

Diversity of freshwater macrobenthos and its use in biological assessment: a critical review of current applications

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Abstract: Numerous procedures for biological assessment employ different measures of benthos diversity as a main or additional metric. This paper argues that biological diversity of freshwater macrobenthos is not a strong metric for biological assessment. It is extremely difficult to estimate accurately the taxonomic diversity of the whole macrobenthos. In particular, taxonomic diversity estimations are typically based on taxonomic misconceptions. Moreover, even if it is accurately estimated, it has too many drawbacks to be a reliable metric: it is affected by many factors important only for particular taxa and dependent on parameters that are extremely difficult to define and to quantify. Certain requirements are presented and discussed that are necessary to apply macrobenthos diversity in biological assessments.

Key words: biodiversity, biological assessment, macrobenthos, macroinvertebrates, methods, taxonomic sufficiency.

Résumé : De nombreuses méthodes pour l'évaluation biologique utilisent différentes mesures de la diversité du benthos mesuration principales ou additionnelles. L'auteur soutient que la diversité biologique du macrobenthos d'eau douce ne constitue pas une mesure robuste pour l'évaluation biologique. Il demeure extrêmement difficile d'estimer précisément la diversité taxonomique de l'ensemble du macrobenthos. En particulier, les estimations de la diversité taxonomique sont typiquement basées sur de faux concepts taxonomiques. De plus, même si on peut l'évaluer précisément, on y trouve trop d'effets indésirables pour qu'elle constitue une mesure fiable; elle est affectée par plusieurs facteurs importants, seulement pour des taxons particuliers et dépendant de paramètres extrêmement difficiles à définir et à quantifier. L'auteur présente et discute certains préalables nécessaires pour appliquer la diversité du macrobenthos dans les évaluations biologiques.

Mots-clés : biodiversité, évaluation biologique, macrobenthos, macroinvertébrés, méthodes, adéquation taxonomique.

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1. Introduction

Sustaining biological diversity is a priority for nature conservation in terrestrial, marine, and freshwater environments (Brooks et al. 2006). Freshwater biodiversity is the overriding conservation priority during the International Decade for Action "Water for Life" 2005 to 2015 (Dudgeon et al. 2006). Therefore, the assessment of biological diversity in freshwaters and its most important element — taxonomic diversity — plays a very significant role as the basis for nature protection. Different measures of biodiversity are often used in biological assessment of freshwaters. In 33 bio-assessment articles published in scientific journals between 2005 and November of 2009 indexed by the Web of Science® (Institute of Scientific Information – Thomson Reuters), various measures of biological diversity calculated for the whole macrobenthos were used. The alteration of invertebrate taxa diversity as compared to an undisturbed reference is an important indicator of quality status of a lake or river in *The Water Framework Directive* (WFD) (European

Commission 2000). That biodiversity of freshwater organisms decreases as a result of environmental disturbance is an important assumption according to this document. This assumption seems, however, to be an unprovable supposition, not a general rule. This article argues the thesis that biological diversity of freshwater macrobenthos is not a good metric for biological assessment.

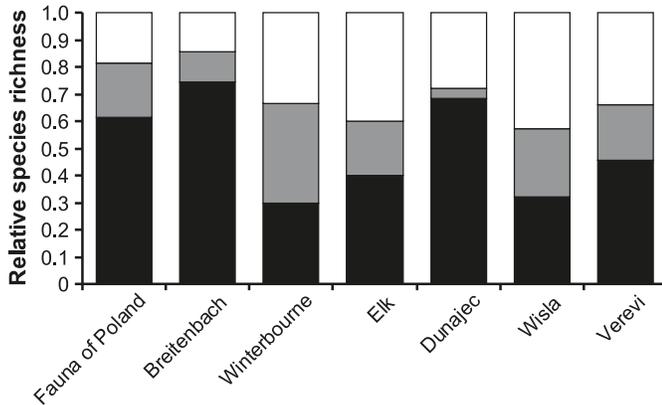
2. What is biological diversity? Which of its meanings is applicable to biological assessment?

The term *biodiversity* (or biological diversity) has at least four meanings: (1) The diversity and distribution of native species present at some time, prior to human settlement, but it can also refer to lower levels of organization, such as the diversity of genetic material within a species, or to higher levels of organizations, such as the diversity of ecosystem structures and functions (Heywood 1995). In this meaning it can be quantified, expressed as the number of species or other taxa (richness) or as the values of any of several indices, that describe the spatial distribution of individuals. (2) The sum of organisms on Earth, their genetic and phenotypic variation, and the communities and environments of which they are a part (Dirzo and Mendoza 2008). (3) Life subject to protection under legislation (e.g., Convention on Biological Diversity 1992). (4) An ethical and philosophical

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Fig. 1. Taxonomic composition of macrobenthos in selected databases (see Table 2). Taxa, which are typically identified in assessment studies to the level of species and genus (EPT larvae, Odonata, Heteroptera, Gastropoda) are presented as black area; to the level of family and order (Diptera, Oligochaeta, Acari) presented as empty area to the mixed level (Bivalvia, Coleoptera, Amphipoda, and other) as grey area.



term, or even mythical notion treated as the value in itself (Ghilarov 1996).

In scientific literature, more than 10 indexes are commonly used to quantify the diversity of individuals. These include richness measures, diversity indices, evenness indices, and taxonomic distinctness. Richness describes the number of taxa found: the number of species, families, or individuals calculated at some other level of taxonomic aggregation. Diversity indices (note the confusing duality of the term) — the best known Shannon–Weaver’s (or Shannon’s), Simpson’s, and Margalef’s indices — are more precisely called indices of “probability of interspecific encounter” or “uncertainty” (DeJong 1975). These indices represent either “heterogeneity” or “dominance” depending on their mathematical construction (Peet 1974). Evenness indices, for example Pielou’s J-index (Pielou 1966), describe “equitability” of assemblages. Taxonomic distinctness (Clarke and Warwick 1998), and its derivatives (Clarke and Warwick 2001), describe an assemblage’s phylogenetic diversity; those measures are difficult to interpret and, because of criticism raised by Abellan et al. (2006), this review excludes taxonomic distinctness from the discussion henceforth. Mathematical peculiarities of various diversity measures, their benefits and objections, and their interrelationships have been described by many authors (e.g., Peet 1974; Heip and Engels 1974; DeJong 1975; Magurran 1988), as have their limitations, terminological misconceptions, and methodological errors (e.g., McNaughton 1977; Ghilarov 1996; Faith 2008).

3. Classifying biodiversity

Two hierarchical biodiversity classifications are common in ecology. One reflects three traditionally recognized levels of organization: intraspecific (genetic diversity), interspecific (species diversity), and hyperspecific (ecosystem diversity). The other, by Whittaker (1972), describes three types

of biodiversity over spatial scales: alpha (α) diversity refers to the diversity within an ecosystem; beta (β) diversity means the differences in species number between ecosystems of the same region; and gamma (γ) diversity is a measure of the overall diversity for the different ecosystems within a region. Alpha and gamma diversity are expressed as the number of species, while beta diversity is relative value, expressing the gamma diversity/alpha diversity quotient. Neither of these two schemes is appropriate for classifying biodiversity of benthic invertebrates in rivers, streams, lakes, and ponds. This is because freshwater ecosystems have special properties that render the boundaries between categories ill defined. Facultative parthenogenesis, mixed-mating, interspecies hybridization (Michailova 1996; Ball 2002; Facon et al. 2005; Jokela et al. 2006; Schaack 2008; Petrauskienė et al. 2009), and the common occurrence of cryptic species (e.g., Brandle et al. 2007; Wilson 2008; Gustafsson et al. 2009) makes it difficult to classify variability as intra-, inter-, or hyper-specific. Furthermore, among certain taxonomic groups, species identification is impossible or questionable for some aquatic life stages (e.g. within Diptera and Trichoptera), which leads to the application of categories known as species groups or morphospecies: categories that blur the borders between genetic, population, and species biodiversity.

Important difficulties in classifying ecosystem diversity are discussed below. These issues relate to differentiation between alpha, beta, and gamma diversity in freshwater environments having vague borders, and in which numerically dominant animals (insects) typically migrate outside and spend a part of their life in terrestrial environments.

4. Uses of biodiversity indices

Biological diversity is primarily used for nature conservation and environmental monitoring, but is also used in non-applied ecological studies as a tool to compare different habitats (Magurran 1988). Therefore, biological diversity exists simultaneously as an ecological metric and as a key matter for nature conservation. Such a dichotomy of meaning, and the scale dependence of its definitions, have resulted in numerous misunderstandings. One of the most common misinterpretations is related to the concept known as “threats to biodiversity” that has been widely discussed in scientific literature and is especially concerned at a global scale. The conclusion that flow modification, pollution, and exotic species are the main threats to freshwater biodiversity (Dudgeon et al. 2006; Johnson et al. 2008) is probably true, but mainly at large scales (landscapes, continents). Whereas, at the scale of single freshwater ecosystems, those factors may result in an increased local biodiversity. This question is discussed in the following text. A threat to biodiversity that can seriously increase the risk of global species extinction is a completely different phenomenon from a factor that locally reduces one of the diversity indices. Unfortunately, these differences have often been confused and their related problems have often been discussed without proper differentiation (Humphries et al. 1995; Johnson et al. 2008). Gontier et al. (2006) argued that the term *biodiversity* is used in en-

Fig. 2. Mean number of species per family (grey bars) and mean number of species per genus (black bars) in selected taxonomic groups of macrobenthos in Polish freshwaters (based on Bogdanowicz 2008).

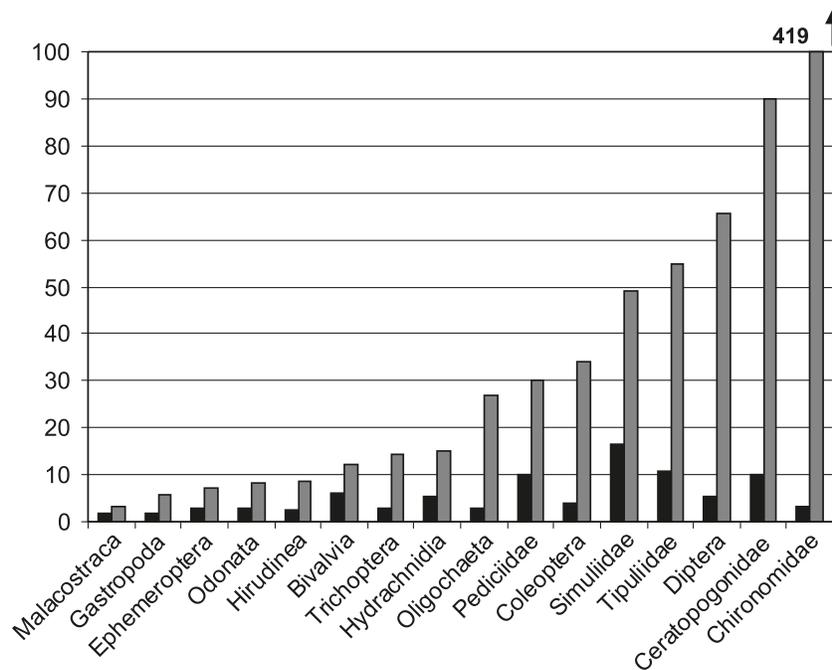


Table 1. Significance of correlations between ecological parameters of lowland streams and diversity of different groups of macrofauna.

Parameter / Taxon	Gastropoda	Hirudinea	Ephemeroptera	Chironomidae	Odonata	All taxa
Pollution	+ ns	+ ns	--	ns ns	ns ns	ns ns
Riparian diversity	ns ns	ns ns	+ ns	+ ns	ns ns	+ ns
Stream width	- ns	- ns	ns ns	ns ns	++	ns ns
Stream depth	- ns	- ns	ns ns	ns ns	ns ns	ns ns
Isolation	--	- ns	ns ns	ns ns	- ns	- ns
Bottom substrate	++	- ns	ns ns	+ ns	ns ns	ns ns
Seasonality	ns ns	+ ns	--	ns ns	ns ns	ns ns
Mean number of species per sample	4.2	3.9	5.2	16.3	2.9	28.1

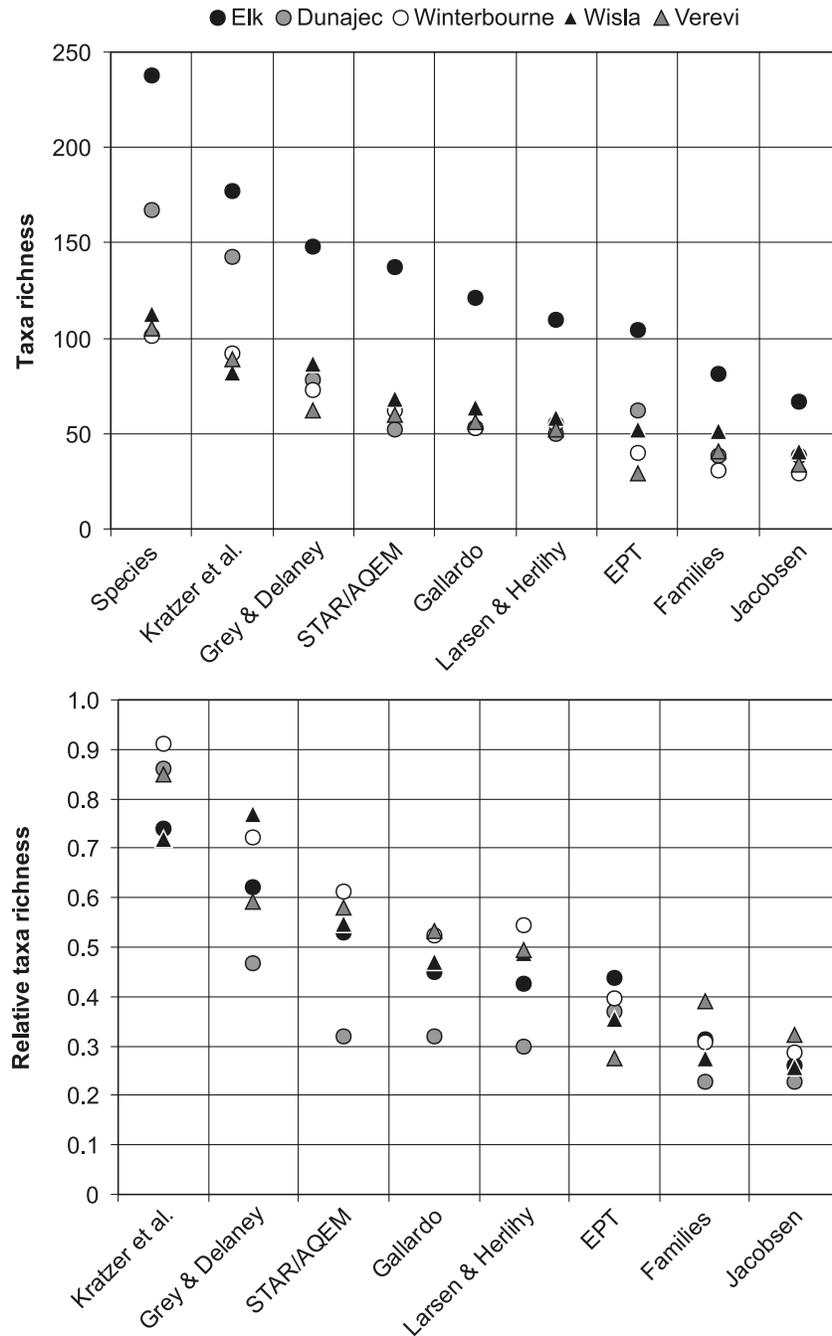
Note: +, positive significant correlation; -, negative significant correlation; ns, nonsignificant. First result in each column based on the number of species while the second one on the number of genera. Presented analysis based on data presented in Koperski (2010a).

Table 2. Data and methods of species identification used in analysis, presented in Figs. 1 and 3, with references.

Environment	References
Stream, Winterbourne, England — 8 km in length	Berrie and Wright 1984
Stream, Elk, Poland — 113 km in length	SEPI, Koperski 2010a
River Wisła, Poland — 1047 km in length	SEPI, Koperski (unpublished)
River Dunajec, Poland — 247 km in length	SEPI, Kownacki et al. 2002
Lake Verevi, Estonia — area 1.26×10^4 m ²	Timm and M—ls 2005
Level of identification	
Species, species groups (Diptera)	
Species or genus (Insecta), order (other taxa)	Kratzer et al. 2006
Species, Chironomidae and Oligochaeta not identified	Gray and Delaney, 2008
Mixed levels	STAR-AQEM (Tończyk 2006)
Genus, family (Diptera), class (Oligochaeta)	Gallardo et al. 2008
Genus (Insecta), tribe (Chironomidae), family (Mollusca), order (other taxa)	Larsen and Herlihy 1998
Sub-family (Chironomidae and Ceratopogonidae), family (other Insecta), order (other taxa)	Jacobsen 2008

Note: SEPI, data from State Environmental Protection Inspectorate, Warsaw, Poland.

Fig. 3. Taxa richness (upper plot) and taxa richness in relation to species richness (lower plot) of macrobenthos in selected databases (see Table 2) calculated on the basis of referred procedures of identification (see Table 1).

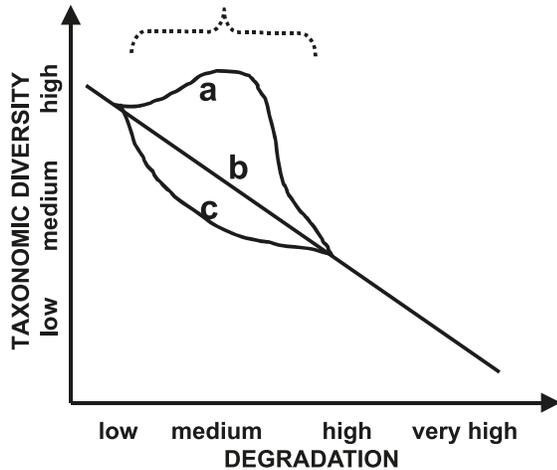


environmental impact assessments without a clearly defined scope and meaning.

Numerous European biological assessment methods use different measures of benthos diversity as a main or supplementary metric (e.g., Lorenz et al. 2004; Hering et al. 2004; Birk and Hering 2006). For example, values of diversity indices based on benthic macrofauna are taken into account in two methods of biological assessment of freshwaters implemented in Poland. These indices are (1) the Margalef index as a supplement to the BMWPP biotic index (Biological Monitoring Working Party score system, Polish modifica-

tion), in which animals are identified to the family level (Fleituch et al. 2002); and (2) the Margalef index and Shannon–Weaver index, as complementary metrics in the STAR–AQEM (Standardisation of River Classifications’ integrated assessment system for the ecological quality of streams and rivers throughout Europe using benthic macroinvertebrates) method, which requires mixed-level taxonomic aggregation (mainly family or genus) (Buffagni et al. 2004; Tończyk 2006). Similarly, Kerans and Karr (1994) used taxa richness of macrobenthos from mixed-level aggregation in their benthic index of biotic integrity (B–IBI). Shannon’s diversity index using mixed-level benthic–inver-

Fig. 4. Taxonomic diversity as a hypothetical function of environmental degradation. Within the range of moderate degradation, between *a* and *c*, many trajectories are possible.



tebrate aggregation has also been used to assess quality of ponds (Trigal et al. 2009).

5. Which ecological factors determine the diversity of macrobenthos as a whole, and which ones do not?

Factors that potentially influence the biodiversity of macrobenthos are many, however, unambiguous examples of strong influence on biodiversity of the whole macrobenthos are rare. Unfortunately, relationships found for certain groups, like diatoms or reef corals (e.g., Connell 1978) are sometimes extended as alleged rules for freshwater macrobenthos (e.g., Magurran 1988; Dudgeon et al. 2006); this extension seems to be fallacious.

It is obvious that the diversity of macrobenthos dwelling in fresh waters is determined by geographic, climatic, and historical factors. The results of a study aiming to find the reasons for notable differences in composition and diversity of benthic assemblages between New Zealand and Palearctic springs show that predator type is a main cause (Barquin and Death 2006). Additionally, the diversity correlated positively with spring stability and productivity, and negatively with altitude. According to Jacobsen (2008), the negative correlation of stream-benthos diversity with altitude reflects oxygen concentration in water. Stability of abiotic parameters and isolation are important and strong determinants of the diversity of benthos, especially in ponds and streams (Scheffer et al. 2006; Shulman and Chase 2007; Koperski 2010a).

Biotic factors, predation and parasitism in particular, are typically omitted as potential determinants of macrobenthos diversity in biological assessment procedures, although they are factors that take place continuously and are able to significantly modify biodiversity. Theoretically, predation is expected to increase diversity (Paine 1966), but, in some environments, selectively feeding vertebrate carnivores are able to extirpate prey populations (Henrikson 1988), or at least significantly reduce their density (Prejs et al. 1997). Macroinvertebrate species lists for fishless ponds tend to be shorter than those for ponds having benthivorous fish (e.g.,

Rosenfeld 2000; Knapp et al. 2005; Koperski 2006). The effect of predatory pressure in complex environments is, however, not visible in the total biodiversity of macrobenthos (Krakowiak and Pennuto 2008); thus, it cannot be used as a metric of the strength or the type of predatory pressure.

An important exception may be constituted by certain invasive predatory species that are able to reduce the diversity of native species (Ratti and Barton 2003; Usio et al. 2009). However, a logical contradiction stands between the conclusions that invasive species are one of the most important threats to freshwater biodiversity (e.g., Dudgeon et al. 2006) and the fact that in some environments (e.g., lowland rivers in Europe) species richness is higher because of the occurrence of nonnative species of invertebrates, mainly molluscs and crustaceans. Biological diversity in northern and central European freshwaters, which dramatically decreased during the last glacial period, significantly increased in recent years as a result of nonnative species' invasions (Kołodziejczyk et al. in press). The potentially negative influence of interaction between native and alien species on the functioning of freshwater environments is an important problem, but is different from numerical change in species richness due to invasions.

In general, the relation between the sampling area and number of species observed is well known (Arrhenius 1921), but the relation between the area of freshwater environment (lake, pond, or catchment area) and diversity is not obvious at all. The results obtained by Davies et al. (2008) suggest that species richness depends more on habitat type than on habitat size. It seems that the application of a measure commonly used in ecology — species density (number of species per area unit) is problematic in the biological assessment of freshwaters where comparisons between environments are required. The heterogeneity and discontinuity of the aquatic environments are their typical features — highest diversity is noted at margins of slowly flowing and standing waters (Principe and Corigliano 2006). The ratio of littoral-zone area to whole-water-body area is not constant, which makes the relation between area and biological diversity unclear.

Stream discharge is an intensively studied biodiversity influence (Dewson et al. 2007a). Moore and Palmer's (2005) results show that taxa richness of stream macrofauna depends on riparian forest cover, however, their taxonomic resolution made for an insufficient surrogate for species diversity (noninsect taxa identified to class or order).

6. Diversity of whole macrobenthos is driven by multiple factors, and thus is a problematic metric of assessment

The influence of certain, potentially very important, environmental parameters on benthic-invertebrate diversity seems to be problematic, weak, and unclear. Different studies on the effects of decreased pH yielded opposite conclusions (Sandin 2003; Petchey et al. 2004; Petrin et al. 2007), and is a good example. One of these parameters is organic pollution, despite its common application as a main parameter in biological environmental quality assessment. For example, no significant relationship, linear or nonlinear, was found between any of the measures of benthic inverte-

Table 3. Parameters of the best-fitted linear regressions between species richness of selected groups of macrobenthos found.

Variables	<i>n</i>	Equation	<i>R</i> ²
Chironomidae richness versus total richness	18	$y = 1.646x + 4.5295$	0.9238
EPT richness versus total richness	18	$y = 2.2752x + 31.161$	0.4701
Other taxa richness versus total richness	18	$y = 2.8761x + 15.769$	0.6676
Chironomidae richness versus EPT richness	34	$y = 0.1445x + 9.9192$	0.0495

Note: Analysis based on data from 10 streams and rivers, where all or almost all macrobenthic invertebrates were identified to the species and species-group level, presented in Berrie and Wright (1984); Lenat (1988); Kownacki et al. (2002); Kornijów and Lechowska (2002) and Koperski (2010a).

brate taxonomic diversity and total phosphorus concentration and nutrient loading in the 45-lake study by Donohue et al. (2009). Likewise, the results of an intensive study of 143 European streams by Johnson and Hering (2009) clearly demonstrated that diversity of macrobenthos was not a significant predictor of nutrient enrichment or habitat degradation and, moreover, was a significantly weaker predictor than was the diversity of any other group of freshwater fauna. Extreme stressors, such as high concentration of toxicants, are evident exceptions: reduced species richness and decreased faunal evenness after pesticide application has been reported by many authors (e.g., Wilson 2008). It must be added, however, that an analysis of biodiversity is not necessary to evaluate the environmental results of catastrophic stress. The relations between macrobenthos diversity and certain intensively studied factors were found to be unimportant (i.e., metal contamination, Spencer et al. 2008; deforestation, McKie and Malmqvist 2009). Strong and convincing determination of evidence that stream benthos diversity is determined by an area's past (ca. 40 years earlier) land uses were presented by Harding et al. (1998) — a rare but important exception.

The strongest and most self-evident driver of macrobenthos diversity is “habitat diversity,” which is expressed and measured in many different ways, for example, as the diversity of water bodies in a river–floodplain ecosystem (Gallardo et al. 2008). Riparian habitat diversity, measured as the quantity of tree species, was found to be the most important factor determining species richness of aquatic insects in the study by Voelzl and McArthur (2000). Streams with greater diversity in floral assemblages and hence potentially greater variation in habitat complexity, food sources, and other factors may be able to support a more varied invertebrate fauna (Metzeling and Miller 2001). Analyses presented in the review by Dewson et al. (2007b) show that a significant decrease in the diversity of macrobenthos along with a decrease in stream discharge is, in fact, a result of the decreased number and diversity of habitats available for fauna. Nevertheless, habitat diversity is not a simple parameter, moreover, it is difficult to compare for different types of environments. Apart from that, strong relationships between taxonomic diversity and habitat diversity seem to be obvious. In fact, habitat diversity is not a factor, but rather a complex of parameters. Decreased habitat diversity is an element of so called “degradation.” There is no possibility to distinguish the effect of any particular element of “habitat diversity” or “degradation” on the basis of whole macrobenthos diversity.

7. Diversity of different groups of macrobenthos is driven by specific factors

Diversity of the whole macrobenthos seems to be related only to complex ecological factors like productivity or habitat heterogeneity (Voelzl and McArthur 2000), while different groups of benthic invertebrates may be strongly affected by simple, abiotic environmental parameters. The number of references in the scientific literature confirming this conclusion is vast. For example, Koperski (2010a), in his study on lowland streams, showed that taxonomic diversity of the main groups of macrobenthos is affected by different environmental parameters (Table 2): Ephemeroptera by stream pollution; Gastropoda by the type of bottom substrate; and Odonata by stream width. Similarly, Scrimgeour et al. (1998) showed that, out of the list of several environmental variables, leech species richness was significantly related only to lake area (larger lakes may provide more habitats for species that are only locally abundant, rare, or absent from smaller lakes). Chemical pollution was found to be the main cause of significant decrease in leech diversity in small, artificial ponds (Krodziewska 2003). Species richness of freshwater gastropods examined at 429 North American sites was significantly correlated with the type of bottom substrate, the richness of aquatic macrophytes, inorganic phosphorus, chloride, total alkalinity, total dissolved solids, pH, and dissolved organic matter (Pip 1987). Tixier and Guerold (2005) demonstrated that Plecopteran diversity was most affected by freshwater acidification. The taxonomic richness of the so called EPT group (Ephemeroptera, Plecoptera, and Trichoptera combined) being sensitive to oxygen concentration is commonly used in biological assessment as a metric of stream pollution (e.g., Growns et al. 1997) and also as a parameter responding along gradients of land-use and riparian cover (Moore and Palmer 2005).

Species diversity, often of species-rich subgroups of site assemblages (like Chironomidae), is sometimes used as a biomonitoring index (e.g., Inoue et al. 2005). Studies of Janssens de Bisthoven and Gerhardt (2003) and Karimmou-savi et al. (2003) present a visible reduction in chironomid species richness as a result of strong heavy metal pollution. Diversity reflects theoretical notions about increasing stress excluding taxa: because each taxon has a limited range of conditions it can tolerate, increasing exposure to stress will lead to sequential deletions of taxa, so that declining richness is viewed as convincing evidence of biological effects. However, species diversity of those taxa has limited effectiveness, because the taxa contained in biotic assemblages are often ecologically divergent (e.g., some being tolerant generalists and others being sensitive specialists). As a

result, even if species substitutions are made, richness may not change along the gradient of certain important and intensively studied environmental factors (Koperski 2010a). Values of richness of species-rich taxonomic subgroups sampled at moderately polluted sites are typically equal or even much higher than those sampled at reference sites — as was presented for Chironomidae (Rabeni and Wang 2001; Kownacki et al. 2002; Kornijów and Lechowska 2002) and Oligochaeta (Kownacki et al. 2002; Kornijów and Lechowska 2002).

8. Units of macrobenthos taxonomic diversity are not comparable

Species richness, the main parameter of biological diversity, increases with time spent collecting and with the number of individuals collected. The relationship is logarithmic (DeJong 1975). Thus, the number of new species added to the list asymptotically approaches some ceiling (Soberon and Llorente 1993). Rarefaction is the group of numerical procedures that correct for significant errors caused by different sample sizes in estimation of species richness. It permits several diversity estimates to be made: it allows the diversities of various habitats to be compared (Palmer 1990; Ugland et al. 2003); and it estimates the sample size necessary to complete the list of species with specified accuracy (e.g., Koperski 2006). Nevertheless, numerous studies' conclusions are based on diversities from different-sized samples, without rarefaction procedures having been applied (e.g., Nedeau et al. 2003; Inoue et al. 2005; Gallardo et al. 2008). Rare species' richness (rarity), although it depends on the number of specimens collected, is regarded by Cao et al. (1998) as an efficient metric of habitat quality. However, Marchant (2002) concluded, that rare taxa are not important in bioassessment.

Biological diversity must be estimated for a certain area but the spatial extent of most areas being biologically monitored is ill defined. Larval stages of winged insects constitute the majority of freshwater animals in freshwater environments (Fig. 1), but following metamorphosis insects typically migrate between freshwater environments to reproduce. Dormant stages of crustaceans and adult gastropods and leeches colonize new environments rapidly via birds (Green and Sanchez 2006), mammals, and humans (e.g., boats and nets). Some freshwater invertebrates may exist in metapopulations, for other temporal dispersal via diapause is functionally equivalent to spatial dispersal, and finally, local extinctions may be rare or absent (Bohonak and Jenkins 2003). In biological assessment, the biological diversity is quantified for an environment (river, stream, lake or pond) on the basis of the values measured at sampling sites. However, many flowing waters in temperate zones are connected with nearby or even distant water bodies during regular or incidental floods allowing for the exchange of species and genes between them (Gallardo et al. 2008). Complexes of continuously or temporarily connected environments between which the exchange of species occurs should be treated as the basic environmental unit in terms of macrobenthos diversity. Such super ecosystems (river valleys with oxbow lakes and riparian marshes, sets of connected lakes with inflows and outflows, sets of small water bodies con-

nected temporarily during floods) should be the basic areas to estimate biodiversity for biological assessment. An analysis of single freshwater environments, especially when sampled one or two times per year probably can record only a fraction of the number of species inhabiting them. The methodology of comparative studies on benthos diversity for the goals of biological assessment needs a definition of environment, which should be as precise as possible. Paillex et al. (2007) demonstrate high importance of lateral connectivity between reaches and Gallardo et al. (2008) present diversity of water-body types as the main factors stimulating high biodiversity. Conclusions of Horsak et al. (2009) coincide with the above, when they suggest that reduced diversity of macrobenthos in a river due to its channelization is directly caused by the reduction in habitat diversity.

Numerous field studies of relationships between freshwater macrobenthos diversity and environmental variables used only one type of sampler, adapted to a specific habitat or even microhabitat (Larsen and Herlihy 1998; Adams et al. 2005; Barquin and Death 2006; Paillex et al. 2007), but taxonomic composition of different habitats in the same environment could be considerably different. This approach seems to be problematic in bioassessment studies based on diversity estimation. More and more studies on diversity, from Lenat (1988) onward, have been considering habitat and microhabitat diversity of rivers and lakes, applying different sampling methods (e.g., Royer et al. 2001; Jacobsen 2008; Gray and Harding 2009). Significant differences in taxonomic composition of macrobenthos sampled with different samplers have been often presented and analysed. It was found that differences in selectivity and sampling efficiency of samplers in relation to different groups of macrobenthos were immense and repeatable (Elliott and Drake 1981; Nalepa et al. 1988; Schloesser and Nalepa 2002; Koperski 2003). Gerth and Herlihy (2006) found significant differences in the diversity of macrobenthos sampled with different procedures (single-habitat method versus multi-habitat-composite methods), but not between riffles and pools. It seems that a factor often neglected — bottom variability — influences the diversity of macrobenthos in flowing waters more strongly than the traditional differentiation into riffles and pools (Robson and Chester 1999; Gerth and Herlihy 2006).

Riparian vegetation is an important element of life habitat for a great part of freshwater macrobenthos such as insects; it is inhabited by them only temporarily and only rarely taken into consideration in studies on freshwater biodiversity (Delettre and Morvan 2000; Rios and Bailey 2006). Soil, sand, and stones close to the shoreline play the same role for certain freshwater animals — amphibiotic leeches and oligochaets, larval dipterans, and Plannipennia — and also for dytiscids and megalopterans during their metamorphosis and hibernation.

9. Macrobenthos taxonomic diversity is a weak metric because diversity estimations are typically based on taxonomic misconceptions

Total biological diversity is difficult to estimate. Therefore, incorrectly estimated diversity of macrobenthos is very

common both in strict ecological studies and in biological assessments. Application of diversity of only a part of macrobenthos occurring in an environment as the total diversity of whole macrobenthos is the most frequent error. Numerous types of methodological errors and inconsistencies that arose due to taxonomic sufficiency in assessment studies were presented at length by Jones (2008). Numerous researchers found detailed identification of certain taxonomic groups difficult or troublesome, yet difficult taxonomy does not excuse methodological errors made when estimating diversity.

Substitution of taxonomic groups by morphospecies in diversity-based rapid bioassessment (Wilson 2008) seems to be impractical. Certain groups of benthic species are extremely difficult to distinguish from one another, in spite of their great ecological divergence — the example of common genus *Cricotopus* (Chironomidae) is notable.¹ Even the approximate number of cryptic species hidden in higher benthic-invertebrate taxa is unknown, but in certain groups it is probably high, such as in Clitellata (Govedich et al. 1999; Beauchamp et al. 2001; Gustafsson et al. 2009), Chironomidae (Sharley et al. 2004; Carew et al. 2007), and Simuliidae (Rivera and Currie 2009). Nevertheless, the analysis of morphospecies seems to be very sensitive to personal differences in classification abilities, resulting from personal knowledge and experience. These arguments support the thesis that this method of analysis will underestimate the real diversity often markedly.

9.1 Diversity of higher taxa may not be efficient surrogate for species diversity of freshwater invertebrates

Detailed identification of animals for biological assessment requires much time, work, and money; therefore, numerous studies present a view that higher taxa can be used as taxonomic surrogates of species richness with equal effectiveness, expressed as an amount of information conveyed (e.g., Bournaud et al. 1996, Doledec et al. 2000, Marshall et al. 2006, Statzner et al. 2008). An important argument against the use of genera, families, or orders as species surrogates for calculating diversity is that there are great differences in the number of species in genera and families among most important groups of macrobenthos (see the result of analysis in Fig. 2). Among macrobenthos present in Polish freshwaters the mean number of species per genus in certain groups of Diptera is five times higher than in Gastropoda, for example; the differences in the mean number of species per family are even much higher (in Diptera and Ephemeroptera, ca. seven times higher; in Chironomidae, 127 times higher than in Malacostraca). Each sample of macrobenthos also contains many more species of Diptera than Ephemeroptera, which makes the richness count unreliable.

Results of species data meta-analysis in available databases (Table 1) highlight the number of species included in the higher taxa, which are typically identified in assessment studies to the level of species or genus, ranged between 14% and 40% of total number of taxa found during the field

study (Fig. 1). Thus, a high portion of total species richness (up to 74%) is contained inside groups that are typically not identified to the species / genus level. In fact, it is unknown how large this fraction is: references for complete lists of freshwater benthic species are extremely rare in scientific literature. Even in species-based datasets some difficult species are assigned only to their genera or families (e.g., Waite et al. 2004). Datasets containing different taxonomic precisions (in which individuals are identified with different levels of taxonomic details) produce erratic results, as it was presented by Nijboer (2006), who analysed samples of stream macrobenthos with clustering method. Humphries et al. (1995, p. 95) emphasized that “for comparisons between areas, accurate identification of the taxa is considered fundamental because the species of each are treated as having equal weight, whatever the range occupied.”

Following Jones (2008, p. 47), it must be emphasized that “species is the lowest group in the taxonomic hierarchy, so individuals of the same species exhibit lower variability in traits than occurs within any other taxonomic group.”² Referring to many studies and analyses related to taxonomic sufficiency, he concludes that, at least for certain databases, aggregating faunistic data at a level coarser than species reduces the effect size that can be detected. All fundamental studies referred to by Welch and Lindell (1980), as classic examples of the predicted decrease of benthos diversity as a result of water pollution, are based on values of diversity indices calculated incorrectly for families, genera or mixed taxonomic levels. Studies of Bournaud et al. 1996, Arscott et al. (2006), and Marshall et al. (2006), for example, belong to the group of articles that present the opinion that genus or family richness is equally informative as species richness, but their conclusions were based on very coarse taxonomy. In spite of the conclusion drawn by Heino and Soininen (2007, p. 78) that “for macroinvertebrates, relatively similar amounts of variation in assemblage structure and taxon richness for species-, genus-, and family level data were accounted for by the environmental variables,” their own results seem to show a decrease in explained variance along with the decrease in the taxonomic precision from species to genus and family. Marshall et al. (2006) provide evidence that even intensive, precisely planned, and scientifically advanced diversity studies can fail to provide any general conclusions about factors determining biological diversity of macrobenthos due to methods applied. The authors concluded that “very little information (< 6%) was lost by identifying taxa to family (or genus), as opposed to species. Species richness was very well represented by genus, family and order richness, so that each of these could be used” Marshall et al. (2006, p. 171). However, 8 of 15 higher taxa occurred in their study area and were identified mainly to family or genus level and in four groups (among others Oligochaeta) no species was identified. Similarly, in the study by Metzeling and Miller (2001), testing optimal sample size in biological assessment, there occurred no significant differences between compared efficiencies of evaluation based on identification to the species and genus levels, but taxa

¹ Only experienced taxonomists are able to identify it to the species level, but some of these species have completely different ecology and food niches (Berg 1995).

² Of course with exception of great ontogenetic shifts in life-history like in Coleoptera.

typically richest in species (Oligochaeta, Acari, and Chironomidae) were not identified in detail. The indicative values of genera and families in results by Arscott et al. (2006) turned to be efficient but only in cases of discrimination between most- and least-impacted sites, while for this level of discrimination the assessment based on macrobenthos identification seems not to be necessary. Chessman et al. (2007) emphasized weak effects of greater taxonomic resolution in discrimination between habitat types but with 10 significant effects at the generic levels and a substantially lower number of significant effects (seven) at the family level. Gayraud et al. (2003) consequently suggest that family and genus identification are sufficient for large river biomonitoring using invertebrate traits even though Diptera and Oligochaeta were excluded from the analysed data in spite of their great importance for river fauna diversity. Similarly, diversity index used in the widespread procedure STAR–AQEM is also calculated without taxonomic identification of the richest groups like Chironomidae (Haase et al. 2004). A large part of freshwater diversity is commonly overlooked when groups that are richest in species are identified only to the level of family (Chironomidae), order (Acari), or class (Oligochaeta), whereas detailed identification are often made for groups that are species poor (Godfrey 1978; Larsen and Herlihy 1998, Melo and Froehlich 2001; Gallardo et al. 2008; Gray and Delaney 2008; Williams et al. 2008).

The values of correlation coefficients for relations between biodiversity of certain groups of macrobenthos of lowland streams and the main environmental parameters, presented in Table 2, explain that 15 of 19 statistically significant correlations were visible only at the species level of identification and only four were recognized at the genus level. Such differences are present despite the strong correlation between the number of species and number of genera in samples.

The results of numerical metaanalysis of marine benthos databases made by Bertrand et al. (2006) led authors to suggest that changing the identification level from species to a higher taxonomic level, commonly used in biological assessment as taxonomic surrogacy, is founded on a misconception about the properties of Linnean classification. Allocation of higher ranks in current taxonomic classifications constitute rather a heterogeneous mixture of various historical and contemporary views than an effect of consistent procedures based on the number of bifurcations on phylogenetic trees. Bertrand et al. (2006) emphasized that there is no strong equivalence between different taxonomic groups in the same rank so they clearly concluded that taxonomic surrogacy lacks justification. As it is suggested by Andersen (1995, p. 39), with reference to terrestrial invertebrates, “it may be applied more generally for taxa in which a relatively small number of genera can contribute a large proportion of species.” Therefore, the diversity of higher taxa does not seem to be an efficient surrogate for species diversity of freshwater invertebrates, especially when the chosen surrogate occupies a different rank, higher than genus.

The results of a meta-analysis, presented in Fig. 3, are based on data from five freshwater environments, from which almost every invertebrate found was identified to the species level or to the level of species-groups (Table 1). The values of species richness were contrasted with the values of

the taxa richness (see below) calculated according to certain methods referred to in Table 1. Clearly at least one fault can be attributed to each method of estimating diversity by taxa richness. These include (1) no equivalence (big difference between taxa richness and species richness — 2–5 times in Gallardo method and Larsen and Herlihy method); and (2) great differences in efficiency when different environments compared (more than 25%: Grey and Delaney method, STAR–AQEM, Larsen and Herlihy method). Low variability in taxa richness calculated with a certain method is generally expected where the ratio of taxa richness to species richness is low (and vice versa). The method of identification by Kratzer et al. (2006) was found to be the best predictor of diversity of the whole macrobenthos. Variability in its results among data from different environments was also low; however, calculations are time consuming. Estimated macrobenthos diversity is incomparable when different taxonomic precisions were used for different environments. All published data on freshwater biodiversity calculated using mixed-level identifications are incorrect (biased), and probably highly incorrect in most cases. Moreover, this bias is impossible to estimate because it is unknown how much diversity is hidden in coarsely identified taxonomic groups.

9.2 Application of “taxa richness” hinders comparisons among studies

It is extremely confusing when mixed-level taxonomic aggregations are used to estimate diversity, but the level of identification applied to each taxon is not completely described (e.g., Rosemond et al. 1992; Astin 2007; Bonada et al. 2008; Tall et al. 2008). This method of estimating diversity is problematic because decisions about which taxa deserve detailed identification is arbitrary. The term “lowest feasible level” or “lowest practical taxonomic level” used for identification (Vinson and Hawkins 1996; Royer et al. 2001; 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 not pragmatic at all for biodiversity studies. This kind of method presentation makes results impossible to compare. In numerous articles, methods of identification are too vaguely described: “invertebrates were (...) identified, usually, to species/genus ...” (Johnson and Hering 2009, p. 177). “Animals were identified, usually to genus or family...” (Angradi 1996, p. 48). “Individuals in (...) subsamples were usually identified to genus level...” (Vinson and Hawkins 1996, p. 394). “Taxonomic identifications were to the lowest feasible level, typically genus, although some groups were left at a coarser level of resolution (e.g., Chironomidae, Oligochaeta) and others were taken to species...” (Royer et al. 2001, p. 628). The scientific value of the data about biological diversity obtained by these methods is, unfortunately, close to zero.

In the study by Marchant et al. (1997), two large datasets were compared in order to construct predictive models of stream macrobenthos for the needs of biological assessment. Marchant’s “species dataset” was composed of 56 species, 10 morphospecies, and 44 taxa identified as genera, families, orders or classes (Nematoda, Oligochaeta, Turbellaria). “Diversity of invertebrates” presented in the results by Gascon et al. 2009 includes only crustaceans and insects. How-

ever, Diptera, probably the richest in species, is not represented there. Statzner et al. (2008) consistently used the term “species richness” of stream macroinvertebrates as a parameter based on datasets identified to the genus level, with Oligochaeta and Diptera excluded from the analysis.

10. Macrobenthos total diversity, even estimated accurately, is a weak metric

Macrobenthos is not a homogenous group of fauna in terms of their ecological preferences (in opposition to assumptions of numerous studies (e.g., Johnson and Hering 2009). The ecological variability of benthic invertebrates dwelling in each freshwater environment is extremely high. In each stream, river or lake, at least several dozen, perhaps even several hundred, benthic species with bodies larger than 2 mm (macrofauna) should be expected. They typically belong to a few phyla and classes, 5–20 orders, and 10–48 families (Zwick’s in Allan 1995; Botos et al. 1990; Bournaud et al. 1996; Bonada et al. 2008; Gallardo et al. 2008). The taxonomic richness of small streams in Poland sampled by Inspectorates of Environment Protection in the years 2006–2008 was found to be 25–47 taxa (STAR–AQEM protocols, mainly genera but also tribes, species, and species groups; unpublished data) per 1000 individuals. Intensive sampling in three lowland streams in northeastern Poland (Koperski 2006) confirmed the occurrence of 54, 62, and 66 families of macrobenthos there (published data, plus families of Oligochaeta).

Taxa found in streams have different preferences for certain conditions such as oxygen concentrations, water chemistry, local water velocity, bottom substrate, and food availability. Biological diversity of macrobenthos is not related in a simple way with any single limiting factor, with the exception of catastrophic factors. Johnson and Hering (2009) investigated how diversity responded to different environmental stressors in streams. They concluded that response trajectories differ between taxonomic groups, stressors and stream type, and they showed diversity of macrobenthos to have lower indicative value than fish, macrophytes, and benthic diatoms.

Relationships between important environmental variables and species diversity of the whole macrobenthos in lowland streams, presented in Table 1, were significant only when it also concerned the groups richest in species (Chironomidae and Ephemeroptera) or all the remaining ones. The observation presented here that the total taxonomic diversity is related mainly to the ecological preferences of the most species-rich taxonomic groups seems to be general, though obvious, evidence.

11. Macrobenthos total diversity is affected by many factors important to particular taxa

Significant positive and negative correlations between environmental variables and diversity of particular groups are neutralized reciprocally when calculated for the whole macrobenthos assemblage. These effects, presented in Table 2 as absence of significant effects for total diversity are probably the main reason for general lack of relations between diversity of the macrobenthos as a whole and important environ-

mental parameters reported in studies presented above. Perhaps this is the reason why total richness of macrobenthos is the least sensitive metric of many tested in multi-metric assessment of river Potomac by Astin (2007). Selected groups of benthic fauna respond to different environmental gradients in different ways, and those factors that stimulate high diversity of a certain taxonomic group may be neutral or negative for the diversity of other groups. The number of references that corroborate this conclusion is, surprisingly, very low (e.g., Waite et al. 2004; Kratzer et al. 2006; Koperski 2010a). Heino (2002) presents visible differences in geographic patterns of diversity for different groups of freshwater fauna. Certain studies, such as the intensive study by Prendergast et al. (1993), emphasize that there is a lack of factors leading to an increase in diversity of many different taxonomic groups.

12. Macrobenthos diversity depends on parameters that are extremely difficult to define and to compare

Certain researchers conclude that major threats to biodiversity are habitat loss and fragmentation (e.g., Wilcove et al. 1998). In numerous studies, direct relationships between taxonomic diversity and certain environmental processes described as degradation, ecological quality, environmental stress, impact or perturbation were observed. An important problem with the description of these complex variables and with prediction of their effects is the essential impossibility to define them. The impossible-to-prove assumption that diversity increases with improving ecological quality (Magurran 1988) is the basic rationale for using diversity indices in biological assessment. This impossibility is a result of the fact that the term *ecological quality* is not clearly defined (Hull et al. 2003). It implies, that “taxa richness should be used carefully in ecological assessment, because it indicates typological differences rather than ecological quality, and the change of taxa richness due to human impact strongly depends on the type of stressor” (Nijboer 2007, p. 85).

While the decrease of total richness of macrobenthos along with increasing environmental perturbations is the important assumption of certain studies (e.g., Astin 2007), García-Criado et al., (2005) found no relationship between different measures of macrobenthos diversity and indices of environmental quality. Also Donohue et al. (2009, p. 118) noted that “the lack of relationship in our data between nutrient status and taxonomic diversity suggests that this parameter, although explicitly stated in the WFD as a requirement, does not provide useful information for classification of eutrophication status with lake littoral invertebrates.”

Our knowledge about benthic diversity responses is especially poor for moderate (and most common) levels of degradation. The majority of modern biological assessment procedures are based on the assumption that diversity responds as in hypothetical curve *b* in Fig. 4. Notwithstanding, curves like *a* and *c* are equally probable — certain anthropogenic transformations of environments, treated unambiguously negatively in WFD as factors reducing biodiversity are able to stimulate higher diversity of macrobenthos. Firstly, it

is not known how to define the degradation objectively, and therefore, nullifies its use as a scientific term. Furthermore, it is probable that the graphic representation of the relation between macrobenthos diversity and moderate degradation has a specific shape for different types of freshwater environments. The level of degradation (disturbance, environmental stress, impact) is typically described and quantified with numerous indices, different in construction, in which certain parameters such as toxic pollution, nutrient loading, type of land-use, anthropogenic changes in stream bottom, macrophytes and riparian vegetation, hydro-engineering constructions, number of nonnative species, and others, have different weight. Certain types of stream degradation, like transformation of the stream shore with stones and boulders as well as acceleration of flow velocity as a result of stream-bed constriction by bridges, caused a significant increase in taxonomic diversity in studies by Casado et al. (1989) and Koperski (2010a), as did transformation of the coastal zone in urban fresh waters (Koperski 2010b). Adams et al. (2005) reported no positive effect of longterm stream remediation on the diversity of macrobenthos, despite chemical recovery. The lack of significant changes in the diversity of stream macrobenthos along with the changes of environmental quality is suggested by Jähnig and Lorenz (2008) as typical and general. A conversion of land cover from forest to human-altered forms is a major driver in the degradation of stream ecosystems (Abell 2002). But high diversity of freshwater fauna in urban environments may be found (Erseus et al. 1999), even higher than in more “natural” lakes and rivers (Koperski 2010b). Streams draining agriculture-dominated watersheds can possess high invertebrate diversity (Moore and Palmer 2005). Maximal values of benthos diversity, typically observed at moderate levels of degradation (Adamek and Jurajda 2001; Nijboer 2006), are a clear corroboration of general regularities, previously noted (e.g., for bird fauna in various types of human-transformed habitats, Marzluff (2008)). In some situations, reduction in pollution loading to a stream may result in the reduction of total taxonomic diversity. It implies that positive changes in water quality, can be, paradoxically, correlated with decrease in biological diversity, which is treated as priority in nature conservation — via the reduction in diversity of other species-rich taxa preferring higher level of pollution. Results of the metaanalysis presented in Table 3 shows that total species richness of macrobenthos is more significantly correlated with species richness of Chironomidae than of EPT larvae. Moreover, species richness of Chironomidae practically does not correlate with the richness of EPT. Ambiguous responses of benthos diversity to environmental variables were explained by Nedeau et al. (2003) in their study on industrial-effluent effect in an urban stream: good riffle-habitat quality had a positive effect and poor water quality had a negative effect.

13. Conclusions: How to apply the diversity of macrobenthos in biological assessment

The ambiguity of conclusions about the relations between diversity of macrobenthos and particular environmental factors compelled specialists to improve the existing methods of biological assessment or to develop new methods (Linke

and Norris 2003). Lamb et al. (2009) concluded that traditional diversity indices are unsuitable for monitoring biodiversity and multivariate indices are sensitive to errors and noise in the data. Their alternative method, however (species intactness based on Buckland’s arithmetic mean index), can only be applied in regularly and intensively assessed environments.

Any method of biological assessment based on total diversity estimates of the whole macrobenthos is problematic. Biological assessment based on the estimation of whole-macrobenthos diversity meets only two of 12 criteria, proposed by Bonada et al. (2006) to define the “ideal biomonitoring tool”: it has “potential to assess ecological function” and “large scale applicability.” To improve upon the current procedure, four requirements must be met: (1) the sampling protocol should count fauna from each habitat occurring in the environment to complete the list of species; (2) all individuals must be assigned to their species or species-group (e.g., Rosenberg et al. 2008); (3) lists of species must be generated on the basis of rarefied data, to avoid the errors caused by unequal sample sizes; and (4) cryptic species must be accounted for, and modern taxonomic methods based on molecular genetics like COI (I-st subunit of cytochrome oxidase) sequencing should be applied for that.

Excluding troublesome groups from datasets (e.g., Rabeni and Wang 2001) is controversial. The list of taxa considered in an assessment should be selected on the basis of their indicative values, not on the basis of their ease of identification. In well thought out procedures, diversity indices calculated for selected taxa are used as metrics to assess selected types of environments affected by selected types of stressors (Trigal et al. 2009). Taxa used in these recommended methods have well known ecological specificity and physiological adaptations.

It must be emphasized, however, that biological assessment based on the diversity of selected taxa only is flawed as a matter of nature conservation. Environmental quality classification based on the diversity of EPT larvae, for example, distinguish streams with high or low quality in terms of EPT’s preferences but not in terms of preferences shown by other stream inhabitants. All species have an equal weight in accordance to the text of the Convention on Biological Diversity (1992) and all wild species are protected by this law. Leech, snail, and midge species are, after all, as important in the stream environment as mayflies, dragonflies and damselflies.

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