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Shallow-water benthic macroinvertebrate community of the limnic part of a lowland Polish dam reservoir

Małgorzata Poznańska[a,*], Jarosław Kobak[a], Norbert Wolnomiejski[b], Tomasz Kakareko[c]

[a]Department of Invertebrate Zoology, Institute of General and Molecular Biology, Nicolaus Copernicus University, Gagarina 9, 87-100 Toruń, Poland
[b]Sea Fisheries Institute in Gdynia, Research Station in Świnoujście, Plac Słowiański 11, 72-600 Świnoujście, Poland
[c]Department of Hydrobiology, Institute of Ecology and Environment Protection, Nicolaus Copernicus University, Gagarina 9, 87-100 Toruń, Poland

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Abstract

Biodiversity, abundance and taxonomic composition of shallow-water zoobenthos were studied in the Włocławek Dam Reservoir (the lower Vistula River, central Poland). The following habitats located near the shore were studied: (1) sandy bottom in the flooded part of the reservoir; (2) sandy bottom close to the main riverine flow in the reservoir and (3) organic-rich bottom covered by a thick layer of plant remnants in a shallow, isolated cove. In each habitat we investigated two sites (ca. 0.5 and 1 m depth). Also examined was the bottom of a phytolittoral site (sandy bottom, with elodeids and nympheids, 1 m depth), located in the flooded zone. In general, the bottom fauna was highly diverse and abundant in these habitats. The highest biodiversity (38 taxa, Shannon–Wiener index = 4.3) was found on the bottom rich in organic matter. However, the zoobenthos abundance in this habitat was comparatively low, probably due to periodical oxygen deficiencies. The highest density of bottom fauna ($>30,000$ individuals per m^2), accompanied by its high biodiversity, occurred at the phytolittoral site. The benthic community of the organic-rich sediments was the most distinct, with many taxa occurring exclusively in this area. The composition of the bottom fauna, from the two sandy habitats and phytolittoral, also differed from one another. The differences in taxonomic composition between the shallower and deeper sites were less pronounced. Lower densities at the shallower sandy sites and a very high variability of taxonomic composition among particular samples from these sites indicated lower stability of their environmental conditions. These were certainly due to water level fluctuations and/or destructive wave action. On the other hand, no such differences were found between the sites of various depths from the organic-rich sediments, showing that this substratum provided better protection against adverse hydrodynamical factors.

Keywords: Near-shore zone; Littoral; Phytolittoral; Sandy bottom; Organic-rich sediments; Zoobenthos community

Introduction

Dam reservoirs are often devoid of a typical littoral, overgrown by emergent plants. Their near-shore zone extends from the shallowest part that is temporarily exposed to air, to the bottom at up to 2 m depth

*Corresponding author. Tel.: +48 056 611 44 52; fax: +48 056 611 47 72.
E-mail address: mpoznan@biol.uni.torun.pl (M. Poznańska).

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(Stańczykowska and Jurkiewicz-Karnkowska, 1983). This zone strongly affects functioning of an entire aquatic ecosystem. In natural lakes, one of its main components is macrophyte cover, which influences the trophic level of a water body, but also depends on it. Plants are extremely important for composition and abundance of bottom fauna, as well as for epiphytic and mining organisms, providing food source and protection against predators and excessive water movements. In dam reservoirs, macrophytes are limited by relatively strong water current. Usually, their succession is slow (may take some decades) and restricted to more stagnant sites (Stańczykowska and Jurkiewicz-Karnkowska, 1983; Allan, 1995).

Composition and abundance of zoobenthos depend on multiple environmental factors and substratum type (e.g. Hoffman et al., 1996; Heino, 2000; Tolonen et al., 2001; Weatherhead and James, 2001). Detritivores prevail in habitats rich in organic matter, e.g. in the vicinity of plants (Kuklińska, 1989; Timm et al., 2001; Kornijów et al., 2003). Bare sand is inhabited by psammophiles (Grigelis, 1980; Kornijów and Gulati, 1992; Mastrantuono et al., 2001; Timm et al., 2001; Tolonen et al., 2001), while habitats experiencing oxygen deficiencies are dominated by organisms resistant to hypoxia (e.g. Wolnomiejski, 1965; Kornijów, 1988; Popp and Hoagland, 1995; Kornijów and Moss, 2002; Brodersen et al., 2004). Most of the above research concerns natural lakes, while similar studies dealing with fauna from manmade reservoirs are less common. Given the strong influence of dam reservoirs upon the environment and their importance for industry, they deserve detailed studies of various parts of their ecosystems. Factors affecting organisms in dam reservoirs differ from those acting in natural water bodies. One of them is water flow, which influences macrophyte distribution and causes dislodgement of bottom fauna (Allan, 1995). The near-shore zone of a dam reservoir is also affected by periodic water level fluctuations, causing temporary exposure of its shallowest parts to air (Stańczykowska and Jurkiewicz-Karnkowska, 1983; Prus et al., 1999; Richardson et al., 2002). The unfavorable effects of these factors on zoobenthos are most pronounced on the sandy bottom, which does not provide any protection for organisms and dries out quickly (Poznańska, 2006).

Studies on the bottom fauna of near-shore zones of dam reservoirs (Stańczykowska and Jurkiewicz-Karnkowska, 1983; Kuklińska, 1989; Żbikowski, 1995; Dusoge et al., 1999; Prus et al., 1999) are less common than those concerning natural water bodies or other parts of reservoir ecosystems. Some of them focus on certain aspects of the functioning of manmade lakes or on selected groups of organisms, e.g. molluscs (Jurkiewicz-Karnkowska, 1998, 2002; Jakubik, 2003; Jurkiewicz-Karnkowska and Żbikowski, 2004; Żbikowski et al., 2007). Few studies deal with the effect of water level fluctuations on bottom fauna and macrophytes of near-shore zones of these water bodies (Hynes, 1961; Richardson et al., 2002). However, general studies concerning entire shallow-water benthic communities of dam reservoirs are still missing.

The Włocławek Reservoir, located on the lower Vistula River is one of the largest Polish dam reservoirs. Previous studies on the benthic fauna in this water body were restricted almost exclusively to its off-shore areas with muddy sediments (Żbikowski, 2000). Little is known about the macroinvertebrate community from its near-shore zone except some fragmentary, unpublished contributions (Żbikowski, 1995). Therefore, the main aim of the present study was to investigate taxonomic composition, biodiversity and abundance of the shallow-water zoobenthos from sites located near the reservoir longshore banks. The main substratum type in this part of the reservoir is bare sand, areas overgrown by submerged plants, appeared only few years ago. Organic matter is accumulated only in sediments of small, isolated coves. Collecting samples from these three habitat types allowed us to relate zoobenthos variability to substratum quality, macrophyte presence and organic matter content. Furthermore, comparison of sites located at different depths (0.5 and 1 m) allowed us to check the adverse impact of water level fluctuations and wave action on zoobenthos. Finally, the effect of the vicinity of riverine flow on bottom fauna was assessed by collecting samples from the flooded part of the reservoir and close to the main river current.

Materials and methods

Study area

The Włocławek Reservoir (Fig. 1) was created in the 1970s when a dam was built across the lower Vistula River at the 675th km along its course (in the town of Włocławek, central Poland). It is the largest dam reservoir in Poland in respect of area (75 km^2), and the second largest in respect of capacity (400 million m^3). This is a shallow (average depth: 5.5 m, maximum: 15 m), highly eutrophic reservoir with a very short water retention time (4–5 days) and mean water flow of 900 $m^3 s^{-1}$ (Giziński, 2000). During the normal operation of a hydropower station located at the dam, water level fluctuates with an amplitude of ca. 0.5 m (data from the Włocławek Hydropower Station).

Samples were collected in the middle part of the reservoir, from three habitat types (Fig. 1): (1) psammolittoral in the flooded part of the reservoir, with sandy bottom devoid of plants, located near the left, flat

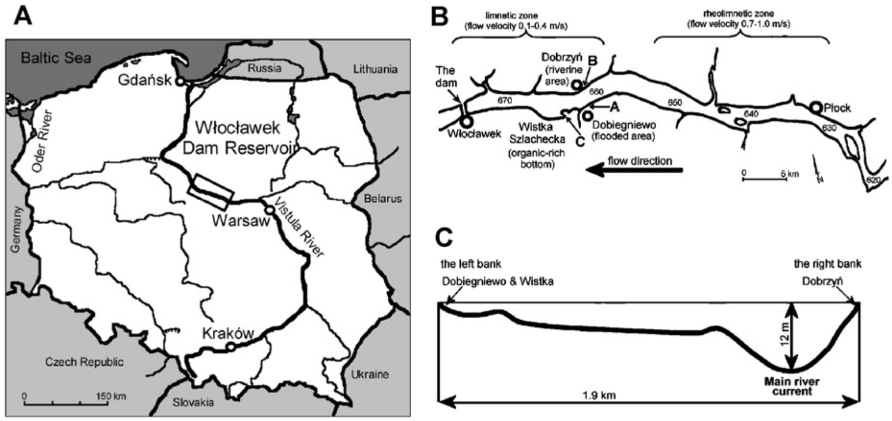


Fig. 1. Study area. (A) Location of the Włocławek Dam Reservoir in Poland. (B) The Włocławek Reservoir with the sampling sites indicated by arrows. (C) Cross-section through the reservoir at the level of the sampling area.

bank at the level of Dobiegniewo village (660th km of the river course) (habitat A in Fig. 1B); (2) psammolittoral close to the main riverine flow in the reservoir, with sandy bottom devoid of plants, located near the right, steep bank of the reservoir, at the level of Dobrzyń village (661th km of the river course) (habitat B, hereafter referred to as "riverine area"); (3) bottom covered by sediments rich in organic matter, mainly plant debris, located on the left bank of the reservoir in Wistka Szlachecka (664th km of the river course), a shallow, isolated cove overgrown by macrophytes (mainly helophytes, elodeids and *Lemna* sp.) (habitat C). In each habitat, we studied two sites, 0.5 and 1 m depth during the normal back-water level at the dam.

To study the effect of macrophytes on zoobenthos we selected an additional, phytolittoral site, overgrown by plants (elodeids and nympheids), located in the flooded area of the reservoir (near Dobiegniewo), at the depth of 1 m, like the deeper psammolittoral sites described above. The samples from this site were collected among plants from its sandy bottom.

Sample collection

Habitats 1 (psammolittoral and phytolittoral from the flooded area) and 3 (organic-rich sediments) were sampled in 2003 at monthly intervals (ten dates). In 2004, samples were taken bimonthly from habitat 1 (continued) and 2 (riverine area) (five dates).

Samples were collected using a core sampler designed by Wolnomiejski (unpublished data), within a catching area of 22 cm^2, penetrating bottom sediments to a depth of 29 cm. Each sample consisted of the contents of five samplers. The collected material was rinsed using a 0.5 mm sieve and preserved in Dorogostajski solution (containing potassium and sodium nitrate, sodium chloride, formalin and glycerin) (Żmudziński, 1974). Diptera (except the family Ceratopogonidae), Oligochaeta, Hirudinea, Mollusca, and Crustacea were identified to species or genus level when practical. Other taxa were not identified beyond order or class.

The daily data on water level fluctuations were made available to us due to the courtesy of the Włocławek Hydropower Station authorities. On the sampling dates in 2003, water temperature and oxygen concentration near the bottom were measured using the MultiLine P4 (WTW) Universal Pocket Sized Meter. Water transparency was estimated with a Secchi disk. Organic mater content in sediments was determined by heating 1 g of dried (24 h at 100 °C) sediments at 550 °C for 2 h.

Data analysis

As the numbers of collected invertebrates differed strongly among various sites, we applied the rarefaction technique to assess a theoretical number of taxa that would be found in a given number of collected individuals (Hurlbert, 1971). We also calculated traditional measures of biodiversity: taxon number (S), Shannon–Wiener index (H') (log base = 2) and evenness ($J' = H'/\log(S)$). To find differences in these parameters among the studied sites, we applied randomization tests using bootstrap technique, available in PAST 1.54 statistical software (Hammer et al., 2001). Sequential Bonferroni correction was applied to control for multiple pairwise comparisons among sites in this analysis.

Total zoobenthos densities at the studied sites were compared using the two-way ANOVA (factors: habitat and site), followed by Tukey test. As the sandy phytolittoral site from the flooded part of the reservoir had no counterparts in the other habitats, two separate analyses were carried out: (1) including all habitats (the flooded area, riverine area and organic-rich sediments) without the phytolittoral site and (2) with all sites (including the phytolittoral) from the flooded part of the reservoir only (two sampling years).

Two-way crossed analysis of similarities (ANOSIM) based on Bray–Curtis distances (Clarke, 1993) was applied to check the differences in community composition between the studied habitats and sites. The statistical significance of differences between groups was tested using a randomisation test (with 1000 replicates), carried out using a procedure written in Microsoft® Visual Basic for Excel 2000. As in the case of the ANOVA, two separate analyses were carried out: (1) including all habitats, without the phytolittoral site and (2) with all sites (including the phytolittoral) from the flooded area only (two sampling years).

To find relationships between habitats, sites and taxa, we applied the correspondence analysis (CA), using PAST 1.54 statistical software (Hammer et al., 2001). The data was log-transformed to dampen the effect of the most common taxa. Rare taxa (represented by three individuals or less) were removed from the data set to reduce noise. As the first analysis showed a strong distinction of the samples collected from the organic-rich sediments, we ran an additional analysis on a reduced data set, including only the samples from the habitats with a sandy bottom. It helped detect less pronounced relationships within the sandy habitats.

Results

Abiotic characteristics

The normal back-water level in the Włocławek Reservoir is 57.3 m above sea level. During the 2 years of the study course, the lowest and the highest measured levels were 56.47 and 57.55 m asl, respectively, with the amplitude being 1.08 m (Fig. 2). The most important, for the purpose of the present study, were drastic reductions of the water level. Such events, lasting for many days, occurred mainly in summer. The longest drastic reductions, up to 76 cm below the normal back-water level, took place in June and July 2003 and lasted up to 28 days (Fig. 2). They were caused by renovation works at the dam. Several very short (a few days) drops of the water level also occurred at the end of the year 2004 (Fig. 2). This resulted in exposing large parts of the upper littoral (including our shallower sampling sites) to air. However, on the sampling dates all the sites were always submerged and the bottom fauna is able to survive quite long periods of air exposure provided that the substratum is wet (M. Poznańska, unpublished data), which was the case in our study.

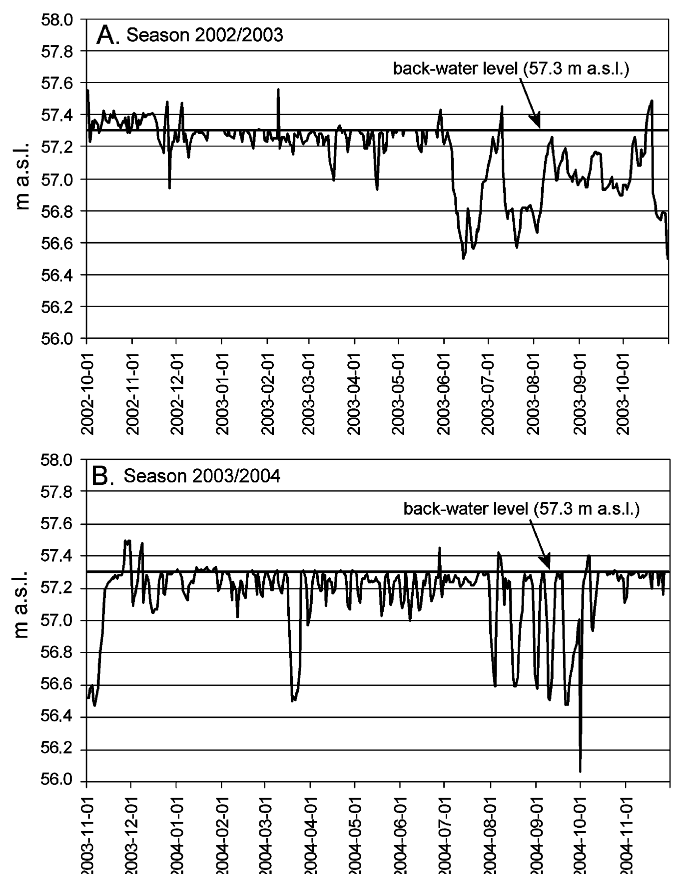


Fig. 2. Water level fluctuations in the Włocławek Reservoir in the season 2002/2003 (A) and 2003/2004 (B). Data from the Włocławek Hydropower Station.

Table 1. Secchi disk visibility and water oxygenation in the littoral from the flooded area and organic-rich sediments.

		Flooded area			Organic-rich sediments		
		Mean	Range	SD	Mean	Range	SD
Secchi disk visibility	(m)	1.2	0.6–2.0	0.6	1.1	0.6–1.1	0.4
Near-bottom water oxygenation	(mg/l)	9.0	6.1–11.2	1.6	3.5	0.4–6.8	3.3
	(%)	81	69–113	15.2	34	4–67	31.3

Table 2. Organic matter content (%) in the sediments at the studied sites: 0.5 m – the shallower submerged site, 1 m – the deeper submerged site, phytolittoral – 1 m – the additional site in the flooded area.

		Organic matter (%)		
Habitat	Site (m)	Mean	Range	SD
Flooded sandy area	0.5	0.1	<0.1–0.1	0.04
	1	0.1	0.1–0.1	<0.01
Phytolittoral	1	0.4	0.2–0.6	0.21
Riverine sandy area	0.5	1.1	0.6–1.5	0.48
	1	0.4	0.3–0.5	0.08
Organic-rich sediments	0.5	48.8	38.1–60.6	11.28
	1	28.9	21.2–39.1	9.21

As the mean Secchi disk visibility was ca. 1 m, light usually reached the bottom of the studied sites (Table 1). Water temperature during the study course varied from 0.1 to 28 °C. The near-bottom water oxygenation in the flooded and riverine parts of the reservoir was good (always above 6 mg l^{-1}), while in the cove with the bottom rich in organic matter, long-term oxygen deficiencies were common and the mean oxygen concentration was rather low (Table 1). Undoubtedly, these poor oxygen conditions resulted from the high amount of detritus in the substratum, overgrowing the water surface by *Lemna* sp., and probably also due to macrophyte respiration at night.

The organic matter content in the bare sand, from the flooded area, was the lowest. Slightly higher values were found at the phytolittoral site and in the riverine area (Table 2). In the cove with the bottom covered by plant remnants, organic matter content was much higher than elsewhere.

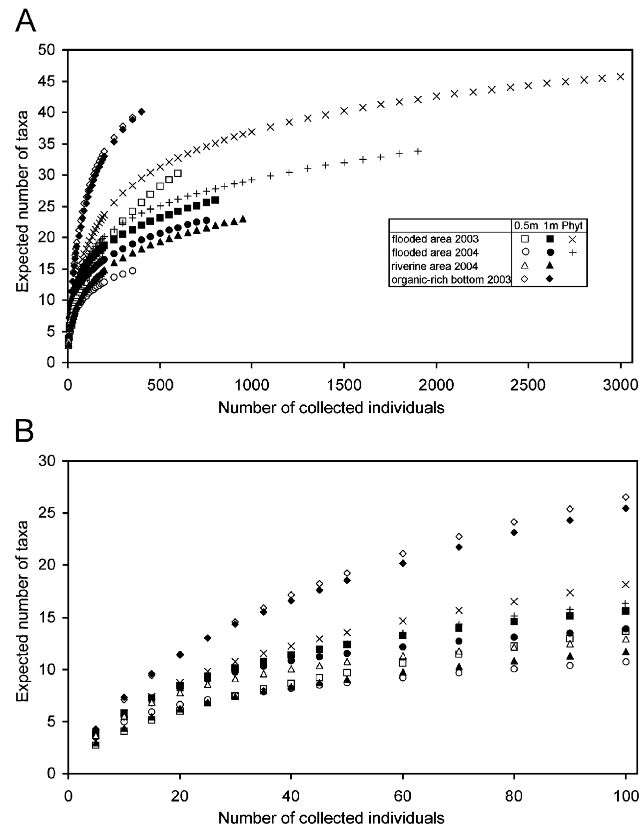


Fig. 3. Rarefaction curves for the studied sites. Fig. B shows the initial parts of the curves, up to 100 collected individuals, which is obscured in Fig. A due to the long scale range on the abscissa. The curve steepness is a function of the community taxon evenness, while its height indicates the taxon richness.

Biodiversity

The rarefaction curves (Fig. 3) showed the highest biodiversity and high taxon richness at the sites with the bottom rich in organic matter. The number of taxa and Shannon–Wiener index (Table 3A) in this habitat differed significantly from the values found in all other habitats, except the number of taxa collected in 2003 from the shallower sandy site in the flooded area (Table 4A). However, contrary to the organic-rich sediments, the latter site was dominated by a few most abundant taxa, mainly *Stictochironomus* sp. (Fig. 4), which is shown by the much lower steepness of its rarefaction curve (Fig. 3B) and low evenness (Table 3A). The highest taxon number (Table 3A), significantly different than at the psammolittoral sites (Table 4B), was found in the phytolittoral (Fig. 3). However, the evenness at this site was comparatively low (Table 3A). The psammolittoral habitats from the flooded and

Table 3. Biodiversity (A), density (B) and biomass (C) of macroinvertebrates in the studied area.

	Flooded area (Dobiegniewo 2003) (Fl03)			Flooded area (Dobiegniewo 2004) (Fl04)			Organic-rich bottom (Wistka) (Org)		Riverine area (Dobrzyń) (Riv)	
Site:	0.5 m	1 m	Phyto	0.5 m	1 m	Phyto	0.5 m	1 m	0.5 m	1 m
A. Biodiversity: S – number of taxa, H′ – Shannon–Wiener index (log base 2), J′ – evenness										
S	27	22	41	14	21	31	37	38	12	22
H′	2.09	3.30	3.37	2.81	3.09	3.10	4.26	4.20	2.93	2.41
J′	0.42	0.70	0.61	0.72	0.68	0.61	0.80	0.78	0.79	0.53
B. Density (ind. m^{-2}): T-total, Ch-chironomids, Ol-oligochaetes, Mol-molluscs, Oth-other										
T	8306	9057	30,624	7346	14,327	36,000	5697	8013	1927	17,346
Ch	5593	4687	6167	2327	2127	4418	2082	2355	345	2273
Ol	1855	2125	20,627	764	4837	22,073	1926	2784	564	14,909
Mol	478	1697	3218	2237	6872	8291	606	1494	109	145
Oth	380	548	612	2018	491	1218	1083	1380	909	19
C. Biomass ($g\,m^{-2}$): T – total, Soft – soft benthos (without molluscs)										
T	66.0	219.5	180.9	62.8	269.2	649.5	123.6	75.6	8.7	158.1
Soft	23.3	28.0	39.7	39.3	27.4	39.4	19.4	20.1	5.5	21.1

Phyto – phytolittoral site.

Table 4. Results of the randomization tests comparing biodiversity indices among habitats (A) and among sites within a given habitat (B).

A	Site:	0.5 m				1 m				Phyto	
	Habitat:	Fl03	Fl04	Org	Riv	Fl03	Fl04	Org	Riv	Fl03	Fl04
	S	a	b	a	b	a	a	b	a	a	b
	H′	a	b	c	b	a	b	c	d	a	b
	J′	a	b	b	b	a	a	b	c	a	a

B	Habitat:	Fl03			Fl04			Org		Riv	
	Site:	0.5 m	1 m	Phyto	0.5 m	1 m	Phyto	0.5 m	1 m	0.5 m	1 m
	S	ab	a	b	a	b	c	a	a	a	a
	H′	a	b	b	a	b	b	a	a	a	b
	J′	a	b	c	ab	a	b	a	a	a	b

Indices labelled with the same letters do not differ significantly from one another ($p<0.05$, after sequential Bonferroni correction). See Table 3 for the abbreviations of the names of indices, habitats and sites.

riverine areas differed from each other with respect to Shannon–Wiener index and evenness only at the depth of 1 m (Table 4A), with the former having more diverse zoobenthos (Table 3A).

Biodiversity and evenness at the sandy sites devoid of macrophytes significantly depended on depth (Table 4B). In the flooded area their values were higher at the deeper sites, while in the riverine area the tendency was opposite (Table 3A). No influence of depth on biodiversity measures was found on the bottom rich in organic matter.

Abundance and biomass

The total densities of bottom fauna in the studied habitats did not differ significantly from one another (ANOVA: all habitats without the phytolittoral site: $F_{3,43} = 0.74$, $p = 0.5357$; the flooded area with the phytolittoral site included: $F_{1,36} = 1.02$, $p = 0.3192$), though the density in the organic-rich sediments was slightly lower (Table 3B). Significant differences were found among sites within particular habitats (ANOVA: all habitats without the phytolittoral site: $F_{1,43} = 6.62$,

$p = 0.0136$; the flooded area with the phytolittoral included: $F_{2,36} = 17.10$, $p < 0.001$). The phytolittoral was the most densely colonised (up to 36,000 individuals per m^2) and differed significantly in this respect from the other sites (Tukey test). The difference in total zoobenthos density between the deeper and shallower sites devoid of plants was significant (Tukey test) only if all habitats were included in the analysis. The highest difference between them was found in the riverine part of the reservoir, where the total density at the deeper site was ca. 9 times higher than at the shallower one (Table 3B).

The psammolittoral in the flooded area was dominated by chironomid larvae (2003) or molluscs (2004). Oligochaetes prevailed in the phytolittoral and in the riverine area. On the bottom rich in organic matter, the domination of oligochaetes and chironomids (with a similar share of both these groups) was observed (Fig. 4, Table 3B).

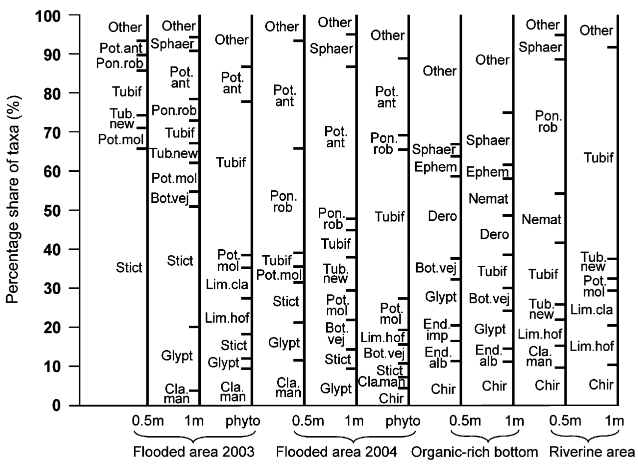


Fig. 4. Taxa dominating at the studied sites (>2% of share in the total zoobenthos density). See Fig. 5 for the abbreviations of the names of taxa.

Total zoobenthos biomass (Table 3C) was affected by the share of molluscs, which at the deeper sites ranged from 73% in the organic-rich sediments to 94% in the phytolittoral. The biomass of soft benthos (without molluscs) at those sites was from $20\,g\,m^{-2}$ in the organic-rich sediments to almost $40\,g\,m^{-2}$ in the phytolittoral. At the shallower sites, the share of molluscs was generally lower (Table 3). The biomass of soft benthos was from $5.5\,g\,m^{-2}$ in the riverine area to more than $39\,g\,m^{-2}$ in the flooded area. At the deeper and shallower site with organic-rich sediments it was similar, though the share of molluscs at the latter case was higher.

Taxonomic composition

Taxonomic composition of zoobenthos differed significantly among the studied habitats and sites (ANOSIM, Table 5). The R_{ANOSIM} values indicated that the differences among habitats were much stronger that those among sites. First of all, the sites with organic-rich sediments deviated significantly from the sandy sites. Significant differences also occurred between the two types of sandy habitats, from the flooded and riverine parts of the reservoir (Table 5A). On the other hand, the taxonomic composition of the samples collected during the two consecutive seasons in the flooded area was similar, showing no effect of the sampling year. Therefore, the comparison of the samples from the organic-rich sediments and riverine

Table 5. Results of the ANOSIM analyses testing the differences between the studied sites and habitats.

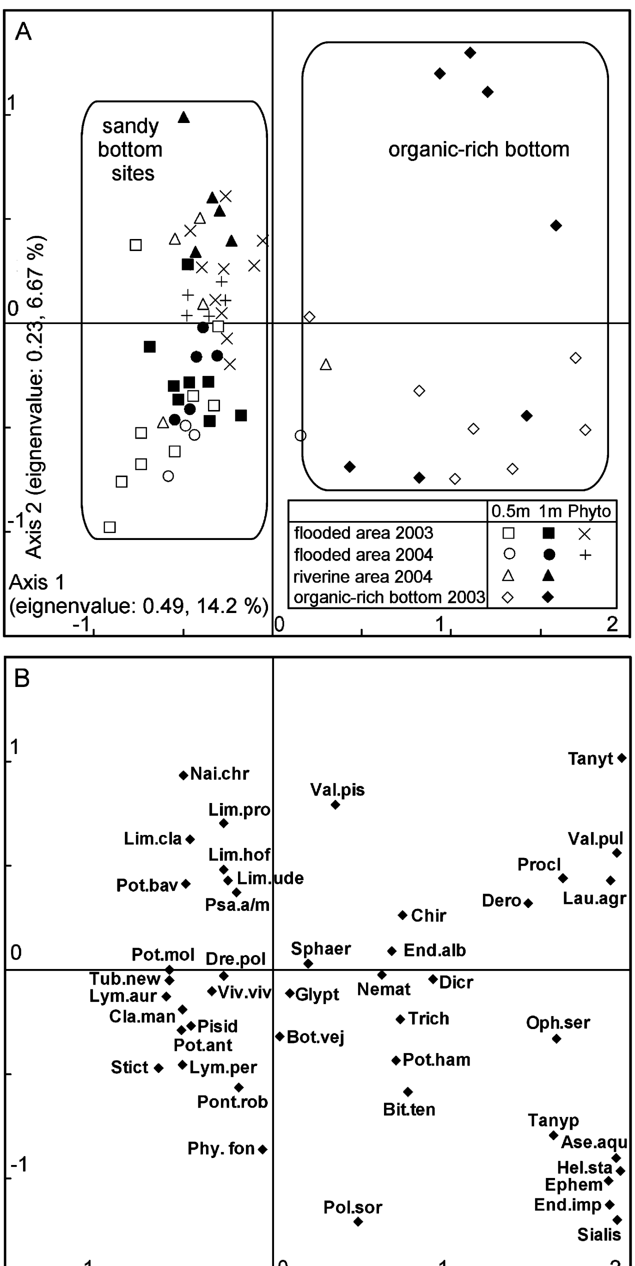
Test	Source of variation	R	*p*-level
A. All habitats, sites: 0.5 and 1 m			
Two-factor crossed test	Between habitats	0.50	<0.001
	Between sites	0.19	0.001
Pairwise comparisons between habitats	Fl03 vs. Fl04	0.12	0.216
	Fl03 vs. Org	0.77	<0.001
	Fl04 vs. Riv	0.47	<0.001
	Org vs. Riv	0.64	<0.001
B. Flooded area (Dobiegniewo) only, all sites			
Two-factor crossed test	Between habitats	0.05	0.235
	Between sites	0.39	<0.001
Pairwise comparisons between sites	0.5 m vs. 1 m	0.19	0.020
	0.5 m vs. Phyto	0.51	<0.001
	1 m vs. Phyto	0.57	<0.001

See Table 3 for the abbreviations of the habitat and site names.

area (Table 5A) seems to be justified, even though they were not collected in the same year.

The zoobenthos community found in the phytolittoral differed significantly from those from the other sites (Table 5B). Although significant differences were also found between the samples collected from the bare bottom at various depths, especially when all the habitats were included into the analysis, these were much weaker (Table 5A).

The correspondence analysis confirmed the results of ANOSIM. The first CA axis separated the samples collected from the bottom rich in organic matter from both sandy habitats (Fig. 5A). Taxa occurring exclusively in the organic-rich sediments were: Ephemeroptera, *Helobdella stagnalis* (L.), *Endochironomus* sp. (impar group), *Valvata pulchella* Studer and *Asellus aquaticus* L. (Fig. 5B). Relatively high densities of a naidid oligochaete *Dero* sp., sphaeriid clams and nematods, identified as plant parasites (Joanna Rokicka-Praxmajer, personal communication) were also observed in this habitat (Fig. 4). Taxa prevailing on sandy substratum were: a snail *Potamopyrgus antipodarum* (Gray), oligochaetes: *Potamothrix moldaviensis* Vejd. et Mr., *Tubifex newaensis* (Mich.) and *Limnodrilus claparedeanus* Ratzel, as well as chironomids: *Stictochironomus* sp. and *Cladotanytarsus* sp. (Figs. 4 and 5B).



Differences among the sites located within the flooded and riverine parts of the reservoir became apparent when the samples collected from the organic-rich bottom were excluded from the analysis (Fig. 6). The first axis of this analysis separated the samples from the psammolittoral in the flooded area from those collected in the phytolittoral and in the riverine area. Taxa occurring mainly in the former habitat were: *P. antipodarum*, *Pontogammarus robustoides* (G.O. Sars), *P. moldaviensis* and *Stictochironomus* sp. The two latter habitats were inhabited by high numbers of *Limnodrilus hoffmeisteri* Clap., *L. claparedeanus* (Fig. 6B), juvenile Tubificidae without hair setae and *Chironomus* sp. (Fig. 4).

In general, the species composition of the samples from the shallower and deeper sites was similar, though

Fig. 5. Position of the studied sites (A) and taxa (B) in the correspondence analysis ordination of the total data set. Only the most important taxa are shown: Ase.aqu-*Asellus aquaticus*, Bit.ten-*Bithynia tentaculata* (L.), Bot.vej-*Bothrioneurum vejdovskyanum*, Chir-*Chironomus* sp., Chir.pup-Chironomidae pupae, Cla.man-*Cladotanytarsus* e.g. mancus (Walk.), Crypt-*Cryptochironomus* sp., Dero-*Dero* sp., Dicr-*Dicrotendipes* sp., Dre.pol-*Dreissena polymorpha* (Pall.), Enchyt-Enchytraeidae juv., End.alb-*Endochironomus* sp. (albipennis group), End.imp -*Endochironomus* sp. (impar group), Ephem-Ephemeroptera, Glypt-*Glyptotendipes* sp., Hel.sta-*Helobdella stagnalis*, Lau.agr-*Lauterborniella agrayloides* Kieff., Lim.cla-*Limnodrilus claparedeanus*, Lim.hof-*L. hoffmeisteri*, Lim.pro-*L. profundicola* (Verrill), Lim.ude-*L. udekemianus* Clap., Lym.aur-*Lymnaea* (*R.*) *auricularia* (L.), Lym.per-*L.* (*R.*) *peregra* (O.F. Műller), Nai.chr-*Nais christinae* Kasprzak, Nemat-Nematoda, Oph.ser-*Ophidonais serpentina* (O.F. Műller), Pei.pus-*Peipsidrilus pusillus*, Phy.fon-*Physa fontinalis* (L.), Pisid-*Pisidium* sp., Pol.nub-*Polypedilum* sp. (nubeculosum group), Pol.sor-*Polypedilum* sp. (sordens group), Pon.rob-*Pontogammarus robustoides*, Pot.ant-*Potamopyrgus antipodarum*, Pot.bav-*Potamothrix bavaricus* (Oschmann), Pot.ham-*P. hammoniensis* (Mich.), Pot.mol-*P. moldaviensis*, Procl-*Procladius* spp., Psa.a/m-*Psammoryctides albicola* or *maravicus*, Sialis-*Sialis* sp., Sphaer-*Sphaerium* sp., Stict-*Stictochironomus* sp., Tanyp-*Tanypus* sp., Tanyt-*Tanytarsus* sp., Trich-Trichoptera, Tub.new-*Tubifex newaensis*, Unc.unc-*Uncinais uncinata*, Val.pis-*Valvata piscinalis* (O.F. Műller), Val.pul-*V. pulchella*, Viv.viv-*Viviparus viviparus* (L.).

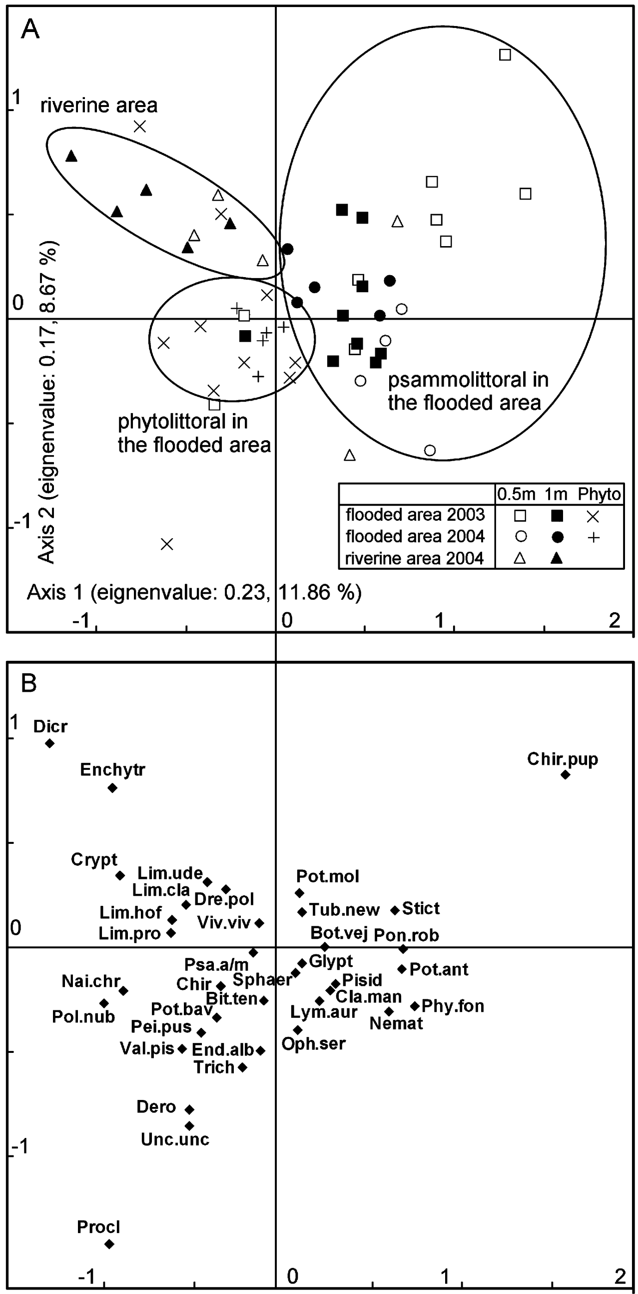


Fig. 6. Position of the studied sites (A) and taxa (B) in the correspondence analysis ordination of the reduced data set containing only the sites from sandy substrata (the flooded and riverine areas). See Fig. 5 for the abbreviations of the names of taxa.

the former tended to locate more to the right along the first CA axis than the corresponding deeper samples (Fig. 6A). The most important difference between these two groups of samples was the higher abundance of an amphipod *Pontogammarus robustoides* at the shallower sites. The share of chironomids in the total zoobenthos abundance was also higher at the shallower sites (Fig. 4). Moreover, the samples from the shallower sites were much more dispersed in the plot, showing that the taxonomic composition of their fauna was more variable than at the deeper sites (Fig. 6A).

The second CA axis of the analysis run on the reduced data set, discriminated between the samples from the riverine area and those from the phytolittoral (Fig. 6A). Taxa typical for the phytolittoral were chironomid *Procladius* spp. and oligochaetes: *Peipsidrilus pusillus* Timm, *Uncinais uncinata* (Oerst.) and *Dero* sp. Chironomids *Dicrotendipes* sp. and *Cryptochironomus* sp. as well as enchytraeid oligochaetes which occurred only in the riverine area (Fig. 6B). However, these taxa did not reach high abundances.

An oligochaete *Bothrioneurum vejdovskyanum* Štolc, a chironomid *Glyptotendipes* sp. and molluscs occurred in the entire flooded area and in the organic-rich sediments, but were rare or absent in the riverine area. On the other hand, high numbers of *Chironomus* sp. larvae were found at all sites except the bare sand in the flooded area (Fig. 4).

Discussion

Differences among habitats

The bottom fauna of the sandy sites devoid of plants was relatively diverse and abundant. The numbers of taxa (21–22) and Shannon–Wiener index (2.4–3.3), found in our study at the depth of 1 m (Table 3A), are relatively high compared to the results of Bänziger (1995), who noted only 10 taxa and Shannon–Wiener index of 1.9 in the sandy littoral in Lake Geneva. In small, shallow, highly eutrophic Lake Zwemlust Kornijów and Gulati (1992) found 30 benthic taxa on bare sand. On the other hand, Kuklińska (1989) found as many as 64 taxa in the near-shore zone of the highly productive Zegrzyński Reservoir. However, the sandy bottom in her study was covered by a thin layer of mud and overgrown by macrophytes, which certainly improved food and habitat conditions, stimulating development of a diverse community. The total zoobenthos abundance and biomass on sandy bottom in the present study (>8000 individuals and more than 20 g of soft benthos per m^2; Table 3A and B) was also rather high. In general, zoobenthos abundances and biomasses found in other reservoirs were similar or lower (Kuklińska, 1989; Sokolova and Sakharova, 1991; Bänziger, 1995; Prus et al., 1999).

Żbikowski (1995), investigating zoobenthos of the Włocławek Reservoir at the depth of 1 m in Dobiegniewo (the flooded area) and Dobrzyń (riverine area) in the years 1988–89, found total densities twice as high as those observed 14 years later in the present study. Perhaps this decrease might result from invasions of predatory Ponto-Caspian gammarids and neogobiid fish, which appeared in the reservoir at the turn of the century (Konopacka, 2004; Kostrzewa et al., 2004) and could affect local communities by feeding on native taxa (Konopacka, 2004; Kakareko et al., 2005). However, verification of this hypothesis would need further studies. Changes in the trophic status of the reservoir and its water level fluctuations between the compared periods could also be responsible for the observed differences (Jurkiewicz-Karnkowska and Żbikowski, 2004).

Another habitat type is sandy bottom overgrown by macrophytes. At the phytolittoral site, the number of taxa (41) was twice as large as at the nearby sandy site devoid of plants (Table 3A). The total zoobenthos density and biomass among macrophytes was the highest in our study (Table 3B and C). Our results confirm those of Stańczykowska and Jurkiewicz-Karnkowska, (1983), who demonstrated that the presence of plants positively affected biodiversity and abundance of bottom fauna in the Uczyński and Goczałkowicki Dam Reservoirs. However, the respective values of biodiversity measures noted in their phytolittoral zones, were much lower than presented here. Comparable biodiversity and abundance of zoobenthos was found among macrophytes in the Zegrzyński Reservoir (Kuklińska 1989).

Macrophytes increase habitat heterogeneity (e.g. Giudicelli and Bournaud, 1997; Tolonen et al., 2001; Weatherhead and James, 2001), improve food conditions, stabilize bottom sediments and provide protection against wave action (e.g. Pieczyńska and Zalewski, 1997; Tolonen et al., 2001, 2005). That is why their presence stimulates development of diverse and abundant bottom fauna (e.g. Kornijow et al., 1990; Kornijów and Gulati, 1992; Bänziger, 1995; Cogerino et al., 1995; Heino, 2000; Tolonen et al., 2005), which was also demonstrated in our study.

In the cove with a thick layer of detritus on the bottom, the high number of taxa (38) and biodiversity (Shannon–Wiener index: 4.2) were accompanied by the comparatively low total abundance and biomass, unlike the phytolittoral site (Table 3B and C). In the phytolittoral of the Zegrzyński Dam Reservoir, zoobenthos density was also very high (Kuklińska, 1989). On the other hand, abundance and biomass of macrofauna in the phytolittoral of eutrophic lakes studied by Kornijów (1988), Kornijow et al. (1990) and Kornijów and Gulati (1992) was lower than in the organic-rich sediments from our study and taxon numbers were similar in both types of habitats. Thus, although the zoobenthos density in the organic-rich sediments was lower than at the sandy phytolittoral site, it was still relatively high compared to the other studies.

Oxygen deficiencies in littoral areas with dense vegetation are quite common (e.g. Miranda and Hodges, 2000; Goodwin et al., 2008). Furthermore, the high abundance of *Lemna* sp. in summer further deteriorated oxygen conditions by shadowing the bottom and directing the produced oxygen into air. Therefore, it is difficult to explain the high biodiversity of the bottom fauna in the organic-rich sediments. It should be noted that it consisted mainly of taxons resistant to oxygen deficiencies and/or associated with plants, which constituted 79% of the total abundance and 50% of the total number of taxa. Some species can migrate actively to water rich in oxygen (e.g. Kuklińska, 1989; Armitage et al., 1995; Marklund et al., 2001; Strayer et al., 2003; Czarnecka, 2005) or exhibit various physiological adaptations allowing them to survive in extremely unfavorable conditions (e.g. Armitage et al., 1995; Hamburger et al., 2000). Perhaps poor oxygen conditions in the organic-rich sediments could be compensated by a very high quantity and quality of food and the vicinity of plants, providing a heterogenous and suitable habitat. At present, it is impossible to determine which of the above-mentioned factors contributed most to the observed taxonomic richness and abundance of zoobenthos at the organic-rich site in our study. Furthermore, the evenness in the cove was very high (Fig. 3, Table 3), showing that no taxon became a clear dominant. Perhaps periodical oxygen depletions happening in the cove prevented development of a stable community, with a permanent domination structure. Such a pattern develops in the presence of a strong limiting factor, like periodical sediment resuspension (Shin, 1989). A similar phenomenon was observed in the study of the molluscan community living in the muddy sediments of the deeper parts of the Włocławek Reservoir (>2 m depth). Periodical resuspensions, during which large amounts of oxygen were consumed, resulted in appearance of a community with high biodiversity and evenness, but low abundance (Żbikowski et al., 2007). In our study, sharp oxygen deficiencies could also be responsible for the occurrence of a similar community type.

Taxonomic composition of the shallow-water zoobenthos of the Włocławek Reservoir was typical for a eutrophic water body with sandy bottom (e.g. Grigelis, 1980; Wiśniewski and Dusoge, 1983; Kornijów, 1988; Kuklińska, 1989; Kornijów and Gulati, 1992; Dusoge et al., 1999). The sandy sites in the flooded and riverine areas were inhabited by similar taxa, but had different domination structures. The former area was dominated by psammophiles: chironomids *Stictochironomus* sp. and *Glyptotendipes* sp., a snail *Potamopyrgus antipodarum*, oligochaetes: *Potamothrix moldaviensis* and *Tubifex newaensis* (e.g. Grigelis, 1980; Kasprzak, 1981; Kornijów and Gulati, 1992; Kołodziejczyk and Koperski, 2000; Krodkiewska et al., 1998; Timm et al., 2001; Milbrink and Timm, 2001), whereas the riverine area was inhabited mainly by pelophilous oligochaetes and *Chironomus* sp. larvae (Fig. 4), strongly depending on amounts of available organic matter in substratum. This was rather unexpected as sandy substrata, with low organic matter content, are usually dominated by psammophilous chironomids (Grigelis, 1980; Kornijów, 1988). Higher organic matter content in substratum near the main river current might be responsible for the observed differences between both psammolittoral habitats. It is also possible that sufficient quantities of food for pelophilous organisms in the riverine area could be constantly supplied by the nearby river current and wave actions and be immediately exploited by animals. Kornijów and Gulati (1992) found the relationship between bioseston quantity in water and development of *Chironomus* sp. larvae. Domination of oligochaetes on sand was also observed in several other studies (Pieczyńska, 1972; Dall et al., 1984; Bänziger, 1995; Żbikowski, 1995). Kuklińska (1989) stated that *Chironomus* sp. larvae, found in sandy substratum, fed in the deeper muddy parts of a reservoir and migrated to sandy areas to avoid poor oxygen conditions occurring periodically in organic-rich sediments.

Similar to the riverine area, the phytolittoral was dominated by oligochaetes, among which several rare taxa and species new to Poland were found: *Bothrioneurum vejdovskyanum*, *Tubifex blanchardi* and *Peipsidrilus pusillus* (Dumnicka and Poznańska, 2006). Its sandy bottom was covered by a thin layer of mud, which provided suitable food for these organisms. Another species common in the phytolittoral was an invasive snail, *Potamopyrgus antipodarum*, which was abundant in the entire flooded area. Usually, it dominates in invaded areas (Wolnomiejski and Furyk, 1968; Brzeziński and Kołodziejczyk, 2001; Żbikowski et al., 2007), due to parthenogenetic reproduction, parental care and high tolerance to unsuitable environmental conditions (Krodkiewska et al., 1998; Kołodziejczyk and Koperski, 2000).

The benthic community living in the bottom, rich in organic matter, clearly differed from those found in the other habitats (Table 5, Fig. 5A). It was dominated by detritivorous organisms capable of surviving oxygen depletions, found in this habitat, such as *Chironomus* sp., *Glyptotendipes* sp. and sphaeriid clams (Fig. 5). Another group of taxa consisted of organisms associated with macrophytes overgrowing a large part of the cove, e.g. a naidid oligochaete *Dero* sp. and nematods. Moreover, many rare taxa occurred exclusively in this habitat, though in low quantities (taxa grouping on the right side of Fig. 5B), making this community the most distinct in the studied area.

Differences among shallower and deeper sites

In general, zoobenthos at the deeper sandy sites was more abundant (particularly in the riverine area) and diverse than at the shallower ones (Table 3), showing that the latter were less suitable for bottom fauna. The slightly higher biodiversity indices at the shallower site in the riverine area were associated with extremely low abundance and taxon richness (Table 3), which suggests the influence of a strong limiting factor and thus confirms our statement. The observed differences could be caused by water level fluctuations or wave actions, which affected shallower sites to a larger extent. In lakes with weak wave actions, where these factors are negligible, density and diversity of littoral fauna may be higher at a depth of 0.5 m than at 2 m (Kornijów, 1988). The effect of hydrodynamics is particularly strong on sandy substratum, which can be easily destabilized and does not provide sufficient protection for bottom organisms (Tolonen et al., 2001). In our study, the communities from the shallower sandy sites were clearly less stable than those from the deeper ones (Figs. 5A, 6A).

Domination structure at the sandy sites of various depths was rather similar (Figs. 5A, 6A), though significant differences in taxonomic composition between sites were also found (Table 5A). The most important difference was the higher abundance of a Ponto-Caspian gammarid *Pontogammarus robustoides* (Fig. 4) often reaching large densities in very shallow, sandy areas (Gruszka, 1999). It was also found in high numbers immediately near the shore in the Włocławek Reservoir (J. Żytkowicz, unpublished data).

No differences in diversity, abundance (Table 3) and taxonomic composition (Fig. 5A) were found between the two sites with the bottom rich in organic matter. Such substratum provides much better protection against desiccation during air exposure (Poznańska, 2006) and better food conditions. Thus, adverse hydrodynamical conditions did not affect the community from this habitat to such extent as that from bare sand.

Conclusions

Zoobenthos of the shallow-water habitats of the Włocławek Reservoir was highly abundant and diverse. Substratum type and presence of plants turned out to be stronger factors shaping the bottom community than water depth and distance from the main river flow. The highest biodiversity was noted in the organic-rich sediments and in the sandy phytolittoral. In these habitats, protection against adverse hydrodynamical conditions and food conditions were better in comparison with bare sandy bottom. In the organic-rich sediments, fauna was limited by oxygen depletions, which resulted in its relatively low abundance, whilst the density of organisms living in the phytolittoral was very high, showing the positive effect of plants upon bottom fauna. Assuming further development of macrophyte cover in the Włocławek Reservoir (especially emergent plants), which is currently in progress, we can expect an increase of overall abundance and richness of zoobenthos in this water body.

The communities from the shallower sandy sites were less stable, less diverse and less abundant than those from the deeper sites, certainly due to the stronger effect of wave action and water level fluctuations on the former. On the other hand, no such differences were found between the sites of various depths from the organic-rich sediments, showing that this substratum provided better protection against adverse hydrodynamical factors.

The two sandy habitats differed from each other with respect to their community structure and biodiversity, with the flooded area providing better conditions for development of bottom fauna than the habitat located in the riverine area.

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