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SAMPLING INTENSITY IN BIODIVERSITY ASSESSMENT: MALACOFAUNA OF SELECTED FLOODPLAIN WATER BODIES

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ABSTRACT: The assessment of completeness of mollusc species lists in selected permanent and temporary floodplain water bodies located within the lower Bug River valley, as well as estimation of the minimum number of samples required to obtain an acceptable efficiency of inventory in individual water bodies, was carried out using sample-based rarefaction curves and non-parametric estimator Chao2. The effect of sampling effort on different measures of species diversity (species richness, Shannon diversity exp(H')) was examined. Dependence of sampling effort, inventories completeness and diversity measures on habitat stability was analysed by comparing permanent and temporary water bodies. Mollusc assemblages of the investigated water bodies showed high temporal and spatial variability, as well as inter-habitat differences (relatively low Jaccard's similarity coefficient, J). Significant differences in diversity and composition of mollusc assemblages were found between permanent and temporary habitats, whereas species richness was similar in both permanence groups. In general, both species richness and diversity increased similarly with growing sampling effort. Total richness accuracy reached at least 90% of the predicted value (calculated with Chao2) with 5 to 14 random samples, depending on the water body (10–14 samples in permanent habitats and 5–10 samples in temporary ones).

KEY WORDS: aquatic molluscs, species richness, diversity, sampling effort, data set completeness

INTRODUCTION

Assessment of species diversity in different sites and comparisons among them demands completeness of species lists. Species accumulation curves are a good way of assessing inventory completeness and standardising the comparisons of different inventories (SOBERÓN & LLORENTE 1993). The cumulative number of species is plotted against some measure of sampling effort: numbers of individuals collected, number of samples, traps, trap-days or some other measures of area or time (COLWELL & CODDINGTON 1994). The curves reach an asymptote when the probability of adding a new species to the list approaches zero. Species accumulation curves may also enable reliable estimates of the effort required to obtain an efficient inventory (MORENO & HALFFTER 2000, HALSE et al. 2002, BERGALLO et al. 2003, THOMPSON et al. 2007).

Natural or slightly affected river floodplains are among the most heterogenous and species-rich areas (NAIMAN et al. 1993, TOCKNER & STANFORD 2002, DUDGEON et al. 2006). Aquatic habitats located there show high spatial and temporal variability in physical and chemical characteristics, which favours diversity in the community composition of water bodies. Temporary hydrological connectivity during flood or higher water level in the river channel enables migration of organisms among habitats.

Aquatic molluscs, especially gastropods, are significant components of macroinvertebrate fauna in many riparian environments (e.g. RICHARDOT-COULET et al. 1987, CASTELLA et al. 1991, FOECKLER et al. 1991, OBRDLIK & FUCHS 1991, VAN DEN BRINK & VAN DER VELDE 1991). Species-rich aquatic malacocoenoses have been reported from river floodplains (e.g. Obrdlik et al. 1995, Weigand & Stadler 2000, Jurkiewicz-Karnkowska 2008, 2009).

Aquatic habitats within the lower Bug River valley are characterised by high diversity despite the presence of a flood control embankment along long sections of its left bank. Earlier investigations of a stretch of 150 km revealed that within this heterogenous area more than 60 samples would be necessary to obtain a nearly complete list of aquatic molluscs (Jurkiewicz-Karnkowska 2009).

The aim of the present study was to assess the completeness of mollusc species lists in selected permanent (more stable) and temporary (less stable) floodplain water bodies located within the lower Bug River valley and to estimate the minimum number of samples required to achieve an acceptable efficiency of inventory in each of them. The effect of sampling effort on different measures of species diversity (species richness, Shannon diversity exp(H')) was examined. Dependence of sampling effort, inventory completeness and diversity measures on habitat stability was analysed.

STUDY AREA AND METHODS

The investigations were carried out in five permanent (relatively stable) and five temporary (unstable) floodplain water bodies located within the lower Bug River valley, between 125 and 53 km of the river course (Fig. 1). The general characteristics of the investigated habitats are presented in Table 1. The active floodplain in the left-bank section is considerably constrained by the flood control embankment except for a short fragment (58–53 km). The right-bank side of the valley has retained a relatively natural character. The investigated sites were located within the fragments of natural floodplain, the active one constrained by the embankment and the former one situated outside the embankment. Most of them represented relatively early succession stages (assessed based on the extent of overgrowing by macrophytes and type of bottom sediments; Jurkiewicz-Karnkowska 2011).

Molluscs were sampled in 2006–2012 during the period from May to September using a hand net with working side of 25 cm, mesh size of 0.5 mm and handle length of 2 m. Individual water bodies were investigated in 4–6 sampling events and 2–6 samples were taken, depending on the habitat size and heterogeneity. Samples were collected within a zone extending from the water body margin to a depth of 1.5 m. Molluscs taken from the bottom (from an area of 1.0 m^2) and macrophytes were washed on a sieve of 0.5 mm mesh and preserved in 75% ethyl alcohol. In the laboratory the animals were sorted, counted and identified using the keys of Piechocki (1979) and Piechocki & Dyduch-Falniowska (1993). The systematic nomenclature follows Piechocki (2008).

Samples were collected until an almost complete list of species was obtained, i.e. when total observed richness exceeded 90% of the predicted value (e.g. Moreno & Halffter 2000, Thompson et al. 2007). Sampling effort necessary to obtain representative data sets (i.e. ≥70% of the total estimated number of species, according to Mackey et al. 1984) in each water body was also assessed.

The total species richness 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 non-parametric estimator Chao2 was chosen to estimate predicted values of species richness in the investigated water bodies based on its observed performance in other stud-

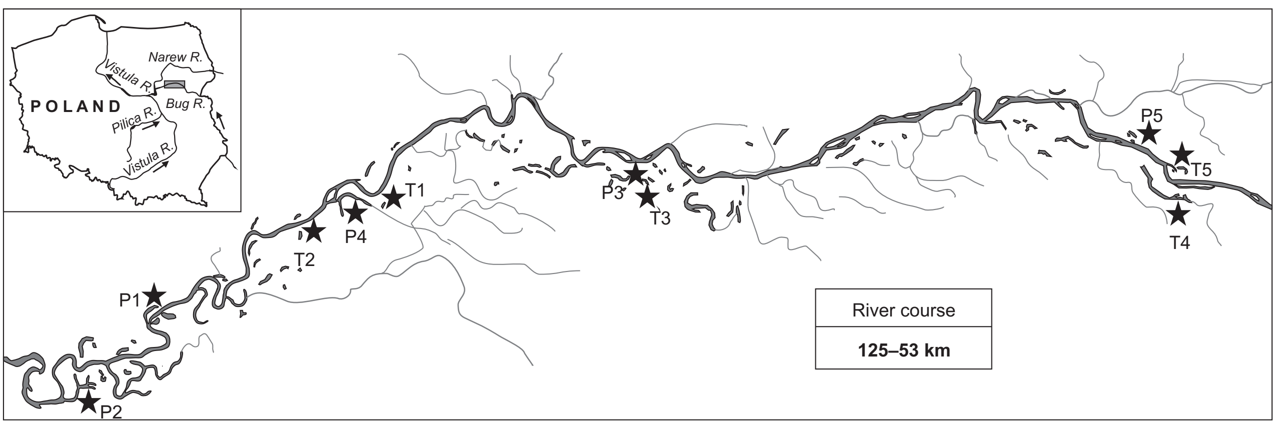

Fig. 1. Study area (grey rectangle) and location of individual water bodies: P1–P5 – permanent habitats, T1–T5 – temporary habitats

Table 1. General characteristics of water bodies; location within the floodplain: n – natural floodplain, w – active floodplain constrained by the embankment, z – outside the embankment; succession stage: 1 – young habitats, 2 – intermediate stages, 3 – old, i.e. with strongly advanced succession; hydrological connectivity: 1 – isolated water bodies (outside the embankment), 2 – sites located outside the embankment which retained a limited connection with the active floodplain (through culverts), 3 – water bodies situated within the active floodplain, but far from the river channel, 4 – sites located relatively close to the river channel, 5 – sites with surface connectivity

	Permanent water bodies				
	P1	P2	P3	P4	P5
Geographical coordinates	52°40.814'N 21°56.388'E	52°36.177'N 21°39.206'E	52°40.695'N 21°56.491'E	52°40.075'N 21°46.974'E	52°40.838'N 22°15.694'E
Approximate size (m^2)	>1,000	>1,000	>1,000	>1,000	>1,000
Approximate depth (m)	>2	>2	>2	<2	<2
Location within the floodplain	n	n	z	w	n
Succession stage	1	1	2	2	1
Connectivity	4	5	2	5	5
	Temporary water bodies				
	T1	T2	T3	T4	T5
Geographical coordinates	52°39.999'N 21°47.190'E	52°39.111'N 21°44.029'E	52°40.522'N 21°57.332'E	52°39.860'N 22°11.494'E	52°40.316'N 22°16.913'E
Approximate size (m^2)	<500	>1,000	<500	<500	500–1,000
Approximate depth (m)	<1	<1	<1	<0.5	<1
Location within the floodplain	z	w	z	z	n
Succession stage	2	1	1	1	3
Connectivity	2	3	2	1	3

ies (e.g. COLWELL & CODDINGTON 1994, HORTAL et al. 2006, SOBERÓN et al. 2007). Chao2 is based on the presence of singletons and doubletons within a data set. The Shannon diversity (exp(H'), where H' = −sum(p_i lnp_i); JOST 2006) was calculated based on mollusc abundance data. Within- and inter-habitat similarity of mollusc assemblages, as well as similarity between different months was analysed using Jaccard's similarity coefficient (J). All the above-mentioned calculations were carried out with EstimateS, v.8.0 software (COLWELL 2004). Data on species richness, diversity and similarity were analysed with non-parametric tests: U Mann-Whitney and Kruskal-Wallis ANOVA. Spearman's correlation between the number of species and diversity (exp(H')) was calculated (STATISTICA 10.0, StatSoft).

RESULTS

Fifty seven mollusc species were recorded in the studied water bodies. Permanent habitats harboured 51 species. In temporary waters only 35 species were found and 29 of them occurred also in permanent ones. The total species richness (i.e. total number of species found in all samples collected in a given water body) was higher in permanent water bodies than in temporary ones (Table 2). The values of species richness differed among the sampling occasions and within a given water body during the same occasion, and their ranges were wider in permanent water bodies than in temporary ones. The mean species richness in individual permanent water bodies was 7.1–10.4 species per sample and it ranged from 6.1 to 11.7 in temporary ones (Fig. 2A). The values of mean species richness were not significantly different when comparing permanent and temporary water bodies or individual habitats within permanent habitats, whereas some differences were found within the group of temporary habitats (Appendix 1).

The species diversity of mollusc assemblages (exp(H')) ranged from 1.65 to 46.06 in permanent water bodies and from 1.67 to 26.05 in temporary ones. The mean exp(H') values were significantly higher in permanent water bodies than in temporary ones, significant differences were also found among individual habitats within the permanence groups (Fig. 2B, Appendix 1).

The considerable spatial and temporal variability of mollusc assemblage composition in the investigated water bodies resulted in relatively low species similarity (Jaccard's similarity coefficient, J). The J values were especially low among different samples taken at one sampling occasion within individual permanent water bodies (Fig. 3A), indicating a high internal variability of the malacofauna. In temporary habitats, compared to permanent ones, the spatial variability of mollusc assemblages (i.e. within-habitat differences) was significantly lower (p=0.0001, see Appendix 1) and it resulted in distinctly higher species similarity among samples taken from a given

Table 2. Total number of species and species richness per sample, Chao2 values and completeness of the inventory in the studied permanent and temporary water bodies

Water body code	Number of samples	Number of sampling events	Total number of species	Species richness per sample	Chao2 value	Completeness of inventory (%)
Permanent water bodies						
P1	13	2	23	2–15	24.85	92.56
P2	14	3	29	3–20	30.11	96.31
P3	17	5	31	2–16	31.63	98.00
P4	16	6	34	4–17	36.35	94.00
P5	18	5	34	2–20	35.98	94.52
Temporary water bodies						
T1	6	4	18	7–11	19.00	94.73
T2	7	4	20	3–13	20.64	96.89
T3	7	4	21	9–14	22.71	92.47
T4	10	5	15	3–8	16.35	91.74
T5	9	5	18	2–13	18.53	97.14

water body (mean J value amounted to 0.57). The composition of malacofauna in different months within one season showed considerable similarity in water bodies from both permanence groups, the mean J value exceeded 0.5 (Fig. 3B, Appendix 1). The similarity among mollusc assemblages of individual water bodies within both permanence groups was slightly lower (mean J value was 0.47 and 0.42 among permanent and temporary water bodies, respectively) (Fig. 3C). Comparison of mollusc assemblages composition of each individual permanent habitat with each temporary one revealed a very low

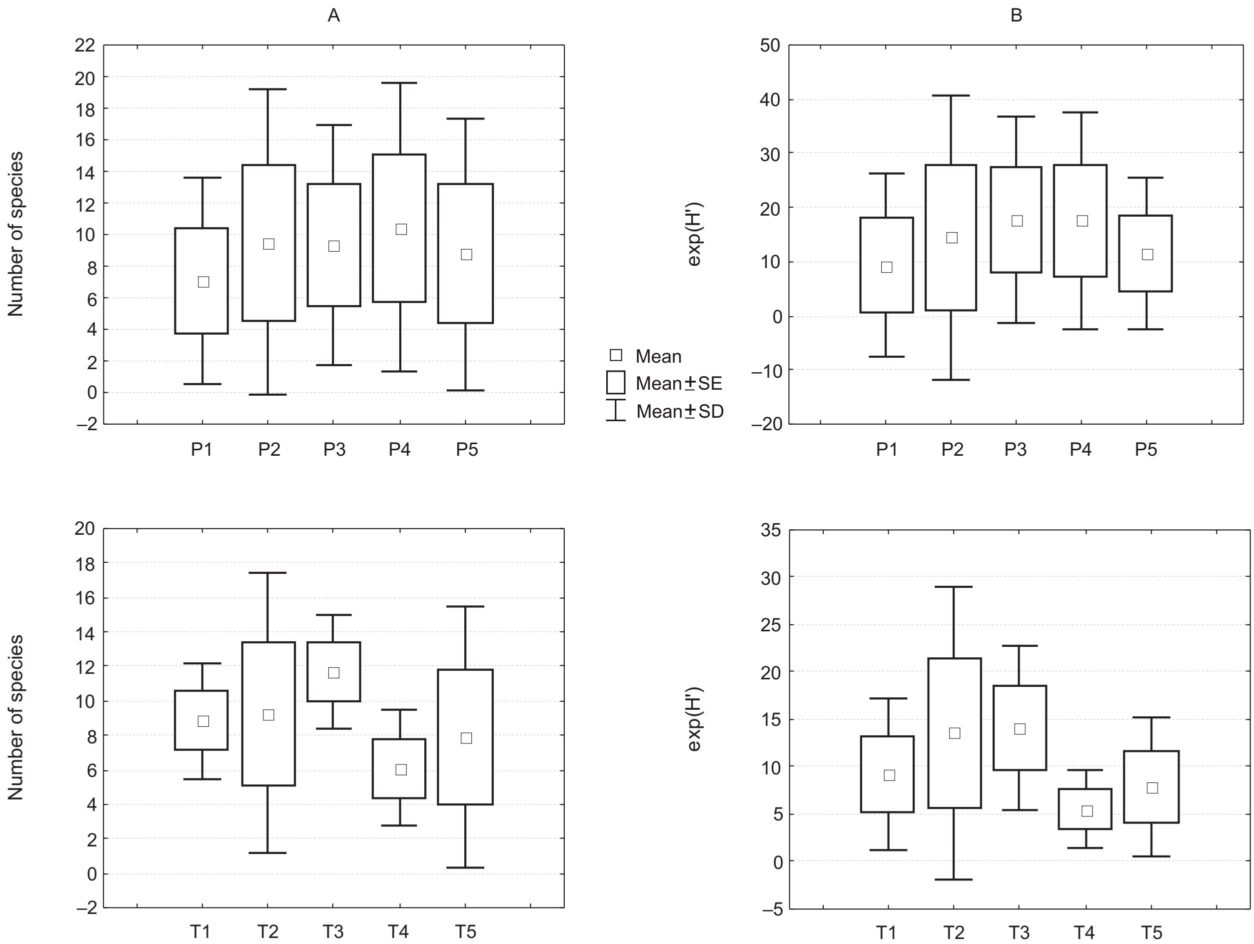

Fig. 2. Mean species richness (A) and mean species diversity (B) of mollusc assemblages in the investigated water bodies; P1–P5 and T1–T5, see Fig. 1

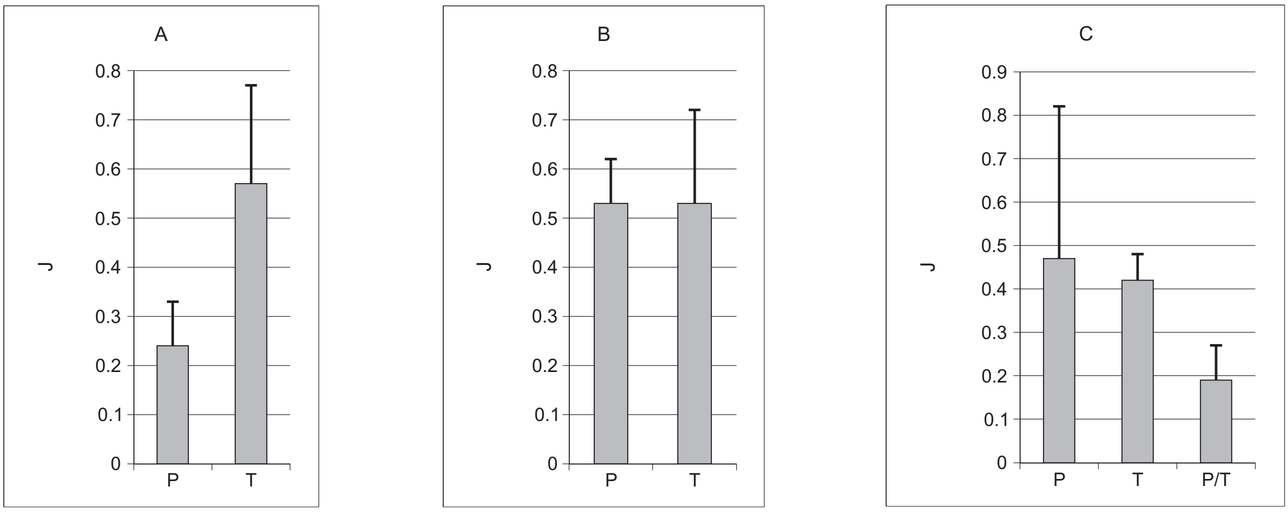

Fig. 3. Similarity of mollusc assemblages composition (J) within individual water bodies from two permanence groups at one sampling occasion (A), within individual water bodies from two permanence groups in different months within one season (B), within and between permanence groups (C) in the same year (2012); P – permanent water bodies, T – temporary habitats, P/T – comparison between each permanent and each temporary water body

species similarity (mean J value was 0.19). The mean J value was significantly lower than in the comparisons within the permanence groups (Appendix 1).

The species diversity (exp(H')) was generally related to species richness (t(N–2) = 9.41, df = 115, R = 0.66, p < 0.0001), the correlation was stronger in temporary water bodies than in permanent ones (t(N–2) = 9.24, df = 37, R = 0.84, p < 0.0001 and t(N–2) = 6.76, df = 76, R = 0.61, p < 0.0001, respectively). The correlation between species richness and diversity in individual water bodies was statistically significant only in half of the cases (Appendix 2). Both the species richness and the diversity (exp(H')) increased with growing number of samples (Figs 4 and 5). In general both the diversity measures approached asymptotes. In the case of temporary water bodies 4–6 samples were sufficient to obtain the value exceeding 90% of the maximum observed exp(H') and 4–7 samples were necessary to get at least 90% of the maximum observed species richness. For permanent water bodies 5–13 samples were enough to obtain at least 90% of the maximum exp(H') and 7–12 samples were necessary to get at least 90% of the maximum species richness.

Permanent water bodies had higher predicted species richness values (Chao2) than temporary ones (Table 2). The completeness of inventories in each of the water bodies studied exceeded 90%, but more sampling effort was necessary to achieve these results in permanent water bodies than in temporary ones. The total observed richness accuracy reached at least 90% of the predicted value (calculated with non-parametric estimator Chao2) with 5 to 14 random samples, depending on the water body (Fig. 6). Generally lower numbers of samples were necessary to complete species list in temporary habitats (5–10) which were characterised by a less variable composition of mollusc assemblages. In the case of

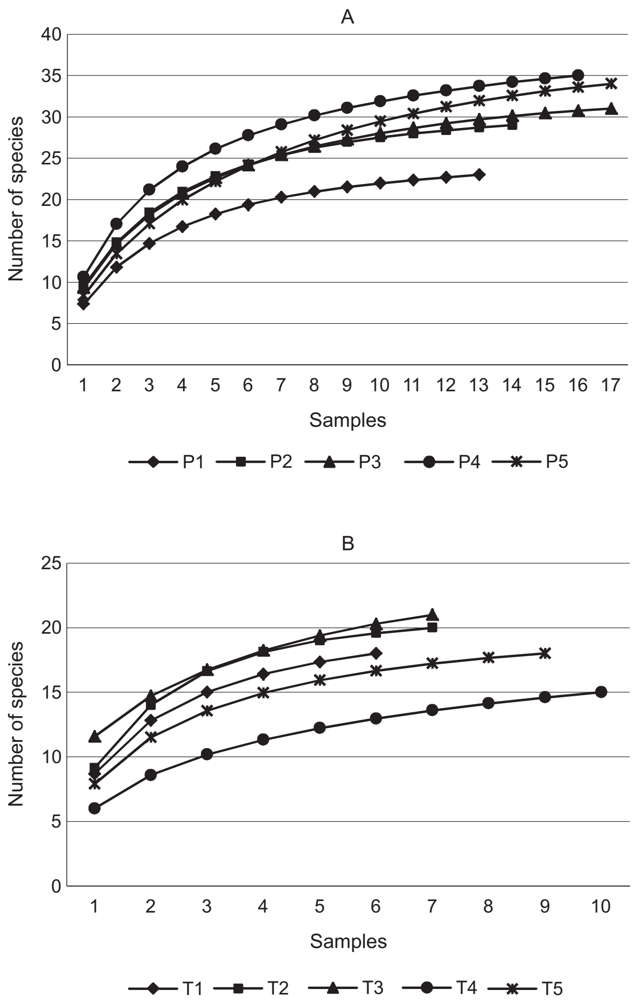

Fig. 4. The effect of sampling effort on species richness: permanent (A) and temporary (B) water bodies

permanent water bodies 10–14 samples were needed to obtain ≥ 90% of the predicted species richness. When representative data were sufficient (i.e. ≥70% of the expected number of species) considerably lower numbers of samples were necessary: 5–7 in the case of permanent water bodies and 3–5 in temporary ones.

DISCUSSION

The total number of species found in permanent water bodies studied (in all samples collected in these habitats) was distinctly higher than the respective value for temporary habitats. The mean species diversity (exp(H')) was significantly higher in permanent habitats than in temporary ones, whereas no difference was found in the mean number of species. However, the composition of mollusc assemblages differed between these two permanence groups and within each of them. Different patterns of mollusc assemblage composition in permanent and temporary water bodies may reflect two different phenomena: spatial turnover and nestedness (Baselga 2010). Variation of the species composition (beta diversity) in permanent water bodies may result mainly from spatial turnover, which implies replacement of some species by others. These habitats were more heterogeneous as compared to temporary ones and a more complex set of environmental factors could shape the species composition, so that different communities with similar numbers of species were found in some cases. Temporary water bodies had more homogeneous environmental conditions, gradually diminishing water surface and volume during vegetation season and a period without water in summer (up to 3 months). Differences in mollusc assemblage composition among these habitats could mainly reflect nestedness. Non-random species loss may be a consequence of different drought-resistance of individual species which promotes an orderly disaggregation of assemblages.

Temporal instability of mollusc assemblage composition in individual habitats may at least partially result from colonisation and local extinctions. Species richness in floodplain water bodies is often driven by rare species, which are more susceptible to local extinction. Connectivity among individual water bodies and with a river channel and its temporal change significantly affect mollusc assemblages facilitating or limiting migration. Biotic interactions, such as competition and predation, may also be important factors (e.g. Lassen 1975, Wellborn et al. 1996). Molluscs have unspecialised demands with regard to food, in general snails are detritivores or micro-herbivores (i.e. feeding on periphyton) and bivalves are filtrators. This is conducive to competition,

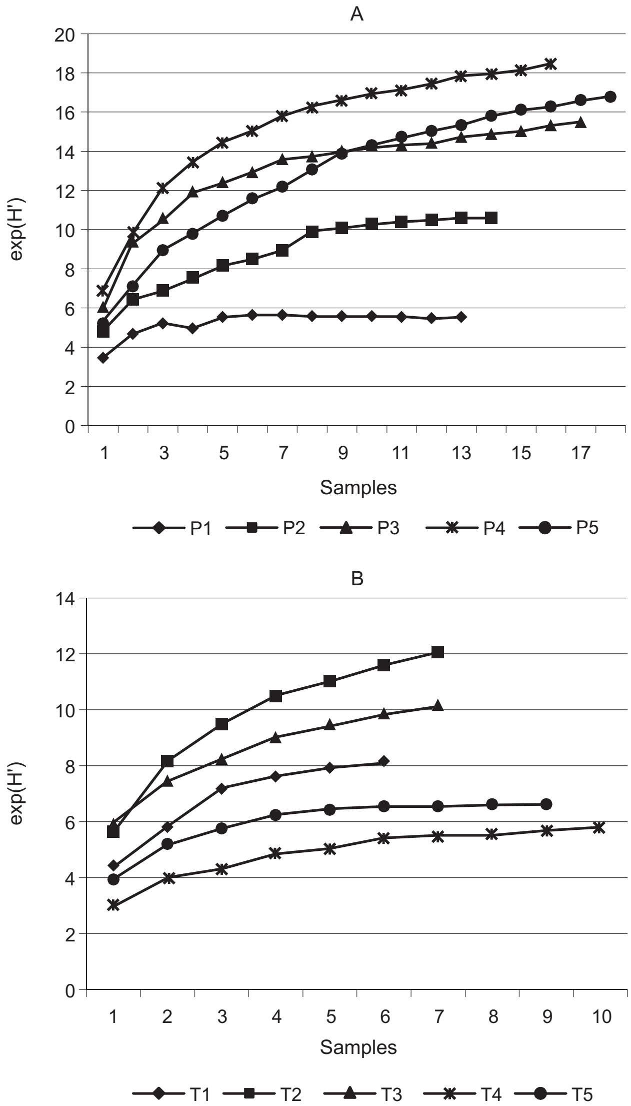

Fig. 5. The effect of sampling effort on species diversity (exp (H')): permanent (A) and temporary (B) water bodies

which especially in small systems leads to extinction of some species (Lassen 1975). Processes of extinction, competitive exclusion and re-colonisation may take place not only within small ponds, but also in different patches of heterogeneous larger water bodies. The presence or lack of fishes may influence the composition and abundance of malacocoenoses. Different invertebrate assemblages were observed in fishless ponds and in those containing benthic-feeding fishes (e.g. Wellborn et al. 1996). Some authors maintain that invertebrate predators, for example dragonflies and leeches, can limit snail populations in fishless ponds (Brönmark 1992, Turner & Chislock 2007).

Sampling effort is related to habitat heterogeneity (Moreno & Halffter 2000). In permanent water bodies which were more heterogeneous, a higher number of species was recorded and inventories approached the asymptote less rapidly than in the case

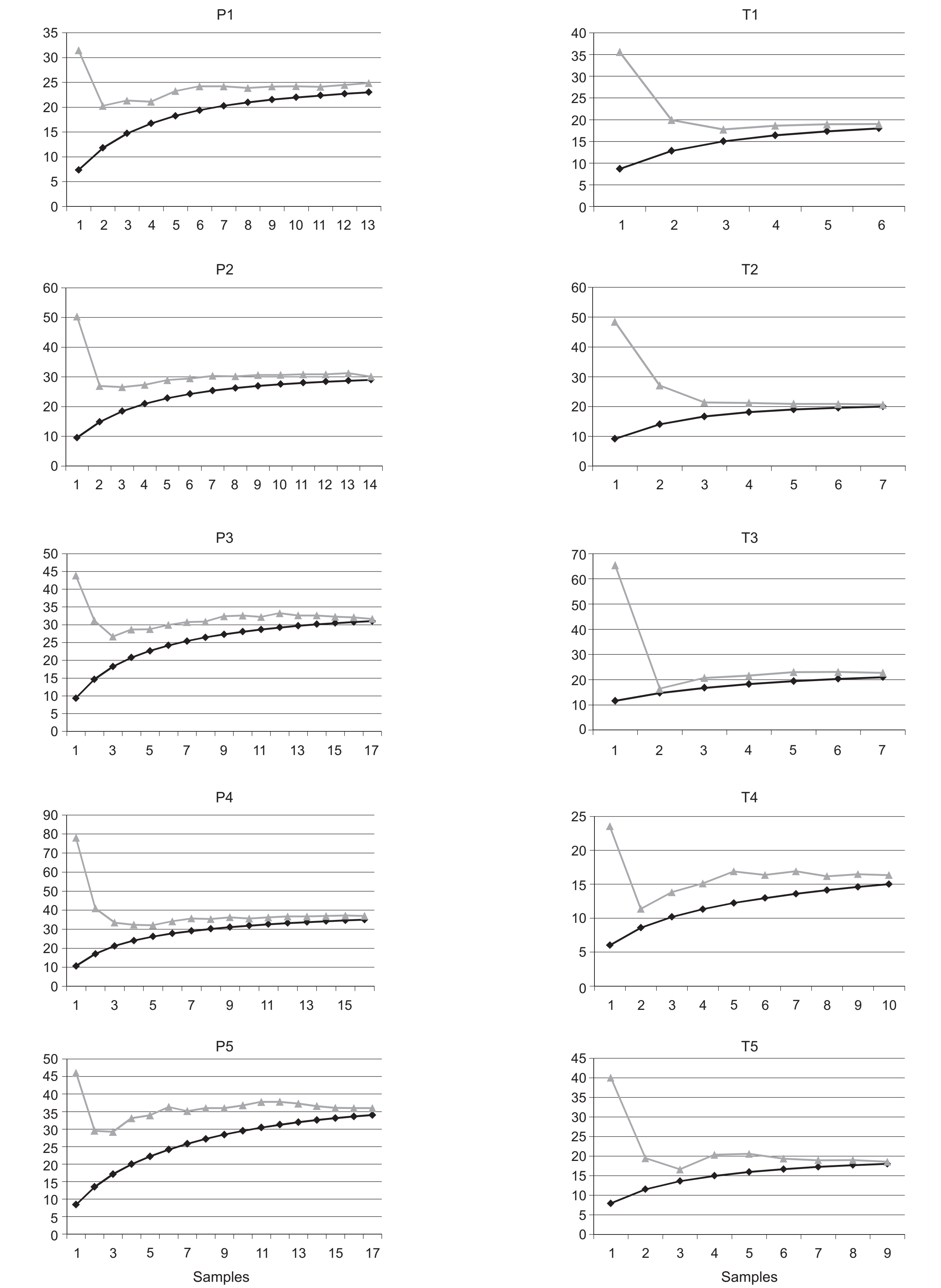

Fig. 6. Accumulation of re-sampled total observed species richness (S_{MaoTau}, in black) and predicted species richness estimated with Chao2 (grey) with increasing number of samples; P1–P5 and T1–T5, see Fig. 1

of less heterogeneous temporary habitats. Species inventory is usually regarded as 'complete' when at least 90% of total species richness (or expected number of species) are collected (Moreno & Halffter 2000, Thompson et al. 2007). Extrapolating of the total species richness is possible when the species accumulation curves have reached or are clearly approaching an asymptote (Willott 2001). This condition was met in the case of mollusc assemblages of the studied water bodies. Simultaneous evaluation of the expected number of species with non-parametric estimator Chao2 revealed a high conformity of the total observed (S_{obs}) and predicted species richness (more than 90%) after collecting 5–14 samples. This confirms that the sampling effort in the investigated water bodies was sufficient. The number of samples required to collect at least 90% of the expected species richness in the investigated water bodies was similar to the results reported by Halse et al. (2002) for macroinvertebrates from five wetlands in south-western Australia (6–10 samples).

Representative collections of molluscs (i.e. at least 70% of the expected number of species) from the investigated habitats were obtained at 3–7 samples per water body. Similar values were reported from lotic sites by Mackey et al. (1984) and Furse et al. (1981). Halse et al. (2002) reported that only two large samples taken from wetlands in south-western Australia were enough to find 75% of species present at the time of sampling, but they did not link the number of species obtained in these two samples to the total number of species occurring in those habitats. According to the results of investigations of invertebrates carried out in heavily vegetated ponds in Ireland, three samples for 3-min multihabitat netting could yield 70% efficiency (Jurado et al. 2008).

The list of molluscs resulting from the intensive investigations carried out in ten selected water bodies within the lower Bug River floodplain contained all species collected by the author during the extensive survey within 186 km section of the lower Bug River floodplain (Jurkiewicz-Karnkowska 2009, Jurkiewicz-Karnkowska & Karnkowski 2013). According to the results, examining the floodplain scale 60–70 samples should be collected to obtain a satisfactory completeness (individual water bodies surveyed not intensively, mostly twice, were treated as samples). Extensive survey in water bodies widely differing in size, succession stage, connectivity and permanence would enable obtaining complete species list of molluscs within a relatively short period. The probability of finding rare species seems to be higher when more habitats are investigated. An intensive study carried out in fewer water bodies, mostly representing less advanced succession stages, might be an alternative approach to the stratified sampling approach presented above, but it demands a longer period of survey and many sampling repetitions to take account of spatial and temporal variability in the water bodies. Relatively young large permanent water bodies appeared to make a high contribution to the total species richness at the landscape scale. They contained species-rich malacofaunas, which showed moderate similarity to each other. The group of temporary habitats harboured a lower total number of species (35 versus 51 in permanent habitats), but the mean species richness did not significantly differ from the respective value in permanent water bodies. However, the malacofaunas living in temporary water bodies were distinct from those inhabiting permanent ones (low values of Jaccard's similarity coefficient, mean J=0.19). They supplemented the species list especially with some drought-resistant molluscs. Most importantly, the comparison of intensive and extensive sampling strategies revealed that similar numbers of samples were needed in both approaches to complete species lists.

Extensive biological databases compiling much taxonomic information and distribution data are important tools in ecological and conservational research, but their usefulness may be limited by sampling bias, lack of sampling effort assessment or lack of coverage of the geographical and environmental variations that affect the distribution of organisms (Hortal et al. 2007, Bruno et al. 2012). Biodiversity databases demand unbiased surveys with standardised sampling effort to be used in biodiversity studies or development of conservation schemes, so the evaluation of data quality including bias in collection of faunistic information and estimation of the degree to which the data represent complete inventories on a given scale are essential (Romo et al. 2006, Hortal et al. 2007, Soberón et al. 2007, Sánchez-Fernández et al. 2008, Bruno et al. 2012).

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Appendix 1. Results of comparisons performed with non-parametric tests: U Mann-Whitney and Kruskal-Wallis ANOVA; P and T – permanent and temporary water bodies

U Mann-Whitney test	N	Z	df	p
Mean number of species: P versus T	117	0.450	1	0.6510
Mean exp(H') values: P versus T	117	2.041	1	0.0413
Kruskal-Wallis ANOVA test	**N**	**χ^2**	**df**	**p**
Jaccard's coefficient (J) in individual P and T water bodies at the same sampling occasion	62	16.01	1	0.0001
Jaccard's coefficient (J) in individual P and T water bodies in different months within one season	7	0.19	1	0.6592
Jaccard's coefficient (J) within P, T and between P and T (P/T)in the same year	36	22.20	2	<0.0001
Mean number of species: P1–P5	78	5.10	4	0.1993
Mean number of species: T1–T5	39	13.40	4	0.0095
Mean exp(H') values: P1–P5	78	13.07	4	0.0109
Mean exp(H') values: T1–T5	39	15.67	4	0.0035

Appendix 2. Results of Spearman's correlation between species richness and species diversity (exp(H')) in individual water bodies

Water body code	R	p	t(N-2)	df
Permanent water bodies				
P1	0.69	0.00948	3.135657	11
P2	0.42	0.42338	1.618866	12
P3	0.38	0.13794	1.567116	15
P4	0.87	0.00001	6.573859	14
P5	0.33	0.17527	1.418370	16
Temporary water bodies				
T1	0.35	0.49237	0.754807	4
T2	0.85	0.01481	3.645745	5
T3	–0.04	0.93712	–0.082931	5
T4	0.69	0.02734	2.693730	8
T5	0.72	0.02783	2.766596	7