FOLIA MALACOLOGICA
Vol. 15(1): 25–38
ISSN 1506-7629
The Association of Polish Malacologists
& Faculty of Biology, Adam Mickiewicz University
Poznań 2007

MALACOFAUNA OF TWO HYDROLOGICALLY DIFFERENT HABITATS IN THE NEAR-SHORE ZONE OF THE WŁOCŁAWEK DAM RESERVOIR (VISTULA RIVER, POLAND)

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ABSTRACT: We studied molluscan fauna at two sites in the Włocławek Dam Reservoir, differing with respect to the hydrological conditions: a rheolimnic site with a comparatively strong water flow (Soczewka) and a limnetic site, dominated by wave action (Dobiegniewo). Within each site, we sampled molluscs from three substratum types (sand, a thin layer of mud on sand and mud). Samples were collected monthly, from April to October. The taxonomic composition differed between the sites, with *Sphaerium corneum* (L. 1758), *Pisidium* sp. C. Pfeiffer, 1821, *Bithynia tentaculata* (L. 1758) and *Viviparus viviparus* (L. 1758) being more abundant in Soczewka, while *Potamopyrgus antipodarum* (Gray, 1843), *Marstoniopsis scholtzi* (Schmidt, 1856) and *Dreissena polymorpha* (Pallas 1771) occurred exclusively in Dobiegniewo. *S. corneum* was a strong dominant in most of the samples, and variation in its abundance was the only cause of the observed differences among the various substrata. Strong differences in the total density and biomass were also observed between the two sites, the molluscs from Soczewka being much more abundant. This phenomenon was particularly apparent on the muddy substratum, which was the most suitable in Soczewka and the poorest in Dobiegniewo. Our study revealed that moderate water flow in Soczewka affected molluscs by improving conditions for them, especially on the muddy substratum.

KEY WORDS: lowland dam reservoir, water flow, water level fluctuations, substratum, Mollusca, hydrological conditions

INTRODUCTION

Dam reservoirs are comparatively young water bodies. Most of them were created in the third quarter of the 20th century (GŁODEK 1985). Therefore, their ecosystems have been much less investigated than those of lakes, rivers and other water bodies. Because of the high diversity of habitats and, in consequence, biocoenoses, as well as a strong impact upon the local environment, dam reservoirs are interesting and important objects of scientific research.

The near-shore zone is the most variable habitat within a dam reservoir. Usually, its range is determined using the depth criterion, although various authors assume different border values, such as 2 m (STAŃCZYKOWSKA & JURKIEWICZ-KARNKOWSKA 1983) or 80 cm (PATERSON & FERNANDO 1969, ARMITAGE 1977). In our opinion, the near-shore zone extends up to areas with decreased environmental heterogeneity and bottom sediments similar to those found in the central part of a reservoir. Obviously, its range strongly depends on local conditions. In the Włocławek Dam Reservoir, the near-shore zone extends up to ca. 100 m from the shore and reaches a depth of 2 m.

In the near-shore zone of a dam reservoir, one can usually distinguish an area that is temporarily exposed to air and inhabited primarily by euryoecious species. Their survival depends mainly on their movement abilities (IZVEKOVA et al. 1997). With respect to mobility, benthic animals can be divided into two groups: 1) species migrating with the decreasing water level (mostly predatory and/or epifaunal, including some snail species), 2) those remaining in the air-exposed area. The latter survive periodic drying and freezing by burying themselves in sediments, building shelters or undergoing physiological changes. This group includes bivalves, which respond to air exposure by closing their valves, and snails which can use an operculum or epiphragm to close their shells. Furthermore, pill clams *Pisidium casertanum* (Poli, 1791) and *Pisidium personatum* Malm, 1855) form protective aggregations ca. 30-40 cm below the sediment surface, and a snail *Valvata piscinalis* (O.F. Müller, 1774) is able to dehydrate its tissues and thus increase its resistance to freezing (STAŃCZYKOWSKA & JURKIEWICZ-KARNKOWSKA 1983). Communities developing in this reservoir zone are similar to those occurring in periodically dried fish ponds. Two areas can be distinguished within this zone: bare sand substratum and sand with various additions of fine detritus (SOKOLOVA & SAKHAROVA 1991). Benthos abundance at such sites strongly depends on the season and duration of air exposure events, and is highly variable among different water bodies (KAJAK 1987).

Below the air-exposed zone, zoobenthos biodiversity and biomass usually reach their maximum values due to the lower variability of environmental factors, high habitat heterogeneity (macrophyte presence) and suitable food and oxygen conditions. Then, with further increasing depth, the benthic community becomes less diverse and abundant (BRINKHURST 1974, KAJAK 1988).

With regard to biomass, the near-shore benthic communities of dam reservoirs are usually dominated by Mollusca (STAŃCZYKOWSKA & JURKIEWICZ-KARNKOWSKA 1983, JURKIEWICZ-KARNKOWSKA 1989, 2004, KUKLIŃSKA 1989, DUSOGE 1989, ŻYTKOWICZ et al. 1990, KRZYŻANEK 1991, ŻBIKOWSKI 1995, JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI 2004). Mollusca dominated also on introduced artificial substrata in the Włocławek Dam Reservoir (CZARNECKA 2005). This shows the great importance of this taxon in the Włocławek Dam Reservoir. Molluscs can greatly affect ecosystem functioning. Bivalves remove chlorophyll (i.e. phytoplankton) from the water column, increasing water transparency, changing its chemical properties (HOLLAND et al. 1995, JOHENGEN et al. 1995, IDRISI et al. 2001) and stimulating development of macrophytes and phytobenthos (LOWE & PILLSBURY 1995). Furthermore, they produce large amounts of faeces and pseudofaeces that improve food conditions for other benthic organisms. Thus, they modify the structure and increase abundance of zoobenthos communities (WOLNOMIEJSKI 1970, STEWART et al. 1998). Substances released by bivalves affect also abundance and metabolic activity of microorganisms living in bottom sediments (GRIFFITHS 1993, NALEPA et al. 1996, KURBATOVA 1998). Therefore, bivalves, especially *Dreissena polymorpha* (Pallas, 1771), are regarded as the so-called ecosystem engineers, i.e. organisms which are able to cause considerable changes in their environment and control the use of resources by other species (KARATAYEV et al. 2002). Moreover, molluscs are a valuable tool in monitoring and typology of water bodies (KRZYŻANEK 1991, ROSENBERG & RESH 1993), and bioindication of toxins, such as heavy metals (OERTEL 1998, JURKIEWICZ-KARNKOWSKA 1999a, GRUNDACKER 2000). They influence element cycling, e.g. phosphorus (JURKIEWICZ-KARNKOWSKA & KRÓLAK 2000) or calcium and are an important item in the diet of fish (MARTYNIAK et al. 1987, PREJS et al. 1990, TERLECKI et al. 1990), and waterfowl (STOCZKOWSKI & STAŃCZYKOWSKA 1995).

The impact of malacofauna upon an aquatic ecosystem obviously depends on its taxonomic composition and abundance, which in turn are influenced by multiple biotic and abiotic factors. In a dam reservoir, organisms are affected especially by its hydrological regime (i.e. water flow, water level fluctuations). The impact of this factor changes with the distance from the dam, which is particularly apparent in strongly rheolimnic reservoirs, such as the Włocławek Dam Reservoir. That is why the relationships between hydrological conditions and the quality and quantity of the bottom fauna, including Mollusca, should be investigated in detail. Therefore, the aim of the present study was to compare the taxonomic composition, abundance and biomass of malacofauna from two hydrologically distinct habitats of the near-shore zone of the Włocławek Reservoir: a lotic site located in its upper part, and a limnetic site from the lower part of the reservoir.

STUDY AREA AND METHODS

STUDY AREA

The Włocławek Dam Reservoir (WDR) is located between 618th and 675th km of the Vistula River course (Fig. 1). It is the first and the only component of the Cascade of the Lower Vistula. The WDR is the largest Polish reservoir with respect to surface area and the second largest considering volume (with the Soliński Dam Reservoir being the biggest). Thus, it is one of the greatest midland water bodies in Poland, smaller only than lakes Śniardwy and Mamry.

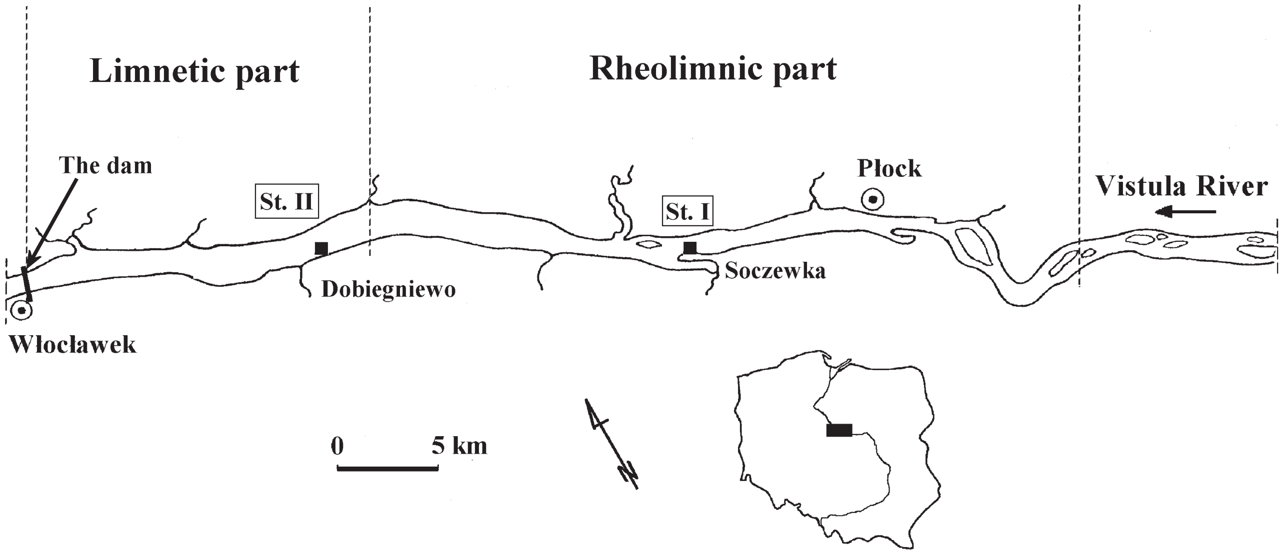

Fig. 1. Location of the sampling sites in the Włocławek Dam Reservoir

The basic morphometric parameters of the WDR (GRZEŚ 1983) are the following: surface area – 75 km^2; volume – total: 400 mln m^3, usable: 55 mln m^3; length – 57 km; shoreline length – 130 km; width – mean: 1,210 m, range: 500–2,500 m; depth – mean: 5 m, maximum: 15 m; mean water flow – 900 m$^3 \cdot$ s^{-1}.

A particular feature of the WDR is its very short water retention time (ca. 4–7 days). Thus, it is strongly rheolimnic, with a very elongated, channel-like shape (the shoreline length is only slightly larger than the double length of the reservoir). The WDR is a highly eutrophic water body, with an elevated nutrient concentration (GIZIŃSKI et al. 1989, ŻYTKOWICZ et al. 1990, KENTZER et al. 1999). On the other hand, its hydrodynamic conditions (such as the high flow rate and intensive wind mixing resulting from the large area and suitable localisation) reduce many negative consequences of the high trophy.

The lack of a clear, long-lasting thermal stratification results in quite good oxygen conditions in the bottom sediments (J. ŻBIKOWSKI, unpublished data). It allows for the development of abundant and diverse benthic fauna (ŻBIKOWSKI 1995, 2000), while cyanobacterial blooms do not occur in the reservoir (DEMBOWSKA & NAPIÓRKOWSKI 2000).

Despite the overall rheolimnic character of the WDR, its hydrodynamic conditions are variable, both along its course and across it. The water body can be divided into the old river bed (with the comparatively strong water flow) and the limnetic, flooded area. Furthermore, in the lower part of the reservoir (below 657th km of the river course), the mean water flow is apparently reduced, compared with its upper, lotic part (GRZEŚ 1983).

The hydrodynamic conditions in the WDR vary not only in space, but also in time. At a long time scale (several years) the hydrology of the WDR depends on the dynamics of the Vistula river, supplying 98% of the water volume to the reservoir. At a daily time scale, it is affected by the activity of the hydropower station, located at the dam. A very important factor, influencing the hydrological conditions in the reservoir, is the small usable volume (14% of the total volume), resulting in low fluctuations of the water level (usually below 0.5 m).

SAMPLING METHODS

Samples were taken in the near-shore zone, close to the left bank of the reservoir, at two sites, differing with respect to their hydrological conditions (Fig. 1). The first group of the sampling stations was located near Soczewka village (643th km of the river course), in the rheolimnic part of the reservoir, with the comparatively strong water flow (ca. 1 m s^{-1} according to GRZEŚ 1983). The second site was situated at the level of Dobiegniewo village (661th km of the river course), in the limnetic zone, with the apparently reduced water flow (0.1–0.4 m s^{-1}). Furthermore, water level fluctuations were higher at the Dobiegniewo site (personal observation).

The selected sites differed also with respect to the abundance and taxonomic composition of vascular plants. Emergent macrophytes (*Phragmites communis* Trin.) were present only at the Soczewka site. On the contrary, *Nuphar lutea* L. occurred only at the Dobiegniewo site. Elodeids, more abundant near Dobiegniewo, were represented by similar species in both locations, with the pond-weeds (*Potamogeton perfoliatus* L., *P. pectinatus* L., *P. lucens* L.), horn-wort (*Ceratophyllum demersum* L.) and water milfoil (*Myriophyllum spicatum* L.) being the most common.

Three sampling stations, located in different habitats, were selected within each site: (1) the sandy bottom at the depth of 0.5–0.7 m, ca. 10 m away from the shore; (2) the sandy bottom covered with a thin layer of muddy sediments, at the depth of 1.1–1.3 m, ca. 20 m away from the shore; (3) the muddy bottom at the depth of 2.0–2.5 m, 60–80 m away from the shore.

Samples were collected from April to the end of October 2004 at monthly intervals, except for the Dobiegniewo site, where the May sample was taken only from the muddy bottom habitat because of technical problems. Moreover, the extremely low water level in August made it impossible to collect samples from the sandy habitat at the Dobiegniewo site, which was exposed to air.

On each sampling date, six replicate samples were taken from the sandy bottom and the sandy bottom covered with mud using a core sampler (catching area of 22 cm^2). The muddy sediments from the Dobiegniewo site were sampled (two replicates) with an Ekman-Birge grab (catching area of 225 cm^2). Due to the tremendous benthos abundance, the samples from the muddy sediments at the Soczewka site were collected by means of a Kajak sampler with the catching area of 40 cm^2 (2–4 replicates).

The samples were sieved through a 0.5-mm mesh size and the collected molluscs were preserved with 4% formaldehyde. Species were identified according to PIECHOCKI (1979) and PIECHOCKI & DYDUCH-FALNIOWSKA (1993). Frequency of particular species was calculated as a percentage of the samples containing a given species in the total number of samples.

Since our sampling methods were inappropriate for quantitative assessment of large species, unionid clams were not included in the statistical analyses described below.

STATISTICAL ANALYSIS

Univariate methods

The differences among the studied sites and habitats in the number of taxa, biodiversity (measured by Shannon-Wiener index), total molluscan density and biomass were tested by means of two-way analyses of variance (separate for each variable), with site (Dobiegniewo or Soczewka) and habitat (mud, sand covered with a layer of mud or sand) as fixed factors. The Bonferroni correction for four analyses was applied to set the p-level, below which the results were regarded as statistically significant ($p < 0.0125$). The density and biomass data were logarithmically transformed ($\ln(x+1)$) to meet the homoscedasticity assumption (checked by Levene test). When the ANOVA results were statistically significant, Tukey test was used to make the post-hoc comparisons.

Multivariate methods

Two-way crossed ANOSIM (analysis of similarities) based on Bray-Curtis distances was applied to test the significance of the differences in community composition between the studied sites and habitats. The R_{ANOSIM} statistic, generated in this analysis, is a measure of separation between a-priori defined groups of samples in ordinate space. The R_{ANOSIM} value close to 0 indicates no differences between groups, while R_{ANOSIM} equal to 1 shows that all samples within groups are more similar among themselves than they are to any samples belonging to the other groups. The statistical significance of differences between groups may be tested using a randomisation test (CLARKE 1993). The overall two-way analysis was followed by the pairwise ANOSIM tests comparing various habitats with one another. Furthermore, two single-factor tests were carried out (separately for each site) to check whether the differences among habitats varied between the sites. The sequential Bonferroni correction was applied to the results of the randomisation tests to control for multiple comparisons (RICE 1989). The randomisation tests (with 10,000 replicates) were carried out using a custom procedure written in Mirosoft® Visual Basic for Excel 2000.

Only the results from those dates on which a full set of samples was taken were used in the above analyses. Therefore, the May and August samples have been excluded from the analysis.

To present the distances between sites and habitats graphically, non-metric multidimensional scaling (nMDS) was carried out using the Bray-Curtis dissimilarity matrix.

Furthermore, to find relationships between the studied samples and molluscan taxa, correspondence analysis (CA) was applied. Rare species (found only once or twice in the entire data set) were removed from this analysis to reduce noise.

A preliminary analysis suggested that *Sphaerium corneum* (L. 1758), a dominant species in the studied area, might be responsible for most of the observed differences among habitats. Therefore, to detect other relationships in the data set, which could be hidden by the strong dominance of this species, the same analyses as described above were run after excluding *S. corneum* from the data set.

RESULTS

GENERAL REMARKS

Nineteen molluscan taxa were found in the near-shore zone of the WDR, including 7 bivalve taxa and 12 gastropods (7 prosobranch and 5 pulmonate) (Table 1). The overall value of Shannon-Wiener biodiversity index was 1.09. With respect to the frequency index, dominant species were: *S. corneum* (85%), *Vivi-*

Table 1. Shannon-Wiener indices (H') (log base = 2) and taxon numbers (S) in the studied area. Db – Dobiegniewo, So – Soczewka

		Sand			Mud on sand			Mud			All habitats		
		Db	So	All	Db	So	All	Db	So	All	Db	So	All
Mollusca	H'	1.49	2.25	2.64	2.23	0.96	2.01	2.66	0.51	0.54	2.25	0.67	1.09
	S	7	12	14	15	8	16	8	11	14	16	13	19
Mollusca	H'	1.20	2.08	2.45	1.93	1.87	2.50	2.42	1.83	1.97	1.96	1.92	2.64
no *S. corneum*	S	6	11	13	14	7	15	7	10	13	15	12	18
Bivalvia	H'	1.30	1.20	1.22	1.78	0.57	0.85	2.04	0.28	0.31	1.89	0.37	0.45
	S	3	4	4	5	5	6	5	4	6	6	5	7
Bivalvia	H'	0.59	0.42	0.45	1.62	0.73	1.54	1.64	0.34	0.53	1.70	0.46	0.92
no *S. corneum*	S	2	3	3	4	4	5	4	3	5	5	4	6
Gastropoda	H'	0.82	1.95	2.08	1.33	1.17	1.73	1.27	1.70	1.76	1.29	1.70	2.16
	S	4	8	10	10	3	10	3	7	8	10	8	12
Prosobranchia	H'	0.61	1.52	1.80	1.07	1.17	1.51	1.27	1.41	1.49	1.05	1.40	1.92
	S	3	5	7	6	3	6	3	5	6	6	5	7
Pulmonata	H'	–	1.50	1.38	1.21	–	1.21	–	0.78	0.78	1.04	1.39	1.39
	S	1	3	3	4	0	4	0	2	2	4	3	5

parus viviparus (L., 1758) (69%), *Pisidium* sp. C. Pfeiffer, 1821 (62%), *Bithynia tentaculata* (L., 1758) (56%) and *Sphaerium rivicola* (Lamarck, 1818) (51%).

The total density of molluscs was very high and reached 10.5 thousand individuals per m^2 (Table 2). Bivalves were more abundant than snails (over 9.3 and 1.2 thousand individuals per m^2, respectively). Within the latter group, prosobranchs strongly dominated (1.1 thousand individuals per m^2). The unquestionable dominant was *S. corneum*, constituting as much as 82% of the total density. A snail *Potamopyrgus antipodarum* (Gray, 1843) and *Pisidium* bivalves were also quite common, but contributed only 6% and 5% of the total density, respectively. Pulmonate snails occurred rarely, with *Lymnaea* (*Radix*) *peregra* (O. F. Müller, 1774), being the most abundant among them (only 38 individuals per m^2, but as much as 72% of the total density of pulmonates).

The molluscan biomass (wet weight including shell) was as high as 1 kg per m^2 on average (Table 3). With respect to biomass, bivalves dominated (more than 720 g/m^2), with *S. corneum* reaching the highest value of 650 g/m^2 (90% of the total bivalve biomass). The gastropod biomass was much lower (275 g/m^2). *V. viviparus* contributed as much as 89% of the total snail biomass (244 g/m^2).

COMPARISON OF THE SITES OF DIFFERENT HYDROLOGICAL CONDITIONS

The molluscan communities at the two compared sites differed from each other (Table 1, Fig. 2). The total numbers of molluscan taxa at both sites were similar (in Dobiegniewo: 6 bivalve and 10 snail taxa; in Soczewka: 5 bivalve and 8 snail taxa), but there was a significant interaction between site and habitat in

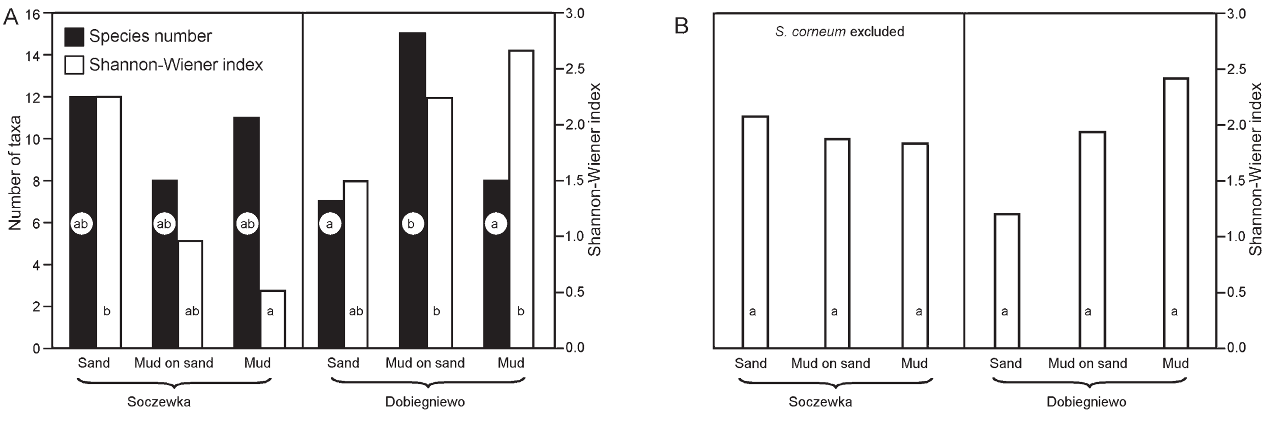

Fig. 2. Numbers of molluscan taxa and values of Shannon-Wiener biodiversity indices in the studied habitats and sites, with *S. corneum* included in (A) or excluded from (B) the analysis. The same letters labelling the bars indicate no significant differences between the corresponding values

Table 2. Molluscan densities (individuals per m^2) in the studied area. Db – Dobiegniewo, So – Soczewka

	Sand			Mud on sand			Mud			All habitats		
	Db	So	All	Db	So	All	Db	So	All	Db	So	All
S. corneum	106	660	383	568	6,126	3,347	51	44,297	22,174	242	17,028	8,635
Pisidium sp.	91	574	332	88	639	363	54	2,001	1,028	78	1,071	574
S. rivicola	15	32	24	215	65	140	60	126	93	97	75	86
D. polymorpha	0	0	0	215	0	107	29	0	14	81	0	41
Unio sp.	0	11	5	0	22	11	0	3	2	0	12	6
S. solidum	0	0	0	13	11	12	0	0	0	4	4	4
Anodonta sp.	0	0	0	0	0	0	3	0	2	1	0	1
Bivalvia	212	1,277	744	1,099	6,863	3,980	197	46,427	23,313	503	18,190	9,347
no *S. corneum*	106	617	361	531	737	633	146	2,130	1,139	261	1,162	712
P. antipodarum	1,030	0	515	2,601	0	1,301	6	0	3	1,213	0	606
B. tentaculata	0	206	103	51	292	171	0	694	347	17	397	207
V. viviparus	15	184	100	215	173	194	41	468	255	90	275	183
M. scholtzi	136	0	68	429	0	215	0	0	0	189	0	94
V. piscinalis	0	22	11	13	22	17	19	54	36	11	32	21
V. pulchella	0	11	5	13	0	6	0	54	27	4	21	13
V. naticina	0	11	5	0	0	0	0	3	2	0	5	2
Prosobranchia	1,181	434	807	3,322	487	1,904	66	1,273	670	1,524	730	1,126
L. peregra	45	11	28	114	0	57	0	60	30	53	24	38
Ph. fontinalis	0	11	5	13	0	6	0	18	9	4	10	7
P. corneus	0	22	11	0	0	0	0	0	0	0	7	4
L. auricularia	0	0	0	13	0	6	0	0	0	4	0	2
A. crista	0	0	0	13	0	6	0	0	0	4	0	2
Pulmonata	45	44	44	153	0	75	0	78	39	65	41	53
Gastropoda	1,226	478	851	3,475	487	1,979	66	1,351	709	1,589	771	1,179
Mollusca	1,438	1,755	1,595	4,574	7,350	5,959	263	47,778	24,022	2,092	18,961	10,526
no *S. corneum*	1,332	1,095	1,212	4,006	1,224	2,612	212	3,481	1,848	1,850	1,933	1,891

the ANOVA carried out on taxa numbers ($F_{2, 33} = 6.46$, $P = 0.0043$). It resulted from the fact that significant differences among various habitats were found only within Dobiegniewo. At this site, the number of taxa found on the sandy substratum covered with a layer of mud was higher than elsewhere (Fig. 2a). In Soczewka, the number of taxa found in the same habitat was the lowest, although this difference was not statistically significant. Furthermore, the number of taxa in the sandy habitat from Soczewka was somewhat higher (although not significantly) than in the same habitat from Dobiegniewo (12 versus 7 taxa).

The Shannon-Wiener index was more than threefold higher in Dobiegniewo (2.25) than in Soczewka (0.67). A significant interaction between site and habitat was found in the analysis of this index (ANOVA: $F_{2, 33} = 9.06$, $P = 0.0007$). In Soczewka, biodiversity decreased with depth (i.e., from the sand to mud substratum), while in Dobiegniewo an opposite tendency (although insignificant) was found. The lowest value of Shannon-Wiener index was observed in the muddy habitat from Soczewka. It differed significantly from indices calculated for the sandy habitat from the same site and the muddy substratum from Dobiegniewo (Fig. 2a). One should also note that in this place (i.e. the muddy habitat from Soczewka) a very low biodiversity was accompanied by a relatively large number of taxa (Fig. 2a), indicating a low evenness (i.e. a strong dominance of one species, viz. *S. corneum*). When this species was excluded from the analysis, all index values (Fig. 2b) became similar to one another (ANOVA: $F_{1, 32} = 0.68$, $p = 0.416$; $F_{2, 32} = 0.73$, $p = 0.488$; $F_{2, 32} = 2.22$, $p = 0.125$ for site, habitat and interaction, respectively).

The frequencies of most of the dominant taxa in Dobiegniewo and Soczewka were usually similar and reached: for *S. corneum* 72% and 100%; for *V. viviparus* 61% and 76%; for *Pisidium* sp. 56% and 67%; and for *S. rivicola* 50% and 52%, respectively. On the contrary, *P. antipodarum* was common in Dobiegniewo (61%)

and absent from Soczewka, while *B. tentaculata* often occurred in Soczewka (90%) and was rare in Dobiegniewo (17%).

The total molluscan density was considerably (9-fold) higher in Soczewka (almost 19 thousand individuals per m^2) than in Dobiegniewo (2 thousand individuals per m^2) (Table 2). Furthermore, considerable differences among various habitats were observed (Fig. 3a): the highest molluscan density was found in the muddy habitat from Soczewka (almost 48 thousand individuals per m^2), while the lowest density occurred in the same habitat from Dobiegniewo (only 263 individuals per m^2) (Table 2, Fig. 3a). Hence, there was a significant interaction between site and habitat in the ANOVA carried out on the molluscan density ($F_{2, 33}$ = 19.37, P < 0.0001). The densities in these two places differed significantly from each other, and from the densities in the remaining habitats. The molluscan densities in the other habitats were similar to one another.

The considerable variation in the molluscan abundance followed mainly from the differences in the distribution of *S. corneum*, by far more common (more than 70-fold) in Soczewka (above 17 thousand individuals per m^2) than in Dobiegniewo (242 individuals per m^2). This difference was observed in all habitat types. After removing *S. corneum* from the data set, the total molluscan densities at both sites became similar (1933 and 1850 individuals per m^2 in Soczewka and Dobiegniewo, respectively). However, differences among habitats were still considerable (a significant interaction between site and habitat in ANOVA: $F_{2, 33}$ = 8.13, p = 0.001), due to the very low density in the muddy habitat from Dobiegniewo, which differed significantly from that found in all other habitats (Fig. 3b). This difference was caused mainly by the distribution of gastropods, which in Dobiegniewo preferred sandy substrata (Table 2). *Pisidium* clams were more common in Soczewka, especially on the muddy substratum, where their density was 37-fold greater than in Dobiegniewo (Table 2).

The total density of snails in Dobiegniewo was twice that from Soczewka (1589 vs. 771 individuals per m^2), but it resulted mainly from the high abundance of *P. antipodarum* (1213 individuals per m^2) and *Marstoniopsis scholtzi* (Schmidt, 1856) (189 individuals per m^2) occurring solely at the former site. On the other hand, two other snail species, *B. tentaculata* and *V. viviparus*, were more abundant in Soczewka (Table 2).

Similarly to density, the total molluscan biomass was greater in Soczewka (1.7 kg/m^2) than in Dobiegniewo (0.27 kg/m^2). It resulted from the high biomass of the dominant taxa in Soczewka: *S. corneum* (almost 1.3 kg/m^2) and *V. viviparus* (nearly 350 g/m^2) (Table 3). In Dobiegniewo, taxa that contributed most considerably to the total biomass were: *V. viviparus* (140 g/m^2), *D. polymorpha* (31 g/m^2) and *S. corneum* (22 g/m^2). In general, differences among habitats in molluscan biomass followed those found in the analysis of density (Fig. 3a). On the sandy substratum, and on the sand covered with a thin layer of mud in Dobiegniewo, the biomass was quite low (compared with density), due to the high abundance of small gastropods: *P. antipodarum* and *M. scholtzi* (Fig. 3b). The muddy habitat from Soczewka had the highest molluscan biomass, differing significantly from that measured in the other places, except for the sand covered with a layer of mud (Fig. 3a, Table 3). It resulted in a significant interaction between site and habitat (ANOVA: $F_{2, 33}$ = 5.34, P = 0.0098). Furthermore, there was a significant difference between the lowest biomass in the study, observed in the sandy habitat from Dobiegniewo, and that found in the sandy habitat covered with a layer of mud from the same site (Fig. 3a, Table 3).

After removing *S. corneum* from the data set, the differences between sites (ANOVA: $F_{1, 33}$ = 7.78, P = 0.0087) and habitats (ANOVA: $F_{2, 33}$ = 6.11, P = 0.0055) were still significant, but the interaction between these factors became insignificant after applying the Bonferroni correction (ANOVA: $F_{2, 33}$ = 3.99, P = 0.0281). The main change in comparison with the

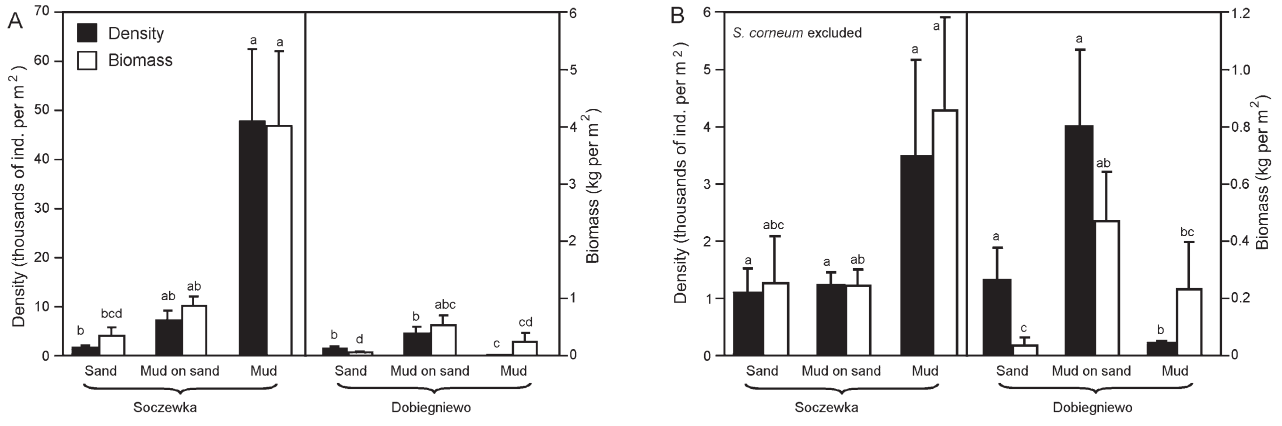

Fig. 3. Total density and biomass of molluscs in the studied habitats and sites, with *S. corneum* included in (A) or excluded from (B) the analysis. The same letters labelling the bars indicate no significant differences between the corresponding values. The error bars show standard errors of mean

Table 3. Molluscan biomass (g per m^2) in the studied area. Db – Dobiegniewo, So – Soczewka

	Sand			Mud on sand			Mud			All habitats		
	Db	So	All	Db	So	All	Db	So	All	Db	So	All
S. corneum	15.50	75.02	45.26	45.85	618.8	332.3	3.33	3,140.6	1,572.0	21.56	1,278.1	649.9
Pisidium sp.	1.35	2.79	2.07	0.48	4.28	2.38	0.64	5.22	2.93	0.82	4.10	2.46
S. rivicola	1.13	2.61	1.87	38.12	5.58	21.85	3.74	8.75	6.25	14.33	5.65	9.99
D. polymorpha	0	0	0	70.25	0	35.12	23.96	0	11.98	31.40	0	15.70
Unio sp.	0	8.54	4.27	0	25.57	12.78	0	99.04	49.52	0	44.38	22.19
S. solidum	0	0	0	0.20	0.14	0.17	0	0	0	0.07	0.05	0.06
Anodonta sp.	0	0	0	0	0	0	146.4	0	73.18	48.79	0	24.39
Bivalvia	17.98	88.95	53.47	154.9	654.4	404.6	178.0	3,253.6	1,715.8	117.0	1,332.3	724.6
no *S. corneum*	2.48	13.94	8.21	109.05	35.57	72.3	174.74	113.01	143.86	95.41	54.18	74.79
P. antipodarum	5.92	0	2.96	15.03	0	7.52	0.10	0	0.05	7.01	0	3.51
B. tentaculata	0	18.16	9.08	3.93	32.09	18.01	0	43.98	21.99	1.31	31.41	16.36
V. viviparus	27.76	170.2	98.98	333.5	175.7	254.6	56.50	700.5	378.5	139.2	348.8	244.0
M. scholtzi	0.03	0	0.02	0.09	0	0.04	0	0	0	0.04	0	0.02
V. piscinalis	0	0.46	0.23	0.26	0.58	0.42	0.45	1.09	0.77	0.23	0.71	0.47
V. pulchella	0	0.01	0.004	0.02	0	0.01	0	0.14	0.07	0.01	0.05	0.03
V. naticina	0	0.15	0.08	0	0	0	0	0.11	0.05	0	0.09	0.04
Prosobranchia	33.71	189.0	111.3	352.8	208.4	280.6	57.04	745.8	401.4	147.9	381.1	264.5
L. peregra	0.70	0.01	0.36	6.84	0	3.42	0	0.95	0.48	2.51	0.32	1.42
Ph. fontinalis	0	0.19	0.09	0.42	0	0.21	0	0.10	0.05	0.14	0.10	0.12
P. corneus	0	50.22	25.11	0	0	0	0	0	0	0	16.74	8.37
L. auricularia	0	0	0	2.19	0	1.09	0	0	0	0.73	0	0.36
A. crista	0	0	0	0.001	0	0.001	0	0	0	0.0004	0	0.00
Pulmonata	0.70	50.42	25.56	9.44	0	4.72	0	1.06	0.53	3.38	17.16	10.27
Gastropoda	34.41	239.4	136.9	362.2	208.4	285.3	57.04	746.9	402.0	151.2	398.2	274.7
Mollusca	52.39	328.3	190.37	517.1	862.8	689.9	235.04	4000.5	2117.8	268.2	1730.5	999.3
no *S. corneum*	36.89	253.3	145.11	471.25	243.97	357.6	231.78	859.91	545.86	246.61	452.38	349.49

analysis of the full data set was disappearance of the difference between the sandy and muddy habitat from Soczewka (Fig. 3b). It suggests that *S. corneum* was responsible for this difference.

The R_{ANOSIM} value for the differences between sites (Dobiegniewo vs. Soczewka) was higher than that for the differences among habitats within the sites (Table 4), indicating that the impact of the former factor upon the molluscan community composition was stronger. The effects of both factors were statistically significant. The single-factor analyses showed that differences among habitats were higher in Soczewka than in Dobiegniewo (Table 4), probably due to the higher within-group variability among samples at the latter site. Only the differences among habitats from Soczewka remained statistically significant after applying the Bonferroni correction. Pairwise tests demonstrated that the sandy and muddy habitats were the most distinct from each other.

The above findings were confirmed by the results of multidimentional scaling (Fig. 4a): the first nMDS axis allowed to discriminate between samples taken from Dobiegniewo and Soczewka. Additionally, the three habitats from Soczewka could be separated from one another along this axis. The distances among particular samples from Dobiegniewo were comparatively larger, and various habitats from this site were split along the second nMDS axis. However, only the samples from sandy and muddy habitats from Dobiegniewo were well separated from each other.

The results of the correspondence analysis allowed to detect taxa contributing to the differences among samples (Fig. 5a). Similarly to the nMDS results, the first CA axis discriminated the two sites from each other. The Soczewka sites, grouped along the left side of the biplot, were characterised by the higher abundances of *S. corneum*, and also *Pisidium* sp., *B. tenta-*

Table 4. Results of the ANOSIM analyses testing the differences between the studied sites and habitats. Asterisks denote the statistical significance of the randomization tests after applying the Bonferroni correction for 13 comparisons: *0.01<p<0.05, **0.001<p<0.01, ***p<0.001

Test	Source of variation	All taxa		*S. corneum* excluded	
		R_{ANOSIM}	p-level	R_{ANOSIM}	p-level
Two-factor crossed test	between sites	0.671	<0.0001**	0.602	<0.0001***
	between habitats	0.424	<0.0001***	0.189	0.0100
	Pairwise comparisons among habitats				
	mud vs. mud on sand	0.360	0.0076*	0.222	0.0257
	mud vs. sand	0.658	0.0003**	0.324	0.0040
	mud on sand vs. sand	0.280	0.0195	–0.013	0.4685
Single-factor test of the Dobiegniewo habitats	between habitats	0.271	0.0170	0.289	0.0132
	Pairwise comparisons among habitats				
	mud vs. mud on sand	0.248	0.0979	0.244	0.0966
	mud vs. sand	0.436	0.0138	0.556	0.0075
	mud on sand vs. sand	0.088	0.2789	0.046	0.3575
Single-factor test of the Soczewka habitats	between habitats	0.576	0.0003**	0.088	0.1920
	Pairwise comparisons among habitats				
	mud vs. mud on sand	0.472	0.0217	0.200	0.1344
	mud vs. sand	0.880	<0.0001***	0.092	0.2759
	mud on sand vs. sand	0.472	0.0158	–0.072	0.6119

culata and *V. viviparus*. The molluscs occurring exclusively in Dobiegniewo (*P. antipodarum*, *M. scholtzi* and *D. polymorpha*) were located in the right part of the biplot. The samples taken in the muddy habitat from Dobiegniewo were the most similar to those from Soczewka.

Various habitats from Soczewka were separated along the second CA axis. The samples taken from mud, dominated by *S. corneum*, were located in the lower left part of the biplot, together with some of the samples taken from sand covered with a layer of mud (Fig. 5a). The samples taken from bare sand were the most variable (dispersed along the entire second axis), mainly due to varying abundances of *V. viviparus*, *S. corneum* and *Pisidium* sp.

The difference between the sites remained high and significant after removing *S. corneum* from the data set (Table 4), indicating that other taxa also contributed to their distinctness. According to the CA biplot, the molluscs typical for Dobiegniewo were *P. antipodarum*, *D. polymorpha*, *M. scholtzi* and *L. peregra*, while those occurring mainly in Soczewka included

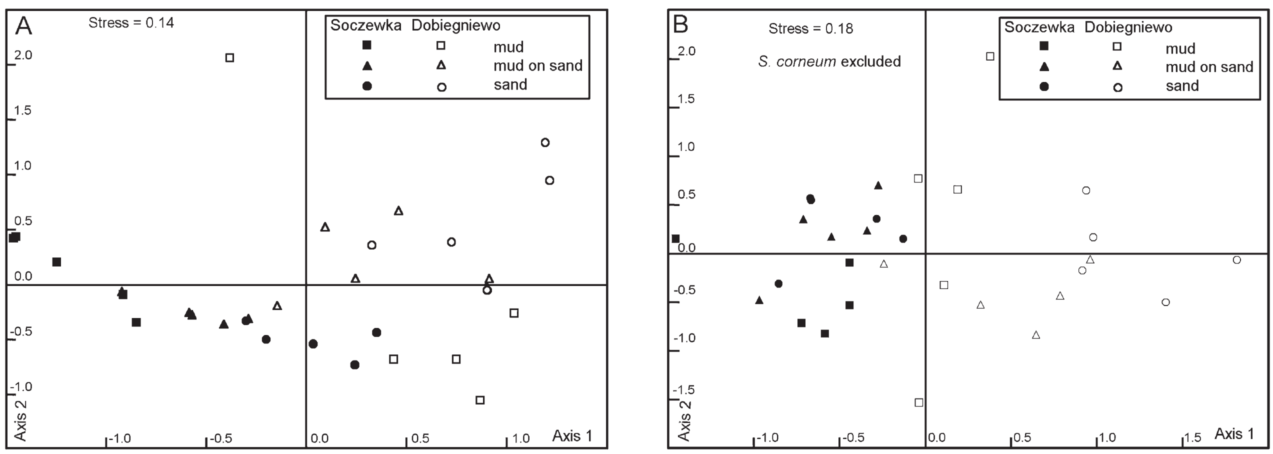

Fig. 4. Non-metric multidimensional scaling ordination of the studied samples, based on the Bray-Curtis distance matrix, with *S. corneum* included in (A) or excluded from (B) the analysis

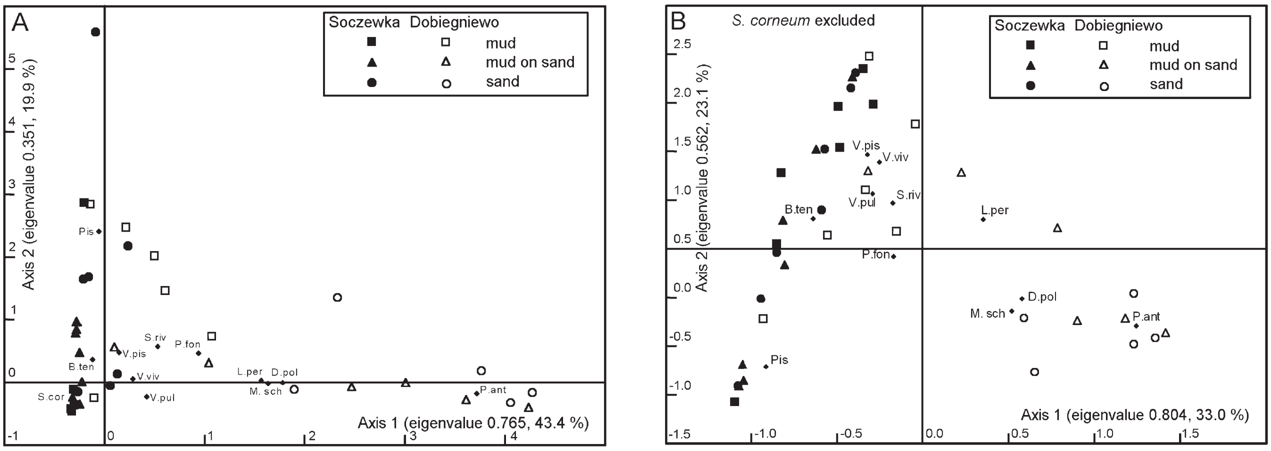

Fig. 5. Correspondence analysis ordination of the studied samples and molluscan fauna, with *S. corneum* included in (A) or excluded from (B) the analysis. Taxon names: B.ten – *Bithynia tentaculata*, D.pol – *Dreissena polymorpha*, L.per – *Lymnaea peregra*, M.sch – *Marstoniopsis scholtzi*, P.ant – *Potamopyrgus atipodarum*, P.fon – *Physa fontinalis*, Pis – *Pisidium* sp., S.cor – *Sphaerium corneum*, S.riv – *Sphaerium rivicola*, Unio – *Unio* sp., V.pis – *Valvata piscinalis*, V.pul – *Valvata pulchella*, V.viv – *Viviparus viviparus*

Pisidium sp., *B. tentaculata* and *V. viviparus* (Fig. 5b). On the other hand, most of the differences between habitats disappeared after removing *S. corneum* from the analysis. It was especially apparent in Soczewka, where the decrease of R_{ANOSIM} value was the highest (Table 4). There was also no separation of various habitats in the biplots of the nMDS (Fig. 4b) and CA (Fig. 5b) run without *S. corneum*, except for the division among the samples taken from sand and mud in Dobiegniewo. It suggests that the distribution of *S. corneum* was the main cause of the differences among various habitats within the sites.

DISCUSSION

Molluscs in the near-shore zone of the WDR were represented by 19 taxa. JURKIEWICZ-KARNKOWSKA (2004) found a similar molluscan richness in other dam reservoirs, viz. Zegrzyński (32), Sulejowski (25) and Siemianówka (18). It should be noted that a lower number of taxa observed in the present study resulted probably from the lack of identification of species of the genus *Pisidium* and family Unionidae, as well as from ignoring empty shells and species living on macrophytes. Thus, the results in both studies are comparable. Therefore, it may be stated that the number of taxa observed in the present study is typical for an old, lowland dam reservoir in Poland. A similar number of molluscan taxa (20) was found in another study dealing with the benthic and epiphytic macroinvertebrates of the WDR (CZARNECKA 2005).

The within-site (i.e. among habitats) molluscan distribution differed between the sites. This result was rather unexpected. One could expect that molluscan communities inhabiting the same substrata (e.g. sand in Dobiegniewo and in Soczewka) would be more similar to each other, than to those occurring in other habitats. This hypothesis was not confirmed, as the differences between the sites turned out to be more important for the molluscan composition than the among-habitat variation. Thus, molluscs were influenced not only by water depth and substratum quality, but also (and above all) by the variability occurring along the reservoir course (DUSOGE et al. 1990). The muddy habitats contributed to most of the differences between the two sites. The Soczewka site, especially the muddy substratum, was extremely suitable for the majority of molluscan taxa, which reached great densities there. A reverse situation was observed in Dobiegniewo, where the muddy habitat was the most unsuitable for molluscs. Soczewka is located in a rheolimnic zone, and Dobiegniewo in a limnetic one. Thus, the most probable reason for the between-site variability is different hydrodynamic regime of the two sites. Soczewka is characterised by a comparatively strong, directional water current, while wave action in this area is low. On the contrary, in Dobiegniewo, wind-induced waves dominate the local hydrodynamics, and the water current is negligible. It is known that moderate water movement is optimal for the bottom fauna, including molluscs (JURKIEWICZ-KARNKOWSKA 2004). It counteracts long-term, sharp oxygen depletions, but is too weak to cause sediment resuspension. Thus, it allows for sedimentation, which is a valuable source of food for bottom macroinvertebrates (KAJAK 1988). It seems probable that a moderate water flow in Soczewka allows for good oxygen conditions in the surface layer of the muddy bottom sediments and provides sufficient amount of suspended particles, which may be used as food. This hypothesis was partially confirmed by the presence of snails *B. tentaculata* and *V. viviparus* in the muddy habitat at this site. These species require good oxygen conditions and may feed by filtering seston from the water column, like bivalves (PIECHOCKI 1979, DUSOGE et al. 1990). One of the reasons for the low abundance of molluscs in Dobiegniewo (especially on muddy substratum) could be a sudden deterioration of environmental conditions, viz. due to oxygen depletions. The oxygen demand of the muddy sediments from Dobiegniewo is very high, so during resuspension they consume large amounts of oxygen in a very short time (ŻBIKOWSKI, unpublished data). Furthermore, resuspension, which is common at this site (due to the strong wave action), may be in itself harmful to a molluscan community (JURKIEWICZ-KARNKOWSKA 1999b). The high biodiversity index, accompanied by the relatively low species number, might suggest indirectly the high probability of resuspension at this site. It indicates the lack of a clear dominant, which seems to be favourable for the ecosystem. However, along with an extremely low abundance, it suggests the strong influence of some limiting factors. One of them could be sediment resuspension, destroying the surface layer of sediments and preventing the development of a stable community with a permanent dominance structure (SHIN 1989).

The species that contributed to most of the differences observed in the present study was *S. corneum*. It should be noted that it was the only cause of the differences among habitats within the studied sites. Most of them disappeared after removing this species from the analysis. On the contrary, the between-site variation depended also on other taxa. *S. corneum* was clearly more abundant in Soczewka, where its density increased with depth, reaching its maximum on the muddy substratum. High densities of Sphaeriidae, particularly *S. corneum*, are often observed in many lowland dam reservoirs, such as the Zegrzyński Dam Reservoir (JURKIEWICZ-KARNKOWSKA 1989) or the Goczałkowicki Dam Reservoir (KRZYŻANEK 1976), especially shortly after their construction. During the subsequent succession, these clams are usually replaced by larger taxa, such as *D. polymorpha* in the Zegrzyński and Sulejowski Dam Reservoir (JURKIEWICZ-KARNKOWSKA 1998, 2002) or Unionidae in the Goczałkowicki Dam Reservoir (KRZYŻANEK 1994). Sometimes, however, the dominance of Sphaeriidae lasts longer, e.g. in the WDR (ŻBIKOWSKI 1995, JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI 2004). LOPEZ & HOLOPAINEN (1987) showed that a great density of these clams in dam reservoirs resulted from suitable food conditions, i.e. sufficient amount of organic particulate matter in the water column and high abundance of bacteria in interstitial water. The presence of Sphaeriidae in muddy substrata is possible mainly due to their high resistance to hypoxia and toxic substances, such as sulfide and ammonium, released by sediments (THIEL 1924, ZHADIN 1952, both cited in PIECHOCKI & DYDUCH-FALNIOWSKA 1993). Because of this resistance, they are sometimes the only representatives of Mollusca in the deeper parts of a dam reservoir (ŻBIKOWSKI 1995). The ability to occupy muddy sediments located far from the shore makes it possible for these clams to avoid competition with other filtrators, especially large bivalves. According to KUDELSKA & SOSZKA (1996) this species is an indicator of low water quality.

The great abundance of molluscs in Soczewka was probably a consequence of very suitable environmental conditions (namely: food and oxygen concentration). That is why the lack of *P. antipodarum* (common in Dobiegniewo) in this zone was a surprise, as this species is very tolerant with respect to substratum quality (sand or mud) and flow speed (stagnant or flowing water) (PIECHOCKI 1979, KOŁODZIEJCZYK & KOPERSKI 2000). Probably, it was more common in those places, where the appearance of a permanent benthic community was inhibited by unstable environmental conditions, such as strong wave action, water level fluctuations and frequent resuspension events in Dobiegniewo. Those habitats could be more susceptible to the invasion of an opportunistic organism, such as *P. antipodarum*. Its dominance in the molluscan community in Dobiegniewo was also noted by CZARNECKA (2005). On the other hand, longer studies on the presence of this species are needed to confirm its preference for Dobiegniewo rather than Soczewka, as it often appears in great numbers, but its occurrence is not permanent (BRZEZIŃSKI & KOŁODZIEJCZYK 2001). Thus, it is possible that its distribution would change in the future.

Dreissena polymorpha was also absent from Soczewka. This may be accounted for by a strong water flow, equal to ca. 1.0 m/s (GRZEŚ 1983). Filtration activity of zebra mussels decreases at the flow speed of 0.2 m/s and higher (ACKERMAN 1999). Futhemore, flow speed above 1–1.5 m/s inhibits settlement of dreissenid larvae (MACKIE et al. 1989), and that above 0.27 m/s suppresses byssogenesis in adults (CLARKE & MCMAHON 1996). Therefore, zebra mussel recruits are known to avoid sites exposed to strong water flow (KOBAK 2004, 2005). JURKIEWICZ-KARNKOWSKA (1998, 2004) noted higher abundances of zebra mussels in the lower region of the Zegrzyński Dam Reservoir and in its parts located outside the old river bed, i.e. at sites with the limited water flow. Another limiting factor for this species is insufficient amount of suitable hard substratum, which could account for the generally low abundance of the zebra mussel at the studied sites.

The greatest number of taxa found in the layer of mud on sand at the Dobiegniewo site resulted probably from the overgrowth of the bottom by macrophytes, which increased habitat heterogeneity, stabilised bottom sediments and improved food conditions (COOPER & KNIGHT 1985, PODDUBNAYA 1988).

The low number of taxa on the sandy bottom in Dobiegniewo could result from the fluctuations of the water level. At the end of the summer, the sampling site was exposed to air for ca. 10 days. This period was too short for the development of terrestrial plants, which would be decomposed after the subsequent submersion and thus would improve food conditions, stimulating the development of benthic macroinvertebrates. The dominance of *P. antipodarum* in this place confirmed this hypothesis, as this snail is able to survive a short-time exposure to air (PIECHOCKI 1979).

Despite the considerable similarity among the sampling sites with respect to the depth, substratum quality and distance from the shore, molluscan communities differed substantially within the studied area. In the rheolimnic part of the WDR (Soczewka), molluscan abundance increased with depth, suggesting an improvement in environmental quality. On the other hand, in its limnetic part (Dobiegniewo), the most suitable conditions for Mollusca were found in the habitat overgrown by macrophytes. Horizontal distribution of molluscs in Dobiegniewo was similar to that found in the near-shore zone of many eutrophic lakes, where a considerable decrease of their abundance and diversity is observed on the muddy bottom. The present study demonstrated that in different hydrodynamic conditions (a moderate directional flow), muddy sediments could be a very suitable habitat for a rich and diverse molluscan community.

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Received: December 20th, 2006
Accepted: June 13th, 2007