FOLIA MALACOLOGICA
Folia Malacol. 27(3): 179–192
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, September 2019
https://doi.org/10.12657/folmal.027.016

COMPARATIVE DIVERSITY OF MOLLUSCAN FAUNA OF DIFFERENT AQUATIC HABITAT TYPES: THE LIWIEC RIVER CATCHMENT (EAST POLAND)

EWA JURKIEWICZ-KARNKOWSKA

Siedlce University of Natural Sciences and Humanities, B. Prusa 12, 08-110 Siedlce, Poland
(e-mail: ewa.jurkiewicz-karnkowska@uph.edu.pl); https://orcid.org/0000-0001-6811-4379

ABSTRACT: Investigations of aquatic mollusc assemblages were conducted within a semi-natural catchment of a medium-sized lowland river Liwiec in five habitat types: the main Liwiec River channel, its secondary channels and six tributaries, as well as in natural ponds and man-made ditches within the river floodplains. To assess the contribution of each habitat type to the diversity, I used the species richness, diversity, rarity (species rarity index, SRI) and abundance, as well as the composition and structure of mollusc assemblages and compared them among the habitat types. The spatial pattern of mollusc diversity was analysed based on hierarchical partitioning. Over five years, 54 mollusc species were found, including three listed on the IUCN Red List or in Annexes II and IV of the EU Habitats Directive (*Unio crassus* Philipsson, *Sphaerium rivicola* (Lamarck) and *Anisus vorticulus* (Troschel)). The mollusc metrics in most cases did not differ significantly among the habitat types. All the habitats contributed relatively evenly to the mollusc diversity. The diversity at the site level was generated mainly by alpha component, whereas at the landscape scale habitat heterogeneity (beta component, i.e. β2) was very important. In order to maintain mollusc diversity, conservation efforts ought to focus specifically on the most heterogeneous fragments of the Liwiec River catchment.

KEY WORDS: aquatic molluscs, threatened species, catchment, drainage ditches, floodplain, river

INTRODUCTION

The river catchment includes various types of lotic and lentic aquatic habitats, which form a complex system. However, macroinvertebrates of different habitat types have not been equally surveyed. Studies on riverine macroinvertebrate diversity focused primarily on main river channels, nonetheless, some of them did include floodplains and diverse aquatic habitats occurring there (e.g. GODREAU et al. 1999, TOCKNER et al. 1999, WARD et al. 1999). Studies conducted in streams were relatively numerous (e.g. LAKE 2000, HEINO et al. 2005, CLARKE et al. 2008 and references therein). Although small water bodies, including natural and man-made ponds and ditches, are very numerous their macroinvertebrate fauna remains under-investigated (e.g. PAINTER 1999, WILLIAMS et al. 2004, BIGGS et al. 2005, GALLARDO et al. 2008, 2009, 2014, VERDONSCHOT et al. 2011).

Studies comparing macroinvertebrate assemblages in different water body types are relatively few (e.g. VERDONSCHOT 1990, WILLIAMS et al. 2004, BIGGS et al. 2007, 2017, DAVIES et al. 2008, VERDONSCHOT et al. 2011), however they still reveal that small water bodies contribute significantly to aquatic biodiversity across landscapes. Ditches (being man-made water bodies) appear important for regional stream biodiversity (SIMON & TRAVIS 2011) and display a considerable contribution to total aquatic biodiversity of the floodplain (ARMITAGE et al. 2003).

Aquatic molluscs are an important component of macroinvertebrate fauna in many riverine and riparian habitats (e.g. JURKIEWICZ-KARNKOWSKA 2015 and references therein). Species-rich malacocoenoses are found in different aquatic habitat types within river-floodplain systems (e.g. PIECHOCKI 1969, OBRDLIK et

Ministry of Science and Higher Education
Republic of Poland
Folia Malacologica is funded by the Ministry of Science and Higher Education, Republic of Poland, under agreement no 534/P-DUN/2018 of April 4th, 2018 allocated to the activities for disseminating science:
Task 1: Preparation of English versions of publications (sum funded by DUN 12,000 PLN) and
Task 2: Digitalisation of publications and scientific monographs to enable their open access in the Internet (sum funded by DUN 11,070 PLN).

al. 1995, Weigand & Stadler 2000, Jurkiewicz-Karnkowska 2008, 2009, 2015, Pérez-Quintero 2011, Beran 2013, Lewin 2014, Bódis et al. 2016). Molluscs were considered to be good descriptors of habitat diversity (e.g. Richardot-Coulet et al. 1987, Foeckler et al. 1991, 1994, Weigand & Stadler 2000, Pérez-Quintero 2011). Their small mobility between habitats and limiting factors in different water bodies result in a particular species composition which is well adapted to specific conditions.

Very few investigations were conducted on molluscs as indicators of biodiversity in European temperate river-floodplain systems, chiefly those including several different habitat types. The literature concerning the diversity in medium-sized and small temperate lowland rivers, which could be comparable with the Liwiec River and its tributaries, is severely limited (e.g. Piechocki 1981, Pliūraitė & Kesminas 2004, Beran 2013). Some data concerning molluscs from floodplain waters representing different degree of hydrological connectivity and successional stage exist (e.g. Richardot-Coulet et al. 1987, Foeckler et al. 1991, Obrdlik et al. 1995, Jurkiewicz-Karnkowska 2009, Jurkiewicz-Karnkowska & Karnkowski 2013). Mollusc diversity in ditches was rarely studied (e.g. Painter 1999, Watson & Ormerod 2004, Verdonschot et al. 2011).

Large scale investigations of aquatic mollusc diversity are very few. One such example of a regional approach may be the studies conducted within the Danube River basin (Bódis et al. 2016), which included the main rivers (Danube and Tisza), their side channels and tributaries; another case worth mentioning regards the investigations within the Thaya River and its tributaries in the Czech Republic (Beran 2013). Another large scale European study (Perez-Quintero 2011) concerned lotic habitats within the Mediterranean Guadiana River basin (SW Iberian Peninsula). Regional studies including not only lotic habitats, but also small natural lentic water bodies, are extremely few (e.g. Piechocki 1969, Lewin 2014).

Molluscs of the main Liwiec River channel were studied by Korycińska (2002) and Jurkiewicz-Karnkowska (2016). Comparative study of aquatic mollusc diversity within a short (about 10 km long) fragment of the Liwiec River and its floodplain included a stretch of the main channel, a secondary channel and a few remnants of the former river channel (Jurkiewicz-Karnkowska 2015). So far, ditches have not been included in the investigations within the Liwiec River floodplain.

The biodiversity characteristics of different water body types within catchments and their contribution to total diversity are important both for sustainable catchment management and for nature conservation. Such information is scanty, particularly for semi-natural catchments. The understanding of the biodiversity's spatial pattern, including the contribution of alpha and beta diversity to the total diversity and determining which spatial scales most influence the diversity to the greatest extent, are crucial to conservation planning.

The main objectives of the present study were to assess the contribution of different aquatic habitat types to mollusc diversity at the landscape scale as exemplified by a semi-natural medium-sized lowland river catchment, as well as to compare conservation values of mollusc assemblages harboured by individual habitat types. The comparison of species richness, diversity, rarity and abundance, as well as composition and structure of mollusc assemblages among five habitat types: the main Liwiec River channel (ML), its secondary channels (SL) and six tributaries (T), natural ponds (P) and man-made ditches (D) within river floodplains was performed. Special attention was paid to the biodiversity and conservation value of ditches, representing the only man-made habitat type within the study area. Diversity partitioning within the individual habitat types and the entire study area was applied to better understand the spatial pattern of mollusc diversity and the contribution of alpha and beta diversity to the total diversity at different spatial scales.

MATERIAL AND METHODS

STUDY AREA

The study area comprised of the Liwiec River and its valley, as well as six of its tributaries (Stara Rzeka, Helenka, Muchawka, Kostrzyń, Miedzanka and Osownica) and their valleys. Liwiec is the biggest left-bank tributary of the Bug River. It is a medium-sized river (ca. 142 km long), with a catchment area of 2,780 km^2. The mean long-term discharge (SSQ) recorded at a water gauge station in the lower course (17 km of the river course counting from the mouth) was 10.2 m^3 s^{-1} (Czarnecka 2005). The source area of the river is located at 160 m a.s.l. (52°36'24"N, 21°33'34"E) and the mouth at 85 m a.s.l. (52°05'39"N, 22°37'39"E), the mean river gradient is 0.52‰.

The valley is 120 km^2 in area, its width not exceeding 2 km, except at two short sections where it widens to over 5 km (within the upper and lower river sections). It has retained its natural character. The land is extensively used, mainly as meadows and pastures, with forests occupying a relatively small area.

The Liwiec River valley is covered by the Natura 2000 network (2 Special Areas of Conservation (SACs): PLB140002 and PLH140032) and partially by the Siedlce-Węgrów Landscape Protection Area. The river channel has been regulated in its upper section, the middle and lower sections have preserved a relatively natural character, however small hydrotechnical constructions (weirs, culverts) are present nearly all along the river except at the mouth section, which has remained exceptionally natural. The river is fed by 10 tributaries, among which Muchawka, Kostrzyń and Osownica are the largest. Substantial fragments of the tributaries have been regulated, but their valleys have retained a relatively natural character. A considerable part of the Kostrzyń River valley is covered by the Natura 2000 network (three SACs:PLB140009 and PLH140036 and a fragment of PLH140032), two nature reserves and partially by the Mińsk Landscape Protection Area. The marshy valley of the Muchawka River within the boundaries of the city of Siedlce is a protected area ("Dolina Muchawki").

The study included 139 sites (Fig. 1): 41 located in the main channel of the Liwiec River (ML1–L41), 11 in its secondary channels (SL1–SL11), 32 within its tributaries (T): Stara Rzeka (S1–S6), Helenka (H1, H2), Muchawka (Mu1–Mu7), Kostrzyń (K1–K5), Miedzanka (M1–M6) and Osownica (O1–O6), 34 in floodplain natural ponds, i.e. lentic water bodies of fluvial origin (P1–P34) and 21 in ditches (i.e. man-made channels) located within river floodplains (D1–D21). At each sampling site within the rivers and other water bodies the width was measured directly in the field with metre tape, the depth was assessed with calibrated pole. Current velocity was measured using a float and stopwatch. The width at the ML sites ranged from <5 to >15 m, in SL and T it ranged from 1 to 10 m, in P from 1 to >15 m and

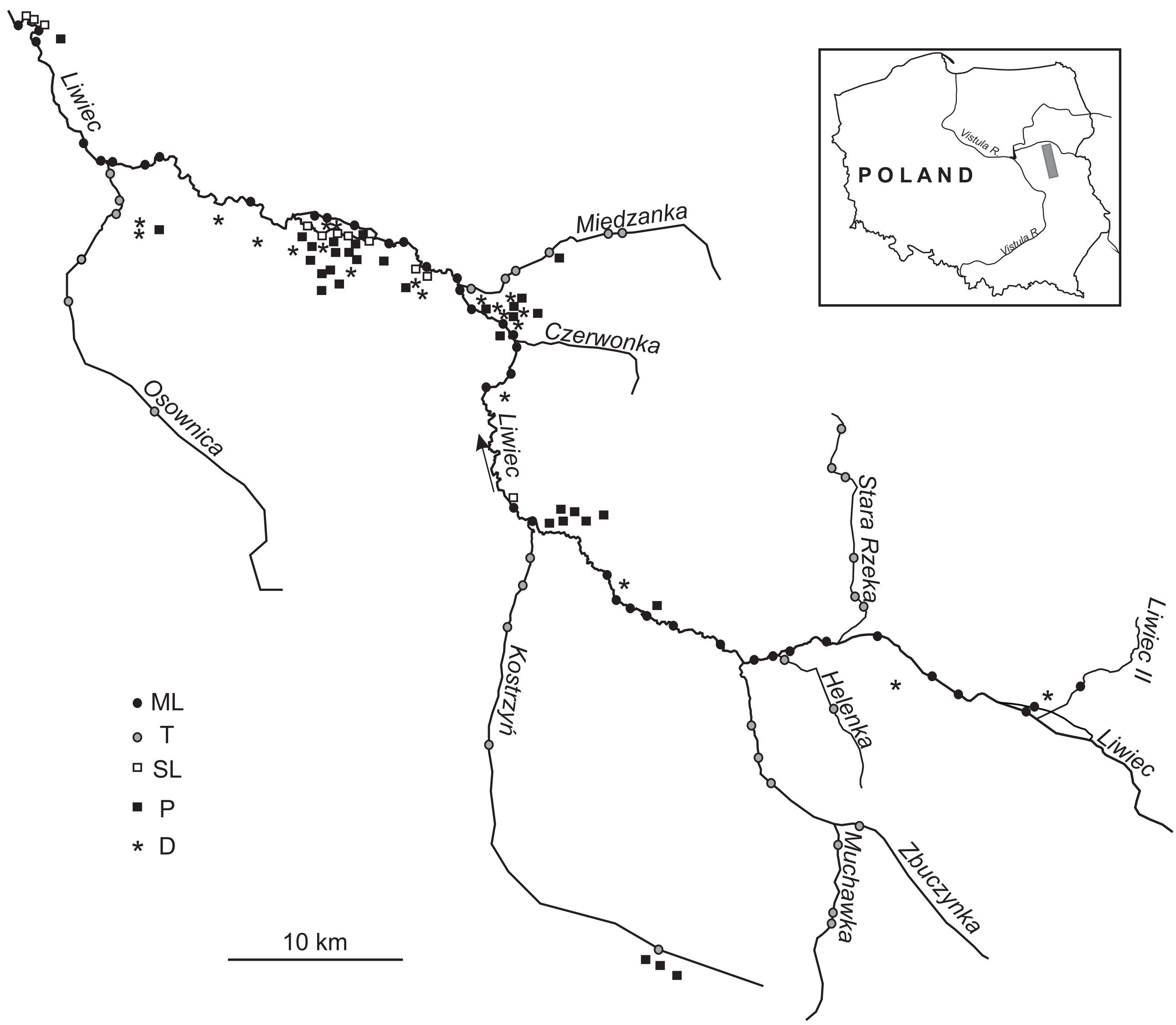

Fig. 1. Study area and location of the investigated sites; ML – main Liwiec River channel, T – tributaries, SL – secondary channels of Liwiec, P – ponds, D – ditches; grey rectangle – location of the study area on the map of Poland

in D from <1 to 5m. The depth ranged from <0.2 to >1 m, with the lowest values in D, as well as in some of T and P sites. Current velocity at ML and T sites ranged from <0.1 to >0.25 m/s (depending on the slope), whereas the other sites were mostly stagnant and only a few of them were characterised by a slight water movement. Bottom sediments in the rivers were sandy or sandy-muddy, often with the admixture of detritus or gravel (depending on current velocity). In the other habitat types bottom sediments were generally muddy or sandy-muddy, mostly with a big admixture of detritus. ML and T sites were characterised by sparse or moderate abundance of macrophytes or lack of vegetation. Within the other habitat types macrophyte abundance was mostly moderate or high (especially in P). Canopy was lacking or it was poor, so most of the sites were open and others were relatively slightly shaded.

MOLLUSC SAMPLING

Molluscs were sampled during summer (July–mid-September) 2012–2016, as well as in late spring (mid-May–the beginning of June) in 2013, 2015 and 2016 using a hand net with a working side of 25 cm, mesh size of 0.5 mm and handle length of 2 m. Individual habitats were investigated during 1–2 sampling events and every time usually 1–2 samples were taken, each of ca. 1 m^2 of the bottom area, covering all visually detected microhabitats. Samples from rivers were collected in the current and near the banks (never deeper than 1.5 m), ponds were investigated within the zone from the margin to the depth of 1.5 m, secondary channels of the Liwiec River and ditches were surveyed mostly in the whole cross sections. In total, 270 samples were collected. Samples were washed directly in the field using a sieve of 0.5 mm mesh size and they were preserved in laboratory with 75% ethyl alcohol (except for the majority of Unionidae, which were identified in the field and returned to the water). In the laboratory the molluscs were sorted, counted and identified using the keys of Piechocki (1979) and Piechocki & Dyduch-Falniowska (1993). Species names were updated according to Piechocki & Wawrzyniak-Wydrowska (2016).

DATA ANALYSIS

Sampling bias was tested with a species accumulation curve and the abundance-based non-parametric estimators Chao1, Chao2 and ACE (Colwell 2004). To compare species richness of the five habitat types, randomization was performed for equal numbers of sites treated as samples in each of them (n=11; the number of samples was constrained by the minimum sample size present in SL).

Dominance patterns of molluscs were estimated as the percentage of individual species within the total mollusc abundance (Górny & Grüm 1981). The frequency of individual species occurrence (i.e. the ratio of sites occupied, %F) within each of the habitat types was calculated (Górny & Grüm 1981). Species were regarded as regionally uncommon when the frequency of their occurrence was lower than 5%. This value was accepted as a halfway between diverse values proposed in the literature (e.g. Verdonschot et al. 2011, Heegaard et al. 2013).

The Shannon index H' (i.e. entropy) and Shannon true diversity (exp(H') (Jost 2006), where H' = -sum(p_i lnp_i)) were calculated based on mollusc abundance data. All these calculations were carried out with the EstimateS, v.9.0 software (Colwell 2004).

Comparison of species rarity within and between the habitat types was conducted using a species rarity index (SRI), conceptually based on the Species Quality Score developed by Foster et al. (1989). To calculate SRI all species present were given a rarity category: common species (score 1), local species (i.e. confined to limited areas or widespread, but represented by few individuals, score 2), nationally scarce (based on Piechocki & Wawrzyniak-Wydrowska 2016, score 4), included in Annexes II or IV of the EU Habitats Directive or legally protected in Poland (8; Council Directive 1992, Dz. U. 2016), included on the IUCN Red List of Threatened Species (IUCN 2018) – near threatened or vulnerable (16), endangered (32). Subsequently, the scores of all species at each site were summed up to obtain the Species Rarity Score, which in turn was divided by the number of species recorded at the site to give the SRI.

Following Whittaker's terminology (Whittaker 1972), total species diversity in a set of communities may be partitioned into additive components within and among communities: $\gamma=\beta+$mean α (Lande 1996, Veech et al. 2002). In contrast to the classical, multiplicative approach (Whittaker 1972) additive partition is more consistent and can be applied to multiple spatial scales. According to Jost (2007) when the sizes of samples or assemblages are unequal, only Shannon diversity measures (diversity indices of order one) can be decomposed into meaningful independent alpha and beta components. Species richness (diversity index of order 0) weights each assemblage equally, regardless of its true weight, and for this reason it is not a satisfactory measure, particularly when weights are important. Additive partitioning of Shannon entropy (H') was used to study the hierarchical partitioning of diversity, because H' is the only diversity index which can be additively partitioned into independent alpha and beta components. The relative contribution of the within and among sample (α_1 and β_1), among site (β_2) and among habitat (β_3) diversity to total diversity (γ) of the study area was assessed. To enable proper interpretation of the results of diversity partitioning the obtained Shannon alpha, beta and gamma entropies were converted to true diversities (their number equivalents, i.e. exponentials). The results of multiplicative decomposition of true Shannon diversity and species richness were compared with the results of additive partitioning of Shannon entropy. MacArthur's homogeneity measure (MacArthur 1965), exp(Hα)/exp(Hγ), was calculated to show the proportion of landscape diversity contained in the average sample.

Beta diversity was used as the measure of dissimilarity among sites to avoid strong bias in Jaccard's index, which may result from small sizes of mollusc assemblages in some cases.

Data on species richness, diversity, abundance and SRI within the five distinguished habitat types (ML, T, SL P and D) were compared with Tuckey RIR post hoc test (one-way ANOVA). The data concerning SRI and abundance were log (x+1) transformed prior to the analysis, because they did not reveal a normal distribution. Differences were considered significant at the 95% level ($P<0.05$). To assess similarity among malacofaunas of distinguished habitat types cluster analysis was performed based on relative abundance of mollusc species in each of 5 habitat types. Ward's linkage method and Euclidean distance were applied. These calculations were carried out using the STATISTICA 12.5 software (StatSoft).

RESULTS

COMPOSITION AND STRUCTURE OF MOLLUSC ASSEMBLAGES

In total, 54 mollusc species were recorded during the study (Table 1). The highest number of species (43) was found in the main channel of the Liwiec River (ML), followed by the tributaries (T, 41 species) and ditches (D, 37 species); the lowest species richness was recorded in secondary channels of the Liwiec River (SL) and ponds (P) – 35 species in each.

Table 1. Frequency distribution (%F) of mollusc species in five habitat types within the Liwiec River catchment: main river (ML), tributaries (T), secondary channels (SL), floodplain ponds (P) and ditches (D); rarity categories of species are given in parentheses; * – alien species

Species		ML	T	SL	P	D
Gastropoda						
Viviparidae						
Viviparus contectus (Millet, 1813)	(1)	3	2	16	20	12
V. viviparus (Linnaeus, 1758)	(1)	1	0	0	0	0
Bithynidae						
Bithynia tentaculata (Linnaeus, 1758)	(1)	31	48	72	34	55
Valvatidae						
Valvata cristata O. F. Müller, 1774	(1)	7	2	24	16	48
V. macrostoma Mörch, 1864	(2)	2	0	4	2	7
V. piscinalis (O. F. Müller, 1774)	(1)	12	8	16	4	12
Acroloxidae						
Acroloxus lacustris (Linnaeus, 1758)	(1)	1	2	0	0	0
Lymnaeidae						
Galba truncatula (O. F. Müller, 1774)	(1)	9	10	8	4	5
Ladislavella terebra (Westerlund, 1885)	(2)	0	0	0	2	2
Lymnaea stagnalis (Linnaeus, 1758)	(1)	9	23	32	40	19
Radix ampla (Hartmann, 1821)	(1)	11	6	4	0	2
R. auricularia (Linnaeus, 1758)	(1)	3	0	8	0	0
R. balthica (Linnaeus, 1758)	(1)	14	31	44	26	19
R. labiata (Rossmässler, 1835)	(2)	0	6	0	0	0
Stagnicola corvus (Gmelin, 1791)	(1)	0	2	12	22	17
S. palustris (O. F. Müller, 1774)	(1)	1	2	12	46	38
Physidae						
Aplexa hypnorum (Linnaeus, 1758)	(2)	1	2	0	16	21
Physella acuta (Draparnaud, 1805)*	(2)*	1	2	0	0	0
Physa fontinalis (Linnaeus, 1758)	(1)	5	25	36	34	36

Table 1. continued

Species		ML	T	SL	P	D
Gastropoda						
Planorbidae						
Ancylus fluviatilis O. F. Müller, 1774	(1)	0	2	0	0	0
Anisus calculiformis (Sandberger, 1875)	(2)	3	2	0	14	10
A. leucostoma (Millet, 1813)	(1)	5	0	4	10	5
A. spirorbis (Linnaeus, 1758)	(1)	1	0	0	4	5
A. vortex (Linnaeus, 1758)	(1)	6	17	56	54	52
A. vorticulus (Troschel, 1834)	(8)	0	0	24	20	0
Bathyomphalus contortus (Linnaeus, 1758)	(1)	0	13	20	26	12
Gyraulus albus (O. F. Müller, 1774)	(1)	9	19	12	4	10
G. crista (Linnaeus, 1758)	(1)	3	0	4	8	2
G. laevis (Alder, 1838)	(4)	0	0	0	0	2
G. rossmaessleri (Auerswald, 1852)	(2)	5	4	0	6	2
Hippeutis complanatus (Linnaeus, 1758)	(2)	1	4	8	10	5
Planorbarius corneus (Linnaeus, 1758)	(1)	5	17	64	64	67
Planorbis planorbis (Linnaeus, 1758)	(1)	5	6	4	46	74
Segmentina nitida (O. F. Müller, 1774)	(1)	3	2	12	36	10
Bivalvia						
Unionidae						
Anodonta anatina (Linnaeus, 1758)	(1)	11	0	4	0	0
A. cygnea (Linnaeus, 1758)	(2)	1	4	0	0	0
Unio crassus Philipsson, 1788	(32)	7	0	0	0	0
U. pictorum (Linnaeus, 1758)	(1)	19	8	12	0	0
U. tumidus Philipsson, 1788	(1)	15	12	4	0	2
Sphaeriidae						
Musculium lacustre (O. F. Müller, 1774)	(2)	0	0	0	0	10
Pisidium amnicum (O. F. Müller, 1774)	(1)	29	15	24	2	0
P. casertanum (Poli, 1791)	(1)	3	6	16	6	12
P. crassum Stelfox, 1918	(2)	0	6	0	0	0
P. henslowanum (Sheppard, 1823)	(1)	27	33	12	8	7
P. hibernicum Westerlund, 1894	(4)	0	12	0	0	0
P. milium Held, 1836	(1)	2	13	20	8	14
P. moitessierianum Paladilhe, 1866	(2)	1	4	0	0	0
P. nitidum Jenyns, 1832	(1)	39	54	20	16	24
P. obtusale (Lamarck, 1818)	(1)	0	2	0	6	5
P. pulchellum Jenyns, 1832	(4)	1	8	0	2	0
P. subtruncatum Malm, 1855	(1)	33	62	40	10	24
P. supinum A. Schmidt, 1851	(1)	46	33	24	0	2
Sphaerium corneum (Linnaeus, 1758)	(1)	53	60	52	24	29
S. rivicola (Lamarck, 1818)	(16)	7	0	12	0	0
Number of species		43	41	35	35	37

Table 2. Comparison of the numbers of species found within five habitat types and the entire study area with the expected species richness calculated with non-parametric abundance-based estimators ACE, Chao1 and Chao2; the values in parentheses show percent of estimated richness comprised by a number of species found

Habitat type	Number of species found	ACE	Chao1	Chao2
The Liwiec River (ML)	43	46.13 (93.2%)	46.00 (93.5%)	50.02 (85.7%)
Tributaries (T)	41	46.48 (88.2%)	42.67 (96.1%)	48.61 (84.3%)
Secondary channels (SL)	35	36.83 (95.0%)	35.00 (100%)	35.73 (98.0%)
Ponds (P)	35	35.5 (98.6%)	35.00 (100%)	35.16 (99.5%)
Ditches (D)	37	38.46 (96.2%)	38.00 (97.4%)	42.33 (87.4%)
Total	54	54.75 (98.6%)	54.25 (99.5%)	54.14 (99.7%)

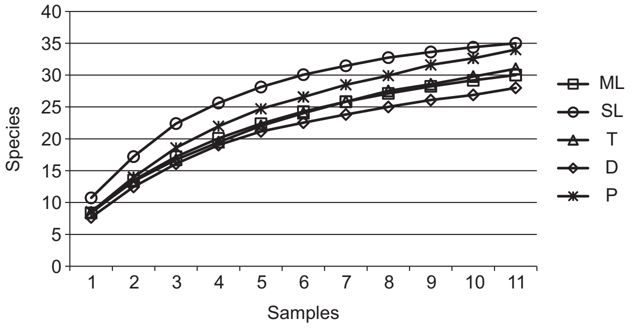

Fig. 2. Sample-based rarefaction curves of mollusc species richness for five habitat types: main Liwiec River channel (ML), tributaries (T), secondary channels of Liwiec (SL), ponds (P) and ditches (D); (n=11)

The accumulation curve for the entire study area approached an asymptote. Although accumulation curves for the habitat types have not achieved asymptotes, the species lists could be considered complete in most of the cases, due to them containing more than 90% of the expected numbers of species calculated with the non-parametric estimators ACE, Chao1 and Chao2, or almost complete in four cases, where they contained 84–88% of the expected numbers of species (Table 2).

The comparison of species richness among the five habitat types, based on equal numbers of sites (n=11) revealed only small differences, with the highest number of species in the secondary channels and ponds and the lowest in the ditches (Fig. 2).

From among all molluscs recorded, 21 species (38.9%) occurred in all habitat types and 8 (14.8%) were unique (i.e. found only in one habitat type): two, four and two species were found exclusively in ML, T and D, respectively.

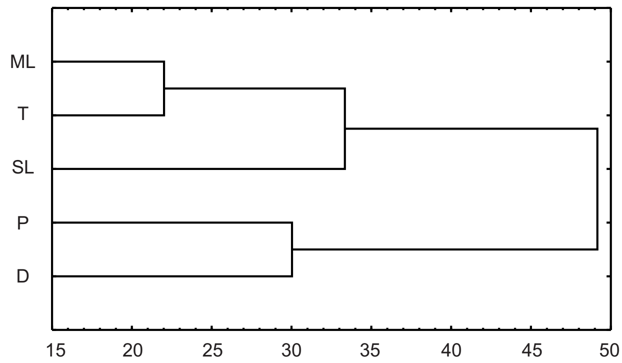

Fig. 3. Dendrogram showing distances among malacofaunas of five habitat types: main Liwiec River channel (ML), tributaries (T), secondary channels of Liwiec (SL), ponds (P) and ditches (D); cluster analysis based on relative abundance of mollusc species

Cluster analysis based on relative abundance of mollusc species in each habitat type revealed a relatively high similarity of the malacofaunas (Fig. 3). The highest similarity (i.e. the lowest distance) was found between ML and T, somewhat smaller between P and D. The malacofauna of SL showed a greater similarity to those in ML and T as compared to P and D.

The dominance pattern varied among the habitat types (Fig. 4). The malacocoenoses of ML and T sites were dominated by small bivalves – *Sphaerium corneum* and representatives of the genus *Pisidium*. *Bithynia tentaculata* was the only gastropod species with a considerable proportion in the dominance structure within the rivers. The mollusc assemblages of SL and D were characterised by a considerable percentage (i.e. over 5% of the total abundance for individual species) of both gastropods and small bivalves. The malacocoenoses of P sites were dominated by pulmo-

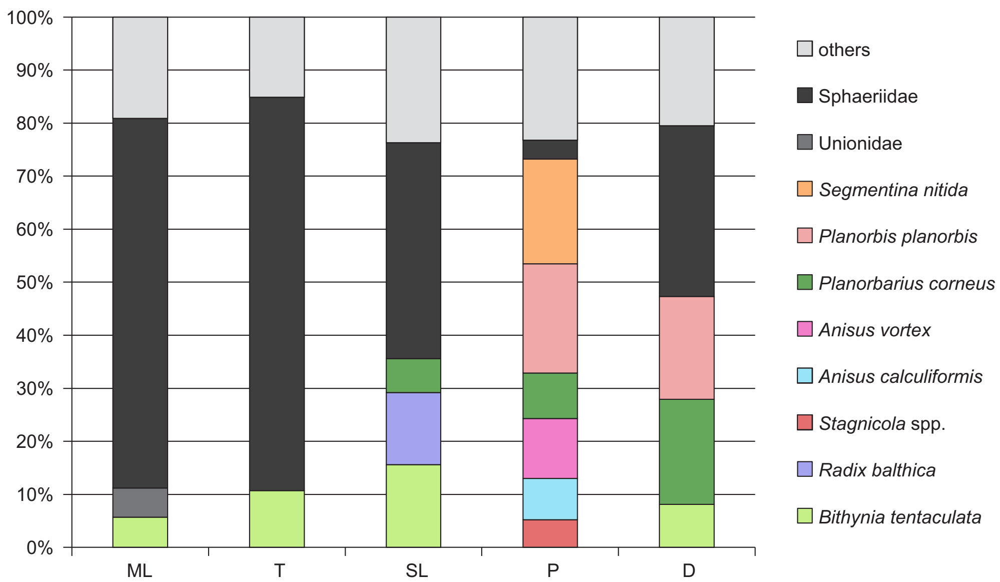

Fig. 4. Dominance patterns of mollusc assemblages in five habitat types: main Liwiec River channel (ML), tributaries (T), secondary channels of Liwiec (SL), ponds (P) and ditches (D)

nate gastropods of the family Planorbidae. In SL and D sites all species contributed more than 2% to the total mollusc abundance. In the other habitat types, the percentage of species with a low contribution to the total abundance (<2%) increased in the following order: P (11.4%), ML (31.7%) and T (34.4%).

None of the species was common (i.e. F>50%) at the scale of the total study area and very few such species occurred within individual habitat types: *S. corneum* in ML, three bivalves (*S. corneum, P. nitidum* and *P. subtruncatum*) in T, *B. tentaculata, P. corneus, A. vortex* and *S. corneum* in SL, two gastropods (*P. corneus* and *A. vortex*) in P and four gastropods (*B. tentaculata, A. vortex, P. planorbis* and *P. corneus*) in D (Table 1). Regionally uncommon species (i.e. with frequencies lower than 5%) were numerous, as they comprised 44.4% of the total number of species within the entire study area. They also formed a large fraction of malacofaunas within individual habitat types: 34.9%, 29.3%, 20.0%, 25.7% and 27.0% in ML, T, SL, P and D, respectively.

Within the study area six nationally rare (rarity category 4) and threatened species were found (over 11% of all mollusc species recorded). They occurred in all habitat types: three in ML, two in T, SL and P, and one in D (Table 1). Three species deserve a special mention: *Unio crassus, Sphaerium rivicola* and *Anisus vorticulus*. *A. vorticulus* is included in Annex II of the EU Habitats Directive (Council Directive 1992) and is legally protected in Poland (Dz. U. 2016). *U. crassus* and *S. rivicola* are included on the IUCN Red List of Threatened Species (IUCN 2018; EN and VU, respectively); furthermore, the first is listed in the EU Habitats Directive (Council Directive 1992, Annexes II and IV) and is legally protected in Poland (Dz. U. 2016). *A. vorticulus* was found at ten sites (8 in P and 2 in SL), *U. crassus* at five sites within the lower Liwiec River section, *S. rivicola* at eight sites (4 in ML and 4 in SL).

Several other species, which are not legally protected in Poland and their conservation status in Europe is LC (Least Concern), also deserve some comments, among others *Valvata macrostoma*, *Anisus calculiformis*, *Gyraulus laevis*, *Pisidium crassum*, *P. moitessierianum*, *P. hibernicum* and *P. pulchellum*. *V. macrostoma* and *G. laevis* exhibit a decreasing population trend, they are relatively rare in Poland and other European countries, in some of them they are legally protected (Piechocki & Wawrzyniak-Wydrowska 2016, IUCN 2018). Within the study area *V. macrostoma* was found at seven sites and *G. laevis* only at one. *A. calculiformis* is relatively common in some regions of Poland, but its population trend in Europe is unknown because of the scarcity of data (Piechocki & Wawrzyniak-Wydrowska 2016, IUCN 2018). It was found at 15 sites within the study area. All three gastropods are threatened with habitat loss and modification (channel regulation, drainage, pollution). *Pisidium moitessierianum* is not threatened through its range in Europe, but it is locally declining. Its general population trend is unknown (Piechocki & Wawrzyniak-Wydrowska 2016, IUCN 2018). Within the study area it was found only at 3 riverine sites. *P. pulchellum* is known from rather few localities in Poland, in Europe it is widely distributed, but locally declining. The general population trend is unknown (Piechocki & Wawrzyniak-Wydrowska 2016, IUCN 2018). It was collected from six sites within the study area. *P. crassum* and *P. hibernicum* are relatively rare in Poland, they are not included in the IUCN Red List of Threatened Species (IUCN 2018), even as DD (Data Deficient). The above mentioned pill-clams are threatened with habitat modification – pollution, changes to flow regime, dredging (Piechocki & Wawrzyniak-Wydrowska 2016, IUCN 2018). Within the study area they were found at three and six sites, respectively.

Table 3. Mean values (±SD) and ranges (in parentheses) of total species richness, mean species richness per site, Shannon index (H'), true diversity (exp(H')), abundance and species rarity index (SRI) of molluscs in the main Liwiec River channel (ML), its tributaries (T), secondary channels of Liwiec (SL), ponds (P) and ditches (D)

	ML	T	SL	P	D
Total species richness	7.78±4.00 (1–19)	8.06±3.37 (3–15)	10.45±4.39 (5–17)	7.82±3.61 (3–18)	8.24±4.65 (2–21)
Mean species richness per site	4.77±2.95 (1–15)	6.34±2.77 (1.5–14)	7.61±2.92 (3.7–13)	6.70±3.29 (2.7–18)	6.32±2.55 (2–11.8)
Shannon index (H')	1.59±0.49 (0–2.56)	1.42±0.52 (0.33–2.43)	1.86±0.77 (0.94–3.70)	1.46±0.42 (0.55–2.15)	1.44±0.49 (0.30–2.30)
True diversity exp(H')	5.50±2.60 (1–12.94)	4.74±2.61 (1.39–11.36)	9.12±10.81 (2.56–40.45)	4.68±1.82 (1.73–8.58)	4.68±2.09 (1.35–9.97)
Mean abundance (indiv./m^2)	25.1±31.1 (1.3–156)	76.2±81.3 (1.5–332)	80.4±66.9 (10.3–210)	140.0±257.6 (7–1,400)	116.9±136.6 (11–422)
Species rarity index (SRI)	1.91±2.20 (1–11.33)	1.16±0.20 (1–1.60)	1.66±0.91 (1–3.50)	1.24±0.29 (1–2.00)	1.11±0.13 (1–1.37)

COMPARISON OF SPECIES RICHNESS, DIVERSITY, ABUNDANCE AND RARITY AMONG HABITAT TYPES

The total number of species at individual sites varied from 1 to 21, but the mean values were fairly similar in all habitat types (Table 3, P>0.05). The highest proportion of sites with total species richness ≥10 was recorded within SL (45.5% of all sites within this habitat type), followed by T (34.4%), ML (29.3%), P (26.5%) and D (23.8%).

The mean number of species per site (i.e. alpha diversity) at individual sites ranged from 1 to 18 and there were no considerable differences among habitat types except the nearly significantly lower value in ML than in P (P=0.0539, Table 3).

The values of Shannon entropy (H') and true diversity (exp(H')) for individual sites varied widely (0–3.70 and 1–40.45 for H' and exp(H'), respectively). The mean H' and exp(H') values in individual habitat types ranged from 1.42 to 1.86 and 4.68 to 9.12, respectively (Table 3), however the differences among the habitat types were mostly not significant except the higher exp(H') value in SL as compared to T, P and D (P=0.0444, P=0.0400 and P=0.0397 for the comparisons with T, P and D, respectively).

The mollusc abundance at individual sites ranged from 1 to 1,400 ind./m^2, with the highest values (>100 ind./m^2) recorded in 11 ponds and seven ditches (mainly due to abundant occurrence of a few desiccation-resistant species), as well as at two ML sites, nine T sites and four SL sites. The mean abundance of molluscs within ML sites was distinctly lower when compared to the other habitat types (Table 3, P=0.0046, P=0.0409, P=0.0000 and P=0.0003 for the comparisons with T, SL, P and D, respectively). Its values were fairly similar among SL, P and D and slightly lower in T as compared to P and D.

The species rarity index (SRI) at individual sites varied widely (1–11.33, Table 3), but the mean SRI values did not differ significantly among the habitat types (P>0.05). The highest SRI value was found in ML (11.33), the maximum value in SL was 3.5, whereas in T, P and D the SRI values were always below two. The proportion of sites with SRI values exceeding one increased as follows: ML (41.5%), T (53.1%), D (57.1%), P (61.8%), SL (63.6%).

PARTITIONING OF MOLLUSC DIVERSITY ACROSS SPATIAL SCALES

Additive partitioning of Shannon entropy (H') proved that the total entropy of 3.11 found within the entire study area can be divided into a mean within habitat type entropy (i.e. α_3) of 2.60 and between habitat type entropy (i.e. β_3) of 0.51 (Fig. 5). The within habitat type entropy consisted of mean

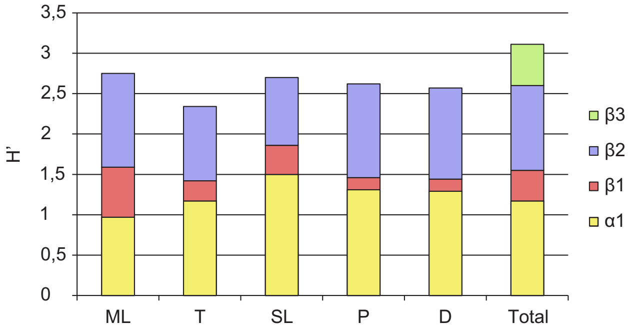

Fig. 5. Shannon entropy partitioning in five habitat types: main Liwiec River channel (ML), tributaries (T), secondary channels of Liwiec (SL), ponds (P) and ditches (D) and in the entire study area (Total); α_1 – mean per sample diversity, β_1 – between sample diversity, β_2 – between site diversity, β_3 – between habitat type diversity

within site entropy (i.e. α_2) of 1.55 and between site entropy (i.e. β_2) of 1.05. The within site entropy can be divided into mean within sample entropy (i.e. α_1) of 1.17 and between sample entropy (i.e. β_1) of 0.38. The total entropy in each of the five habitat types can be divided into additive components in a similar way (Fig. 5). Based on additive partitioning the percentages of total landscape diversity attributed to site-specific diversity ($\alpha_1+\beta_1$), habitat heterogeneity (β_2) and habitat variability (β_3) were 49.84% (i.e. 37.62% +12.22%), 33.76% and 16.40%, respectively. This indicates a relatively high proportion of alpha diversity at the site level and the highest beta diversity at the medium scale (i.e. habitat heterogeneity, β_2). This regularity was also visible in all habitat types. The results of additive partitioning of Shannon entropy were generally consistent with the results of multiplicative decomposition of Shannon true diversity and species richness (Table 4).

Table 4. Results of multiplicative decomposition of species richness and Shannon true diversity (exp(H')) in the distinguished habitats (ML, T, SL, P, D) and the entire study area (Total)

	α_1	β_1	β_2	β_3	γ
		Species richness			
ML	4.42	1.76	5.53		43
T	6.00	1.35	5.10		41
SL	7.40	1.41	3.35		35
P	6.90	1.13	4.50		35
D	6.90	1.19	4.50		37
Total	5.80	1.40	4.60	1.40	54
		exp(H')			
ML	3.10	1.77	2.81		15.46
T	3.74	1.27	2.18		10.35
SL	4.92	1.85	1.63		14.85
P	4.10	1.14	2.92		13.67
D	4.04	1.16	2.80		13.09
Total	3.71	1.43	2.55	1.67	22.47

The proportions of diversity components varied among the habitat types. The highest proportion of site-specific diversity was found in SL. The highest within sample diversity (α_1) was found in SL and the lowest in ML, whereas the highest between sample diversity (β_1) was recorded in ML and the lowest in P. The highest between site diversity (habitat heterogeneity, β_2) was noted in P and the lowest in SL.

The proportion of regional diversity contained in the average sample reflected by MacArthur's homogeneity measure ($M=\exp(H_\alpha)/\exp(H_\gamma)$) was relatively low both for the entire study area (M=0.165) and for individual habitat types (0.201, 0.361, 0.331, 0.300 and 0.309 for ML, T, SL, P and D, respectively).

DISCUSSION

During the study, rich and diverse malacofauna was found within a semi-natural Liwiec River catchment. In terms of landscape species richness (i.e. γ-diversity) lotic habitats – the Liwiec River and its tributaries – collectively supported a slightly richer malacofauna than the ponds, secondary channels of the Liwiec River and ditches together (50 and 44 species, respectively). However, species richness and Shannon diversity measures (H' and exp(H')) were relatively equally distributed among the five habitat types.

The high mollusc gamma diversity in the Liwiec River and its tributaries could result from the high beta diversity, despite the connectivity within the river channels. This might be caused by the influence of stochastic events on the mollusc assemblages, such as the interaction of dispersal with local competition (and/or predation). The considerable disturbance of the river bed (with mostly sandy bottom sediments), low productivity within the river channel and stochastic extinction of less adapted species may also be important (Jurkiewicz-Karnkowska 2016 and references therein).

The total mollusc species richness found in the Liwiec River and its tributaries was similar to that recorded by Bódis et al. (2016) from the Danube, Tisza and their tributaries and higher than in the Wkra River and its tributaries in Poland (Lewin 2014) or the Mediterranean Guadiana River (Perez-Quintero 2011). It was also similar or higher, compared to the values reported from other lowland and upland medium-sized rivers in Poland (Piechocki 1981), as well as some Lithuanian and Czech rivers of a similar nature (Pliūraitė & Kesminas 2004, Beran 2013).

The comparison of species richness for equal numbers of sites in every habitat type revealed that the secondary channels of the Liwiec River were the most species-rich habitat within the study area (but only slightly richer than ponds). This is consistent with the results of Bódis et al. (2016) reporting the highest mollusc species richness and Shannon index (H') in side channels of the Danube, as well as with the earlier study within a short section of the Liwiec River and its valley (Jurkiewicz-Karnkowska 2015) and may result from both favourable environmental conditions (low water flow or even lentic conditions and abundant macrophytes) and habitat heterogeneity.

Ponds and ditches have been reported to make an important contribution to aquatic biodiversity (e.g. Painter 1999, Armitage et al. 2003, Biggs et al. 2007, Davies et al. 2008, Gallardo et al. 2009, Simon & Travis 2011). Ponds are commonly recognised as a very heterogeneous habitat type which results in a high variability of their invertebrate assemblages, including molluscs (e.g. Scheffer et al. 2006, Davies et al. 2008). The malacofauna found in the investigated ponds was poorer than that of the Liwiec River and its tributaries. Similar results were obtained by Lewin (2014), who found more mollusc species in the Wkra River than in its oxbow lakes. However, when equal numbers of sites were compared, ponds investigated within the valleys of the Liwiec River and its tributaries supported more species than the main Liwiec channel, its tributaries and ditches, which is consistent with the results of Williams et al. (2004) from agricultural landscape in Southern England. The total number of mollusc species found in the studied ponds was lower than in the young permanent floodplain water bodies of the Bug River and higher than in the considerably desiccating and temporary ones (Jurkiewicz-Karnkowska 2009). It was also higher than in oxbow lakes of the Polish rivers Grabia and Wkra (Piechocki 1969, Lewin 2014) and 12 oxbow lakes of the Odra River (Piechocki & Szlauer-Łukaszewska 2013). The number of gastropod species was similar to the value reported from the water bodies of an active floodplain of the upper Rhine (Obrdlik & Fuchs 1991).

The number of species collected in ditches was similar to the value reported from Wicken Fen, UK (Painter 1999) and higher than in ditches within agricultural areas in the Netherlands (Verdonschot et al. 2011). This resulted most likely from the location within river floodplains and the permanent presence of water in almost all surveyed ditch sites. According to the literature, species-rich ditches typically occur in floodplain and coastal environments or low-lying fen landscapes (e.g. Painter 1999, Armitage et al. 2003, Biggs et al. 2007).

Ditches, being the only habitat type of anthropogenic origin included in the present study, supported species-rich and abundant malacocoenoses with the number of species similar to that in the ponds and secondary channels of the Liwiec River (slightly smaller compared to equal numbers of sites, n=11). It was the only habitat type where *Gyraulus laevis*, rare in Poland, was found, as well as *Musculium lacustre*. This bivalve, like several other species recorded from the ditches (*Valvata macrostoma*, *Ladislavella terebra*, *Aplexa hypnorum*, *Anisus calculiformis*, *Gyraulus rossmaessleri*), is not legally protected in Poland, but those species are threatened with extinction due to the disappearance of suitable habitats, resulting from land drainage. The importance of ditches, as a habitat supporting uncommon gastropods, has been previously reported, for example by WATSON & ORMEROD (2004).

Similarity among the malacofaunas of the five habitat types was relatively high, indicating connectivity (hydrological or via biotic vectors, e.g. birds, insects, amphibians) among them. Some authors reported a large proportion of freshwater species in a range of water body types, which reflected the occurrence of a network among different kinds of freshwater habitats (e.g. WILLIAMS et al. 2004, BIGGS et al. 2017, BÓDIS et al. 2016). The relatively low habitat variability (β_3), revealed by hierarchical partitioning of diversity, was consistent with the relatively high similarity among malacofaunas of different habitat types.

In conclusion, within the semi-natural river-floodplain systems belonging to the Liwiec River catchment, the mollusc diversity was relatively equally distributed among the habitat types, only the mean species richness was lower in the main Liwiec River channel compared to the ponds and exp(H') was higher in the secondary channels of the Liwiec than in its tributaries, ponds and ditches. However, the mollusc diversity was not distributed evenly across the landscape. The diversity at the site level was generated mainly by alpha component, whereas at the landscape scale habitat heterogeneity (beta component) was very important. The significance of habitat variability (β_3) was distinctly smaller. The aquatic malacofauna of the Liwiec River catchment was rich and almost free of alien species (save for a few individuals of *Physella acuta* only, which were found at two riverine sites). Conservation value of mollusc assemblages of the five habitat types did not differed significantly. Nationally rare and threatened species were present in all of them. Although the highest SRI value was recorded in the main Liwiec River channel, a higher proportion of sites with SRI>1 was found in the secondary channels of the Liwiec, ponds and ditches. All the habitat types deserve attention in order to maintain diversity at the landscape scale. The care for their good ecological condition, particularly protection against pollution and eutrophication, is vastly important to maintain alpha diversity at individual sites. In the case of semi-natural habitats (main Liwiec River channel, its side channels and tributaries, small floodplain water bodies) preservation of hydrological processes structuring the habitat heterogeneity would be important for maintaining beta diversity at a medium scale (β_2). This seems at least partially achievable, due to the fact that a substantial part of the Liwiec River valley and some parts of the valleys of its tributaries are encompassed by different forms of areal protection (the Natura 2000 network, landscape protection areas) and the entire area is extensively used, mainly as meadows and pastures. Maintaining a high biodiversity of ditches requires their management in rotation, which ensures the presence of a range of ditch ages (e.g. CLARKE 2015). For this reason, such a way of management should be executed within the Liwiec River catchment. Conservation efforts should focus mainly on the most heterogeneous fragments of the Liwiec River catchment to support mollusc diversity at the regional scale.

REFERENCES

ARMITAGE P. D., SZOSZKIEWICZ K., BLACKBURN J. H., NESBITT I. 2003. Ditch communities: a major contributor to floodplain biodiversity. Aquatic Conservation: Marine and Freshwater Ecosystems 13: 165–185. https://doi.org/10.1002/aqc.549

BERAN L. 2013. Freshwater molluscs of the Dyje (Thaya) River and its tributaries – the role of these water bodies in expansion of alien species and as a refuge for endangered gastropods and bivalves. Folia Malacologica 21: 143–160. https://doi.org/10.12657/folmal.021.018

BIGGS J., FUMETTI S. VON, KELLY-QUINN M. 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiologia 793: 3–39. https://doi.org/10.1007/s10750-016-3007-0

BIGGS J., WILLIAMS P., WHITFIELD M., NICOLET P., BROWN C., HOLLIS J., ARNOLD D., PEPPER T. 2007. The freshwater biota of British agricultural landscapes and their sensitivity to pesticides. Agriculture, Ecosystems and Environment 122: 137–148. https://doi.org/10.1016/j.agee.2006.11.013

BIGGS J., WILLIAMS P., WHITFIELD M., NICOLET P., WEATHERBY A. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of

Pond Conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 693–714. https://doi.org/10.1002/aqc.745

Bódis E., Tóth B., Sousa R. 2016. Freshwater mollusc assemblages and habitat associations in the Danube River drainage, Hungary. Aquatic Conservation: Marine and Freshwater Ecosystems 26: 319–332. https://doi.org/10.1002/aqc.2585

Briers R. A., Biggs J. 2005. Spatial patterns in pond invertebrate communities: separating environmental and distance effects. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 549–557. https://doi.org/10.1002/aqc.742

Clarke A., MacNally R., Bond N., Lake P. S. 2008. Macroinvertebrate diversity in headwater streams: a review. Freshwater Biology 53: 1707–1721. https://doi.org/10.1111/j.1365-2427.2008.02041.x

Clarke S. J. 2015. Conserving freshwater biodiversity: The value, status and management of high quality ditch systems. Journal for Nature Conservation 24: 93–100. https://doi.org/10.1016/j.jnc.2014.10.003

Colwell R. K. 2004. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8.0. Available online at http://viceroy.eeb.uconn.edu/estimates

Council Directive 1992. Directive 92/43/EEC the Council of the European Communities of 21st May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities (L206/7): 1–44.

Czarnecka H. (ed.). 2005. Atlas podziału hydrograficznego Polski. IMGW, Warszawa.

Davies B., Biggs J., Williams P., Whitfield M., Nicolet P., Sear D., Bray S., Maund S. 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. Agriculture, Ecosystems & Environment 125: 1–8. https://doi.org/10.1016/j.agee.2007.10.006

Dz. U. 2016. Dziennik Ustaw nr 2183 z dnia 28 grudnia 2016 r., poz. 2183. Rozporządzenie Ministra Środowiska z dnia 16 grudnia 2016 r. w sprawie ochrony gatunkowej zwierząt.

Foeckler F., Diepolder U., Deichner O. 1991. Water mollusc communities and bioindication of lower Salzach floodplain waters. Regulated Rivers, Research & Management 6: 301–312. https://doi.org/10.1002/rrr.3450060408

Foeckler F., Kretschmer W., Deichner O., Schmidt H. 1994. Bioindication of former floodplain waters of the lower Salzach River (Bavaria) by macroinvertebrate communities. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 25:1618–1623. https://doi.org/10.1080/03680770.1992.11900456

Foster G. N., Foster A. P., Eyre M. D., Bilton D. T. 1989. Classification of water beetle assemblages in arable fenland and ranking of sites in relation to conservation value. Freshwater Biology 22: 343–354. https://doi.org/10.1111/j.1365-2427.1989.tb01109.x

Gallardo B., Dolédec S., Paillex A., Arscott D. B., Sheldon F., Zilli F., Mérigoux S., Castella E., Comin F. A. 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains. Freshwater Biology 59: 630–648. https://doi.org/10.1111/fwb.12292

Gallardo B., Garcia M., Cabezas A., González E., González M., Ciancarelli C., Comin F. A. 2008. Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. Aquatic Sciences 70: 248–258. https://doi.org/10.1007/s00027-008-8024-2

Gallardo B., Gascón S., González-Sanchis M., Cabezas A., Comin F. A. 2009. Modelling the response of floodplain aquatic assemblages across the lateral hydrological connectivity gradient. Marine and Freshwater Research 60: 924–935. https://doi.org/10.1071/MF08277

Godreau V., Bornette G., Frochot B., Amoros C., Castella E., Oertli B., Chambaud F., Oberti D., Craney E. 1999. Biodiversity in the floodplain of Saône: a global approach. Biodiversity and Conservation 8: 839–864. https://doi.org/10.1023/A:1008807328566

Górny M., Grüm L. 1981. Metody stosowane w zoologii gleby. Państwowe Wydawnictwo Naukowe, Warszawa.

Heegaard E., Gjerde I., Sætersdal M. 2013. Contribution of rare and common species to richness patterns at local scales. Ecography 36: 937–946. https://doi.org/10.1111/j.1600-0587.2013.00060.x

Heino J., Parviainen J., Paavola R., Jehle M., Louhi P., Muotka T. 2005. Characterizing macroinvertebrate assemblage structure in relation to stream size and tributary position. Hydrobiologia 539: 121–130. https://doi.org/10.1007/s10750-004-3914-3

IUCN 2018. IUCN Red List of Threatened Species. Version 2018-2. Available online at https://www.iucnredlist.org/ (accessed 28 February 2019).

Jost L. 2006. Entropy and diversity. Oikos 113: 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439. https://doi.org/10.1890/06-1736.1

Jurkiewicz-Karnkowska E. 2008. Aquatic mollusc communities in riparian sites of different size, hydrological connectivity and succession stage. Polish Journal of Ecology 56: 99–118.

Jurkiewicz-Karnkowska E. 2009. Diversity of aquatic malacofauna within a floodplain of a large lowland river (lower Bug River, eastern Poland). Journal of Molluscan Studies 75: 223–234. https://doi.org/10.1093/mollus/eyp017

Jurkiewicz-Karnkowska E. 2015. Diversity of aquatic molluscs in a heterogenous section of a medium-sized lowland river-floodplain system: an example of intermediate disturbance hypothesis. Polish Journal of Ecology 69: 559–572. https://doi.org/10.3161/15052249PJE2015.63.4.008

Jurkiewicz-Karnkowska E. 2016. Longitudinal pattern of mollusc assemblages within a medium-sized lowland river: Liwiec (East Poland). Folia Malacologica 24: 209–222. https://doi.org/10.12657/folmal.024.018

Jurkiewicz-Karnkowska E., Karnkowski P. 2013. GIS analysis reveals the high diversity and conservation value of mollusc assemblages in the floodplain wetlands of the lower Bug River (East Poland). Aquatic Conservation: Marine and Freshwater Ecosystems 23: 952–963. https://doi.org/10.1002/aqc.2351

Korycińska M. 2002. Molluscs of the Liwiec River (South Podlasie and Middle Mazovian lowlands). Folia Malacologica 10: 17–23. https://doi.org/10.12657/folmal.010.003

Lake P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19: 573–592. https://doi.org/10.2307/1468118

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5–13. https://doi.org/10.2307/3545743

Lewin I. 2014. Mollusc communities of lowland rivers and oxbow lakes in agricultural areas with anthropogenically elevated nutrient concentrations. Folia Malacologica 22: 87–159. https://doi.org/10.12657/folmal.022.012

MacArthur R. 1965. Patterns of species diversity. Biological Reviews 40: 510–533. https://doi.org/10.1111/j.1469-185X.1965.tb00815.x

Obrdlik P., Falkner G., Castella E. 1995. Biodiversity of Gastropoda in European floodplains. Archiv für Hydrobiologie – Supplement 101 (Large Rivers/River Systems 9): 339–356. https://doi.org/10.1127/lr/9/1996/339

Obrdlik P., Fuchs U. 1991. Surface water connection and the macrozoobenthos of two types of floodplains on the upper Rhine. Regulated Rivers, Research & Management 6: 279–288. https://doi.org/10.1002/rrr.3450060406

Painter D. 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. Journal of Applied Ecology 36: 33–48. https://doi.org/10.1046/j.1365-2664.1999.00376.x

Pérez-Quintero J. C. 2011. Distribution patterns of freshwater molluscs along environmental gradients in the southern Guadiana River basin (SW Iberian Peninsula). Hydrobiologia 678: 65–76. https://doi.org/10.1007/s10750-011-0821-2

Piechocki A. 1969. Mięczaki (Mollusca) rzeki Grabi i jej terenu zalewowego. Fragmenta Faunistica 15: 111–197. https://doi.org/10.3161/00159301FF1969.15.10.111

Piechocki A. 1979. Mięczaki (Mollusca). Ślimaki (Gastropoda). Fauna słodkowodna Polski, 7. Polish Scientific Publishing House: Warszawa–Poznań.

Piechocki A. 1981. Współczesne i subfosylne mięczaki (Mollusca) Gór Świętokrzyskich. Acta Universitatis Lodziensis, Łódź.

Piechocki A., Dyduch-Falniowska A. 1993. Mięczaki (Molluscs). Małże (Bivalvia). Fauna Słodkowodna Polski, 7A. Polish Scientific Publishing House: Warszawa.

Piechocki A., Szlauer-Łukaszewska A. 2013. Molluscs of the middle and lower Odra: the role of the river in the expansion of alien species in Poland. Folia Malacologica 21: 73–86. https://doi.org/10.12657/folmal.021.008

Piechocki A., Wawrzyniak-Wydrowska B. 2016. Guide to freshwater and marine Mollusca of Poland. Bogucki Scientific Publishing House, Poznań.

Pliūraité V., Kesminas V. 2004. Species composition of macroinvertebrates in medium-sized Lithuanian rivers. Acta Zoologica Lithuanica 14: 10–25. https://doi.org/10.1080/13921657.2004.10512586

Richardot-Coulet M., Castella E., Castella C. 1987. Classification and succession of former channels of French Upper Rhône alluvial plain using Mollusca. Regulated Rivers, Research & Management 1: 111–127. https://doi.org/10.1002/rrr.3450010203

Scheffer M., Van Geest G. J., Zimmer K., Jeppesen E., Søndergaard M., Butler M. G., Hanson M. A., Declerc S., De Meester L. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112: 227-231. https://doi.org/10.1111/j.0030-1299.2006.14145.x

Simon T. N., Travis J. 2011. The contribution of man-made ditches to the regional stream biodiversity of the new river watershed in the Florida panhandle. Hydrobiologia 661: 163–177. https://doi.org/10.1007/s10750-010-0521-3

Tockner K., Schiemer F., Baumgartner C., Kum G., Weigand E., Zweimüller I., Ward J. V. 1999. The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. Regulated Rivers, Research & Management 15: 245–258. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<245::AID-RRR540>3.0.CO;2-G

Veech J. A., Summerville K. S., Crist T. O., Gering J. C. 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos 99: 3–9. https://doi.org/10.1034/j.1600-0706.2002.990101.x

Verdonschot P. F. M. 1990. Ecological characterization of surface waters in the Province of Overijssel (the Netherlands) (PhD thesis). University of Wageningen, the Netherlands.

Verdonschot R. C. M., Keizer-Vlek H. E., Verdonschot P. F. M. 2011. Biodiversity value of agricultural drainage ditches: a comparative analysis of the aquatic invertebrate fauna of ditches and small lakes. Aquatic Conservation: Marine and Freshwater Ecosystems 21: 715–727. https://doi.org/10.1002/aqc.1220

Ward J. V., Tockner K., Schiemer F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers, Research & Management 15: 125–139. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E

Watson A. M., Ormerod S. J. 2004. The distribution of three uncommon freshwater gastropods in the drainage ditches of British grazing marshes. Biological Conservation 118: 455–466. https://doi.org/10.1016/j.biocon.2003.09.021

WEIGAND E., STADLER F. 2000. Die aquatischen Mollusken der Regelsbrunner Au. Abhandlungen der Zoologisch-Botanischen Gesellschaft, Osterreich 31: 99–124.

WHITTAKER R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251. https://doi.org/10.2307/1218190

WILLIAMS P., WHITFIELD M., BIGGS J., BRAY S., FOX G., NICOLET P., SEAR D. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biological Conservation 115: 329–341. https://doi.org/10.1016/S0006-3207(03)00153-8

Received: April 12th, 2019
Revised: June 22nd, 2019
Accepted: June 30th, 2019
Published on-line: August 2nd, 2019