A peer-reviewed version of this preprint was published in PeerJ on 26 September 2018.

View the peer-reviewed version (peerj.com/articles/5662), which is the preferred citable publication unless you specifically need to cite this preprint.

Pakulnicka J, Zawal A. 2018. Effect of changes in the fractal structure of a littoral zone in the course of lake succession on the abundance, body size sequence and biomass of beetles. PeerJ 6:e5662
https://doi.org/10.7717/peerj.5662
Effect of changes in the fractal structure of a littoral zone in the course of lake succession on the abundance, body size sequence and biomass of beetles

Joanna Pakulnicka Corresp., 1, Andrzej Zawal 2

1 Department of Ecology and Environmental Protection, Faculty of Biology and Biotechnology, University of Warmia and Mazury Olsztyn, Olsztyn, Poland
2 Department of Invertebrate Zoology and Limnology, Institute for Research for Biodiversity, Centre of Molecular Biology and Biotechnology, Faculty of Biology, University of Szczecin, Szczecin, Poland

Corresponding Author: Joanna Pakulnicka
Email address: joanna.pakulnicka@uwm.edu.pl

Dystrophic lakes undergo natural disharmonic succession, in the course of which an increasingly complex and diverse, mosaic-like pattern of habitats evolves. In the final seral stage, the most important role is played by a spreading *Sphagnum* mat, which gradually reduces the lake’s open water surface area. Long-term transformations in the primary structure of lakes cause changes in the structure of lake-dwelling fauna assemblages. Knowledge of the succession mechanisms in lake fauna is essential for proper lake management. The use of fractal concepts helps to explain the character of fauna in relation to other aspects of the changing complexity of habitats. Our 12-year-long study into the succession of water beetles has covered habitats of 40 selected lakes which are diverse in terms of the fractal dimension. The taxonomic diversity and density of lake beetles increase parallel to an increase in the fractal dimension. An in-depth analysis of the fractal structure proved to be helpful in explaining the directional changes in fauna induced by the natural succession of lakes. Negative correlations appear between the body size and abundance. An increase in the density of beetles within the higher dimension fractals is counterbalanced by a change in the size of individual organisms. As a result, the biomass is constant, regardless of the fractal dimension.
Effect of changes in the fractal structure of a littoral zone in the course of lake succession on the abundance, body size sequence and biomass of beetles.

Joanna Pakulnicka¹ and Andrzej Zawal²

¹Department of Ecology and Environmental Protection, University of Warmia and Mazury, Olsztyn, Poland
²Department of Invertebrate Zoology and Limnology, Institute for Research for Biodiversity, Centre of Molecular Biology and Biotechnology, Faculty of Biology, University of Szczecin, Szczecin, Poland

Corresponding Author:
Joanna Pakulnicka¹

Email address: joanna.pakulnicka@uwm.edu.pl
ABSTRACT

Dystrophic lakes undergo natural disharmonic succession, in the course of which an increasingly complex and diverse, mosaic-like pattern of habitats evolves. In the final seral stage, the most important role is played by a spreading Sphagnum mat, which gradually reduces the lake’s open water surface area. Long-term transformations in the primary structure of lakes cause changes in the structure of lake-dwelling fauna assemblages. Knowledge of the succession mechanisms in lake fauna is essential for proper lake management. The use of fractal concepts helps to explain the character of fauna in relation to other aspects of the changing complexity of habitats. Our 12-year-long study into the succession of water beetles has covered habitats of 40 selected lakes which are diverse in terms of the fractal dimension. The taxonomic diversity and density of lake beetles increase parallel to an increase in the fractal dimension. An in-depth analysis of the fractal structure proved to be helpful in explaining the directional changes in fauna induced by the natural succession of lakes. Negative correlations appear between the body size and abundance. An increase in the density of beetles within the higher dimension fractals is counterbalanced by a change in the size of individual organisms. As a result, the biomass is constant, regardless of the fractal dimension.

INTRODUCTION

Ecological succession is a natural course of events that occurs in lakes (Kajak, 1998). Lake succession manifests itself in the growth of macrophytes along lake shores, which initially create increasingly diverse and compact communities (Mc Farland, Carse & Sandin, 2009; Drinan et al., 2013; Beadle, Brown & Holden, 2015; Šiling & Urbanič, 2016; Stryjecki et al., 2017), only to have the littoral zone ultimately dominated by a single species. If the succession is disharmonic, the dominant species is Sphagnum sp. (Kajak, 1998), whereas in lakes undergoing harmonic succession the prevalent species are most often Phragmites australis (Ciecierska, 2008; Pakulnicka, Górski & Bielecki, 2015b), and less frequently Carex sp., Sparganium sp. or Acorus sp. Many hydrobiologists emphasize the important role of the littoral zone in the secondary production of lakes and as a zone having the highest species richness and density of macroinvertebrates (Cremona, Planas & Lucotte et al., 2008; Mieczan et al., 2014; Plaska &
Mieczan, 2018). The littoral zone is also considered to be the most sensitive part of a lake, and its character provides evidence on the ecological condition of the whole lake (Czachorowski, 1998; Šiling & Urbanič, 2016).

The succession of lakes entails changes in the lake-dwelling fauna (Kowalik, 1968; Pakulnicka & Bartnik, 1999; Ranta, 1985; Kordylas, 1990; Lundkvist, Landin & Milberg, 2001; Pakulnicka & Zawal, 2007). This problem is rarely raised in research, and when it is, it most often consists of brief studies into zooplankton (e.g. Demetraki-Paleolog, 2012; Kuczyńska-Kippen, 2008; Jasser, 1997; Lepisto & Saura, 1998; Odland & del Moral, 2002; Filoc & Kupryjanowicz, 2015). More detailed investigations pertaining to changes in lake fauna during consecutive seral stages are conducted on anthropogenic rather than natural ecosystems (Pakulnicka, 2008; Bloechl et al., 2010; Buczyński, 2015; Pakulnicka, Górski & Bielecki, 2015b). Hence, despite the wealth of references, our knowledge of the succession mechanisms in lake fauna is modest and fragmentary, even though it is extremely important for developing proper lake management practice (Šiling & Urbanič, 2016; Shadrin et al., 2016).

Another challenge for researchers is to find an adequate measure for the determination of changes in fauna induced by the succession of water bodies. Hydrobiologists most often draw attention to changes in the abundance and species richness while comparing small groups of lakes with different trophic states (Kowalik, 1968; Ranta, 1985; Kordylas, 1990; Lundkvist, Landin & Milberg, 2001; Pakulnicka & Zawal, 2007; Soldán et al., 2012; Barndt, 2012; Drinan et al., 2013; Pakulnicka et al., 2013; Baars et al., 2014; Beadle, Brown & Holden, 2015). A measure that has been gaining popularity over the last twenty years consists of an analysis of quantitative relations between components (generalists and diversified specialists) distinguished on the basis of their affinity towards specific habitat conditions (e.g. Kowalik, 1968; Kordylas, 1990; Czachorowski, 1998; Pakulnicka & Zawal, 2007; Plaska & Tarkowska-Kukuryk, 2014; Pakulnicka et al., 2016a; Pakulnicka et al., 2016b; Plaska et al., 2016; Stryjecki et al., 2017). However, the results obtained from this approach are discrepant and therefore not highly reliable, often because of a small number of samples or analysed objects.

An important addition to research consists of analyses based on biometric measurements, found also in studies on small water organisms, including beetles (Jeffries, 1993; McAbendroth et al., 2005; Ulrich, 2007; Vamosi, Naydani & Vamosi, 2007; Cremona, Planas & Lucotte, 2008;
Scheffer et al., 2014, Scheffer and van Nes, 2005; Tokeshi & Arakaki, 2012; Désamoré et al., 2018). In recent years, biometric measures have become a tool applied in evolutionary ecology. Some hydrobiologists, e.g. Scheffer & van Nes (2005) and Scheffer et al. (2014), analyse the structure of body sizes of organisms in specific communities from the viewpoint of coevolution of concurrent species. Others, e.g. Désamoré et al. (2018), search for relationships between the evolution of a body size and the environment, as well as the diversification of species in various water habitats.

Data regarding the body mass and body size of macroinvertebrates often appear in the context of studies on a fractal structure, a notion which still awaits a better understanding (Jeffries, 1993; Tokeshi & Arakaki, 2012; Barnes, Vaughan & Ormerod, 2013), and a fractal dimension, a borrowing from mathematical sciences (Mandelbrot, 1983). According to Andrejczuk (2014), all landscapes with inner diversity demonstrate fractality, i.e. they are composed of smaller fragments, self-similar fractals, which are self-reproducing duplicators of parameters on a different scale. Thus, a fragment of any system should contain all the system’s characteristics in a nutshell (on a smaller scale). The littoral zone of ecologically young lakes can serve as an example of a linear structure of spatial organisation which demonstrates properties of fractality. However, as the succession progresses, the shoreline becomes more diverse and turns into a multifractal system, i.e. heterogeneous, composed of fragments (separate subsets) with different, local characteristics, each presenting self-similar properties (Miałdun, 2010; Miałdun & Ostrowski, 2010). Thus, similar fragments (fractals) of the littoral zone of different objects should be characterised by similar habitat traits, offering the same niches to the organisms which populate them. A convenient and valuable object in studies on the fractal structure are dystrophic lakes, in which various habitats (fragments of the littoral zone) appear during the course of succession: from a plant-free zone to zones overgrown with macrophyte communities of various compactness to a compact Sphagnum mat with small pools.

In our study we looked at water beetles because they are particularly numerous organisms in the littoral zone as well as being very sensitive and responsive to any unfavourable changes in the environment (Eyre, Foster & Foster, 1992; Foster & Eyre, 1992; Corbet, 1999; Winfield Fairchild, Faulds & Matta, 2000; Bosi, 2001; Menetrey et al., 2005; McFarland, Carse & Sandin, 2009; Gioria, Bacaro & Feehan, 2010a; Gioria et. al., 2010b; Yee, 2014). Furthermore,
many species are predators, which defines their important role as organisms regulating the abundance and species richness of concurrent taxa (Yee, 2014; Frelik & Pakulnicka, 2015; Frelik et al., 2015; Perissinotto, Bird & Bilton, 2016; Miller & Bergsten, 2016; Płaska & Mieczan, 2018). Water beetles penetrate both the ground and the water column, so according to McAbendroth et al., (2005), their ecological niche is three-dimensional. Consequently, the fractal dimension of the habitats they occupy is within the range of 2<D<3 (increasing from the least to the most compact habitats) (Cremona, Planas & Lucotte, 2008; Tokeshi & Arakaki, 2012).

In the light of the above considerations, our aim has been to investigate whether 1) the distinguished habitats are populated by similar assemblages of organisms with respect to body size and trophic preferences, 2) if there is a relationship between the body mass and abundance of water beetles, 3) if the fractal dimension of a habitat has an effect on the total biomass of beetles, and whether the total biomass of beetles in particular habitats is the same, and finally 4) if there are changes in the sequence of body size of organisms occurring in the course of disharmonic succession.

**MATERIAL & METHODS**

**Study area and field studies**

The study covered 40 dystrophic lakes located in northern Poland: the South Baltic Coastland, the West Pomeranian, Olsztyn, Mrągowo Lakelands and the Suwałki Lakeland (Fig. 1, Appendix 1). The lakes chosen for the study were of various surface areas and having a floating peat mat growth belonging to *Sphagnum* sp. that varied in size. The lakes represented various succession stages in a disharmonic series – from oligo- to polyhumic lakes. The oligohumic lakes were inhabited by *Juncus bulbosus, Eleocharis palustris, Phragmites australis, Typha angustifolia, Typha latifolia, Sphagnum sp., Lobelia dortmanna, Isoëtes lacustris, Drosera rotundifolia, D. anglica, D. intermedia, Sparganium angustifolium, Lycopodiella inundata*. In polyhumic lakes, the dominant species included *Sphagnum* sp., *Oxycccus quadripelatus, Andromeda polifonia, Eriophorum vaginatum, Calluna vulgaris, Erica tetralix, Empetrum nigrum*. The lakes were arranged *a priori* according to the seral stages of succession (Bloechl, 2010), and the point of reference was assumed to be the coverage of a lake’s surface by a *Sphagnum* mat (0 – 75%) (Appendix 1). The percentage cover by a *Sphagnum* mat in each lake was calculated in the GIS...
system, supported by ArcMap 9.3.1 software. For charting the research sites, data made available through Geoportal 2 in the WMS format were employed.

The study was carried out from 2002 to 2014, in spring, summer and autumn. The fauna samples were collected with a dip net from a surface area of about 1 m². In the compacted Sphagnum mat environment, a sample comprised 10 subsamples (aggregated afterwards), which were collected using a 0.1m² strainer. Sampling sites were chosen so as to represent the biggest array of the littoral habitat diversity and areas of individual lakes. Thus, five different littoral components (habitats) were identified: 1) the Sphagnum mat, 2) sparse macrophyte zone, 3) dense macrophyte zone, 4) sandy bottom zone and 5) pockets and ponds within a Sphagnum mat. The vegetation cover was assessed using Braun-Blanquet (1964) phytosociological records. All lakes were identified with respect to the surface area, extent of the lake’s surface covered with a Sphagnum mat, which corresponds to succession stages (1 – 3), percent share of individual habitats in the littoral zone (1 – 4) and a seral stage (1 – 40) (Appendix 1). It was assumed that these habitats, due to different degrees of complexity, represent different fractal dimensions, all within an interval of $2.0 > D > 3.0$ (Tokeshi & Arakaki, 2012). A schematic representation of fractals different in size can be seen in Figure 2. The smallest size (1) corresponds to the sandy bottom zone, while the largest one (5) is assigned to the Sphagnum mat. The intermediate sizes belong to: 2) pockets and ponds within the Sphagnum mat, 3) sparse macrophyte zone, and 4) dense macrophyte zone. Field studies were conducted in accordance with field-study-approvals: Certificate of RDOS in Olsztyn (WOPN.070.21.2018.AKI), WNP Certificate (PNE 08-070/18) and ZPK Certificate (060.1.2018).

In total, 499 samples were collected. Subsequently, the collected samples were described according to the chosen environmental parameters: habitat (1 – Sphagnum mat, 2 – sparse macrophytes, 3 – dense macrophytes, 4 – sandy bottom, 5 – pockets and ponds within Sphagnum mat), place (location) (1 – ecotone, 2 – pockets and ponds within the Sphagnum mat, 3 – compacted Sphagnum mat), bottom (soil substrate) (1 – sand, 2 – sand and mud, 3 – Sphagnum), depth (1 – 0-10 cm, 2 – 0-20 cm, 3 – 20-40 cm, 4 – 40-60 cm), nymphaeids (1 – none, 2 – present), elodeids (1 – none, 2 – present), (detritus (1 – none, 2 – scarce and fine, 3 – abundant and fine, 4 – abundant and coarse), debris (1 – none, 2 – present), fractal dimension (1 – 5), stage – seral stage of succession (1 – 40).
Ecological and statistical analyses

Species diversity was calculated using: S – number of species, N – number of individuals and D – percent share. All collected beetles were divided into 5 classes of different body size (where a body size meant the total length of an organism), i.e. 1 – very small beetles (< 3.0 mm), 2 – small beetles (3.0 – 5.0 mm), 3 – medium beetles (5.1 – 10.0 mm), 4 – large beetles (10.1 – 20.0 mm) and 5 – very large beetles (> 20.0 mm). In addition, the body weight was measured within each of the five classes. The ranges of body weight values of beetles in the distinguished body size classes are shown in Table 1. Three functional groups were distinguished in the trophic structure of beetles: predators (families: Gyrinidae, Dytiscidae and Noteridae), polyphages (Haliplidae) and saprophages (Helophoridae, Hydrophilidae and Hydraenidae) (Appendix 2).

Collected adult water beetles were identified using standard identification keys (Galewski, 1990; Galewski & Tranda, 1978; Friday, 1988; Hansen, 1987; Holmen, 1987).

Because the samples of water beetle fauna were collected several times (taking into account the phenological aspect) from the same lakes and from the habitats distinguished within these lakes, we used a GLM (Generalized Linear Model) for repeated measures ANOVA (Hocking, 1996) to determine the significance of differences in the number of beetles within each functional group in the distinguished habitats, and to identify dependencies between the type of habitats, body size, abundance and biodiversity of Coleoptera. First, we checked the assumptions of normality (the Shapiro-Wilk test) and homogeneity of variances (the Levene’s test), respectively. The GLM repeated measure models were calculated on the basis of Type III sums of squares so as to take the unbalanced design into account. Significant results were tested for pair-wise comparisons by the Tukey’s HSD post-hoc tests. Dependent variables (abundance and number of species) were transformed where necessary to fulfil the requirements of parametric tests (Saint-Germain et al., 2007; Cremona, Planas & Lucotte, 2008).

In four separate analyses, we calculated the Pearson's correlation coefficients ($r_p$) in order to determine correlations between: 1) body size and counts of beetles in the distinguished habitats, 2) cover of the Sphagnum mat and counts of beetles, 3) cover of the Sphagnum mat and functional groups, and 4) species and environmental variables.
Linear regression analysis was performed to determine the influence of: 1) the body size on the abundance of beetles, 2) fractal dimension on the mean body size on, 3) fractal dimension on the mean weight, and 4) the seral stage of succession on the mean body size.

Multidimensional correspondence analysis (MCA) (Clausen, 1998) served to determine dependencies between the abundance of water beetles within the identified body size classes, the share of the distinguished habitats in the littoral zones and in the analysed lakes. MCA has been used in similar studies, e.g. Usseglio-Polatere, Bournaud & Tachet, 2000; Obolewski, Glińska-Lewczuk & Kobus, 2009. The average density of body size classes in a sample was adjusted by the value corresponding to the total contribution of a given littoral zone type in individual lakes, thus giving the weighted average. The analysis included two dimensions, of which the first explained the biggest part of the general chi-squared statistics (% of inertia), whereas the inclusion of the other dimension increased the percentage of explained inertia. Similarities in the fauna between particular lakes were also analysed by the single linkage method for the hierarchical clustering of objects. The distance measure is an Euclidean distance. The results are presented in the form of a dendrogram drawn for 40 lakes.

Relationships between the presence of beetles and the analysed environmental parameters in individual lakes were determined with the help of a principal component analysis, PCA. All calculations were performed in Statistica, ver. 13.0 (StatSoft, Tulsa, USA).

RESULTS

General description of the collected material

The collected material comprised 10 139 specimens representing 124 species classified to seven families (Gyrinidae, Haliplidae, Noteridae, Dytiscidae, Hydraenidae, Hydrochidae and Hydrophilidae) (Appendix 1). Most species (55.6%) belonged to the two smallest body size classes. In total, they composed 84.75% of all collected specimens. The remaining beetles represented the consecutively higher body size classes, of which the largest one had the fewest representatives (Table 1). Most beetles (28.8% of the entire material) were collected in pockets and ponds of the Sphagnum mat. It was also there that the highest species richness was determined (91 spp.). The species diversity was lower in the dense macrophytes zone (26.6%; 74 spp.), sparse macrophytes zone (19.64%; 66 spp.), compacted Sphagnum mat (18.9%; 64 spp.),
and finally in the sandy bottom (5.9%; 39 spp.). Very small beetles, which represented the first
type of habitat and body size class, demonstrated the highest species richness in the compacted Sphagnum mat
(41.5% of the whole collected material) (Fig. 3), while being the most numerous in the dense
macrophyte zone. Small beetles (class 2 of the body size) were most numerous in the pockets and ponds within the Sphagnum mat (73.4%). The presence of very large beetles was
notable in the sparse macrophytes zone, pockets and ponds in the Sphagnum mat and in the
sandy bottom zone, although they made up a small share of the collected material (around 1%).

In the trophic structure, the highest percentage (71.9%) was achieved by predatory
beetles, represented mainly by Dytiscidae (Fig. 4). Although their species diversity was similar
in all the habitats, they were most numerous in the dense macrophyte zone (91.3%) and in the
sandy bottom zone (84.5%). Most saprophages (47.2%) were noted in the compacted Sphagnum
mat, while the number of species representing polyphages was low in all of the habitats, with the
highest score (6 spp.) determined in the compacted Sphagnum mat. The GLM Repeated Measure
Anova results \( F(2, 499) = 6.74, p = 0.0089 \) indicate significant differences in counts of the
distinguished trophic groups in the particular habitats. The counts of predatory beetles in the
habitats in question did not differ significantly (the Tukey’s HSD test, \( p = 0.18 \)). Conversely,
differences in the counts of predators and polyphages were significant (\( p = 0.0003 \)).

Dependencies between types of habitats, body size and abundance as well as biodiversity of
Coleoptera

The results of the GLM repeated measure Anova analysis point to a significant influence of the
synergistic effect between the type of habitat and body size class on the abundance of beetles
\( F(16, 1996) = 7.25, p = 0.000002 \). Significant differences (the Tukey’s HSD post-hoc test)
between the analysed subclasses are illustrated in Figure 5A (cf. Appendix 3). Moreover, a
significant influence of the synergistic effect was determined between the indicated factors
(habitat and body size class) and the number of species \( F(16, 1996) = 16.22, p = 0.00002 \)
(Appendix 3). Results of the GLM repeated measure also point to a significant influence of the
type of habitat on the number of beetles \( F(4,499) = 6.75, p = 0.00003 \) (Figure 5B). Significant
differences (the Tukey’s HSD post-hoc test) were determined between the compacted Sphagnum
mat and sparse macrophytes zone (\( p = 0.031 \)), dense macrophytes zone and sparse macrophytes
zone (\( p = 0.00014 \)), dense macrophytes zone and pockets (\( p = 0.0479 \)). Moreover, significant
differences were demonstrated in the numbers of beetles representing the distinguished body size
classes ($F_{(4, 1996)} = 77.61$, $p = 0.00002$). The Tukey’s *post-hoc* test reveals significant differences
in the counts of beetles representing all the classes of body size ($p = 0.00002$), except 3 and 4
class ($p = 0.77$). Both factors, the type of habitat ($F_{(4, 499)} = 11.04$, $p = 0.000003$) and body size
($F_{(4, 1996)} = 375.61$, $p = 0.000001$), also had a significant impact on the number of species
determined. With respect to the species diversity, significant differences were found between the
*Sphagnum* mat and sparse macrophytes ($p = 0.0048$), and between the pockets and ponds in the
*Sphagnum* mat and sandy bottom zone ($p = 0.0046$), and between the *Sphagnum* mat and sparse
macrophytes ($p = 0.00018$) and dense macrophytes ($p = 0.0014$). Significant differences in the
number of species were shown between all body size classes ($p = 0.00002$), except 1 and 3 ($p =
0.24$).

Negative correlations were observed in all the habitats between the body size and the
number of beetles. It was only in the sandy bottom zone that these correlations were not
significant ($p = 0.47$) (Table 2). Similarly, negative correlations appeared between the body size
and species richness in the compacted *Sphagnum* mat ($p = 0.01$) and in the sparse macrophytes
zone ($p = 0.0008$) (Table 2).

**Dependencies between the type of habitats, body size and abundance of Coleoptera in lakes**

Our analysis of the body size structure of beetles in the fauna populating every lake
demonstrated significant differences in the counts of beetles representing different body size
classes ($x^2 = 171.18$, $df = 156$; $p = 0.0001$). The plotted diagram points to lakes with a more
strongly developed *Sphagnum* mat concentrating small organisms (two smallest body size
classes) (Fig.6). In the dendrogram (Fig. 7), these lakes create centrally located clusters (2 – 7).
In the lakes less densely overgrown with *Sphagnum* sp., with the littoral zone either bare or
weakly overgrown by sparse macrophytes, a larger contribution of organisms that belonged to
the other body size classes, especially middle-size ones, was notable (clusters 8 – 9) (Fig.6,
Fig.7). Lakes included in cluster 1 are characterized by a minimal share of the smallest beetles
(prevalent are the beetles that belong to the second body size class). The lakes Żabionek and
Wielkie Gacno were distinguished by a demonstrably large contribution of big beetles.

**Presence of beetles in lakes versus the fractal structure**
Our analysis of the correlations confirmed a strong positive correlation between the development of a *Sphagnum* mat in the littoral zone of each lake and the abundance of beetles which belong to the first body size class \((r_p = 0.7025, p = 0.000013)\), while the correlation with the number of the largest beetles was negative \((r_p = -0.21, p = 0.04)\). Both relationships were linear: \(\log(\text{Body size 1}) = 0.9045 + 0.4736 \times \log(\text{Sphagnum mat %})\); \(\log(\text{Body size 5}) = 0.1531 - 0.101 \times \log(\text{Sphagnum mat %})\). The remaining correlations were not significant statistically (Table 3).

A negative relationship between the size of body and the number of organisms in lakes emerged from our analysis conducted on the level of samples \((r_p = 0.7046, p = 0.00001)\). This correlation was linear as well (Fig. 8A). The relationship between the weight and abundance of beetles was similar in character (Fig. 8B).

The results of the linear regression analysis showed that as the fractal dimension increased, the mean body size \((r_p = -0.86, p = 0.037)\) and the mean weight of Coleoptera \((r_p = -0.91, p = 0.032)\) decreased (Fig. 9). In turn, the relationship between the total biomass of beetles and the fractal dimension was not significant \((r_p = -0.31, p = 0.623)\).

Our analysis performed for all the lakes (arranged according to the seral stages of succession), which took into account the extent of the *Sphagnum* mat cover and the shares of the other habitats with different fractal dimensions, also indicated negative correlations between the seral stage of succession and the mean body size \((r_p = -0.465, p = 0.0034)\) (Fig. 10).

The principal component analysis of the variables representing the parameters of habitats and trophic groups distinguished in our study (Fig. 11) suggests that the first axis corresponding to the highest own values most strongly corresponds with the variables ‘predators’ and ‘saprophages’, while the second axis shows the strongest correlations with the variables ‘body size’, ‘weight’, ‘N – abundance’, ‘place’, ‘depth’, ‘stage’ and ‘fractal dimension’. Positive correlations were determined between ‘abundance’ and fractal dimension \((r_p = 0.26, p = 0.003)\), ‘abundance’ and ‘stage’ \((r_p = 0.06, p = 0.001)\), ‘saprophages’ and ‘detritus’ \((r_p = 0.75, p = 0.004)\), ‘polyphages’ and ‘fractal dimension’ \((r_p = 0.81, p = 0.003)\), while negative correlations appeared between ‘abundance’ and ‘depth’ \((r_p = -0.41, p = 0.003)\), ‘saprophages’ and ‘depth’ \((r_p = -0.85, p = 0.001)\), ‘abundance’ and ‘weight’ and ‘body size’ \((r_p = -0.15, p = 0.008)\) and between
‘predators’ and place ($r_p = -0.85$, $p = 0.004$) and between ‘abundance’ and ‘nympheids’ ($r_p = -0.78$, $p = 0.006$).

**DISCUSSION**

**Influence of the habitat and architecture on the richness, abundance and body size of Coleoptera**

This article is an outcome of 12 years of field studies, during which time we acquired a very rich amount of comparative material (124 species) from 40 lakes. Among the numerous references dedicated to water beetles, there are few which document a larger number of lakes (e.g. Nilsson & Södenberg, 1996; Buczyński, 2012).

In our study, same as Linzmeier & Costa (2011), we observed the highest species diversity and density of beetles representing two smallest body size classes, mostly of the genus *Hydroporus*. According to Ulrich (2007), empirical studies show the highest species richness among the medium-size species, while simulation models point to the smallest species. A contrary opinion is held by Scheffer & van Nes (2006) and Scheffer et al. (2015), who maintain that intermediate body sizes in animal assemblages are found extremely rarely because coevolution in competitive systems favours the co-occurrence of species either very similar to or very different from one another.

Thus, it seems to be the matter of assigning the criteria distinguishing body size categories. At the same time, we demonstrated very scarce presence of the largest species, a finding also reported by Nilsson & Södenberg (1996), Ulrich (2007) and Linzmeier & Costa (2011).

Similarly to Nilsson & Södenberg (1996), Saint-Germain et al. (2007) and Linzmeier and Costa (2011), we revealed negative correlations between the body size (and the individual body mass) and the abundance of beetles, as well as between the body size and the species richness. According to Nilsson & Södenberg (1996), a negative relationship between the abundance and body size is typical for most aquatic organisms. On the other hand, Saint-Germain et al. (2007) emphasise the negative correlation between the abundance of species and body size.
For clarification, we made an in-depth analysis of the dependencies between the body size and the number of beetles relative to the aspects defining the complex nature of each habitat. Such an approach enjoys a long tradition, as suggested by Urlich (2007), although it is rarely implemented in hydrobiological research (Cremona, Planas & Lucotte, 2008; Tokeshi & Arakaki, 2012; Désamoré et al., 2018). We demonstrated significant differences between the abundance and species richness of beetles representing different body size classes in the particular habitats. Figure 5 shows that the highest abundance and species richness occurred in the Sphagnum mat and mostly with respect to the smallest beetles (body size classes 1 and 2), mainly of the genera Anacaena and Hydroporus. In the same habitat, the least numerous were large beetles and the largest ones, such as Dytiscus or Cybister, were completely absent. A reverse situation was observed in the sandy bottom zone and in the pockets and ponds within the Sphagnum mat, where the smallest beetles (class 1) were the least numerous, while the largest ones were more abundant than elsewhere. Medium-size beetles (classes 2 and 3), e.g. Noterus, Agabus, and Ilybius, were numerous in all habitats. These relationships are explained perfectly well by the fractal structure. Should we take into consideration an increase in the fractal dimension from the smallest one (the less complex form of a habitat) in the sandy bottom zone to the highest (the more complex form of a habitat with increasingly small structural elements) in the Sphagnum mat, then our observations are in accord with the ones reported by other hydrobiologists, who conclude that the species diversity and density increase as the fractal dimensions increases (e.g. Verberk, 2001; Tokeshi & Arakaki, 2012). Meanwhile, small spaces between leaves in a Sphagnum mat inhibit the presence of very large beetles, a conclusion supported by the results provided by Tokeshi & Arakaki (2012). Similar conclusions were drawn by Scheffer et al. (2015), who suggest that the maximum body size is limited by the available space in which beetles could move.

In our study, negative correlations between the body size, weight or abundance of water beetles were determined in particular habitats. Considering the total biomass of beetles in individual habitats, we were unable to identify any significant differences, which again agrees with the conclusions drawn by Tokeshi & Arakaki (2012), namely that biomass does not change in the fractal dimensions. An increase in the density of beetles is offset by a decrease in the individual size of the body, which is concordant with the results of Tokeshi & Arakaki’s research (2012).
A very compact structure of vegetation creates niches for small beetles, offering them egg-laying safety, food for larvae (much humus) and a shelter from predators (Verberk, 2001). How is the co-occurrence of these smallest beetles possible if, according to Scheffer et al. (2015), specimens of the same size compete with one another most strongly? Some hydrobiologists, e.g. Scheffer & van Nes (2006) and Scheffer et al. (2015), draw attention to the fact that these organisms create self-organising assemblages, the presence of which is the result of co-evolution between potential competitors.

In the trophic structure we analysed we discovered that 70% of beetles were predators, being the most numerous groups in all habitats. According to Bloechl et al. (2010), the number of predatory beetles depends on the amount of their prey. In our study, the smallest quantitative impact of predatory beetles (same as the number of saprophages) was identified in the Sphagnum mat. There they represented classes of organisms with small body size, e.g. Hydroporus, which do not limit the presence of other water beetles, as they use other food resources, e.g. zooplankton, smaller insects, like mayflies, or insect eggs (Frelik & Pakulnicka, 2015; Frelik, Koszalka & Pakulnicka, 2016; Perissinotto, Bird & Bilton, 2016). According to Scheffer & van Nes (2006), Pakulnicka et al. (2013) and Scheffer et al. (2015), what happens here is the evident division of functions, which relies on the principle of minimising similarity (being similar albeit different), as this minimizes competitiveness. As Scheffer et al. (2015) maintain, these mechanisms ensure a certain measure of redundancy of similar species in the environment, which is essential for the functioning of ecosystems during unfavourable changes.

**Implications of the disharmonic succession of lakes on coleopteran fauna**

The species diversity and density of organisms are the properties most often applied to measuring both biodiversity and quality of the environment, also in the context of succession changes (Kowalik, 1968; Ranta, 1985; Kordylas, 1990; Linzmeier & Costa, 2011). According to Vamosi et al. (2007), species richness and body size change predictably along the spatial gradient, whereas Linzmeier & Costa (2011) suggest that changes in the body size can be an important indicator, while Saint-Germain et al. (2007) claim that body mass is a better measure than abundance.
Lake succession is a phenomenon that occurs in a given place and over a certain period of time, and with time (in subsequent stages) habitat conditions, mostly shaped by macrophytes, change as well. For particular organisms, optimal living conditions appear here and now, and then they disappear. Thus, changes in the primary structure of lakes result in changes in the secondary structure, formed by assemblages of various organisms. Many ecologists, including Siemann, Haarstad & Tilman (1999), Brown (2003), White et al. (2007) and Linzmeier & Costa (2011), underline that body size is correlated with numerous morphological, physiological and ecological features, such as an ability to disperse, metabolic capacity, digestion capacity, reproduction rate and duration of a generation, as well as biodiversity. Scheffer & van Nes (2006) claim that these characteristics act as specific mechanisms which prevent competition between species, especially ones with similar body size.

We have demonstrated that body size and body mass are also useful measurements in investigations into the mechanisms of succession of beetles in dystrophic lakes. Communities of lake-dwelling beetles representing different seral stages are characterised by diverse shares of species representing different body size classes. This is a consequence of changes in the fractal structure, that is the representativeness of habitats (fractals) with different fractal dimensions. Hence, in young lakes (see the Dendrogram), where the littoral zone is very modestly overgrown with plants, we noted very few smallest beetles associated with peats (tyrphophiles), e.g. Anacaena, Helophorus or Hydroporus, which agrees with the results reported by Bloechl et al. (2010). However, these beetles were very numerous in mature lakes, where a Sphagnum mat dominates. Thus, we determined negative correlations between the body size and the percentage of an area overgrown with Sphagnum moss in the littoral zone of lakes, as well as between the body size (and mean weight) and the abundance of beetles in lakes. Also, we observed that as the fractal dimension of lakes increased, the mean body size (and mean weight) decreased. As spaces between the habitat’s components, i.e. plants, decrease in size and become more and more complex, smaller organisms are evidently preferred, even though larger ones may occur in such habitats as well, because they can push away or move plant stems, small shoots or leaves, an observation also made by McAbendroth et al. (2005). This could be the reason why large beetles were found in the pockets and ponds within the Sphagnum mat, and in the ecotone between the Sphagnum mat and the open water surface.
We support the view of other researchers, e.g. McAbendroth et al. (2005), Bloechl et al. (2010), Linzmeier & Costa (2011), and believe that large species gain benefits during the early stages of succession, while smaller and specialised ones are at an advantage in the final stages. We have shown (see Fig. 11) that the abundance of beetles is correlated with the age of lakes (the seral stage) (contrary to Bloechl et al. (2010), and with the fractal dimension (McAbendroth et al., 2005). These relationships are connected with the development of plants, which offer a shelter from predators, places for laying eggs and food supply. Like Bloechl et al. (2010) and Cremona, Planas & Lucotte (2008), we demonstrated a relationship between polyphages (Haliplidae) and submerged, more compact plants, while a negative correlation was proven with nymphiids, which restrain the growth of food (algae) eaten by polyphages. In turn, the presence of saprophages is correlated with detritus and drifters (which additionally contribute to a growth in the fractal dimension by creating microhabitats that can be used by smaller organisms), which has been confirmed by Verberk (2001) and Cremona, Planas & Lucotte (2010). Moreover, we found out that the abundant presence of predatory beetles in all lakes, and especially among loose vegetation, is favoured by the availability of potential prey, a conclusion also supported by the findings made by Bloechl et al. (2010), whereas a more compact structure is clearly a barrier to the occurrence of the largest organisms. Another factor that limits the number of beetles is the depth. This suggestion is confirmed by the research completed by Brittain (1978), Pakulnicka, Górski & Bielecki (2015b) and Pakulnicka et al. (2013, 2015a). Among the lakes which we analysed, the ones that contained dark brown water with acidic reaction (Pakulnicka & Zawal 2018) there were no fish or amphibians, which are usually considered as one of the major factors limiting the presence of water beetles (Ericsson et al. 1980; Solé & Rödder 2010).

CONCLUSIONS

Our research has revealed that an application of fractal concepts enables a more comprehensive explanation regarding the character of fauna relative to the complex natural aspects of habitats. This approach is also helpful in explaining directional changes in fauna induced by the natural succession of lakes. The taxonomic diversity and various densities of beetles in lakes increase as the fractal dimension increases. There are negative correlations between the body size and abundance. An increase in the density of beetles in fractals with a higher dimension is offset by a
lower individual body size of specimens. Consequently, the biomass is constant regardless of the fractal dimension.

REFERENCES

Andrejczuk W. 2014. About the landscape space. *Dissertations of Cultural Landscape Commission* 24:45–64.

Baars JR, Murray DA, Hannigan E, Kelly-Quinn M. 2014. Macroinvertebrate assemblages of small upland peatland lakes in Ireland. *Biology & Environment: Proceedings of the Royal Irish Academy* 114B:233-248 DOI 10.3318/BIOE.2014.31.

Barnes JB, Vaughan IP, Ormerod SJ. 2013. Reappraising the effects of habitat structure on river macroinvertebrates. *Freshwater Biology* 58: 2154–2167 DOI 10.1111/fwb.12198.

Barndt D. 2012. Beitrag zur Kenntnis der Arthropodenfauna der Zwischenmoore Butzener Bagen, Trockenes Luch und Möllnsee bei Lieberose (Land Brandenburg) (Coleoptera, Heteroptera, Hymenoptera part., Auchenorrhyncha, Saltatoria, Diptera part., Diplopoda, Chilopoda, Araneae, Opiliones, u.a.). *Märkischen Entomologischen Nachrichten* 14:147–200.

Beadle JM, Brown LE, Holden J. 2015. Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes. *WIREs Water* 2:65–84 DOI 10.1002/wat2.1063.

Bloechl A, Koenemann S, Philippi B, Melber A. 2010. Abundance, diversity and succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in the North German Lowlands. *Limnologica* 40:15–225 DOI 10.1016/j.limno.2009.08.001.

Bosi G. 2001. Abundance, diversity and seasonal succession of dytiscid and noterid beetles (Coleoptera: Adephaga) in two marshes of the Eastern Po Plain (Italy). *Hydrobiologia* 459:1–7 DOI 10.1023/A:1012594615880.
Braun-Blanquet J. 1964. *Pflanzensociologie: Grundzüge der Vegetationskunde*, 3rd edn. Wien–New York: Springer–Verlag, 1–607.

Brown JH. 2003. *Macroecología*. Mexico: Fondo de Cultura Económica, 1–397

Buczyński P. 2012. VI.2. Aquatic beetles (Coleoptera: Adephaga, Hydrophiloidea, Staphylinioidea, Byrrhoidea). In: Kornijów R, Buczyński P, eds. *Lake Skomielno (Łęczna - Włodawa Lakeland, Eastern Poland). Environment monograph*. Olsztyn: Wydawnictwo Mantis, 257–272.

Buczyński P. 2015. *Dragonflies (Odonata) of anthropogenic waters in middle-eastern*. Olsztyn: Wydawnictwo Mantis, 1–272.

Ciecierska H. 2008. Macrophytes as indicators of the ecological state of lakes. *Dissertations and Monographs*. 139. Olsztyn: Wydawnictwo Mantis, 1–202.

Clausen SE. 1998. *Applied correspondence analysis*. California: Sage Publications, Thousand Oaks, 1–215.

Corbet S, Perrin R, Hartley D, Lancashire P, Mace H, Mc Clay A, Morton J, Parfitt R, Tomiak H, Wheatley K, Willmer R, Willows R. 1980. Diel changes in plankton and water chemistry in Wicken Brickpit. *Hydrobiologia*** 74**:249–271.

Cremona F, Planas D, Lucotte M. 2008. Biomass and composition of macroinvertebrate communities associated with different types of macrophyte architectures and habitats in a large fluvial lake. *Fundamental and Applied Limnology* 171/2:119–13 DOI 10.1127/1863-9135/2008/0171-0119.

Czachorowski S. 1998. *Caddisflies (Trichoptera) of Polish lakes - description of the distribution of larvae*. Olsztyn: Wydawnictwo WSP, 1–155.
Demetraki-Paleolog A. 2012. Long term changes of planktonic rotifers of ten lakes of different trophic status. *Teka Komisji Ochrony i Kształtowania Środowiska Przyrodniczego O.L. PAN* 9:44–57.

Désamoré A, Laenen B, Miller KB, Bergsten J. 2018. Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae). *Molecular Ecology* 27(4):979-993 DOI 10.1111/mec.14492. Epub 2018 Feb 11.

Drinan TJ, Foster GN, Nelson BH, O’Halloran J, Harrison SSC. 2013. Macroinvertebrate assemblages of peatland lakes: Assessment of conservation value with respect to anthropogenic land-cover change. *Biological Conservation* 158:175–187 DOI 10.1016/j.biocon.2012.10.001.

Eyre MD, Foster GN, Foster AP. 1992. Factors affecting the distribution of water beetle species assemblages in drains of eastern England. *Journal of Applied Entomology* 109:217–225 DOI: 10.1111/j.1439-0418.1990.tb00043.x.

Eriksson MOG, Henrikson L, Nilsson B-I, Nyman G, Oscarson HG, Stenson AE, Larsson K. 1980. Predator–prey relations important for the biotic changes in acidified lakes. *Ambio* 9: 248–249.

Fiłoc M, Kupryjanowicz M. 2015. Non-pollen palynomorphs characteristic or the dystrophic stage of humic lakes in the Wigry National Park, NE Poland. *Studia Quaternaria* 32:31–41 DOI 10.1515/squa-2015-0003.

Friday LE, 1988. A key to the adults of British water beetles. *Field Studies* 7: 1–151.

Foster GN, Eyre MD. 1992. Classification Ranking of Water Beetle Communities. *UK Nature Conservation*: 1. Peterborough: Joint Nature Conservation Committee, 1–110.

Frelik A, Koszalka J, Pakulnicka J. 2016. Trophic relations between adult water beetles from the Dytiscidae family and fly larvae from the Chironomidae family. *Biologia* 71:931–940 DOI 10.1515/biolog-2016-0115.
Frelik A, Pakulnicka J. 2015. Relations Between the Structure of Benthic Macro-Invertebrates and the Composition of Adult Water Beetle Diets from the Dytiscidae Family. *Environmental Entomology* **44**:1348–1357 DOI 10.1093/ee/nvv113.

Galewski K, Tranda E, 1978. Fauna słodkowodna Polski. Chrząszcze (Coleoptera). Rodziny: Pływakowate (Dytiscidae), Flisakowate (Haliplidae), Mokrzelicowate (Hygrobiidae), Krętakowate (Gyrinidae). *Fauna Słodkowodna Polski*. PWN Warszawa – Poznań, Poland, 1–396.

Galewski K, 1990. Chrząszcze (Coleoptera). Rodzina: Kałużnicowate (Hydrophilidae). *Fauna Słodkowodna Polski*. PWN Warszawa, Poland, 1–261.

Gioria M, Bacaro G, Feehan J. 2010a. Identifying the drivers of pond biodiversity: the agony of model selection. *Community Ecology* **11**:179–186 DOI 10.1556/ComEc.11.2010.2.6.

Gioria M, Schaffers A, Bacaro G, Feehan J. 2010b. The conservation value of farmland ponds: Predicting water beetle assemblages using vascular plants as a surrogate group. *Biological Conservation* **143**:1125–1133 DOI 10.1016/j.biocon.2010.02.007.

Hocking RR, 1996. Methods and applications of linear models. Regression and the Analysis of Variance. *Journal of the American Statistical Association* **70**: 707–712.

Holmen M, 1987. The aquatic Adephaga (Coleoptera) of Fennoskandia and Denmark. I. Gyrinidae, Haliplidae, Hygrobiidae and Noteridae. Fauna Entomologica Scandinavica **20**: 1–168.

Hansen M, 1987. The Hydrophiloidea (Coleoptera) of Fennoskandia and Denmark. Fauna Entomologica Scandinavica **18**: 1–254.

Jasser I. 1997. The dynamics and importance of picoplankton in shallow, dystrophic lake in comparison with surface waters of two deep lakes with contrasting trophic status. *Hydrobiologia* **342/343**:87–93 DOI 10.1007/978-94-011-5648-6_10.

Jeffries M. 1993. Invertebrate colonization of artificial pondweeds of differing fractal dimension. *Oikos* **67**:142–148.
Kajak Z. 1998. *Hydrobiology–Limnology. Ecosystems of Inland Water Bodies*. Warszawa: Wydawnictwo Naukowe PWN, 1–356.

Kordylas A. 1990. Water beetles (Coleoptera) of the lobelian Krzemno Lake. *Fragmenta Faunistica* 33:71–81.

Kowalik W. 1968. Water beetles (Coleoptera aquatica) in the Sosnowickie Lakes in the Łęczna-Włodawa Lake District. *Annales Universitatis Mariae Curie-Skłodowska* 18:283–300.

Kuczyńska-Kippen N. 2008. Spatial distribution of zooplankton communities between the sphagnum mat and open water in a dystrophic lake. *Polish Journal of Ecology* 56:57–64.

Lepistö L, Saura M. 1998. Effects of forest fertilization on phytoplankton in a boreal brown-water lake. *Boreal Environment Research* 3:33–43.

Linzmeier AM, Ribeiro-Costa CS. 2011. Body size of Chrysomelidae (Coleoptera, Insecta) in areas with different levels of conservation in South Brazil. In: Jolivet P, Santiago-Blay J, Schmitt M, eds. *Research on Chrysomelidae* 3. *ZooKeys* 157:1–14 DOI 10.3897/zookeys.157.1083.

Lundkvist E, Landin J, Milberg P. 2001. Diving beetle (Dytiscidae) assemblages along environmental gradients in an agricultural landscape in southeastern Sweden. *WETLANDS* 21:48–58 DOI 10.1672/0277-5212(2001)021[0048:DBDAAE]2.0.CO;2.

Mandelbrot B. 1983. *The fractal geometry of nature*. New York: WH Freeman and Company, 1–468.

McAbendroth L, Ramsay PM, Foggo A, Rundle SD, Bilton DT. 2005. Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions? *Oikos* 111: 279–290 DOI https://doi.org/10.1111/j.0030-1299.2005.13804.x.

McFarland B, Carse F, Sandin L. 2009. Littoral macroinvertebrates as indicators of lake acidification within the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20:105–116 DOI 10.1002/aqc.1064.
Menetrey N, Sager L, Oertli B, Lachavanne JB. 2005. Looking for metrics to assess the trophic state of ponds. Macroinvertebrates and amphibians. Aquatic Conservation: Marine and Freshwater Ecosystems 15:653–664 DOI 10.1002/aqc.746.

Miałdun J. 2010. Effect of ground sample distance and impulse noise on fractal dimension of littoral vegetation of Lake Łuknajno. Archiwum Fotogrametrii, Kartografii i Teledetekcji 21:257–266.

Miałdun J, Ostrowski M. 2010. Fractal dimension of fragments of aerial images of shoreline zones of the Lakes Mikołajskie, Śniardwy and Łuknajno. Archiwum Fotogrametrii, Kartografii i Teledetekcji 21:267–279.

Mieczan T, Tarkowska-Kukuryk M, Plaska W, Rechulicz J. 2014. Abiotic predictors of faunal communities in an ombrotrophic peatland lagg and an open peat bog. Israel Journal of Ecology & Evolution 60: 62–74.

Miller KB, Bergsten J. 2016. Diving Beetles of the World. Systematics and biology of the Dytiscidae. Baltimore: Johns Hopkins University Press, 1–320.

Nilsson AN, Söderberg H. 1993. Abundance and species richness patterns of diving beetles (Coleoptera, Dytiscidae) from exposed and protected sites in 98 northern Swedish lakes. Hydrobiologia 321:83–88 DOI 10.1007/BF00018680.

Obolewski K, Glińska-Lewczuk K, Kobus S. 2009. Effect of hydrological connectivity on the molluscan community structure in oxbow lakes of the Łyna River. Oceanological and Hydrobiological Studies 38:75–88 DOI 10.2478/v10009-009-0045-1.

Odland A, del Moral R. 2002. Thirteen years of wetland vegetation succession following a permanent drawdown, Myrkdalen Lake, Norway. Plant Ecology 162:185–198 DOI 10.1023/A:1020388910724.

Pakulnicka J. 2008. The formation of water beetle fauna in anthropogenic water bodies. Oceanological and Hydrobiological Studies 37:1–12 DOI 10.2478/v10009-007-0037-y.

Pakulnicka J, Bartnik W. 1999. Changes in the fauna of aquatic beetles (Coleoptera aquatica) in Lake Luterskie (Olsztyn Lake District) in 1981-1993. Fragmenta Faunistica 42:71–93.
Pakulnicka J, Buczyńska E, Buczyński P, Czachorowski, S, Kurzątkowska A,
Lewandowski K, Stryjecki R, Frelik A. 2015a. Are beetles good indicators of insect
diversity in freshwater lakes? *Oceanological and Hydrobiological Studies* **44**:487–499 DOI 10.1515/ohs-2015-0046.

Pakulnicka J, Buczyński P, Dąbkowski P, Buczyńska E, Stępień E, Stryjecki R, Szlauer-
Łukaszewska A, Zawal A. 2016a. Aquatic beetles (Coleoptera) in springs situated in the
valley of a small lowland river: habitat factors vs landscape factors. *Knowledge and
Management of Aquatic Ecosystems* **417**, 29:1–13 DOI 10.1051/kmae/2016016.

Pakulnicka J, Buczyński P, Dąbkowski P, Buczyńska E, Stępień E, Stryjecki R, Szlauer-
Łukaszewska A, Zawal A. 2016b. Development of fauna of water beetles (Coleoptera)
in waters bodies of a river valley habitat factors, landscape and geomorphology.
*Knowledge and Management of Aquatic Ecosystems* **417**, 40:1–23 DOI
10.1051/kmae/2016027.

Pakulnicka J, Górski A, Bielecki A. 2015b. Environmental factors associated with biodiversity
and the occurrence of rare, threatened, thermophilous species of aquatic beetles in the
anthropogenic ponds of the Masurian Lake District). *Biodiversity and Conservation* **24**:429–
445 DOI 10.1007/s10531-014-0774-7.

Pakulnicka J, Górski A, Bielecki A, Buczyński P, Tończyk G, Cichocka JM. 2013.
Relationships within aquatic beetle (Coleoptera) communities in the light of ecological
theories. *Fundamental and Applied Limnology* **183**:249–258 DOI 10.1127/1863-
9135/2013/0413.

Pakulnicka J, Zawal A. 2007. Water beetles (Coleoptera) of ‘Szare Lake’ Reserve and water
bodies situated in its vicinity. *Parki Narodowe i Rezerwaty Przyrody* **25**:121–133. [in
Polish]

Pakulnicka J, Zawal A. 2018. Model of disharmonic succession of dystrophic lakes based on
aquatic beetle fauna (Coleoptera). *Marine and Freshwater Research*. DOI 10.1071/MF17050.
Perissinotto R, Bird MS, Bilton D. 2016. Predaceous water beetles (Coleoptera, Hydradephaga) of the Lake St Lucia system, South Africa: biodiversity, community ecology and conservation implications. *ZooKeys* **595**:85–135 DOI 10.3897/zookeys.595.8614.

Plaska W, Mieczan T. 2018. Effects of water bugs on crustacean zooplankton in a shallow littoral zone. *Knowledge and management of aquatic ecosystems* **419**, 16:1–7 DOI 10.1051/kmae/2018012.

Plaska W, Kurzątkowska A, Stępień A, Buczyńska E, Pakulnicka J, Szlauer-Lukaszewska A, Zawal A. 2016. The effect of dredging of a small lowland river on aquatic Heteroptera. *Annales Zoologici Fennici* **53**:139–153 DOI 10.5735/086.053.0403.

Plaska W, Tarkowska-Kukuryk M. 2014. Influence of abiotic factors on species spectrum of zoopleuston in different types of peatlands. *Polish Journal of Environmental Studies* **23** (2): 441–447.

Ranta E. 1985. Communities of Water-Beetles in Different Kinds of Waters in Finland. *Proceedings of the Academy of Natural Sciences of Philadelphia* **137**:33–45.

Saint-Germain M, Buddle CM, Larrivée M, Mercado A, Motchula T, Reichert E, Sackett TE, Sylvain Z, Webb A. 2007. Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *Journal of Applied Ecology* **44**:330–339 DOI 10.1111/j.1365-2664.2006.01269.x.

Shadrin NV, EL-Shabrawy GM, Anufriieva EV, Goher ME, Ragab E. 2016. Long-term changes of physicochemical parameters and benthos in Lake Qarun (Egypt): Can we make a correct forecast of ecosystem future? *Knowledge and management of aquatic ecosystems* **417**, 18:1–11 DOI 10.1051/kmae/2016005.

Siemann E, Haarstad J, Tilman D. 1999. Dynamics of plant and arthropod diversity during old field succession. *Ecography* **22**: 406–414 DOI 10.1111/j.1600-0587.1999.tb00577.x.

Scheffer M, van Nes EH. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences of the United States of America* **103** (16): 6230–6235 DOI 10.1073/pnas.0508024103.
Scheffer M, Vergnon R, van Nes EH, Cuppen JGM, Peeters ETHM, Reijs R, Nilsson AN. 2015. The Evolution of Functionally Redundant Species; Evidence from Beetles. *PLoS ONE* 10(10): e0137974 DOI 10.1371/journal.pone.0137974.

Soldán T, Bojková J, Vrba J, Bitušík P, Chvojka P, Papáček M, Peltanová J, Sychra J, Tátosová J. 2012. Aquatic insects of the Bohemian Forest glacial lakes: Diversity, long-term changes, and influence of acidification. *Silva Gabreta* 18:123–283.

Solé M, Rödder D. 2010. Dietary assessments of adult amphibians. In: Dodd CK, Jr, ed. *Amphibian Ecology and Conservation A Handbook of Techniques*. Oxford: University Press, 1–180.

Stryjecki R, Zawal A, Szlauer-Łukaszewska A, Michoński G, Buczyńska E, Buczyński P, Pakulnicka J, Śmietańska P. 2017. Water mite (Acari, Hydrachnidia) assemblages in relation to differentiation of mesohabitats in a shallow lake and its margins. *Turkish Journal of Fisheries and Aquatic Sciences* 17:323-332 DOI 10.4194/1303-2712-v17_2_11.

Šiling R, Urbanič G. 2016. Do lake littoral benthic invertebrates respond differently to eutrophication, hydromorphological alteration, land use and fish stocking? *Knowledge and management of aquatic ecosystems* 417, 35:1–31 DOI 10.1051/kmae/2016022.

Timm H, Möls T. 2012. Littoral macroinvertebrates in Estonian lowland lakes: the effects of habitat, season, eutrophication and land use on some metrics of biological quality. *Fundamental Applied Limnology* 180: 145–156 DOI 10.1127/1863-9135/2012/0203.

Tokeshi M, Arakaki S. 2012. Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia* 685: 27–47 DOI 10.1007/s10750-011-0832-z.

Ulrich W. 2007. Body weight distributions of central European Coleoptera. *European Journal Of Entomology* 104:769–776. DOI 10.14411/eje.2007.098.

Usseglio-Polatera, P., Bournaud, M. and Tachet, H. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* 43, 175–205. DOI 10.1046/j.1365-2427.2000.00535.x.
Vamosi SM, Naydani CJ, Vamosi JC. 2007. Body size and species richness along geographical gradients in Albertan diving beetle (Coleoptera: Dytiscidae) communities. Canadian Journal of Zoology 85:443–449 DOI 10.1139/Z07-021.

Verberk WCEP, van Duinen GJA, Peeters TMJ, Esselink H. 2001. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society 12:121–128.

Winfield Fairchild G, Faulds A, Matta JF. 2000. Beetle assemblages in ponds: effects of habitat and site age. Freshwater Biology 44:523–534 DOI 10.1046/j.1365-2427.2000.00601.x.

White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ. 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22:323–330 DOI 10.1016/j.tree.2007.03.007.

Yee DA (ed.) 2014. Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae). Dordrecht: Springer, 1–468.
FIGURE CAPTIONS

Figure 1 Study area – Location of lakes (1-40). 1, Żabie; 2, Szare; 3, Wygoda; 4, Krypko; 5, Pałsznik; 6, Małe Gacno; 7, Wielkie Gacno; 8, Długie; 9, Moczadło; 10, Sosnówek; 11, Żabionek; 12, Klimontek; 13, Nierybno; 14, Małe Łowne; 15, Czarne; 16, Piecki; 17, Babionek Duży; 18, Babionek Mały; 19, Białe; 20, Kociołek; 21, Żabie; 22, Motylek; 23, Purdka; 24, Jonkowo; 25, Borkowskie; 26, Bobrówko; 27, Gryżewskie; 28, Skarp; 29, Zakręt; 30, Kruczy Stawek; 31, Kruczek Duży; 32, Kruczek Mały; 33, Krucze Oko; 34, Kruczy Staw; 35 Suchar Wielki; 36, Suchar 1 Lake; 37, Suchar 2; 38, Suchar 3; 39, Suchar 4; 40, Suchar 5.

Figure 2 Distinguished habitats in the littoral zone of lakes (A) and hypothetical fractal dimensions (B) (after Tokeshi & Arakaki (2012), modified).

Figure 3 The structure of body size of Coleoptera in distinguished habitats: N - abundance, S – number of species.

Figure 4 The trophic structure of Coleoptera in distinguished habitats: N - abundance, S – number of species.

Figure 5 Results of a Tukey post hoc test for GLM repeated measure Anova. The diagram shows the influence of the statistically significant synergistic effect between habitats and body size classes on: A) abundance and B) number of species in the habitats distinguished with the analysed lakes. Habitats: sandy – sandy bottom zone, pockets – pockets and ponds in a Sphagnum mat, sparse – sparse macrophytes, dense – dense macrophytes, Sphagnum – compacted Sphagnum mat. (Bars indicate 0.95 confidence intervals). 1 – very small beetles, 2 – small beetles, 3 – medium beetles, 4 – large beetles, 5 – very large beetles.

Figure 6 Multidimensional correspondence analysis (MCA). Relationship between identified classes of body size, distinguished habitats and individual lakes along the first and second MCA.

Figure 7 Results of dendrogram for 40 lakes. Single Linkage, Euclidean distances (1-10 – cluster distinguished.
Figure 8 Linear regression for Coleoptera in lakes. Abundance vs body size (A) and abundance vs weight (B).

Figure 9 Linear regression for Coleoptera in lakes. Mean body size vs fractal dimension (A) and mean weight vs fractal dimension (B).

Figure 10 Linear regression for Coleoptera in lakes. Mean body size vs seral stage of succession.

Figure 11 Principal Component Analysis (PCA) ordination plot of functional groups, and environmental variables in samples along the first and second PCA axis.

APPENDIX CAPTIONS

Appendix 1 General characteristics of the lakes. % – contribution in the littoral zone (Sm – Sphagnum mat, Di – Sparse macrophytes, De – Dense macrophytes, A – sandy bottom zone), T – Stage of succession (O – oligohumic, M – mesohumic, P – polyhumic), S – number of species.

Appendix 2 Quantitative occurrence of beetles in humic lake. N – number of individuals, NS – number of samples. L – number of lakes, Bs – body size class, F – functional group (P – predators, S – saprophages, F – polyphages), P – Legal protection, EN,VU, LC – threat status (Polish Red List), min – minimum abundance of the species in a single sample (excluded samples where the species did not occur), max – abundance of the species in a single sample, Mean – average abundance of the species in a single sample, SD – standard deviation.

Appendix 3 Results of HSD Tuckey post hoc test for GLM repeated measure Anova. Influence of significant interaction between habitats and body size on A) abundance of beetles, B) number of species. SN – Subclass number, BS – Body size class, Habitat: Sphagnum – compacted Sphagnum mat, dense – dense macrophytes zone, sparse - sparse macrophytes zone, sandy bottom – sandy bottom zone, pockets – pockets and ponds in Sphagnum mat. Values statistically significant are in bold.

Appendix 4 Database - source data.
Figure 1

Study area.

Location of lakes (1-40). 1, Żabie; 2, Szare; 3, Wygoda; 4, Krypko; 5, Pałsznik; 6, Małe Gacno; 7, Wielkie Gacno; 8, Długie; 9, Moczadło; 10, Sosnówek; 11, Żabionek; 12, Klimontek; 13, Nierybno; 14, Małe Łowne; 15, Czarne; 16, Piecki; 17, Babionek Duży; 18, Babionek Mały; 19, Białe; 20, Kociołek; 21, Żabie; 22, Motylek; 23, Purdka; 24, Jonkowo; 25, Borkowskie; 26, Bobrówko; 27, Gryżewskie; 28, Skarp; 29, Zakręt; 30, Kruczy Stawek; 31, Kruczek Duży; 32, Kruczek Mały; 33, Krucze Oko; 34, Kruczy Staw; 35 Suchar Wielki; 36, Suchar 1 Lake; 37, Suchar 2; 38, Suchar 3; 39, Suchar 4; 40, Suchar 5.
Figure 2

Distinguished habitats in the littoral zone of lakes (A) and hypothetical fractal dimensions (B).

(after Tokeshi & Arakaki (2012), modified).
Figure 3

The structure of body size of Coleoptera in distinguished habitats:

N - abundance, S - number of species.
Figure 4

The trophic structure of Coleoptera in distinguished habitats.

N - abundance, S - number of species.
Figure 5

Results of a Tukey *post hoc* test for GLM repeated measure Anova. The diagram shows the influence of the statistically significant synergistic effect between habitats and body size classes on:

A) abundance and B) number of species in the habitats distinguished with the analysed lakes. Habitats: sandy – sandy bottom zone, pockets – pockets and ponds in a *Sphagnum* mat, sparse – sparse macrophytes, dense – dense macrophytes, *Sphagnum* – compacted *Sphagnum* mat. (Bars indicate 0.95 confidence intervals). 1– very small beetles, 2 – small beetles, 3 –medium beetles, 4 – large beetles, 5 – very large beetles.
Figure 6

Multidimensional correspondence analysis (MCA).

Relationship between identified classes of body size, distinguished habitats and individual lakes along the first and second MCA.
**Figure 7**

Results of dendrogram for 40 lakes.

Single Linkage, Euclidean distances (1-10 – cluster distinguished).
Figure 8

Linear regression for Coleoptera in lakes.

Abundance vs body size (A) and abundance vs weight (B).
A

\[ \text{LOG (mean body size)} = 0.8657 - 0.36 \times \text{LOG (N)} \]

\[ R^2 = 0.49 \]

B

\[ \text{LOG (mean weight)} = 1.523 - 0.4256 \times \text{LOG (N)} \]

\[ R^2 = 0.369 \]
Figure 9

Linear regression for Coleoptera in lakes.

Mean body size vs fractal dimension (A) and mean weight vs fractal dimension (B).
A

\[ \text{LOG (mean body size)} = 0.8535 - 0.061 \times \text{Fractal dimension } D \]
\[ R^2 = 0.769 \]

B

\[ \text{LOG (mean weight)} = 2.0245 - 0.19 \times \text{Fractal dimension } D \]
\[ R^2 = 0.827 \]
Figure 10

Linear regression for Coleoptera in lakes.

Mean body size vs seral stage of succession.
Figure 11

Principal Component Analysis (PCA) ordination plot of functional groups, and environmental variables in samples along the first and second PCA axis.
Table 1 (on next page)

General description of the lake beetles.

Min – minimum value, max – maximum value, mean - average value, SD – standard deviation.
Table 1 General description of the lake beetles. Min – minimum value, max – maximum value, mean - average value, SD – standard deviation.

| Body size class | Abundance | Number of species | Body size (mm)  | Body weight (mg) |
|-----------------|-----------|-------------------|-----------------|------------------|
|                 |           |                   | (mean ± SD)     | min – max        |
| very small      | 2953      | 32                | 2.25 ± 0.38     | 1.30 – 2.95      |
| small           | 5640      | 37                | 3.47 ± 0.56     | 3.00 – 4.90      |
| medium          | 945       | 26                | 5.82 ± 1.12     | 5.00 – 9.80      |
| large           | 565       | 24                | 13.06 ± 2.37    | 10.5 – 18.6      |
| very large      | 36        | 5                 | 31.79 ± 2.09    | 27.5 – 35.1      |
Table 2 (on next page)

Results of the Pearson’s analysis of correlation ($r_p$).

Dependencies between body size and the abundance and diversity of Coleoptera in the distinguished habitats (Pearson’s analysis of correlation). Statistically significant data are in bold ($p < 0.05$).
Table 2 Results of the Pearson’s analysis of correlation ($r_p$). Dependencies between body size and the abundance and diversity of Coleoptera in the distinguished habitats (Pearson’s analysis of correlation). Statistically significant data are in bold ($p < 0.05$).

| Habitat                              | Abundance $r_p$ | Abundance $p$ | Number of species $r_p$ | Number of species $p$ |
|--------------------------------------|----------------|--------------|-------------------------|-----------------------|
| Compacted *Sphagnum* mat             | $-0.140$       | $0.011$      | $-0.13$                 | $0.011$               |
| Dense macrophytes zone               | $-0.265$       | $0.0008$     | $-0.04$                 | $0.40$                |
| Sparse macrophytes zone              | $-0.265$       | $0.00001$    | $-0.18$                 | $0.0008$              |
| Sandy bottom zone                    | $-0.31$        | $0.47$       | $-0.09$                 | $0.48$                |
| Pockets and ponds in *Sphagnum* mat  | $-0.10$        | $0.06$       | $-0.04$                 | $0.40$                |
Table 3 (on next page)

Results of the Pearson’s analysis of correlation.

Changes in the abundance (LOG N) of the distinguished body size and the growth of the *Sphagnum* mat (LOG %) in lakes. Statistically significant data are in bold (p < 0.05).
1 Table 3 Results of the Pearson’s analysis of correlation. Changes in the abundance (LOG N) of the distinguished body size and the growth of the Sphagnum mat (LOG %) in lakes.

2 Statistically significant data are in bold (p < 0.05).

| Variables                        | $r_p$ | $r^2$ | $t$   | $p$     |
|----------------------------------|-------|-------|-------|---------|
| Body size class 1 & Sphagnum mat (%) | 0.702 | 0.449 | 6.085 | 0.00004 |
| Body size class 2 & Sphagnum mat (%) | – 0.19 | 0.03  | – 1.236 | 0.22    |
| Body size class 3 & Sphagnum mat (%) | – 0.155 | 0.02  | – 0.97 | 0.338   |
| Body size class 4 & Sphagnum mat (%) | – 0.16  | 0.027 | – 1.03 | 0.308   |
| Body size class 5 & Sphagnum mat (%) | **0.207** | **0.043** | **– 1.307** | **0.04** |