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MALACOCOENOSES OF LARGE LOWLAND DAM RESERVOIRS OF THE VISTULA RIVER BASIN AND SELECTED ASPECTS OF THEIR FUNCTION

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ABSTRACT: Spatio-temporal variation in qualitative and quantitative occurrence of malacofauna was analysed in three large lowland dam reservoirs. Differences between the malacofauna of flooded land areas and former river beds persist even in middle-aged reservoirs. Quick turnover of water has a positive effect on mollusc abundance and species richness of the whole reservoir, and on the frequency of occurrence in the former river bed. Considerable dynamics of the malacocoenoses and a possibility to revert to earlier development stages, as a result of considerable disturbance, were observed at an advanced stage of biocoenosis development. Besides water dynamics and composition and distribution of bottom deposits, a significant effect on the malacocoenoses is exerted by dominant species, especially *D. polymorpha*. Abundance and dominance structure of malacocoenoses determine their role in the ecosystem, including accumulation of phosphorus and heavy metals, and their cycling as a result of filtration activity, faeces production, excretion and trophic transfer. Generally, the quantities of elements, especially heavy metals, accumulated in molluscs, are much smaller than the quantities which flow through the malacocoenoses. A large part of the pool of these elements contained in the shells is excluded from circulation for many years. Food chains seem to have relatively little effect on the transfer of heavy metals in the reservoir.

KEY WORDS: aquatic molluscs, dam reservoirs, spatio-temporal changes, heavy metals, phosphorus, trophic transfer, ecology

CONTENTS

INTRODUCTION

Small water resources of Poland, widely varying water flow in rivers, and increasing water deficit make it necessary to construct dam reservoirs in order to increase retention and improve water balance. A project of constructing a cascade of dam reservoirs on the Vistula River was prepared in 1956 (the concept arose as early as the 1930s) (TUSZKO 1967, GLAZIK 1976, GŁODEK 1985), and later much modified. The cascade of the lower Vistula was to consist of nine reservoirs, but till now only one – the Włocławek Reservoir – has been built. Dams were to be constructed also on larger tributaries to the Vistula (e.g. MIKULSKI 2001). Large objects built on tributaries to the middle and lower Vistula are the reservoirs Zegrzyński and Siemianówka on the Narew River, Sulejów Reservoir on the Pilica River and Koronowo Reservoir on the Brda River. Constructing dam reservoirs disturbs the continuity of river environment and leads to changes in communities of living organisms; the changes may affect the functioning of the reservoir ecosystem and, indirectly, also water quality.

Tracing the development of bottom malacocoenoses of lowland dam reservoirs and their succession make it possible to distinguish characteristic phases of the process (among others SOKOLOVA 1971, KRZYŻANEK et al. 1986, MORDUKHAY-BOLTOVSKOY 1961, KAJAK 1962, BUTORIN 1978b). These are associated with environmental changes caused by the decrease in water flow speed and flooding of adjacent land. The resulting new hydrological regime affects development and transformation of bottom deposits and bottom morphology (e.g. MCLAHLAN & MCLAHLAN 1971, GERASIMOV & PODDUBNYI 1999, ZAKONNOV & PODDUBNYI 2002). Especially great changes occur in the zone of extensive shallows which are subject to strong wave action, wind-induced water currents and water table changes. Because of the more intense transformation of habitat conditions in flooded land areas, compared to river beds which were incorporated into the reservoir, changes in communities of the bottom macrofauna are much greater in the former kind of habitat.

In the intial stage, in most cases including the first year of the reservoir's existence, dynamic transformations of macrobenthic communities take place in the flooded areas. The soil fauna dies out, most often (in conditions of a high proportion of flooded land in the total area of the reservoir) a mass development of chironomid larvae takes place, favoured by increased trophic level and large food resources resulting from decomposition of flooded terrestrial vegetation and soil organic matter; oligochaets are few and molluscs may appear (ARMITAGE 1977, MORDUKHAY-BOLTOVSKOY 1961, BUTORIN 1978b, VOROPAEV & VENDROV 1979). In the second year of the reservoir's existence the proportion of oligochaetes and molluscs increases, as well as species diversity. The bottom fauna is rather randomly distributed, but gradual dispersal of particular species leads to their increased frequency. The fauna of flooded floodplain water bodies colonises the flooded land. At that time, in the former river beds the abundance of bottom macrofauna increases. Simultaneously, in that zone the species diversity decreases, since rheophilic and oxygen-loving species recede as a result of decreased flow. During a certain period, in most cases of a few years duration, macrozoobenthos is characterised by a dynamic development, high species diversity and high density (ZAĆWILICHOWSKA 1965a, b, PATERSON & FERNANDO 1969, KRZYŻANEK 1970, PETR 1972, BUTORIN 1978b, VOSHELL & SIMMONS 1984), then its abundance stabilises at a certain value, mainly dependent on the trophic level (BAXTER 1977, STAŃCZYKOWSKA & JURKIEWICZ-KARNKOWSKA 1983). In conditions of limited influx of nutrients from the outside, an impoverishment of the benthos occurs (e.g. MURDUKHAY-BOLTOVSKOY 1961, 1971, SOKOLOVA 1971, PODDUBNAYA 1966, HRUŠKA 1973, ARMITAGE 1977, KRZYŻANEK 1986, KRZYŻANEK et al. 1986, KRZYŻANEK & KASZA 1995). At present, however, the phenomenon is usually only temporary because of anthropogenically-enhanced eutrophication. The increased trophic level stimulates development of bottom fauna whose abundance may stabilise at a higher level (e.g. KRZYŻANEK et al. 1986, KRZYŻANEK & KASZA 1995, DUSOGE et al. 1990, 1999, PEROVA & SHCHERBINA 1998). In reservoirs where low abundance of bottom fauna is maintained for a long time, following a brief peak observed in the first years of the reservoir's existence, e.g. in the Rybinsk, Gorki or Iwankovo Reservoirs, an increase in abundance and stabilisation at a higher level were observed after about a dozen years or even later (e.g. SMERNOY & MITROPOLSKIY 1978, BAKANOV & MITROPOLSKIY 1982, BUTORIN 1978a, b, ABAKUMOV et al. 2000, SHCHERBINA 2000). This was associated on the one hand with the gradual increase in the trophy level of the reservoir, on the other with the development of bottom deposits. Formation of bottom deposits, consisting in transformations of the flooded substratum, development of proper bottom deposits distributed in accordance with hydrodynamic conditions of the reservoir and being in dynamic equilibrium, was in such cases a long-lasting process, of even dozens of years (e.g. KURDIN 1976). Generally, in conditions of a greater influence of the river on the reservoir (higher proportion of river bed in the reservoir's total area), the bottom deposits are quicker to develop (e.g. in the Kuybyshev Reservoir of greater flow compared to the Rybinsk Reservoir), which favours earlier stabilisation of zoobenthos and higher levels of abundance (e.g. MITROPOLSKIY &

BISEROV 1982, BORODICH & LYAKHOV 1983). The environmental conditions change through time, to a large extent in accordance with the ageing of the reservoir. The changes are manifested, among others, as an increase in the layer of bottom deposits, and a considerable unification of environment conditions. This in turn contributes to a decrease in species diversity and a shift of dominance structure toward a clear dominance of oligochaetes (COOPER & KNIGHT 1985, PEROVA & SHCHERBINA 1998). The first symptoms of the reservoir's ageing are seen in the shallows (ZIMBALEVSKAYA et al. 1984). In areas of the slowest current, a thick layer of fine-particle deposits of high organic content develops, oxygen conditions deteriorate, and the quantity of nutrients from surface run-off increases (e.g. DENISOVA et al. 1985).

The excessive eutrophication observed in the last decades of the 20th c., as well as pollution load, lead to a reduction of abundance of some components of the bottom fauna, at maintained high values of total benthos abundance and biomass, to a limitation of species diversity and to changes in the dominance structure (e.g. BUTORIN 1978b, BORODICH & LYAKHOV 1983, KRZYŻANEK et al. 1986, KRZYŻANEK 1994, KRZYŻANEK & KASZA 1995, JURKIEWICZ-KARNKOWSKA 1998a). Similar changes were observed in lakes (e.g. HARMAN & FORNEY 1970, MORGAN 1970, STAŃCZYKOWSKA et al. 1983, HARMAN 1997, KANGUR et al. 1998, PIECZYŃSKA et al. 1999, GONG & XIE 2001). In the 1990s, some reservoirs started to show symptoms of a change of the above tendency, which was associated with an improvement in their water quality (e.g. PEROVA 1998, PEROVA & SHCHERBINA 1998, JURKIEWICZ-KARNKOWSKA 1998a). A similar phenomenon was observed in lakes and rivers (e.g. DAUBA et al. 1997, KILGOUR et al. 2000). Such tendencies of changes in the communities of the bottom malacofauna can be seriously disturbed by physical (e.g. hydrological or climatic) factors. In such cases abundance and species diversity of the bottom malacofauna increase (e.g. GIZIŃSKI & WOLNOMIEJSKI 1982, DUSOGE et al. 1985, 1990, 1999, DUSOGE 1989, JURKIEWICZ-KARNKOWSKA 1986, 1989a, KRZYŻANEK et al. 1986, PODDUBNAYA 1988), indicating a reversal to earlier stages of succession. The described changes in abundance and diversity of the bottom fauna are more dynamic in areas of flooded land, which is associated with larger fluctuations of habitat conditions compared to the zone of the former river beds.

Hydrological regime and kind of substratum are crucial factors in the development of macrozoobenthos. Hydrology of dam reservoirs, especially rheolimnic, is much variable. In reservoirs of short retention time, and especially in those which are channel-like, the conditions are similar to those found in rivers. When the proportion of flooded land in the whole area of the reservoir is high, the conditions over large areas are similar to those in lakes. In the littoral zone water dynamics is mostly associated with wave action, wind-induced water currents and changes in water table (among others DUSSART et al. 1972, DUBNYAK 1997, GERASIMOV & PODDUBNYI 1999, ZAKONNOV & PODDUBNYI 2002).The character of the substratum depends both on the type of flooded soil, especially in the first years of the reservoir's existence, and on the properties of the developing bottom deposits, rate of their deposition and changes in time. Hydrological factors determine the development of bottom organisms, affecting formation and stability of the deposits (e.g. MITROPOLSKIY & BISEROV 1982, PODDUBNAYA 1988, GERASIMOV & PODDUBNYI 1999, ZAKONNOV & PODDUBNYI 2002).

It follows from the above that the trophic status of the reservoir is an important factor determining the course of macrobenthos development through its effect on food resources, as well as chemistry of water and of the surface layer of bottom deposits, including oxygen concentration. In eutrophic reservoirs of high content of organic matter in bottom deposits, oxygen concentration may be the factor limiting development and production of bottom malacofauna (e.g. MCLACHLAN & MCLACHLAN 1971, FERRARIS & WHILM 1977, KAJAK & PRUS 2001). In rheolimnic reservoirs negative effects of the high trophic level, including oxygen deficit, are smaller. In conditions of large instability of bottom deposits, associated with intense mixing and resuspension, the development and production of macrozoobenthos may be clearly limited in spite of good food and oxygen conditions (e.g. GERASIMOV & PODDUBNYI 1999). In littoral habitats, little exposed to the wind, higher aquatic vegetation develops rather well, thus favouring diversity and abundance of the bottom fauna through stabilisation of bottom deposits and increased spatial diversity (among others COOPER & KNIGHT 1985, PIP 1987, PODDUBNAYA 1988).

Macrozoobenthos communities may undergo a clear effect of single animal species. The zebra mussel can affect various components of aquatic ecosystems and their functioning to a considerable extent. The effect of the mussel on the structure and abundance of the benthic communities was studied by many authors (among others DERMOTT et al. 1993, GRIFFITHS 1993, STEWART & HAYNES 1994, HOWELL et al. 1996, NALEPA et al. 1996, STEWART et al. 1998, SHCHERBINA 2000, PEROVA & SHCHERBINA 2001); most of the papers pertained to lake ecosystems.

Molluscs are important components of the bottom macrofauna of lowland dam reservoirs, especially because of their high proportion in the total biomass (e.g. DUSOGE et al. 1990, 1999, JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press). The abundance of malacocoenoses, their dominance structure and size structure of populations of the dominant species have an effect on the significance of malacofauna in the ecosystem. Studies on the role of molluscs in freshwater ecosystems, including dam reservoirs, focused mainly on bivalves, especially their filtration activity (for a review see STAŃCZYKOWSKA & LEWANDOWSKI 1997).The most numerous papers dealt with *D. polymorpha*, an invasive species which can reach high densities of several dozen or even hundreds thousands individuals per m^2.

Much work has been devoted to the possibility of using freshwater molluscs in biomonitoring of quality of aquatic habitats, especially pollution with toxic substances, including heavy metals (e.g. IMLAY 1982, BALOGH 1988, BUSCH 1991, KRAAK et al. 1991, KRAAK 1992, PEROVA 1996, OERTEL 1998, JAMIL et al. 1999, JURKIEWICZ-KARNKOWSKA 1999b, 2000, GRUNDACKER 2000), though such studies are much less numerous compared to papers on marine habitats and only rarely pertain to dam reservoirs (e.g. JURKIEWICZ-KARNKOWSKA 1999b, 2000, 2003, JURKIEWICZ-KARNKOWSKA & KRÓLAK 2003). It is believed that molluscs meet requirements of good indicator organisms (e.g. PHILLIPS 1977, ROSENBERG & RESH 1993). The important feature determining their suitability as indicators is their ability to accumulate large quantities of metals (and other toxic substances), associated with their limited capability of regulating the level of metals in the organism (e.g. NAIMO 1995, LANGSTON et al. 1998). Many studies deal with mollusc mechanisms of uptake and excretion of heavy metals, their accumulation and distribution in tissues, and responses to increased metal concentrations in the environment (for review see JURKIEWICZ-KARNKOWSKA 1994, 1998b).

Heavy metals and phosphorus, penetrating to inland waters with sewage, surface runoff and atmospheric precipitation, accumulate in various components of aquatic ecosystems. They are intensively accumulated in bottom deposits (among others KAJAK 1995, TANG & XIE 2000, WOJTKOWSKA 2000). However, under certain conditions phosphorus can be rather rapidly released from the deposits (e.g. KAJAK 1991, RAMM 1997, NOGES et al. 1998, PENN et al. 2000, SELIG & SCHLUNGBAUM 2002). Contrary to phosphorus, the quantity of heavy metals released from the bottom deposits is fairly small (WIECHUŁA et al. 1997, VAN DEN BERG et al. 1999). A part of heavy metals is immobilised in the bottom deposits as insoluble compounds. The remaining part, bound in less durable compounds, adsorbed on particles of bottom deposits and triptone (i.e. mineral particles and dead organic matter being a part of seston), or bound in living components of the ecosystem, undergoes constant transformations. A real decrease in the quantity of phosphorus and heavy metals in the ecosystem is possible mainly through their export. The most effective export of elements associated with the deposits and suspension may take place during increased flow (e.g. KENNEDY 1999, TANG & XIE 2000). Dynamic flow changes affect the variability of element retention in reservoirs (e.g. TURNER et al. 1983, JURKIEWICZ-KARNKOWSKA 2001b). A rather intense export of elements from reservoirs (poorer retention) occurs through outflow via bottom outlets (e.g. DURAS & HEJZLAR 2001). Heavy metal concentration in the deposits may be high in relation to that found in biota, but only a part of them is available to organisms. The level of metal accumulation in living organisms, e.g. molluscs, reflects the concentration of biologically available metal fraction in the environment.

Phosphorus concentration in freshwater habitats is the main factor determining their trophic status. Molluscs can play a significant part in both accumulation and cycling of phosphorus, especially in habitats where they are numerous (STAŃCZYKOWSKA et al. 1976, STAŃCZYKOWSKA 1983, 1984, 1997, STAŃCZYKOWSKA & PLANTER 1985, KASPRZAK 1986, KRZYŻANEK 1989, NALEPA et al. 1991, STAŃCZYKOWSKA & LEWANDOWSKI 1993, 1997). The papers mentioned deal with lake ecosystems; only KRZYŻANEK (1989) attempted an estimate of the role of unionids in phosphorus circulation in a dam reservoir. Studies on various aspects of the role of molluscs in cycling of heavy metals or other toxic substances in freshwater habitats are very few (e.g. BRUNER et al. 1994, JURKIEWICZ-KARNKOWSKA 2001c); there are no data on the significance of malacofauna in accumulation of these elements in ecosystems.

Ecotoxicological effect of metals once introduced in aquatic ecosystems can be very long-lasting, especially when the chemistry of the environment (e.g. pH, oxygen conditions, redox potential) favours maintaining biologically available forms of metals in the water. These forms can be assimilated and accumulated by various organisms and transferred along the food chains. Autotrophic organisms (producers) accumulate metals from water solution; in the case of heterotrophic organisms (consumers) two ways of metal uptake are possible: from water and from food. Significance of the metal sources varies between animals, even for the same metal. The quantity of heavy metals assimilated with food depends on the feeding mode, size and composition of food rations, form in which the metal occurs (e.g. BAUDO 1985, CHAPMAN et al. 1998).

Molluscs are parts of an array of trophic chains, feeding on diverse food and providing food for numerous other organisms. The basic bivalve food is particulate organic matter obtained from filtered suspension. Sphaeriids may supplement their food requirements through feeding on bottom deposits with foot ciliary mechanism, or absorbing dissolved organic matter from the water (MITROPOLSKIY 1966a, b, MONAKOV 1972, EFFORD & TSUMURA 1973, HORNBACH et al. 1983). PARDY (1980) found that *Anodonta* sp. assimilated certain quantities of organic matter as a result of symbiosis with Zoochlorellae. Snails feed mainly on dead and live plant matter (algae, tissues of higher plants, debris), and can supplement their diet through filtration (prosobranchs) or consuming some animal matter (CIKHON-LUKANINA

1961a, b, Fretter & Graham 1962, Fretter & Peake 1978, Piechocki 1979, Tashiro & Colman 1982, Aldridge 1983, Höckelmann & Pusch 2000, and others).

Molluscs are important components in the diet of some fishes (e.g. French III & Morgan 1995, French III & Bur 1996, Stańczykowska 1977, 1987). They may constitute the main food of roach (Budzyńska et al. 1956, Prejs 1973, 1976, Olszewski 1978, Prejs et al. 1990, Terlecki et al. 1990), an important component of bream (Budzyńska et al. 1956, Pliszka 1956, Martyniak et al. 1987), carp (Stein et al. 1975, Tucker et al. 1996), and white bream food (Terlecki et al. 1990, Tadajewska 1993) – fish species which dominate in the ichthyofauna of the Zegrzyński Reservoir and many other lowland dam lakes (Wajdowicz 1964, Kakareko & Giziński 2001, Szlakowski & Wiśniewolski 2001). Molluscs are also consumed by benthophagous birds (e.g. Stempniewicz 1974, Mikulski et al. 1975, Stańczykowska 1977, Suter 1982, Kuć & Stańczykowska 1990, Stańczykowska et al. 1990, Cleven & Frenzel 1993, Hamilton et al. 1994, Stoczkowski & Stańczykowska 1995) and crayfish (Piesik 1974, Love & Savino 1993), leeches (Smit et al. 1993, Molloy et al. 1997), turtles (Serrouya et al. 1995) and small mammals (Bedulli & Franchini 1978, Wołk 1979). Mollusc faeces, enriching the debris pool of the bottom deposits, may constitute an important food source for various bottom invertebrates, e.g. chironomid larvae (Izvekova & Lvova-Katchanova 1972), Gammaridae and other detritivores (Griffiths 1993, Bruner et al. 1994). Elements contained in faeces of molluscs included in food chains return to circulation in ecosystems.

Studies on trophic transfer of heavy metals in freshwater environments are few (e.g. Blanchard et al. 1999, Chen et al. 2000) and only rarely pertain to molluscs (e.g. Blanchard et al. 1999, Jurkiewicz-Karnkowska 2001c). Fairly much attention has been devoted to the analysis of heavy metal uptake by representatives of various species (and trophic levels) or dependences between metal concentration in fragments (two consecutive links) of food chains.

It follows from the above that studies on the occurrence and succession of the bottom macrofauna of lowland dam reservoirs have focused on formation and initial development of macrozoobenthos, while much less attention has been given to long-term changes, including the stage of stabilised biocoenosis. Later periods of existence of the bottom macrofauna were of less interest because of the common opinion about a short time of succession leading to a unification of the communities, especially in flooded floodplain water bodies and land areas, followed by stabilisation which is characterised by the absence of greater qualitative and quantitative changes. Generalisations on the development of macrozoobenthos of dam reservoirs, found in literature, are mainly based on analyses of basic components of soft benthos. Molluscs are important components of the bottom macrofauna of lowland dam reservoirs, but data on formation of malacocoenoses and their further development, as well as on spatial diversity of these processes, are fragmentary. Many studies do not consider participation of large molluscs in the bottom macrofauna communities, and data on qualitative occurrence, dominance structure and spatial distribution of malacoenoses are scanty and often incomplete (e.g. they pertain only to small molluscs or the most abundant species). Data on abundance of malacoenoses, dominance structure and also size structure of populations of dominant species are important for estimates of the role of malacofauna in the functioning of dam reservoir ecosystems.

Many studies on the role of molluscs in freshwater ecosystems deal with the effects of filtration activity of bivalves, especially *D. polymorpha.* The main issues are filtration potential expressed as the quantity of filtered suspension, volume of water filtered by a population, while the quantity of produced faeces and pseudofaeces is less often discussed. The studies focus on lakes, while data on dam reservoirs are scanty. Likewise, papers on the role of the zebra mussel or other bivalves in nutrient cycling are few; studies on the role of freshwater molluscs in circulation of heavy metals and various toxic substances are very few. There is no information on the role of malacofauna in accumulation of metals in the ecosystem. Few papers analyse transfer of these elements in freshwater food chains, and studies on such transfer in which molluscs take part are very rare.

The objective of this paper was a description of temporal and spatial changes of malacocoenoses of large lowland dam reservoirs of the mid Vistula River basin, and an analysis of selected aspects of the role of molluscs in the functioning of these ecosystems.

In order to analyse the spatial variation of the malacofauna, I compared the composition, species diversity, dominance structure and abundance of molluscs in three reservoirs (Zegrzyński, Sulejów, Siemianówka), considering differences between flooded land areas (shallow habitats) and former river beds (habitats of greater depth and faster water exchange). An attempt was also made at presenting the development of malacocoenoses with special emphasis on the stage of stabilised biocoenosis, based on long-term changes in the Zegrzyński Reservoir and on literature data. To determine the effect of particular mollusc species on malacocoenoses, the effect of the main dominants on the number of species, and the abundance of the remaining components of these communities were analysed in the Zegrzyński and Sulejów Reservoirs.

Within studies on selected aspects of the role of molluscs in the functioning of dam reservoir ecosystems, an attempt was made at an estimate of the significance of molluscs for accumulation of phosphorus and heavy metals, compared to the quantities of these elements contained in the water and bottom deposits, and their load and retention, based on the Zegrzyński Reservoir. The estimated values of accumulation of the studied elements by molluscs were compared for four reservoirs of different structure and abundance of malacocoenoses (Zegrzyński, Sulejów, Siemianówka, Włocławek). One of the aims of the study was calculation of clearance rate of molluscs and biodeposition of phosphorus and heavy metals with faeces (and pseudofaeces), which made it possible to assess the effect of the malacofauna on the cycling of these elements in the dam reservoir ecosystem (Zegrzyński Reservoir). Another objective was an analysis of transfer of phosphorus and heavy metals in short food chains with molluscs as one of the links, based on selected examples from the Zegrzyński Reservoir.

STUDY AREA

The studies included three large lowland dam reservoirs: Zegrzyński (lower Narew River), Siemianówka (upper Narew River) and Sulejów (Pilica River), located in the mid Vistula River basin (Fig. 1). Additionally, the Włocławek Reservoir located in the lower section of the Vistula River was included in comparative studies on phosphorus and heavy metal concentration in molluscs. The reservoirs are rather shallow (Table 1), but based on decreasing proportion of shallow habitats in the whole area of the reservoir they can be ranked as follows: Siemianówka, Sulejów, Zegrzyński, Włocławek. The water column in the shallow zone is intensely mixed by the wind, while bottom deposits undergo constant resuspension. Decrease in water level causes periodical uncovering of considerable parts of the bottom, especially in the Siemianówka Reservoir.

Though comparable in terms of their surface area (especially the first three), the reservoirs are fed by rivers of different size (Table 1), hence different mean discharge (SSQ). The Włocławek and Zegrzyński Reservoirs are rheolimnic, the remaining two are limnic. The water retention time determines the intensity of the effect of intra-reservoir processes on chemical properties of water. The flow in the rivers feeding the reservoirs differs considerably, which results in a varied significance of hydrology in the formation, development and functioning of the reservoir biocoenoses. The proportion of river bed in the total area of the reservoirs increases in the following order: Siemianówka, Sulejów, Zegrzyński, Włocławek. In the last case it is over 70% (over 50% excluding floodplains), in the remaining ones the majority of the area is flooded land.

All four reservoirs are characterised by a high trophic level (Table 2), and concentrations of suspension and chlorophyll a exceed the standards during some periods. The bottom deposits are most often sandy, muddy or sandy-muddy; near shores sandy deposits often occur, sometimes with an admixture of coarser mineral fractions or debris. In the Siemianówka Reservoir, a considerable part of the bottom is covered by peat. Bottom deposits of the reservoirs have a high phosphorus content (from ca. 0.20 to 0.57%). Macrophytes are rather poorly developed, among others because of the negative effect of waves and water table fluctuations (the smallest in the Zegrzyński Reservoir). A general environmental characteristics of the Zegrzyński Reservoir was presented by KAJAK (1990, 1991), KAJAK & DUSOGE (1989) and others (OLSZEWSKI & MÓWIŃSKA 1985, WOJTKOWSKA 1997). Data on the Sulejów Reservoir are contained in GALICKA & PENCZAK (1989), GALICKA (1990, 1999), GIERCUSZKIEWICZ-BAJTLIK (1992), GALICKA & DROŻDŻYK (1996), on the Siemianówka Reservoir – in

Table 1. General charactersitics of the studied reservoirs (after GIZIŃSKI et al. 1989, KAJAK 1990, 1991, GALICKA 1990, 1999, GÓRNIAK & JEKATIERYNCZUK-RUDCZYK 1995a); dates of reservoir construction given in parentheses

	Reservoir			
	Włocławek (1969/1970)	Zegrzyński (1962)	Sulejów (1973)	Siemianówka (1990)
Area [km^2]	75	33	22	23
Max. volume [10^6 m^3]	408	100	75	79.5
Catchment area [km^2]	171,000	103,600	4,860	1,050
Depth [m]: mean	5.5	3.5	3.3	2.5
max.	15	9	15,5	9
Length [km]	57	55 (42+13)	15.5	13.5
Mean discharge (SSQ) [m^3 s^{-1}]	900	312	29.8	~6
Mean retention time [days]	4–5	4–5	15–40	120
Water level fluctuations [m]	0.8	~0.5	2–2.5	1–3

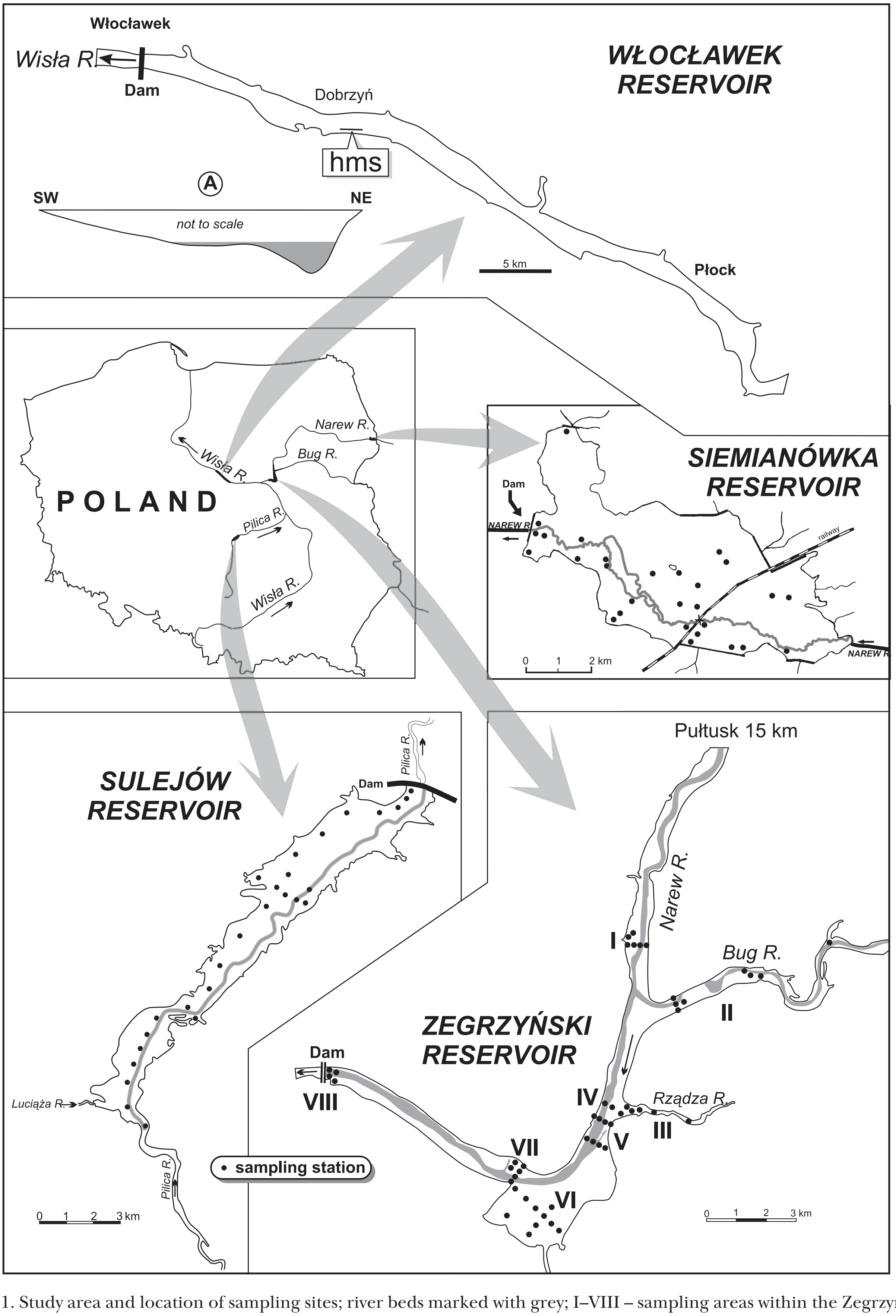

Fig. 1. Study area and location of sampling sites; river beds marked with grey; I–VIII – sampling areas within the Zegrzyński Reservoir; hms – sites in the Włocławek Reservoir where molluscs were sampled for phosphorus and heavy metal analyses; A – location of the Vistula River bed within the Włocławek Reservoir

Table 2. Chemical characteristics of the studied reservoirs (according to KAJAK 1990, GÓRNIAK & JEKATIERYNCZUK-RUDCZYK 1995b, GÓRNIAK 1996, GALICKA & DROŻDŻYK 1996, KENTZER et al. 1999, KENTZER 2000, Environmental Reports – REPORT 2000a, b, c)

	Reservoir			
	Włocławek	Zegrzyński	Sulejów	Siemianówka
pH	8.1	7.9	8.1	7.4
O_2 [mg dm^{-3}]	8.3–11.2	7.1–8.8	10.7–11.9	8.7–9.3
Ca [mg dm^{-3}]	71.3–73.1	76.6–81.8	–	44.5–53.2
N-NH_4 [mg dm^{-3}]	0.47–0.79	0.21–0.29	0.26–0.50	0.16–0.49
N-NO_2 [mg dm^{-3}]	0.02–0.03	0.014–0.016	0.012–0.035	–
N-NO_3 [mg dm^{-3}]	1.35–1.40	0.57–0.67	0.32–0.85	0.28–0.49
P-PO_4 [mg dm^{-3}]	0.09–0.14	0.189–0.217	0.150–0.320	0.069–0.100
TP [mg dm^{-3}]	0.26–0.28	0.100–0.270	0.610–0.780	0.142–0.218
seston [mg dm^{-3}]	10.8–16.8	18.3 (13.9–30.4)	25 (2.0–31.8)	29.8 (22.2–41.1)
chlorophyll a [μg dm^{-3}]	3.2–221.7	27	3–58	53.2–62.6

GÓRNIAK & JEKATIERYNCZUK-RUDCZYK (1995a, b), GÓRNIAK (1996), GÓRNIAK & GRABOWSKA (1996), GÓRNIAK & PIEKARSKI (1999), GÓRNIAK et al. (1999), JEKATIERYNCZUK-RUDCZYK et al. (2002), on the Włocławek Reservoir – in GIZIŃSKI et al. (1989), ŻYTKOWICZ et al. (1990), KENTZER & GIZIŃSKI (1995), ŻBIKOWSKI 1995, 2000, KENTZER et al. (1999), KENTZER (2000). Information on physico-chemical parameters of water in the reservoirs is also published in Environment Reports of Mazovian, Podlaskie and Kujawsko-Pomorski provinces (REPORT 2000a, b, c), hydrological data – among others in the monthly bulletin of IMGW [Institute of Meteorology and Water Management] in Warsaw – "Zasoby Wodne Kraju" [State Water Resources].

MATERIAL AND METHODS

Malacofauna of the Zegrzyński Reservoir was studied in 1980–1981, 1995 and 1997–2000. Molluscs were usually sampled three times during the season (May, July, September). Most of the 47 sampling sites were situated in eight sampling areas (I–VIII), located in various parts of the reservoir (Fig. 1). In the Siemianówka Reservoir molluscs were sampled from 28 sites in 1996, 1997, 1999 and 2000, once or twice during the season (June, September). In the Sulejów Reservoir molluscs were studied in 28 sites, once during each season (July) in 1999–2001. Two zones were distinguished in the studied reservoirs: former river beds and flooded land. The position of the river beds within the reservoirs was determined based on maps published prior to and after damming. Molluscs were sampled with Ekman-Birge's grab, of 225 cm^2 catching area and with a rectangular dredge, towed along a definite distance (semi-quantitative samples, especially useful when studying large molluscs). The samples were washed on a sieve of 0.5 mm mesh. Parallelly, qualitative search was made, especially for macrophyte-associated molluscs. Macrophytes were rather poorly developed and occupied small areas, besides – as shown by earlier observations (JURKIEWICZ-KARNKOWSKA 1986 and unpublished) molluscs were not very abundant on plants compared to the bottom, and it was assumed that the vegetation had no significant effect on the density of the malacofauna. Similar conclusions follow, for example, from studies in reservoirs of the upper Volga River (SOKOLOVA 1971). The molluscs were preserved with 4% formaldehyde and 75% ethyl alcohol. Species were identified using keys of PIECHOCKI (1979) and PIECHOCKI & DYDUCH-FALNIOWSKA (1993); molluscs were counted and, following drying to constant mass, weighed with laboratory scales to the nearest 0.01 g.

The data made it possible to analyse the spatial diversity of the malacocoenoses in the studied reservoirs, and in the Zegrzyński Reservoir also long-term changes were analysed, including data from the second half of the 80s (DUSOGE et al. 1990, 1999, GRUŻEWSki 1988, 2000). The frequency of individual species in the reservoir (%F) was expressed as percentage of samples containing the species to the total number of samples. The similarity of species composition (S) (MARCZEWSKI & STEINHAUS 1959) and the percentage similarity (Psc) (WHITTAKER & FAIRBANKS 1958) of the malacocoenoses were calculated from the following formulae:

$S=w/(a+b-w)$, where a, b – number of species in sites A and B, w – number of species in common for A and B.

$Psc = \Sigma \min (a, b)$, where a, b – percentage of a given species in the total abundance in sites A and B.

The species diversity in the studied sites was estimated with Shannon-Weaver index (MARGALEF 1958), with the formula:

$H' = -\Sigma p_i \ln p_i$, where p_i – relative abundance of ith species.

Molluscs for the analysis of phosphorus and heavy metal concentration (Cu, Zn, Mn, Fe, Pb, Cd) were collected in May, July and September 1997, 1998 and 1999 in eight sampling plots located in various parts of the Zegrzyński Reservoir (I–VIII, Fig. 1). In the sites samples of water from above the bottom were also taken (3 times during the vegetation season 1998 – May, July and September and 10 times in the hydrological year 1998/1999), as well as samples of bottom deposits, periphyton, higher aquatic plants (*Nuphar lutea* (L.) Sibth. & Sm., *Lemna* spp., *Potamogeton* spp., *Elodea canadensis* Rich.) and detritus. Samples of newly deposited fine organic seston (floc) were also taken with the method of SMITH et al. (1996). The suspension above the bottom is similar in its composition to the most recent layer of the bottom deposits. This is associated on the one hand with increased triptone proportion and decrease of live plankton with settling of the suspension in the water column, on the other – with disturbing the deposits as a result of water mixing by wind (high proportion of shallow habitats in the reservoir), and flow-associated resuspension. In this study floc was assumed as bivalve food, instead of seston, since it seems to better correspond to chemical composition of the matter available to bivalves. The values of concentrations of the analysed elements in the seston samples were probably overestimated resulting from the small mass of the samples. The values of concentration of the elements in floc were comparable to data on suspension from relatively little polluted waters (e.g. BALOGH 1988, BREKHOVSKIKH et al. 1999).

Additionally, mollusc samples for the analysis of phosphorus and heavy metal content were taken from the reservoirs Siemianówka (June 1997 and 1999), Sulejów (July 2000 and 2001) and Włocławek (June 2001). Moreover chironomid larvae were sampled, and fish obtained in 1998–1999 (the fish were obtained from fishing cooperative exploiting the reservoir in July 1998 and October 1999).

Molluscs which were abundant and widely distributed in the reservoirs were selected for analyses of heavy metal (Cu, Zn, Mn, Fe, Pb, Cd) and phosphorus content. In the Zegrzyński Reservoir they were three snail species (*Viviparus viviparus* (L.), *Lymnaea stagnalis* (L.) and *L. peregra* (O. F. Müll.) and five bivalves (*Dreissena polymorpha* (Pall.), *Anodonta anatina* (L.) *A. cygnea* (L.), *Unio pictorum* (L.), *Sphaerium rivicola* (Lamarck), in the Sulejów Reservoir – *D. polymorpha, A. cygnea* and *U. pictorum*, in the Siemianówka Reservoir – *L. stagnalis, L. peregra, A. anatina* and *A. cygnea*, in the Włocławek Reservoir – *V. viviparus, D. polymorpha, A. anatina, U. tumidus* (Philipsson) and *Sphaerium corneum* (L.). In order to avoid age (and weight)-related differences in concentration of the analysed elements, animals of standardised size were selected (JURKIEWICZ-KARNKOWSKA & KRÓLAK 2000).

Samples of molluscs, bottom deposits, seston, floc, detritus, periphyton, macrophytes, chironomid larvae, fish, mollusc faeces and water were prepared and then mineralised in concentrated nitric acid and 30% perhydrol (Merck suprapur), according to the protocol described in earlier papers (JURKIEWICZ-KARNKOWSKA & KRÓLAK 2000, JURKIEWICZ-KARNKOWSKA 2001c). Heavy metal concentrations were determined with ASA technique: Cu, Zn, Mn and Fe with flame method, Pb and Cd in graphit tray (Carl Zeiss Jena, AAS 30). Certified reference material was used (prawn, GBW 08572). Comparative analyses with ICP-AES method were also made. Phosphorus content was determined with molybdate blue method, using Novaspec 2 (Pharmacia LKB) spectrophotometer.

In the Zegrzyński Reservoir concentration of phosphorus and heavy metals was estimated in the water column and bottom deposits (as total content and converted to 1 m^2 in the whole reservoir), as well as load of these elements introduced into the reservoir and their retention in the reservoir (based on the difference between the quantity of metals brought by the rivers and flowing out through the dam, multiplying values of mean flow in the Narew and Bug rivers and on the dam in Dębe by mean concentration of the elements in the water obtained in this study). Likewise, an estimate was made of the quantity of heavy metals and phosphorus accumulated in molluscs living on 1 m^2 bottom and in the whole reservoir, based on data on their mean biomass, proportion of soft tissues and shell in the mass of dominant species and mean values of concentration of the analysed elements in the tissues and shells. The role of molluscs in retention of these elements in the reservoir was estimated.

Filtration activity of bivalves and filtration potential of *V. viviparus* were assessed based on literature data on clearance rate (Table 3), and on the density of species which were abundant in the Zegrzyński Reservoir, as estimated in this study. Adopting literature values of clearance rates of bivalves inhabiting the Zegrzyński Reservoir, the effect of several factors on filtration was considered (for more details see Discussion), as well as methods applied by various authors to estimate such values. For *D. polymorpha*, on which many literature data exist, results of studies in natural or close-to-natural conditions were adopted. Values reported by various authors varied widely (Table 3). It was assumed that water re-filtration in the conditions of the Zegrzyński Reservoir is rather small because of water mixing and exchange, while food supply is good which is indirectly supported by the good condition of *D. polymorpha* (DUSOGE et al. 1990). For this reason clearance rate values close to the so called effective values (ECR according to YU & CUL-

VER 1999) were adopted. Based on data on the concentration of phosphorus and heavy metals (Cu, Zn, Mn, Fe, Pb, Cd) in floc (to avoid overestimation) and the suspension concentration in the water, the quantity of these elements cleared by molluscs was estimated. Rough values of snail consumption were calculated based on MONAKOV's (1972), KOŁODZIEJCZYK's (1983) and BRENDELBERGER's (1997) data. Quantities of phosphorus and heavy metals ingested with food were estimated from the mean concentration of particular elements in plant matter (periphyton, macrophytes, detritus).

The faeces (and pseudofaeces) production was assessed from the data on quantitative occurrence of molluscs in the reservoir and the mean quantity of faeces produced by a single specimen of each of the studied species. Data on the quantity of biodeposits were obtained based on the mass of faeces collected after bringing the molluscs in the laboratory and placing them in crystallizers with filtered water from the sites where the animals were collected. In one crystallizer of 500 cm^3 most often 5–20 specimens were placed, depending on the species (size). After 12 hours the faeces-containing water was filtered through filters of pore diameter 0.45 µm and the samples were dried. The values were compared with the literature data on the studied species (Table 4). It was found that the estimated faeces production for the studied snail species was similar to that obtained experimentally, while for the bivalves (*D. polymorpha*, unionids) the estimated values were higher than in Mikołajskie Lake (LEWANDOWSKI & STAŃCZYKOWSKA 1975, STAŃCZYKOWSKA et al. 1976), which might result from higher biodeposits production in conditions of higher suspension content in the Zegrzyński Reservoir compared to the lake. Because of the method of faeces collecting, the proportion of pseudofaeces could be rather slight (most pseudofaeces rejected during filtration in the environment, while the time of passage through the alimentary tract is longer and thus mainly faeces were collected). Data of other authors (Table 4) indicate a possibility of producing higher quantities of faeces by bivalves (for more details see Discussion). It was assumed that in conditions of the Zegrzyński Reservoir (moderate flow, consider-

Table 3. Filtration rates of the studied mollusc species or closely related taxa (cm^3 indiv.$^{-1}$ h^{-1})

Taxa	Filtration rate	Source
V. viviparus	141.7	SCHAFER (1953)
	up to 141.7	HÖCKELMANN & PUSCH (2000)
D. polymorpha	43	MIKHEYEV (1966b)
	135	ALIMOV (1969)
	43.0–56.3	LVOVA-KATCHANOVA (1971)
	13.0–70.7	HINZ & SCHEIL (1972)
	35 (10–100)	STAŃCZYKOWSKA (1968), STAŃCZYKOWSKA et al. (1976)
	286.8	KRYGER & RIISGARD (1988)
	123 (78–170)	REEDERS et al. (1989)
	260	WIŚNIEWSKI (1990)
	18–75	REEDERS & BIJ de VAATE (1990)
	33.3–79.2	REEDERS et al. (1993)
	61	FISHER et al. (1993)
	8.3–370	SPRUNG (1995)
	74	LEI et al. (1996)
	114 (97–133)	RODITI et al. (1996)
	41.7–62.5	JAMES et al. (1997)
	40–80	MADON et al. (1998)
	15.3–68.6*	*YU & CULVER (1999)
	60–200	ACKERMAN (1999)
	18–402	BALDWIN et al. (2002)
Unionidae	300 (60–490)	LEWANDOWSKI & STAŃCZYKOWSKA (1975)
	389.5	LEWANDOWSKI & STAŃCZYKOWSKA (1975) recalculated after ALIMOV (1965)
S. corneum	0.16–5.71	HINZ & SCHEIL (1972)
S. suecicum	5.46	ALIMOV & BULON (1972)
Sphaeriidae	2.2 (0.6–8.3)	STAŃCZYKOWSKA et al. (1976) basing on ALIMOV (1965)

*ECR (effective clearance rate)

Table 4. Quantities of faeces produced by the studied mollusc species or closely related taxa (mg dry wt indiv.$^{-1}$ d^{-1})

Taxa	Faeces (and pseudofaeces)	Source
V. viviparus	21.0	KOŁODZIEJCZYK (1983)
	19.2	*MONAKOV (1972)
	1–26.9	*SIEFERT (1996) after HÖCKELMANN & PUSCH (2000)
	12.0	JURKIEWICZ-KARNKOWSKA (1986)
	20.2±1.7	this work
Lymnaea sp.	11.4–43.0	*PIECZYŃSKA (1976)
	11 (4.6–16.4)	KOŁODZIEJCZYK (1983)
	14.0	BIJOK (1984)
	4.3–15.5	*BRENDELBERGER (1997)
	5.2	JURKIEWICZ-KARNKOWSKA (1986)
	10.4±2.8	this work
	10.0–12.0	*RYBAK (2002)
D. polymorpha	1.6	STAŃCZYKOWSKA et al. (1976)
	5–60	*REEDERS et al. (1993)
	15.2 (14.2–22)	*KLERKS et al. (1996)
	55.0 (43–65)	*RODITI et al. (1997)
	1.1–16.0	*DOBSON & MACKIE (1998)
	3.7±0.3	this work
Unionidae	4.2	LEWANDOWSKI & STAŃCZYKOWSKA (1975)
	2.3–107.0	*SIEFERT (1996) after HÖCKELMANN & PUSCH (2000)
	31.4±3.2	this work

* values were recalculated based on data on consumption reported in the papers

able but not excessive concentration of suspension with a high proportion of organic matter) the data obtained by the author could be used for calculations. Based on the results of analyses of phosphorus and heavy metal concentration in the faeces, quantities of these elements contained in the faeces of molluscs inhabiting 1 m^2 bottom were estimated.

Based on data on the concentration of the studied elements in the molluscs, their potential food, faeces, mollusc-eating fish and predatory fish, chironomid larvae feeding on mollusc faeces, transfer of these elements in selected short trophic chains of which molluscs form a part, was analysed.

All the results were statistically analysed with Statistica (version 5, '97 edition). The data were logarithmically transformed when the distribution was not normal. Variance analysis and comparisons with T-tests were made, and dependence between the occurrence of molluscs and selected factors was analysed (Pearson correlation). In the case of small data series (concentrations of the elements in faeces of particular mollusc species), significance of differences was tested with non-parametric Mann-Whitney U-test. The level of $p<0.05$ was adopted as statistically siginificant.

RESULTS

1. MALACOCOENOSES OF THE STUDIED RESERVOIRS – OCCURRENCE AND SPATIO-TEMPORAL CHANGES

1.1. Qualitative and quantitative occurrence of molluscs, spatial diversity

1.1.1. Species composition

The malacofauna of the studied reservoirs showed a considerable species richness. In 1996–2001, 18 species of molluscs were found in the Siemianówka Reservoir (13 snail and 5 bivalve species), 25 species in the Sulejów Reservoir (11 and 14, respectively), and 32 species in the Zegrzyński Reservoir (18 and 14) (Table 5). Besides, other species of molluscs were recorded in the particular reservoirs based on empty shells, such species being especially numerous (7) in the Siemianówka Reservoir. In all three reservoirs more species were found in the zone of flooded land compared to the former river beds (Fig. 2), but the comparison of the mean numbers of molluscs in the two habitats showed no significant differences

(ANOVA). The greatest species richness in the reservoirs Siemianówka and Sulejów in the study period was observed in the upper parts of the reservoirs (Fig. 3) which may be associated both with the heterogeneity of the habitats and with their ecotone character, representing intermediate conditions between a river and a reservoir. In the Zegrzyński Reservoir the highest species richness was observed in the mid part with its heterogeneous habitats, resulting on the one hand from a strong effect of the two main rivers which differ in many physico-chemical characters, and a more local effect of small tributaries (river Rządza, Żerański canal), on the other the presence of relatively large areas of stagnant character, extensive shallows of different development of macrophytes and different exposure to wind action. The mean numbers of species found in particular parts of the reservoirs did not differ significantly, except for the Sulejów Reservoir where that number in the mid part was significantly lower than in the lower part (NIR test, p=0.0024).

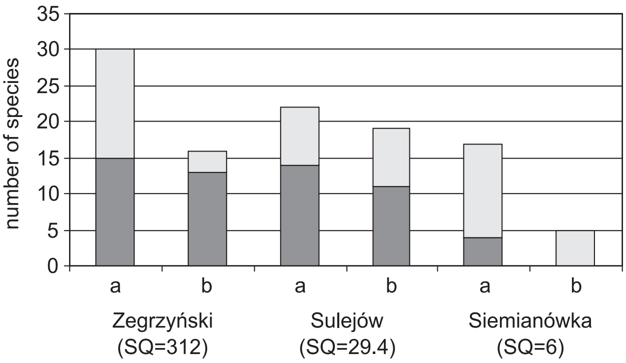

Fig. 2. Numbers of mollusc species in the investigated reservoirs and proportion of species with frequencies higher than 10% (grey parts of the bars); a – flooded land, b – former river beds; SQ – mean discharge in the late 1990s

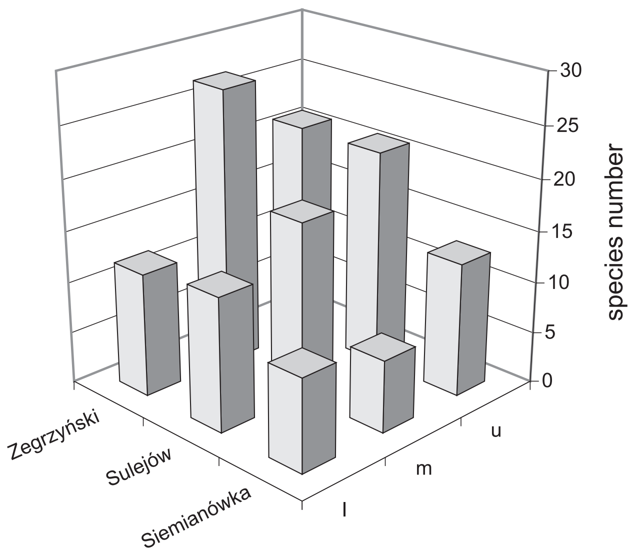

Fig. 3. Numbers of mollusc species in the upper (u), mid (m) and lower (l) parts of the investigated reservoirs

Table 5. The occurrence of molluscs in the investigated reservoirs (numbers in parentheses include species represented by empty shells); plus – present, minus – absent, o – empty shells

Species	Reservoir		
	Zegrzyński	Sulejów	Siemianówka
1. *Theodoxus fluviatilis* (L.)	+	–	–
2. *Viviparus viviparus* (L.)	+	–	–
3. *V. contectus* (Millet)	–	–	o
4. *Valvata cristata* O. F. Müller	–	+	–
5. *Valvata pulchella* Studer	–	–	o
6. *V. piscinalis* (O. F. Müller)	+	+	o
7. *V. naticina* Menke	o	–	–
8. *Potamopyrgus antipodarum* (Gray)	–	+	–
9. *Lithoglyphus naticoides* (C. Pfeifer)	o	–	–
10. *Bithynia tentaculata* (L.)	+	+	+
11. *Physa fontinalis* (L.)	+	–	o
12. *Lymnaea stagnalis* (L.)	+	–	+
13. *L. (Radix) peregra* (O. F. Müller)	+	+	+
14. *L. (Radix) auricularia* (L.)	+	+	+
15. *L. (Galba) corvus* (Gmelin)	+	–	o
16. *L. (Galba) turricula* (Held)	+	–	o
17. *Planorbis planorbis* (L.)	+	+	+
18. *P. carinatus* O. F. Müller	–	o	+
19. *Anisus leucostomus* (Millet)	+	o	+
20. *A. septemgyratus* (Rossmässler)	–	–	+
21. *A. vortex* (L.)	+	+	–
22. *A. contortus* (L.)	+	+	+
23. *Gyraulus albus* (O. F. Müller)	+	+	+
24. *Armiger crista* (L.)	–	+	+
25. *Hippeutis complanatus* (L.)	–	–	+
26. *Segmentina nitida* (O. F. Müller)	–	–	+
27. *Planorbarius corneus* (L.)	+	–	o
28. *Ancylus fluviatilis* O. F. Müller	+	–	–
29. *Acroloxus lacustris* (L.)	+	o	–
30. *Unio tumidus* Philipsson	+	+	–
31. *U. pictorum* (L.)	+	+	–
32. *Anodonta cygnea* (L.)	+	+	+
33. *A. anatina* (L.)	+	+	+
34. *Dreissena polymorpha* (Pall.)	+	+	–
35. *Sphaerium corneum* (L.)	+	+	+
36. *S. rivicola* (Lamarck)	+	o	–
37. *S. solidum* (Normand)	+	–	–
38. *Musculium lacustre* (O. F. Müll.)	+	+	–
39. *Pisidium amnicum* (O. F. Müller)	+	–	–
40. *P. casertanum* (Poli)	+	+	+
41. *P. crassum* Stelfox	–	+	–
42. *P. henslowanum* (Sheppard)	+	+	–
43. *P. moitessierianum* Paladilhe	–	+	–
44. *P. nitidum* Jenyns	+	+	–
45. *P. subtruncatum* Malm	+	+	+
46. *P. supinum* Schmidt	–	+	–
Number of species	32 (34)	25 (29)	18 (25)

The malacocoenoses of all three reservoirs showed a comparable species diversity (H=1.7 in the Zegrzyński Reservoir, 1.6 in the Sulejów and 2.3 in the Siemianówka Reservoirs), characteristic of moderate trophic level (TUDORANCEA et al. 1979, GONG & XIE 2001). A comparison of species diversity between the flooded land area and the zone of the former river bed revealed a higher value of Shannon-Weaver coefficient in the former zone in the reservoirs Zegrzyński and Siemianówka (1.6 and 1.2, 2.2 and 1.2, respectively), while in the Sulejów Reservoir the situation was reversed (1.4 and 2.2).

Only few among the recorded species showed a high frequency of occurrence (%F). In the Zegrzyński Reservoir frequency of at least 50% was reached by *Viviparus viviparus*, *Dreissena polymorpha* and *Sphaerium rivicola*, and in the Sulejów Reservoir by *Valvata piscinalis*, *Dreissena polymorpha* and *Pisidium henslowanum* (Fig. 4). In the Siemianówka Reservoir the occurrence of molluscs was to a large extent random, the highest frequency was that of *Gyraulus albus* and *Lymnaea peregra* (13.2% each). The proportion of species of frequency higher than 10% in the malacocoenoses of the flooded land zone and former river beds varied between the reservoirs. In the Zegrzyński Reservoir it was clearly higher in the river beds, in the Sulejów Reservoir the situation was similar in both zones, in the Siemianówka Reservoir species of frequencies of over 10% were noted only in the flooded land zone (Figs 2 and 4). The data indicate that in conditions of a greater influence of a river, associated with the flow value, the proportion of species of higher frequency of occurence in the former river bed increased. A reverse tendency was also observed (decrease in the number of species of higher frequency with increasing river size), involving the malacocoenoses of the flooded land. A comparison of the Sulejów and Zegrzyński Reservoirs indicates a larger effect of intra-reservoir processes on the molluscs of this zone in the former reservoir. The malacofauna of the Siemianówka Reservoir, characterised by a highly random character of occurrence, is not comparable with the malacocoenoses of the remaining two reservoirs.

1.1.2. Dominance structure

The dominance structure of the malacofauna of the Zegrzyński and Sulejów Reservoirs showed a high similarity (Fig. 5), resulting especially from the dominance of *D. polymorpha*. In the Zegrzyński Reservoir the co-dominant species was *Viviparus viviparus*. The porportion of other bivalve and prosobranch species was higher in the Sulejów than in the Zegrzyński Reservoir. In both reservoirs the proportion of prosobranchs, unionids and *Pisidium* spp. in the former river beds was fairly high, while in the zone of flooded land the proportion of *D. polymorpha* was the highest. Pulmonate snails constituted an insignificant component of the malacocoenoses, they occurred mainly in the zone of flooded land, and in the upper part of the

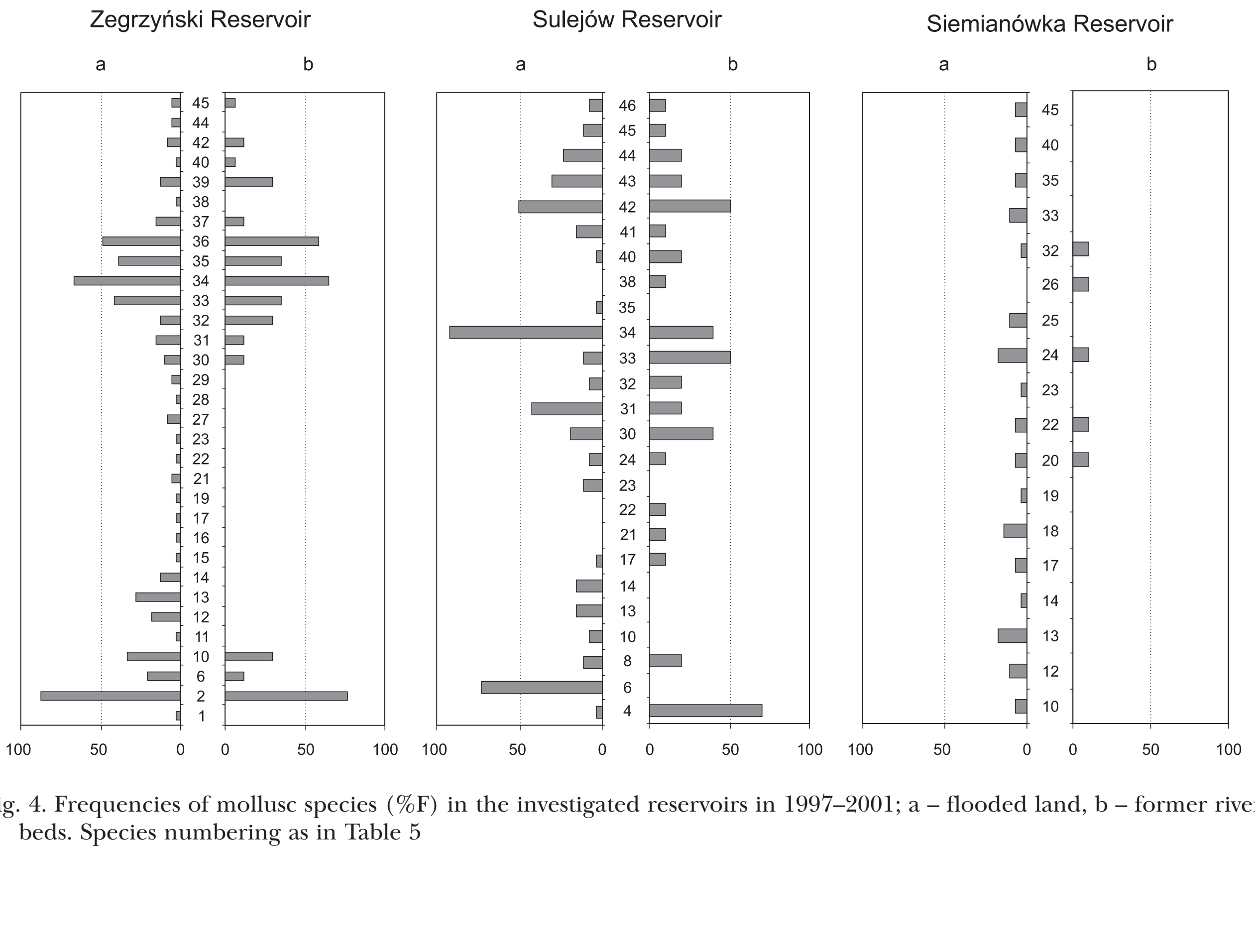

Fig. 4. Frequencies of mollusc species (%F) in the investigated reservoirs in 1997–2001; a – flooded land, b – former river beds. Species numbering as in Table 5

Sulejów Reservoir also in the former river bed. A considerable similarity in the structure of the malacocoenoses of these reservoirs is reflected in the percentage similarity values; the species composition similarity was not much lower. The dominance structure of the malacofauna of the Siemianówka Reservoir departed considerably from that observed in the other two reservoirs. Pulmonate snails dominated there, especially small planorbids (including species characteristic of small water bodies), and constituted 100% molluscs within the river bed. In the flooded land areas a significant proportion was constituted, besides planorbids, by lymnaeid snails which were the most numerous in the littoral. The distinct character of the malacofauna of this reservoir compared to the other two was expressed, among others, as low coefficients of species similarity, especially percentage similarity (Fig. 6). Rather small or moderate (when comparing the Zegrzyński and Sulejów Reservoirs) species similarity (S) and percentage similarity (Psc) values of the malacofauna indicate an effect of individual characters of the studied reservoirs on the development of their malacocoenoses. The species composition similarity and percentage similarity of the malacocoenoses of the flooded land and former river beds within

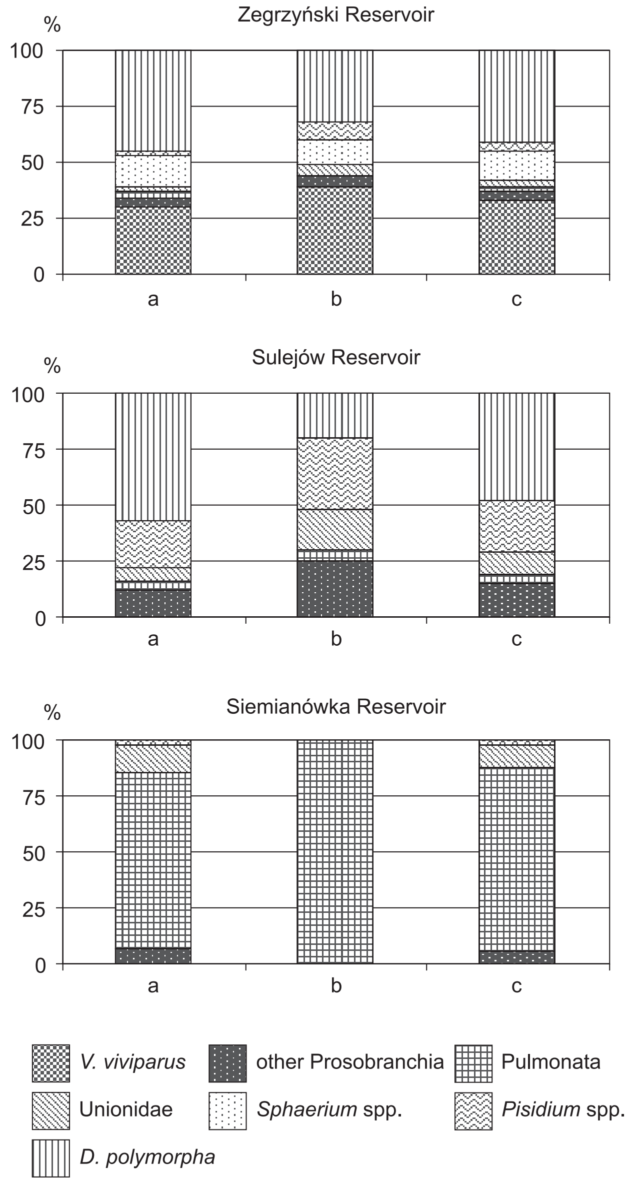

Fig. 5. Proportion (%) of abundant molluscs in the total density of the malacofauna in the investigated reservoirs; a – flooded land, b – former river beds, c – whole reservoir

A (upper right: S; lower left: Psc)

	I	II	III
I		0.46	0.40
II	0.50		0.44
III	0.06	0.05	

B (upper right: S; lower left: Psc)

	I	II	III
I		0.43	0.00
II	0.24		0.00
III	0.00	0.00	

Fig. 6. Species (S) and percentage (Psc) similarity of malacocoenoses in the flooded land areas (A) and former river beds (B) of the investigated reservoirs; I – Zegrzyński, II – Sulejów, III – Siemianówka

Table 6. Species (S) and percentage (Psc) similarity between malacofauna of flooded land and former river bed in three reservoirs

	Reservoir		
	Zegrzyński	Sulejów	Siemianówka
Species similarity	0.67	0.64	0.22
Percentage similarity	0.75	0.50	0.25

each reservoir were generally higher than the similarity between the malacofaunas of corresponding zones of different reservois (Fig. 6, Table 6).

The main dominants in terms of abundance had also a high biomass proportion. In the dominance structure of the biomass, contrary to the abundance, there was a clear participation of large unionid bivalves, especially in the Sulejów and Siemianowka Reservoirs (higher in the flooded land zone) (Fig. 7).

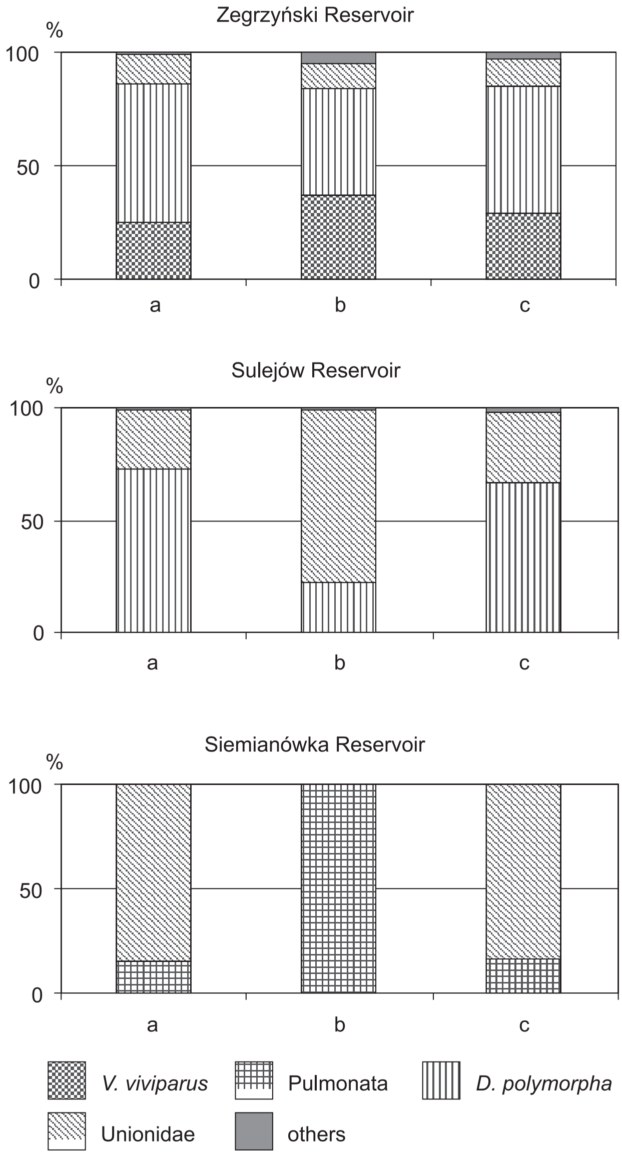

Fig. 7. Dominance relations in mollusc biomass in the investigated reservoirs; a – flooded land, b – former river beds, c – whole reservoir

1.1.3. Density and biomass

The malacofaunas of the studied reservoirs differed in abundance. In the Zegrzyński Reservoir the mean density of molluscs was ca. 900 indiv. m^{-2}, in the Sulejów Reservoir ca. 320 indiv. m^{-2}, in the Siemianówka Reservoir ca. 95 indiv. m^{-2} (Fig. 8A). Differences in the mean densities were more obvious in the case of malacocoenoses of the former river beds compared to flooded land (Table 7). Comparison of mean abundance of molluscs in the zones of flooded land and river beds in the studied reservoirs showed that, despite the higher values in the former zone in all three reservoirs, the difference was statistically significant only for the Sulejów Reservoir (NIR test, $p=0.0320$). The absence of significant differences in the remaining two reservoirs resulted mainly from a high variability of mollusc density in the studied habitats.

Large differences were found in the mean mollusc biomass between the reservoirs, the values being 291.4 g dry weight m^{-2}, 113.5 g dry weight m^{-2} and only 0.32 g dry weight m^{-2} for Zegrzyński, Sulejów and Siemianówka Reservoirs, respectively (Fig. 8B). Like with the density, larger biomass differences between the malacocoenoses were found when comparing the river beds, in relation to the flooded land (Table 7). No significant differences in the mean mollusc biomass in the zone of flooded land and former river beds were found in the studied reservoirs (ANOVA, $p>0.05$). In the compared reservoirs, there is a de-

Table 7. Differences in quantitative occurrence of molluscs in the studied reservoirs (Scheffe-test); A – abundance, B – biomass

		Reservoirs	
		Sulejów	Siemianówka
Whole reservoir			
Zegrzyński:	A	p=0.022104	p=0.000004
	B	p=0.029904	p=0.000000
Sulejów:	A		p=0.000000
	B		p=0.000000
Flooded land			
Zegrzyński:	A	ns	p=0.000000
	B	ns	p=0.000000
Sulejów:	A		p=0.000000
	B		p=0.000000
Former river beds			
Zegrzyński:	A	p=0.009973	p=0.000000
	B	p=0.013569	p=0.000000
Sulejów:	A		p=0.000000
	B		p=0.000000

creasing tendency of mean density and biomass of molluscs with decreasing effect of the river on the reservoir ecosystem, and thus in the following order: Zegrzyński→Sulejów→Siemianówka Reservoirs (Fig. 8A, B). The described tendency seems to be confirmed by the mean density of molluscs in the Włocławek Reservoir (in the 1990s 2,537 indiv. m^{-2}, Fig. 8A) where the Vistula discharge is much greater (see Table 1) than that of the rivers feeding the other reservoirs. The mean biomass of moluscs in the Włocławek Reservoir was of the same order of magnitude, though lower than in the Zegrzyński Reservoir: 127 and 291 g dry weight m^{-2} (Fig. 8B), respectively (JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press), which was associated with the dominance of small bivalves of the family Sphaeriidae (mainly *Sphaerium corneum*). In the reservoirs Zegrzyński, Sulejów and Siemianówka a distinct correlation was found between the mollusc abundance and the biomass. For the whole reservoirs the correlation coefficient values were 0.71, 0.51 and 0.61, respectively; in the flooded land areas the values ranged from 0.48 for the Sulejów Reservoir to 0.60 for the Siemianówka Reservoir and 0.86 for the Włocławek Reservoir. For the former river beds the correlation coefficients were 0.65 in the Zegrzyński Reservoir and 1.00 in the Siemianówka Reservoir. Only in the Sulejów Reservoir, where the abundance was dependent on small molluscs

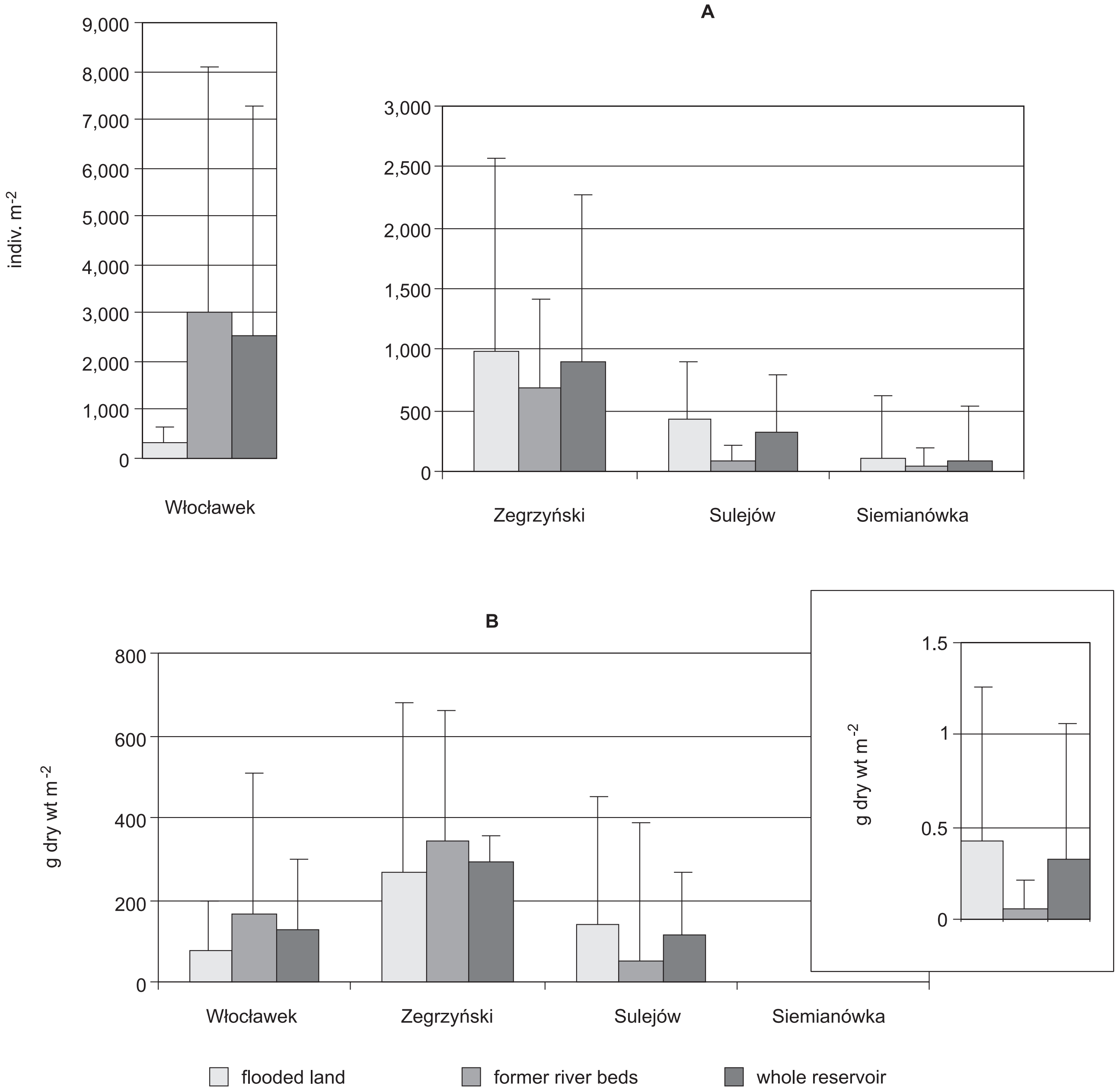

Fig. 8. Mean density (A) and biomass (B) of molluscs in the investigated reservoirs

(*Pisidium* spp., *Valvata piscinalis*), and the biomass – on large unionids in those sites where they occurred, the correlation of abundance and biomass within the river bed was not significant. In the other cases the dominant species differed much less in their size (and weight).

1.2. Long-term changes in malacocoenoses based on the Zegrzyński Reservoir

Studies including a twenty-year period of development of malacocoenoses of the Zegrzyński Reservoir made it possible to observe qualitative and quantitative changes of its malacofauna.

The number of mollusc species in the studied habitats varied widely during the analysed period, showing a general decreasing tendency (Fig. 9). At the beginning of the 1980s 49 mollusc species were found (8 species of prosobranchs, 19 pulmonates and 22 bivalves), in the second half of the 1980s the number decreased slightly (DUSOGE et al. 1990, GRUŻEWSKI 2000), while at half of the 1990s the number of species was reduced to 28 (6 prosobranchs, 9 pulmonates, 13 bivalves). At the end of the 1990s the species richness increased somewhat (32 species: 4 prosobranchs, 14 pulmonates, 14 bivalves). The tendency varied between the habitats, but on the whole the number of species at the end of the 1990s was much lower than several years earlier (Fig. 9). At the same time, there were significant changes in the dominance structure. Both these phenomena were reflected in the dynamics of species diversity (Shannon-Weaver index, H'). In the 1990s the index decresed in a part of habitats (Table 8). The largest decrease in species diversity was observed in habitats of slow water exchange, i.e. in bays in the upper, mid and lower parts of the reservoir, and in the stagnant habitat in its southern part (areas I, III, VI and VII, Fig. 1). In two areas – mouth section of the Bug River and the western side in the mid part of the reservoir (areas II and IV) the species diversity increased, while on the eastern side the value of Shannon-Weaver index remained unchanged.

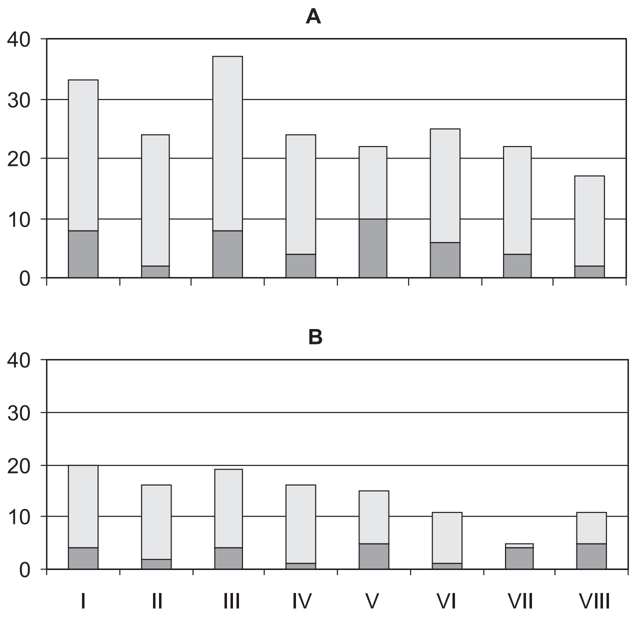

Fig. 9. Spatial and temporal changes in the number of mollusc species in the Zegrzyński Reservoir; A – 1980s, B – 1990s, I–VIII – sampling areas, see Fig. 1; species with frequencies exceeding 50% are shown as grey parts of the bars (after JURKIEWICZ-KARNKOWSKA 1986, 1998a, modified and supplemented)

During the twenty-year period the frequency of occurrence of particular mollusc species underwent considerable changes, some species disappeared from the reservoir. At the beginning of the 1980s only three species (*Lithoglyphus naticoides*, *Pisidium casertanum, P. henslowanum*) showed a high frequency (F>50%), while the frequency of most of the remaining species was fairly equalised, and for only a few species it dropped below 10%. In the 1990s the frequency of most species changed. In 1995 its values decreased for most species, only in a few cases there was a reverse tendency (Table 9). Four species: *V. viviparus*, *Bithynia tentaculata*, *Sphaerium rivicola* and *D. polymorpha*, reached a frequency over 50%. Except for *B. tentaculata*, these molluscs showed the highest constancy also at the end of the 1990s. The total number of species and the proportion of absolutely constant species in the discussed period changed to various extent depending on the habitat; the changes were more distinct in the stagnant habitat close to the southern shore of the reservoir and in its lower part (areas VI and VII) (Fig. 9). Generally, there was a decrease in both the total number of species and in absolutely constant species (F>50%), except for the vicinity of the dam where the number of absolutely constant species increased.

During the twenty years the dominance structure underwent changes which are better documented for habitats located in the zone of flooded land (Fig. 10).

Table 8. Long-term changes in mollusc species diversity (Shannon-Weaver's index, H') in the sampling areas of the Zegrzyński Reservoir

Part of the reservoir	Sampling area	Shannon-Weaver's index value		
		1981	1995	1997–1999
upper	I	2.1	0.9	0.8
	II	1.3	1.5	2.0
mid	III	2.0	0.7	1.6
	IV	1.4	0.4	2.0
	V	1.9	0.8	1.8
	VI	0.8	1.3	0.1
lower	VII	1.7	1.0	0.8
	VIII	–	0.7	0.6

Table. 9. Changes in frequency (%F) of mollusc species which were the most widespread in the 1980, in the following years (till 1999); a – littoral zone, b – central zone; according to JURKIEWICZ-KARNKOWSKA 2001a, modified; * – from GRUŻEWSKI (1988); *Sphaerium* sp. and *Pisidium* sp. are included in the absence of data on the species identity from 1986–1987

Taxon	1980–1981	*1986–1987	1995	1997–1999		
	a	a+b	a	a	b	a+b
Vviparus viviparus	44.3	60.3	86.3	84.8	78.3	80.4
Lithoglyphus naticoides	51.7	21.8	11.1	0	0	0
Valvata piscinalis	42.5	37.8	19.4	17.6	21.7	19.3
Bithynia tentaculata	21.8	35.9	65.3	39.4	26.1	32.0
Anodonta anatina	22.4	27.6	41.8	38.2	47.8	42.1
Sphaerium rivicola	45.4	–	63.4	54.5	33.3	50.1
S. corneum	23.7	–	10.0	42.4	30.3	36.8
Sphaerium sp.	60.3	68.6	66.7	67.6	65.2	66.7
Pisidium henslowanum	50.8	–	12.6	5.4	15.8	8.9
P. casertanum	56.3	–	13.9	2.7	5.3	3.4
Pisidium sp.	70.1	50.6	16.7	23.5	30.4	26.3
Dreissena polymorpha	23.0	18.6	72.9	66.7	73.9	64.3

At the beginning of the 80s, the proportion of bivalves of the genus *Pisidium* in the total abundance of molluscs was high in that zone; this was also true of some prosobranch species (*Lithoglyphus naticoides*, *Theodoxus fluviatilis*, *Valvata* spp.). It was especially clear in the upper part of the reservoir and in the habitats of its mid part which were under the effect of the Bug River. In the remaining habitats there was a clear dominance of *Viviparus viviparus* (along the western shore of the mid part of the reservoir, and in the lower part) and *D. polymorpha* (mainly in the southern, stagnant and in the lower parts). In the second half of the 1980s, the proportion of *V. viviparus* in the studied malacocoenoses increased; likewise there was a certain increase in the porportion of *D. polymorpha* and *Sphaerium* spp., while the proportion of *Pisidium* spp. and of some prosobranchs decreased. The dominance of *V. viviparus* persisted till the half of the 1990s, though in some habitats of the discussed zone the species was partly replaced by the spreading zebra mussel. At that time *D. polymorpha* reached a high proportion in the dominance structure of the malacocoenoses of the mid and lower parts of the reservoir (except the western shore of its mid part). The dominance structure became even further simplified. At the end of the 1990s, the main dominants were still *D. polymorpha* and *V. viviparus*, but there was an increase in the proportion of sphaeriid bivalves in most of the studied habitats. Reclamation work carried out in 1997 at the eastern shore in the mid part of the reservoir (by the District Water Management) caused a distinct change in the dominance structure of the malacofauna of that area. After colonies of *D. polymorpha* had been covered with a thick layer of sand, *V. viviparus* and *Sphaerium* sp. became dominants. The changes in the dominance structure in the zone of former river beds were less marked than in the flooded land areas (Fig. 10). This could result partly from a shorter period of observations, but also from smaller habitat changes (especially bottom deposits) compared to the flooded land. In the mid part of the reservoir the proportion of sphaeriids increased, and in the lower part – that of *D. polymorpha* which became the main dominant there.

Long-term changes in the mollusc biomass and density are, like the qualitative occurrence, rather well documented for habitats located in the flooded land zone. A comparison of the density in the 1980s and 1990s showed a general decrease in its values (t test, $p=0.0012$), especially in the upper and mid parts of the reservoir (except area VI, t test, $p>0.05$). The differences were more obvious on the eastern side of the reservoir which was under the effect of the Bug River (area V), then on the western side where the Narew River enters (area IV). In the 1990s, in the lower part of the reservoir, and on the southern shore in its mid part, the density increased (area VIII) or the values remained roughly unchanged (areas VI, VII). On the whole, in the 1990s the highest densities were observed close to the dam (areas VI, VIII), while in the 1980s the density was the highest in the upper part of the reservoir and on the eastern side of its mid part (I, II, III) (Fig. 11A). In the analysed period the density fluctuations were rather large. During the 1980s its values increased (JURKIEWICZ-KARNKOWSKA 1986, 1989a, GRUŻEWSKI 1988, DUSOGE et al. 1990, 1999), especially in the mouth section of the Bug River. In 1995 the density decreased significantly, while at the end of the 1990s it increased again (JURKIEWICZ-KARNKOWSKA 2001a).

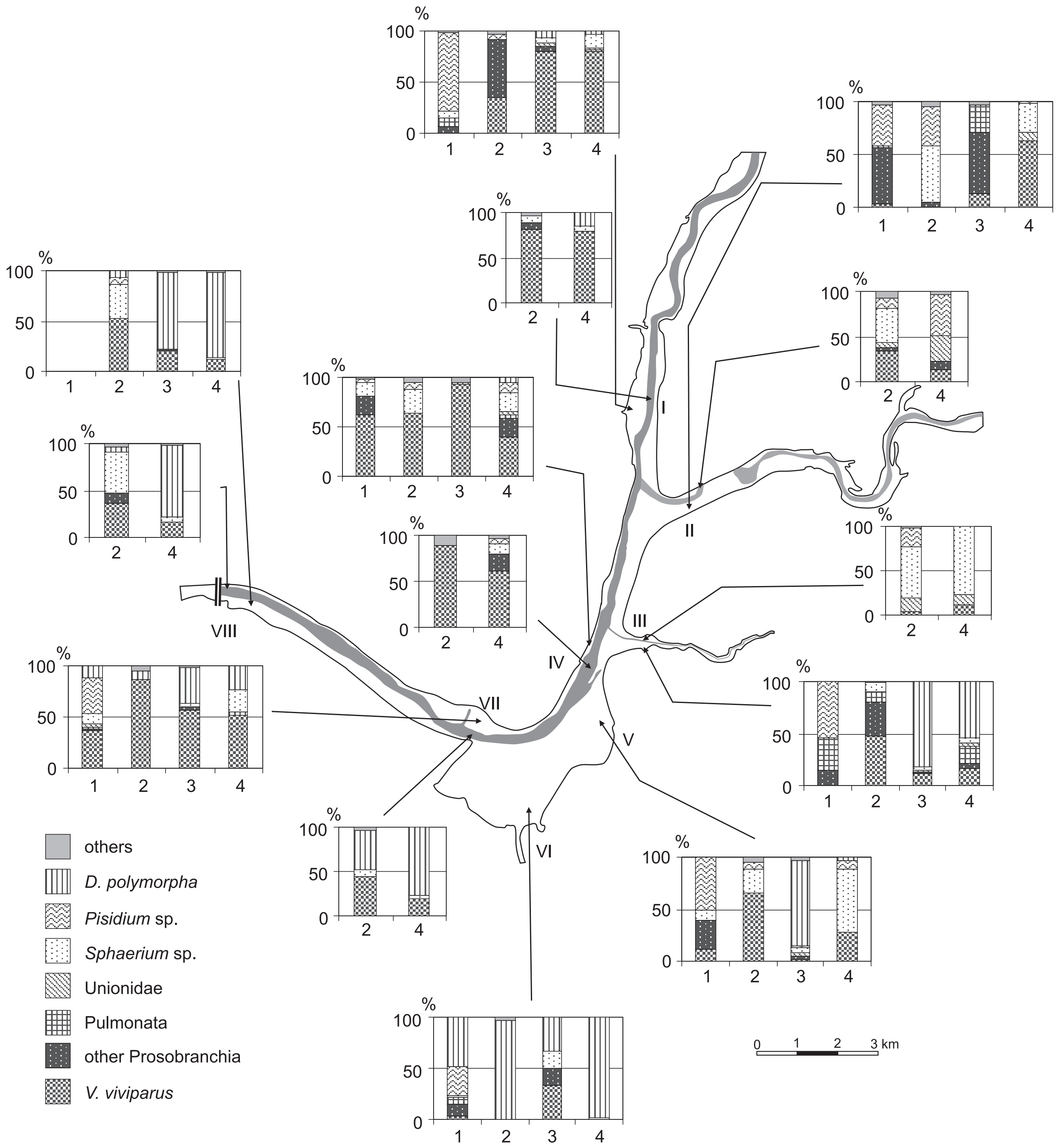

Fig. 10. Long-term changes in dominance structure of malacocoenoses in the investigated habitats of the Zegrzyński Reservoir; 1–4 – successive periods of investigations (1980–1981, 1986–1987, 1995, 1997–1999) (after JURKIEWICZ-KARNKOWSKA 1986, 1998a, modified, years 1986–1987 after GRUŻEWSKI 1988, modified)

A similar shift in the maximum density of the malacofauna toward the lower parts of the reservoir, like in the zone of flooded land, was observed in habitats of the former river beds (Fig. 11B). In such habitats, however, there were no significant differences in the mollusc density between the 1980s and 1990s.

A comparison of the mollusc biomass in the flooded land zone in the 1980s and 1990s indicates its increase (t test, p=0.0343). In the 1990s the biomass in most habitats was higher, but the differences were significant only in the case of the mouth section of the Narew River (I) and in the lower part of the reservoir (Fig. 12). The increase in biomass was associated with the increase in abundance in the 1980s and with the higher proportion of large molluscs in the total density in the 1990s. In the 1980s the maximum biomass was observed in the mid part of the reservoir, while in the 1990s it was the highest near the dam and in three

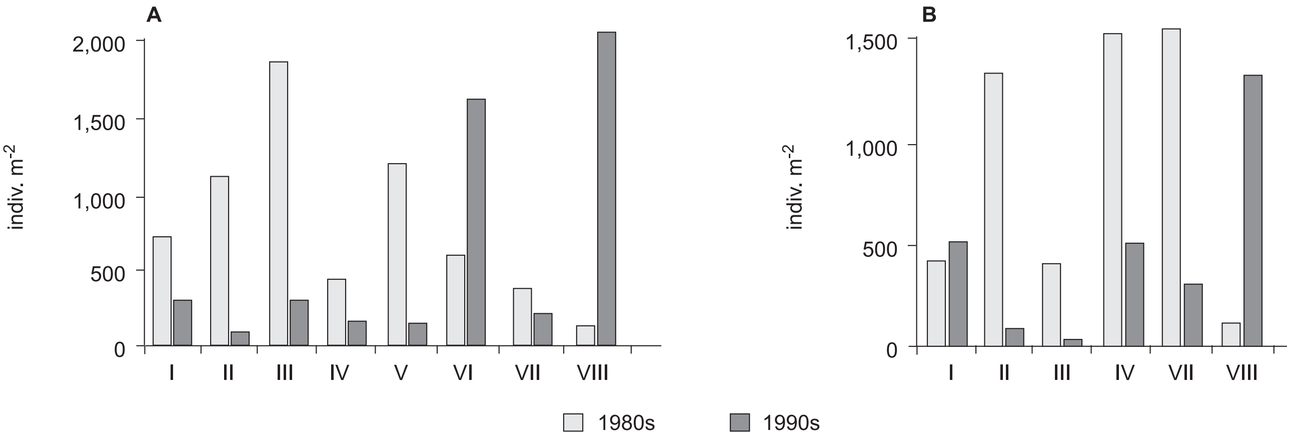

Fig. 11. Long-term changes in mollusc density in the investigated habitats within the flooded land areas (A) and former river beds (B) of the Zegrzyński Reservoir; I–VIII – see Fig. 1

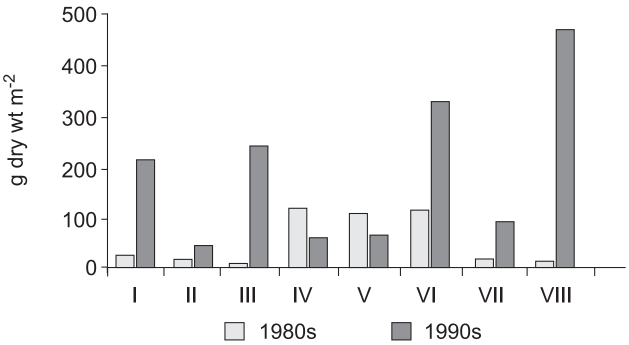

Fig. 12. Long-term changes in mollusc biomass in the investigated habitats within the flooded land areas of the Zegrzyński Reservoir; I–VIII – see Fig. 1

different habitats with strong dominance of *D. polymorpha* and *V. viviparus* (areas I, VI, VII, VIII). Only a rough comparison of biomass changes in the zone of former river beds was possible, because of the absence of data from the end of the 1980s for the habitats studied in this paper. Mean biomass values reported for the reservoir malacofauna of that period (1987) by DUSOGE et al. (1990), characterised by a strong increase in abundance of the malacofauna, were of similar order of magnitude as those obtained by the author at the end of the 1990s.

1.3. Effect of the main dominants on the malacocoenoses

In the Sulejów Reservoir, where *D. polymorpha* dominated in the malacocoenoses, and in the Zegrzyński Reservoir, with *D. polymorpha* and *V. viviparus* as co-dominants, these molluscs were observed to affect the number of species and density of other molluscs in habitats where one or both of them were abundant. The limiting effect of *D. polymorpha* on the species richness of malacocoenoses of the Sulejów Reservoir was especially marked. In habitats where the density of the zebra mussel exceeded 500 indiv. m^{-2}, only eight species of other molluscs were found, while where *Dreissena* was scarce or absent, 24 species were present. A similar limiting effect of the dominants could be observed in the Zegrzyński Reservoir, the effect of *D. polymorpha* being more distinct there, compared to *V. viviparus*. The fewest mollusc species (8) were found in habitats in which both dominants were abundant (>500 and >200 indiv. m^{-2}, respectively), a richer malacofauna was found in sites with high abundance of only *D. polymorpha* (13 species) and still richer in habitats with high densities of *V. viviparus* (15 species). In habitats where both species were scarce or absent, the number of other mollusc species was the highest (26). The dominants were also found to have an effect on the density of other components of malacocoenoses (Fig. 13). In the presence of *D. polymorpha* and *V. viviparus* at fairly high densities (>500 and >200 indiv. m^{-2}, respectively), the density of the remaining molluscs was lower compared to situations where the dominants were absent or sparse. The negative effect on the number of species and density of the remaining molluscs was always statistically significant in the case of high abundance of *D. polymorpha* (Table 10), and statistically insignificant in the case of *V. viviparus*. High positive values of correlation coefficients between the density of *D. polymorpha* and the density and biomass of malacocoenoses of the studied habitats of the Zegrzyński and Sulejów Reservoirs confirm the dominant position of the species. High abundance of *V. viviparus* had a significant effect on the biomass of the malacocoenoses (Table 10). No negative dependence, which might indicate a competition between the two co-dominants, was found between the abundace of *D. polymorpha* and *V. viviparus* in the Zegrzyński Reservoir. In the lower part of the reservoir both species reached high densities, but fragments of bottom occupied by them overlapped only to a slight extent, which may result from competition-induced habitat partitioning. In the mid

Table 10. The influence of dominant species on the occurrence of other molluscs and whole malacocoenoses (Pearson's correlation indices – r) in the Zegrzyński and Sulejów Reservoirs; * – statistically significant correlations

Characteristics of dominants	Whole malacocoenosis		Malacocoenosis with exclusion of *D. polymorpha* and *V. viviparus*		
	Density	Biomass	Number of species	Density	Biomass
Zegrzyński Reservoir (N=49)					
Abundant/scarce:					
D. polymorpha	0.69*	0.66*	–0.32*	–0.35*	–0.04
V. viviparus	0.22	0.38*	0.01	0.16	0.03
together	0.60*	0.53*	–0,18	–0.26	–0.10
Density:					
D. polymorpha	0.99*	0.72*	–0.17	–0.20	0.06
V. viviparus	0.25	0.42*	0.07	0.19	0.03
together	1.00*	0.77*	–0.15	–0.16	0.06
Sulejów Reservoir (N=35)					
D. polymorpha:					
Abundant/scarce	0.90*	0.63*	–0.34*	–0.32	–0.16
Density	0.93*	0.61*	–0.34*	–0.29	–0.17

part of the reservoir, at the eastern shore, an increase in abundance of *V. viviparus* was observed following recultivation measures which eliminated *D. polymorpha* as a result of covering it with a thick layer of sand. The phenomenon might suggest that *V. viviparus* is a weaker competitor compared to *D. polymorpha*. This was reflected in the changes in proportions of the two dominants in the structure of the malacocoenoses of the reservoir (see previous chapter, changes of dominance structure).

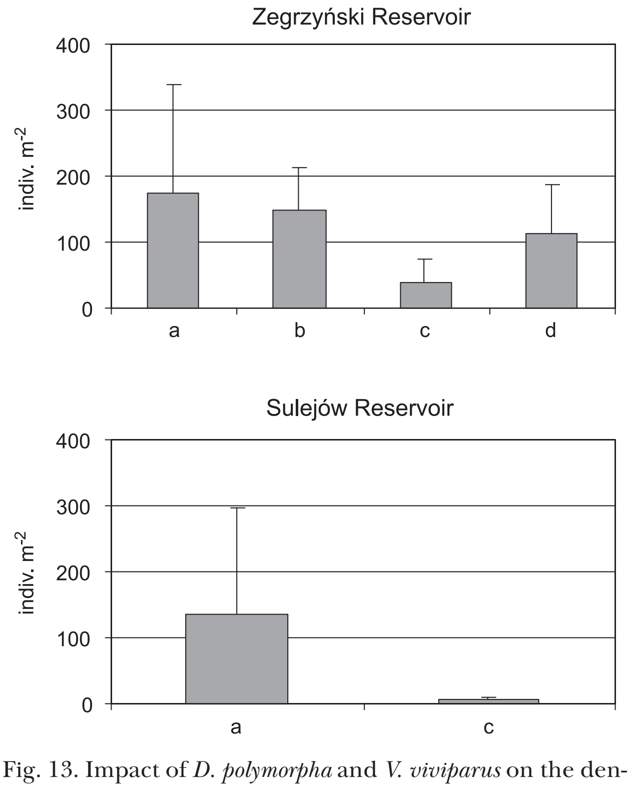

Fig. 13. Impact of *D. polymorpha* and *V. viviparus* on the density of the other mollusc species; a – low density or lack of *D. polymorpha* and *V viviparus*, b – high density of *V. viviparus* (>200 indiv. m^{-2}), c – high density of *D. polymorpha* (>500 indiv. m^{-2}), d – high density of *D. polymorpha* and *V. viviparus*

2. ROLE OF MOLLUSCS IN HEAVY METALS AND PHOSPHORUS ACCUMULATION IN THE RESERVOIR ECOSYSTEM

2.1. Concentration of phosphorus and heavy metals in molluscs and their accumulation in the reservoir malacocoenoses

Phosphorus concentration in soft tissues of the studied mollusc species ranged from below 10 to over 20 mg g^{-1} dry weight (from 0.63% to 2.42% dry weight). The highest values were noted for unionids. Concentrations of analysed essential metals in tissues of molluscs from the Zegrzyński, Sulejów, Siemianówka and Włocławek Reservoirs were most often within the range from tens to hundreds μg g^{-1} dry weight, only the level of Cu in bivalves was usually below 10 μg g^{-1} dry weight, while concentration of Mn and Fe in unionids and sphaeriids (except Mn in *Sphaerium corneum*) was of an order of thousands μg g^{-1} dry weight (Table 11). Lower values were noted for non-essential metals (from over 1 to over 10 μg g^{-1} dry weight for Pb, and below 1 μg g^{-1} dry weight for Cd). Concentration of phosphorus and the studied metals in the shells was usually much lower, most often by an order of magnitude, compared to soft tissues (Table 12).

The level of the studied elements in mollusc tissues varied rather much between species, while their concentration in the shells varied much less (Table 13). Instances of statistically significant differences in the concentration in tissues in the studied reservoirs

Table 11. Concentrations of phosphorus and heavy metals (μg g^{-1} dry wt ±SD) in soft tissues of the studied molluscs from four reservoirs (Zegrzyński, Sulejów, Siemianówka, Włocławek); * – *Sphaerium rivicola*, ** – *S. corneum* (data on metal concentrations in molluscs from the Zegrzyński Reservoir based on JURKIEWICZ-KARNKOWSKA & KRÓLAK 2000, supplemented and modified)

Reservoir	P	Cu	Zn	Mn	Fe	Pb	Cd
			Viviparus viviparus				
Zegrzyński	6,250±1,490	54.0±32.3	193.0±51.9	80.7±39.1	232.2±203.6	10.8±5.6	0.05±0.03
Włocławek	6,200±1,920	174.6±24.3	377.2±53.6	206.1±36.9	965.5±617.0	1.1±0.2	0.11±0.06
			Lymnaea sp.				
Zegrzyński	7,440±1,020	27.4±18.1	70.3±20.1	240.1±103.6	507.5±230.6	15.6±25.0	0.29±0.21
Siemianówka	3,970±580	20.7±2.5	87.7±23.6	468.7±63.2	1,082±355.8	1.7±0.9	0.48±0.07
			Dreissena polymorpha				
Zegrzyński	9,390±2,480	8.1±3.4	95.1±35.6	93.0±59.2	279.6±136.9	14.4±5.5	0.20±0.18
Sulejów	9,860±340	20.5±5.0	133.1±20.2	579.6±97.5	912.2±364.3	1.5±0.8	0.71±0.36
Włocławek	11,400±1,000	7.3±1.0	177.1±2.8	316.4±21.3	534.0±11.6	1.0±0.1	0.29±0.01
			Anodonta sp.				
Zegrzyński	25,900±25,230	7.2±3.0	226.3±125.1	5,850±2,790	1,615±928.1	13.2±14.4	0.21±0.16
Siemianówka	18,800±5,840	9.6±4.0	131.8±24.8	3,840±1,034	2,210±1,060	7.0±6.2	0.42±0.05
Sulejów	11,330±4,070	9.3±4.3	247.0±64.0	3,981±46.6	1,590±742.1	1.4±0.04	0.71±0.40
Włocławek	14,980±3,930	10.7±1.1	318.7±45.5	4,770±51.3	1,170±1,240	0.7±0.3	0.73±0.30
			Unio sp.				
Zegrzyński	19,740±4,480	7.1±3.6	282.8±120.4	4,830±1,090	2,580±1,810	6.8±9.0	0.30±0.13
Sulejów	18,300±1,020	8.5±3.0	233.6±117.8	3,230±1,950	4,070±2,900	1.2±0.1	0.49±0.28
			Unionidae				
Zegrzyński	22,250±7.410	7.2±3.0	238.2±123.1	5,635±2,530	1,880±1,160	11.6±13.3	0.23±0.16
Siemianówka	1,880±5,840	9.6±3.7	129.2±24.3	3,670±1,130	2,240±1,010	7.0±6.2	0.42±0.04
Sulejów	15,150±3,680	8.9±3.6	240.9±87.4	3,640±1,290	2,410±2,000	1.3±0.3	0.68±0.29
Włocławek	13,450±4,880	8.5±3.4	278.9±69.8	3,620±1,660	888.0±432.8	0.7±0.3	0.56±0.35
			Sphaeriidae				
Zegrzyński*	8,600±5,940	39.8±17.2	112.8±34.3	104.2±63.0	547.8±401.2	6.7±6.3	0.21±0.13
Włocławek**	5,170±3,060	73.5±17.6	139.6±10.7	218.0±32.4	1,380±317.4	4.1±0.1	0.56±0.21

were much more numerous in the case of P, Cu, Zn, Mn and Fe compared to Pb and Cd. The differences in phosphorus concentration in tissues of conspecific molluscs from two to four reservoirs were fewer (ANOVA, $p<0.05$) than inter-specific differences within the same reservoir, while the phosphorus level in the shells usually did not differ significantly between conspecific molluscs from different reservoirs, or between different species within the same reservoir. Contrary to phosphorus, differences between conspecific molluscs from two to four reservoris were more numerous for the analysed metals (ANOVA, $p<0.05$) than inter-specific differences, especially for non-essential metals. For shells, most intra- and interspecific diferences in the concentration of the elements were insignificant.

The differences in the level of phosphorus and heavy metals in molluscs, and different values of biomass and dominance structure of the malacocoenoses of the studied reservoirs had an effect on the possibilities of accumulation of the analysed elements by the malacofauna in particular reservoirs (Fig. 14). The quantities of accumulated elements were negligible in the Siemianówka because of the low values of mollusc biomass in that reservoir. In the Zegrzyński, Sulejów and Włocławek Reservoirs the quantities were significantly higher (most often by two orders of magnitude), but not in direct proportion to the biomass values. In spite of lower mollusc biomass in the studied habitats of the last two reservoirs, compared to the Zegrzyński Reservoir, quantities of some elements (P, Cu, Zn, Mn, Cd) accumulated by the molluscs were relatively high which resulted from the high proportion of unionids in the biomass of the malacocoenoses. Fairly high concentrations of Cu and Cd in small bivalves *Sphaerium corneum*, dominant in the Włocławek Reservoir (JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press), may significantly increase the value of accumulation of these elements in the malacofauna.

Table 12. Concentrations of phosphorus and heavy metals (μg/g dry wt ±SD) in shells of the studied molluscs from four reservoirs (Zegrzyński, Sulejów, Siemianówka, Włocławek); * – *Sphaerium rivicola,* ** – *Sphaerium corneum* (data on metal concentrations in molluscs from the Zegrzyński Reservoir according to JURKIEWICZ-KARNKOWSKA & KRÓLAK 2000, supplemented and modified)

Reservoir	P	Cu	Zn	Mn	Fe	Pb	Cd
			Viviparus viviparus				
Zegrzyński	353±159	3.8±1.6	8.8±3.1	342.8±336.4	899.5±755.1	2.9±3.5	0.03±0.04
Włocławek	437±32	4.7±0.1	7.8±0.5	274.8±25.9	1164.7±43.7	0.6±0.5	0.02±0.01
			Lymnaea sp.				
Zegrzyński	183±90	2.4±2.2	5.5±3.4	369.4±178.8	134.8±112.9	5.2±6.8	0.02±0.02
Siemianówka	317±150	2.1±0.6	4.6±4.2	179.1±52.4	198.3±134.1	0.3±0.3	0.02±0.01
			Dreissena polymorpha				
Zegrzyński	297±161	3.4±1.8	6.2±2.4	177.1±142.2	347.0±276.6	2.0±1.7	0.02±0.01
Sulejów	383±129	1.9±0.8	5.3±1.3	244.9±84.4	627.6±2291.5	0.4±0.1	0.02±0.01
Włocławek	400±98	3.3±0.5	7.4±0.9	257.5±33.5	560.7±72.4	0.3±0.2	0.04±0.03
			Anodonta sp.				
Zegrzyński	239±153	5.6±2.5	5.5±3.3	334.6±175.1	696.3±747.9	3.0±3.3	0.03±0.04
Siemianówka	300±107	4.3±2.4	7.1±4.6	308.7±20.1	259.7±53.9	0.6±0.7	0.08±0.10
Sulejów	397±158	4.4±0.2	3.4±0.6	320.6±17.3	406.4±84.7	0.3±0.1	0.02±0.01
Włocławek	310±117	5.8±0.3	10.1±7.2	480.2±106.4	136.4±2.0	0.3±0.2	0.03±0.03
			Unio sp.				
Zegrzyński	320±186	2.4±1.1	5.5±3.3	230.5±96.2	187.1±184.6	0.3±0.2	0.01±0.01
Sulejów	300±115	3.7±0.8	4.4±0.8	244.1±79.4	378.3±136.8	0.4±0.2	0.02±0.01
			Unionidae				
Zegrzyński	247±148	4.8±2.6	5.3±3.5	310.1±163.7	576.6±689.5	2.4±3.1	0.02±0.01
Siemianówka	300±107	4.3±2.3	6.9±4.5	296.2±45.7	315.6±192.3	0.6±0.6	0.07±0.09
Sulejów	333±58	4.0±0.7	4.0±0.9	276.9±71.1	390.4±114.2	0.3±0.1	0.02±0.01
Włocławek	302±102	5.3±0.8	11.3±6.0	391.8±157.0	125.5±30.1	0.3±0.2	0.03±0.02
			Sphaeriidae				
Zegrzyński*	203±126	3.0±2.6	3.8±1.8	80.0±102.3	263.0±168.7	1.3±0.9	0.01±0.01
Włocławek**	333±129	8.3±0.5	26.0±0.6	69.0±18.1	574.1±22.4	0.2±0.1	0.07±0.03

2.2. Role of molluscs in accumulation of phosphorus and heavy metals in the Zegrzyński Reservoir

Though the concentration of the studied elements in mollusc tissues is usually by an order of magnitude higher compared to the shells, due to the high proportion of shell in mollusc dry weight (Table 14), elements contained in it may constitute a considerable portion of the entire pool accumulated in the animals. Especially great significance of shell was noted for accumulation of manganese and iron, it was also considerable for copper, lead and cadmium, while phosphorus and zinc were accumulated mainly in tissues.

Mean quantities of particular elements accumulated in molluscs inhabiting 1 m^2 bottom in different parts of the reservoir, and significance of shell and tissues in accumulation of particular elements varied considerably (Fig. 15). The greatest quantities of the studied elements were accumulated by molluscs in the lower part of the reservoir, where the animals reached the highest biomass values. Large differences with respect to accumulation of phosphorus and metals by molluscs were observed also within each of the three parts of the reservoir. Comparison of accumulation of some elements, especially phosphorus and manganese, by molluscs of the mouth sections of the Bug and Narew Rivers, indicates the effect of dominance structure on the quantities of elements accumulated by the malacocoenoses. In spite of much lower mean biomass in the first habitat (only ca. 40% biomass compared to the second), the quantities of phosphorus and manganese accumulated in molluscs were similar. The dominance of unionid bivalves in the biomass of the malacofauna determined the great capacity for accumulating phosphorus and manganese in the malacocoenosis of the mouth section of the Bug River. The unionids were characterised by an exceptionally high level of manganese and phospho-

Table 13. Inter-specific differences in concentration of the studied elements in soft tissues and shells of molluscs from the Zegrzyński Reservoir (symbols of elements denote significant inter-specific differences, shading denotes high number of inter-specific differences; ANOVA, p<0.05); *V.v.* – *Viviparus viviparus*, *L.s.* – *Lymnaea stagnalis*, *L.p.* – *L. peregra*, *D.p.* – *Dreissena polymorpha*, *A.a.* – *Anodonta anatina*, *A.c.* – *A. cygnea*, *U.t.* – *Unio tumidus*, *U.p.* – *U. pictorum*, *S.r.* – *Sphaerium rivicola*

Soft tissues

	V.v.	*L.s.*	*L.p.*	*D.p.*	*A.a.*	*A.c.*	*U.t.*	*U.p.*	*S.r.*
V.v.		Cu, Zn, Mn, Fe, Cd	Zn, Mn, Fe, Cd, P	Cu, Zn, Cd, P	Cu, Mn, Fe, Cd, P	Cu, Mn, Fe, Cd, P	Cu, Mn, Fe, Cd, P	Cu, Zn, Mn, Fe, Pb, Cd, P	Zn, Mn, Fe, Pb, Cd
L.s.	Cu, Zn, Fe, P		Cu	Cu, Mn, Fe, Pb, P	Cu, Zn, Mn, Fe, P	Cu, Zn, Mn, Fe, P	Zn, Mn, Fe, P	Cu, Zn, Mn, Fe, P	Cu, Zn
L.p.	Fe, Pb			Cu, Mn Fe, Cd	Cu, Zn, Mn, Fe, Cd, P	Cu, Zn, Mn,Fe, P	Cu, Zn, Mn, Fe, P	Cu, Zn, Mn, Fe, Pb, P	
D.p.	Zn, Fe, Mn	Cu, Mn, Fe, P	Mn, Pb		Zn, Mn, Fe, P	Zn, Mn, Fe, P	Zn, Mn, Fe, P	Zn, Mn, Fe, Pb, P	Cu, Fe
A.a.	Zn, Fe, P	Cu	Mn, Pb	P			Cd	Zn, P	Cu, Zn, Mn, P
A.c.	Zn	Cu, Fe	Fe	Mn, Fe	Mn, Fe			P	Cu, Zn, Mn, P
U.t.	Zn		Pb						Cu, P
U.p.	Fe, Zn, Pb		Pb	Pb		Fe, Pb			Cu, Zn, Mn, P
S.r.	Cu, Zn, Mn,Fe	Mn, Fe	Zn, Mn	Zn	Mn	Mn, Fe	Mn	Mn	

Shells

rus in their tissues, compared to other molluscs. A similar situation follows from a comparison of accumulation of the studied elements in molluscs from two habitats located on opposite sides of the mid part of the reservoir. Participation of tissues and shell in accumulation of particular elements by malacocoenoses varied within the reservoir, which was associated with the diverse dominance structure. Especially wide ranges of values were observed for manganese and zinc. For the remaining metals and phosphorus the differences in participation of tissues and shell in accumulation in various habitats ranged from a few to over 10%.

Heavy metals contained in molluscs living on the bottom of the Zegrzyński Reservoir constituted only a small fraction of annual retention of these elements

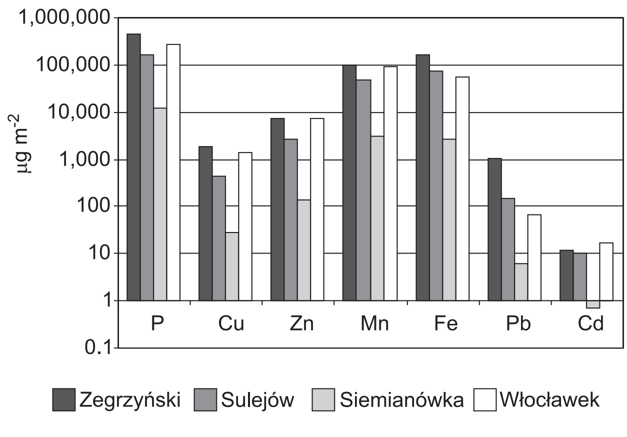

Fig. 14. Accumulation of phosphorus and heavy metals in molluscs living on 1 m^2 bottom in four reservoirs

Table 14. Significance of mollusc shells in accumulation of phosphorus and heavy metals in the Zegrzyński Reservoir

	% of mollusc dry mass	Participation of shells in metal accumulation (%)						
		P	Cu	Zn	Mn	Fe	Pb	Cd
Viviparus viviparus	85	24	30	20	96	96	60	77
Lymnaea sp.	67	5	15	14	76	35	40	11
Dreissena polymorpha	91	24	81	40	95	93	58	50
Unionidae	85	5	78	13	22	57	52	36
Sphaeriidae	88	35	37	20	17	48	57	25

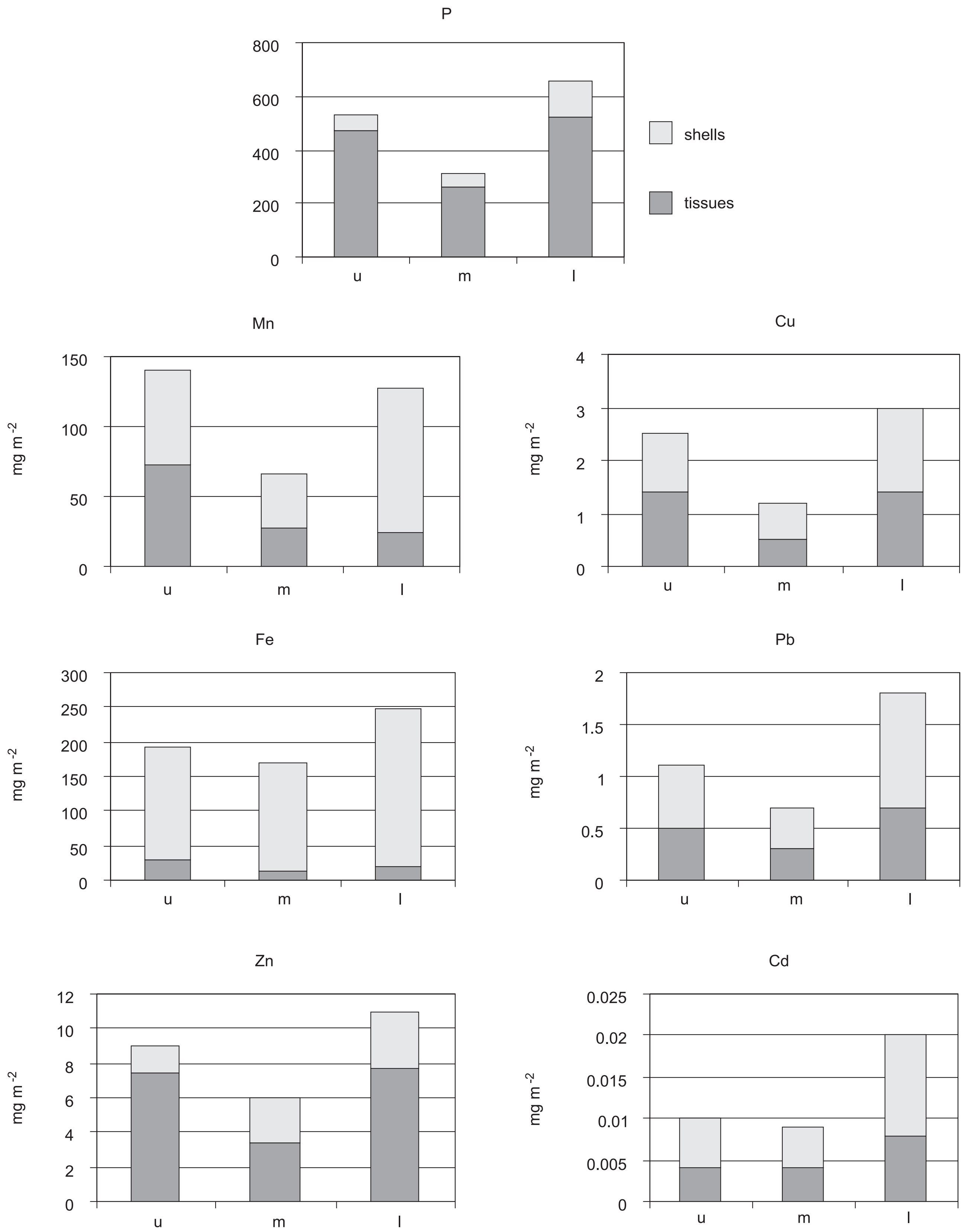

Fig. 15. Accumulation of the investigated elements in soft tissues and shells of molluscs inhabiting 1 m^2 bottom in the upper (u), mid (m) and lower (l) parts of the Zegrzyński Reservoir

in the reservoir (most often below 1%, only for Mn over 2%); the corresponding value for phosphorus was ca. 6%. Compared to the content of the analysed elements in water (whole volume of the reservoir), quantities of metals accumulated in molluscs constituted from over 4% (Pb) to ca. 48% (Mn) and over 90% for phosphorus (Table 15). In the case of phosphorus, molluscs were a significant trap. The mollusc-accumulated pool of the studied elements formed a small part of the quantity accumulated in bottom deposits, the highest values were noted for phosphorus, copper and manganese (4%, 1.9% and 1.8%, respectively). However, considering the great significance of shell in heavy metal accumulation (except Zn) by molluscs, ranging from over 46% to nearly 90%, the animals may, when abundant, exclude considerable quantities of these elements from circulation. Shells, especially more massive, remain in the bottom deposits during many years, preserving considerable fraction of their content of phosphorus and heavy metals (Table 16). Comparison of the level of the studied elements in shells of live molluscs (*D. polymorpha, V. viviparus*) and empty shells of these species from a few to about a dozen years ago, indicates in most cases a significant decrease in their concentration with time, but the concentrations were still of a similar order of magnitude. In the case of Zn and Fe, the concentrations in old shells were even higher compared to shells of live molluscs.

Table 15. Amounts of the investigated elements accumulated in molluscs inhabiting the Zegrzyński Reservoir against the pools contained in bottom sediments deposited during one year (1 cm thick), water column (the volume of the reservoir) and yearly retention, 1998–1999

Element	Accumulation in molluscs (kg)	The share (%) of molluscs in pools of elements		
		Bottom sediments	Water	Retention
P	14,777.4	4.0	92.4	5.7
Cu	59.7	1.9	17.2	0.4
Zn	240.2	1.3	14.5	0.8
Mn	3,269.3	1.8	47.7	2.6
Fe	5,243.7	0.2	18.0	0.6
Pb	34.3	0.6	4.1	0.6
Cd	0.38	0.5	22.4	0.3

Table 16. Concentrations of phosphorus and heavy metals (μg g^{-1} dry wt) in shells of *Dreissena polymorpha* and *Viviparus viviparus* from the Zegrzyński Reservoir – comparison of living individuals and shells found in sediments deposited at least a few years ago; significant differences (t-test, $p<0.05$) marked with an asterisk

Element	Living individuals	Old shells
	Dreissena polymorpha	
P*	297±161	170±11
Cu*	3.4±1.8	2.5±0.4
Zn*	6.2±2.4	15.1±2.0
Mn	177.1±14.2	112.1±39.7
Fe*	347.0±276.6	689.9±420.5
Pb	2.0±1.7	1.2±0.8
Cd*	0.02±0.01	0.048±0.001
	Viviparus viviparus	
P*	350±119	160±10
Cu*	3.8±1.6	2.2±0.2
Zn*	8.8±3.1	13.1±3.0
Mn	342.8±336.4	133.1±39.7
Fe*	899.5±755.1	1,354.5±152.0
Pb*	2.9±3.5	9.9±1.0
Cd	0.03±0.04	0.01±0.002

3. SELECTED ASPECTS OF THE ROLE OF MOLLUSCS IN MATTER CIRCULATION, BASED ON THE ZEGRZYŃSKI RESERVOIR

3.1. Effect of filtration activity on the circulation of phosphorus and heavy metals

Filtratory activity of bivalves and filtrationist snails (prosobranchs, in the Zegrzyński Reservoir especially *V. viviparus*) is limited to the vegetation season (200 days were assumed here). The quantity of water (4,052 mln m^3) which could be filtered during that time by bivalves at a mean density observed in the reservoir, exceeds the reservoir's capacity many times and reaches values which are comparable to the amount of water contributed by the Bug and Narew Rivers (in 1999 the mean 4,769.3 mln m^3) (Fig. 16A). The quantity of water equal to the volume of the reservoir could be filtered by molluscs within a few days. Considering filtration activity of the abundant snail *V. viviparus*, the volume of mollusc-filtered water would be comparable to the water discharge during the vegetation season. It follows from the calculations that during the vegetation season (1998 and 1999) bivalves could potentially clear the quantity of suspension equal to about half of total suspension introduced during that period by the Bug and Narew Rivers (Fig. 16B). It should be noted that suspension content in the water during the vegetation season was much higher than in winter.

A similar situation to that described for suspension, could be observed for suspended fraction of phosphorus and heavy metals (Fig. 17) which indicates that bivalves could clear a considerable part of these elements introduced in the reservoir during the vegetation season (in the case of P and most analysed metals over 50% maximum value, for manganese – over 80%).

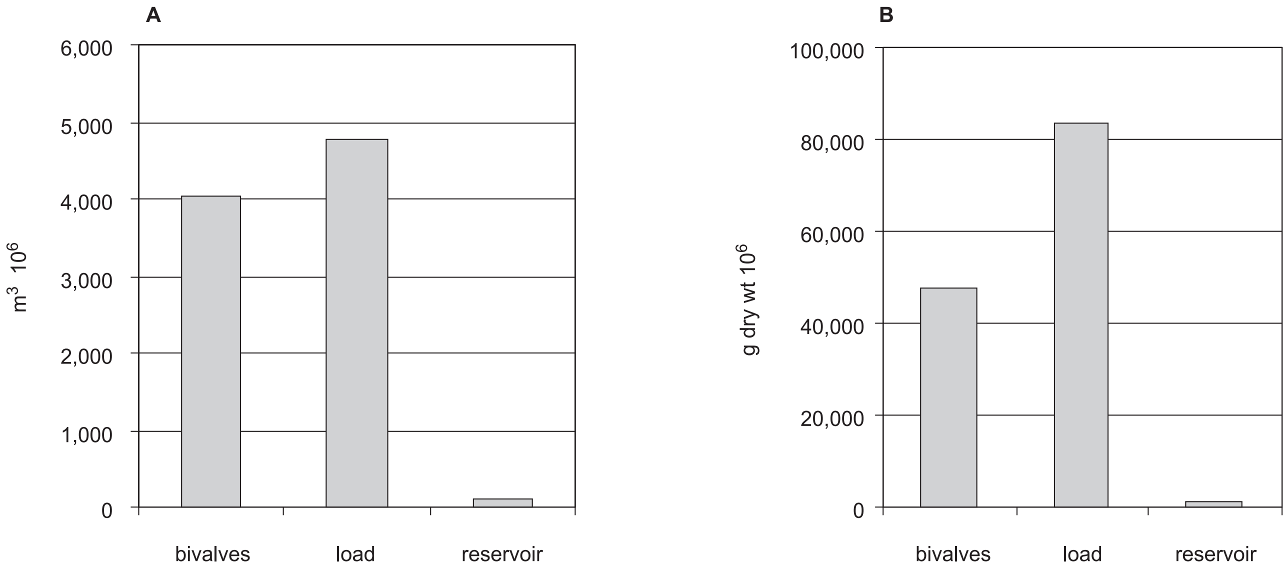

Fig. 16. Filtration activity of bivalves in the Zegrzyński Reservoir: A – volume of water filtered during season compared with seasonal water discharge of the Bug and Narew rivers and the reservoir's capacity, B – the amount of seston cleared by bivalves during season compared with seston load assessed for the same period and mean amount of seston contained in the reservoir

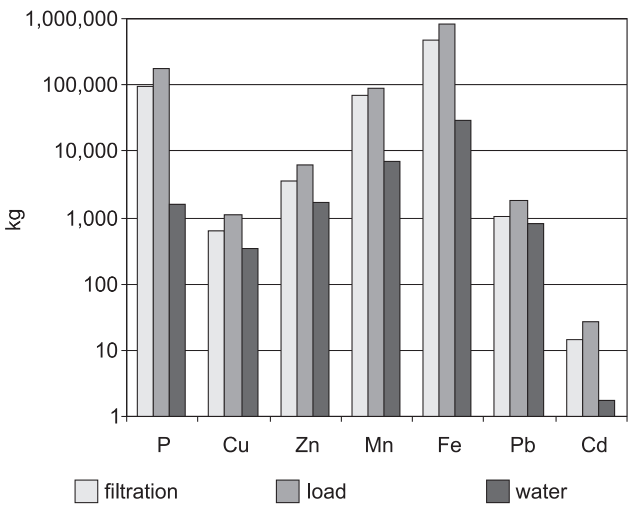

Fig. 17. Amounts of the analysed elements potentially cleared with seston by bivalves during season on the background of seasonal inputs through rivers and the pool contained in the water column in the Zegrzyński Reservoir

Table 17. Quantities of faeces (and pseudofaeces) estimated for the investigated molluscs from the Zegrzyński Reservoir; all inter-specific differences statistically significant (ANOVA, p<0.05)

Taxon	Faeces (and pseudofaeces) mg dry wt indiv^{-1} day^{-1}
Viviparus viviparus	20.2±1.7
Lymnaea sp.	10.4±2.8
Dreissena polymorpha	3.7±0.3
Unionidae	31.4±3.2

Biodeposition of elements (faeces and pseudofaeces) by molluscs depends on the abundance of the animals, but also on the dominance structure of the malacocoenoses. The dominant snail, *V. viviparus*, produced more faeces per individual compared to the dominant bivalve, *D. polymorpha* (Table 17). On the average, in the pool of faeces and pseudofaeces (biodeposits) deposited on 1 m^2 bottom inhabited by molluscs, snail faeces constituted at least a half, while the whole of biodeposits formed ca. 10% of the annual layer of bottom deposits (according to WIĘCKOWSKI 1979; layer ca. 1 cm thick). The quantity of the studied heavy metals and phosphorus in faeces of molluscs inhabiting 1 m^2 bottom constituted from over 13% (Fe) to over 62% (Zn) quantity of these elements contained in a 1 cm layer of bottom deposits. In many cases (Cu, Zn, Mn, Pb, Cd), the values were clearly higher in faeces produced by bivalves, compared to the faeces of the dominant snail *V. viviparus* (Mann-Whitney U-test, p<0.05). Concentration of phosphorus and heavy metals reached higher values in mollusc faeces compared to the level of these elements in bottom deposits (Fig. 18) (t test, p<0.05); mollusc faeces enrich bottom deposits with both phosphorus and heavy metals. As a result of bivalve biodeposition, a considerable part of suspension, with metals and phosphorus contained in it, is transferred from the water column to the bottom deposits. Phosphorus contained in bivalve biodeposits formed ca. 12% load of suspension fraction of the element introduced into the reservoir during the vegetation season; corresponding values for heavy metals were usually much higher (from over 15% for Mn to over 90% for Cu and Zn). Detritus-feeding snails participate

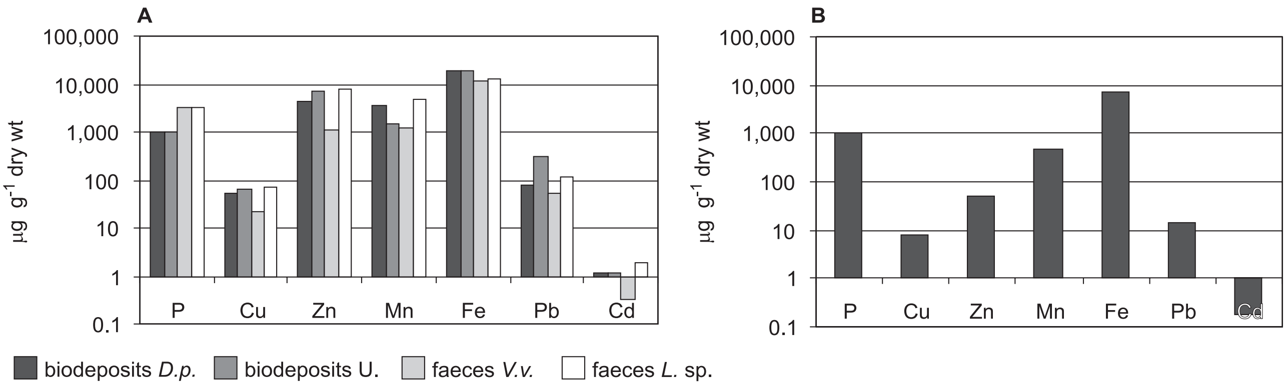

Fig. 18. Concentrations of the analysed elements in mollusc faeces (A) and bottom sediments (B); *D.p.* – *D. polymorpha*, U. – Unionidae, *V.v.* – *V. viviparus*, *L.* sp. – *Lymnaea* sp.

Table 18. Role of molluscs in accumulation and circulation of the studied elements in the Zegrzyński Reservoir ecosystem

	P	Cu	Zn	Mn	Fe	Pb	Cd
	mg m^{-2} season^{-1}						
Biodeposition:							
bivalves	600	30.9	250	1,800	7,810	29.6	0.336
gastropods	1,900	9.8	113	730	3,680	13.3	0.240
together	2,500	40.7	363	2,530	11,490	42.9	0.576
Filtration – bivalves	2,448	19.0	106.3	2,160	14,650	31.1	0.446
Consumption – gastropods	2,840	11.4	40.5	2,290	2,246	31.2	0.305
Load during season	21,197	649	2,389	11,548	240,069	1,200	3.26
Retention during season	1,927	212.4	229.5	1,599	7,275	104.8	0.47
Bottom sediments*	12,240	97.1	582	5,400	87,936	171.7	2.16
Accumulation:							
bivalves	335.3	0.97	3.3	27.3	71.4	0.4	0.003
gastropods	112.5	0.84	4.0	71.8	87.5	0.7	0.008
together	447.8	1.81	7.3	99.1	158.9	1.1	0.011

* – yearly layer of bottom sediments (1 cm, according to WIĘCKOWSKI 1969)

mainly in deposit processing, while consuming plant material results in a certain quantity of matter, contained in macrophytes and periphyton, being transferred to the detritus pool in bottom deposits.

The flow of phosphorus and heavy metals through malacocoenoses was many times higher compared to the quantity of these elements accumulated in mollusc tissues and shells (Table 18). This indicates a considerable effect of the malacofauna on cycling of the discussed elements in the reservoir ecosystem. The quantity of phosphorus cleared with suspension by bivalves during the vegetation season was many times (ca. 9 times) higher than its quantity accumulated in the animals. Corresponding differences for heavy metals were much greater (from ca. 20 to ca. 200 times), especially for Fe and non-essential metals (Pb and Cd). This indicates a more intense flow of metals, compared to phosphorus, through bivalve populations. Intense flow of the studied elements, compared to their accumulation values, was found also for snails. The quantities of phosphorus and heavy metals potentially taken up with food by the animals during the vegetation season were from over 10 to over 40 times higher than the quantities accumulated in tissues and shells (Table 18).

3.2. Phosphorus and heavy metals in short food chains

The studies focused on four short food chains with molluscs as one of the links:
periphyton – *V. viviparus* – *Rutilus rutilus* – *Esox lucius*;
macrophytes – *Lymnaea stagnalis* – *R. rutilus* – *E. lucius*;
floc – *D. polymorpha* – *R. rutilus* – *E. lucius*;
mollusc faeces – chironomid larvae – *R. rutilus* – *E. lucius*.

Food spectrum of molluscs is extensive, and particular species, especially snails, often utilise several different food sources. Periphyton and macrophytes were assumed as potential food of snails (*V. viviparus* and *Lymnaea* spp.), floc – as food of bivalves

(*D. polymorpha*). Besides, detritus as food for snails and *Anodonta* spp. as filtrationist were taken into account.

Phosphorus concentration in mollusc tissues was significantly higher than in their food or faeces (t test, p<0.05), only differences between the level of this element in snail tissues and snail faeces were insignificant. In the analysed food chains, the highest phosphorus concentration was found in the second link – molluscs and chironomid larvae (Fig. 19). Within the studied mollusc species (consumers I) there were significant differences in P concentration in tissues (see chapter 2.1), in spite of the lack of significant differences in P concentration in food in most cases (ANOVA, p>0.05). Relatively high phosphorus concentrations (contrary to heavy metals) were found at higher trophic levels (fish).

Concentration of the studied metals in potential food of molluscs varied, but in most cases the differences were statistically insignificant (ANOVA, p>0.05). The level of P in bivalve tissues was usually lower than or similar to that found in their potential food, only Mn and Fe concentration in *Anodonta* sp. was higher than in the floc (Table 19). Significantly lower concentration of Mn and Fe, and partly Pb and Cd (most differencs for Cd were insignificant) was noted also in snail tissues compared to their level in food, while Cu and Zn concentration (in case of *V. viviparus* – detritus) was higher than in the food.

Phosphorus concentration in mollusc faeces did not differ significantly from corresponding values in their potential food. The level of essential metals in the faeces was (in over half of the cases) higher than (t test, p<0.05) or similar to the concentration in potential food of molluscs which could be associated, among others, with a fairly weak assimilation of the studied metals and with selective uptake of food particles, especially suspension and detritus (fine particles contain more adsorbed metals). Lower metal concentrations in mollusc tissues, compared to the level in faeces (t test, p<0.05), may confirm poor assimilation of metals or a capability of regulation of their concentration in the organism.

Metal concentration in chironomid larvae was lower than in the mollusc faeces which constituted their potential food; statistically significant differences were noted for Zn, Mn, Fe, Pb and Cd (t test, p<0.05). The level of analysed metals in fish tissues (*R. rutilus*) was significantly lower than in molluscs and chironomid larvae (except the insignificant difference in Pb concentration between mollusc tissues and fish muscles).

Transfer of microelements, such as heavy metals, in food chains, differed from the fate of phosphorus.

Table 19. Significance of differences between phosphorus and heavy metal concentrations in consecutive links of the studied food chains (t-test); (p – probability level; ns – not significant). In the case of fish metal concentrations in muscles were compared

	p – values						
	P	Cu	Zn	Mn	Fe	Pb	Cd
Chain: detritus/periphyton – *Viviparus viviparus* – *Rutilus rutilus* – *Esox lucius*							
detritus – *V. viviparus*	0.003145	0.000000	0.000000	0.000000	0.000000	ns	0.000000
periphyton – *V. viviparus*	0.001074	0.000000	ns	0.000000	0.000000	0.000000	0.000000
V. viviparus – *R. rutilus*	ns	0.000000	0.000000	0.000000	0.000000	ns	0.000462
R. rutilus – *E. lucius*	ns	ns	ns	ns	ns	ns	0.042019
Chain: detritus/periphyton/macrophytes – *Lymnaea* sp. – *Rutilus rutilus*							
detritus – *Lymnaea* sp.	0.002102	0.002405	ns	0.000002	0.001291	ns	ns
periphyton – *Lymnaea* sp.	0.021541	ns	ns	0.001886	0.000000	0.000264	ns
macrophytes – *Lymnaea* sp.	0.000018	0.000287	0.000131	0.000002	0.000335	ns	0.000177
Lymnaea sp. – *R. rutilus*	ns	0.000001	0.000028	0.000000	0.000000	ns	0.000001
Chain: floc – *Dreissena polymorpha*/*Anodonta* sp. – *Rutilus rutilus*							
floc – *D. polymorpha*	0.000004	0.012927	ns	0.000000	0.000000	ns	ns
floc – *Anodonta* sp.	0.000017	0.018689	0.000000	0.000000	0.000000	ns	ns
D. polymorpha – *R. rutilus*	0.003920	0.000668	0.000000	0.000000	0.000000	ns	0.000000
Anodonta sp. – *R. rutilus*	0.000004	0.010431	0.000000	0.000000	0.000000	ns	0.000000
Chain: mollusc faeces – chironomid larvae – *Rutilus rutilus*							
faeces – Chironomidae	0.000689	ns	0.000000	0.000003	0.000015	0.007978	0.001499
Chironomidae – *R. rutilus*	0.000186	0.000002	0.011840	0.000014	0.000000	0.049228	0.000035

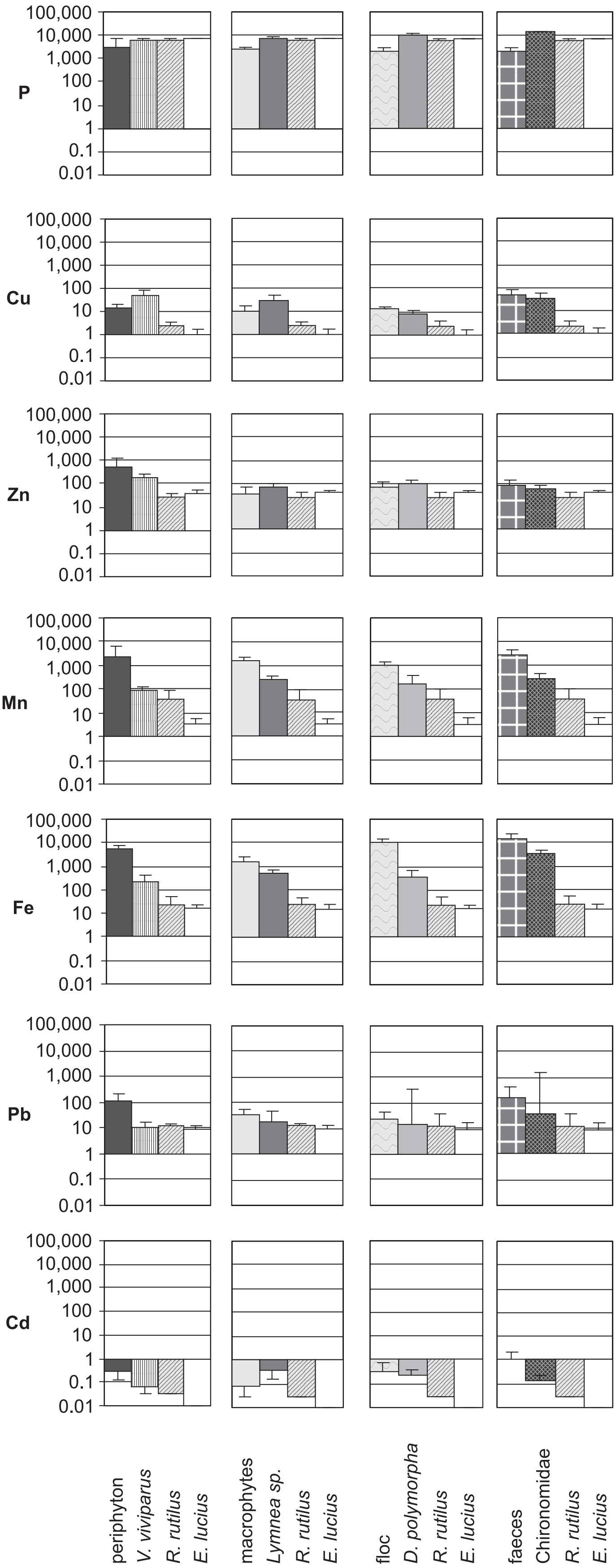

Fig. 19. Changes in concentrations of the analysed elements in consecutive links of four food chains including molluscs (data concerning heavy metal concentrations after JURKIEWICZ-KARNKOWSKA 2001c, modified and supplemented)

Generally, there was a decrease in concentration of heavy metals at higher levels of the food chains (fish). Differences between the level of these elements in particular links of the food chains were mostly statistically significant (Table 19), only comparison of metal concentration in tissues of zoobenthos-feeding fish and predatory fish showed no significant differences except Cd – its content in the tissues of predatory fish was higher (but because of the low concentrations of the element, the measurements were burdened with a relatively great error).

DISCUSSION

1. MALACOCOENOSES OF LOWLAND DAM RESERVOIRS – OCCURRENCE, TEMPORAL AND SPATIAL CHANGES

1.1. Significance of molluscs in the structure of bottom macrofauna

In many lowland dam reservoirs, molluscs may constitute a significant component of bottom macrofauna. The proportion of these animals in the total abundance of macrobenthos of the Zegrzyński, Koronowo and Włocławek Reservoirs was generally of an order of a few per cent (in the last reservoir in the second half of the 1980s on an average about a dozen per cent) (GIZIŃSKI & WOLNOMIEJSKI 1966, DUSOGE et al. 1990, 1999, JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press), in the Rybinsk and Siemianówka Reservoirs temporarily even higher (up to a few dozen per cent), however benthos of these reservoirs was quantitatively poor, especially in the last case (SHCHERBINA 1998, and own, unpublished data). A much greater proportion of molluscs was noted in the total benthos biomass, often of an order of a few dozen per cent or even over 90%, when large molluscs dominated (e.g. SOKOLOVA 1959, TSEEB & DENISOVA 1973, DUSOGE et al. 1990, 1999, SHCHERBINA 1998). In some Volga reservoirs authors reporting biomass disregarded large molluscs, and then the proportion of molluscs was lower. In the Włocławek Reservoir, in spite of the dominance of relatively small molluscs (*Sphaerium corneum*) in its malacocoenoses, their proportion in the benthos biomass was often of an order of a few dozen per cent (JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press). It can be supposed that the proportion of molluscs in the total biomass of the Sulejów Reservoir benthos is also high, especially because of abundant occurrence of *D. polymorpha* (ABRASZEWSKA-KOWALCZYK et al. 1999, JURKIEWICZ-KARNKOWSKA 2002a). In such cases, considering the zebra mussel biomass, the proportion of molluscs in the total biomass of benthos increases from a few or a few dozen per cent to over 90% (e.g. TIMM et al. 1996). Excluding biomass of large molluscs when analysing dominance structure may be justified because of great differences in the biomass of individuals of such species and representatives of other zoobenthos components, but it should be considered in studies on the role of molluscs in the functioning of ecosystems.

1.2. Qualitative occurrence of molluscs

The malacofauna of the studied reservoirs was relatively species-rich, like in an array of other dam reservoirs of the temperate zone: e.g. Gorky, Rybinsk (MITROPOLSKIY & BISEROV 1982, PEROVA 1998, SHCHERBINA 1998, 2000), Ivankovo (BUTORIN 1978b, ABAKUMOV et al. 2000), Uchinsk (SOKOLOVA 1959, SOKOLOVA et al. 1980), Kuybyshev (BUTORIN 1978a), Goczałkowice (KRZYŻANEK 1970, 1976, 1994, KRZYŻANEK et al. 1986, KRZYŻANEK & KASZA 1995), and Koronowo (GIZIŃSKI & WOLNOMIEJSKI 1966, 1982).

Low frequency of occurrence of individual mollusc species is characteristic not only of the initial succession stages, when the organisms have not managed to spread on the flooded land. It may also be favoured by instability of habitats, e.g. uncovering of large bottom fragments for a longer period. This is the case in the Siemianówka Reservoir (especially since 2000), the situation is common in the Volga (GERASIMOV & PODDUBNYI 1999) and Dnepr reservoirs (ZIMBALEVSKAYA et al. 1984). In the period of rapid development of malacocoenoses many species may reach rather high frequencies (e.g. JURKIEWICZ-KARNKOWSKA 1998a, GRUŻEWSKI 2000), while in older ecosystems of dam reservoirs, in conditions of increasing habitat homogeneity (bottom deposits) and high trophy, the number of species of higher frequency is low (1–4), but %F values in such cases are much higher than in the earlier period (e.g. JURKIEWICZ-KARNKOWSKA 1998a, 2001a, PEROVA & SHCHERBINA 1998). Usually species of higher frequency are also dominants or subdominants in the malacocoenoses.

1.3. Dominance structure of malacoenoses

In many lowland dam reservoirs, at least during some periods, small sphaeriid bivalves form a considerable proportion of the malacofauna, e.g. in many reservoirs on the Volga and Dnepr (MORDUKHAY-BOLTOVSKOY 1961, PODDUBNAYA 1966, BUTORIN 1978a, MITROPOLSKIY & BISEROV 1982, BORODICH & LYAKHOV 1983), in the Zegrzyński (JURKIEWICZ-KARNKOWSKA 1989a, GRUŻEWSKI 2000) and Goczałkowice Reservoirs (KRZYŻANEK 1970, 1973, 1976). At later stages of succession, they are most often replaced by large bivalves – *D. polymorpha*, e.g. in the reservoirs Kuybyshev (BORODICH & LYAKHOV 1983), Rybinsk (MITROPOLSKIY & LUFEROV 1966, PEROVA & SHCHERBINA 1998), Zegrzyński and Sulejów (JURKIEWICZ-KARNKOWSKA 1998a, 2001a, 2002a), or unionids, e.g. in the Goczałkowice Reservoir (KRZYŻANEK 1976, 1994), but in some cases the sphaeriid dominance persists for a long time of biocoenosis stabilisation, e.g. in the Włocławek Reservoir (JURKIEWICZ-KARNKOWSKA & ŻBIKOWSKI in press). *D. polymorpha* is often dominant in malacocoenoses of lowland dam reservoirs of the temperate zone, in many cases already at early stages (during the first few years) of their development it plays a considerable part, e.g. in the reservoirs Uchinsk (SOKOLOVA 1959), Gorky, Saratov, Volgograd (BUTORIN 1978a), Kiev (GAK et al. 1972, TSEEB & DENISOVA 1973), Koronowo (WOLNOMIEJSKI & GIZIŃSKI 1976, GIZIŃSKI & WOLNOMIEJSKI 1982).

Among snails, prosobranchs, e.g. *V. viviparus* (JURKIEWICZ-KARNKOWSKA 1989a, 1998a, 2001a, LEWANDOWSKI et al. 1989, LEVINA 1993), or *Valvata* spp. (e.g. PEROVA & SHCHERBINA 2001) may play an important part in the dominance structure of the malacofauna. High proportion of fluviatile species, e.g. *Lithoglyphus naticoides* or *Theodoxus fluviatilis* was also observed in habitats closely associated with the former river bed, especially at early stages of reservoir development or following rejuvenation of biocoenosis as a result of particularly great flows (e.g. GAK et al. 1972, TSEEB & DENISOVA 1973, JURKIEWICZ-KARNKOWSKA 1986, 1989a, GRUŻEWSKI 2000). Pulmonate snails play a certain part in shallow habitats, especially in the littoral zone. At the beginning of succession in flooded land areas they are pioneer species, especially lymnaeids (e.g. ZAĆWILICHOWSKA 1965a, b, PATERSON & FERNANDO 1969, KRZYŻANEK 1970, GIZIŃSKI & WOLNOMIEJSKI 1966). They dominate also in habitats with unstable physical conditions, e.g. when large areas of bottom are exposed for a longer period (e.g. GIZIŃSKI & WOLNOMIEJSKI 1982). In the Siemianówka Reservoir in 2001–2002 the proportion of *Lymnaea* spp. increased when the water level significantly decreased during a greater part of the vegetation season (own, unpublished data).

Generally, with progressing succession the dominance structure, after a period of rapid development, becomes simplified, with a pronounced dominance of single species which already in the period preceding stabilisation played an important part in the dominance structure of the malacocoenoses.

1.4. Density and biomass

The malacofauna of the Zegrzyński and Sulejów Reservoirs shows a fairly high abundance, compared to molluscs of other lowland dam reservoirs and also lakes. Comparable abundance and biomass of molluscs were noted e.g. in the Włocławek (GIZIŃSKI et al. 1989) and Koronowo (GIZIŃSKI & WOLNOMIEJSKI 1982) Reservoirs, and in the Goczałkowice Reservoir during a period of intense development of unionids (KRZYŻANEK 1976, 1977, 1986), as well as in an array of Volga and Dnepr reservoirs (SOKOLOVA 1959, BUTORIN 1978a, TSEEB & DENISOVA 1973, SHCHERBINA 1998). The Siemianówka Reservoir harbours a qualitatively poor malacofauna and generally poor macrobenthos (own, unpublished data) which results from its environmental specificity, associated with numerous limiting factors (JURKIEWICZ-KARNKOWSKA 1999a). A similar poverty has been observed e.g. in parts of some large dam reservoirs of sandy bottom, subject to strong wave action (e.g. BUTORIN 1978a, SOKOLOVA 1988) or with peat bottom (e.g. PODDUBNAYA 1988) and in reservoirs of high humus content in the water (e.g. SOROKIN 1972, ARMITAGE 1977).

1.5. Changes in malacocoenoses on the background of macrozoobenthos succession

Many studies on the bottom macrofauna report incomplete information on the occurrence of molluscs; it often pertains only to species of small size while large molluscs, even those reaching high abundance, are disregarded. However, in many cases estimates of quantitative occurrence of all molluscs, even based on fragmentary literature data, indicate high values, comparable to those for the reservoirs described in this paper and other water bodies with a high mollusc abundance. Malacofauna of lowland reservoirs may be richer compared to lakes of a similar trophic level, because of a positive effect of moderate flow (more favourable oxygen conditions). Data on quantitative occurrence of molluscs and its temporal and spatial variation may be important for the estimate of the role of these animals in the functioning of the reservoir ecosystem.

Generally, malacofauna of lowland dam reservoirs undergoes changes similar to those experienced by the whole bottom macrofauna. When the trophic level is low, at first stages of the reservoir's existence the increase in mollusc abundance is less obvious than that of soft benthos which develops faster, utilising increased food resources which result from decomposition of flooded terrestrial vegetation. In such reservoirs, a clear increase in mollusc abundance was observed after 10 years or later, e.g. sphaeriids in the Ivankovo Reservoir (BUTORIN 1978b) or unionids in the Goczałkowice Reservoir (KRZYŻANEK 1994). The ecosystem development is quicker when the river feeding the reservoir is large, and the proportion of the river bed in the reservoir's total area is considerable. The effect of the river on the processes that take place in the reservoir may also be associated with the water quality, and especially its trophy. A moderate trophy of the reservoir favours qualitative and quantitative richness of the malacofauna, while excessive fertility of the water causes a decrease in species diversity (e.g. species of the genus *Pisidium* recede), and then mollusc abundance and mollusc proportion in the macrobenthos structure decrease. At that time abundance of soft macrobenthos remains at a high level. Improvement in water quality causes increase in species diversity and abundance of molluscs, while abundance of soft benthos decreases. More sphaeriids appear (e.g. PEROVA 1998, JURKIEWICZ-KARNKOWSKA 2001a). Rejuvenation of biocoenoses resulting e.g. from sudden changes in hydrological regime or exposure of large areas of the bottom for longer periods and then flooding them again, is marked in the case of malacocoenoses. On bottom areas re-flooded after a longer period of exposure, pioneer species appear (often in great numbers), such as e.g. lymnaeids in the Koronowo (e.g. GIZIŃSKI & WOLNOMIEJSKI 1982) and Siemianówka Reservoirs (own, unpublished data). After the 1980 flood and next year, exceptionally high mollusc species richness was observed in the Zegrzyński Reservoir (JURKIEWICZ-KARNKOWSKA 1986, 1989a). The fauna included rheophilic species, and some reached high densities, e.g. *Lithoglyphus naticoides*, *Theodoxus fluviatilis* or *Sphaerium solidum*. The species were found in many habitats, including some of slow flow or stagnant.

Lowland dam reservoirs, shallow, extensive and rather varied with respect to habitats, may favour development of malacofauna, but these possibilities are to a large extent modified by the complex of factors characteristic for a given water body; this is confirmed by the situation in the studied reservoirs.

The Zegrzyński Reservoir harbours a rich and diverse malacofauna. The direction of development of its malacocoenoses seems to depend mainly on the trophic level and changes associated with the ageing of the ecosystem (kind and thickness of bottom deposits, their increased homogeneity) and stabilisation of biocoenoses, but great disturbances of hydrological regime may change it, resulting in a reversal to earlier succession stages (JURKIEWICZ-KARNKOWSKA 1998a, 2001a). A limiting effect on the species composition and abundance of molluscs was exerted by excessive eutrophication and consequent deterioration of environment quality (among others periodical oxygen deficits above the bottom, receding of submerged macrophytes); the results were visible in the first half of the 1990s, while the decrease in the trophic level in subsequent years seems to be the main reason for a certain increase in the richness and species diversity of molluscs, though the number of species was still lower than in the 1980s. The abundant occurrence of *D. polymorpha*, and to a lesser extent *V. viviparus*, also seems to limit the mollusc species richness.

The malacofauna of the Sulejów Reservoir is also rather rich, but poorer in species compared to the Zegrzyński Reservoir. Important factors for the development of mollusc communities in this reservoir are, among others, the kind of bottom deposits, wave action, changes in water level over considerable areas, and also the limiting effect of the zebra mussel on the occurrence of an array of species, especially filtrationists (JURKIEWICZ-KARNKOWSKA 2002a).

The mollusc density and biomass in the Siemianówka Reservoir are low in spite of the high trophy level; the situation results probably from many limiting factors. The kind of bottom deposits (poorly advanced development of proper deposits in flooded areas and loose, muddy deposits within the river bed) and their constant resuspension over large areas, as well as instability resulting from small depths and strong wave action, seem to be the most important among them. High humus content in the water and deposits, limited availability of calcium ions, poor development of macrophytes and algal blooms may also affect mollusc abundance (JURKIEWICZ-KARNKOWSKA 1999a). A considerable species richness and at the same time a highly random character of the occurrence of molluscs in the reservoir may be associated on the one hand with habitat diversity of the reservoir and the presence of numerous small water bodies and courses (especially on polders) which may be sources of colonisers, on the other – instability of the habitats in the reservoir, especially in the littoral where large areas are often exposed and dried during decreased water level.

1.6. Effect of *D. polymorpha* on other molluscs and the whole macrozoobenthos

Invasion of *D. polymorpha* may cause an array of structural and functional changes in freshwater ecosystems. Especially clear effects of its invasion were observed in lakes and rivers of N America, where the zebra mussel reached very high abundance. They included, among others, changes in trophic structure, in pathways of energy flow in the system, increased water transparency and changes in its chemistry, as well as decrease in chlorophyll concentration resulting from decreased phytoplankton density, changes in the structure of bacterio-, phyto- and zooplankton, increased abundance of bottom algae and changes in their communities, macrophyte development, and also some changes in fish and bottom macrofauna communities (among others GRIFFITHS 1993, HOLLAND et al. 1995, JOHENGEN et al. 1995, LOWE & PILLSBURY 1995, NALEPA et al. 1996, KURBATOVA 1998, STEVART et al. 1998, JOHANSSON et al. 2000, IDRISI et al. 2001, MAYER et al. 2001).

Generally, *D. polymorpha* was observed to have a positive effect on bottom invertebrates, especially soft benthos, which was expressed as increased abundance and in some cases also species richness (DERMOTT et al. 1993, GRIFFITHS 1993, STEWART & HAYNES 1994, PEROVA & SHCHERBINA 1998, STEWART et al. 1998, 1999, HORVATH et al. 1999, GONZÁLEZ & DOWNING 1999, BIALLY & MACISAAC 2000, GREENWOOD et al. 2001, COBB & WATZIN 2002). According to the authors just named, the positive effect of the zebra mussel could result from creating new microhabitats – bivalve colonies – providing substratum, shelter and food (faeces and pseudofaeces, mussel-covering algae, detritus accumulated in spaces between shells). The increase in abundance and species richness of the bottom macrofauna in the presence of *D. polymorpha* was observed both in habitats of hard bottom (e.g. HORVATH et al. 1999) and soft bottom (e.g. BIALLY & MACISAAC 2000). Less often negative effects were noted, on the soft benthos, especially filter-feeders or species utilising freshly settled detritus (e.g. NALEPA et al. 1998, STRAYER & SMITH 2001).

The effect of *D. polymorpha* on other molluscs is less clear. In the case of other bivalve species it is, as a rule, negative. Especially much attention was paid to disappearance of large unionid bivalves in the waters of N America, where densities of the zebra mussel were extremely high. In many lakes and river systems an array of unionid species were observed to recede rapidly, their density decreased and their communities changed (GILLIS & MACKIE 1994, NALEPA 1994, HAAG et al. 1993, HOWELL et al. 1996, NALEPA et al. 1996, RICCIARDI et al. 1996, 1998, SCHLOESSER 1998, MARTEL et al. 2001). Usually the process continued for only a few years (4–8), and the main mechanism of depleting populations of the native bivalves was the zebra mussel attaching to their shells, thus disturbing functioning, causing stress, starvation symptoms and energy losses (e.g. RICCIARDI et al. 1996, BAKER & HORNBACH 1997, HALLAC & MARSDEN 2000). As demonstrated by TOCHYLOWSKI's et al. (1999) study, settling of *D. polymorpha* on unionid shells is not associated with any particular preference, and in habitats with much hard substratum densities of the zebra mussel on large bivalve shells and on other substrata are similar. LEWANDOWSKI (1976) observed a certain preference of the zebra mussel for live unionids and conspecific colonies in experimental conditions. The mortality of unionids depends on the intensity of overgrowing with the zebra mussel. RICCIARDI et al. (1995) reported an over 90% mortality of unionids with more than 100 individuals of *Dreissena* attached to their shells. KHARCHENKO & ZORINA-SAKHAROVA (2000) found that unionids could survive when the mass of attached zebra mussels did not exceed their individual mass, and the number of zebra mussels per individual unionid ranged from 100 to 160; comparable values follow from observations of LEWANDOWSKI (1976). Mortality of unionids depends also on the biology of the species, and especially its shell morphology (e.g. HAAG et al. 1993, NALEPA 1994), species of very delicate shells are the first to recede. This leads to changes in the community composition. Most European unionids have rather massive shells, while shells of many of the several dozen of N American species are very delicate. ABRASZEWSKA-KOWALCZYK (2002) showed a negative effect of the zebra mussel on the growth and body size of unionids from the Sulejów Reservoir, even when the coverage of their shells by the mussel was lower than critical values reported in the literature. In conditions of moderate overgrowing of unionids by *D. polymorpha* KHARCHENKO & ZORINA-SAKHAROVA (2000) observed a symbiotic relation (commensalism) between these bivalves, which made it possible for the zebra mussel to expand to areas of temporarily exposed shallows. It was possible due to migration, with unionids which constituted the substratum, from temporarily dry habitats to deeper places, and back again to the shallows when the water level increased.

It appears that also small sphaeriid bivalves can be affected by *D. polymorpha*. It was observed, among others, by SHCHERBINA (2001) based on experiments; also results of other authors (e.g. HOWELL et al. 1996, DERMOTT & KEREC 1997, PEROVA & SHCHERBINA 1998, STRAYER & SMITH 2001) indirectly point to competition. In lake Michigan, LAUER & MCCORNISH (2001) observed overgrowing of sphaeriids by the zebra mussel, and a drastic decrease in sphaeriid density within a few years.

Some studies show a positive effect of *D. polymorpha* on the occurrence of snails (e.g. STEWART et al. 1998, 1999, GREENWOOD et al. 2001), among others through improvement of food and habitat conditions. Results of other authors indicate a limiting effect of the zebra mussel, associated with e.g. competition for space or overgrowing snail shells by the bivalve (e.g. DUSOGE 1966, GIZIŃSKI & WOLNOMIEJSKI 1982, TUCKER 1994, WISENDEN & BAILEY 1995, HOWELL et al. 1996, RICCIARDI et al. 1997, GREENWOOD et al. 2001).

In the Sulejów Reservoir only negative correlations between the abundant *D. polymorpha* and the abundance of the remaining bivalves, and also the prosobranch snail *Valvata piscinalis*, were noted; they might suggest competition. No such dependence was found for pulmonate snails (JURKIEWICZ-KARNKOWSKA 2002a).

Some studies suggest a possibility of negative influence of other mollusc species, e.g. invasive *Potamopyrgus antipodarum* (Gray), on malacocoenoses (KRODKIEWSKA et al. 1998, STRZELEC 1992, 2000), contributing to disappearance of native snail species. STAŃCZYKOWSKA (1963) observed, in the Vistula shoal Konfederatka, migration of large molluscs (unionids, *Lymnaea* spp., *Planorbarius corneus*) from the bottom, where dense aggregations of *V. viviparus* were formed, which might indicate a competition for space. In this study the limiting effect of *V. viviparus* on other molluscs was observed only to a small extent and pertained mainly to the number of species, but was not visible in the case of abundance.

2. SELECTED ASPECTS OF MOLLUSC EFFECT ON THE FUNCTIONING OF THE RESERVOIR ECOSYSTEM

2.1. Filtration activity of molluscs

2.1.1. Conditions and consequencies

Malacocoenoses of dam reservoirs are dominated by filter-feeding species. The main filtrationists are bivalves; some prosobranch snails may also use this feeding mode but its proportion in meeting the energy requirements of these organisms is little known. Filtration rate and efficiency, as well as the quantity of produced faeces and pseudofaeces, depend on many factors, associated with the environment, the size of the organisms, species-specific factors, population density and age structure.

Generally, the clearance rate increases with individual size (e.g. ALIMOV 1965, HINZ & SCHEIL 1972, LEI et al. 1996, YOUNG et al. 1996, HÖCKELMANN & PUSCH 2000), but when it is converted to unit gill area, the resulting values are rather constant within species (LEI et al. 1996).

One of important external factors affecting filtration activity is temperature. For freshwater bivalves of the temperate zone the range of temperatures permitting filtration is 5–30°C, but optimum values reported by various authors are within a much narrower range (MIKHEYEV 1966a, b, MORTON 1971, STAŃCZYKOWSKA et al. 1976, WALZ 1978, ALIMOV 1981, REEDERS et al. 1989, FANSLOW et al. 1995, LEI et al. 1996).

Mollusc filtration activity depends on many qualitative and quantitative properties of suspension – its concentration in water, proportion of inorganic particles, size structure, quality of particulate organic matter, species composition of plankton (especially dominant species). Filtration rate is the highest in conditions of low concentration of suspension and decreases clearly with increasing quantity of seston in the water, after values close to natural have been exceeded (CIKHON-LUKANINA 1961a, b, ALIMOV & BULON 1972, FOSTER-SMITH 1975, WALZ 1978, ALIMOV 1981, SPRUNG & ROSE 1988, REEDERS & BIJ DE VAATE 1990, FANSLOW et al. 1995, HÖCKELMANN & PUSCH 2000). In spite of the decrease in the volume of water filtered per unit time, the quantity of cleared suspension, and also its unassimilated fraction, increases. The excess of filtered suspension is removed as pseudofaeces. Values of suspension concentration above which bivalves produce pseudofaeces, reported in the literature, vary from a few to 10 mg dm^{-3} (WALZ 1978, STAŃCZYKOWSKA & PLANTER 1985, MADON et al. 1998) or 17–27 mg dm^{-3} (HORNBACH 1984, LEI et al. 1996, YU & CULVER 1999). In conditions of high water turbidity pseudofaeces may constitute a very large proportion, even 90% filtered suspension (REEDERS & BIJ DE VAATE 1992, MACISAAC & ROCHA 1995, MADON et al. 1998).

Limiting filtration and production of large quantities of pseudofaeces make it possible to regulate consumption in conditions of high suspension level. Mechanisms of this regulation vary with suspension composition. When proportion of inorganic particles in the seston is high, a high rate of filtration is maintained and at the same time large quantities of pseudofaeces are produced (KRYGER & RIISGARD 1988, WIŚNIEWSKI 1990, REEDERS & BIJ DE VAATE 1992, MACISAAC & ROCHA 1995, KLERKS et al. 1996, RODITI et al. 1996, YU & CULVER 1999), which results from the necessity of uptake of an adequate quantity of food. An alternative mechanism is selective uptake of particles which is of more advantage in habitats with constant, high proportion of bottom deposits (mineral fraction of seston) in the suspension (PAYNE et al. 1995). Limited filtration and increased production of pseudofaeces are very good strategies in habitats where the increased content of deposits in the water is only temporary (FOSTER-SMITH 1975, REEDERS & BIJ DE VAATE 1990). In conditions of high content of organic matter in the suspension, regulation of cunsumption is effected mainly due to limited filtration (WALZ 1978, SPRUNG & ROSE 1988, REEDERS et al. 1989).

At a given suspension concentration, filtration rate may depend on particle size (e.g. MIKHEYEV 1967, ALIMOV 1981, TEN WINKEL & DAVIDS 1982, LEI et al. 1996, RODITI et al. 1996, HORGAN & MILLS 1997, WELKER & WALZ 1998). An effect of food quality on filtration rate, consumption and assimilation was also observed (STAŃCZYKOWSKA et al. 1975, BIRGER et al.1978, DORGELO 1993, GARDNER et al. 1995).

Hydrodynamic conditions are also a very important, though rarely analysed factor; they affect both rate and efficiency of filtration, as well as growth and development of filter-feeding molluscs. Studies in inland rivers showed that relatively small flow velocity (below 10 m s^{-1}) caused increase in the quantity of cleared suspension, while greater flow had an inhibitory effect (for review see ACKERMAN 1999). Strong mixing causing increased resuspension has a limiting effect on filtration (ALDRIDGE et al. 1987, WIŚNIEWSKI 1990, MADON et al. 1998). SCHAFER's (1953) studies indicate that the prosobranch *V. viviparus* filters at a flow speed of 3 m s^{-1}. The favourable effect of slight water flow consists in mixing, due to which food resources are replenished in the thin layer of water (a few cm) above the bottom which is available to bivalves and filtrationist snails. As a result of filtration activity within this layer food deficits occur, causing intensified filtration of water already filtered by other individuals (FRECHETTE et al. 1989, MONISMITH et al. 1990, O'RIORDAN et al. 1995). In such situations the actual effect of filtration on suspension concentration in the water column may be considerably smaller than that suggested by calculations based on the reservoir volume and quantity of suspension cleared by organisms from unit bottom area (calculated as product of volume of bivalve-filtered water and suspension concentration in the water). Such an estimate is the most exact in shallow, well mixed habitats, while it may considerably depart from the actual values in poorly mixed waters, especially at high densities of bottom filtrationists and increased food competition. YU & CULVER (1999) introduced the so called effective clearance rate (ECR) which makes it possible to eliminate the error resulting from water refiltration.

2.1.2. Filtration activity of molluscs in the Zegrzyński Reservoir

In the Zegrzyński Reservoir suspension concentration, especially during the vegetation season, remains at a rather high level which is characteristic of eutrophic waters, however, except some (short) periods and some parts of the reservoir (especially the part under the effect of the Bug waters), these values should not have a limitng effect on filtration. Seston concentrations in the Włocławek Reservoir (16.8–30 mg dm^{-3}) did not limit filtration activity of *D. polymorpha* (WIŚNIEWSKI 1990). Suspension of the Zegrzyński Reservoir contains a large proportion of organic matter (own, unpublished data) which, in the light of the earlier considerations, should rather favour the mechanism of regulation of the quantity of cleared suspension through limited filtration, instead of increased production of pseudofaeces. During strong winds which cause deposit resuspension over large areas of the reservoir bottom, bivalves could be expected to produce more pseudofaeces. Flow velocity in the littoral and stagnant zones of the reservoir ranges from 1 to a few cm s^{-1}, and in parts closer to the current it is even higher by an order of magnitude (JURKIEWICZ-KARNKOWSKA 1986); it is generally within the range of values which is favourable for bivalves (ACKERMAN 1999), favouring inflow of new supplies of seston and oxygen from higher water layers to the thin boundary layer over the filtering animals. Assuming filtration values from the literature (i.e. water volume filtered in unit time), for bivalves living in the Zegrzyński Reservoir, the effect of the above factors on filtration was considered, as well as methods applied by different authors to estimate its values. In the case of *D. polymorpha* for which there are many literature data, results of studies conducted in natural or close to natural conditions were taken into account. The reported values vary widely (Table 3). It was assumed that water refiltration in conditions of the Zegrzyński Reservoir is rather small, and trophic conditions good, which is indirectly supported by the good fitness of *D. polymorpha* (DUSOGE et al. 1990). Thus the assumed filtration values were close to the so called effective values (ECR, according to YU & CULVER 1999). Clearance rate in *V. viviparus* may reach 140 ml per hour for large specimens (SCHAFER 1953, HÖCKELMANN & PUSCH 2000). As shown by HÖCKELMANN & PUSCH (2000) in their studies on *V. viviparus* from the Spree River, in summer, at suspension concentration of 7 to 15 mg dm^{-3}, at least large specimens can balance their energy expenditure through filter-feeding. The proportion of filter feeding in the total consumption by the snails in the Zegrzyński Reservoir is not known, but calculations based on filtration rate data (HÖCKELMANN & PUSCH 2000) and the mean concentration of suspension in the reservoir indicate that filter-feeding could completely meet the energy requirements (reported by many authors). SCHAFER (1953) found that *Bithynia tentaculata* could completely satisfy its energy requirements through filtration when suspension content is ca. 20 mg dm^{-3}.

A great effect of bivalve filtration activity in lotic conditions was found e.g. in the Spree River below the productive lake Neuendorfer (WELKER & WALZ 1998), in the Hudson River estuary (RODITI et al. 1996) and canalised section of the Mosel River (BACHMANN & USSEGLIO-POLATERA 1999). Filtration potential of unionids, which are rather abundant in the Goczałkowice Reservoir (KRZYŻANEK 1989), was many times smaller than this of bivalves from the Zegrzyński Reservoir. Volume of water filtered by *D. polymorpha* in one to a few days in many lakes, especially N American, equalled the volume of these water bodies (HEBERT et al. 1991, MACISAAC et al. 1992, KLERKS et al. 1996). A lower filtration potential of these bivalves was reported from European lakes, which is associated with the lower density (STAŃCZYKOWSKA 1968, LEWANDOWSKI & STAŃCZYKOWSKA 1975, STAŃCZYKOWSKA et al. 1975, KASPRZAK 1986, REEDERS et al. 1989).

It can be supposed that water, contributed during the vegetation season by the rivers feeding the Zegrzyński Reservoir, could be mostly filtered by molluscs, especially assuming that *V. viviparus* at least partly utilises this way of feeding. Filtration efficiency, however, may vary depending, among others, on the rate of water exchange in the habitat and on mollusc density. It should be stressed that the flow (Q) of the main rivers feeding the reservoir, and the water exchange rate, are generally much lower in the vegetation season, compared to the remaining months (water budget of the Zegrzyński Reservoir in 1998/1999 – Regional Water Management, Dębe, JURKIEWICZ-KARNKOWSKA 2001b). It appears that molluscs could significantly control suspension content in water during the vegetation season, but a high increase in seston concentration in some periods (up to ca. 40 mg dry weight dm^{-3} and more, like e.g. in June/July 1999) may have a limiting effect on their filtration activity. REEDERS & BIJ DE VAATE (1990) found that to stop the process of phytoplankton increment in lake Wolderwijd in summer, filtration of its whole volume every three days would be enough. According to estimates, molluscs of the Zegrzyński Reservoir can filter its volume during ca. 5 days. It seems that, considering sedimentation of a large part of phytoplankton introduced by the rivers (BUBIEŃ 1989, SIMM 1990), the possibility of control of its part that remains in the water column by filtrationists, including molluscs, should be considerable.

The above considerations and chapter 1.2 suggest that the balance between the reservoir's food resources and mollusc abundance has been adjusted to changes in the dominance structure of malacocoenoses which are associated with recession of many sphaeriid species and spreading of *D. polymorpha.* A certain decrease in the reservoir trophy is also observed (TP concentration, suspension) which may limit quantitative increase of filtrationists. In the second half of the 1980s the malacofauna was more abundant compared to the present situation, but the suspension load (and load introduced by the rivers) was also higher (DUSOGE et al. 1990, 1999, KAJAK 1990, 1991). At that time the proportion of the most active filtrationist – *D. polymorpha* – among bivalves was less pronounced, probably the effect of some bivalves on suspension concentration was smaller, and due to this maintaining a higher biomass of less efficient filtrationists was possible. Perhaps *V. viviparus* at least partly utilised suspension, and certainly freshly sedimented fine detritus, which would be indicated by high densities of the species and the condition of the specimens (LEWANDOWSKI et al. 1989, JAKUBIK 1998) in the upper part of the reservoir where there is an intense seston sedimentation (SIMM 1990).

With cleared suspension, among others, nutrients and heavy metals are removed from water. Analyses in this paper are consitent with the results obtained by other authors (e.g. REEDERS & BIJ DE VAATE 1992, REEDERS et al. 1993, LA VALLE et al. 1999) indicating that bivalve biodeposits contain more toxic substances than the suspension, which might be associated, among others, with clearing relatively fine and more polluted organic particles. The considerable load of metals in bivalve faeces may also result from uptake of certain quantities of these elements directly from water, in their ionic form (BAUDO 1985), and also poor assimilation. Different metals are to a different degree assimilated from food by consumers, e.g. Pb and Cd are poorer assimilated than Fe, Cu, Mn and Zn (BURRELL 1974 after BAUDO 1985, REINFELDER & FISHER 1994).

The quantity of phosphorus that could be cleared by bivalves during the season in the Zegrzyński Reservoir was probably a part of a phorphorus pool contained in the ecosystem, of a similar size as that for *D. polymorpha* in Lake Mikołajskie (STAŃCZYKOWSKA & LEWANDOWSKI 1993). In relation to P contained in 1 cm (annual) layer of bottom deposits of the Zegrzyński Reservoir, the quantity of this nutrient cleared by bivalves during the season was of an order of 10%. Quantities of metals cleared by bivalves, compared to the quantity of these elements contained in 1 cm deposit layer, were much higher, which may indicate a great effect of filtration activity of bivalves on sedimentation of heavy metals compared to phosphorus.

Suspended fraction of metals studied here forms a high proportion of their total pool in the water (WOJTKOWSKA 1997, 2000); for this reason both natural sedimentation and its acceleration as a result of mollusc filtration activity may cause a fairly intense flow of heavy metals and phosphorus from water column to bottom deposits. Filtration activity of bivalves is conducive to a shift of dynamic equilibrium between element deposition and release towards deposition in bottom sediments. Increase in deposition of heavy metals during the vegetation season increases the chances of their transfer to detritus food chains. Return of P and heavy metals to the water column, as a result of deposit resuspension, is also possible, especially with strong resuspension in shallow habitats, or release of ionic forms during decomposition of organic matter on the bottom, oxidation of sulphides and desorption during oxygen deficits above the bottom and in superficial layers of deposits (especially P), which may occur periodically in the reservoir (KAJAK 1991). Release of phorphorus from bottom deposits is rather intense (KAJAK 1991), while return of ionic forms of metals to the reservoir water is fairly limited because of high proportion of more durable fractions (WOJTKOWSKA 1997, 2000) and generally low intensity of metal release from deposits in both aerobic and anaerobic conditions (CHAPMAN et al. 1998). Poor internal feeding of the Goczałkowice Reservoir by interstitial waters was observed, for copper, by WIECHUŁA et al. (1997), though mixing of bottom deposits increased the intensity of the process. Small possibilities of mobilisation of ionic forms of metals from bottom deposits were also shown in studies on the Meuse River (VAN DEN BERG et al. 1999). On the other hand, experiments of RODITI et al. (1997) indicate that biodeposits of *D. polymorpha* are more liable to resuspension compared to bottom deposits. This may cause their decomposition in the water column and release of ionic forms. Bottom deposit resuspension increases not only as a result of stronger mixing of water, but also due to increased deposit erosion by burrowing organisms, including freshwater molluscs, especially unionid and sphaeriid bivalves (e.g. CHAPMAN et al. 1998, VAUGHN & HAKENKAMP 2001). WILLOWS et al. (1998) demonstrated that a population of a rather small marine bivalve *Macoma balthica* living in a tidal zone contributed to increase in resuspension by 420 g m^{-2} per tide. Bioturbation, especially in case of depositivores, concentrates mainly in the topmost 10 cm layer of bottom deposits (e.g. BOUDREAU 1998), causing their disturbance and consequent loosening of their structure which makes them more liable to resuspension, and also inflow of dissolved forms of elements from interstitial waters characterised by increased concentrations of both phosphorus and metals (e.g. WIECHUŁA et al. 1997, LINNIK 1999).

2.2. Role of biodeposition in circulation of phosphorus and heavy metals

Importance of biodeposition in circulation of phosphorus and heavy metals depends on the quantity of produced faeces and concentration of the studied elements in the faeces. The dominant snail of the Zegrzyński Reservoir, *V. viviparus*, produced more faeces than the dominant bivalve *D. polymorpha*; concentrations of the analysed metals were higher in bivalve faeces or similar to those found in snail faeces; phosphorus concentration was higher in snail faeces. Producing high quantities of faeces by snails may result from their high food rations, especially in the case of pulmonates, which may be associated with their rather high activity and metabolic rate (MONAKOV 1974, KOŁODZIEJCZYK 1983, BRENDELBERGER 1997). Estimated faeces production for specimens of the studied snails from the Zegrzyński Reservoir is comparable to values reported in other papers (Table 4).

Higher concentration of some heavy metals in bivalve faeces, compared to corresponding values for snails, observed in this study (despite the similar level in food in most cases) might be associated with uptake of considerable quantities of metals in ionic form by bivalves (e.g. PENTREATH 1973, ABBE & SANDERS 1990, LUOMA et al. 1992, KLERKS & FRALEIGH 1997) which is also confirmed by significant correlations between metal concentration in the water and in tissues of molluscs from the Zegrzyński Reservoir, especially *D. polymorpha* (JURKIEWICZ-KARNKOWSKA 2000). Some authors regard the pool of ionic forms of these elements dissolved in the water as their main source for bivalves (e.g. ABBE & SANDERS 1990), and also for snails (e.g. REED-JUDKINS et al. 1998). Bivalves may be more capable of regulating metal concentration compared to snails (e.g. GRUNDACKER 2000), which could explain higher concentrations of these elements in their faeces. Some authors (among others JARMILLO et al. 1992, REEDERS & BIJ DE VAATE 1992, REEDERS et al. 1993, HOWELL et al. 1996) found higher concentrations of heavy metals and other toxic substances in bivalve biodeposits compared to their level in bottom deposits. No increased levels of toxicants were found in biodeposits of *D. polymorpha* from Lake Erie (DOBSON & MACKIE 1998) which might result from a high proportion of pseudofaeces and small differences in their composition, compared to passively sedimenting suspension particles. However, bottom sediments were significantly enriched with heavy metals and other toxic substances due to their increased sedimentation. In the light of earlier considerations (chapter 2.1) the diluting effect of pseudofaeces on the concentration of metals in bivalve biodeposits in the Zegrzyński Reservoir could be rather small in conditions of moderate suspension concentrations observed in this reservoir.

The effect of mollusc faeces on the pool of phosphorus and heavy metals in bottom deposits is rather little known. It follows from papers by STAŃCZYKOWSKA et al. (1976), STAŃCZYKOWSKA (1968, 1978), STAŃCZYKOWSKA & LEWANDOWSKI (1993) and KOŁODZIEJCZYK (1983, 1984) that they can significantly enrich detritus pool in bottom deposits. Phosphorus contained in faeces produced by *D. polymorpha* at high density (2,000 indiv. m^{-2}) constituted 1% total quantity of the element in Mikołajskie Lake (STAŃCZYKOWSKA & LEWANDOWSKI 1993). Proportion of mollusc faeces in sedimentation in the Zegrzyński Reservoir (estimated based on quantity of sediments deposited during a year, according to WIĘCKOWSKI 1969) was comparable with respective data for Mikołajskie Lake studied by the above authors, and also with participation of *D. polymorpha* in sedimentation in the estuary of the Hudson River (RODITI et al. 1996). Most studies on organic matter biodeposition by *D. polymorpha* contain no data which would make it possible to ascertain the proportion of faeces and elements contained in the faeces in the deposits or their sedimentation. DOBSON & MACKIE (1998) found 8–10 times higher values of biodeposition of organic matter, cadmium and polychlorinated biphenyls (PCBs) by *D. polymorpha* in the eastern part of Lake Erie, compared to natural sedimentation. Increase in the content of nutrients, heavy metals and various toxic substances in bottom deposits as a result of biodeposition was indirectly found also by other authors (e.g. NALEPA et al. 1991, REEDERS & BIJ DE VAATE 1992, MACKIE & WRIGHT 1994, KLERKS & FRALEIGH 1997, LA VALLE et al. 1999). In the Zegrzyński Reservoir enriching deposits with phosphorus and heavy metals (except Fe) was from twice to several times higher compared to enrichment with particulate matter.

Phosphorus excretion by molluscs also plays a certain role in element cycling in aquatic ecosystems. Nutrients are excreted in dissolved forms and thus directly available to phytoplankton and periphyton. Daily phosphorus excretion by molluscs from 1 m^2 bottom surface in the Zegrzyński Reservoir, estimated based on literature data (KUENZLER 1961, LAURITSEN & MOZLEY 1989, NALEPA et al. 1991, ARNOTT & VANNI 1996, JAMES et al. 1997, 2000, 2001, RYBAK 2002) on the studied species (or species of similar life style and size) was about 3–4 mg m^{-2} day^{-1}. The value is comparable with the mean values reported for excretion of *D. polymorpha* in Lake Pepin (JAMES et al. 2000). Converted to 1 l water it constitutes a value below 2 µg P per day, i.e. from ca. 2 to about a dozen per cent of the value of regeneration of this nutrient by zooplankton of the reservoir, noted by EJSMONT-KARABIN &

WĘGLEŃSKA (1989). In habitats with higher mollusc densities, e.g. in the region of the dam, the values would be higher (over 3 μg P dm^{-3} day^{-1} and from 3 to 25%, respectively). However, the role of phosphorus regeneration by molluscs is slight (by two orders of magnitude smaller) compared to the total amount of PO_4-P released from bottom deposits of the reservoir (KAJAK 1991), but it should be emphasised that phosphorus release from the deposits in the reservoir is very intense.

Phosphorus excretion by molluscs may be of a similar order as quantities of P released from bottom deposits in high trophy lakes (e.g. ANDERSEN & RING 1999, SONDERGAARD et al. 1999, the lowest values reported by ANDERSEN 1974). Results of experiments of JAMES et al. (1997) showed that the zebra mussel at a density of ca. 1,300 indiv. m^{-2} may excrete phosphorus quantities comparable to those released from bottom deposits of a eutrophic lake in anaerobic conditions (ca. 2.5 mg m^{-2}). The value is comparable to the one resulting from the calculation made for bivalves of the Zegrzyński Reservoir. Phosphorus (and nitrogen) regeneration may be of greater significance in ecosystems with very high densities of molluscs. The studies focused on the role of *D. polymorpha*, because of its extremely high densities. EFFLER et al. (1996) demonstrated the effect of zebra mussel on the changes of water chemistry in a river. Phosphorus excretion by *D. polymorpha* in the eastern part of Lake Erie exceeded both regeneration by zooplankton, and release from macrophytes and bottom deposits (ARNOTT & VANNI 1996). As demonstrated in the studies of these authors, and also JAMES et al. (2000) N:P ratio in excretions of *D. polymorpha* was low which might significantly affect changes in the proportion of these nutrients in the water, so that nitrogen (and not phosphorus) became a limiting factor for phytoplankton. Such a situation is conducive to dominance of blue-green algae (Cyanophyta). In the Sulejów Reservoir in places the zebra mussel reached densities of ca. 30 thousand indiv. m^{-2} (ABRASZEWSKA-KOWALCZYK et al. 1999), and in such habitats it could regenerate nutrients at least 10 times quicker, compared e.g. to the mean value for the Zegrzyński Reservoir. Considering that in the Sulejów Reservoir blue-green algal blooms occurred before the zebra mussel invasion (TARCZYŃSKA et al. 1997), the bivalve may contribute to an increase in blue-green algae dominance.

Certain quantities of phosphorus and heavy metals may be secreted from mollusc organism with mucus, and in the case of *D. polymorpha* also with byssus (e.g. KUENZLER 1961, DAVIES & HATCHER 1999). Because of the similar composition of byssus and shell periostracum, quantities of phosphorus in the byssus should be rather small (KUENZLER 1961), contrary to heavy metals which may accumulate more intensely in byssus compared to tissues (e.g. SZEFER et al. 1997). Metal concentration in mucus may be much higher than in mollusc tissues which might indicate a detoxicating function of mucus with respect to metals. Metals secreted with mucus are bound in mineral granules. DAVIES & HATCHER (1999) found that during one day snails removed from their organisms quantities of lead comparable to those accumulated in tissues.

2.3. Role of molluscs in accumulation of phosphorus and heavy metals in the reservoir

2.3.1. Concentrations of phosphorus and heavy metals in molluscs – intra- and inter-specific differences

Comparison of phosphorus level in the studied molluscs with the rather scanty literature information (e.g. STAŃCZYKOWSKA & PLANTER 1985, JURKIEWICZ-KARNKOWSKA 1986, 2002b, KRÓLAK 1997, MARKOWSKA 2000) indicates that the concentration of this element in tissues of particular species is relatively independent from the trophic status of the water body. Significant inter-specific differences in phosphorus concentration in mollusc tissues may reflect species-specificity of its accumulation, associated with phosphorus requirements.

Concentrations of the studied heavy metals in molluscs from the Zegrzyński, Sulejów, Siemianówka and Włocławek Reservoirs were usually comparable with corresponding values for habitats unpolluted or only slightly polluted with heavy metals (among others MANLY & GEOGRE 1977, TESSIER et al. 1984, BIAS & KARBE 1985, BUSCH 1991, VAN HATTUM et al. 1991, SMITH et al. 1996). Inter-specific differences in the content of essential metals in mollusc tissues were more frequent, compared to non-essential elements (Pb, Cd). They might result, among others, from species-specificity of requirements for essential elements, their selective uptake and different degree of development of mechanisms regulating their content in the organism (BROOKS & RUMSBY 1965, PARSONS et al. 1973, CHAPMAN et al. 1996), as well as the lack of capability to regulate, and the consequent passive uptake of non-essentials, e.g. Pb and Cd (e.g. SUNILA 1981, SIMKISS et al. 1982, SIMKISS & MASON 1983, AMIARD et al. 1987, KRAAK 1992), which are isolated in mineral granules or vacuoles and bound by low-molecule proteins, e.g. tioneine (for review see JURKIEWICZ-KARNKOWSKA 1994, 1998b).

2.3.2. Role of molluscs in accumulation of phosphorus and heavy metals in the reservoir

Molluscs of the Zegrzyński Reservoir can accumulate relatively high quantities of phopshorus, e.g. ca. 3 times more than unionids in the Goczałkowice Reservoir of comparable size during the period of their highest density of ca. several dozen indiv. m^{-2} (KRZYŻANEK 1989). Converted to unit bottom area, their phosphorus accumulation values are by an order of magnitude higher compared to unionids (density about a dozen indiv. m^{-2}) in Lake Zbęchy in Wielkopolska (KASPRZAK 1986). Compared to data for *D. polymorpha* from mesotrophic Lake Mikołajskie (STAŃCZYKOWSKA & PLANTER 1985), the content of this element in molluscs from 1 m^2 bottom of the Zegrzyński Reservoir was from over two to several times higher, and in the zebra mussel alone it was comparable. The quantity of phosphorus contained in molluscs from the studied habitats in the Zegrzyński Reservoir was comparable to or even higher than that in the water column (see Table 15), and thus molluscs were a significant trap for this element. Similar results on *D. polymorpha* from Lake Huron were presented by JOHENGEN et al. (1995).

The role of molluscs in phosphorus and heavy metal accumulation depends not only on their abundance, and especially biomass, but also on the dominance structure. This is associated with species-specificity of concentration of essential elements in tissues, and different proportion of soft tissues and shell in accumulation of particular elements. Population size (age) structure is also of some importance, since both phosphorus and heavy metal concentration vary with individual age (size) (KUENZLER 1961, BOYDEN 1974, 1977, MANLY & GEORGE 1977, BOUQUEGNEAN et al. 1979, WILLIAMSON 1979, STAŃCZYKOWSKA & PLANTER 1985, SZEFER et al. 1999, JURKIEWICZ-KARNKOWSKA 2002b). Pool of phosphorus and heavy metals contained in mollusc tissues is excluded from circulation for the period of mollusc life, while elements contained in the shell become immobilised for a much longer time. Shells can be rather well preserved in bottom deposits (SKOMPSKI & SŁOWAŃSKI 1961, SKOMPSKI 1983, JURKIEWICZ-KARNKOWSKA 1986), implying unavailability of a considerable part of elements contained in them. Such a situation was observed in these studies, for both phosphorus and heavy metals. On the other hand, a high proportion of tissues in accumulation of most of the studied elements, except manganese and iron, by malacocoenoses (see Table 14) is conducive to transfer of these elements via food chains in the reservoir ecosystem, and including them in circulation as a result of quick mineralisation of dead mollusc bodies, lasting only a few days (e.g. KOŁODZIEJCZYK 1983, RYBAK 2002).

2.4. Role of molluscs in trophic transfer of phosphorus and heavy metals

Because of high abundance of molluscs in the Zegrzyński Reservoir they may be expected to play a significant part in the food web of the ecosystem. Many authors regard food as a very important source of heavy metals for aquatic organisms, including molluscs, but the role of trophic pathways in pollution with these elements varies and depends on many factors associated with organism (e.g. feeding mode, food preferences), and with environment (e.g. food composition, its availability, size of food ration, concentration of bio-available metal fractions in food and water, interaction between metals) (PENTREATH 1973, YOUNG 1977, BRYAN 1979, PHILLIPS 1979, GEORGE 1980, LUOMA et al. 1992, REINFELDER & FISHER 1994, ABSIL et al. 1996, SMITH et al. 1996). Some authors maintain that the main source of metals for molluscs is their uptake from water solution (e.g. ABBE & SANDERS 1990, REED-JUDKINS et al. 1998). Phosphorus is assimilated by molluscs mainly from food, but some studies indicate a possibility of its uptake in ionic form (e.g. SOLOMATINA 1981).

The higher level of phosphorus in mollusc tissues, compared to its concentration in potential food observed in this study, as well as high (but lower than in molluscs) phosphorus content in mollusc- and fish-feeding fish may indicate species-specificity of phosphorus requirements and accumulation. This is confirmed by significant differences in phosphorus concentration between the studied mollusc species.

Lower (or similar) concentrations of the analysed metals in bivalve tissues, compared to their level in floc might have a variety of reasons, among others small proportion of food in accumulation of heavy metals in spite of high proportion of plankton in the suspension (up to 60% according to KAJAK 1990). According to some authors metals passively taken up by algae may be bound by them in inactive form, unavailable to bivalves (e.g. AMIARD 1988, CONELL et al. 1991, PAWLIK-SKOWROŃSKA 2002). The factor limiting assimilation of metals from seston in the Zegrzyński Reservoir might be high concentrations of suspension during summer (up to 48 mg dm^{-3}, own data) and consequent greater food ration and shorter gut passage (e.g. RODITI & FISHER 1999). Limited assimilaton of metals from food seems to be confirmed by significantly lower or comparable levels of these elements in freshly sedimented suspension (and seston), compared to mollusc faeces (t test, $p<0.05$). Author's own earlier studies (JURKIEWICZ-KARNKOWSKA 2000) indicate a relatively strong correlation between the level of metals in bivalves, especially *D. polymorpha*, and in water. The dependences may suggest a significant assimilation of dissolved forms of metals. Exceptionally high concentrations of Mn and Fe in unionid tissues seem to be characteristic of these bivalves, as indicated also by the author's earlier studies (JURKIEWICZ-KARNKOWSKA & KRÓLAK 1999, 2000, 2003).

Significantly higher (in most cases) Cu concentrations (in some cases Zn level) in tissues of the studied snails, compared to plant material they consume, may result, among others, from active accumulation of these elements according to metabolic requirements. They may be also associated with the inability to regulate their level in organism or with sources of these metals other than food. Studies of some authors (e.g.

AMIARD-TRIQUET et al. 1987, DALLINGER 1993, GRUNDACKER 2000) indicate more limited possibilities of regulation of metal level in snail tissues, compared to bivalves, though e.g. LANGSTON et al. (1998 and references contained therein) advocate an opposite view. Clearly higher Cu concentration in snail tissues, compared to bivalves, observed in this study, confirms the results of GRUNDACKER (2000) and may testify to inter-specific differences in regulation capability. Correlation between the level of heavy metals in snails and in their potential food, especially clear in the case of non-essential metals (JURKIEWICZ--KARNKOWSKA 2000), seems to confirm the significance of the trophic pathway in accumulation of these elements. However, values of metal concentration in snail faeces, in most cases higher than in plant material, may indicate a limited assimilation of these elements from food. Limitation of metal uptake through alimentary tract may result from e.g. their binding by glycoproteins (e.g. CONRAD et al. 1991, ELANGOVAN et al. 1997), shorter passage time associated with high food rations (e.g. RODITI & FISHER 1999, MUNGER & HARE 2000) or interaction between metals (VIARENGO & NOTT 1993).

As demonstrated in some studies (among others LANGSTON et al. 1998), metal load in species from higher trophic levels is mainly of trophic origin, and most metals are deposited in the digestive gland. Relatively high metal concentrations in fish liver, compared to the level in muscles (JURKIEWICZ-KARNKOWSKA 2001c), may indicate a significant proportion of trophic pathway in accumulation of these elements, though on the other hand high concentrations in the liver are also associated with the role of this organ in organism detoxication, irrespective from the source of metal. In spite of participation of soluble forms of metals in fish contamination, food – characterised by higher metal concentration compared to water – is always an important metal source (DALLINGER & KAUTZKY 1985). In fish both ways of metal accumulation are regarded as significant (KUMADA et al. 1973, DALLINGER et al. 1987), but metal content in food must exceed a certain threshold value before the metal is absorbed (JACOBS 1978, MURAI et al. 1981). Accumulation of metals from food by fish may be influenced by feeding frequency, food rations, food quality, interactions with metals taken up from water etc.

Decrease in metal concentration at higher trophic levels, observed in the studied food chains, in most cases confirms results of numerous other studies, namely that metals are concentrated to the greatest extent by primary producers or by the first two links of short food chains, but never in small or large fish (BRYAN 1979, HODSON 1980, BAUDO 1985, PRAHALAD & SEENAYYA 1986, DALLINGER et al. 1987, DEVI et al. 1996, NOTT 1998, BLANCHARD et al. 1999, MASON et al. 2000, CHEN et al. 2000). The reason is a limited availability of metals resulting from ligand binding and compartmentalisation. Only metals associated with soluble fraction of the prey are available to higher trophic levels (e.g. WALLACE & LOPEZ 1996). Forms bound as insoluble phosphates and sulphur compounds are unavailable to predators, since they are not absorbed by alimentary tract, and thus not transferred along food chains. Molluscs may bind excess of heavy metals in mineral granules which are a result of detoxication (HODSON 1980, NOTT & LANGSTON 1989, NOTT & NICOLAIDOU 1990, 1993, BURBRIDGE et al.1996, NOTT 1998). Thus inactivated metals are, after a certain time, excreted with faeces and enrich bottom deposits. Limiting of trophic transfer of metals may be effected also through binding metals, released from digested food, by indigestible matter and excretion with faeces (HODSON 1980). Due to the mentioned processes, availability of metals contained in mollusc faeces to detritivores may be considerably limited, which would be confirmed by relatively low concentrations of these elements in tissues of chironomid larvae compared to their level in mollusc faeces.

Molluscs constitute an attractive food for many species of fish, benthophagous birds and an array of other animals (see: Introduction). In the Zegrzyński Reservoir they are the main food of roach; they constitute up to 100% food of individuals over 15 cm long (TERLECKI et al. 1990). Remains of shells of *V. viviparus, Valvata piscinalis, Bithynia tentaculata, Sphaerium* sp., *D. polymorpha* and also unionids were found in alimentary tracts of roach (own, unpublished data). Other fish species dominant in the reservoir (bream, white bream) also feed on molluscs, though to a lesser extent (TADAJEWSKA 1993).

Metals contained in granules consumed with mollusc tissues and in shells are unavailable to fish, which may be an important reason for the lower metal concentrations in fish muscles (often also in liver; JURKIEWICZ-KARNKOWSKA 2001c), compared to the level found in prey. Besides, fish were shown (e.g. SMITH et al. 1996) to control the uptake and elimination of heavy metals more effectively, compared to invertebrates. Probably, they reject considerable quantities of consumed metals (HAMDY & PRABHU 1979, TARIFENO-SILVA et al. 1982).

The role of molluscs in the transfer of heavy metals is complex. As a rule, they exploit more than one food source (especially snails), and the composition of their diet is varied. Molluscs may also assimilate heavy metals directly from water solution and transfer them to food chains. Because of limited bio-availability of metals contained in mollusc tissues, caused by ligand binding and compartmentalisation, a considerable part of these elements is unavailable to either molluscs or predators. A similar phenomenon is observed in e.g. detritus chain, where the food source is mollusc faeces. In ecosystems of rather slight heavy metal pollution molluscs, in spite of a certain accumulation of these elements in their tissues and increased concentrations in the faeces, constitute no threat to mollusc-feeding predators, detritus-feeders or higher trophic levels.

CONCLUDING REMARKS

The studied reservoirs have a rich malacofauna, like an array of other lowland eutrophic dam lakes of the temperate zone. Higher mollusc species richness is observed in conditions of higher proportion of the former river bed in the total area of the reservoir, and quicker water exchange, though always more numerous species are found in the zone of flooded land. In the zone of former river beds, where the effect of the river on the reservoir is greater, the proportion of widespread species is higher. There is a certain distinctness in the dominance structure of the malacofauna in the former river bed and the flooded land, which persists even in mature reservoirs. This may be associated mainly with the effect of hydrological regime and changes in the structure of bottom deposits and distribution of various kinds of sediments. Mean values of mollusc densities in the studied reservoirs are the highest in conditions of the greatest effect of the river on the reservoir. Differences in abundance of malacofauna of the studied reservoirs become clearer when the zones of former river beds are compared. This may be associated with the favourable effect of flow, among others, improved oxygen conditions above the bottom and continuous food supply, especially for filtrationists and detritus-feeders.

Long-term changes in the malacocoenoses are more distinct in the zone of flooded land, compared to the former river beds. In reservoirs of advanced development (middle-aged), malacocoenoses are subject to factors associated mainly with the reservoir's ageing and eutrophication, whose effects are more obvious in flooded land areas, especially in habitats of the slowest water exchange. However, even at that development stage there may occur considerable changes resulting from large disturbance by physical (especially hydrological) factors which cause reversal of malacocoenoses to earlier stages of succession. Significant changes in the structure of malacocoenoses may take place also as a result of invasion by *D. polymorpha*.

Distribution and temporal changes in malacocoenoses affect their significance in the functioning of the reservoir ecosystem. Filtration potential and intensity of production of faeces which enrich bottom deposits (and excretion) depend not only on the density of molluscs but also on the dominance structure. An efficient filtrationist – *D. polymorpha* – tends to be more abundant outside the zone of former river beds. The bivalve may have a great effect on the water quality in the shallows, especially that water exchange there is much slower. A much smaller effect can be expected from e.g. abundant occurrence of small sphaeriids in the former river bed, both because of their low filtration efficiency and the fast water exchange in the current. In older reservoirs, especially of higher trophic status, often more efficient filtrationists dominate, when their occurrence is not limited by other factors. Snails produce more faeces than bivalves, but their food is derived from the water column to a lesser extent than bivalve food, and thus their significance is more local.

As a result of inter-specific differences in concentration of phosphorus and heavy metals in molluscs, not only biomass but also structure of malacocoenoses influence the quantity of accumulated elements. These quantities in the Zegrzyński Reservoir constitute only from 1 to several per cent compared to their retention in the reservoir or their content in bottom deposits. A large part of these elements is, however, accumulated in shells because of their high proportion in the total mollusc mass, and thus excluded from circulation. Phosphorus cycling, and to an even greater extent metal circulation through malacocoenoses many times exceed the quantity of these elements accumulated in mollusc tissues and shells.

Phosphorus and heavy metals assimilated by molluscs are subject to trophic transfer. A part of metals, as a result of detoxication and isolation mechanisms, are excluded from circulation due to which there is a decrease tendency in their concentration at higher trophic levels. Phosphorus does not conform to these regularities. It appears that participation of trophic pathway in transfer of heavy metals is rather small (greater for phosphorus), much lower than quantities of these elements contained in molluscs, since the part of them contained in shells and mineral granules in tissues is biologically unavailable to potential consumers.

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