

Are beetles good indicators of insect diversity in freshwater lakes?

by

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Abstract

The study verifies the usefulness of aquatic beetles as an indicator of biodiversity of a simple ecological system. Detailed analyses were carried out at the elementary level for the purpose of determining the significance of correlations between the biodiversity of Coleoptera and other groups of aquatic insects in single samples. The relation of selected taxa to selected habitats of the lake Wukśniki (north-eastern Poland) was also investigated. Moreover, the possibility of application of biodiversity surrogates, i.e. higher taxonomic units (genera and orders), in the determination of biodiversity was examined. A significant high correlation was determined between Coleoptera and the total remaining taxa (RR – Remaining Richness) in samples collected in the entire lake. The correlation has the highest value at the species level. The complementarity analysis reveals that the percentage contribution of Coleoptera in the overall biodiversity of the lake is similarly high at the species and genus level, and substantially lower at the family level. In accordance with the hypothesis, aquatic beetles can be used as indicators of the overall biodiversity of insects in the ecosystem of a mesotrophic lake. Biodiversity surrogates, i.e. higher taxonomic units (genera and families), can be applied instead of the species level.

Key words: Coleoptera, macroinvertebrates, lake, biodiversity indicators, surrogates

Introduction

The primary objective of nature protection is the preservation of particularly environmentally valuable habitats and the biodiversity of organisms inhabiting such habitats (Margules and Pressey 2000; Myers et al. 2000; Moore et al. 2003; Sánchez-Fernández et al. 2006). The full assessment of the biodiversity of aquatic environments poses considerable practical problems. They mainly result from the vast taxonomic diversity of many groups of organisms, in particular macroinvertebrates (including insects). Consequently, it is necessary to involve a number of high-class specialists in the research. Therefore, the assessment is usually performed based on selected taxa, although their choice may raise controversies.

Certain solutions are provided by new theories developed over the recent years based on the biodiversity concept. They particularly concern bioindication in lotic waters (e.g. Paszkowski and Tonn 2000; Sahlén and Ekestubbe 2001; Heino 2002; Briers and Biggs 2003; Kati et al. 2004; Sánchez-Fernández et al. 2006; Sebastião and Grelle 2009). Little research has so far been conducted on bioindicators in stagnant freshwaters, including lakes (Sánchez-Fernández et al. 2006; Heino 2010).

One of the theories is the so-called biodiversity indicator theory. According to the theory, the biodiversity of a number of co-occurring groups of organisms can be determined based on one selected taxon. Another theory – the so called surrogate concept, applying substitutes to biodiversity indicators, draws attention to several levels of biodiversity (Noss 1990). Instead of species richness, it suggests performing biodiversity assessment based on higher-level taxa (genus or family), i.e. biodiversity indicators, representing one of the components of surrogates (Humphries et al. 1995; Caro and O'Doherty 1999). This would facilitate the biodiversity assessment, particularly in large areas where the identification of organisms at the species level is frequently too problematic, or impossible (Noss 1990; Williams P.H. 1996; Reyers and van Jaarsveld 2000; Heino et al. 2005).

It remains an open question what groups of organisms can fulfil the function of biodiversity indicators in stagnant waters to the highest degree. They should undoubtedly be organisms with high

importance to the taxonomic diversity of lacustrine fauna. Insects meet this condition. The best represented insects are Coleoptera, Odonata, and Trichoptera (Williams D.D. 1996). Coleoptera and Odonata are recognized as biodiversity indicators of the macrobenthos in freshwater ecosystems (Davis et al. 1987; Foster et al. 1990; Foster and Eyre 1992; Hornung and Rice 2003; Heino et al. 2005; Lee Foote and Rice Hornung 2005; Sánchez-Fernández et al. 2006). This opinion, particularly in relation to Coleoptera, is in accordance with the view of a number of authors emphasizing the high importance of this group of insects (Eyre et al. 1992; Winfield Fairchild et al. 2000; Bosi 2001). Coleoptera usually occur in high abundance in lakes. They show high species and ecological diversity. They are also very sensitive to environmental factors, and usually respond rapidly to changes in such factors (Eyre et al. 1992; Foster and Eyre 1992; Menetrey et al. 2005; Pakulnicka and Nowakowski 2012). Another reason for recognizing beetles as the best biodiversity indicators is the fact of their occurrence in water at both the larval and imaginal stage. Their prevailing occurrence in shallow littoral is very convenient for practical reasons.

Considering the current scarcity of data regarding analyses of biodiversity indicators and the surrogate concept based on invertebrates in stagnant waters (Sánchez-Fernández et al. 2006; Heino 2010), this paper presents an analysis of these issues based on the example of a single lake. Such an approach permits a more thorough insight into a well-defined system instead of a number of varied and difficult to assess relations. The primary objective of the paper is to verify the hypothesis that Coleoptera can be an indicator used in the assessment of total biodiversity of the co-occurring taxa in a lake ecosystem. The research involved the application of methods described by Sánchez-Fernández et al. (2006), as well as our own methods, including modifications. Detailed analyses were performed at the elementary level. The occurrence of a significant correlation between the biodiversity of Coleoptera and other taxonomic groups inhabiting the lake ecosystem and its habitats was verified. Another objective is to verify the hypothesis that instead of the species level, the assessment of the biodiversity of insects in an ecosystem can be performed based on the biodiversity surrogates, i.e. higher taxonomic

units – genera and families. For this purpose, the correlations between Coleoptera and other taxa at various taxonomic levels were verified. The paper also attempts to answer the question whether the ecological state of a lake can be determined based on mutual relations between the species richness of beetles and other invertebrate taxa inhabiting various habitats of a lake.

Materials and methods

The study object was Lake Wukśniki located in north-eastern Poland in the Olsztyńskie Lakeland (53°58'40"N – 53° 57'46"N, 20°5'18"E – 20°6'22.3"E) (Fig. 1). The lake is the deepest water body of the Masurian Lakeland (the maximum depth is 68.0 m, and the surface area – 117.1 ha). No significant inflows of surface waters occur here. The direct vicinity of the lake is dominated by agricultural lands, mostly meadows and pastures. Forests are located only at the south-eastern shore of the lake. No substantial traces of anthropopressure have been recorded. Most of the lake shore is steep with a weakly developed rush zone. Lake Wukśniki is a mesotrophic lake with waters representing class I of cleanliness. It is included in the Natura 2000 network. The very good

condition of the lake is confirmed by the occurrence of *Chara* meadows (*Chara tomentosa*, *Ch. contraria*, *Ch. fragilis*, *Nitella flexilis*, and *Nitellopsis obtusa*), as well as e.g. *Fontinalis antipyretica*, or very rare in the region *Butomus umbellatus* (Ciecierska et al. 2008).

The faunistic material was sampled four times in 2009 (on 27 April, 10 June, 9 July, and 27 September). The samples were collected by means of a hydrobiological sampler with a surface area of approximately 1 m². The sampling sites were selected so that they represent possibly the highest habitat variability of the littoral. A total of 122 samples were collected in five habitats (the environment of bare bottom; loose community of *Phragmites australis*, *Schoenoplectus lacustris*, or *Butomus umbellatus*; community of *Equisetum* sp. and *Carex* sp.; floats of the shallowest littoral; the environment of dense helophytes with high amounts of organic matter; Table 1). They were described in terms of selected environmental parameters: substrate (1 – sand, 2 – sand with stones, 3 – sand with silt, 4 – boggy bottom), depth (1 – 0-10 cm, 2 – 10-20 cm, 3 – 20-40 cm, 4 – 40-60 cm), detritus (1 – absent, 2 – scarce and fine, 3 – abundant), degree of vegetation cover (1 – absent, 2 – loose, 3 – dense and varied), shore (1 – flat, 2 – steep), other elements (1 – absent, 2 – present). Each parameter was described in qualitative terms, and classified in accordance with the degree of intensity of a given characteristic.

The entire material includes 2893 individuals belonging to Coleoptera, Ephemeroptera, Odonata, Plecoptera, Heteroptera, and Trichoptera. The analysis was conducted at the elementary level, based on single samples. This permitted more thorough observation of the situation encountered at the level of all of the collected single samples (Pakulnicka et al. 2013, 2015).

At the first stage of the statistical analysis, the RR (Remaining Richness) parameter was calculated

Table 1

The number of families, genera, and species of the six groups of macroinvertebrates recorded in the study lake

	Families	Genera	Species
Coleoptera	9	27	44
Odonata	7	15	24
Ephemeroptera	6	9	15
Plecoptera	2	2	2
Heteroptera	8	10	15
Trichoptera	9	19	41

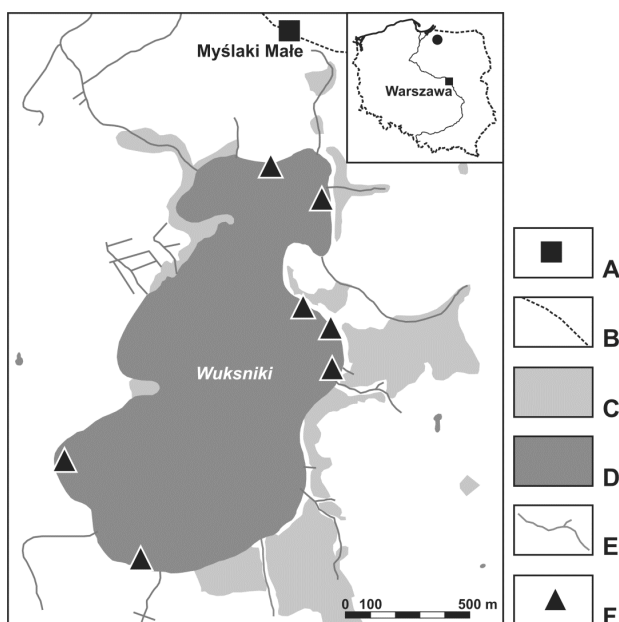


Figure 1

Study area: Legend: A – villages, B – main roads, C – forests, D – stagnant waters, E – streams and ditches, F – sampling sites

for particular taxa, defined as the total of all species (from all taxa) minus the number of species of the selected taxon (Sánchez-Fernández et al. 2006). The RR parameter was calculated for all of the collected samples and for particular habitats. Then, the correlation was determined between Coleoptera and other groups of organisms and RR for all the samples collected, followed by the correlation between Coleoptera and other groups of organisms and RR in samples collected in particular habitats. The analysis involved the application of the Spearman correlation levels. Correlations with the significance of $p < 0.05$ were deemed significant (Sokal and Rohlf 1995). The strength of correlations was determined at a scale commonly applied in the statistical analysis, where: $r_{XY} = 0$ – variables not correlated, $0 < r_{XY} < 0.1$ – very weak correlation, $0.1 \leq r_{XY} < 0.3$ – weak correlation, $0.3 \leq r_{XY} < 0.5$ – average correlation, $0.5 \leq r_{XY} < 0.7$ – high correlation, $0.7 \leq r_{XY} < 0.9$ very high correlation, $0.9 \leq r_{XY} < 1$ – close to full correlation.

Next, in order to determine the co-occurrence of species representing various invertebrate taxa, the modified method of a complementary network was applied (Kirkpatrick 1983; Sánchez-Fernández et al. 2006). A number of authors emphasize that complementarity methods complement correlation analyses (Pressey et al. 1993; Margules and Pressey 2000; Sánchez-Fernández et al. 2006; Williams et al. 2006; Heino 2010). Therefore, complementarity can be an effective guidance how to select places where conservation measures should be implemented (Brooks et al. 2001; Sauberer et al. 2004).

The analysis concerned 10 samples distinguished by the highest frequency (the highest number of species) in a particular taxon. Then, the percentage contribution of species of such a taxon was calculated, as well as the percentage contribution of species representing the remaining taxa in an entire assemblage (10 samples analyzed), and RR

for such a taxon. The procedure was repeated for all the analyzed taxa in subsequent 10 samples with the highest number of species.

At the next stage of the statistical analyses, the correspondence analysis (CA) was applied (Clausen 1998) to determine the relation between the species richness of particular taxa and the type of habitat. The analysis is frequently used in similar studies (Usseglio-Polatera et al. 2000; Obolewski et al. 2009). With the application of the multidimensional method of principal components analysis (PCA), frequently used in the analyses of assemblages (Jurkiewicz-Karnkowska 2006, 2011; Lenda et al. 2012), the correlation was examined between the co-occurrence of the analyzed taxa and the environmental parameters specific to a given sampling site. The principal components analysis (PCA) was based on the occurrence of species representing various groups of organisms in the samples collected. The data used for the analyses were subject to prior logarithmic transformation to obtain a distribution close to normal. The normal character of the distribution was tested using the Shapiro-Wilk test. All the calculations were performed with the Statistica 10 software.

Results

Coleoptera as indicators of the biodiversity in a lake

The study material included 141 species representing 82 genera, 41 families, and six orders of insects: Coleoptera, Trichoptera, Odonata, Ephemeroptera, Heteroptera, and Plecoptera (Table 1). All the taxa with the exception of Plecoptera were recorded in all the habitat types. The highest frequencies in the samples were reached by Ephemeroptera and Trichoptera (Table 2).

Table 2

The number of samples with the presence of each group of macroinvertebrates in different types of habitats

	Bare sandy bottom (n=36)	Community with scarce reed (n=19)	Community of sedge and horsetail (n=18)	Floats from the shallowest littoral (n=21)	Community of dense macrophytes (n=25)	All samples
Coleoptera	13	10	10	11	15	59
Odonata	21	16	10	12	15	75
Ephemeroptera	25	19	10	11	16	81
Plecoptera	1	0	0	1	0	2
Heteroptera	20	11	10	15	20	76
Trichoptera	30	19	10	11	16	86

Table 3 shows that for the entire lake (in all the samples collected), only the species richness of Odonata and Ephemeroptera was significantly correlated ($p < 0.05$) with the relevant RR value. The analysis of correlations between particular taxa showed significant correlations between Odonata and Ephemeroptera, Odonata and Trichoptera, Trichoptera and Ephemeroptera, Odonata and Plecoptera, as well as Plecoptera and Ephemeroptera.

The analysis of the correlation between the species richness of particular taxa in various types of environments presents the situation somewhat differently (Table 4). The statistical significance generally increases between particular taxa and their respective RR, whereas the strongest – high positive correlation was observed in the environment of floats from the shallowest littoral, and concerned Ephemeroptera and the respective RR value. The

Table 3

Values of the Spearman correlation coefficient between the species richness of six groups of macroinvertebrates in all samples collected ($p < 0.05$) (significance of correlations in bold)

	Coleoptera	Odonata	Ephemeroptera	Plecoptera	Heteroptera	Trichoptera	RR
Coleoptera		0.08	-0.06	-0.11	0.02	-0.16	-0.09
Odonata			0.31	0.20	0.01	0.25	0.36
Ephemeroptera				0.19	-0.05	0.23	0.19
Plecoptera					0.01	0.02	0.09
Heteroptera						-0.13	-0.08
Trichoptera							0.04

Table 4

Values of the Spearman correlation coefficient between the species richness in each habitat type (significance of correlations in bold)

	Coleoptera	Odonata	Ephemeroptera	Plecoptera	Heteroptera	Trichoptera	RR	Total (all species)
Bare sandy bottom (n=36)								
Coleoptera		0.09	0.17	-0.12	-0.11	0.27	0.17	0.33
Odonata			0.38	0.30	-0.15	0.29	0.27	0.49
Ephemeroptera				0.28	-0.25	0.44	0.39	0.70
Plecoptera					0.07	0.26	0.29	0.29
Heteroptera						-0.15	-0.26	0.55
Trichoptera							0.40	0.84
Community with scarce reed (n = 19)								
Coleoptera		0.21	0.27		0.13	-0.19	0.15	0.39
Odonata			0.40		0.04	0.33	0.49	0.63
Ephemeroptera					-0.16	0.34	0.46	0.66
Plecoptera								
Heteroptera						0.15	0.41	0.38
Trichoptera							0.26	0.68
Community of sedge and horsetail (n=18)								
Coleoptera		0.44	-0.07		-0.20	-0.27	-0.11	0.51
Odonata			0.09		0.34	0.09	0.32	0.52
Ephemeroptera					0.13	0.12		
Plecoptera								
Heteroptera						-0.34	-0.28	0.09
Trichoptera							-0.47	0.18
Floats of the shallowest littoral (n=21)								
Coleoptera		-0.49	-0.34	-0.22	0.19	-0.29	-0.50	0.13
Odonata			0.47	0.25	-0.03	0.21	0.40	0.49
Ephemeroptera				0.57	0.13	0.12	0.60	0.77
Plecoptera					0.00	-0.21	-0.14	0.18
Heteroptera						-0.26	0.48	0.24
Trichoptera							-0.14	0.29
Community of dense helophytes with high amounts of organic matter (n=25)								
Coleoptera		0.40	-0.27		-0.15	-0.20	-0.41	0.59
Odonata			-0.34		-0.40	-0.19	-0.02	0.07
Ephemeroptera					-0.06	0.21	-0.22	0.18
Plecoptera								
Heteroptera						0.16	-0.11	0.29
Trichoptera							0.05	0.60

highest negative correlation was recorded between Coleoptera and RR. The analysis of the correlation between the species richness of particular taxa in pairs suggests that the highest significant correlations were recorded in the environment of floats of the shallowest littoral. They were determined between Odonata and Ephemeroptera (positive correlation), and between Coleoptera and Odonata (negative correlation). In the environment of bare bottom, the highest correlations in pairs of taxa were recorded between Odonata and Ephemeroptera, as well as

Application of biodiversity surrogates in the assessment of the lake's total biodiversity

The analysis of Spearman's correlation between the species richness of Coleoptera and the total species richness in the lake, as well as between beetles and other groups of organisms in the total RR, conducted at various taxonomic levels (Table 6), reveals the highest significant correlations at the species level. The complementarity analysis (Table 7) shows that the percentage contribution of Coleoptera

Table 5

Percentage of species that could be represented in complementary networks for each group

		Complementary network of					
		Coleoptera	Odonata	Ephemeroptera	Plecoptera	Heteroptera	Trichoptera
		%					
Coleoptera	%	59.3	14.29	8.47	0	8.47	11.86
Odonata		23.08	24.6	12.3	3.08	10.8	26.15
Ephemeroptera		23.8	13.04	28.3	4.35	10.9	39.1
Plecoptera							
Heteroptera		17.02	8.51	8.51	0	29.8	36.2
Trichoptera		5.36	14.29	12.5	3.58	12.5	51.78
RR		40.77	75.13	71.7		70.21	48.21
Total		24.13	44.8	31.7		9.65	38.6

between Trichoptera and Ephemeroptera. In the environment of loose reed beds, they occurred between Odonata and Ephemeroptera, and in the environment of dense helophytes – between Odonata and Coleoptera (positive correlation), as well as between Odonata and Heteroptera (negative correlation). In the community of horsetail and sedge, no correlations were recorded in any of the pairs of taxa.

The complementary method applied suggests that in 10 samples analyzed for particular taxa, the highest contribution of a given taxon was determined for Coleoptera (approximately 60%) (Table 5). They are relatively most frequently accompanied by Odonata. A somewhat lower contribution of a given taxon in 10 analyzed samples was determined for Trichoptera (51.8%), mostly accompanied by Odonata, followed by Ephemeroptera and Heteroptera. The highest percentage contribution of RR was determined for Odonata, Ephemeroptera, and Heteroptera.

in the total biodiversity of the lake is similarly high both at the species and genus level, and substantially lower at the family level.

Impact of environmental factors on the occurrence of particular taxa

The correspondence analysis (CA), determining the correlation between the species richness of particular taxa and the type of environment (Fig. 2), shows the strongest correlation with the environment of dense helophytes in the case of Coleoptera. Trichoptera and Ephemeroptera clearly prefer the environment of bare bottom, or bottom sparsely overgrown with *Phragmites australis*. Higher species richness of Heteroptera and Odonata was recorded in the environment of floats and in the plant community with horsetail and sedge.

The principal components analysis (PCA) shows weak negative correlations in the case of Coleoptera

Table 6

Spearman correlation coefficient between the richness of Coleoptera at different taxonomic levels (families, genera, species), and richness of other groups of insects and the RR value in the collected samples ($p < 0.05$) (significance of correlations in bold)

Taxonomic levels	Coleoptera	RR
Species	0.52	0.61
Genera	0.37	0.06
Families	0.35	0.04

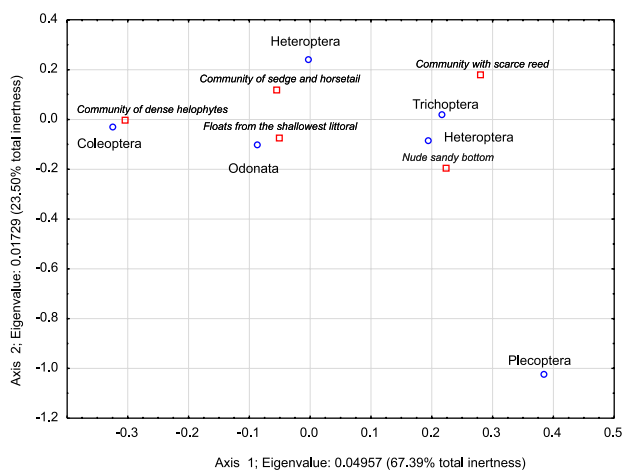
Table 7

Percentage of insects that could be represented in complementary networks at different taxonomic levels (families, genera, species)

		Complementary network of		
		Coleoptera species	Coleoptera genera	Coleoptera families
Coleoptera	%	59.3	55.9	33.3
Ephemeroptera		8.47	8.8	16.6
Heteroptera		8.47	14.7	22.2
Odonata		10.2	11.8	33.3
Plecoptera		0	0	0
Trichoptera		11.9	8.8	22.2

and Heteroptera in the habitat of bare bottom. This is weakly related to detritus and height of the shore (Fig. 3a).

In the community of loose reed beds, the highest positive correlations occur in the case of Odonata, Trichoptera, and Ephemeroptera. This is


Figure 2

Multidimensional correspondence analysis (CA). Relation between the species richness of particular taxa and type of habitat along the first and second CA axis.

in a weak or average relation to the substrate, depth, and degree of vegetation cover (Fig. 3b). In the community including horsetail and sedge, Odonata, Coleoptera, and Heteroptera show a high negative correlation with Trichoptera and a high degree of vegetation cover (Fig. 3c). In the environment of floats, Coleoptera show a high and very high negative correlation with Odonata, Ephemeroptera, and Trichoptera. This is weakly related to the depth, the height of the shore, and the presence of other elements (e.g. roots) (Fig. 3d). In the environment of dense helophytes, Coleoptera show close to full negative correlation with other taxa, primarily with Trichoptera (very high correlation) as well as Ephemeroptera and Odonata (high correlation). This is related to the substrate (average correlation) and, to a lesser extent, the height of the shore, the degree of insolation, and the amount of organic matter (detritus) (Fig. 3e).

Discussion

Coleoptera as the lake's biodiversity indicators

One practice in assessing the ecological condition of ecosystems is to determine the contribution of stenobiotic species in the studied environment (Biesiadka and Kowalik 1991; Zawal 1993, 1994; Pakulnicka and Bartnik 1999). A different approach would consist in applying the biodiversity indicators. Studies regarding the usefulness of biodiversity indicators for monitoring the condition of the natural environment have a long tradition, not only in ecology, but also in environmental toxicology or forestry (Noss 1990). Usually, however, they are conducted at large scales – at the level of countries, regions, or ecological landscapes (Noss 1990; Ricketts et al. 1999; Myers et al. 2000; Sánchez-Fernández et al. 2006). Some authors (Noss 1990; Heino 2010) emphasize the need to study the biodiversity at a smaller scale, namely at the ecosystem scale.

Considering the opinions of a number of authors regarding the high importance of water beetles in the shallow littoral zone of lakes (Eyre et al. 1992; Foster and Eyre 1992; Menetrey et al. 2005; Sánchez-Fernández et al. 2006; Pakulnicka and Nowakowski 2012) and the usefulness of this group of insects as an indicator for areas with high biodiversity (Davis et al. 1987; Foster et al. 1990; Foster and Eyre 1992;

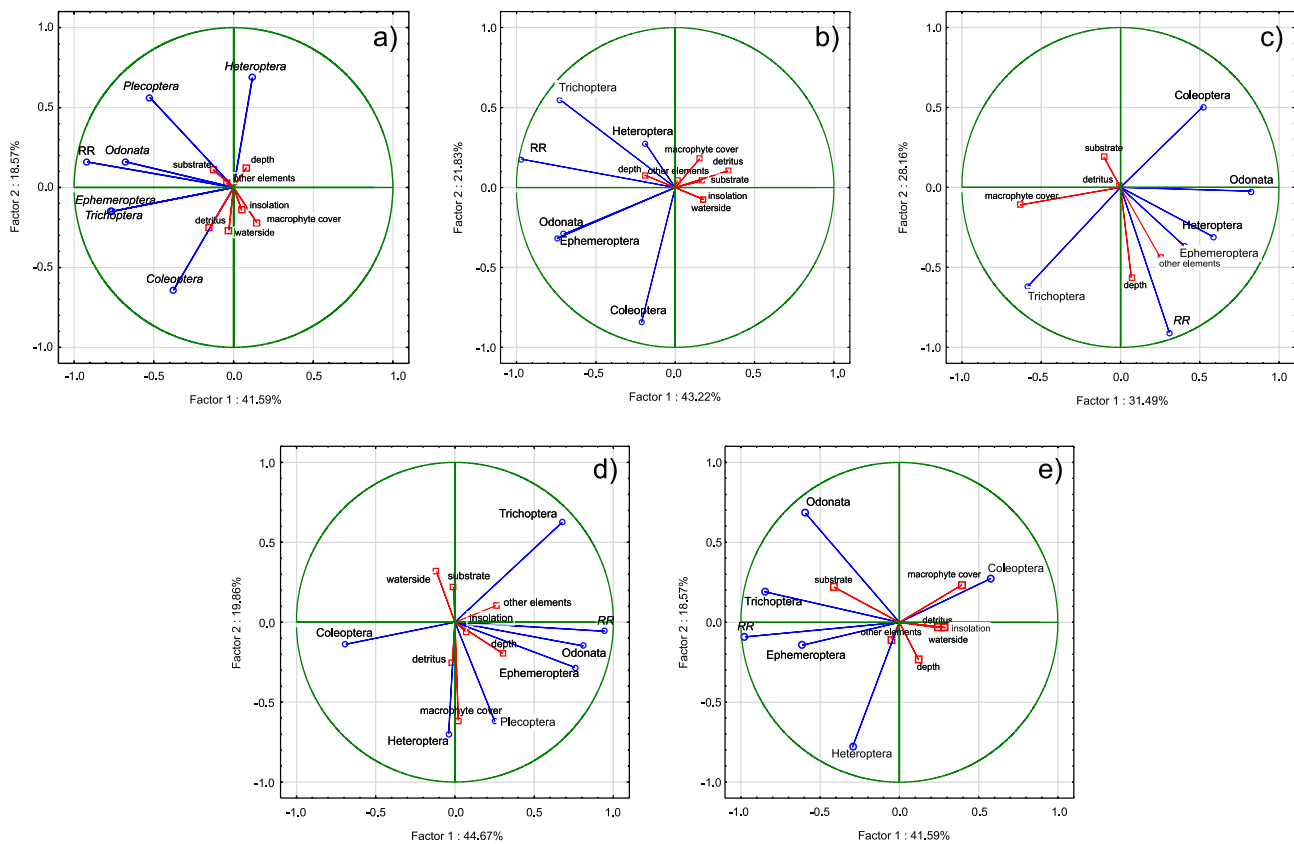


Figure 3

Principal Component Analysis (PCA) ordination plot of number of species (S) Coleoptera, RR index and the remaining taxa and environmental variables along the first and second PCA axis: a) Bare sandy bottom, b) Community with scarce reed, c) Sedge community of the shallowest littoral, d) Floats from the shallowest littoral, e) Environments of dense vegetation with high amounts of organic matter.

Sánchez-Fernández et al. 2006; Heino et al. 2005), it is worth following the suggestion of certain authors (Noss 1990; Heino 2010) to analyze the usefulness of Coleoptera as indicators of the biodiversity at the level of a single ecosystem, namely a lake. This may be of importance to monitoring and protection of a given lake.

Due to their high environmental values, mesotrophic lakes, for example Lake Wukśniki, are objects important to the preservation of local biodiversity. In comparison with significantly more eutrophicated lakes, mesotrophic lakes are usually characterized by lower species diversity. This is evident in a number of groups of organisms (Czachorowski 1998; Bernard et al. 2002; Wendzonka 2004; Zawal 2007; Kurzątkowska and Zawal 2007), including water beetles (Pakulnicka and Bartnik 1999; Pakulnicka and Zawal 2007), and is primarily

the result of poor habitat diversity observed in the littoral zone of such lakes.

In Lake Wukśniki, Coleoptera are represented by the highest number of species and genera. This defines Coleoptera as potential biodiversity indicators, which is in accordance with the approach adopted by e.g. Sánchez-Fernández et al. (2006).

It is assumed that the species richness of a taxon representing a potential indicator of the overall biological diversity should be correlated with the species richness of the remaining taxa, and influence the total biodiversity in the ecosystem (Sánchez-Fernández et al. 2006). This should be a positive and high correlation (Noss 1990; Pearson 1994).

Analyses of the correlations between Coleoptera and the remaining taxa in samples collected in the entire lake revealed lack of a very strong correlation between Coleoptera and particular individual taxa.

A high significant correlation was observed between Coleoptera and the total remaining taxa (RR) in samples collected in the entire lake. A similar situation was recorded in the stagnant waters of the basin of the Segura River (Sánchez-Fernández et al. 2006). The analysis of the distinguished types of habitats in the lake shows an increase and a varying correlation between particular taxa in samples. This results from the differences in the species richness of particular taxa. The apparent correlation between Coleoptera and other taxa is additionally emphasized by the applied complementarity method. We believe that water beetles can be an effective indicator of the total biodiversity assessed at the ecosystem level.

Aquatic beetles are a group varied in terms of trophic preferences (Pakulnicka and Bartnik 1999). They include phytophagous, saprophagous, and predatory organisms. A wide trophic spectrum permits their occurrence in various habitats. In the studied lake, beetles are most strongly associated with the environment of dense helophytes with high amounts of detritus, which has been also confirmed in studies of the fauna of beetles inhabiting other lakes (Biesiadka 1980; Pakulnicka and Bartnik 1999). A high positive correlation with the total determined species richness was recorded for this environment. This suggests a high importance of beetles to the development of an assemblage of organisms, particularly in such habitats. Considering the fact that the foremost part of the fauna of water beetles is represented by species related to slightly eutrophicated waters, characterized by a broad environmental tolerance, an increase in the significance of this group is to be expected as the eutrophication of the lake progresses (Pakulnicka and Bartnik 1999). However slow this process might be at the moment, given that current anthropogenic pressure is low, the successive spatial expansion of such habitats is inevitable, and an increase in the contribution of species typical of minor water bodies is bound to follow. Researchers may expect that in such a situation the correlation between the species richness of Coleoptera and overall biodiversity will be significantly higher (with a simultaneous decrease in the number of aerophilous species – Ephemeroptera and Trichoptera). This paper is in many ways a case study, therefore similar analyses are recommended to be carried out in lakes of different habitat structure.

It is evident that as predators, aquatic beetles compete with other insects for food, particularly with Heteroptera and Odonata (Shalan and Canyon 2009; Klecka and Boukal 2012). Competition, however, is not the only trophic relation between the mentioned taxa. An important interaction between Coleoptera and Odonata is the predator-prey relation (Ohba 2009a,b; Ohba and Inatani 2012; Frelik and Pakulnicka 2015), which seems to be of asymmetric nature. This results not only from the organisms' morphology, but also their behavior. Therefore, most probably Odonata become the prey of aquatic beetles more often than the other way round. The effects of both biotic interactions between the beetles and other co-occurring taxa in the studied lake seem to be the strongest in the habitat of the shallowest littoral influx, where the highest negative correlation with other taxa, mainly Odonata, was recorded.

The remaining habitats represented in the lake – the habitats of bare bottom or loose helophytes, do not seem to be an optimal place of occurrence for beetles, in contrast to other taxa of Trichoptera, Ephemeroptera, and Odonata, as suggested by an average or no correlation. Also the complementarity analysis and PCA suggest that aquatic beetles are to a small extent accompanied by Odonata and Trichoptera. Therefore, the invertebrate fauna of the lake includes three groups of organisms preferring varied habitats in the lake. Coleoptera is relatively most strongly correlated with the environment of dense helophytes.

Moreover, each ecosystem, also the limnic one, should be treated as a system largely representing a set of incidental elements. Apart from the most typical species and those specific to limnic fauna, they are mostly represented by eurytopic species. They largely determine the species structure and the number of taxa representing the limnic fauna. Considering the fact that the most important part of the fauna of aquatic beetles is represented by species related to smaller eutrophicated waters distinguished by a wide ecological tolerance, an increase in the importance of the group along with the proceeding eutrophication of the lake should be expected (Pakulnicka and Bartnik 1999). In mesotrophic Lake Wukśniki, beetles evidently prefer habitats of dense vegetation with organic matter on the bottom. Irrespective of the slow rate of the process and the current insignificant anthropopressure,

the phenomenon of successive expansion of this type of habitats is inevitable, and so is an increase in the contribution of species preferring small water bodies. It should be expected that in such a situation, the correlation between the species richness of Coleoptera and the overall biodiversity, as well as between Coleoptera and the total remaining taxa (RR), following the definition of a good indicator, will be much higher (with a simultaneous decrease in the number of rheophilic species, typical of weakly eutrophicated lakes). In our opinion, aquatic beetles can be an efficient indicator of the overall biodiversity determined at the ecosystem level. Such a level of correlation between the species diversity of Coleoptera and the overall biodiversity can reflect the current trophic status of Lake Wukśniki.

Application of biodiversity surrogates in the assessment of the lake's total biodiversity

It remains an open issue whether higher-level taxa can be applied in the assessment of the overall biodiversity based on Coleoptera used as indicators following the concept of surrogates (Noss 1990; Humphries et al. 1995; Williams P.H. 1996; Caro and O'Doherty 1999; Reyers and van Jaarsveld 2000; Heino et al. 2005; Sánchez-Fernández et al. 2006). This concerns genera or families which would fulfil the function of surrogates of the biodiversity indicator. It also remains to be determined whether such surrogates can be applied as indicators of biodiversity at the level of a single ecosystem, similarly as in the case of the examined areas with high biodiversity (Noss 1990; Williams P.H. 1996; Reyers and van Jaarsveld 2000; Heino et al. 2005; Sánchez-Fernández et al. 2006).

Data resulting from the conducted analyses suggest that although the correlation between the number of species of Coleoptera and the overall species richness in the lake is high, similarly as the correlation between the biodiversity of Coleoptera and the richness of the total remaining taxa, the correlation between the biodiversity of beetles and the overall biodiversity in the lake considered at the genus or family level is weak, and statistically insignificant between the biodiversity of beetles and the total remaining taxa. Our analyses suggest that such an assessment is not possible, which is in accordance with the opinion of Heino (2010).

More promising data are provided by the complementarity analysis which according to a number of authors should be conducted simultaneously with the correlation analysis (Pressey et al. 1993; Margules and Pressey 2000; Sánchez-Fernández et al. 2006; Williams et al. 2006; Heino 2010). Our analyses suggest that the percentage contribution of other taxa in the complementarity network remains approximate, or even higher at the family or genus level than at the species level.

According to our suggestion, the assessment of biodiversity of insects in the ecosystem of a mesotrophic lake based on Coleoptera can apply biodiversity surrogates, i.e. higher taxonomic levels (genera and families), instead of the species level. This would be in accordance with the opinion of Sánchez-Fernández et al. (2006) on the usefulness of this group of insects for the determination of the biodiversity of other groups of organisms in the ecosystems of large stagnant waters, namely lakes, and the possibility of application of biodiversity surrogates (genera and families) in the monitoring and protection of the species richness in lakes. According to their definition, surrogates can also be useful for the initial and faster assessment of the biodiversity of an aquatic ecosystem (Heino 2010). This can be a starting point for further, more detailed or time-consuming analyses with the application of orders of insects analyzed in this paper.

Our findings and conclusions are promising, although other lakes should also be examined in such terms, particularly those representing various stages of ecological succession.

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