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The formation of bottom macrofauna communities in three dam reservoirs in Silesia (southern Poland) from the beginning of their existence

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Abstract — In the Goczałkowice, Wisła-Czarne, and Rybnik dam reservoirs the process of formation of bottom macrofauna occurred in three stages: 1 — the stage of development of pioneer communities during the first two years after filling; 2 — the stage of transition communities from the third to the tenth year after filling; 3 — the stage of permanent communities ten years after filling. Two types of dam reservoir were identified: 1 — of the Oligochaeta type, Wisła-Czarne, and 2 — of the midge type, Goczałkowice and Rybnik.

Key words: dam reservoirs, bottom macrofauna, settlement succession, numbers, biomass.

1. Introduction

Throughout the world the regulation of numerous rivers and the construction of dam reservoirs necessitate comprehensive hydrobiological studies, frequently carried out by scientific centres especially founded for this purpose. From these investigations monographs of many reservoirs have been elaborated (Tsyeyeb 1964, Kuzin 1972, Tsyeyeb, Maystryenko 1972, Butorin 1978), this also making available rich literature data concerning the bottom macrofauna in dam reservoirs (Mordukhay-Boltovsky 1961, Jankovič 1972, Mordukhay-Boltovsky et al. 1972, Peter 1972, Hruška 1973, Shilova 1976, Prat 1980).

In Poland there are 123 dam reservoirs (Głodek 1985). In most of them hydrological studies have been carried out. They were begun by German scientists (Wundsch 1942, 1949) in the reservoirs of

Lower Silesia (Otmuchów, Turawa). After World War II the investigations on the above-mentioned reservoirs and also in southern Poland were chiefly conducted by the Laboratory of Water Biology of the Polish Academy of Sciences in Kraków. Periodical hydrobiological studies were carried out in the reservoirs of the River Dunajec (Olszewski 1946, 1953, Starmach 1965), cascades of the River Soła (Kownacki 1963, Smagowicz 1963, Krzanowski 1971, Krzyżanek 1971, Paluch et al. 1975), and in Silesia (Starmach, Zaczyński 1957, Zaczyński 1958). Also in other regions of Poland where dam reservoirs were constructed hydrobiological studies were made (Włocławek, Dębe, Sulejów, Koronowo). The investigations on such reservoirs also concerned the bottom macrofauna (Grzybowska 1958, 1965, Kownacki 1963, Giziński, Wolnomiejski 1966, Krzyżanek 1971, Giziński, Paliwoda 1972, Paluch et al. 1975, Wolnomiejski, Giziński 1976).

The present work covers the investigations on the communities of bottom macrofauna in the Goczałkowice, Wisła Czarne, and Rybnik Reservoirs. Its basic part concerns the results of the author's study carried out in the Goczałkowice Reservoir in the period 1961—1982. Some fragments of these results have already been published (Krzyżanek 1965, 1966a, b, 1970, 1973, 1976, 1977, 1986a). The results of investigations from the first years of existence of the reservoir were also taken into consideration (Kysela 1956, 1958, Zaćwilichowska 1965a, Grzybowska unpubl.).

All investigations on the Wisła-Czarne Reservoir were carried out by the author from 1975—1984, part of the obtained results having already been published (Krzyżanek 1986b). In the case of the Rybnik Reservoir the present work was chiefly based on the results of an investigation carried out by the author in the years 1978—1981 and fragmentarily published (Krzyżanek 1979), and on data given by other authors (Bielańska 1973, Grzybowska unpubl.).

In attempts to classify the dam reservoirs their morphology and the rate of water exchange were used as the chief criteria (Starmach 1958, Zhadin 1961, Benson 1982). On this basis the Wisła-Czarne Reservoir would exemplify rheolimnic gorge reservoirs and Goczałkowice limnic flood water reservoirs, the Rybnik Reservoir occuppying an intermediate position.

The aim of the present work was to investigate the process of formation of bottom macrofauna communities in three dam reservoirs in Silesia from the moment of their filling. The reservoirs differed with regard to their morphology and geology, their purpose, and the impact of anthropogenic factors on them.

2. Study area, material, and methods

2.1. Description of catchment basins of the Upper Vistula and the Wisła-Czarne and Goczałkowice Reservoirs

With regard to its morphology the catchment basin of the Upper Vistula is divided into a montane part (276 km^2), a submontane area (216 km^2), and lowlands (247 km^2). The basin of the Wisła-Czarne Reservoir lies in the mountainous region. In the structure of land use forests prevail, covering 80% of the area; meadows and pastures cover 17%, and arable land 2%.

The basin of the Goczałkowice reservoir lies in montane, submontane, and lowland terrain. In the structure of land use arable constitutes 46%, and forests 40% of the total area. Forests dominate in the basin of the Bajerka streem, which feeds the reservoir from the south. In this area, particularly in Ustroń and Skoczów, numerous industrial plants have been developed. The population is over 75 thousand, increasing in summer and winter owing to tourism and rest-houses (Pasternak 1962, Kasza 1986a, b, Mazur 1972, Wróbel 1975). The Wisła Czarne and Goczałkowice Reservoirs lie on the Upper Vistula (figs 1, 2A),

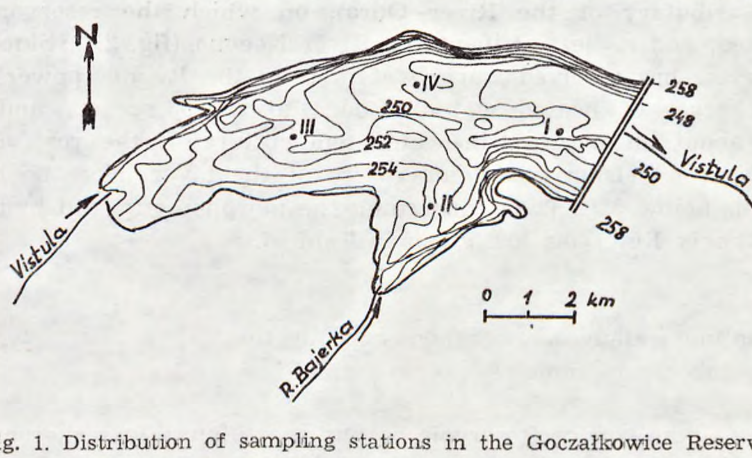

Fig. 1. Distribution of sampling stations in the Goczałkowice Reservoir

their chief purpose being water supply. The more important morphometrical and hydrological parameters of the investigated reservoirs are presented in Table I.

2.2. Description of the basin of the River Ruda and the Rybnik Reservoir

The catchment area of the Rybnik Reservoir lies on the Rybnik Plateau (maximum altitude 288 m) in the Rybnik Coal Region, this

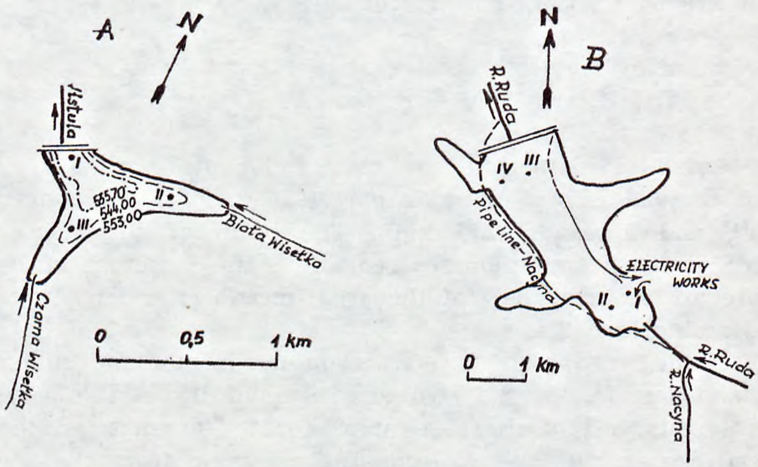

Fig. 2. Distribution of sampling stations in the Wisła-Czarne (A) and Rybnik (B) Reservoirs

bringing about the inflow of enormous amounts of industrial and municipal wastes. The chief sources feeding the reservoir are the River Ruda (a right tributary of the River Odra), on which the reservoir was constructed, and its left affluent the River Nacyna (fig. 2B). Since 1973 the reservoir has received warm waters from the Rybnik power plant. The discharges of heated water amount to 25—33 m^3 s^{-1} and have brought about an increase in water temperature in the reservoir by a few degrees Celsius. The temperature of the layer near the bottom never falls below 5°C. Data concerning the morphometry and hydrology of the Rybnik Reservoir are given in Table I.

2.3. Sampling stations and methods of collecting and elaborating samples

In the Goczałkowice Reservoir bottom macrofauna was characterized
of the Rybnik Reservoir are given in Table I.
I—IV, fig. 1), in 1955—1960 at 16 stations, and in 1961—1975 at 19 stations (K r z y ż a n e k 1986a). In the period 1955—1970 the numbers only were investigated but from 1971 also the biomass. For the earlier period (1955—1970) the biomass of *Chironomus* sp. I (? *Ch. plumosus* L.) and *Procladius* spp. larvae and of Bivalvia was approximately reconstructed on the basis of detailed lists of collected animals reported by A. K y s e l a and K. Z a ć w i l i c h o w s k a (K y s e l a 1956, 1958, Z a-ć w i l i c h o w s k a 1956a, b, c).

In 1972 the water level was reduced in the Goczałkowice Reservoir,

Table I. Some morphometric and hydrological parameters of Wisła Czarna, Goczałkowice, and Rybnik reservoirs

Parameter	Dam reservoir		
	Wisła Czarne	Goczałkowice	Rybnik
Localization	9.3 km below the Czarna Wisełka sources and 6.7 km below the Biała Wisełka sources	67 km below the River Vistula sources	15 km below the River Ruda sources (right tributary of the River Odra)
Geographical position	49°36′N, 18°56′E	49°51′N, 18°52′E	50°25′N, 18°32′E
Purpose	retention, intake for water supply	retention, intake for water supply	cooling of waters discharged by the power plant
Year of construction	1974	1955	1972
Maximum depth m	30	11	11
Mean depth m	9	5	5
Maximum area ha	55	3200	555
Maximum volume m^3	5 mln	168 mln	27 mln
Frequency of water exchange in a year	9—14	2—4	5—6
Area of catchment basin km^2	30	523	280
Type of catchment basin	mountainous, forest, touristic	forest-agricultural, average urbanized	agricultural, industrial, strongly urbanized

this causing the emergence of over 600 ha of the bottom. Taking this opportunity, Bivalvia were investigated both on the emerged part of the bottom and on that under water (Krzyżanek 1976).

In the Wisła-Czarne Reservoir the investigation was carried out at one station only in 1975—1980 (Station I) and at three stations in 1981—1984 (Stations I—III, fig. 2A). A detailed description of the stations was given by Krzyżanek (1986b).

In the Rybnik Reservoir the investigation was carried out at four stations in 1974—1981 (fig. 2B).

In all reservoirs similar methods of sampling were used during the entire period of the investigation (Krzyżanek 1986a). Samples were taken with an Ekman mud grab with the catching area of 225 cm² (2—4 grabs per sample) and a bottom scraper of 20 cm side length. The content was rinsed through 0.5 mm mesh bolting cloth. The animals were selected from the samples and fixed in a 4% solution of formalin. The biomass was determined by weighing various groups and selected taxa with a torsion balance exact to 0.001 mg.

Apart from Chironomidae the species nomenclature of the investigated groups was based on Illies's work (1978). In the case of Chironomidae, whose larvae cannot always be identified as to species, the accepted nomenclature has also been used by other workers, among others by Lehman (1971).

3. Hydrochemical and biological description of the investigated reservoirs

3.1. The Goczałkowice Reservoir

The River Vistula pays a decisive role in feeding this reservoir, It supplies 77.1% of the water and has the most important effect on its chemical composition there. The waters of the River Vistula also supply the greatest amount of biogenic components: 82% of total N and 67% of total P. The small Bajerka stream was more polluted than the Vistula (only in some periods certain parameters were contained in purity class II). Its share in the water balance of the reservoir (4%) and the load of nutrients supplied to it (4% N and 8% P, Kasza 1977) were small. In comparing the chemical composition of the feeders and of the reservoir it was found that the concentration of chemical parameters (with the exception of oxygen consumption) was usually higher in the water of the affluents (Table II).

The results achieved in detailed hydrochemical investigations of the reservoir (Kasza, Winochradnik 1986) revealed two periods in its existence. In the first (1956—1961) a greater content of organic matter (measured as oxygen consumption), a higher degree of water colour, and increased amounts of mineral suspension were observed, but in the second (1962—1982) greater amounts of nutritive components and of compounds indicating the degree of salinity.

In the development of macrophytes three periods were distinguished: I — 1956—1959 (an intense development of *Elodea canadensis* Rich.), II — 1960—1972 (a poorer development and almost complete decline of *E. canadensis*), III — from 1973 (the development of submersed vegetation, Kuflikowski 1986).

However, after filling of the reservoir in 1955 a very intense develop-

Table II. Average chemical composition of water in Goczałkowice, Wisła Czarne, and Rybnik dam reservoirs and in their affluents (Kasza 1986b, Kasza unpubl.), a — data from 1960; b — data from 1978; c — data from 1983; — — trace amounts

Parameter	GOCZAŁKOWICE 1955—1982				WISŁA CZARNE 1976—1984			RYBNIK 1979		
	affluents		reservoir		affluents			affluents		
	Vistula	Bajerka	1955—1961	1962—1982	Biała Wisełka	Czarna Wisełka	reservoir	Ruda	Nacyna	reservoir
Alkalinity mval dm^{-3}	1.2	0.9	1.0	1.1	0.51	0.35	0.44	1.15—1.75	3.75—5.60	1.30—1.90
Hardness °G	5.4[c]	3.6[a]	4.0[a]	5.5[c]	2.8[c]	1.7[c]	2.7[c]	7.90—8.70	24.00—44.80	10.20—13.10
Chlorides mg Cl dm^{-3}	16.2	10.3	9.1	13.3	3.5	3.3	3.8	56.0—71.0	1094.0—1245.0	198.5—207.0
Calcium mg Ca dm^{-3}	30.0	22.6	24.2	28.6	12.7	6.8	10.2	36.45—51.45	108.99—336.62	49.67—63.25
Magnesium mg Mg dm^{-3}	3.8	4.4	3.0	4.2	3.8	4.0	3.8	10.41—14.31	59.63—100.18	13.44—21.25
Silica mg SiO_2 dm^{-3}	5.91	7.82	4.70	2.86	2.6	2.95	2.54	8.342—10.802	7.059—11.337	0.021—5.946
Iron mg Fe dm^{-3}	0.46	0.46	0.19	0.13	—	—	—	0.65—6.1[b]	0.30—1.80[b]	0.15—0.6[b]
Mineral nitrogen mg N dm^{-3}	1.58[c]	—	—	1.11[c]	1.61[c]	1.31[c]	1.22[c]	1.970—7.417	2.657—6.316	0.669—2.677
Organic nitrogen mg N dm^{-3}	0.46[c]	—	—	0.55[c]	0.19[c]	0.10[c]	0.25[c]	—	—	—
Total nitrogen mg N dm^{-3}	2.04[c]	—	—	1.66[c]	1.80[c]	1.41[c]	1.47[c]	—	—	—
Pphosphates mg P-PO_4 dm^{-3}	0.022	0.064	0.005	0.009	0.008	0.005	0.006	0.670—1.13	0.89—1.16	tr. —0.103
Total phosphorus mg P dm^{-3}	0.059	0.088	—	0.047	0.041	0.031	0.028	1.270—1.808	1.86—3.588	0.080—0.452
Oxidability mg O_2 dm^{-3}	3.9	6.8	6.1	4.4	2.8	3.5	4.1	8.72—18.96	13.16—25.10	5.72—9.16
BOD_5 mg O_2 dm^{-3}	3.0	3.5	3.2	2.9	2.6	1.8	2.1	4.2—8.4[b]	4.0—19.0[b]	0.48—4.99[b]
Loading of the reservoir:										
mineral nitrogen g N m^{-2} a^{-1}				5.42			6.60[c]			18[b]
phosphates g P m^{-2} a^{-1}				0.08			0.03[c]			—
total phosphorus g P m^{-2} a^{-1}				0.18			0.24[c]			1.6[b]

ment of phytoplankton took place, bringing about periodical blooms. From 1960—1975 there occurred a decrease in the phytoplankton. From 1976 observations showed greater numbers and periodical blooms of blue-green algae, chiefly *Microcystis aeruginosa* Kütz. (Pająk 1986).

In 1955 a mass development of Cladocera and from 1956 of Rotatoria (chiefly in the period 1960—1961) was observed in zooplankton communities. Up to 1969 the quantitative growth of zooplankton was fairly intensive, but from 1970 it began to decrease, this state being maintained until 1982 (Krzyżanowski 1986).

3.2. The Wisła-Czarne Reservoir

In the period of the investigation the waters of both the reservoir and its feeders, the Rivers Biała and Czarna Wisełka, were unpolluted. The River Biała Wisełka brought in more nutritive salts and electryltes. In Table II average values of selected chemical parameters are given.

As compared with the water of the rivers, only slight changes were found in the water of the reservoir. There was an increase in the content of organic nitrogen and in oxygen consumption while the amount of total phosphorus decreased. A comparison of the results obtained during the 10-year period of existence of the reservoir showed that the values of electrolytes, the abundance of trophic compounds, content of organic matter, and transparency (3.30 m) were maintained at the same level. Only the content of total phosphorus was slightly greater in the first two years of the investigation, while in periods of drought the content of electrolytes usually increased (Kasza 1986b).

The average annual temperature on the water was low in this reservoir, amounting to 7—8°C. Differences between the surface and water layer near the bottom were small, reaching no more than 2°.

In the period 1975—1976 the average annual numbers of phytoplankton reached $4—5 \cdot 10^3$ indiv. cm^{-3} with Bacillariophyceae as dominants. In 1976—1980 the numbers increased to $15 \cdot 10^3$ indiv. cm^{-3}, chiefly of Chlorophyceae and Bacillariophyceae, while from 1981 there occurred a decrease to $2.5 \cdot 10^3$ indiv. cm^{-3} with the dominance of Chlorophyceae, Cyanophyceae, and Peridiniales. From 1974—1975 average annual numbers of zooplankton were 440 indiv. dm^{-3} with an average biomass of 3.9 mg dm^{-3}; from 1976—1980 the respective values were 300 and 1, and in 1981—1984 200 and 1.5. During the entire period of the investigation the dominants were Rotatoria, mainly *Polyarthra vulgaris* Carb., *Keratella cochlearis* Gosse, *Synchaeta pectinata* Ehr., and *Conochilus unicornis* Rouss. Also Crustacea constituted a considerable percentage of the biomass (Krzyżanowski 1987).

3.3. The Rybnik Reservoir

In the River Ruda, the main tributary of this reservoir, the water was highly polluted, chiefly with dissolved mineral and also organic components (Table II). In the period 1974—1981 the water of its left affluent, the River Nacyna, was still more polluted (coal-dust suspension, sodium and potassium chlorides, calcium and magnesium salts, and organic compounds). The loads of nutrients and pollution caused by oils (1.3—4.5 mg dm^{-3}) and volatile phenols (0.016—0.025 mg dm^{-3}) were greater than in the River Ruda.

From 1974—1976 the total annual primary production was 140—473 g C m^{-2} $year^{-1}$ the maximum daily gross production amouhting to 5.456 g m^{-2} $24h^{-1}$ (Pasternak, Kasza 1978). In the period 1972—1981 a constant tendency to increase was observed in the numbers (from 400 to 700 thousand cells dm^{-3}) and biomass (from 200 to 400 mg dm^{-3}) of phytoplankton. Bacillariophyceae and Dinoflagellatae dominated and blue-green alga blooms were also periodically observed (Strzelecki unpubl.).

Slight quantitative and qualitative changes took place in the zooplankton in the period 1974—1978. The species composition was fairly rich (43 species, comprising 5 Protozoa, 26 Rotatoria, 10 Cladocera, and 2 Copepoda) with average numbers of 1047—1596 indiv. dm^{-3} and average annual biomass of 5.7—8.2 mg dm^{-3} (Krzanowski 1979).

Macrophytes were found only in the period 1972—1973, forming small aggregations of *Polygonum amphibium, Lemna minor, Phragmites communis*, and *Glyceria aquatica*. Owing to the introduction of the herbivorous fish *Ctenopharyngodon idella* Val., almost no higher plants have been noted in the reservoir since 1974 (Kuflikowski unpubl.).

4. Results

4.1. The share of more important groups of bottom macrofauna in settling the bottom of the investigated dam reservoirs

4.1.1. Chironomidae

Throughout the period of investigation on the Goczałkowice Reservoir Chironomidae constituted the most numerous group, characterized by the greatest differentiation of its taxonomic composition (fig. 3A, Table III). 70 taxa were identified, among them 42 of the Chironominae subfamily (Chironomini — 36, Tanytarsini — 6); 19 of the Orthocladiinae, and 9 of the Tanypodinae subfamilies. In the Chironominae subfamily *Chironomus* sp. I (? *Ch plumosus* L.) chiefly dominated in the period

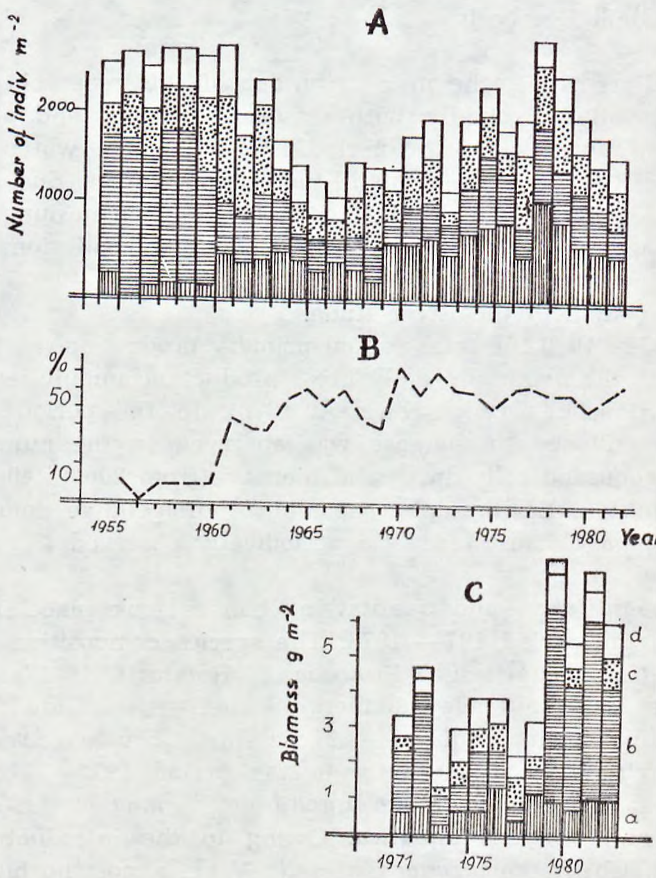

Fig. 3. Course of changes of average annual numbers (A), of percentage share of *Procladius* spp. in the Chironomidae family (B), of average annual biomass without Unionidae (C) in the Goczałkowice Reservoir from 1955—1982. a — *Procladius* spp.; b — others Chironomidae; c — Oligochaeta; d — other organisms

1955—1963. In the first five years after filling of the reservoir the occurrence of another taxon of this genus — *Chironomus* sp. II (? *Ch. thummi* K.) — was periodically recorded. Beginning from 1961 frequent constituents of Chironominae were predatory forms of the genus *Cryptochironomus*, mainly *C. defectus* K., pelophile *Microchironomus* sp. (? *M. tener* K.), and phytophilous *Dicrotendipes* sp. (? *D. nervosus* Staeg.). In the periods 1955—1963 and 1970—1982 pelophile *Polypedilum* sp. (? *P. nubeculosum* Mg.) was often found. The Tanytarsini tribe was usually represented by two taxa, i.e. *Tanytarsus* spp. and *Cladotanytarsus* sp. (? *C. mancus* Wulp.), and the Orthocladiinae subfamily by *Cricotopus sylvestris* (Fabr.) and *Psectrocladius* spp. In the Tanypodinae subfamily the genus *Procladius* dominated (figs 3 A, C). A

Table III. Succesion of more important Chironomidae taxa in the Goczałkowice dam reservoir from 1955—1982. + — single specimens; ● — 200—500 indiv. m^{-2}; ○ — over 500 indiv. m^{-2}

Taxa			1955					1960					1965					1970					1975				1980	
Pseudosmittia sp.	+																											
Smittia sp.	+																											
Chironomus sp. I (?Ch. plumosus L.)	○	○	○	○	○	○	○	○	○	●	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	●	●
Procladius spp.	●		+	+	+	+	●	●	●	○	●	●	●	●	●	○	○	○	○	○	○	●	○	○	○	○	○	○
Polypedilum sp. I (?P. nubeculosum Mg.)	+		+	+	+	+	+	+	+	+						+	+	+	+	○	+	+	+	+	+	+	+	+
Chironomus sp. II (?Ch. thummi K.)	+	●	+	+	+																							
Paratendipes sp.			+	+	+	+	+																		+	+	+	+
Clinotanypus nervosus Mg				+	+	+	+	+	+																			
Ablabesmyia sp.				+	+	+	+	+	+	+			+			+				+	+	+	+	+	+	+	+	+
Cryptochironomus defectus K.							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Microchironomus sp. (?M. tener K.)							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	●	●	●	●	●
Dicrotendipes sp. (?D. nervosus Staeg.)							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tanypus sp. I (?T. punctipennis Meig.)							+			+	+		+	+		+		+	+	+	+	+	+	+	+	+	+	+
Polypedilum sp. II (?P. pedestre Mg.)								+	+	+																		
Stictichironomus sp. I (?S. histrio Fabr.)								+	+	+			+		+													
Stictochironomus sp.											+	+	+	+	+													
Xenochironomus xenolabis K.										+						+	+	+	+	+	+	+	+	+	+	+	+	+
Micropsectra spp.																+	+		+	+	+	+	+		+			
Tanypus sp. II (?T. kraatzi Kieff.)										+								+	+		+	+	+	+	+	+	+	+

Table IV. Succession of more important Chironomidae taxa in the Wisła Czarne dam reservoir from 1975—1984. + — single specimens

Taxa	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
Potthastia sp.	+	+	+	+	+					
Prodiamesa olivacea (Mg.)	+	+	+	+	+	+				
Cricotopus spp.	+	+	+		+			+		
Dicrotendipes sp. I (?D. nervosus Staeg)	+		+	+	+	+	+			
Psectrocladius spp.	+	+	+	+	+	+	+	+		
Ablabesmyia sp. (?A. monilis L.)	+	+	+	+	+	+	+	+	+	+
Procladius spp.	+	+	+	+	+	+	+	+	+	+
Chironomus sp. I (?Ch. plumosus L.)	+	+	+	+	+	+	+	+	+	+
Tanypus sp. I (?T. punctipennis Mg.)	+		+	+		+	+	+	+	+
Cladotanytarsus sp. (?C. macus Wulp.)										
Cladotanytarsus spp.		+	+	+	+	+	+	+	+	+
Microchironomus sp. (?M. tener K.)						+	+	+	+	+

constant increase in settlement density and also in biomass, and hence in the share of the genus *Procladius* in the Chironomidae family, was observed throughout the later period of the investigation up to 1982. Its quantitative share in this family constantly varied between 40 and 60%. In the period 1958—1963 *Clinotanypus* sp. (? *C. nervosus* M g.) and *Ablabesmyia* sp., and in later years chiefly *Microchironomus* sp. (? *M. tener*), *Cryptochironomus defectus,* and *Dictrotendipes* sp. (? *D. nervosus*) were fairly frequently noted. The succession of more important taxa is presented in Table III.

In the Wisła-Czarne Reservoir Chironomidae did not play such a great role as in the Goczałkowice or Rybnik Reservoirs. Their percentage share was 1.5—12% at Station I, 8—12% at Station I, and 6.5—30% at Station III. 25 taxa were identified (12 Chironomini, 3 Tanytarsini, 5 Tanypodinae, and 5 Orthocladinae). The succession of more important taxa is given in Table IV. During the first five years after filling of the reservoir among the recorded taxa there also occurred those living in the river before the construction of the dam reservoir, e.g., *Prodia-*

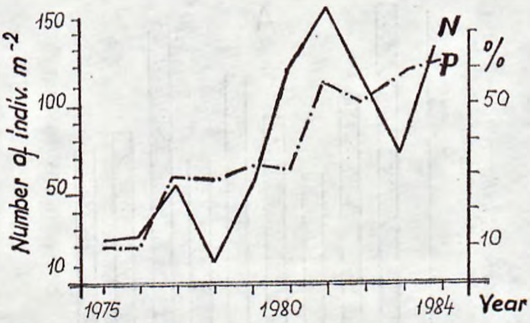

Fig. 4. Course of changes of average annual numbers of *Procladius* spp. (N) and of percentage share of *Procladius* spp. in the Chironomidae family (P) in the Wisła-Czarne Reservoir

mesa olivacea, Potthastia sp. and *Harnischia* sp., and *Chironomus* sp. I. From 1977 the genus *Procladius* was the main component of Chironomidae with respect to numebrs (fig. 4). At Station I its percentage share increased from 10 to 60%, from 11 to 16% at Station II, and from 16 to 28% at Station III.

In the Rybnik Reservoir Chironomidae constituted a dominant group from 1974 (figs 5, 6). A total number of 31 taxa was identified, the succession of the most important being shown in Table V.

The Chironominae subfamily and among them the Chironomini tribe, chiefly *Chironomus* sp. I, *Cryptochironomus defectus,* and *Polypedilium* sp. I, dominated. The Tanytarsini tribe was represented by *Tanytarsus* spp. and *Cladotanytarsus* sp. up to 1978 but from 1979—1980 only by *Cladotanytarsus* sp.

The Tanypodinae subfamily was represented by 5 taxa with *Procladius* spp. as the dominant (fig. 5). The Orthocladiinae subfamily was represented by 5 taxa, occurring only at Stations I and II. The most abundant was shown by *Psectrocladius* spp. and *Criotopus sylvestris* (F a b r.).

4.1.2. Oligochaeta

In the Goczałkowice Reservoir Oligochaeta constituted the second group of bottom macrofauna with respect to numbers (K r z y ż a n e k 1970, 1973, 1977, 1986a). During the first ten years an aggregation of Oligochaeta developed and was maintained throughout the entire later period, when the main role was played by *Limnodrilus* sp., *L. hoffmeisteri* C l a p., *Tubifex tubifex* O.F. M ü l l., *Nais* spp., and *Stylaria lacustris* L. In the following years mainly quantitative changes occurred in this group. The density of settlement by Oligochaeta was lower, the

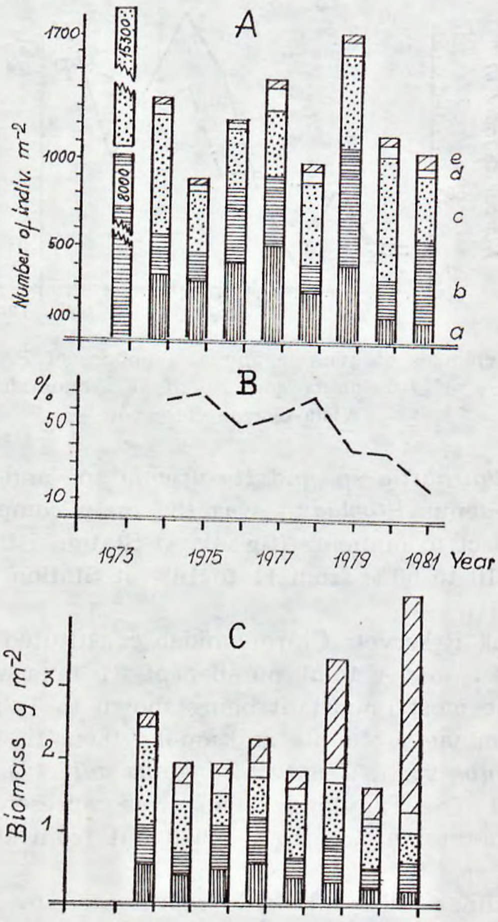

Fig. 5. Course of changes of average annual numbers (A), of percentage share of *Procladius* spp. in the Chironomidae family (B), and of biomass (C) in the Rybnik Reservoir. a — *Procladius* spp.; b — other Chironomidae; c — Oligochaeta; d — other organisms; e — Gastropoda

greatest reduction in numbers being recorded in 1967 and 1973 (figs 3, 7).

In the Wisła-Czarne Reservoir the communities of bottom macrofauna were almost exclusively (over 90%) composed of Oligochaeta with the dominants *Limnodrilus hoffmeisteri* and *Tubifex tubifex* (fig. 8). Table VI shows the succession of more important species. Particularly great numbers of Oligochaeta were observed in the first years after filling of the reservoir, chiefly at Station I (fig. 9A).

In the Rybnik Reservoir Oligochaeta group dominated in the period 1972—1974 (fig. 5), their numbers reaching 15 000 indiv. m^{-2}. From

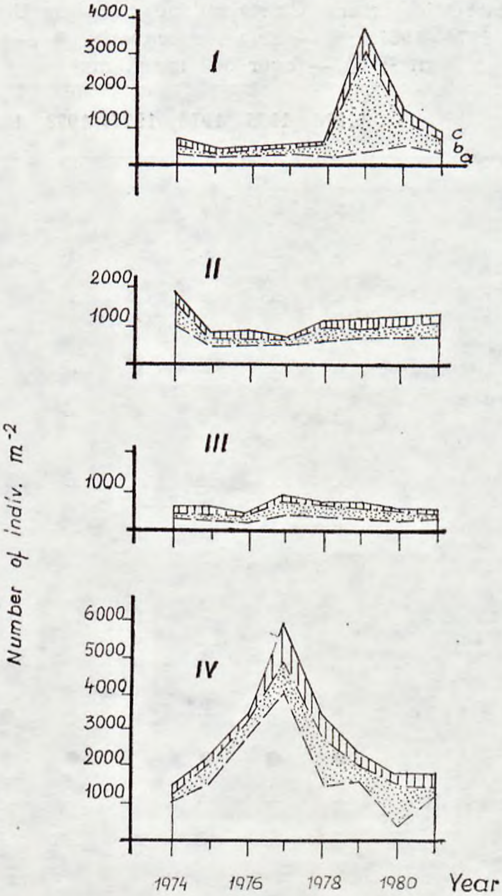

Fig. 6. Course of changes of average annual numbers of bottom macrofauna in the Rybnik Reservoir at Stations I—IV. a — Chironomidae; b — Oligochaeta; c — others

1975—1977 their occurrence was less abundant. In 1978 the density of settlement again increased, particularly at Station I, in the region where warm waters from the power plant were discharged (fig. 6).

4.1.3. Mollusca

In the Goczałkowice Reservoir Bivalvia developed very abundantly (Table VII). The first specimens of this group appeared in 1956, i.e. in the second year after filling. These were small species from *Pisidium* genera. Their greater density was noted at Station I, where *Pisidium amnicum* and *P. casertanum* dominated. In 1958 *Anodonta cygnea*, a representative of the Unionidae family, was caught for the first time.

Table V. Succesion of more important Chironomidae taxa in the Rybnik dam reservoir from 1974—1981. + — single specimens; ● — 200—500 indiv. m⁻²; ○ — over 500 indiv. m⁻²

Taxa	1974	1975	1976	1977	1978	1979	1980	1981
Dicrotendipes sp. II (?D. tritomus K.)	+	+	+	+				
Microtendipes sp.	+	+	+	+				
Tanytarsus spp.	+	+	+	+	+			
Dicrotendipes sp. I (?D. nervosus Staeg.)	+	+	+	+	+			+
Harnischia sp.	+	+	+	+	+			+
Cladotanytarsus sp. (?C. mancus Wulp.)	+	+	+	+	+	+	+	
Endochironomus spp.	+	+				+	+	+
Chironomus sp. II (?Ch. thummi K.)			+	+				
Einfeldia sp.			+	+		+		
Chironomus sp. I (?Ch. plumosus L.)	+	+	+	+	+	●	+	●
Procladius spp.	●	●	●	○	●	●	+	+
Cryptochironomus defectus K.	+	+	+	+	+	+	+	+
Glyptotendipes spp.	+	+	+	+	+	+	+	+
Polypedilum sp. I (?P. nubeculosum Mg.)	+	+	+	+	+	+	+	+
Psectrocladius spp.		+	+	+	+	+	+	+
Cricotopus sylvestris (Fabr.)			+	+	+	+	+	+
Cricotopus spp.				+	+	+	+	+

Its maximum development occurred in the period 1966—1973. In 1965 the determination of the numbers of molluscs on the exposed part of the bottom (Krzyżanek 1966a) showed the greatest density of *Anodonta cygnea* (80%) at Station II. From 1970 the share of *Unio pictorum* gradually increased. The occurrence of this species in the reservoir was for the first time recorded in 1962, i.e. in the 8th year after filling (Krzyżanek 1970).

When in 1972 the water level was again reduced and a 600-hectare area of the bottom was exposed, the whole malacofauna was investigated in detail, both on the emerged part and on that under water (Krzy-

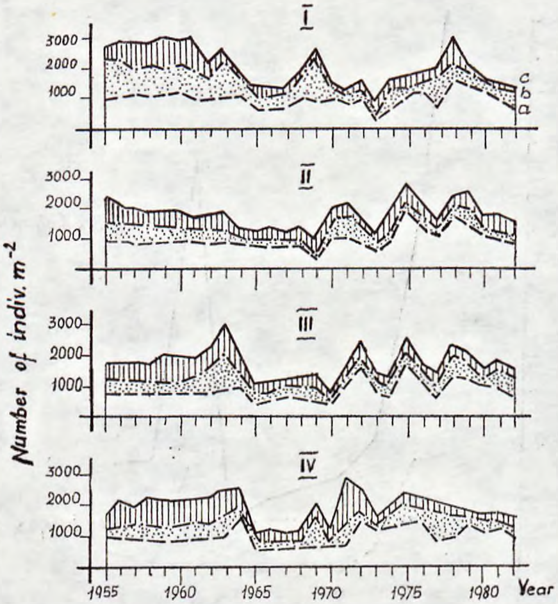

Fig. 7. Course of changes of average annual numbers of bottom macrofauna in the Goczałkowice Reservoir at Stations I—IV. a — Chironomidae; b — Oligochaeta; c — others

ż a n e k 1976). It was computed that on the whole emerged area about 18 million molluscs of the biomass of 1114 tons had been left. An investigation carried out in the submerged part of the reservoir, using the diving method, at 4 cross-sections from depths of 2, 4, 6, and 8 m also showed that greater numbers of molluscs settled the northern than the southern zone. The greatest number of molluscs was caught at a depth of 2 m. In the submersed and exposed parts the qualitative composition of molluscs was similar. *Unio pictorum* dominated in the northern zone and *Anodonta cygnea* in the southern. The computation showed that about 106 million Unionidae with a biomass of over 5000 tons (in the measurement of biomass the weight of shells was taken into consideration) were settling the reservoir.

The aim of biometric measurements, whihe were also carried out, was to determine the age structure of the dominant Unionidae species. Four age classes were determined, using the length as the basis of classification (K r z y ż a n e k 1976). The investigation showed that most individuals examined belonged decisively to size class III (*Unio pictorum* 6—9 cm in length, *Anodonta cygnea* 8—12 cm). On the basis of annual growth rings it was concluded that these were specimens aged 6—8 years in the case of *Unio pictorum* and 8—10 years in that of *Anodonta cygnea*.

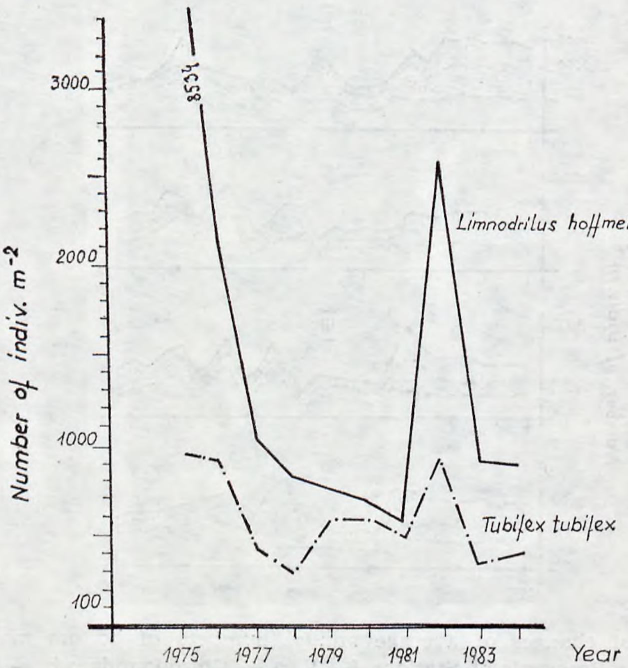

Fig. 8. Course of changes of average annual numbers of *Limnodrilus hoffmeisteri* and *Tubifex tubifex* in the Wisła-Czarne Reservoir

The studies continued in the years 1973—1982 showed that the structure of molluscs communities observed in 1972 changes distinctly. The domination of *Unio pictorum* increased in the northern zone while in the southern one the density of settlement by *Unio pictorum* and *Anodonta cygnea* was similar. The density of settlement and the biomass of all Unionidae constantly decreased. In 1972 the mean annual density of settlement was 53 indiv. m^{-2} and the biomass 700 g m^{-2}, in 1976 the respective numbers were 16 indiv. m^{-2} and 200 g m^{-2}, and in 1982 10 indiv. m^{-2} and 120 g m^{-2} (Krzyżanek 1986a).

In the littoral zone of the Goczałkowice Reservoir also Gastropoda constituted an important component of the bottom macrofauna. In the first 2 years after filling *Lymnaea stagnalis* L., *Physa fontinalis* L., and *Gyraulus albus* Müll. were most frequently encountered. Subsequently, this zone was settled by *Valvata piscinalis* Müll., *V. pulchella* Studer, *V. naticina* Menke, *Lymnaea peregra* Müll., *L. auricularia* L., *Planorbis planorbis* L., and *Planorbarius corneus* L.

In the Wisła Czarne Reservoir Mollusca constituted a very small percentage of invertebrate macrofauna and were represented by the genus *Pisidium*.

Table VI. Succession of more important Oligochaeta species in the Wisła Czarne dam reservoir from 1975—1984. + — single specimens; ● — 300—1000 indiv. m^{-2}; ○ — over 1000 indiv. m^{-2}

Taxa	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
Limnodrilus hoffmeisteri Clap.	○	○	●	●	●	●	●	○	●	●
Tubifex tubifex (Müll.)	●	●	●	●	●	●	●	○	+	●
Limnodrilus spp.	+		+	+	+					
Potamothrix hammoniensis (Mich.)	+	+	+	+	+	+	+			
Nais spp.										
Stylaria lacustris (L.)			+	+	+	+	+	+	+	+
Tubifex spp.				+	+	+	+	+	+	+

In the Rybnik Reservoir among the more important groups were Gastropoda (Table VIII) represented by the families Planorbidae (*Planorbarius corneus, Gyraulus albus, Anisus vortex, A. spirorbis* L., *Anisus* sp.), Lymnaeidae (*Lymnaea peregra*), and Physidae (*Physa fontinalis, Ph. acuta*). The thermophilous species *Physa acuta* was caught for the first time in 1974, i.e. in the third year after filling, at Station I. Its average density of settlement gradually increased from 5 to 200 indiv. m^{-2} (fig. 5). At the same time. *Physa fontinalis* L. was found at Station IV. In this reservoir Bivalvia played a less important role than Gastropoda, small numbers of their representatives being encountered almost exclusively at Station IV. Of the Sphaeridae family *Pisidium amnicum* Müll., *P. subtruncatum* Malm., *P. nitidum* Jen., *P. pulchellum* Jen., *Pisidium* sp., and *Sphaerium lacustre* Müll. occurred.

4.1.4. Other groups of bottom macrofauna

Other groups of animals played great role in the communities of bottom macrofauna. In the Goczałkowice Reservoir only the following groups occurred periodically in greater numbers: Trichoptera (*Polycentropus flavomaculatus* Pict., *Oecetis ochracea* Curt.), Ephemeroptera (*Caenis moesta* Bgts, *Caenis* sp.), Hirudinea (*Helobdella stagnalis* L., *Glossiphonia complanata* L., and *Hemiclepsis marginata* O.F. Müll.), and Nematodes, *Sialis* sp., *Asellus aquaticus* O.F. Müll., and Ceratopogonidae.

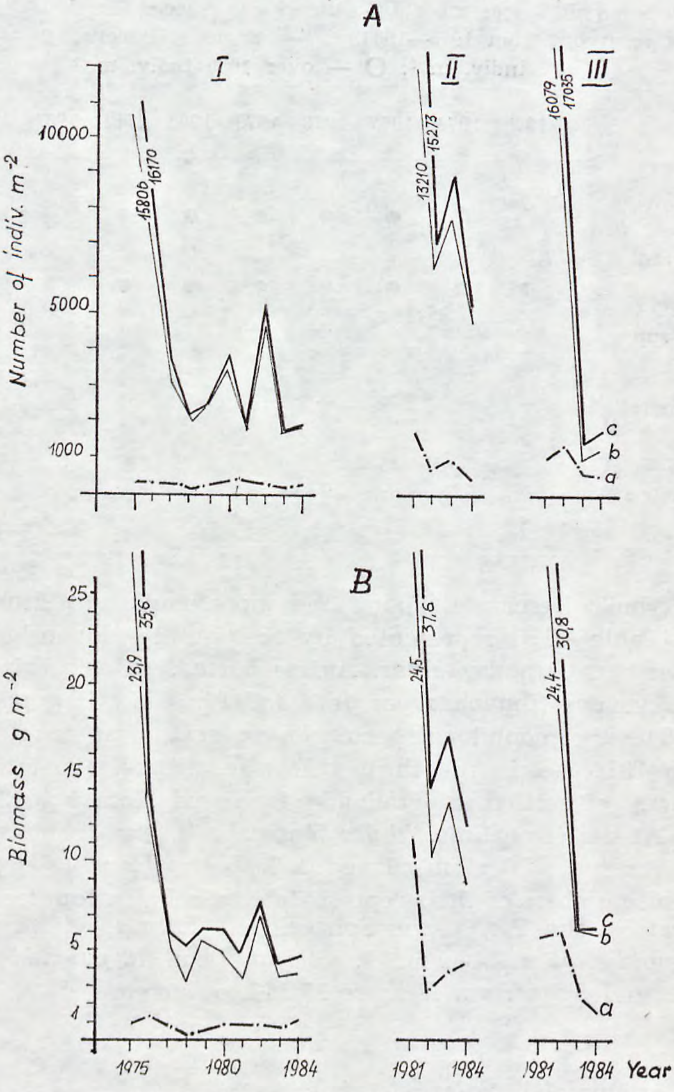

Fig. 9. Course of changes of average annual numbers (A) and biomass (B) of bottom macrofauna in the Wisła-Czarne Reservoir at Stations I—III. a — Chironomidae; b — Oligochaeta; c — all invertebrates

4.2. Ecological succession of bottom macrofauna communities in dam reservoirs

4.2.1. General remarks

The investigation carried out in three dam reservoirs showed that two stages (periods) could be determined in the formation of bottom

Table VII. Sucession of more important species of the Bivalvia class in the Goczałkowice dam reservoir from 1955—1962. + — single specimens; ● — 10—20 indiv. m^{-2} (Sphaeridae), 3—5 indiv. m^{-2} (Unionidae); ○ — over 20 indiv. m^{-2} (Sphaeridae), over 5 indiv. m^{-2} (Unianidae)

Taxa		1955					1960					1965					1970					1975				1980	
Sphaeriidae																											
Pisidium amnicum Müll.	+	+	+	+	+	●	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pisidium casertanum Poli			+	●	○	○	○	●	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pisidium subtruncatum Malm.						+	●	●	●		+				+	+	+	+	+	+	+	+	+	+	+	+	+
Pisidium henslowanum Shepp.																+	+	+		+		+				+	+
Pisidium nitidum Jenyns																+	+							+	+		+
Pisidium pulchellum Jenyns																								+			+
Unionidae																											
Anodonta cygnea L.			+	+	+	+	+	+	+	+	+	●	●	●	○	○	○	○	●	●	●	●	●	●	●	●	●
Unio pictorum L.							+	+	+	+	+	+	+	●	●	●	●	●	○	○	○	○	○	○	○	○	○
Unio tumidus Phil.												+				+	+	+	+	+	+	+	+	+	+	+	+
A. piscinalis Nilss.												+				+	+	+	+	+	+	+	+	+	+	+	+

macrofauna communities during the first ten years after filling. The first period, which included the initial two years after filling of the reservoir, may be determined as that of the first (pioneer) communities. During this time land and riverine animals (e.g., rheophilous forms) unadopted to the new conditions, dramatically diet out. They were replaced by communities chiefly composed of detrivorous animals. In the Wisła-Czarne and Rybnik Reservoirs there occurred a mass de-

Table VIII. Succession of more important species of Gastropoda in the Rybnik dam reservoirs in the years 1974—1981. + — single specimens; ● — 10—30 indiv. m^{-2}; ○ — over 30 indiv. m^{-2}

Taxa	1974	1975	1976	1977	1978	1979	1980	1981
Planorbarius corneus L.	+	+	+	+	+	+	+	+
Physa acuta Drap.	+	+	+	+	+	+	●	○
Anisus vortex L.	+		+	+				
Lymnaea peregra Müll.		+	+	+	+	+	+	●
Gyraulus albus Müll.		+	+	+	+	+	+	+
Physa fontinalis L.			+	+	+	+	+	+

velopment of Oligochaeta (*Limnodrilus hoffmeisteri*) and in the Goczałkowice Reservoir of Chironomidae (*Chironomus* sp. I)). The second period, which lasted 8—9 years, i.e. from the second or third to the tenth year after filling, may be determined as that of transitional communities. Apart from Chironomidae and Oligochaeta other groups of animals, above all Mollusca (Bivalvia in the Goczałkowice Reservoir and Gastropoda in the Rybnik impoundment), began to play a more important role.

In the Goczałkowice Reservoir where the investigation covered 28 years, a third stage should also be differentiated: the period of formation of permanent communities.

4.2.2. The Goczałkowice Reservoir

The first period began after the reservoir was filled in February 1955 and lasted to the end of that year. After the decline of land forms, unadapted to the now environmental conditions, there appeared Chironomidae, chiefly *Chironomus* sp. I (? *Ch. plumosus*) and *Chironomus* sp. II (? *Ch. thummi*), feeding on decomposing plants and rapidly increasing in density of settlement. Within two months of filling the reservoir, land forms, i.e. Enchytreidae (Oligochaeta) and amphibiotic

Chironomidae, chiefly *Pseudosmittia* sp. and *Smittia* sp., were found only in small numbers (Table III). Subsequently, the formation of invertebrate macrofauna mainly depended on the quality and quantity of bottom sediments and on the degree to which the littoral zone was overgrown by macrophytes. Chironomidae with 27 identified taxa dominated. Of these 15 taxa were new, previously not found in the river or ponds in the flooded area (Grzybowska, unpubl.).

The second stage covered the years 1958—1963. Bottom sediments had not yet formed, while the bottom was covered with a layer of decomposing plants. In the early years of this period (1956—1959) dramatic processes of biochemical decomposition of the flooded vegetation occurred on the bottom of the reservoir and enriched the water and sediments with organic and mineral components, this favouring the development of bacterial flora, the food basis of most benthos organisms. These conditions brought about the mass development of Chironomidae, chiefly *Chironomus* sp. I whose greatest numbers were found in the years 1956—1957. In the littoral zone the abundant occurrence of *Glyptotendipes* spp. and *Harnischia* sp. and in the central zone of *Procladius* spp. was also observed. Apart from the ubiquitous forms there occurred greater numbers of phytophilous taxa and also those such as *Chironomus* sp. II (? *Ch. thummi*) which, according to the literature data (Romaniszyn 1958), tolerates putrid processes and is resistant to oxygen deficiency. In the Goczałkowice Reservoir this taxon occurred abundantly to the end of 1956 but later in markedly smaller numbers. Mollusca were represented by Gastropoda (*Lymnaea stagnalis* and *L. peregra*) and small Bivalvia (*Pisidium casertanum* Poli and *P. amnicum*). The first representatives of the Unionidae family, *Anodonta cygnea*, were caught in 1958.

In the period 1960—1963 other groups, above all Oligochaeta and in the littoral zone also Mollusca, Trichoptera, Ephemeroptera, and Hirudinea began to play an ever greater role. The biomass of Bivalvia also increased. In the Chironomidae family *Chironomus* sp. produced a considerable biomass. During this time in the Chironomidae family 50 taxa were identified, 30 of them being representatives of the Chironominae subfamily (27 Chironomini, 3 Tanytarsini), 15 of Orthocladiinae, and 5 of Tanypodinae.

The third period was taken from 1964—1973. Bottom sediments were already formed and spatially differentiated. Specific zones of the reservoir and characteristic pelophile, phytophilous, and psammophilous zoocenoses had developed. The characteristic trait of the first 8 years of this period was a rapid decrease in the numbers of bottom macrofauna (fig. 3). The very small numbers of bottom macrofauna in 1973 were caused by the reduction in the water level in 1972. The poorer composition was observed in all groups of animals, especially in Mollusca and Oligochaeta at all stations here. In the period 1964—1973 changes constantly occurred in the taxonomic composition of Chironomidae. Such taxa as *Chironomus* sp. II and *Paratendipes* sp. disappeared and new ones, such as *Stictochironomus* sp. I (? *S. histrio* F.). *Stictochironomus* sp., *Tanypus* sp. I (? *T. punctipennis* M g.), *Microchironomus* sp. (? *M. tener*), *Cryptochironomus defectus*, and *Xenochironomus xenolabis* K. were recorded (Krzyżanek 1986a). 49 taxa were identified, including 32 from the subfamily Chironominae (29 Chironomini and 5 Tanytarsini), 10 of Orthocladiinae, and 7 of Tanypodinae. An increase in the numbers of the genus *Procladius* took place. Great qualitative and quantitative changes were observed among Bivalvia. In the sixties *Anodonta cygnea* dominated, while in the early seventies *Unio pictorum* began to do so. Throughout 1964—1973 the spatial differentiation was remarkable. The greatest abundance of these animals was found at stations III and IV (figs. 3, 7).

From 1974 there was a gradual increase in the numbers of bottom macrofauna in the reservoir, with a maximum in 1978 (fig. 3). The growing density of settlement of Chironomidae was particularly distinct, their taxonomic composition being already stabilized. The total number of taxa did not change; in the group of 49 were found 31 Chironominae (26 Chironomini, and 5 Tanytarsini), 10 Orthocladiinae, and 8 Tanypodinae. Among the new taxa were *Tanypus* sp. II (? *T. kraatzi* Kieff.) and *Micropsectra* spp. The share of larvae of the genus *Procladius* rose (60% of the total number of Chironomidae). With regard to numbers this group was followes by Oligochaeta, Mollusca were found in the third place. They were represented by Unionidae and Valvatidae at stations II and IV, and by Sphaeridae at Station I. *Unio pictorum* was the dominant taxon. 1964 was determined as the beginning of the third period, above all on account of qualitative changes in the group of Chironomidae and Bivalvia (Tables III, VII).

4.2.3. The Wisła-Czarne Reservoir

The investigation chiefly concerned Station I lying in that part of reservoir near the dam (fig. 9). The first period, covered the years 1974—1975. There developed then bottom sediments, chiefly mineral of fairly considerable thickness, originating from allochtonous components constantly transported from the catchment basin. The accumulation of large amounts of inorganic and organic matter brought about an abundant development of Oligochaeta as organisms feeding on detritus. They constituted 98% of the numbers and biomass of the total bottom macrofauna, with *Limnodrilus hoffmeisteri* as the dominant species. Chironomidae constituted only 1.5% of absolute numbers. In this family

Prodiamesa olivacea and *Ablabesmyia* sp. attained greater numbers, while *Chironomus* sp. I (? *Ch. plumosus* L.) showed the greatest biomass. In bays of the reservoir at Stations II and III representatives of Oligochaeta were only sporadically found.

The second period was from 1976—1984. As compared with the first period the numbers and biomass of Oligochaeta were reduced to 1/3; in this group 38% of absolute numbers were constituted by *Limnodrilus hoffmeisteri* and 20% by *Tubifex tubifex*. Chironomidae constituted 4% of numbers with *Chironomus* sp. I (? *Ch. plumosus* L.) as the dominant. From 1977—1980 a further decrease in numbers and biomass of Oligochaeta was observed. The share of *Tubifex tubifex* rose to 30% while that of *Limnodrilus hoffmeisteri* fell to 30%. In the Chironomidae family *Procladius* spp. dominated. Towards the end of the seventies the numbers of *Ablabesmyia* sp. and *Dictrotendipes* sp. I (? *D. nervosus* Staeg.) were reduced and *Prodiamesa olivacea* and *Potthastia* sp. taxa completely died out, while the appearance of *Microchironomus* sp. (? *M. tener*) was observed.

Early in the eighties (1981—1984) a further decrease in numbers and biomass of Oligochaeta was found at Station I in the central zone of the reservoir. The share of *Limnodrilus hoffmeisteri* in this group constantly increased (fig. 8). In the Chironomidae family, which constituted 10—15% of the total number and biomass of bottom macrofauna, *Procladius* spp. attained a distinct dominance (50—60% of numbers and 30—54% of biomass).

The investigation carried out in 1981 at Stations II and III showed a rich macrofauna there (fig. 9). Oligochaeta constituted 86% of absolute numbers at Station II (*Limnodrilus hoffmeisteri* 60%) and 94% at Station III (*Limnodrilus hoffmeisteri* 70%). Chironomidae constituted 12% of macrofauna numbers at Station II and 6% at Station III. The dominant taxa were *Chironomus* sp. I and *Procladius* spp. From 1982—1984 the numbers and biomass of Oligochaeta decreased, while the percentage share of Chironomidae larvae was 8—12% at Station II and 15—20% at Station III. In the Chironomidae family 23 taxa were identified, with *Chironomus* sp. I dominating at Station II *Procladius* spp. at Station III. During three years no quantitative or qualitative changes were observed in this group. In the Wisła-Czarne Reservoir the division into two periods was chiefly based on quantitative changes in Oligochaeta.

4.2.4. The Rybnik Reservoir

The first period covered the years 1972—1973. The investigation begun im March 1972 showed that the bottom was settled by Oligochaeta. In this group Tubificidae decidedly dominated (over 90% of numbers), their rapid development being especially visible at Station III. In 1973 the development of bottom macrofauna was even more intensive.

The second period was from 1974—1981. In 1974 a dramatic decrease in the settlement density of bottom macrofauna resulted in its reduction to 1/5 (fig. 5) this density was maintained until 1977 when a slight increase in settlement occurred. This was particularly visible at Station IV (figs 5, 6) and chiefly concerned Chironomidae larvae. *Procladius* spp. (Tanypodinae) dominated, constituting 50—60% of the numbers of all Chironomidae. *Cryptochironomus defectus* and *Polypedilum* sp. I (? *P. nubeculosum*) were also fairly numerous. From 1976—1977 the occurrence of *Chironomus* sp. II (? *Ch. thummi*), characteristic of polluted waters, was periodically observed. In 1974 the thermophilous species *Physa acuta* L. (Gestropoda) was caught at Station I and in subsequent years became more and more numerous at this station.

In 1979 the numbers and biomass of bottom macrofauna increased, particularly at Station I, where Oligochaeta dominated. In the following years (1980—1981) the numbers fell while the biomass increased, reaching the highest value in 1981 (fig. 5). The increase in biomass was caused by the occurrence of Gastropoda (*Physa acuta* at Station I and *Lymnea peregra* at Station IV). In the period 1979—1981 17 taxa were identified in the Chironomidae family. The domination of *Procladius* spp. fell to 20% of the numbers of Chironomidae (fig. 5) while the share of phytophilous forms (*Cricotopus sylvestris, Cricotopus* spp., and *Psectrocladius* spp.) rose. *Dicrotendipes* sp., *Microtendipes* sp., and *Tanytarsus* spp. completely disappeared, while *Endochironomus* spp., not noted in the years 1976—1978, reappeared. The division into two periods resulted both from quantitative and qualitative changes of the bottom macrofauna.

5. Discussion

5.1. Factors decisive for the process of formation of bottom macrofauna in dam reservoirs

After the construction of a dam reservoir on a river the composition and magnitude of communities of bottom macrofauna chiefly depend on the morphology and position of the reservoir, the kind of land use before the flooding of the territory, the area overgrown by higher plants, chemical composition of the substratum, the size of existing aquatic areas in the territory of the reservoir, the size of the main river, the character and area of the catchment basin, and the quality of water flowing into the reservoir. Therefore, in shallow, floodwater, limnic reservoirs, whose bottom was in a great part covered with vegetation before filling, as was the case in the Goczałkowice Reservoir, the mass development of animals feeding on decomposing plants, chiefly Chironomidae larvae, followed the filling of the reservoir. In deep, rheolimnic, gorge reservoirs, e.g., the Wisła-Czarne Reservoir, where the accumulation of mineral and organic components brought in by river water prevails, detrivorous organisms, chiefly Oligochaeta, developed abundantly. After the first communities of bottom macrofauna have formed, i.e. after 1—2 years, further changes take place, leading to the formation of transitional communities. In this period the process of settlement and formation of these communities depends both on external factors, particularly the magnitude of loads of biogenic substances fed with the river waters, and on internal ones in the reservoir biocoenosis, i.e. the development of plankton and macrophytes. The process of settlement of the bottom usually occurs from two directions: from the part near the dam, as muddy sediments develop up the reservoir along the axis formed by the former riverbed by pelophilous animals, and from the upper littoral zone along the banks, as the growth of macrophytes and then their decomposition progress, mainly by phytophilous taxa. In the early period of existence of the reservoir changes occurring in the environment to a great degree depend upon anthropogenic factors. They bring about changes also manifested in the spatial distribution of animal communities. Here the Goczałkowice and Rybnik Reservoirs may be mentioned as examples. Owing to the constant inflow of nutrients and organic matter brought in to the Goczałkowice Reserovir with the waters of the River Vistula, and increased sedimentation and accumulation in the upper part of the reservoir, it was precisely in this part that the most abundant communities developed. In the Rybnik Reservoir the most abundant development of bottom macrofauna was found in the littoral zone in the lower part near the dam. In the upper part the poorer development was to a great degree affected by the inflow of toxic substances contained in mine waters fed to the River Ruda and activated by warm waters discharged from the power plant. In the Wisła-Czarne Reservoir bottom sediments were formed only in bays and in the central part of the main reservoir. In these places the quantitatively abundant fauna, though of little differentiated species composition (90% Oligochaeta), developed during the 10-year period of existence of the reservoir. At that time the banks of the reservoir were only very slightly covered with sediments, hence pelophile animals did not find there favourable conditions of development. In the central zone of the Goczałkowice Reservoir the abundantly developed fauna was little differentiated. In the Rybnik Reservoir the bottom macrofauna of this zone was quantitatively and qualitatively poor because the accumulation of toxic substances from the River Ruda was most intensive along the reservoir in the old riverbed. After about 10 years, permanent communities of bottom macrofauna began to develop in the dam reservoirs, though they are nevertheless subject to slow changes chiefly caused by anthropogenic factors. Their further development has also been affected in great part by periodical changes occurring in the reservoirs, e.g., frequent fluctuations in the water level in reservoirs built fo energetic purposes. In the Goczałkowice Reservoir falls in water level, necessitated by conservation works carried out on the dam, periodically though fairly considerably affected the development of bottom macrofauna. Such decreases took place in 1965, 1972, and 1978, and each time almost 1/3 of the bottom emerged for a period of about a year. On the emerged area many animals remained and died out. After refilling of the reservoir, changes in faunistic communities could be observed. Thus, after the lowering of the water level in 1965 and its raising in 1966, the reproduction of bivalves of the Unionidae family, chiefly of *Anodonta cygnea,* was intensified. The next reduction of the water level in 1972 contributed to a change in dominance in this family, *Anodonta cygnea* being replaced as dominant species by *Unio pictorum.*

5.2. The share of more important faunistic groups in the process of formation of bottom macrofauna communities in dam reservoirs

Usually the first animals to begin settling the bottom sediments in dam reservoirs and then abundantly reproduce are Chironomidae larvae. Numerous data concerning the role of this insect in dam reservoirs are to be found in the literature (Peter 1972, Shilova 1976, Musatov 1979). In general, taxonomic lists usually include 50—100 forms in different reservoir. The Rybinsk impoundment was an exception with 168 taxa of these insects identified there (Shilova 1976). Apart from cosmopolitan forms, regional ones which only occur in certain reservoirs (Ioffe 1961) were also found there. The first organisms to settle the bottom of a dam reservoir are forms living on flooded and then decomposing land vegetation. These are chiefly *Chironomus plumosus*, *Ch. thummi*, *Dicrotendipes nervosus*, and *Glyptotendipes* spp. In numerous dam reservoirs in the first years after filling the mass development of *Chironomus plumosus* was observed (Jankovič 1972, Krzyżanek 1986a). After a few, usually five to six, years after the filling predatory forms *(Ablabesmyia*, *Procladius*, and *Cryptochironomus*) were observed to begin to play an ever greater role and then to dominate. The particularly great importance of the genus *Procladius* was observed. The present author is currently carrying an investigation on the taxonomy of the genus *Procladius* in the Goczałkowice Reservoir, including culture from eggs to adult forms. In natural lakes, *Procladius* prefers the littoral zone (Kajak 1961) and in dam reservoirs occures most abundantly in those zones where the environmental conditions to a great degree resemble it (Grzybowska 1965, Giziński, Wolnomiejski 1982). In the Goczałkowice Reservoir absolute numbers of *Procladius* were greater in the central zone, while its percentage share in relation to other Chironomidae was uniform throughout the reservoir. This genus also numerously occurred in a reservoir with heated water (Skalskaya 1975), as was confirmed by the investigation conducted in the Rybnik dam Reservoir (Krzyżanek 1979).

The great share of *Procladius* in dam reservoirs was confirmed by numerous workers both in Poland (Kownacki 1963, Grzybowska 1965, Krzyżanek 1971, Giziński, Wolnomiejski 1982) and abroad (Jankovič 1972, Mordukhay-Boltovskoy et al. 1972, Hruška 1973, Prat 1980). It domination among Chironomidae increases with the passage of years after the construction of the reservoir.

Oligochaeta are another group whose representatives settle bottom sediments soon after the filling and then reproduce in masses. The rate at which these animals appear and the intensity of their propagation are different in different reservoirs. In the investigated Silesian ones, both in the montane Wisła-Czarne Reservoir and in the lowland reservoir at Rybnik, a sudden mass development of Oligochaeta occurred during the first two years after filling. In the Goczałkowice Reservoir their numbers increased at a slower rate than those of Chironomidae, with a maximum in the seventh year after filling. Such a process of formation of macrofauna communities with an enormous domination of Oligochaeta during a short period, as was the case in the Wisła--Czarne Reservoir, is rather rare. A similar pattern was observed only in a few reservoirs (Kubiček 1956, Zelinka 1962, Krzyżanek 1971). In most dam reservoirs, e.g. in the cascades on the Rivers Volga, Dnieper, or Vltava the changes observed were similar to those in the Goczałkowice Reservoir. In the Oligochaeta group cosmopolitan species usually dominate, chiefly *Limnodrilus hoffmeisteri, L. claparedeanus* Ratzel., *Tubifex tubifex,* and *Potamotrix hammoniensis* (Mich.), though in some cases rare species also reproduced in masses, e.g. *Arcteonais lomondi* Mart. (Zelinka 1962).

In bottom macrofauna communities Mollusca constitute a great percentage share of numbers and above all of biomass. In some reservoirs these are chiefly Bivalvia (Goczałkowice) and in other Gastropoda (Rybnik). Such intensive reproduction and the formation of large populations of Unionidae as observed in the Goczałkowice Reservoir were also found in other dam reservoirs, e.g. in southern Poland in those on the River Soła cascades (Tresna and Porąbka, Krzyżanek 1971), and in the Soviet Union in the Novosibirsk Reservoir (Popova et al. 1972). The possibility of rapid development and formation of great Unionidae populations in numerous dam reservoirs is associated with their geographical distribution. Therefore, in regions where suitable conditions appear after the construction of a new reservoir (e.g., great contents of organic suspension and calcium, suitable conditions for the development of glochidia, and also weak competition from other species, especially *Dreissena polymorpha* Pall.) large populations of Unionidae may develop.

In the Soviet Union, Czechoslovakia, and also in northern Poland in most dam reservoirs Bivalvia of the family Dreissenidae are more numerous than Unionidae (Giziński, Wolnomiejski 1982). After the construction of such reservoirs on the River Volga and Dnieper they propagated in masses and spread throughout the cascade of these rivers (Lubyanov et al. 1967, Pligin 1979).

Among the dam reservoirs where Gastropoda constitute one of the more important groups in the Rybnik Reservoir. Here *Physa acuta* was the chief component of Gastropoda. In most dam reservoirs the most frequently and most numerously encountered snails belong to the families Lymnaeidae, Planorbidae, and Valvatidae (Ioffe 1961, Krzyżanek 1986a).

5.3. The importance of bottom macrofauna in dam reservoirs

Bottom macrofauna above all play an important role in the metabolism of dam reservoirs and constitute the basic food of benthophagous fish. A knowledge of the qualitative and quatitative composition of these animals is exceedingly important in hydrobiological investigations, permitting evaluation of the current productive capacity of the reservoir, its trophy, and the current stage of its development.

On the basis of the magnitude of biomass of these animals dam reservoirs in the Soviet Union were divided into five groups: 1 — those with a very high biomass of over 120 kg ha^{-1}, 2 — with a high biomass of 60—120 kg ha^{-1}, 3 — with a mean biomass of 30—60 kg ha^{-1}, 4 — with a small biomass of 15—30 kg ha^{-1}, 5 — with a very small biomass under 15 kg ha^{-1}. Chironomidae and Oligochaeta constituting the so-called soft benthos are the most valuable food for fish. In the cascades of reservoirs on the River Dnieper the biomass of these animals varies from 7—50 g m^{-2} and in the cascade on the River Volga from 2—10 g m^{-2} (Musatov 1979). Of the investigated Silesian reservoirs benthophagous fish find the best feeding conditions in the Goczałkowice Reservoir. Apart from soft fauna, fish, e.g. *Mylopharyngodon piceus*, also consume molluscs, chiefly of Dreissenidae and even Unionidae. In dam reservoirs of water supply system the largest bottom filtrators, bivalves of the Unionidae family (*Unio, Anodonta*), play a very useful role. Intensive reproduction and development of great populations of these animals bring about the accumulation of considerable amounts of organic matter and biogenic substances in their bodies (Stańczykowska 1983). With high density considerable amounts of phosphorus may be accumulated in Unionidae populations. Using the data obtained in Lake Mikołajskie (Lewandowski, Stańczykowska 1983), it was calculated that in the seventies in the Goczałkowice Reservoir these organisms accumulated about 5 tons of phosphorus (2 tons in their bodies and 3 tons in the shells). The most important role of molluscs in the cycling of organic matter in a reservoir is its accumulation through their filtration activity. The measurements carried out in Lake Mikołajskie may be used to compute with fairl probability that 106 million molluscs (chiefly *Anodonta cygnea* and *Unio pictorum*, in most cases individuals aged 8—10 years) were able to filtrate the entire mass of water of the Goczałkowice Reservoir twice to three times in a year. Populations of *Dreissena*, abundantly occurring in dam reservoirs, also play the important role of filtrators (Lvova 1979). On the other hand, it is worth remembering that with a constant increase in numbers the larval stages of Unionidae may cause glochidiosis of fish and also intensify the invasion of their bodies by sporocysts and cercaria, dangerous parasites of fish (Castagnolo et al. 1972). The role if indirect hosts of trematodes, which bring about diseases dangerous to fish is also played by other animals, suck as numerous species of Gastropoda and Tubificidae.

5.4. Formation of bottom macrofauna communities in dam reservoirs against the background of the reservoir ecosystem

On the basis of data obtained from three different dam reservoirs, i.e. Wisła-Czarne, Goczałkowice, and Rybnik, the process of formation of bottom macrofauna could be investigated against the background of changes occurring in other ecological formations, i.e. in plankton, higher vegetation, and the environment. The division of the formation of macrofauna communities into three stages, presented in the preceding chapters, is schematic and simplified. The limits of stages are not distinct and differ in individual reservoirs. In the montane, gorge rheolimnic reservoir at Wisła-Czarne the transport of allochthonous organic and mineral matter played a decisive role. In this reservoir with poor vegetal and animal plankton, the process of formation of bottom macrofauna could be observed in the central zone only, in the course of the old riverbed. In the Rybnik Reserovir, which holds an intermediate position between the gorge, rheolimnic and pool limnic reservoirs, the process of formation of bottom macrofauna communities was above all affected by the inflow of pollution in the waters of the rivers feeding this reservoir (the Ruda and the Nacyna) and also by warm waste water from the power plant.

The limnic Goczałkowice Reservoir is of the flood waters type. It seems that the large area of flooded territories in relation to the river formerly flowing through them, played, it would seem, a very decisive role in the process of formation of the bottom macrofauna. It was possible to show dependences between plankton and benthos communities, higher vegetation, and the abiotic environment, which occurred in the process of formation of the whole ecosystems. In the first period, only a few organisms from flooded water bodies were propagated profiting from the lack of competition (some aquatic plants such as *Utricularia vulgaris*, *Lemna minor*, and *Elodea canadensis*: Kuflikowski 1986). Of land animals scarce numbers Oligochaeta and amphibiotic Chironomidae (*Pseudosmittia* sp., *Smittia* sp.) were observed for some weeks only. On the other hand, the occurred a mass development of aquatic Chironomidae, which utilized the decomposing vegetation as their feeding ground. In this early period only greater numbers of Crustacea were noted in the animal plankton, while in the vegetal one there occurred blooms of blue-green alga *Aphanizomenon flos aquae*. In the second period he decomposition of the flooded vegetation and the leaching of primary soils were continued. The banks of the reservoir were observed to change. In some places the scouring of banks reached 20—35 m, though the formation of coastal beaches and submerged shoals, which limited the process of bank erosion, occurred at the same time (Pasternak 1964). In the phytoplankton great numbers of algae and frequent diatom blooms, in most cases caused by *Asterionella formosa*, were observed. The dynamic development of zooplankton with Rotatoria as dominants, took place there. Macrophytes, at first submersed, then emerged, and formed large overgrown areas, creating a swamp zone. In the communities of bottom macrofauna Chironomidae, especially *Chironomus* sp. I, dominated. Other groups, especially Oligochaeta and Bivalvia of the Unionidae family, began to play an ever greater role. In the third period the formation of permanent biocenoses of the reservoir was completed, though at the sometime their numbers fell. The abundance of bottom macrofauna also decreased. Among Chironomidae the dominant taxon was *Procladius* spp. Molluscs, chiefly *Anodonta cygnea* (in the first part of this period) and *Unio pictorum* (in the second part) were important constituents of the biomass. From

1966—1974 a dramatic decrease in the numbers of phytoplankton was recorded. The filtratory action of *Anodonta cygnea* may have played a significant role here. Fig. 10 shows the concomitance of the most intensive development of these molluscs with the period of the greatest quantitative reduction of phytoplankton. The change of domination from *Anodonta cygnea* to *Unio pictorum* in the first part of the seventies was probably caused by the lowering of the water level in 1972, when a great number of these animals remained and died on the exposed part of the bottom. The fall in the water level occurred in the summer season, when *Anodonta* had as yet no progeny, while glochidia of *Unio pictorum* had been produced in spring. In the second part of the seventies the numbers of phytoplankton increased and blooms of blue--green algae (*Microcystis aeruginosa*) began to occur priodically. This was caused by the increased water fertility in the reservoir on account of the more intensive inflow of nutrients. In the years 1975—1976 and in 1978 the mean content of phosphorus did not fall below 10 μg $P\text{-}PO_4$ dm^{-3}. This value is regarded as the limit above which the mass development of phytoplankton is possible. It is also possible that a decrease in the numbers of Unionidae might have contributed to the more anundant development of phytoplankton. The great content of mineral suspension in the water of this reservoir, negatively affecting Cladocera

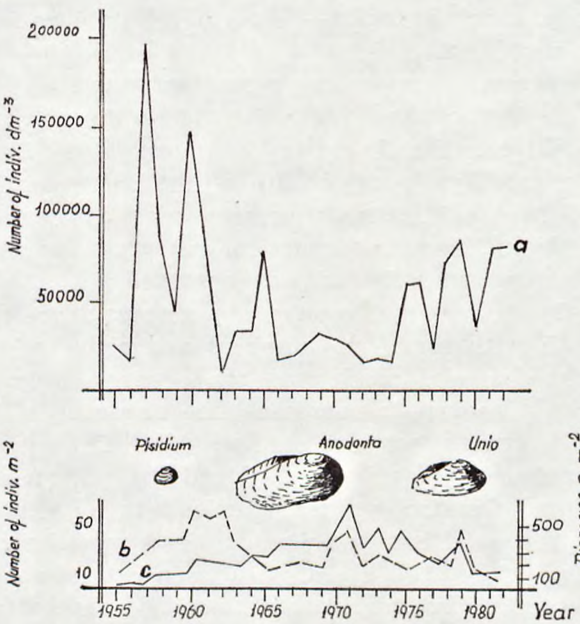

Fig. 10. Course of changes of average annual numbers of phytoplankton (a) and course of changes of average annual numbers (b) and biomass (c) of Bivalvia in the Goczałkowice Reservoir

and, to a small degree, Rotatoria (Żurek 1980), probably accounted for the domination of the latter in the zooplankton and for the small numbers of Crustacea during the entire 28-year period of the reservoir's existence. An attempt at biocoenotically connecting the different trophic links and also the zones of the Goczałkowice Reservoir was presented by Kownacki and Krzyżanek (1986).

5.5. General rules in the formation of bottom macrofauna communities in dam reservoirs

From the first moment of existence of a dam reservoir there occur quantitative and qualitative changes in the ecosystem, which after a certain period result in the formation of a fairly stable one. The formation of the entire ecosystem of the reservoir takes place according to a regular pattern. This well-ordered process, i.e. the ecological succession, is also observed in bottom macrofauna communities.

In dam reservoirs of the Soviet Union three periods of formation of bottom macrofauna communities were in general distinguished: 1 — a period of gradual devastation and decline of land biocoenoses and of remodelling of existing aquatic ones; 2 — a period of formation of transitional communities with a mass settlement of the flooded area by a varied Chironomidae fauna; 3 — a period of stabilization accompanied by a decrease in biomass.

In these reservoirs the entire period of stabilization of animal communities of the bottom took 3—5 years (Musatov 1979). Thie priodicity is similar to that found in the investigated Silesian reservoirs. The only difference lies in the length of the particular periods. In the Soviet Union the stabilization processes were faster. In most dam reservoirs in which Chironomidae dominated succession changes occurred within this family, similarly as was observed in the Goczałkowice Reservoir. In the first years *Chironomus plumosus* developed abundantly, dominating both with regard to numbers and above all to biomass. In later years the share of predatory forms, with *Procladius* spp. as a decisive dominant, began to increase. The sequence of settelemen by different animal groups was also similar. After Chironomidae an icreasingly important role began to be played by Oligochaeta, Mollusca (Sphaeriidae) and Ceratopogonidae, particularly in central parts, and Mollusca (Gastropoda, Bivalvia-Unionidae, and sometimes Dreissenidae), Ephemeroptera, Trichoptera, and Crustacea in littoral zones. Usually the mass development of bottom macrofauna lased several years and was then followed by a distinct decrease un numbers and biomass. In the period of stabilization of the ecosystem an increase in the biomass of bottom macrofauna was observed in some reservoirs. This concerned those were the mass development of *Dreissena* took place and also those where new Caspian crustaceans had been introduced (e.g., in the reservoirs on the Dnieper — L u b y a n o v et al. 1967). However, in many cases a decrease in biomass, especially of soft fauna, was observed in this period. Probably, it also took place in the Goczałkowice Reservoir in the period 1963—1970 as it was manifested by reduced numbers (the biomass was investigated in 1971). The biomass of this reservoir, estimated together with molluscs certainly increased, since the numbers of the Unionidae family rose.

The obtained results of studies on bottom macrofauna show that in the two types of reservoir the processes occurring during the formation of communities of these animals differed both with regard to numbers and quality. In rheolimnic reservoirs the fauna which settles the bottom is little differentiated and is basically limited to one grup, Oligochaeta. The process of settling the bottom occurs very unevenly over its whole area. In limnic reservoirs the bottom is settled by a very varied fauna with the domination of midges (Chironomidae) and is basically similar over the entire area. Since to animal groups play a decisive role in the formation of communities of bottom macrofauna, dam reservoirs may be divided into two categories: a) reservoirs of the Oligochaeta type include a few small rheolimnic gorge reservoirs, similar to the Wisła-Czarne one, and b) reservoirs of the midge type (the Chironomidae type) include most dam reservoirs, particularly the pool limnic ones, similar to those at Goczałkowice and Rybnik.

The above division is very general. In each dam reservoir are to be found such dominant animal organisms, particular species (taxa), genera, families, and even classes, as can be used in classifying the given reservoir to a separate type. On the basis of Mollusca the reservoirs of a) Bivalvia type (Goczałkowice) and b) Gastropoda type (Rybnik) may be distinguished, and on the basis of Bivalvia themselves may be sclassified as of a) Unionidae type (Goczałkowice, Tresna, Novosibirsk) and b) of Dreissenidae type (the reservoirs of the Dnieper and Volga cascades, reservoirs in northern Poland, e.g. Koronowo). Similarly, on the basis of snails (Gastropoda) settling the bottom, dam reservoirs of a) Valvatidae type (Goczałkowice) and b) Physidae type (Rybnik) may be distinguished.

The Chironomidae family is an excellent material in the formation of separate classification. The indicatory species of these flies living in the profundal have frequently been used in the classification of lakes by, among others, B r u n d i n (1949) and T h i e n e m a n n (1954).

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6. Polish summary

Formowanie się zgrupowań makrofauny dennej w trzech zbiornikach zaporowych na Śląsku (południowa Polska) od początku ich istnienia

Proces formowania się zgrupowań makrofauny dennej w zbiornikach zaporowych przedstawiony został w oparciu o wieloletnie badania przeprowadzone w trzech zbiornikach zaporowych na Śląsku, uzupełnione danymi literaturowymi. Dwa z tych zbiorników — Wisła-Czarne i Goczałkowice położone są na Górnej Wiśle, trzeci — Rybnik na rzece Rudzie, prawym dopływie Odry (ryc. 1, 2, tabela I). Wyniki badań przedstawiono na tle zmian składu chemicznego jego wody (tabela II) oraz składu zbiorowisk planktonowych i makrofitów.

W formowaniu się makrofauny dennej zbiorników Goczałkowice i Rybnik główną rolę odgrywały Chironomidae (tabele III, V, ryc. 3, 4) i Mollusca (tabele VII, VIII), zaś zbiornika Wisła-Czarne Oligochaeta (tabela VI, ryc. 5, 8). Proces formowania się tych zgrupowań przebiegał etapowo. W zbiorniku Goczałkowice przebiegał w 3 okresach (ryc. 3, 7). Pierwszy, obejmujący rok 1955, charakteryzował się wymieraniem form lądowych i pojawieniem się fauny wodnej głównie z Chironomidae. Drugi okres obejmował lata 1956—1963. Nastąpił wówczas masowy rozwój Chironomidae, głównie *Chironomus* sp. I, a także innych grup bezkręgowców, przede wszystkim Oligochaeta i Mollusca. Trzeci okres rozpoczął się w 1964 roku. W latach 1964—1973 nastąpił spadek liczebności makrofauny dennej, a następnie ponownie jej wzrost. W rodzinie Chironomidae wzrósł udział *Procladius* spp., w rodzinie Unionidae (Bivalvia) po początkowej dominacji *Anodonta cygnea* L. na początku lat 70-tych zaczęła dominować *Unio pictorum* L. (ryc. 9). W zbiorniku Wisła-Czarne w pierwszym etapie obejmującym lata 1974—1975, doszło do masowego rozwoju Oligochaeta. Drugi okres, obejmujący lata 1976—1984, charakteryzował się znacznym spadkiem liczebności i biomasy tej grupy zwierząt (ryc. 3). W zbiorniku Rybnik wyróżniono dwa okresy (ryc. 4, 6). W pierwszym (1972—1973) nastąpił najpierw bardzo silny rozwój Oligochaeta, następnie Chironomidae. W drugim okresie (1974—1981) w pierwszych pięciu latach notowano spadek liczebności, zaś w latach 1979—1981 wzrost liczebności i biomasy. Wzrost ten spowodowały głównie Oligochaeta, natomiast wzrost biomasy spowodowany został przez Gastropoda, głównie *Physa acuta* Drap.

Wyniki badań trzech zbiorników zaporowych oraz dane literaturowe pozwoliły ustalić, że proces formowania się makrofauny dennej przebiega w następujących etapach: — pierwszy okres to tworzenie się pierwszych (pionierskich) zgrupowań, drugi jest okresem zgrupowań przejściowych, trzeci to okres tworzenia się zgrupowań trwałych. W procesie tym dwie grupy zwierzęce odgrywają decydującą rolę: owady z rodziny Chironomidae (tabele III, V) i Oligochaeta (tabela VI). Na

tej podstawie można wyodrębnić dwie grupy zbiorników zaporowych: a) zbiorniki typu skąposzczetowego (typ Oligochaeta), do których należy zbiornik Wisła-Czarne, b) zbiorniki typu ochotkowatego (typ Chironomidae) do których należą zbiornik Goczałkowice i Rybnik.

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