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LONGITUDINAL PATTERN OF MOLLUSC ASSEMBLAGES WITHIN A MEDIUM-SIZED LOWLAND RIVER: LIWIEC (EAST POLAND)

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Abstract: The Liwiec River, the biggest left-bank tributary of the Bug River, drains South Podlasie and Middle Mazovian Lowlands. This study aimed at tracing longitudinal changes in the composition, diversity, dominance pattern and abundance of its mollusc assemblages. Special attention was paid to the role of spatial disturbances in the river continuum, of both natural (tributaries) and anthropogenic origin (sewage treatment plants, small dam). Forty two mollusc species were recorded, with the respective values within the upper (UR), middle (MR) and lower (LR) river sections of 27, 19 and 34. The composition of mollusc assemblages showed some longitudinal changes, but without any clear progression along the river course. However, some differences among the malacofaunas of UR, MR and LR were observed, including large variation in species richness along the river. A relatively small species richness (less than 5 species) was found at 26% of the sites. The rather high total species diversity (γ) resulted mostly from considerable differences in the species composition among the sites. The effect of spatial discontinuities in the river course on the mollusc assemblages was rather weak, but they were more visible than the differences between consecutive sites within free-flowing river sections.

Key words: mollusc assemblages, diversity, longitudinal changes, river discontinuities

INTRODUCTION

Longitudinal patterns of macro-invertebrate community changes along the river course have been explained in different ways. The River Continuum Concept (RCC, Vannote et al. 1980) emphasises the importance of large-scale patterns of energy partitioning. The Hierarchical Patch Dynamics Concept (HPDC, Townsend 1989, Poole 2002) recognises local scale habitat patchiness as the main community-shaping factor. The Link Discontinuity Concept (LDC, Rice et al. 2001) emphasises the fundamental importance of water and sediment fluxes at moderate spatial scales.

Natural disturbances resulting from hydrological regime and related factors create temporal discontinuities which have a strong effect on macro-benthic assemblages of lotic habitats (Statzner & Higler 1986, Resh et al. 1988, Poff & Ward 1989, Poff 1992, Townsend et al. 1997). Tributaries, constituting natural spatial disturbances in the river continuum, are also recognised as crucial physical factors which affect community structure and species richness of benthic invertebrates (Minshall et al. 1985, Lake 2000, Rice et al. 2001, Benda et al. 2004a, b). Habitat heterogeneity resulting from temporal and spatial disturbances potentially promotes biological diversity in riverine systems (Townsend 1989, Townsend & Hildrew 1994, Poole 2002, Ward et al. 2002, Benda et al. 2004a, b). However, many anthropogenic disturbances in the river continuum, for example dams, weirs, or pollution, negatively affect macro-invertebrate assemblages (e.g. Munn & Brusven 1991, Fruget 1992, Käiro et al. 2012, Manfrin et al. 2013, Feio et al. 2015, Ellis & Jones 2016).

Aquatic molluscs are important components of macro-invertebrate fauna in many river habitats

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(e.g. Fruget 1992, Humpesch 1996, Pliūraitė & Kesminas 2004, Królak & Korycińska 2008, Jiang et al. 2010). Species-rich aquatic malacocoenoses have been reported from river channels (e.g. Piechocki 1969, 1972, Beran 2013, 2015, Piechocki & Szlauer-Łukaszewska 2013, Lewin 2014).

Molluscs of the Liwiec River were studied by Korycińska (2002) based on samples from 12 sites along the entire river. Malacofauna of a short (ca. 10 km) section of the lower Liwiec was recently investigated by Jurkiewicz-Karnkowska (2015).

The present study aimed at tracing longitudinal changes in the composition, diversity, dominance pattern and abundance of mollusc assemblages. Special attention was paid to the role of spatial discontinuities of both natural (tributaries) and anthropogenic origin (discharge from sewage treatment plants, small dam).

STUDY AREA

The Liwiec River is the biggest left-bank tributary of the Bug River; it drains South Podlasie and Middle Mazovian Lowlands (52°36'24"–52°05'39"N, 21°33'34"–22°37'39"E). It is a medium-sized river (ca. 142 km long), with the catchment area of 2,780 km². The upper river course extends from the source to the village of Chodów (52°21'09"N, 22°13'28"E), the middle course ends in the village of Liw (52°22'30"N, 21°58'01"E). The lower course is almost as long as the two preceding sections combined.

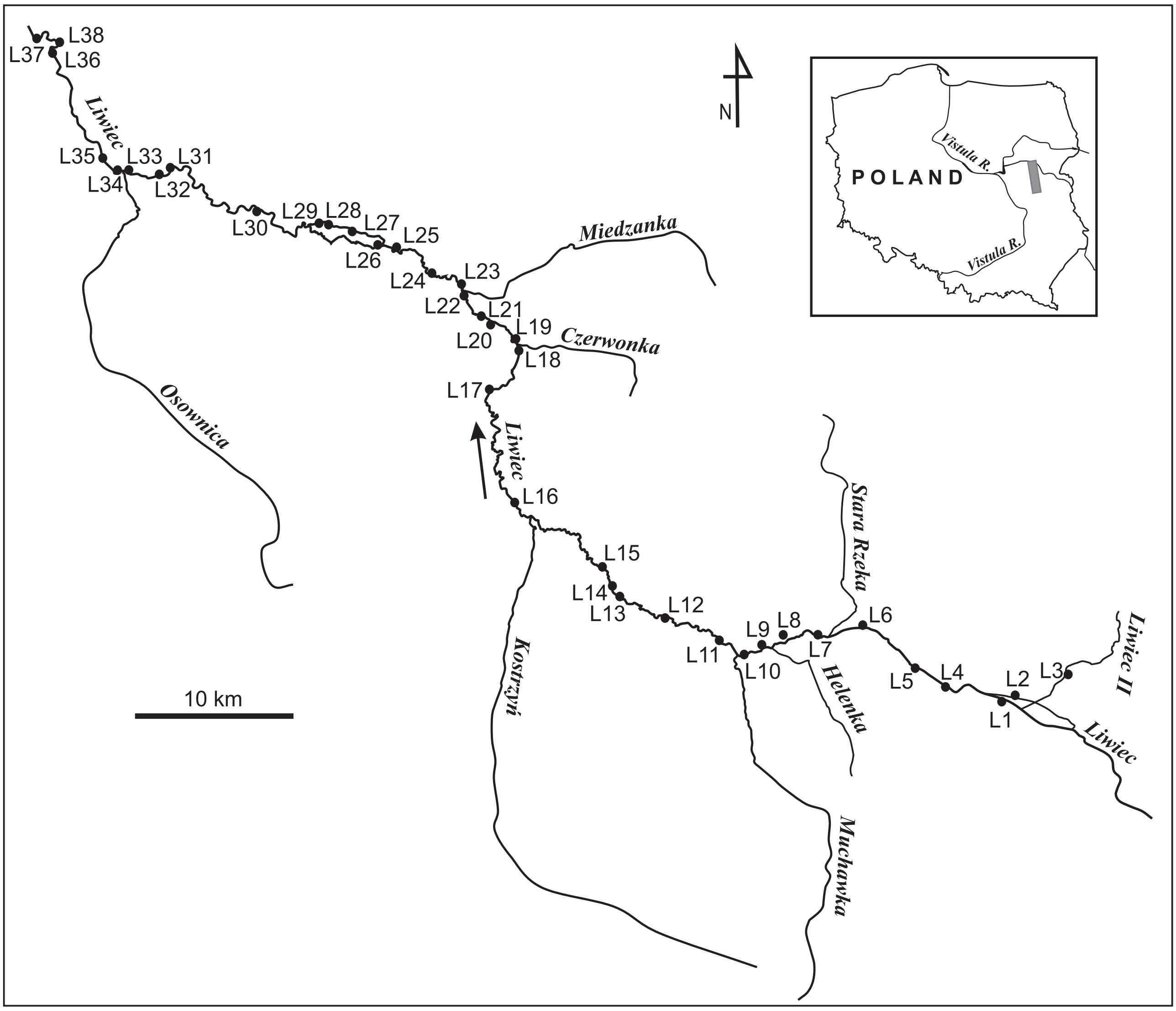

Fig. 1. Study area and location of sites: L1–L9 – upper Liwiec River section (UR), L10–L17 – middle section (MR), L18–L38 – lower section (LR); solid circles – sites, dark grey rectangle – study area

The mean long-term discharge (SSQ) recorded at the water gauge station in the lower section (17th km of the river course counting from the mouth) was 10.2 m^3s^{-1} (Czarnecka 2005). The source area of the river is located at 160 m a.s.l. (ca. 20 km E of Siedlce) and the mouth at 85 m a.s.l.; the mean river gradient is 0.52‰.

The valley is 120 km^2 in area, its width is mostly up to 2 km except 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: PLB 140002 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, but small hydrotechnical constructions (weirs, culverts) are present nearly all along the river except the mouth section which has remained exceptionally natural. The river is fed by 10 tributaries among which Muchawka, Kostrzyń and Osownica are the largest. The water quality is the best in the upper section. Recently, it has improved within the entire river, reaching II quality class in terms of physico-chemical parameters (Report 2015). However, the ecological condition JCWP varies from good within the headwaters to moderate and poor in the middle and lower sections.

The study included 38 sites located along the Liwiec River (Fig. 1), with the numbers of sites in the upper (UR), middle (MR) and lower (LR) river sections approximately proportional to their lengths (9, 8 and 21 sites, respectively). The sections upstream and downstream of selected tributaries (Helenka, Czerwonka, Miedzanka and Osownica) were included. The confluences with the Muchawka and Kostrzyń rivers were not taken into consideration because of the difficult access and the lack of molluscs in the samples.

General characteristics of the sampling sites are presented in Appendix 1; six qualitative environmental parameters were expressed as categorical variables: width, depth, current velocity, bottom sediment type, macrophyte abundance, canopy.

METHODS

Molluscs were sampled in late spring (mid-May – early June) in 2013 and 2015, as well as in summer (July – mid-September) of 2012–2015, 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 on each occasion 2–3 samples were taken. The samples were collected in the current and near the banks from ca. 1 m^2 of the bottom area. They were washed on a sieve of 0.5 mm mesh and preserved with 75% ethyl alcohol (except *Unio crassus*, which was returned alive into the water). In the laboratory, the molluscs were sorted, counted and identified based on shell morphology and previous experience, using the keys of Piechocki (1979) and Piechocki & Dyduch-Falniowska (1993). Species names were updated according to Piechocki (2008). Mean values of mollusc abundance (indiv./m^2) were calculated for each site. Species were regarded as common when present in at least 50% of samples and as rare when they occurred at one or two sites.

The true total species richness in the whole study area and in the three river sections (UR, MR and LR) was estimated with sample-based rarefaction curves (Gotelli & Colwell 2001, Colwell et al. 2004), which are the expected species accumulation curves based on re-sampled total observed species (S_{obs}). The samples were randomised for all 38 sites or separately for each of the three river sections. The non-parametric abundance based estimator Chao2 was used to estimate the predicted values of species richness based on its observed performance in other studies (e.g. Foggo et al. 2003, Hortal et al. 2006, Soberón et al. 2007, Jurkiewicz-Karnkowska 2014). Datasets were regarded as complete when at least 90% of the number of species predicted with Chao2 were found and as representative when over 70% of the predicted number of species were recorded. The Shannon index H' (entropy) and Shannon true diversity (exp(H') Jost 2006, where $H' = -\mathrm{sum}(p_i \ln p_i)$) were calculated based on mollusc abundance data. The Jaccard similarity coefficient (J) was calculated for each pair of consecutive sites. The calculations were carried out with EstimateS, v.8.0 software (Colwell 2004).

The data on species richness, diversity and abundance were compared with the Kruskal-Wallis test; the Mann-Whitney test was applied to compare species similarities (J) of disturbed sites (tributary confluences, discharge from sewage plants, small dam) and sites located within free-flowing river sections. The calculations were carried out with STATISTICA 10.0 software (StatSoft).

RESULTS

COMPOSITION OF MOLLUSC ASSEMBLAGES

During the study 42 mollusc species were recorded from the Liwiec River (Table 1). The respective values within the upper, middle and lower river sections were 27, 19 and 34. The datasets for UR, MR and LR were representative, containing 76.5–88% of the expected number of species calculated with the non-parametric estimator Chao2 (Fig. 2). The dataset for the entire river may be regarded as almost complete (89% of the expected number of species). From among all molluscs recorded 13 species were

Table 1. Frequency distribution (%) of mollusc species in three sections of the Liwiec River channel: upper (UR), middle (MR) and lower (LR); * – species included in IUCN European Red List of Threatened Species

Species	Species labels	UR	MR	LR
Prosobranchia				
Bithynia tentaculata (Linnaeus, 1758)	B.t.	47.4	57.9	19.4
Valvata cristata O. F. Müller, 1774	V.cr.	15.8	0	6.5
V. macrostoma Mörch, 1864	V.m.	0	0	3.2
V. piscinalis (O. F. Müller, 1774)	V.p.	5.3	15.8	11.3
Viviparus viviparus (Linnaeus, 1758)	V.v.	0	0	1.6
V. contectus (Millet, 1813)	V.c.	15.8	0	0
Pulmonata				
Lymnaea stagnalis (Linnaeus, 1758)	L.s.	21.1	10.5	4.8
Radix ampla (W. Hartmann, 1821)	R.am.	0	26.3	9.7
R. auricularia (Linnaeus, 1758)	R.a.	0	5.3	3.2
R. balthica (Linnaeus, 1758)	R.b.	0	10.5	19.4
Stagnicola palustris (O. F. Müller, 1774)	S.p.	5.3	0	0
Galba truncatula (O. F. Müller, 1774)	G.t.	26.3	0	6.5
Aplexa hypnorum (Linnaeus, 1758)	A.h.	5.3	0	0
Physa fontinalis (Linnaeus, 1758)	P.f.	15.8	0	3.2
Physella acuta (Say, 1817)	P.ac.	0	5.3	0
Planorbarius corneus (Linnaeus, 1758)	P.c.	15.8	5.3	1.6
Planorbis planorbis (Linnaeus, 1758)	P.pl.	5.3	0	6.5
Anisus leucostoma (Millet, 1813)	A.l.	21,1	0	1.6
A. septemgyratus (Rossmässler, 1835)	A.sep.	15.8	0	0
A. spirorbis (Linnaeus, 1758)	A.s.	0	0	1.6
A. vortex (Linnaeus, 1758)	A.v.	15.8	5.3	3.2
Gyraulus albus (O. F. Müller, 1774)	G.a.	10.5	15.8	4.8
G. rossmaessleri (Auerswald, 1852)	G.r.	26.3	0	0
G. crista (Linnaeus, 1758)	G.cr.	5.3	0	1.6
Hippeutis complanatus (Linnaeus, 1758)	H.c.	0	0	1.6
Segmentina nitida (O. F. Müller, 1774)	S.n.	5.3	0	3.2
Bivalvia				
Anodonta anatina (Linnaeus, 1758)	A.a.	0	0	16.1
A. cygnea (Linnaeus, 1758)	A.c.	0	0	1.6
Unio crassus Philipsson, 1788*	U.c.	0	0	11.3
U. pictorum (Linnaeus, 1758)	U.p.	0	10.5	27.4
U. tumidus Philipsson, 1788	U.t.	5.3	10.5	17.7
Sphaerium corneum (Linnaeus, 1758)	S.c.	57.9	47.4	51.6
S. rivicola (Lamarck, 1818)	S.r.	0	15.8	6.5
Pisidium amnicum (O. F. Müller, 1774)	P.a.	26.3	15.8	32.3
P. casertanum (Poli, 1791)	P.cas.	0	0	1.6
P. henslowanum (Sheppard, 1823)	P.h.	15.8	15.8	33.9
P. milium Held, 1836	P.m.	10.5	0	0
P. moitessierianum (Paladilhe, 1866)	P.moit.	0	0	1.6
P. nitidum Jenyns, 1832	P.n.	63.2	47.4	27.4
P. pulchellum Jenyns, 1832	P.p.	5.3	0	0
P. subtruncatum Malm, 1855	P.s.	84.2	10.5	22.6
P. supinum A. Schmidt, 1851	P.sup.	36.8	42.2	46.8
Number of species		27	19	34

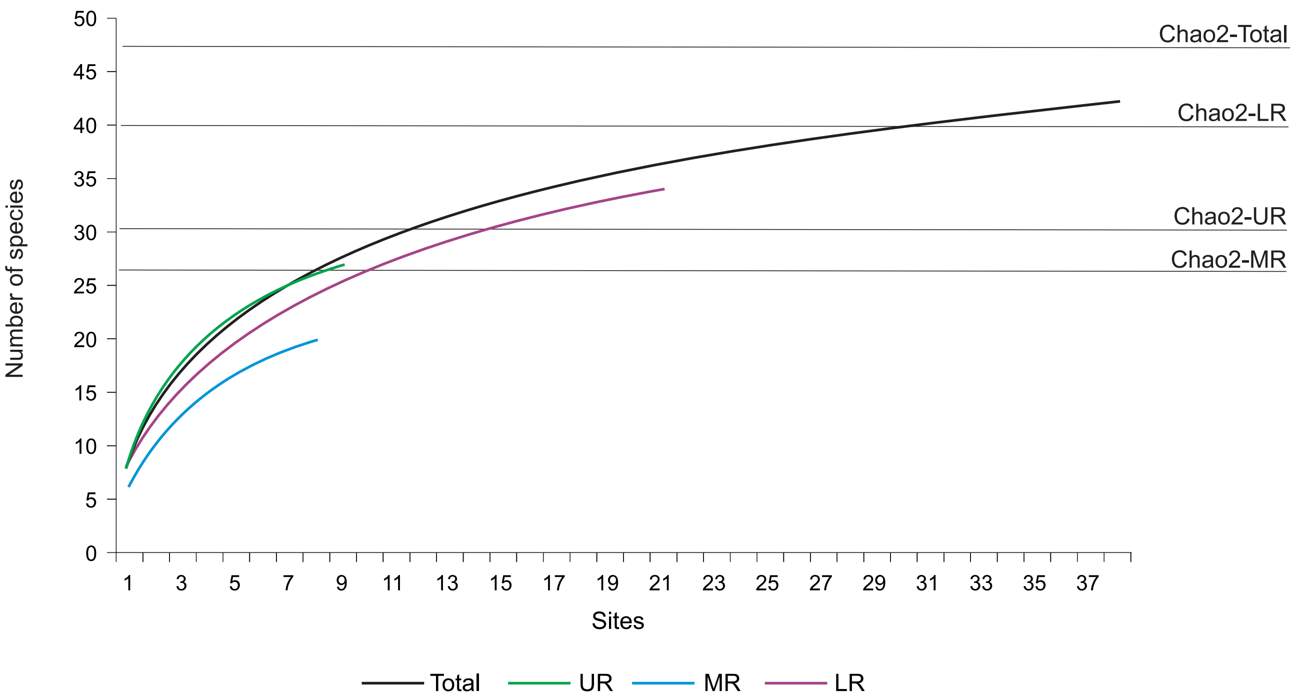

Fig. 2. Sample-based rarefaction curves of mollusc species richness for the whole study area and three river sections (UR, MR, LR); accumulation of re-sampled total observed species richness and expected species richness estimated with Chao2; Chao2-Total, Chao2-UR, Chao2-MR, Chao2-LR – expected species richness within the entire study area and in the upper, middle and lower river sections, respectively

common for the three river sections and 17 species were section-specific. UR and LR contributed to the pool of specific species (7 and 9 species, respectively) to a large extent, whereas only one species (*Physella acuta*) was found exclusively within MR.

Unio crassus deserves a special comment. It is included in the European Red List of Threatened Species (IUCN 2015) and is protected in Poland (Dz. U. 2014). *U. crassus* was found within the lower river section (7 sites).

STRUCTURE OF MOLLUSC ASSEMBLAGES IN THE UPPER, MIDDLE AND LOWER RIVER SECTIONS

The dominance pattern of mollusc assemblages varied among the sites, but there were some differences among the upper (UR), middle (MR) and lower (LR) sections (Table 2). UR was characterised by a smaller number of species, with the relative abundance exceeding 5% as compared to MR and LR. Overall, a high proportion of bivalves, especially Sphaeriidae, to the total mollusc abundance was observed both in the entire river (ca. 78%) and within UR, MR and LR (72.9%, 68.3% and 82.2%, respectively) (Table 2). A considerable proportion of large bivalves of the family Unionidae was observed only within LR (10.4%). From among prosobranch gastropods only *Bithynia tentaculata* constituted a significant percentage in the mollusc assemblages (UR and MR, 10.1% and 9.7%, respectively), whereas pulmonate snails *Radix ampla* and *R. auricularia* formed a considerable percentage only within MR (7.3% and 5.9%, respectively). The species abundance distribution along the river was characterised by a relatively high percentage of species represented by one or two individuals (23.8%).

Three species were common within UR – *Sphaerium corneum* (F = 57.9%), *Pisidium subtruncatum* (F = 84.2%) and *P. nitidum* (F = 63.2%) (Table 1). Both in MR and LR only one species occurred in more than 50% of the samples (*B. tentaculata* in MR and *S. corneum* in LR). Rare species, i.e. those found at one or two sites, formed a large fraction of the river malacofauna (13 species, i.e. 31%). Five rare species were recorded in UR, one in MR and eight in LR.

COMPARISON OF SPECIES RICHNESS, DIVERSITY AND ABUNDANCE AMONG THREE RIVER SECTIONS

The number of species at individual sites varied from 3 to 19. The mean species richness per site ranged from 6.6 ± 1.8 in MR to 9.0 ± 3.5 in UR (Table 3), but the values did not differ significantly ($p > 0.5$). The number of gastropod species at individual sites ranged from 0 to 12. The highest mean value was found in UR (the difference was marginally significant; $H(2, N = 38) = 3.99$, $p = 0.136$). The number of bivalve species at individual sites ranged from 2 to 10, but the mean values were similar within UR, MR and LR.

The mean values of Shannon index (H') and true diversity (exp(H')) were similar in UR, MR and LR. The values for individual sites varied widely (0.19–2.40 and 1.25–11.02 for H' and exp(H'), respectively), especially in UR and LR (Table 3). The abundance at individual sites ranged from 2 to 156, the maximum value was recorded at the beginning of LR, just below the junction with the Czerwonka River (L19). The mean abundance was the lowest within MR, and the difference was marginally significant ($H(2, N = 38) = 4.68$, $p = 0.096$).

Table 2. Percentage composition of mollusc assemblages in three sections of the Liwiec River: upper (UR), middle (MR), lower (LR) and whole river (Total)

Species	UR (%)	MR (%)	LR (%)	Total (%)
Prosobranchia	11.27	12.70	7.30	9.51
Bithynia tentaculata	10.12	9.68	2.44	6.12
Valvata cristata	0.04	0	0.34	0.31
V. macrostoma	0	0	0.07	0.04
V. piscinalis	0.14	3.02	1.67	1.26
Viviparus viviparus	0	0	2.78	1.42
V. contectus	0.97	0	0	0.36
Pulmonata	13.73	18.75	10.58	12.79
Lymnaea stagnalis	0.65	0.61	0.24	0.43
Radix ampla	0	7.26	1.38	1.54
R. auricularia	0	5.89	3.60	2.53
R. balthica	0	0.91	1.85	1.07
Stagnicola palustris	0.28	0	0	0.12
Galba truncatula	1.86	0	0.44	0.91
Aplexa hypnorum	0.56	0	0	0.20
Physa fontinalis	1.50	0	0.24	0.71
Physella acuta	0	2.27	0	0.28
Planorbarius corneus	1.25	0.30	0.91	0.99
Planorbis planorbis	0.28	0	0.15	0.20
Anisus leucostoma	1.25	0	0.10	0.51
A. septemgyratus	1.81	0	0	0.67
A. spirorbis	0	0	0.04	0.03
A. vortex	0.56	0.30	0.51	0.51
Gyraulus albus	1.53	1.21	0.81	1.1
G. rossmaessleri	1.83	0	0	0.67
G. crista	0.28	0	0.10	0.16
Hippeutis complanatus	0	0	0.14	0.08
Segmentina nitida	0.09	0	0.07	0.08
Unionidae	0.09	3.55	10.39	5.72
Anodonta anatina	0	0	2.07	1.03
A. cygnea	0	0	0.04	0.03
Unio crassus	0	0	0.70	0.36
U. pictorum	0	1.59	2.29	1.34
U. tumidus	0.09	1.96	5.29	2.96
Sphaeriidae	72.77	64.76	71.77	71.97
Sphaerium corneum	25.13	11.03	18.28	20.22
S. rivicola	0	2.20	0.17	0.36
Pisidium amnicum	6.96	1.51	14.24	10.08
P. casertanum	0	0	0.04	0.03
P. henslowanum	1.25	5.14	8.70	5.48
P. milium	0.28	0	0	0.12
P. moitessierianum	0	0.91	0.10	0.16
P. nitidum	7.75	7.25	3.66	5.60
P. pulchellum	0	0	0.04	0.03
P. subtruncatum	27.08	6.19	17.99	20.42
P. supinum	4.32	30.53	8.55	9.47

Table. 3. Species richness, diversity and abundance in the upper (UR), middle (MR) and lower (LR) sections of the Liwiec River – mean values ±SD and ranges of values (in parentheses); * – marginally significant differences

	UR	MR	LR
Number of mollusc species	9.0 ± 3.5 (3–15)	6.6 ± 1.8 (5–8)	8.3 ± 4.5 (3–19)
Number of gastropod species	4.8 ± 3.3* (0–11)	2.5 ± 1.9 (0–6)	2.7 ± 3.1 (0–12)
Number of bivalve species	4.2 ± 1.5 (2–6)	4.4 ± 2.1 (2–8)	5.5 ± 2.0 (3–10)
Shannon index (H')	1.33 ± 0.52 (0.71–2.18)	0.92 ± 0.34 (0.49–1.28)	1.06 ± 0.57 (0.19–2.40)
True diversity (exp(H'))	4.40 ± 2.43 (2.06–8.85)	2.78 ± 0.84 (1.82–3.72)	3.66 ± 2.33 (1.25–11.02)
Mean abundance	39.7 ± 32.1 (4–107)	12.8 ± 9.9* (4–34)	24.4 ± 35.6 (2–156)

LONGITUDINAL PATTERN OF MOLLUSC ASSEMBLAGES AND INFLUENCE OF SELECTED SPATIAL DISTURBANCES

The composition of mollusc assemblages within the Liwiec River showed some longitudinal changes, but there was no distinct trend along the river course. However, there were differences among the malacofauna of the upper, middle and lower river sections. Fourteen of the species present within UR were not found in MR (Table 1). Most of them were desiccation-tolerant and characteristic of small water bodies. Six additional species appeared in MR – four pulmonate gastropods regarded as tolerant of poor water quality and two bivalves. Seven gastropod species (mainly characteristic of small water bodies), recorded in UR, were found again in LR and nine new species appeared within this section – 4 gastropods and 5 bivalves.

The species richness varied much along the river (Fig. 3). Relatively more numerous gastropod species were recorded within UR and LR (up to 11 and 12 species, respectively) except the sites within the lower part of LR (L29 – L38) where only 0–3 species per site were found. The bivalve species richness showed smaller variation compared to gastropods and reached the highest values within LR (maximum 10 species at site L21). At 18 sites (over 47% of all sites) the bivalve species richness amounted to at least 5. Overall, the mollusc species richness was the smallest within MR, where only 25% sites held assemblages consisting of ≥ 7 species. The respective values for UR and LR were 88.6% and 47.6%. The value of Shannon index (H') exceeded 2.0 at only four sites, two of them located within the tributary confluences (L9, UR and L19, LR) and two within the links, i.e. sections between confluences (L5, UR and L35, LR) (Fig. 4). At 19 sites H' did not exceed 1.0. True diversity changes along the river course were compatible with those of Shannon index. The values of exp(H') exceeded 7 at four sites only (L5, L9, L19 and L35). The mean mollusc abundance at most of the sites ranged from a few to under 40 individuals per 1 m^2 of the bottom, higher values were recorded only at three sites in UR (maximum 107 indiv./m^2) and four sites in LR (maximum 156 indiv./m^2) (Fig. 5). Two sites with the greatest mollusc abundance were located downstream of the tributary confluences (L9, L19) and one within the dammed section of the river (L28).

The comparison of mollusc assemblages of the tributary confluences and the links revealed that the effect of tributaries on the changes in mollusc assemblages within the main channel was relatively weak (not statistically significant). The mean species similarity (J) between the sites positioned directly upstream and downstream of the studied confluences did not differ compared to J values between pairs of consecutive sites located within the links (J = 0.31 ± 0.15 and J = 0.34 ± 0.12, respectively; U = 51.00, Z = 0.2581, p = 0.7964). However, a distinct increase in species richness (from 6 to 15 species) (Fig. 3) was observed within the junction with Helenka (UR). In the case of the next tributary (Czerwonka, MR) the species number downstream of the confluence increased by six, whereas the tendency was not observed in the other two junctions located within the lower Liwiec (with Miedzanka and Osownica). The Shannon index increased downstream of the confluences with Helenka, Czerwonka and Miedzanka (from 0.96 to 2.0, 1.66 to 2.02 and 0.72 to 1.29, respectively), whereas it showed a decreasing trend below the junction with Osownica (from 1.55 to 1.12). The course of changes in true diversity (exp(H')) downstream of the confluences was similar to that of the Shannon index. The mollusc abundance increased considerably downstream of the confluences with Helenka and Czerwonka, but no distinct changes were observed in the junctions with Miedzanka and Osownica (Fig. 5). Some differences in the dominance pattern of mollusc assemblages at sites upstream and downstream of the tributary junctions were observed (Figs 6–9). The differences concerned mainly changes in proportions of dominant species, replacement of dominants was rare. They were more distinct than the differences between consecutive sites within the links (e.g. Fig. 10).

Another potential source of the Liwiec River discontinuity – discharge from sewage treatment plants – seemed to have a more distinct effect on the mollusc assemblages, compared to the tributaries. The

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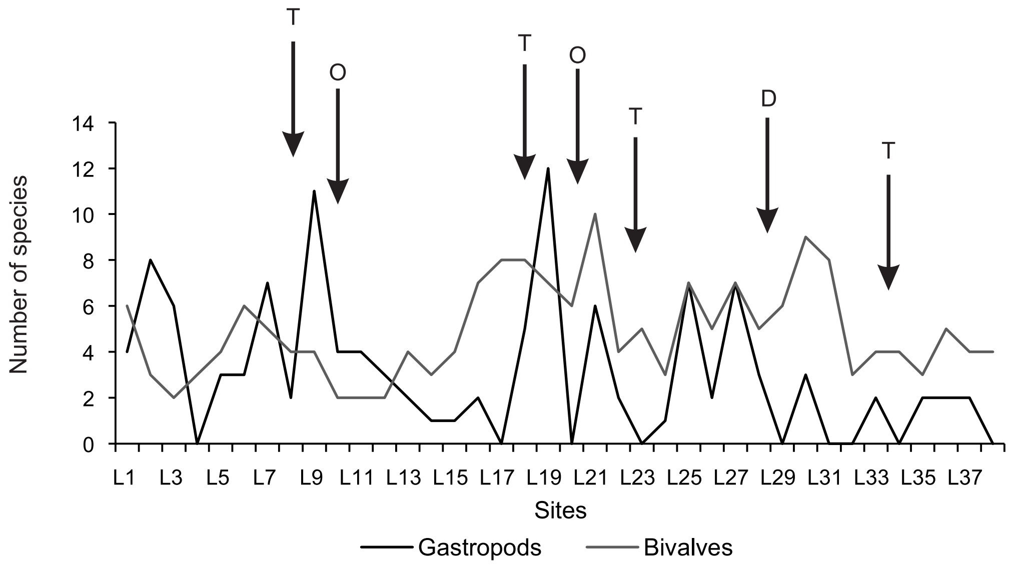

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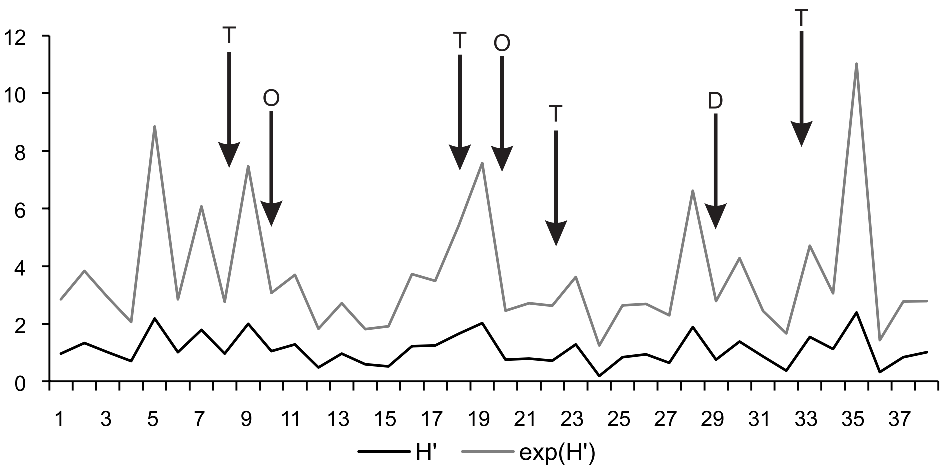

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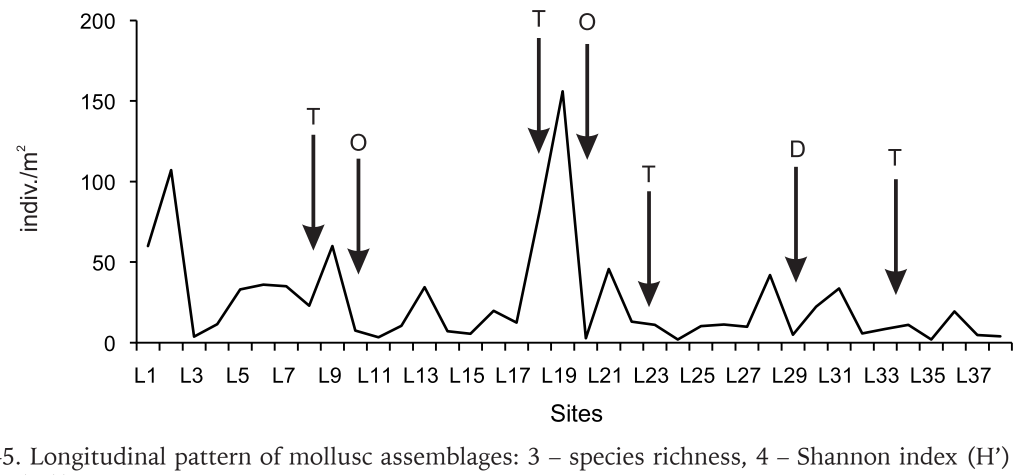
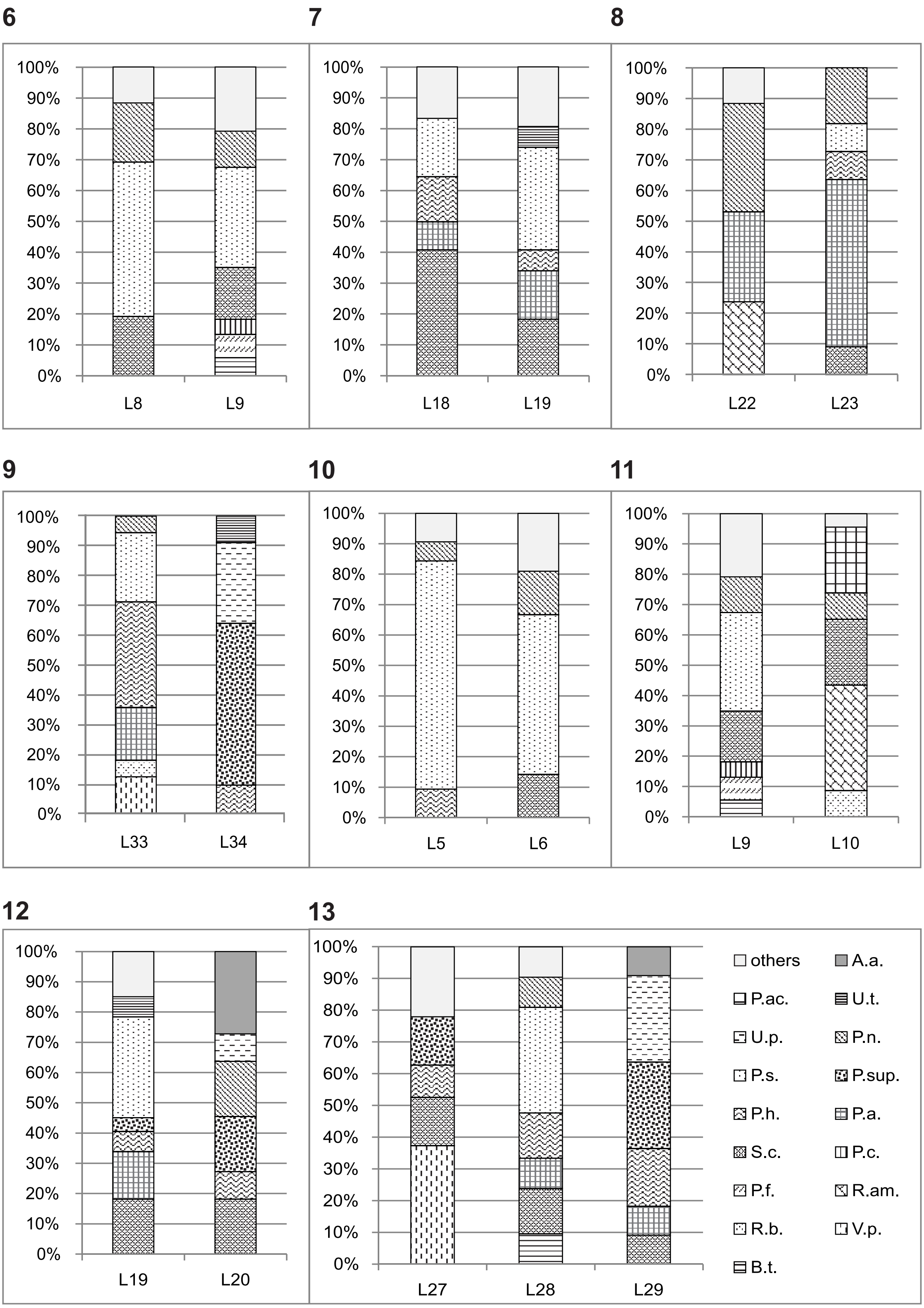


Figs 3–5. Longitudinal pattern of mollusc assemblages: 3 – species richness, 4 – Shannon index (H') and true diversity (exp (H')), 5 – abundance; arrows indicate discontinuities in the river course which have been included in the study; T – tributaries, O – discharge from sewage treatment plants, D – small dam



Figs 6–13. Comparison of dominance patterns of mollusc assemblages upstream and downstream of discontinuities studied within the Liwiec River: 6 – the confluence with Helenka (UR), 7 – the confluence with Czerwonka (MR), 8 – the confluence with Miedzanka, 9 – the confluence with Osownica, 10 – selected pair of sites located within river section between consecutive discontinuities and characterised by the largest difference in dominance patterns (treated as a reference), 11 – discharge from sewage treatment plant in Siedlce, 12 – discharge from sewage treatment plant in Węgrów, 13 – sites above, within and below dammed river section; for species labels see Table 1

malacofauna of the sites located upstream and downstream of the channel outlets differed substantially (J values 0.17 and 0.19, respectively). The species richness sharply declined below the outlets – from 15 to 6 and from 19 to 6 below the sewage treatment plants in Siedlce and Węgrów, respectively. Likewise, the Shannon index distinctly decreased (from 2.0 to 1.05 and from 2.02 to 0.76, respectively) and the true diversity (exp(H')) showed a similar trend (Fig. 4). A considerable decrease in mollusc abundance downstream of the outlets was observed – from 60 to 7 indiv./m^2 and from 156 to 3 indiv./m^2, respectively (Fig. 5). Differences in the dominance pattern of mollusc assemblages upstream and downstream of the outlets were also rather distinct (Figs 11–12). Replacement of dominants was more frequent than in the case of tributary junctions.

The small dam in the village Kalinowiec was another disturbance in the river continuity. The mollusc assemblages differed between the free-flowing and the dammed river sections (L27 and L28), as well as upstream and downstream of the dam (L28 and L29), in both composition (J = 0.375 and J = 0.273, respectively) and dominance pattern (Fig. 13). The number of species increased slightly from L27 (7 species) to L28 (8 species) and decreased from L28 to L29 (6 species). The Shannon index distinctly increased in the dammed river section and declined below the dam (0.64, 1.88 and 0.76 at sites L27, L28 and L29, respectively) (Fig. 4). A similar trend was observed for exp(H'). The mollusc abundance was the highest within the dammed section (42 indiv./m^2 at L28) and the lowest downstream of the dam (5 indiv./m^2 at L29) (Fig. 5).

DISCUSSION

The species richness found in this study along the entire length of the Liwiec River was distinctly higher than that recorded by Korycińska (2002). Only two of the earlier recorded gastropods (*Planorbis carinatus* and *Bathyomphalus contortus*) were not re-found, whereas another 12 species, not found previously, were recorded (*Viviparus viviparus*, *Valvata cristata*, *V. macrostoma*, *Radix ampla*, *Aplexa hypnorum*, *Anisus septemgyratus*, *A. spirorbis*, *A. leucostoma*, *Gyraulus albus*, *G. rossmaessleri*, *Gyraulus crista*, and *Physella acuta*). These species are mostly relatively desiccation-resistant and associated with shallow habitats near the river banks; it is likely that the majority of them is of the floodplain origin. The present study revealed the occurrence of additional bivalve species – two unionids (*Anodonta anatina* and *A. cygnea*) and 11 sphaeriids. The exact comparison of bivalve species richness was not possible, because in the earlier study (Korycińska 2002) small bivalves of the genera *Sphaerium* and *Pisidium* were not identified to the species level.

The mollusc species richness in the Liwiec River channel was higher than or similar to the values reported from some other medium-sized lowland and upland rivers in Poland (Piechocki 1981) and some Czech rivers of similar nature (Beran 2013). It was considerably higher than in a number of medium-sized Lithuanian rivers (Pliūraitė & Kesminas 2004), as well as in tributaries of the Danube and Tisza rivers (Bódis et al. 2016). A relatively small total species richness (up to 5 species) was found at 26% of all sites and a small mean species richness (i.e. α-diversity) up to 3 was noted at 32% of sites. However, a considerable turnover in the mollusc species sets (i.e. 1-S_j, where S_j – Jaccard similarity) was observed among individual sites (0.50–0.91), which resulted in a rather high total richness (γ-diversity). A high possibility of migration due to connectivity within the river channel should be expected to reduce the β component of the diversity (i.e. variation among sites) and increase the α-diversity. However, dispersal may interact with local competition (and/or predation) to control the balance between α and β diversity in different ways in individual patches of the river channel (e.g. Loreau 2000). Another reason for small α-diversity within the river channel may be low productivity, which may be conducive to stochastic extinction of less well adapted species, maintained by dispersal in the patches. River bed disturbance dependent on particle size of the bottom substratum may also be a very important factor affecting species richness (e.g. Townsend et al. 1997). In the Liwiec River sandy bottom prevails, which is unstable and thus conducive to disturbance.

According to Mouthon (1999) who described longitudinal changes in mollusc assemblages in a theoretical French river, the highest mollusc diversity should be expected in lower reaches. A similar pattern was reported from the Dyje River in the Czech Republic (Beran 2013). The results presented here, as well as the earlier data of Korycińska (2002) generally confirm this pattern. However, a rich malacofauna was also found within the upper section which is consistent with Piechocki's (1979) opinion concerning headwaters of lowland rivers. In contrast to the middle and lower sections, the upper Liwiec River is canalised. The high mollusc diversity in UR may result partially from the connectivity with the floodplain, which has retained its natural character and may supply a number of species characteristic of small water bodies. Local habitat conditions and land use are recognised as important factors shaping invertebrate diversity patterns in streams (e.g. TONKIN et al. 2016). The good water quality (REPORT 2015) may also promote species richness within this river section.

MOUTHON (1999) pointed to differences in the composition of mollusc assemblages among upper, middle and lower river sections. The results of the present study generally confirm such differences, but the wide variation among individual sites located within each of the three river sections may considerably obscure any longitudinal trends of mollusc assemblages. On the other hand, the Liwiec being a lowland river lacks abrupt changes in slope which are important in determining faunal zones (STATZNER & HIGLER 1986 and references therein).

The longitudinal patterns of mollusc assemblages may be disturbed by the discontinuities of natural and anthropogenic origin existing along the Liwiec River, for example tributaries, discharge from sewage treatment plants, weirs and dams. According to the Link Discontinuity Concept (RICE et al. 2001), characteristics of macro-invertebrate communities tend to change significantly and suddenly at confluences while exhibiting less remarkable, gradual changes or unstructured variation along the links (i.e. sections between two consecutive tributaries). The effect of the tributaries on the mollusc assemblages in the Liwiec River was varied and rather weak. The increase in species richness and abundance found at two confluences, with Helenka (UR) and Czerwonka (MR), may have resulted from a supply of molluscs by these tributaries and an enhanced local habitat heterogeneity within the confluences, which provided refuges (e.g. RICE et al. 2001, BENDA et al. 2004a, b). The lack of similar changes in the mollusc assemblages within the other two confluences (with Miedzanka and Osownica) located within LR is not clear. It may partially result from the small size of those tributaries compared to the main channel. In such cases the influence on the channel morphology and indirectly on the mollusc assemblages may be expected to be small (RHOADS 1987, BENDA et al. 2004a). By contrast, it is likely that the mouths of those tributaries are considerably affected by the main river during high flow (BECKMANN et al. 2005). This could be also the cause of the small species richness in those highly variable habitats (3 species including single individuals of one species not found in the Liwiec River; own observations).

A considerable decrease in the species richness was recorded at sites below the discharge from the sewage treatment plants in Siedlce and Węgrów, despite the good chemical parameters of the discharged water after recent modernisation. However, slowing down of the river velocity by weirs in the downstream sections may be conducive to eutrophication. The bottom sediments, especially those accumulated in the section below Siedlce, are still muddy and tubificid worms (Oligochaeta) are abundant there (own observation), indicating low quality of the habitat. The ecological condition of the river within this section was characterised as poor, whereas its macro-invertebrate benthos index was assessed as moderate (REPORT 2015). However, ARCE et al. (2014) showed that recovery in invertebrate communities following wastewater treatment improvement may take more than a few years.

The small dam and hydroelectric power station in the village Kalinowiec seemed to affect the mollusc assemblages even more than the tributaries and the discharge from sewage treatment plants. River damming is regarded as the factor which strongly affects mollusc assemblages, leading to changes in their composition and decrease in diversity due to changes in hydrological regime and physico-chemical characteristics, development of bottom sediments differing from riverine deposits etc. (e.g. FRUGET 1992, DETHIER & CASTELLA 2002, JURKIEWICZ-KARNKOWSKA 2004 and references cited therein).

Despite the lack of spectacular influence of river discontinuities on the species richness, diversity, composition and abundance of mollusc assemblages, the observed changes were more visible than the differences among consecutive sites within the free flowing river sections.

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Appendix 1

Environmental characteristics of sampling sites. * – side channel (main river channel width >15 m); bottom sediments: s – sandy, sg – sandy-gravelly, sc – sandy-clayey, sm – sandy-muddy, smd – sandy-muddy with detritus, md – muddy with detritus, cd – clayey with detritus; macrophytes: 0 – absent, 1 – sparse, 2 – moderate; canopy: 0 – absent, 1 – poor, i.e. few trees or high shrubs, 2 – moderate

Site	River section	Geographic coordinates		Width (m)	Depth (m)	Current velocity (m s^{-1})	Bottom sediments	Macrophytes	Canopy
		latitude	longitude						
L1	UR	52°10'25"N	22°29'09"E	<5	<0.5	0.2–0.25	smd	1	0
L2	UR	52°10'33"N	22°29'50"E	<5	<0.5	<0.1	cd	2	0
L3	UR	52°11'15"N	22°33'25"E	<5	<0.5	<0.1	sm	1	2
L4	UR	52°10'58"N	22°26'07"E	<5	<0.5	0.1–0.2	sm	2	0
L5	UR	52°11'42"N	22°24'24"E	<5	0.5–1	0.1–0.2	smd	2	0
L6	UR	52°13'19"N	22°21'23"E	5–10	<0.5	0.1–0.2	smd	1	0
L7	UR	52°13'05"N	22°16'38"E	5–10	0.5–1	0.1–0.2	sm	2	2
L8	UR	52°12'45"N	22°15'22"E	5–10	0.5–1	0.1–0.2	sm	1	1
L9	UR	52°12'44"N	22°15'22"E	5–10	0.5–1	0.1–0.2	smd	1	0
L10	MR	52°12'31"N	22°13'16"E	5–10	>1	<0.1	md	1	0
L11	MR	52°12'55"N	22°12'47"E	5–10	0.5–1	0.1–0.2	sm	1	0
L12	MR	52°13'48"N	22°09'40"E	5–10	0.5–1	0.1–0.2	sm	1	0
L13	MR	52°15'07"N	22°05'42"E	5–10	0.5–1	0.2–0.25	sg	2	1
L14	MR	52°15'31"N	22°05'26"E	10–15	>1	0.2–0.25	sm	2	0
L15	MR	52°15'12"N	22°05'39"E	5–10	>1	0.2–0.25	s	1	0
L16	MR	52°18'09"N	22°00'19"E	10–15	>1	0.2–0.25	sm	2	1
L17	MR	52°22'55"N	21°59'18"E	10–15	>1	>0.25	sm	1	0
L18	LR	52°24'42"N	21°59'54"E	10–15	>1	0.2–0.25	s	1	0
L19	LR	52°24'57"N	21°59'21"E	>15	>1	0.2–0.25	sm	1	1
L20	LR	52°25'19"N	21°58'09"E	10–15	0.5–1	>0.25	s	0	0
L21	LR	52°25'27"N	21°57'51"E	10–15	0.5–1	0.2–0.25	sg	0	0
L22	LR	52°26'16"N	21°57'22"E	10–15	0.5–1	0.2–0.25	sm	1	0
L23	LR	52°26'18"N	21°57'19"E	>15	0.5–1	0.2–0.25	smd	1	1
L24	LR	52°26'47"N	21°55'41"E	5–10	>1	0.2–0.25	s	0	0
L25	LR	52°27'40"N	21°54'38"E	10–15?	0.5–1	0.2–0.25	sg	0	0
L26	LR	52°27'45"N	21°53'31"E	10–15?	0.5–1	0.2–0.25	s	1	0
L27	LR	52°28'16"N	21°52'03"E	5–10	0.5–1	0.2–0.25	s	1	1
L28	LR	52°28'33"N	21°50'38"E	>15	>1	<0.1	smd	1	0
L29	LR	52°28'37"N	21°50'07"E	10–15	0.5–1	0.2–0.25	sc	0	1
L30	LR	52°29'06"N	21°46'25"E	>15	0.5–1	0.2–0.25	s	0	0
L31	LR	52°30'49"N	21°41'23"E	>15	0.5–1	0.1–0.2	sm	1	1
L32	LR	52°30'35"N	21°40'45"E	>15	<0.5	0.1–0.2	s	0	0
L33	LR	52°30'40"N	21°38'25"E	>15	0.5–1	0.2–0.25	s	1	0
L34	LR	52°30'37"N	21°38'16"E	>15	>1	0.2–0.25	s	1	0
L35	LR	52°31'12"N	21°37'30"E	>15	0.5–1	0.2–0.25	sg	1	0
L36	LR	52°32'26"N	21°36'14"E	>15	0.5–1	0.2–0.25	s	1	0
L37	LR	52°35'38"N	21°33'47"E	<5*	0.5–1	>0.25	s	1	1
L38	LR	52°35'28"N	21°35'02"E	>15	0.5–1	<<0.1	smd	2	1