Polish Journal of Ecology
Pol. J. Ecol. (2014) 62: 335–348

Regular research paper

Beata JAKUBIK [1], Paweł KOPERSKI [2]*, Krzysztof LEWANDOWSKI [1]

[1] Institute of Biology, Siedlce University of Natural Sciences and Humanities, B. Prusa 12, 08–110 Siedlce, Poland; e-mail: *ekologia@uph.edu.pl*
[2] Department of Hydrobiology, Faculty of Biology, Center of Biological and Chemical Research, University of Warsaw, Żwirki i Wigury 101, 02-089 Warszawa, Poland;
*e-mail: p.t.koperski@uw.edu.pl (*corresponding address*)

DIVERSITY OF MOLLUSCA IN LOWLAND RIVER-LAKE SYSTEM: LENTIC VERSUS LOTIC PATCHES

ABSTRACT: Longitudinal organisation of macroinvertebrate fauna along river is one of the most important problem commonly used to explain the functioning of flowing water ecosystems. The river system can be treated as a mosaic of landscapes patches and riverine macroinvertebrates' community structure is a function of longitudinal changes in its key abiotic patterns. The aims of the study was to analyse the taxonomic structure of molluscs in the river-lake system, to compare river and lake malacofauna and to determine the factors responsible for its diversity in lakes and river stretches. The study based on comprehensive analysis of malakofauna sampled at 10 sites in the Krutynia River and in all 19 lakes it flows through were performed in the years 2008–1011. River Krutynia is one of the most important rivers in Masurian Lakeland (north-eastern Poland) with length of 100 km and mean annual discharge of 10.6 m^3 h^{-1}. It forms a characteristic river-lake system typical for the lakeland landscape in Central Europe. The density and taxonomic composition of molluscs were found as strongly dissimilar in a local scale – between closely located lakes and between particular parts of flowing waters, divided by the lakes. Multivariate methods were used to demonstrate a clear dissimilarity of lake and river malakofauna and to show that the mean content of phosphorus, nitrogen and organic matter in bottom sediments were correlated with each other in lakes but not in the river. The most important species differentiating river sites into larger groups with respect to the similarity was *Theodoxus fluviatilis* while *Stagnicola corvus* and *Anisus vortex* were such species differentiating lakes. The numbers and percentages of *Dreissena polymorpha* and Unionidae were negatively correlated with nutrients in river sediments. There was a strong positive relationship between nutrients' concentrations in sediments and the percentages of *Viviparus*, Obtained results of multiple regression indicate a strong effect of nutrient and organic matter concentrations in the sediments and the distance from the site to the lake on the domination structure of molluscs.

KEY WORDS: diversity, Mollusca, river system, water chemistry

1. INTRODUCTION

Longitudinal organisation of macroinvertebrate fauna along river systems in one of the most important problem commonly used to explain the functioning of flowing water ecosystems. The authors of the River Continuum Concept (Vannote *et al.* 1980), as it is concluded by Statzner and Higler (1985): "*consider it as a framework for a characterization of pristine running water ecosystems, describing the structure and function of communities along a river system in relationship to the abiotic environment*". Ecological processes and macroinvertebrate community structure are at least in part, a function of longitudinal changes in key abiotic factors like discharge, channel width, and bed sediment size (Rice *et al.* 2001). The river system can be treated as a mosaic of landscapes patches differed in morphology and function (*e.g.* Wiens 2002). This longitudinal trends can be disturbed by tributaries (Minshall *et al.* 1983) and, probably, by lakes, which disconnect fragments of a river-system. Woodward and Hildrew (2002) presented the roles of biotic factors and certain physical habitat features (*e.g.* geology, land-use, habitat fragmentation) in moulding riverine food web structure at the landscape scale. Among others, riverine molluscs, both bivalve filterers and algivorous gastropods, play a great role in lotic food-webs (Atkinson *et al.* 2013) .

The Krutynia is one of the most important rivers in Masurian Lakeland. It is 100 km long and flows through 19 lakes inflowing to the Lake Bełdany, forming a characteristic river-lake system typical for the lakeland landscape of northern Poland. The Krutynia River was an object of many detailed physical, chemical and biological studies (*e.g.* Szczepański 1958, Hillbricht-Ilkowska *et al.* 1996). Mean discharge of the River Krutynia was determined by Radwan *et al.* (1992) as 10.6 m^3 h^{-1} with a range of 1.26–25.7 m^3 h^{-1}. The dynamics of phosphorus and other important elements in sediments of different parts of Krutynia river-lake system was detailly studied and presented by Rzepecki (2010, 2012). The history of studies on Mollusca in the Krutynia River dates back 100 years ago (Hilbert 1913, Berger 1960, 1962) while current research is still conducted (Jakubik and Lewandowski 2011), hence the community is relatively well recognised. Long-term changes in riverine assemblages of molluscs, noted in European rivers (*e.g.* Mouthon and Daufresne 2010) should be, however, taken into consideration. The studies, mostly qualitative, pertain, however, to either old times (the begining of the 20th century), selected river stretches or selected species. The effect of selected habitat conditions like: the type of bottom, vegetation coverage, nutrient and organic matter content in bottom sediments on the occurrence and species richness was presented in certain previous studies involved in different geographical regions (*e.g.* Cremona *et al.* 2008). The great importance of hydrological and genetic effects functioning in local-scale on mollusc fauna in river systems was empahasized *e.g.* in Mediterranean water-courses (Perez-Quintero 2012). The effects of trophic status on mollusc assemblages in Masurian river-lake system, similar to Krutynia system were presented in details by Kołodziejczyk *et al.* (2009). Complex studies on molluscs in the river and lakes from the river springs to its mouth were never conducted.

The aim of this study was to comprehensively analyse the taxonomic structure of molluscs in the river-lake system of the Krutynia River, to compare river and lake malacofauna and to determine the factors responsible for qualitative and quantitative diversity of malacofauna in lakes and river stretches. The effect of certain important abiotic factors like nutrient concentrations and organic matter content in sediments and distance from riverine sampling site to a lake outflow on molluscs structure and diversity was also analysed. One of important aim of the study is explaining the role of local spatial patterns, which determine diversity and dissimilarity of mollusc assemblages in river-lake system

2. STUDY AREA AND METHODS

Studies on molluscs were made in the years 2008–2009 in river stretches and in the years 2010–2011 in lakes. Ten sampling sites spread from springs to river mouth were selected in river sections between lakes (Fig. 1). When selecting the sites we attempted to account for a full diversity of lotic sections of the river. The river in sites situated at different distances from its outlet from a lake had different width, maximum depth, different type of bottom and was overgrown by vegetation to a different degree (Table 1).

Studied lakes were mainly eutrophic but had different size and depth. The smallest lakes had an area slightly more than 20 ha (Lake Malinówka, Lake Kujno), the surface area of the largest Lake Mokre was over 840 ha (Table 2).

In each lake the samples of molluscs were collected from two sites at depths of 0.5, 1.0, 2.0 and 3.0 m. At greater depths there was a

Table 1. Characteristics of study sites in the Krutynia River (according to Jakubik and Lewandowski 2011; modified).

No.	River width (m)	Maximum depth (m)	Distance from the river outlet from a lake (m)	Type of the bottom	Approximate plant coverage (%)	Dominant plant species
1	2–3	0.5	50	sand, gravel, stones	40	*Nuphar lutea, Sparganium ramosum, Potamogeton perfoliatus*
2	8	0.5	100	sand, gravel, stones	20	*N. lutea, Acorus calamus, Phragmites australis*
3	10–12	0.5	500	sand, gravel	80	*N. lutea, S. ramosum*
4	12–15	0.5	100	gravel, stones	30	*Typha latifolia*
5	12	1.0	200	sand, stones	30	*N. lutea, P. australis*
6	12–15	1.0	2000	sand, gravel	30	*N. lutea, P. australis*
7	15	0.5	100	gravel	no plants	–
8	20	1.0	2000	sand, stones, mud	30	*Carex* sp., *Utricularia vulgaris*
9	15	1.0	25 000	gravel, stones, mud	80	*N. lutea, P. australis, A. calamus, Carex* sp., *Sagittaria sagittifolia, Fontinalis antipyretica, Ceratophyllum demersum*
10	12–20	1.0	200	sand, mud	20	*N. lutea, P. australis*

Table 2. Characteristics of study lakes (data from the Institute of Inland Fisheries and Hillbricht-Ilkowska *et al.* 1996).

No.	Lakes	Area (ha)	Maximum depth (m)	Mean depth (m)	Trophic status
1	Warpuńskie	49.0	6.9	2.6	hyper/eutrophy
2	Zyndackie	39.5	10.3	4.0	hyper/eutrophy
3	Gielądzkie	475.5	27.0	6.8	eutrophy
4	Lampackie	198.6	38.5	11.1	eutrophy
5	Lampasz	88.2	21.7	4.9	eutrophy
6	Kujno	24.0	6.0	2.8	eutrophy
7	Dłużec	123.1	19.8	6.3	eutrophy
8	Białe	341.0	31.0	7.0	eutrophy
9	Gant	75.3	28.3	9.5	mezo/eutrophy
10	Zyzdrój Wielki	210.0	14.5	4.9	eutrophy
11	Zyzdrój Mały	50.7	12.8	3.9	eutrophy
12	Spychowskie	48.8	7.7	2.3	eutrophy
13	Zdrużno	250.2	23.9	5.4	eutrophy
14	Uplik	60.6	9.2	2.8	eutrophy
15	Mokre	841.0	51.0	12.7	mezo/eutrophy
16	Krutyńskie	55.0	3.2	1.7	eutrophy
17	Gardyńskie	82.6	11.5	2.4	eutrophy
18	Malinówka	21.0	no data	no data	eutrophy
19	Jerzewko	29.0	3.0	no data	eutrophy

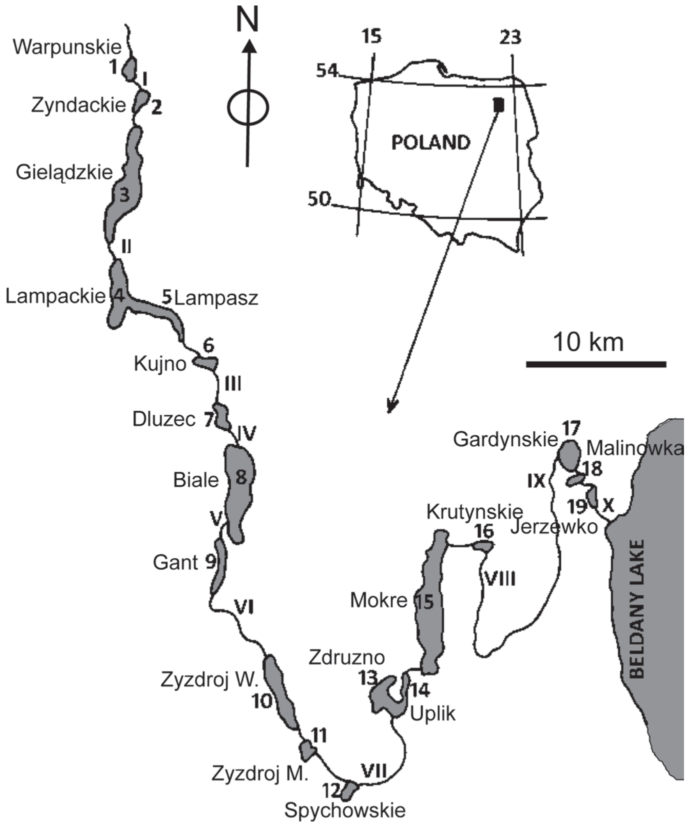

Fig. 1. River-lake system of the Krutynia River: 1–19 – lakes (see Table 2), I–X – sampling sites in river sections.

thick sediment layer and molluscs were not recorded.

In each river site and in shallow lake sites (0.5 and 1.0 m) a frame of an area of 0.25 m^2 was randomly placed 4 times on the bottom and the whole material (bottom sediments and plants) was collected with a grab. In deeper lake sites (2.0, 3.0 m) the Günther's sampler of an active area of 276 cm^2 was used four times. Collected material was transferred onto benthos sieve of 1 mm mesh size. After washing this content alive molluscs and empty shells were collected. Apart from quantitative analyses, qualitative samples were also taken to find out the richness of micro-habitats.

Bivalves of the family Unionidae, their age and size were determined directly in the field and live animals were then released to water. Other live molluscs were transported to the laboratory, determined and weighted. Only small part of collected material was conserved in 50% alcohol. All live molluscs after accomplished analyses were released to water.

Fresh biomass of bivalves of the family Unionidae was determined from species composition and size structure based on rich documentation from the Krutynia River from the year 1989 (Lewandowski 1996).

Moreover, in each river and lake site, bottom sediments were sampled for the determination of total phosphorus (with the molybdenum blue method), total nitrogen (with the indophenol method of Marczenko 1979) and percent of organic matter.

Three types of multidimensional statistical and numerical procedures (TWINSPAN, MDS and PCA) and multiple regression were used to analyse the similarity of sites in taxonomic composition and the relationship between the latter and measured abiotic parameters. The first and second analyses were performed with the Community Analysis Package Software, Pisces Inc., while the third and fourth – with the software Statistica 6, Statsoft. Primary data were log transformed and arc-sin transformation was used in the case of percentage share.

Table 3. Concentrations of nitrogen and phosphorus (mg g dry wt.$^{-1}$) and percent of organic matter in bottom sediments in river presented as annual means and ranges.

Sites	N	P	Organic matter (% dry wt)
1	0.54 (0.34–0.66)	0.26 (0.22–0.31)	1.25 (1.11–1.49)
2	0.55 (0.21–1.02)	0.44 (0.33–0.55)	1.29 (1.01–1.50)
3	0.35 (0.18–0.59)	0.29 (0.20–0.45)	1.04 (0.91–1.15)
4	0.51 (0.31–0.78)	0.39 (0.30–0.52)	1.74 (1.47–2.21)
5	0.30 (0.17–0.66)	0.34 (0.21–0.57)	0.90 (0.60–1.50)
6	0.29 (0.22–0.45)	0.27 (0.23–0.33)	0.88 (0.57–1.07)
7	2.41 (0.10–0.42)	0.38 (0.32–0.44)	0.94 (0.59–1.40)
8	0.62 (0.30–1.15)	0.29 (0.20–0.38)	1.62 (0.87–2.97)
9	0.86 (0.53–1.19)	0.45 (0.35–0.59)	15.50 (3.10–29.70)
10	0.32 (0.12–0.43)	0.37 (0.28–0.47)	0.66 (0.29–1.07)

1. TWINSPAN is a method based on correspondence analysis (reciprocal averaging) which was made from data on percentage share of particular species in classes 0, 1, 5, 10 and 50%. As a result, we obtained a dendrograph of site similarity, nodes of which bear the names of species most important at particular stages of grouping.
2. Non-hybrid multidimensional scaling (MDS) is a method of the analysis of similarity among sites where results are presented in a form of ordination map. Two types of this analysis were made: the first based on Euclidean distances calculated from the numbers of particular species in samples and the second based on the values of the Jaccard's function.
3. Principal Component Analysis (PCA) was performed based on correlations. Four PCA analyses were calculated from the numbers of particular species and their percentage share, separately for river and lake sites. Data on species richness and the total number of molluscs in particular sites were also used in these analyses. Resulting ordination maps contain also the representation of measured abiotic parameters and the distribution of particular sites.
4. With the multiple regression we estimated the relationships between abiotic parameters and the numbers or percentage shares of particular taxa. In the forward stepwise regression we considered only those variables of R^2> 0.95 at P <0.05.

3. RESULTS

Concentrations of total nitrogen in bottom sediments of particular river sites varied from 0.10 to 1.19 mg g^{-1} dry wt. and those of total phosphorus – from 0.20 to 0.59 mg g^{-1} dry wt. The content of organic matter ranged from 0.29 to 29.70% (Table 3). In lake sediments the respective figures for nutrients were from 0.13 to 22.82 mg g^{-1} and from 0.06 to 3.10 mg g^{-1} and the content of organic matter varied between 0.34 and 65.84% (Table 4).

Chemical parameters in particular river sites showed similar mean values and ranges. Distinct differences were found only in site 9 where the content of organic matter was ten times higher and the content of total nitrogen was also highest. Among lakes one may distinguish a group in the lower river course (lakes Mokre, Krutyńskie, Gardyńskie, Malinówka and Jerzewko) with highest concentrations of total nitrogen, total phosphorus and organic matter. Sediments of lakes in the middle and upper course of the river had markedly lower chemical parameters. From among these lakes two showed slightly higher concentrations of nutrients and organic matter – Lake Białe situated in the middle course of the Krutynia River and the uppermost situated Lake Warpuńskie.

In total 39 species of molluscs (22 species of snails – Gastropoda and 17 species of bivalves – Bivalvia) were found in the whole system (Table 5). River sections were inhabited by 38 species and lakes – by 23 species. Apart from live molluscs, the presence of empty shells of *Valvata cristata* O.F. Müller, 1774 was noted in the river and of *V. macrostoma* Mőrch, 1864 and *Borysthenia naticina*

(Menke, 1845) in lakes. Twenty two species were common for river and lake sites. There were 16 species present exclusively in river sections and 1 species present only in lakes. Species richness of molluscs was bigger in river stretches – in various sites there were from 13 to 26 species; the number of species in lakes varied from 6 to 15. Most common species noted in river and lake sites were: *Bithynia tentaculata*, *Viviparus contectus*, *Unio tumidus*, *Anodonta anatina* and *Dreissena polymorpha* (Table 5).

Mean densities of molluscs in river sections ranged from less than 50 ind. m^{-2} to more than 300 ind. m^{-2} and in lakes – from less than 50 ind. m^{-2} to over 3000 ind. m^{-2} (Fig. 2). The lowest mean biomasses in river stretches and in lakes were similar (less than 20 g m^{-2}) and the highest exceeded 1300 g m^{-2} in the river and 1500 g m^{-2} in lakes (Fig. 2). The highest density, locally exceeding 11.5 thousand ind. m^{-2} was noted for *D. polymorpha* in Lake Lampasz and the largest biomass (up to 3 kg m^{-2}) – for *U. tumidus* in Lake Zyzdrój Mały.

Mollusc fauna in lakes distinctly differed from that in the river which was seen in both the TWINSPAN dendrograph and ordination maps MDS. The differences pertain to data expressed as percentage share (Fig. 3), as the numbers of particular species and as the values of the Jaccard's function (Fig. 4), according to which similarity is expressed as relative number of common species. The most important species differentiating river sites into larger groups with respect to the similarity of malacofauna was *Theodoxus fluviatilis*. Such species differentiating lakes were *Stagnicola corvus* and *Anisus vortex* (Fig. 3). The difference between river and lake sites was complete when we used in MDS the Jaccard's function as a measure of distance. After using Euclidean distances and the numbers of species, two river sites (3 and 6) seemed to be closer to lake sites than to other river sites. Results of both analyses had, however, a rather low explanatory power due to high values of stress (0.44 and 0.47) (Fig. 4).

According to PCA based on both the numbers (Fig. 5) and percentage shares (Fig. 6), a clear identity of three groups of river sites (8 and 9, 2 and 7 and the other) and three groups of lake sites (Lampasz – Lampackie – Giełądzkie, Krutyńskie – Gardyńskie – Malinówko – Jerzewko and the others) was clearly visible. All these analyses explained from 61 to 77% of variance. PCA showed that the concentrations of phosphorus, nitrogen and organic matter in sediments were interrelated in lakes but independent in the river. The numbers and percentage share of *Dreissena polymorpha* and Unionidae were negatively correlated with nutrients in river sediments. There were no such relationships in

Table 4. Concentrations of nitrogen and phosphorus (mg g dry wt.$^{-1}$) and percent of organic matter in bottom sediments of lakes (mean and range).

Lakes	N	P	Organic matter (% dry wt)
Warpuńskie	1.50 (0.66–2.25)	0.60 (0.14–1.08)	6.41 (2.58–11.26)
Zyndackie	0.59 (0.23–0.90)	0.33 (0.28–0.40)	1.29 (0.74–1.73)
Giełądzkie	0.28 (0.25–0.33)	0.48 (0.38–0.59)	0.53 (0.47–0.56)
Lampackie	0.35 (0.28–0.38)	0.33 (0.22–0.45)	0.95 (0.73–1.16)
Lampasz	0.81 (0.38–1.87)	0.29 (0.17–0.44)	2.75 (0.93–7.56)
Kujno	0.22 (0.13–0.41)	0.29 (0.27–0.31)	0.64 (0.44–1.18)
Dłużec	0.28 (0.23–0.35)	0.38 (0.20–0.49)	0.61 (0.54–0.69)
Białe	3.93 (0.25–12.45)	0.51 (0.18–1.28)	11.61 (0.55–31.41)
Gant	0.89 (0.46–1.45)	0.24 (0.12–0.50)	3.32 (2.07–4.57)
Zyzdrój Wielki	0.31 (0.23–0.36)	0.25 (0.24–0.27)	0.65 (0.46–0.88)
Zyzdrój Mały	0.69 (0.45–0.95)	0.17 (0.13–0.21)	2.00 (1.29–2.71)
Spychowskie	0.48 (0.42–0.55)	0.37 (0.31–0.43)	1.57 (1.43–1.72)
Zdrużno	0.43 (0.20–0.55)	0.21 (0.06–0.41)	0.86 (0.44–1.08)
Uplik	0.36 (0.20–0.44)	0.28 (0.08–0.40)	1.02 (0.34–1.95)
Mokre	5.61 (0.14–22.82)	1.02 (0.23–2.53)	22.67 (0.37–65.84)
Krutyńskie	6.55 (4.81–8.98)	0.96 (0.88–1.04)	22.94 (21.74–24.15)
Gardyńskie	19.72 (17.58–21.50)	1.81 (2.91–1.14)	43.00 (40.84–45–89)
Malinówka	8.87 (0.47–21.33)	1.52 (0.13–3.10)	25.12 (2.51–48.14)
Jerzewko	10.88 (1.09–20.58)	1.17 (0.66–1.75)	30.75 (3.40–45.29)

Table 5. Composition of molluscs sampled in the river-lake system of the Krutynia River, presented as number of individuals sampled (N), frequency of occurence (F %) and the dominance (D %).

		River			Lakes		
Higher taxa	Species	N	F (%)	D (%)	N	F (%)	D (%)
Gastropoda							
Acroloxidae	*Acroloxus lacustris* (Linnaeus, 1758)	4	5	0.1	9	26	0.3
Ancylidae	*Ancylus fluviatilis* (O.F. Müller, 1774)	13	10	0.5	0	0	0
Bithyniidae	*Bithynia tentaculata* (Linnaeus, 1758)	517	85	18.3	313	95	9.4
Hydrobiidae	*Potamopyrgus antipodarum* (J.E. Gray, 1843)	361	55	12.8	63	10	1.9
Lymnaeidae	*Bathyomphalus contortus* (Linnaeus, 1758)	2	10	0.1	0	0	0
	Galba truncatula (O.F. Müller, 1774)	2	5	0.1	0	0	0
	Lymnaea stagnalis (Linnaeus, 1758)	24	35	0.8	42	68	1.3
	Radix auricularia (Linnaeus, 1758)	25	25	0.9	53	74	1.6
	Radix balthica (Linnaeus, 1758)	29	45	1	0	0	0
	Stagnicola corvus (Gmelin, 1791)	8	5	0.3	2	10	< 0.1
	Stagnicola palustris (O.F. Müller, 1774)	1	5	< 0.1	0	0	0
Neritidae	*Theodoxus fluviatilis* (Linnaeus, 1758)	740	50	26.2	215	42	6.5
Physidae	*Aplexa hypnorum* (Linnaeus, 1758)	0	0	0	2	5	< 0.1
Planorbidae	*Anisus leuctostomus* (Millet, 1813)	3	15	0.1	0	0	0
	Anisus vortex (Linnaeus, 1758)	12	10	0.4	3	10	0.1
	Gyraulus albus (O.F. Müller, 1774)	1	5	< 0.1	2	5	< 0.1
	Planorbarius corneus (Linnaeus, 1758)	26	30	0.9	11	26	0.3
	Planorbis carinatus (O.F. Müller, 1774)	2	5	0.1	6	5	0.2
	Planorbis planorbis (Linnaeus, 1758)	1	5	< 0.1	1	5	< 0.1
Valvatidae	*Valvata piscinalis* (O.F. Müller, 1774)	41	35	1.4	1	5	< 0.1
Viviparidae	*Viviparus contectus* (Millet, 1813)	80	50	2.8	77	58	2.3
	Viviparus viviparus (Linnaeus, 1758)	6	5	0.2	42	21	1.3
Bivalvia							
Dreissenidae	*Dreissena polymorpha* (Pallas, 1771)	125	55	4.4	2102	63	63.9
Sphaeriidae	*Musculium lacustre* (O.F. Müller, 1774)	2	5	0.1	0	0	0
	Pisidium amnicum (O.F. Müller, 1774)	13	20	0.5	0	0	0
	Pisidium casertanum (Poli, 1791)	12	15	0.4	0	0	0
	Pisidium crassum Stelfox, 1918	4	5	0.1	0	0	0
	Pisidium henslowanum (Sheppard, 1823)	10	25	0.3	0	0	0
	Pisidium nitidum Jenyns, 1832	8	10	0.3	4	16	0.1
	Pisidium subtruncatum Malm, 1855	7	20	0.2	0	0	0
	Pisidium supinum A. Schmidt, 1851	4	10	0.1	0	0	0
	Sphaerium corneum (Linnaeus, 1758)	202	65	7.1	14	26	0.4
	Sphaerium rivicola (Lamarck, 1818)	1	5	< 0.1	0	0	0
Unionidae	*Anodonta anatina* (Linnaeus, 1758)	104	55	3.7	51	84	1.5
	Anodonta cygnea (Linnaeus, 1758)	22	20	0.8	25	58	0.7
	Pseudanodonta complanata (Rossmässler, 1835)	4	5	0.1	0	0	0
	Unio crassus Philipsson, 1788	6	15	0.2	0	0	0
	Unio pictorum (Linnaeus, 1758)	53	50	1.9	29	32	0.9
	Unio tumidus Philipsson, 1788	361	50	12.8	243	74	7.3

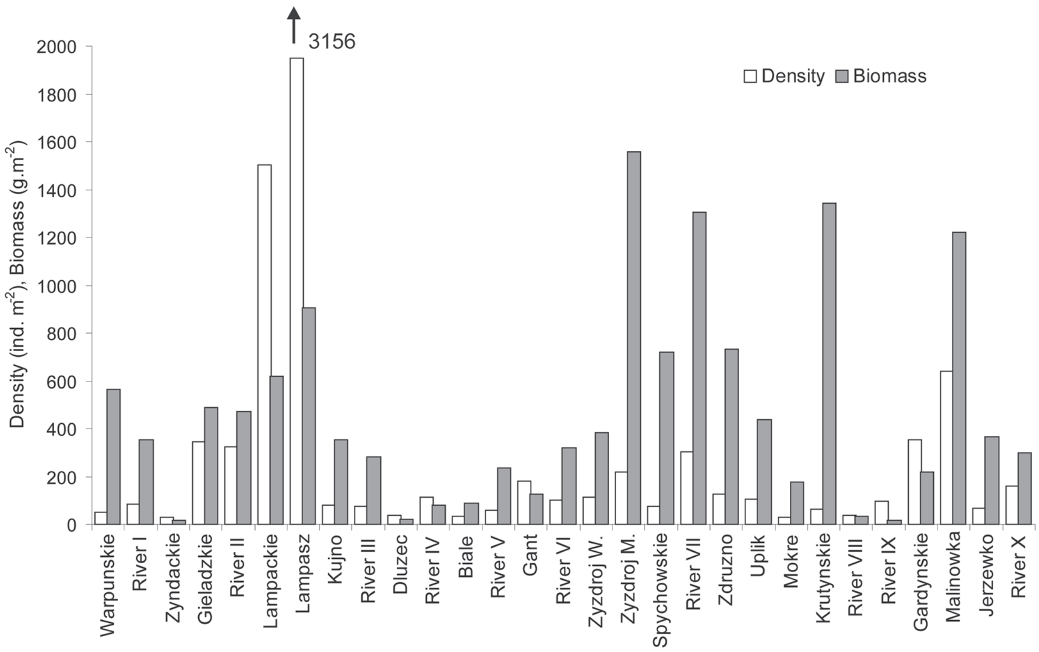

Fig. 2. Mean density and mean biomass of molluscs in lakes and in river sections (I–X) of the Krutynia River system.

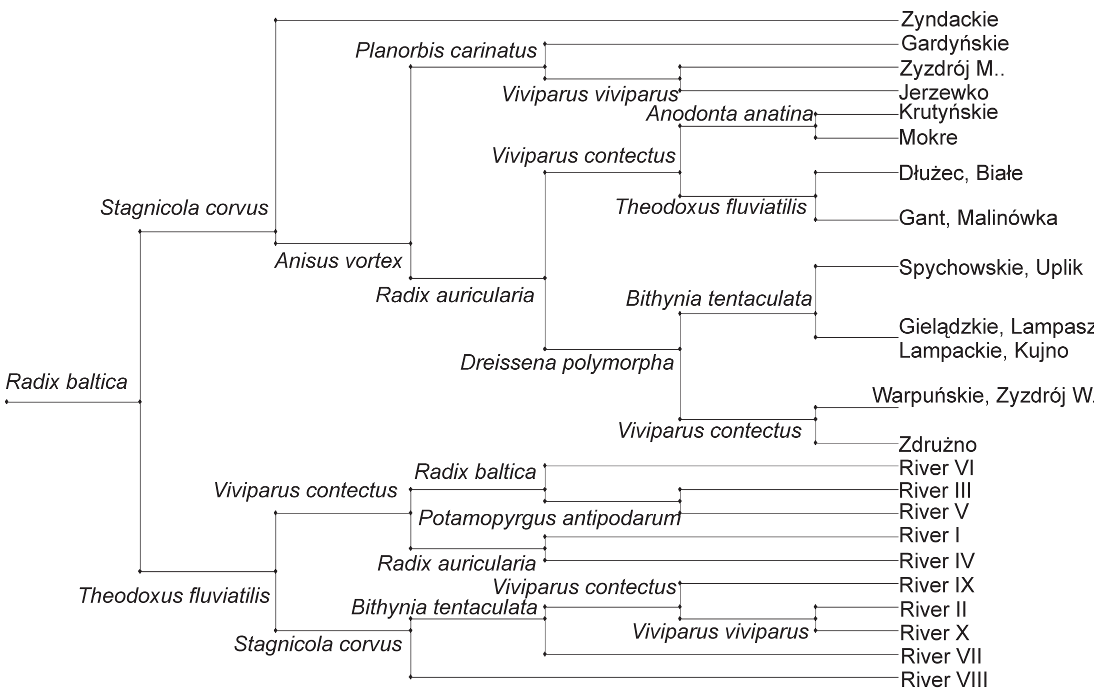

Fig. 3. Twinspan analysis of the taxonomic composition of molluscs in particular sites based on percentage shares.

lakes with the exception of a positive relationship between nutrients in sediments and the numbers and percentage share of *Viviparus.*

Multiple regression revealed a strong effect of some measured abiotic parameters on the domination structure of malacofauna (Table 6). Presented models were highly significant (R^2 close to 1, low *P* values), indicated positive or negative relationships and had a high explanatory power. There was a strong positive relationship between phosphorus and nitrogen concentrations in sediments and the percentage share of *Viviparus*, *Anodonta anatina* and *Radix balthica* have a strong negative relationship with the percentage share of *Planorbarius corneus*, *Pisidium subtruncatum* and *Anodonta cygnea*. One may notice distinctly different relationship between the percentage share of species from the family Sphaeriidae and organic matter content in sediments. The relationship was positive for *P. nitidum*, *P. amnicum* and *Spherium rivicola* and negative for *P. subtruncatum*, *P. henslowanum* and *P. supinum*. A strong positive relationship between organic matter and percentage share was also found for *Viviparus* and a negative – for *Planorbis carinatus* and *Planorbarius corneus*. There was a strong positive relationship between the distance of a river site from a lake and percentage share of snails of the genus *Anisus* and a negative relationship with the percentage share of bivalves *Anodonta cygnea*, *S. corneum* and *P. amnicum*.

4. DISCUSSION

The range of nutrients and organic matter concentrations in sediments of studied lakes was much broader than in river sites and their concentrations in lakes situated downstream the river was much higher than in the river. These results are quite opposite to data presented for the Krutynia River system in the 1980s by Hillbricht-Ilkowska and Kostrzewska-Szlakowska (1996) where the concentrations in the river were similar or slightly higher than in lakes. Temporarily and spatially independent dynamics of nitrogen and phosphorus in lotic habitats of the Krutynia River was similar to that noted in morphologically comparable Liwiec River by Królak and Korycińska (2008).

Species composition and the numbers of molluscs in the river-lake system of the Krutynia River seems typical for a medium size lowland rivers (Zettler 1996, Królak and Korycińska 2008, Koperski 2011). Studies carried out in the years 2008–2011 showed a great species richness of molluscs (39 species). Compared with data of Hilbert (1913) and Berger (1960) from the beginning and the middle of the 20th century, respectively, the composition of malacofauna in the Krutynia River remained generally unchanged. In Polish rivers of similar size, slightly higher numbers of species were recorded; for example 50 in the Grabia River (Piechocki 1969) or 43 in the Pasłęka River (Piechocki 1972). In the Liwiec River, Korycińska (2002) noted 21 taxa of molluscs but without detailed identification of bivalves of the family Sphaeriidae. Species richness in these rivers of similar length may result from the fact that they are relatively less modified by human activity.

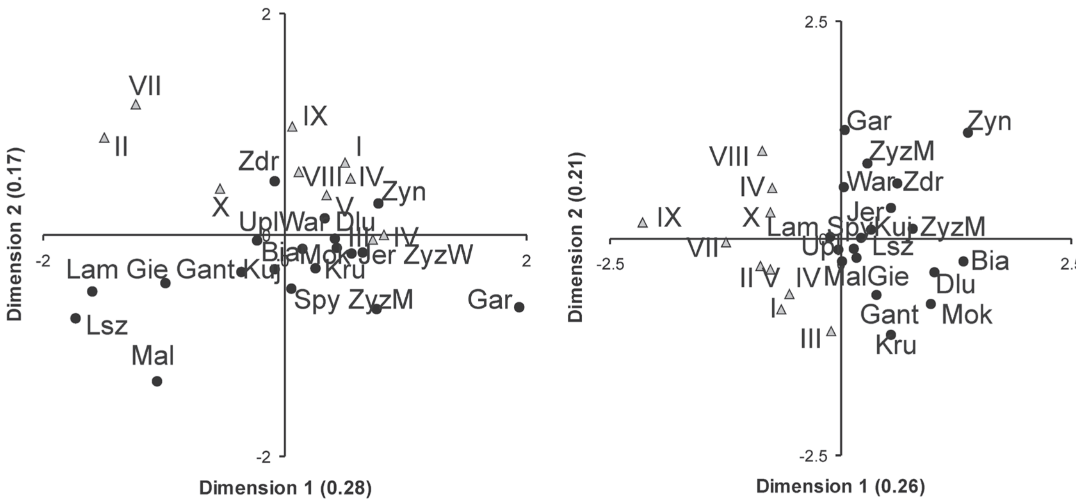

Fig. 4. Similarity map of the taxonomic composition of molluscs in particular lake sites (black circles) and sites at River Krutynia (empty triangles) obtained with the MDS method based on: a – the numerical composition and the euclidean distance, b – Jaccard's function.

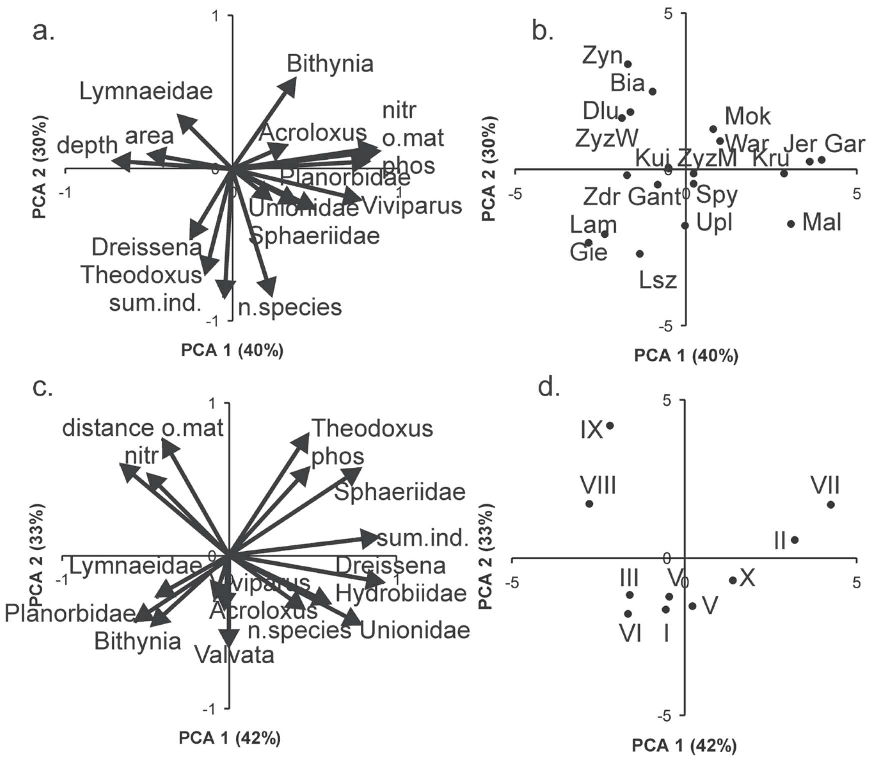

Fig. 5. Results of the PCA based on numerical values, presented as correlation of main abiotic parameters, number of particular mollusc species and sampling sites variability in lakes (a, b) and in riverine section (c, d) of the Krutynia River system.

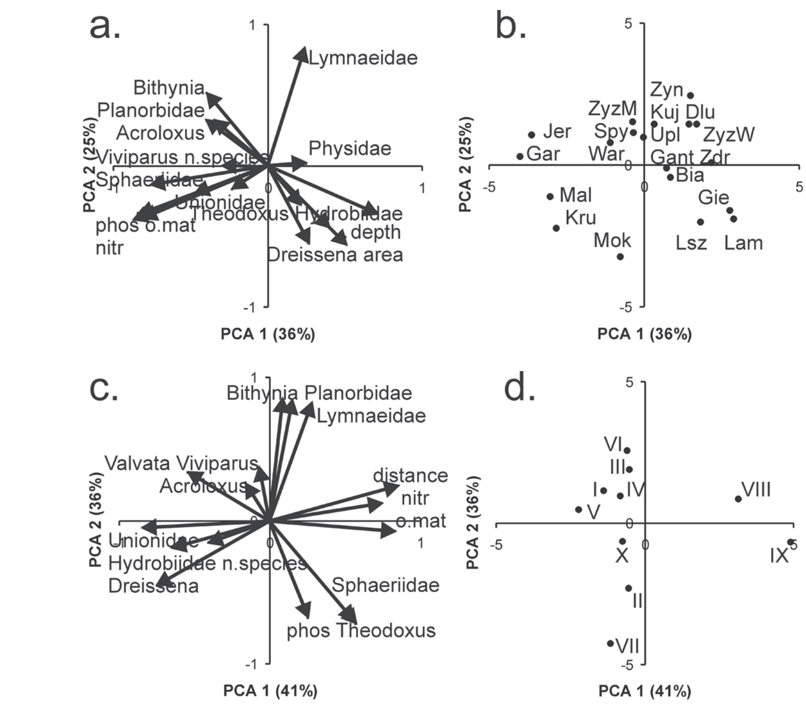

Fig. 6. Results of the PCA, based on percentage shares presented as correlation of main abiotic parameters, percentages of particular mollusc species and sampling sites variability in lakes (a, b) and in riverine section (c, d) of the Krutynia River system.

Table 6. Results of four models of multiple regression analysis (stepwise progressive procedure) presented as values of BETA and p for percentages of particular mollusc species and values of R^2 and p for each model. Only 26 species with at least one significant relationship with any of analysed parameter are included – they are ordered on the basis of the number of significant relationships. ns – non-significant. *P* values: * 0.01–0.05, ** 0.001–0.01, *** <0.001

	Nitrogen		Phosphorus		Organic matter		Distance from lake	
species	BETA	*P*	BETA	*P*	BETA	*P*	BETA	*P*
Aplexa hypnorum	–	ns	–0.258	**	0.464	*	–0.305	**
Pisidium subtruncatum	–0.545	**	–0.57	***	–2.014	*	–	ns
Planorbarius corneus	–0.828	***	–0.852	***	–0.629	*	–	ns
Viviparus contectus	0.751	***	0.698	***	0.907	*	–	ns
Viviparus viviparus	0.849	***	0.725	***	1.021	**	–	ns
Anisus leucostomus	–	ns	–	ns	–1.776	**	0.759	*
Anodonta anatina	0.371	*	0.283	*	–	ns	–	ns
Anodonta cygnaea	–0.505	*	–0.388	**	–	ns	–	ns
Gyraulus albus	0.455	**	–	ns	0.527	**	–	ns
Lymnaea stagnalis	–	ns	–	ns	0.579	**	0.032	*
Pisidium amnicum	–	ns	–	ns	2.241	*	–0.101	*
Radix baltica	0.42	*	0.351	*	–	ns	–	ns
Sphaerium corneum	–	ns	–	ns	1.67	**	–0.147	*
Unio tumidus	–	ns	–	ns	0.345	*	0.193	**
Anisus vortex	–	ns	–	ns	–	ns	0.64	*
Bathyomphalus contortus	–	ns	–0.246	*	–	ns	–	ns
Bithynia tentaculata	–	ns	–	ns	0.578	*	–	ns
Dreissena polymorpha	–	ns	–	ns	1.24	**	–	ns
Pisidium henslowanum	–	ns	–	ns	–1.748	*	–	ns
Pisidium nitidum	–	ns	–	ns	1.732	*	–	ns
Pisidium supinum	–	ns	–	ns	–0.87	**	–	ns
Planorbis carinatus	–	ns	–	ns	–0.228	*	–	ns
Planorbis planorbis	–	ns	–	ns	0.233	*	–	ns
Radix auricularia	–	ns	–	ns	0.416	*	–	ns
Sphaerium rivicola	–	ns	–	ns	2.602	**	–	ns
Unio pictorum	–0.293	*	–	ns	–	ns	–	ns
model R^2	0.927		0.932		0.998		0.999	
model *P*	***		***		**		**	

There are a lot of strong arguments for treating the river system as a mosaic of landscapes (*e.g.* Wiens 2002); also Hillbricht-Ilkowska and Węgleńska (2003) present the river-lakes system of Krutynia as a mosaic pattern of landscape patches. It should be emphasized that the influence of nutrients' exchange between lake outflows and inflows on the secondary production and food web functioning is still not well understood (Woodward and Hildrew 2002). Benthic fauna of this type of ecological system should also be treated as complex of habitat-specified assemblages of populations with different ecological preferences (Robinson *et al.* 2002). Malacofauna of the river and of lakes forming the system of the Krutynia River is diverse – much richer in river stretches than in lakes. As many as 16 species (38% of all species) were found exclusively in river sites. Particularly interesting seems a clear preference for lotic habitats in the representatives of the genus *Pisidium* which were rarely determined to species. From among 6 species of *Pisidium* found only in river sites, four are described as typically eurytopic species and one as specifically lake species (Piechocki and Dyduch-Falniowska 1993). A strong negative relationship between the occurrence of species from the family Sphaeriidae (*P. amnicum* and *Spherium rivicola*) and organic matter content is a result of their preference for clean or slightly polluted waters (oligo- and ß-mezosaprobic zone). A strong positive relationship with organic matter demonstrated *P. subtruncatum* and *P. henslowanum* which prefer more polluted waters and sediments.

The literature provides evidence for positive relationship between the number of *Viviparus* and nutrient content in bottom sediments of lakes and rivers which was also shown for the Krutynia River system with PCA and multiple regression (Jakubik 2009, 2012). Food choice is evidently affected by its availability and by food preferences (Kołodziejczyk and Martynuska 1980). *Viviparus* is an obligatory detritus feeder. Experiments made by Kołodziejczyk (1984) demonstrated that snails when offered detritus and live plant tissues chose the former as food because partly decomposed tissues are easier to bite into and to digest. When eating large amounts of sediments or decomposing tissues of higher plants, snail acquire associated algae as it is the case in grazing periphyton. Algae are wholesome and calorific food for snails. Small algal contribution to viviparids' diet is a result of their facultative filter-feeding (Berg and Ockelmann 1959, Newerkla *et al.* 1979, Brendelberger 1995, Höckelmann and Pusch 2000, Jurkiewicz-Karnkowska and Żbikowski 2004). If the habitat is rich in plankton, filtration may be one of the main ways of feeding in viviparids.

In contrast with detritus feeding snails of the genus *Viviparus*, bivalves of the family Unionidae and *Dreissena polymorpha* are typical filter-feeders. Chemical composition of bottom sediments will be of less importance for these bivalves. Negative relationship between the number of bivalves and nutrient concentrations found in the Krutynia River is confirmed in the literature but rather for more eutrophic habitats (Arter 1989, Lewandowski 1991, Stańczykowska and Lewandowski 1993).

Strong positive relationship between the distance of a river site from a lake and the content of nitrogen and organic matter in sediments shown by PCA is probably indirect. It should be interpreted as an effect of the two sites (8 and 9) most distant from lakes situated downstream the Krutynia and thus containing sediments richer in nutrients. Strong relationship between the distance of a river site from a lake and the number and percentage share of both species of the genus *Anisus* might reflect their known from the literature preference for sites abundant in macrophytes (as sites 3 and 6) (Piechocki 1979, Terrier *et al*. 2006).

It seems relatively easy to find the factors responsible for the differences in malacofauna between river sites 8 and 9 and all other and between lakes Giełądzkie, Lampackie, Lampasz and other lake sites. In the first case, the sites are situated at the end of the river-lake system, rich in nutrients and remote from lake outlets. In the second case, the three lakes are larger and of relatively lower nutrient content. Abiotic factors responsible for distinguishing other groups of sites as shown by PCA and MDS analyses are less unambiguous.

AKNOWLEDGMENTS: Authors are grateful to all reviewers for valuable comments to previous version of the article and to Professor Ewa Jurkiewicz-Karnkowska for identification of difficult species of family Sphaeriidae.

5. REFERENCES

Arter H.E. 1989 – Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland) – Aquat. Sci. 51: 87–99.

Atkinson C.L., Vaughn C.C., Forshay K.J., Cooper J.T. 2013 – Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics – Ecology, 94: 1359–1369.

Berg K., Ockelmann K.W. 1959 – The respiration of freshwater snails – J. Experiment. Biol. 36: 690–708.

Berger L. 1960 – Badania nad mięczakami (Mollusca) Pojezierza Mazurskiego [Studies on Mollusca in Masurian Lakeland] – Bad. Fizjogr. Pol. Zach. 6: 7–49 (in Polish).

Berger L. 1962 – Uwagi o rozmieszczeniu małżów Sphaeriidae w Krutyni na Pojezierzu Mazurskim [Notes on the distribution of bivalves Sphaeriidae in the Krutynia River in Masurian Lakeland] – Fragm. Faun. 10: 1–9 (in Polish).

Brendelberger H. 1995 – Dietary preference of three freshwater gastropods for eight natural foods of different energetic content – Malacologia, 36: 147–153.

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 – Fund. Appl. Limnol. 171: 119–130.

Hilbert R. 1913 – Die Molluskenfauna des Kruttinflusses, Kr. Sensburg – Ostpr. Arch. Naturges. 12: 91–96.

Hillbricht-Ilkowska, A., Kostrzewska-Szlakowska, I., Wiśniewski, R.J. 1996 – Zróżnicowanie troficzne jezior rzeki Krutyni (Pojezierze Mazurskie) – stan obecny, zmienność wieloletnia, zależności troficzne [Trophic differentiation of lakes along the Krutynia River (Masurian Lakeland) – present situation, long-term variability and trophic relationships] – Zeszyty Naukowe Komitetu „Człowiek i Środowisko", 13: 125–153 (in Polish).

Hillbricht-Ilkowska A., Kostrzewska-Szlakowska I. 1996 – Zmienność stężenia wybranych związków chemicznych oraz retencja fosforu i azotu w układzie rzeczno-jeziornym rzeki Krutyni (Pojezierze Mazurskie) [Variability of concentrations of selected chemical elements and the retention of phosphorus and nitrogen in the river-lake system of the Krutynia River (Mazurian Lakeland)] – Zeszyty Naukowe Komitetu „Człowiek i Środowisko", 13: 187–210 (in Polish).

Hillbricht-Ilkowska A., Węgleńska T. 2003 – River-lake system as mosaic pattern of landscape patches and their transition zones (ecotones) – Pol. J. Ecol. 51: 163–174.

Höckelmann C., Pusch M. 2000 – The respiration and filter-feeding rates of the snail *Viviparus viviparus* (Gastropoda) under simulated stream conditions – Arch. Hydrobiol. 4: 553–568.

Jakubik B. 2009 – Food and feeding of *Viviparus viviparus* (L.) (Gastropoda) in dam reservoir and river habitats – Pol. J. Ecol. 57: 321–330.

Jakubik B. 2012 – Life strategies of snails from the family Viviparidae in various aquatic habitats – Folia Malacol. 20: 145–179.

Jakubik B., Lewandowski K. 2011 – Molluscs of the Krutynia river (Masurian Lakeland) – Fol. Malac. 19: 19–29.

Jurkiewicz-Karnkowska E., Żbikowski J. 2004 – Long-term changes and spatial variability of mollusc communities in selected habitats within dam reservoir (Włocławek Reservoir, Vistula River, Central Poland) – Pol. J. Ecol. 52: 491–503.

Kołodziejczyk A., Martynuska A. 1980 – *Lymnaea stagnalis* (L.) - feeding habits and production of faeces – Ekol. Pol. 28: 201–217.

Kołodziejczyk A. 1984 – Occurrence of Gastropoda in the lake littoral and their role in the production and transformation of detritus II. Ecological activity of snails – Ekol. Pol. 32: 469–492.

Kołodziejczyk A., Lewandowski K., Stańczykowska A. 2009 – Long-term changes of mollusc assemblages in bottom sediments of small semi-isolated lakes of different trophic state – Pol. J. Ecol. 57: 331–339.

Koperski, P. 2011 – Diversity of macrobenthos in lowland streams: ecological determinants and taxonomic specificity – J. Limnol. 69: 88–101.

Korycińska M. 2002 – Molluscs of the Liwiec River (South Podlasie and Middle Mazovia Lowlands) – Fol. Malacol. 10: 17–23.

Królak E., Korycińska M. 2008 – Taxonomic composition of macroinvertebrates in the Liwiec River and its tributaries (Central and Eastern Poland) on the basis of chosen physical and chemical parameters of water and season – Pol. J. Environ. Stud. 17: 39–50.

Lewandowski K. 1991 – Long-term changes in the fauna Unionidae bivalves in the Mikołajskie Lake – Ekol. Pol. 39: 265–272.

Lewandowski K. 1996 – Występowanie *Dreissena polymorpha* (Pall.) oraz małży z rodziny Unionidae w systemie rzeczno-jeziornym Krutyni (Pojezierze Mazurskie) [The occurrence of *Dreissena polymorpha* (Pall.) and bivalves of the family Unionidae in the Krutynia river-lake system (Mazurian Lakeland)] – Zeszyty Naukowe Komitetu „Człowiek i Środowisko", 13: 173–185 (in Polish).

Marczenko Z. 1979 – Spektrofotometryczne oznaczanie pierwiastków [Spectrophotometric determination of elements]. PWN, Warszawa. 757 pp. (in Polish).

Minshall G.M., Petersen R.C., Cummins K.W., Bott T.L., Sedell J.R., Cushing C.E., Vannote R.L. 1983 – Interbiome comparison of stream ecosystem dynamics – Ecol. Monogr. 53: 1–25.

Mouthon J., Daufresne M. 2010 – Long-term changes in mollusc communities of the Ognon river (France) over a 30-year period – Fund. Appl. Limnol. 178: 67–79.

Newerkla P.D., Dolezal E., Eder R. 1979 – Populationsdichte und respiration von *Viviparus viviparus* (L.) im litoral des Jeserzer oder Saisser Sees, Kärnten – Carinthia II, 169: 352–355.

Perez-Quintero J.C. 2012 – Environmental determinants of freshwater mollusc biodiversity and identification of priority areas for conservation in Mediterranean water courses – Biodiv. Conserv. 21: 3001–3016.

Piechocki A. 1969 – Mięczaki (*Mollusca*) rzeki Grabi i jej terenu zalewowego [Molluscs of

the Grabia River and its floodplain] – Fragm. Faun. 15: 111–197 (in Polish).
Piechocki A. 1972 – Materiały do poznania mięczaków (*Mollusca*) rzeki Pasłęki [Materials to recognising molluscs of the Pasłęka River] – Fragm. Faun. 18: 121–139 (in Polish).
Piechocki A.1979 – Mięczaki (*Mollusca*). Ślimaki (*Gastropoda*). Fauna Słodkowodna Polski, 7, [Molluscs (*Mollusca*). Snails (*Gastropoda*). Freshwater fauna of Poland, 7] – PWN, Warszawa-Poznań, 187 pp. (in Polish).
Piechocki A., Dyduch-Falniowska A. 1993 – Mięczaki (*Mollusca*), Małże (*Bivalvia*). Fauna Słodkowodna Polski. 7A. [Molluscs (*Mollusca*), Bivalves (*Bivalvia*). Freshwater fauna of Poland 7A] – PWN, Warszawa-Poznań, 187 pp. (in Polish).
Radwan S., Kornijów R., Kowalczyk C. 1992 – Organic matter in the River Krutynia (Masurian Lakeland, Poland) – Hydrobiologia, 243: 449–456.
Rice S.P., Greenwood M.T., Joyce C.B. 2001 – Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems – Can. J. Fish. Aquat. Sci. 58: 824–840.
Robinson C.T., Tockner K., Ward J.V. 2002 – The fauna of dynamic riverine landscapes – Freshwat. Biol. 47: 661–677.
Rzepecki M. 2010 – The dynamics of phosphorus in lacustrine sediments: contents and fractions in relation to lake trophic state and chemical composition of bottom deposits – Pol. J. Ecol. 58: 409–427.
Rzepecki M. 2012 – The dynamics of phosphorus in lacustrine sediments: the process of uptake/release of dissolved phosphorus by sediments in different habitats and lakes – Pol. J. Ecol. 60: 717–740.
Stańczykowska A., Lewandowski K. 1993 – Thirty years of studies of *Dreissena polymorpha* ecology in Mazurian Lakes of Northeastern Poland (In: Zebra mussels biology, impacts, and control, Eds: T.F. Nalepa, D.W. Schloesser) – Lewis Publischers, Boca Raton, Ann Arbor, London, Tokyo, 3–37.
Statzner B., Higler B. 1985 – Questions and comments on the River Continuum Concept – Can. J. Fish. Aquat. Sci. 42: 1038–1044.
Szczepański A. 1958 – Die schwebende Fauna des Krutynia-Flusses – Pol. Arch. Hydrobiol. 4: 153–162.
Terrier A., Castella E., Falkner G., Killeen I.J. 2006 – Species account for *Anisus vorticulus* (Troschel, 1834) (Gastropoda: Planorbidae), a species listed in annexes II and IV of the habitats directive – J. Conchol. 39: 193–205.
Vannote R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing C.E. 1980 – The River Continuum Concept – Can. J. Fish. Aquat. Sci. 37: 130–137.
Wiens J.A. 2002 – Riverine landscapes: taking landscape ecology into the water – Freshwat. Biol. 47: 501–515.
Woodward G., Hildrew A.G. 2002 – Food web structure in riverine landscapes – Freshwat. Biol. 47: 777–798.
Zettler M. 1996 – Die aquatische malakofauna (Gastropoda et Bivalvia) im Einzugsgebiet lines norddeutschen Tieflandflusses, der Warnow – Limnologica, 26: 327–337.

Received after revision February 2014