistix version 8.0, Analytical Software).

The significance of the effects of the categorical parameters: seasonality (categories: spring, summer and autumn) and the type of bottom substrate (categories: bottom deposits, macrophytes, solid substrates – stones, logs, artificial substrate) was tested using Kruskal-Wallis nonparametric analysis of variance with χ^2 approximation and pairwise comparisons (Statistix version 8.0, Analytical Software).

Two models of multiple regression were used to evaluate relative influence of the diversity of particular higher taxa on total diversity of analysed organisms. In the first one, values of Shannon-Weaver index, calculated for all taxa were the explained variable and the values of the index calculated for the higher taxa were used as explaining variables. In the second model, the same procedure involved with the values of Pielou evenness index. Those relative effects were expressed as values of β coefficients and probabilities of their significance.

3. RESULTS

The results are based on 25198 individuals, collected in 59 samples in seven streams (Tab. 2). The specimens of larval Chironomidae, Odonata and Ephemeroptera as well as Hirudinea and Gastropoda were identified as 177 species and species groups. Fourtyfive species and species groups found with the frequency lower than 10% were treated as rare species.

Tab. 2. Number of samples, number of individuals sampled and the level of identification of higher taxa.

Taxon	Samples	Individuals	Level of identification	
			Species	Groups of species
Chironomidae	46	11850	51	45
Gastropoda	50	2629	20	-
Hirudinea	50	2856	20	-
Odonata	48	1021	19	-
Ephemeroptera	49	6927	22	-
Total	59	25198	132	45

The values of the environmental parameters (Tab. 1) show that ecological divergences both between streams and between sites of the same stream were high. There were high differences in taxonomic diversity of benthic animals between the studied streams. The estimated species richness was visibly higher in streams Orzysza, Elk, Swiecek and Osa than in all the other streams under investigation (Fig. 2). The values of Shannon-Weaver index of diversity and evenness were similar in all streams except for Wilkus, with visibly lower values (Fig. 3). The values of extrapolated rarity in Orzysza, Elk and Osa were more than two times higher than in Wilkus (Fig. 4). High or low values of total taxonomic diversity in streams did not coincide with the values of diversity of higher taxa. For example, the highest values of estimated total species richness and estimated richness of Chironomidae and Hirudinea were found in Orzysza with simultaneously the lowest values of Ephemeroptera species richness (Fig. 2). High values of species diversity for Chironomidae, Gastropoda and Hirudinea were found in Swiecek and Konopka with extremely low values for Odonata (Fig. 3).

The results of estimation of total species richness and total species diversity are seriously affected by the values of the taxon richest in species – Chironomidae (Tab. 3). The diversity of odonate larvae in Wilkus was very high but simultaneously the total diversity there was extremely low (Fig. 2). Apparently paradoxically, the estimated species richness of chironomid larvae in Swiecek and Orzysza are higher than the total species richness in both these streams – it means that the number of species found in a sample of chironomids is higher than the number of species found in a sample of benthic invertebrates of the same number of individuals. The most diverse group of animals in almost all streams was Chironomidae, which contributes about half of all the species found, only in Wilkus the odonates were the most diversed group of fauna (Fig. 3) in terms of Shannon-Weaver index.

Tab. 3. Determination of the values of Shannon-Weaver Index and Evenness Index calculated for all taxa by the diversity of higher taxa, analized by multiple regression and expressed as the Beta values and probabilities.

Taxon	Shannon-Weaver Index		Evenness Index	
	Beta	*p*	Beta	*p*
Chironomidae	0.559	<0.00001	0.447518	0.003
Gastropoda	0.188	ns	0.167761	ns
Hirudinea	0.444	0.00004	0.246415	0.05
Odonata	0.141	ns	0.062829	ns
Ephemeroptera	0.185	ns	0.164703	ns
R^2	0,833		0,621	

The estimated values of rarity were strongly dependent on the number of animals sampled and on the relative number of species-rich taxa in the sample. High or low value of the rare species richness found in particular streams was not correlated with the number of rare species of specific higher taxa. The comparisons of the estimated number of rare species expected in the same number of sampled individuals between streams place Orzysza, Osa nad Elk much higher than the other streams in terms of rare species richness (Fig. 4). Stream Wilkus was found as the poorest in terms of rare species richness. In streams Osa and Ełk the highest number of rare species of Gastropoda, but not Ephemeroptera, should be expected, while in Stream Orzysza the highest number of rare species of Chironomidae and Hirudinea and in Swiecek – Ephemeroptera (Fig. 4).

The correlations between total diversity of the analysed benthic fauna and the values of environmental parameters were highly divergent. It did not correlate with pH, conductivity, hardness, concentrations of oxygen, ortho-phosphates, nitrates, ammonia, chloride, anionic surfactants and sulphide, or with Ext/Int and DeBS indices. It seems to be generally positively correlated with the diversity of riparian vegetation and negatively correlated with the degradation of riparian vegetation and the distance to the nearest standing water-body (Tab. 4).

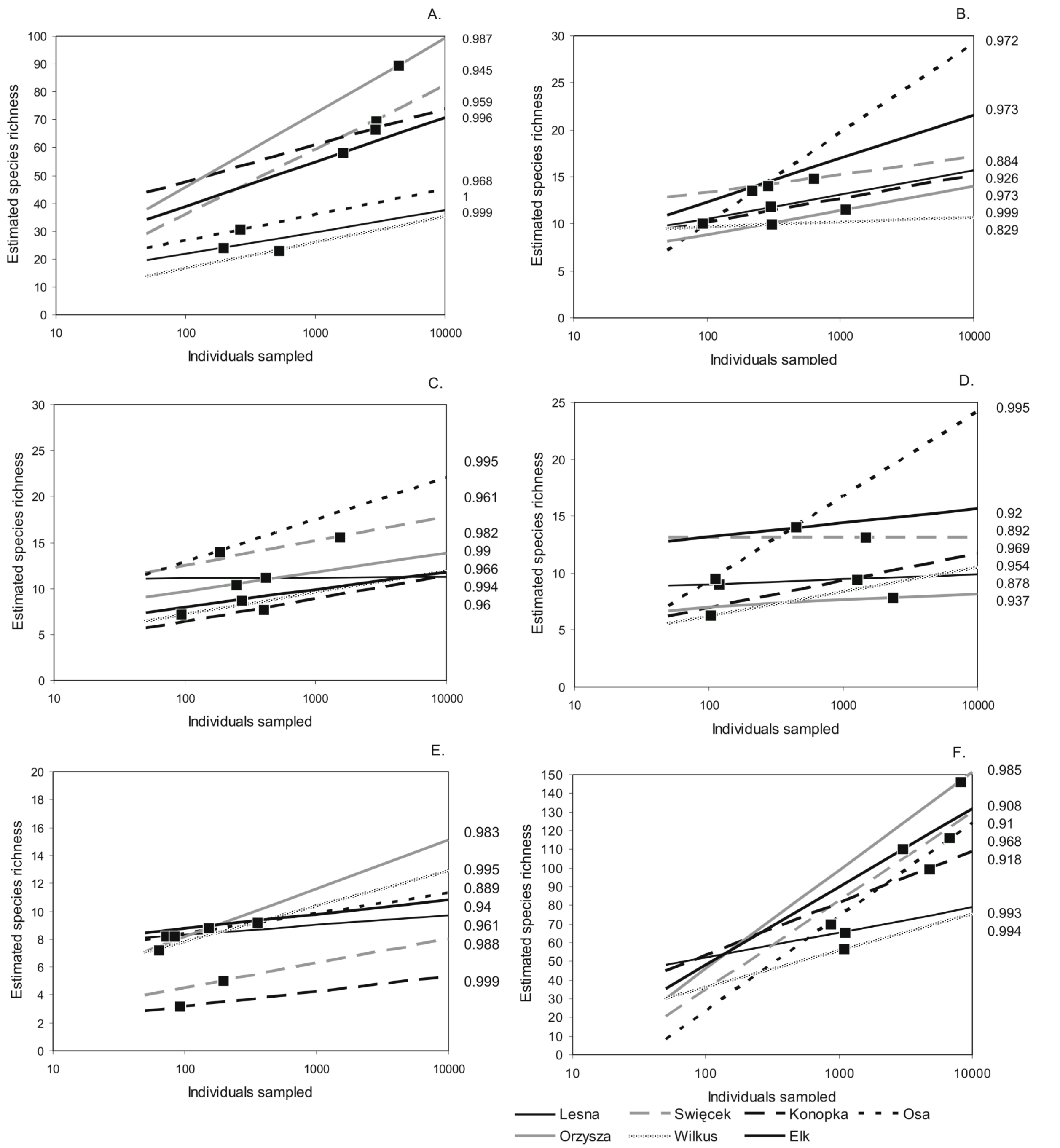

Fig. 2. Rarified species richness, estimated as Michaelis-Menten's function during rarefaction procedure and based on the samples from the seven streams. Values of R^2 coefficient between species richness and number of individuals sampled are added. **A**. larval Chironomidae, **B**. Gastropoda, **C**. Hirudinea, **D**. larval Ephemeroptera, **E**. larval Odonata, **F**. all the above taxa. Note the differences in scale on axis Y.

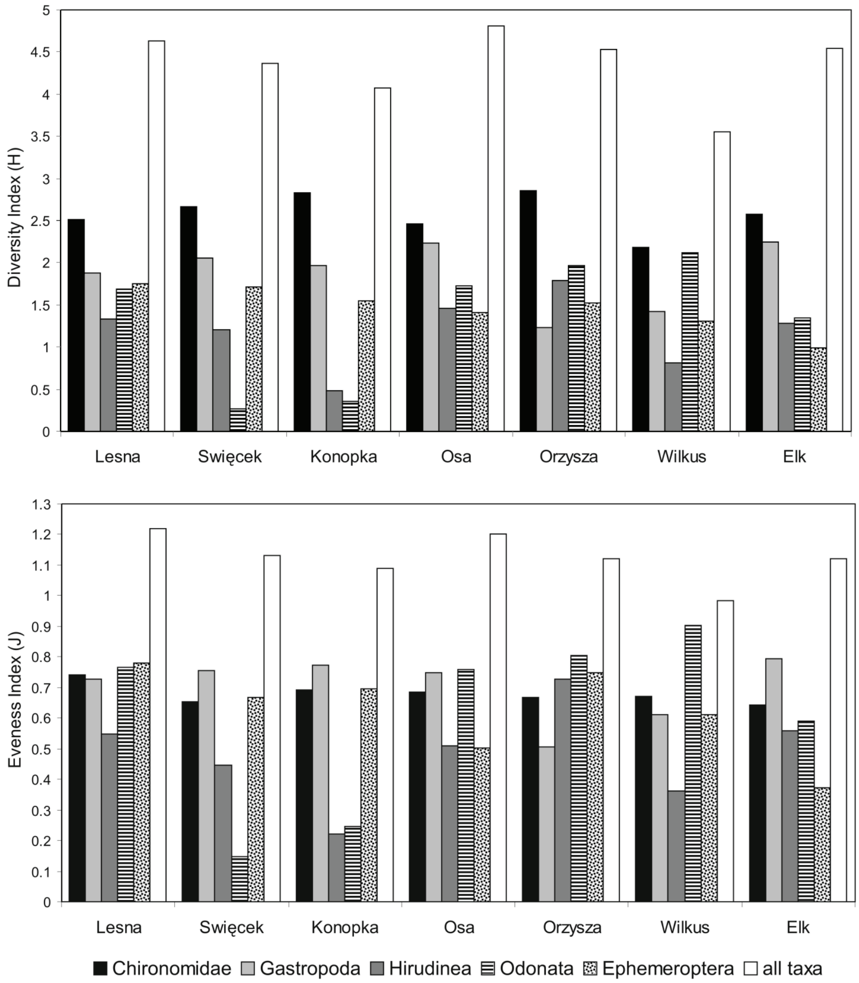

Fig. 3. Values of Shannon-Weaver index of diversity (upper plot) and values of Pielou evenness index (lower plot) for higher taxa sampled in the seven streams. Values of indices estimated for 1000 individuals (see Methods for details).

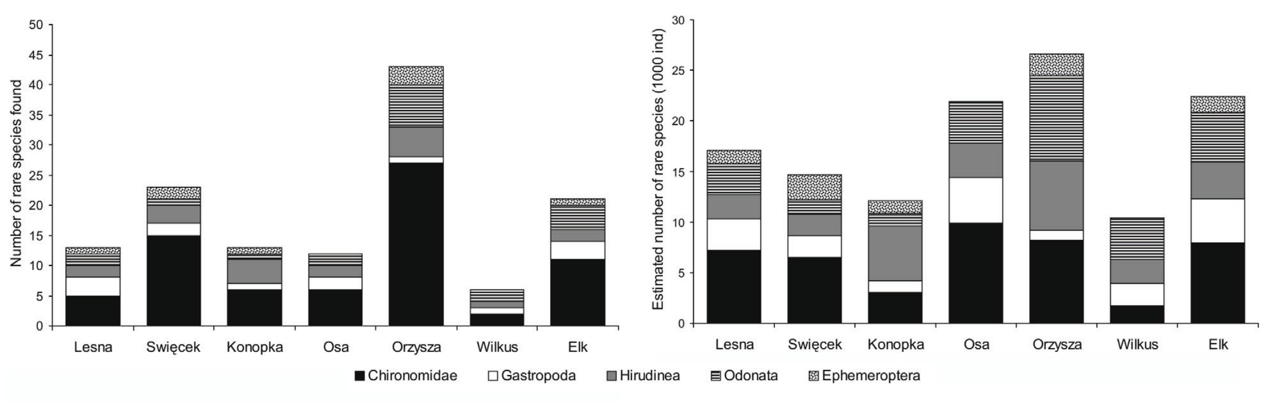

Fig. 4. Rare species richness and estimated rare species richness per 1000 individuals of higher taxa in the seven streams (see Methods for details).

Tab. 4. The significance and direction of Spearman correlations between 6 ecological parameters and the biodiversity metrics (total species richness, Shannon-Weaver's index, rare species richness, evenness and general effect on diversity) of 5 higher taxa of macrobenthos. Only those ecological parameters which correlate significantly with biodiversity metrics are presented: 1. mean width of a stream, 2. mean depth of a stream, 3. diversity of the riparian vegetation (DiRV - see Methods for details), 4. additive index of pollution (AIP - see Methods for details), 5. Isolation - distance to the nearest standing water body, 6 - seasonality. - denotes significant negative correlation (0.01 <*p* <0.05), -- highly significant negative correlation (*p* <0.01), + significant positive correlation (0.01 <*p* <0.05), ++ highly significant positive correlation (*p* <0.01), 0 non-significant correlation.

Taxon	Parameter Metric	Stream width	Stream depth	DiRV	DeRV	AIP	Isolation
Chironomidae	Species richness	0	0	++	-	0	0
	Shannon-Weaver	0	0	0	0	0	0
	Rarity	0	0	+	-	0	0
	Eveness	0	0	0	0	0	0
	General Effect	**0**	**0**	**+**	**-**	**0**	**0**
Gastropoda	Species richness	0	--	0	0	0	-
	Shannon-Weaver	0	0	0	0	++	--
	Rarity	-	0	0	0	+	-
	Eveness	-	0	0	0	+	-
	General Effect	**0/-**	**-**	**0**	**0**	**+**	**-**
Hirudinea	Species richness	-	-	0	0	+	-
	Shannon-Weaver	0	-	0	0	+	0
	Rarity	0	0	0	0	0	-
	Eveness	-	-	0	0	+	-
	General Effect	**0/-**	**-**	**0**	**0**	**+**	**-**
Odonata	Species richness	++	0	0	0	0	--
	Shannon-Weaver	+	0	0	0	0	0
	Rarity	0	0	0	0	0	--
	Eveness	+	0	0	0	0	-
	General Effect	**+**	**0**	**0**	**0**	**0**	**-**
Ephemeroptera	Species richness	0	0	+	0	-	0
	Shannon-Weaver	0	0	+	-	-	0
	Rarity	0	0	0	0	-	0
	Eveness	0	0	+	0	-	0
	General Effect	**0**	**0**	**+**	**-**	**-**	**0**
All taxa	Species richness	0	0	+	-	0	-
	Shannon-Weaver	0	0	0	0	0	-
	Rarity	0	0	+	-	0	-
	Eveness	0	0	0	0	0	-
	General Effect	**0**	**0**	**+**	**-**	**0**	**-**

The correlation between diversity and pollution has different direction and strength in various taxa. The Spearman's correlation between stream morpholgy, diversity of riparian vegetation, pollution and the distance to the nearest standing water-body and various metrics expressing the taxonomic diversity of groups of fauna were found highly significant (Tab. 4). Three groups of taxa were featured on the basis of strength and direction of the relation between their diversity and the values of environmental parameters. In the first group, the diversity of Gastropoda and Hirudinea increased with the increasing of pollution index and decreased at deeper sites and at sites removed from water-bodies. The diversity of only those two taxa significantly differed as a result of seasonality. In the second group, the diversity of larval Chironomidae and Ephemeroptera are correlated with the diversity and degradation of riparian environments. The diversity of larval Odonata, being a third group, was higher in wider streams and lower when the distance to the nearest standing water-body increased.

The diversity of higher taxa throughout the season and between the types of bottom substrate changed in different ways (Tab. 5). There was no effect of seasonality on total diversity, while the maximum diversity of Hirudinea was noted in summer and larval Epheroptera in spring. The highest diversity of Gastropoda and larval Chironomidae was noted on the parts of bottom covered by macrophytes, but the highest diversity of Hirudinea on solid bottom structures. Nevertheless, the total diversity did not vary significantly between the types of subtrate.

Tab. 5. The significance of the effect of the bottom substrate type (B - bottom deposits, M - macrophytes, S - solid structures) and seasonality (Sp - spring, Su - summer, Au - autumn) on the biodiversity metrics (total species richness, Shannon-Weaver's index, rare species richnes (rarity), Evenness Index and general effect on diversity) of 5 higher taxa of macrobenthos. * - significant effect in Kruskall-Wallis analysis of variance p <0.05), ns - non-significant.

taxon	Parameter Metric	Type of bottom substrate	Seasonality
Chironomidae	Species richness	*	ns
	Shannon-Weaver	*	ns
	Rarity	*	ns
	Eveness	*	ns
	General Effect	**M>B>S**	**ns**
Gastropoda	Species richness	*	ns
	Shannon-Weaver	ns	ns
	Rarity	ns	ns
	Eveness	ns	ns
	General Effect	**M and S>B**	**ns**
Hirudinea	Species richness	ns	ns
	Shannon-Weaver	*	*
	Rarity	ns	ns
	Eveness	*	*
	General Effect	**S>M and B**	**Su>Sp and Au**
Odonata	Species richness	ns	ns
	Shannon-Weaver	ns	ns
	Rarity	ns	ns
	Eveness	ns	ns
	General Effect	**ns**	**ns**
Ephemeroptera	Species richness	ns	ns
	Shannon-Weaver	ns	*
	Rarity	ns	*
	Eveness	ns	ns
	General Effect	**ns**	**Sp>Su and Au**
All taxa	Species richness	ns	ns
	Shannon-Weaver	ns	ns
	Rarity	ns	ns
	Eveness	ns	ns
	General Effect	**ns**	**ns**

4. DISCUSSION

As it was emphasized in Methods, the results and discussion presented in this study are based on diversity values relating only to five of 10-20 higher taxa commonly occuring in typical, lowland Central European streams. Five higher taxa used in the study as the metrics of total diversity of macrofauna: Chironomidae, Gastropoda, Hirudinea, Odonata and Ephemeroptera were selected on account of special features. They were most common and most numerous of all higher taxa having at least ten species, which occurred in studied environments. All of these groups are relatively well known and their ecology is often studied and presented in scientific literature, additionally, the keys for their identification are relatively easy available. To what extent are these conclusions representative for the whole freshwater benthic macrofauna? The answer is not easy to obtain. References containing datasets arranged as complete lists of benthic species inhabiting Central European streams are extremely rare in international scientific literature. Even in species-based datasets some awkward groups (most often Diptera and certain non-insect taxa) are identified only on genus or family levels. The same tendencies were observed by Waite *et al.* (2004) in North American highlands and quantified by Jones (2008). Typically, aggregating data on coarser levels than species reduces the amount of information contained in a dataset in spite of providing sufficient resolutions for sensitive and accurate bioassessment, as it was presented in Jones' (2009) review. In the materials of Botos *et al.* (1990) from Hungarian rivers, five taxa analysed in detail in the present study, Chironomidae, Gastropoda, Hirudinea, Odonata and Ephemeroptera, represent *ca* 50% of all macroinvertebrate taxa found, similarly to the findings of Narloch (1975) in a small Polish stream (54%). In the study of Kownacki *et al.* (2002), in River Dunajec in Poland the corresponding percentage was *ca* 68% and in the data of Berrie & Wright (1984) from an English stream – 52%. However, these two latter values should be decreased because certain taxa in this dataset were not identified on species level. The data of Zwick (Allan 1995) from a small German stream are quite different: in this habitat, much better studied and much richer in species, those five higher taxa represent only 26% of the total macrobenthic diversity. Cited faunistic datasets show a great divergence in taxonomic richness between watercourses, which is probably the result of diverse intensity of sampling and different taxonomic knowledge and abilities. *Ca* 700 out of 1044 species, which are presented as a complete list of fauna collected in a German stream by Zwick (Allan 1995), could be determined as macrobenthos, while only 42 and 54 species were found in two Hungarian rivers by Botos *et al*. (1990) during an intensive sampling. Clearly, the species richness of insect larvae found there seems to be highly underestimated. In the present paper, an approximately three times higher number of species was found in the most taxonomically diversed Stream Orzysza than in Wilkus, which is the least numerous with respect to species richness (138 to 45). In terms of the estimated species richness for 1000 specimens this proportion equals 1.75 (98 to 56 species).

The relatively high diversity of macrobenthic assemblages in the present study is definitely related to the sampling method, with three time-points in season and all types of bottom substrate available for fauna. To draw a comparison, faunistic materials in the studies of Narloch (1975), Botos *et al*. (1990) and Kownacki *et al*. (2002) were collected with one type of bottom sampler (dip-net or Surber sampler), one or two times per year; in another study (Berrie & Wright 1984) only the kick-sampling method was used. A great influence of sampling methods on the composition of qualitative collection was presented in numerous studies involved in various habitats (e.g., Lenat 1988; Koperski 2003). Differences in taxonomic composition are also dependent on micro-habitat divergence (Ormerod 1988; Jähnig & Lorenz 2008; Koperski 2009) – the occurrence of common taxa frequently differed between types of bottom-substrate or along the stream cross-section.

The answer to the questions included in aims allowed to tentative evaluation which environmental features favour the maximal total taxonomic diversity and which ones favour only the diversity of specific taxa. The diversity of riparian vegetation, the level of its degradation and the distance to the nearest water-body were the only ecological patterns determining the total diversity of the analysed taxa (Tab. 4). The remaining parameters did not significantly affect the stream biodiversity (the diversity of aquatic habitat, degradation of bottom substrate, type of land-use) or influence the diversity of higher taxa in different ways. The lack of effect in the first case could probably be explained by the relatively weak effect of man-made transformation and relatively low level of habitat degradation in the studied area. It seems surprising that seasonal variability in taxonomic diversity was noted only in the assemblages of Hirudinea and Gastropoda, whereas seasonal changes in taxonomic composition have been well studied in stream assemblages of larval insects (e.g., Hilsenhoff 1998). Similar incongruence between seasonal changes in diversity and composition of aquatic insects was found by Schütz *et al*. (2001) in a mountain stream.

Significantly higher taxonomic diversity of larger streams, Orzysza and Elk, when compared with much smaller Wilkus and Leśna are impressive. Nonetheless, the smallest Stream Osa has highly diversified fauna, which suggests that solely the stream size (expressed as length or width) is not a decisive factor. One of the important factors is probably the specificity of a stream. The case of Stream Swiecek is meaningful. One of its sites, previously highly degraded, was in 2006 an object of reconstruction being in fact some kind of re-naturalisation – as a result, a high increase in the diversity of ephemeropteran and odonate larvae, Hirudinea and Gastropoda were observed, while the values of Ext/Int (the type of land use), DeRV (the degradation of the riparian vegetation), DiAH (the diversity of the aquatic habitat) and DiRV (the diversity of the riparian vegetation) did not change visibly (author's unpublished data). The diversity of macrobenthos collected at certain transformed parts of the studied streams, localized close to the bridges (Swiecek, Lesna and Elk) are relatively high, which is probably due to the fact that the diversity of aquatic habitat there was higher than at other sites. Certain types of stream degradation, like reinforcement of the stream shore with stones and boulders as well as acceleration of flow velocity as a result of stream-bed straiting beside the bridge, caused a significant increase in taxonomic diversity. A similar effect was observed in transformed parts of the coastal zone in urban freshwaters (Koperski 2009, in press).

Rarefaction methods based on analytical function used to evaluate species richness may help to avoid errors which are a consequence of unequal samples. In spite of great value of these methods, they can produce other types of errors: an analysis of trend lines makes it possible to also count species that are not found in any sample. In the case of a large abundance in a virtual sample, the evaluated species richness could be even higher than the number of species potentially possible to be found in this type of habitat, e.g. higher than *ca* 40 leech species found in Polish freshwaters. Therefore, the values of rarified species richness should rather be treated as an evaluation of potential ecological diversity of the studied environment. An extrapolated value of species richness equaling 124 at 10,000 specimens collected in Stream Osa (Fig. 2) is thus only a theoretical value because of the extremely small size of this diverse watercourse (few hundred meters in length). Higher slope of species saturation curve for Osa than for Wilkus shows that the first habitat is more diversified and offers many more potential niches for invertebrates possible to be found on a small area.

Benthic fauna of lowland streams is typically abundantly inhabited by animals mainly occur in lentic environments. Only a few species of Gastropoda prefer lotic habitats, the rest of species occur in flowing waters only at sites with slowly flowing water – only five of 21 species presented in this study are typical inhabitants of flowing waters. In common with gastropods also Hirudinea are mainly a lentic species. Only three out of 19 leech species found in the studied streams are assumed to be typically reophilic (*Erpobdella vilnensis*, *Glossiphonia nebulosa*, *Cystobranchus respirans*), whereas the predominant species (*Erpobdella octoculata*, *Glossiphonia complanata*) are typically eurytopic (Koperski 2006). Frequent occurence of lentic species of Gastropoda and Hirudinea in flowing waters is common and has been presented by various authors (e.g., Kołodziejczyk 1992; Strzelec & Królczyk 2004; Koperski 2006). The largest number of rare species of Hirudinea found in the streams and about half of the rare species number in Odonata and Chironomidae are known as preferring lentic environments (Wiederholm 1983; Nesemann & Neubert 1999; Bernard *et al.* 2002). *Ca* 90% of Ephemeroptera species prefer lotic habitats during the period of larval development; the larvae simultaneously need a large amount of oxygen dissolved in water. About half of the species of Odonata and Chironomidae are typically lotic species as larvae. Species richness of chironomids in the Polish rivers Dunajec (79 species and species groups, Kownacki *et al.* 2002) and Pilica (82 species, Siciński 1990) was similar to high values in Orzysza. Unfortunately, a lack of total number of identified specimens in the first study impedes an accurate comparison. The presented values of diversity are much higher and the values of evenness similar when compared with those from Swedish lowland streams revealed by Janssens de Bisthoven & Gerhardt (2003).

A stronger correlation with the quality of riparian vegetation of aquatic insects' diversity than of the diversity of animals spending whole life in water (Gastropoda and Hirudinea) is evident and easy to explain. Similar relationships have been presented either for Chironomidae (Delettre & Morvan 2000) or Ephemeroptera (Rios & Bailey 2006). Nevertheless, the present results do not confirm the observations of Smith *et al.* (2007) on the highest sensitivity of odonates to the differences in riparian vegetation. Adult Odonata, especially Anisoptera, as more efficient fliers than adult midges and mayflies, seem to be less dependent in their occurence on the local structure of vegetation. Five odonate species found in the studied streams are rather typical inhabitants of lake littoral and small, permanent or astatic ponds (Heidemann & Seidenbusch 1993). Thus, the strong correlation of odonate diversity with the distance from the nearest standing water-body is easy to explain.

In a faunistic study on Gastropoda collected in lowland watercourses, which presents data on the species richness in the lakeland area in north-eastern Poland (Kołodziejczyk 1992), the values of diversity were highly divergent and visibly lower than in the present work. The author of the study concludes that the main pattern determining species richness seems to be the connectivity of streams with lakes. The number of species found in streams flowing through the lakes was much higher than in the others, and this difference was mainly caused by the presence of typically lentic species, similar to those in the present article. Taxonomic compositions and species richness of Gastropoda in lowland watercourses in Lithuania (Włosik-Bieńczak 2005) were similar to those in Orzysza, Elk or Swiecek, but the values of diversity were higher. Korycińska (2002) found 19 species of gastropods in a lowland Polish River Liwiec – many more than in each of the streams studied in the present paper, but the taxonomic composition in her dataset was almost identical to the joined species lists for the seven streams under present investigation. The same similarity between larval Odonata in Liwiec and in the streams under current study were found by Królak & Korycińska (2008).

The taxonomic diversity of Ephemeroptera in Siberian streams (Beketov 2004), explained as species richness, and the values of Shannon-Weaver index were affected by various ecological variables, but to the largest extent by chemical parameters of water. Moreover, the maximum species richness was found at low altitudes, high water temperatures, relatively slow current velocities, medium stream widths, and on the bottom with medium-small particle sizes (Beketov 2008). However, the strength of these relationships was rather low.

The results presented in table 5 clearly illustrate the mechanism of increased diversity of macrobenthos along the increasing of diversity in bottom substrate. The presence of macrophyte stands stimulates the diversity of chironomids and snails, while the presence of solid substrate forces high diversity of leeches.

As it was shown in my previous paper (Koperski 2009), taxonomic diversity of Chironomidae in three of the studied streams (Orzysza, Swiecek and Konopka) is significantly lower at the sites determined as degraded on the basis of multimetric index of environmental quality. The results presented in table 2 suggest that the level of pollution, being the component of this index, does not significantly affect the chironomids' diversity – it seems to be rather reduced by degradation of riparian vegetation. It must be emphasized that the higher level of pollution in the streams under present investigation did not decrease the total taxonomic diversity. Generally low congruence in the species richness patterns across different groups of organisms were shown by Kati *et al.* (2004), who compared the value of six assemblages as terrestrial biodiversity indicators at a local scale. Whereas moderate pollution significantly declined diversity of ephemeropterans in the streams under present study (Tab. 2), which is congruent with the results of numerous other studies (e.g., Fleituch *et al*. 2002; Beketov 2008), the diversity of Gastropoda and Hirudinea is visibly high. If one takes into account that the diversity of the last group is more important than Ephemeroptera in determining total diversity of stream macrobenthos (Tab. 3), one can expect that, in some situations, reduction in pollution loading to a stream may result in the reduction of total taxonomic diversity. Metrics used in biological assessment procedures based on the diversity of selected taxa, like pollution-sensitive EPT group, may in this way promote significant decrease in the main parameter, which is treated as priority in nature conservation. To beware of such paradoxical errors more attention in bioassessment protocols should be paid to the metrics explaining total taxonomic diversity of a stream fauna. Leech, snail and midge species are, after all, as valid in the stream environment as mayflies, dragonflies and damselflies.

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