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Consequences of the basin morphology for fish community in a deep-storage submontane reservoir

Antoni AMIROWICZ

Karol Starmach Institute of Freshwater Biology, Polish Academy of Sciences, ul. Sławkowska 17, 31-016 Kraków, Poland

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Abstract – In the Dobczyce Reservoir (49°52' N, 20°02' E, the River Raba, Carpathian Mts; area 9.85 km^2, volume 0.108 km^3, maximum depth about 27 m, mean water residence time 0.34 yr), which fills up the river valley with flat floor and steep sides, distinct longitudinal and vertical gradients in Secchi depth, temperature and dissolved oxygen were recorded in 1988–1997. Owing to reservoir operation the water level fluctuated between -5.9 and 1.7 m in relation to the standard damming ordinate (269.9 m a.s.l.) which resulted in changes in the area (7.02–10.63 km^2) and volume (0.059–0.126 km^3) and influenced substantially some habitat conditions. Ecological effects on fish populations are discussed.

Key words: freshwater fishes, ecology, habitat diversity, littoral, pelagial.

1. Introduction

A reservoir is a water body created by constructing a dam across a river valley to store impounded water to satisfy such human demands as municipal and industrial water supply, irrigation, hydropower generation, flood control, navigation, etc. Contrary to natural lakes reservoirs are fully engineered systems designed and controlled according to their purposes. For this reason they may be influenced by seasonal hydrological phenomena only to a limited extent, but at the same time every reservoir modifies significantly the hydrological regime in river channel below the dam. Usually reservoirs are localized where lakes or other large natural water bodies do not exist. Thus, most of reservoirs as a rule are aquatic ecosystems not previously existing in their river basins. As there is a wide variety of local conditions, natural ones such as geology and climate, as well as those altered by human activity (e.g. water quality influenced by waste water discharge and land use in drainage basin) each of such man-made "lakes" may be regarded as a unique ecosystem that offers specific living conditions to local associations of aquatic organisms. Therefore, each reservoir is an interesting subject of limnological studies.

Investigations carried out in last decades helped to develop general paradigms for reservoirs (Thornton et al. 1990). However, as the number of reservoirs increases continuously they will provide research problems for many years. Results of these studies not only enhance our knowledge but also may be useful for management of reservoirs and may help to solve environmental problems caused by these water bodies. In Poland there are about forty reservoirs with volumes greater than 10 10^6 m^3 (Głodek 1985). These reservoirs are located in mountains in southern Poland and in the lowland area of the central part of the country. In several reservoirs more detailed research work was carried out (among others Kajak 1990, Pająk and Kiss 1990, Krzyżanek 1991, Galicka et al. 1992, Rakowska and Rakowski 1992, Bednarz and Starzecka 1993, Dumnicka 1993, Krzyżanek et al. 1993, Kwandrans et al. 1994, Górniak and Jekatierynczuk-Rudczyk 1995, Gwiazda 1995, Wilk-Woźniak 1996; see also Kasza 1991). The results of these studies provided valuable contribution to the ecology of aquatic organisms in Central European reservoirs.

Despite being constructed for purposes other than inland fishery development, in most cases the Polish reservoirs are water bodies of great importance for recreational and commercial fishing (Mastyński 1985, Mastyński and Wajdowicz 1994). Therefore, they need fishery management including: (1) professional monitoring of fish community, (2) improvement of species composition by stocking valuable species and reduction of unwanted ones, and (3) controlled exploitation. These measures, if properly taken may produce both direct and indirect (e.g. maintenance of desired water quality by biomanipulation) economic profits. As the fish production in reservoirs may be strongly influenced by habitat conditions specific to these ecosystems (O'Brien 1990), in every study of reservoir fish populations a special attention should be paid to the ranges of possible fluctuations of essential abiotic and biotic factors, i.e. water level, physico-chemical features of water, presence of suitable microhabitats for each development stage, available food resources, and intensity of competition and predation.

The aim of this work is to characterize the main habitats and their ecological conditions in a typical Carpathian submontane reservoir.

2. Study area, material and methods

The Dobczyce Reservoir (49°52' N, 20°02' E) is located between the upper and middle course of the River Raba (a tributary of the Vistula) about 30 km southward of Cracow. The dam 31 m high and 700 m long was constructed near the town of Dobczyce to create a medium-size reservoir designed for water storage of about 90 10^6 m^3 for potable water supply, and to maintain a volume reserve of 25 10^6 m^3 for flood control.

The drainage basin of the Dobczyce Reservoir has an area of 763 km^2 (Pasternak 1980) and includes parts of several montane (up to the altitude 1310 m) and submontane geographical units of the western Carpathian Mts built of Tertiary sandstone. Local climate in the reservoir area may be characterized by the mean annual temperature of about 7 °C. Water temperature in running waters in the catchment basin fluctuates between 0.1–0.2 °C in winter and 20–25 °C in summer. Annual precipitation ranges from 800 to 1000 mm depending on the altitude. It results in the average runoff of about 13 L s^{-1} km^{-2} and yields the mean annual discharge of about 10 m^3 s^{-1} in the Raba at the reservoir dam (Punzet 1969). The inflow of water to the Dobczyce Reservoir is dominated by the flow from the Raba, which supplies 88.6% of the total amount of water entering reservoir, while seven other tributaries provide only 6.7%, the direct (non-channelized) flow 2.1%, and the precipitation on the reservoir surface 2.6% (Mazurkiewicz 1988).

The reservoir catchment area is inhabited by a population of 90,000–100,000 people. In the land use predominate arable fields and permanent crops (pastures, meadows and orchards), which constitute 40.5% and 10.5% of the total area, respectively, while the natural vegetation (deciduous and mixed forest) occupies 39.2% (Gawlikowski and Jarosz 1980). This results in feeding the Dobczyce Reservoir with relatively fertile water (Mazurkiewicz 1988). The water quality in its catchment is influenced mainly by discharge of raw municipal sewage from two small towns (Rabka and Mszana Dolna), domestic effluents from numerous villages, runoff from arable fields, and continuous ingress of dissolved compounds of nitrogen and phosphorus from sewage treatment work in the town of Myślenice (Wróbel 1980). Nutrient rich water entering the reservoir leads to increased growth of planktonic algae which causes periodical water blooms. It should be taken into consideration that eutrophic conditions in the Dobczyce Reservoir may seriously effect its main function. During episodic storm-related inflows the reservoir also receives considerable loads of particles eroded from soils in the agricultural portions of drainage basin. According to Łajczak (1995) the 50% of the initial volume of the Dobczyce Reservoir will have been filled with sediment in 650 years.

The dam was closed in early 1986 and the filling of reservoir was finished in December 1987. Since 1988 three damming ordinates determine the reservoir operation: the standard (269.9 m above sea level), minimum (256.7 m), and maximum (272.6 m) damming level. The water mass retained behind the dam fills up the typical submontane river valley with flat floor up to 1.5 km wide and relatively steep (the slope gradient exceeds 30% in several places) and high (up to about 100 m) sides (Galarowski 1980). There is only one large lateral valley, the Wolnica stream valley (left-side tributary of the Raba) within the reservoir area. In general, the main channel keeps a NE direction excluding a stretch near the dam where the River Raba winded between three hills, the Zuchówka, Góra Jałowcowa, and Góra Zamkowa. As a result of the landscape configuration the Dobczyce Reservoir consists of three distinct parts (Fig. 1). The downreservoir sub-basin, the Dobczyce Basin, is separated from the upreservoir portion, the Myślenice Basin, by the narrowed section of the main valley. The Wolnica Bay extends to the NW of the lower part of the Myślenice Basin. The shape of the basin determines some of the useful characteristics of a reservoir. They are: (1) the water residence time which is calculated by dividing the volume (i.e. water surface area multiplied by the mean depth) by the inflow rate; (2) its reciprocal, the flushing rate; and (3) the morphoedaphic index calculated as a ratio of the concentration of total dissolved solids to the mean depth (i.e. reservoir volume divided by the water surface area). Basin morphology also determines the structure of habitats in a water body and affects their ecological conditions.

Comparisons between natural lake and dam reservoir ecosystems were published twenty years ago (Margalef 1975, Ryder 1978). Nowadays it is commonly accepted that ecological characteristics of reservoirs are markedly divergent from properties of lakes and they are considered as being "semifluvial" systems known for their dynamic and heterogeneous nature (Thornton et al. 1990). It is emphasized that reservoirs, as inundated river valleys are often relatively long and receive majority of the water, nutrient and sediment load from one large tributary. This produces longitudinal gradients in main abiotic and biotic factors. Typically, three zones are distinguishable along the longitudinal axis of a reservoir (Kimmel et al. 1990):

1. The riverine zone at the mouth of large tributary. This part of reservoir is narrow, shallow, and characterized by short water residence time, high nutrient concentration and turbidity.

2. The transitional zone with high primary productivity caused by significant decrease of the amount of allochthonous suspended particles to sedimentation.

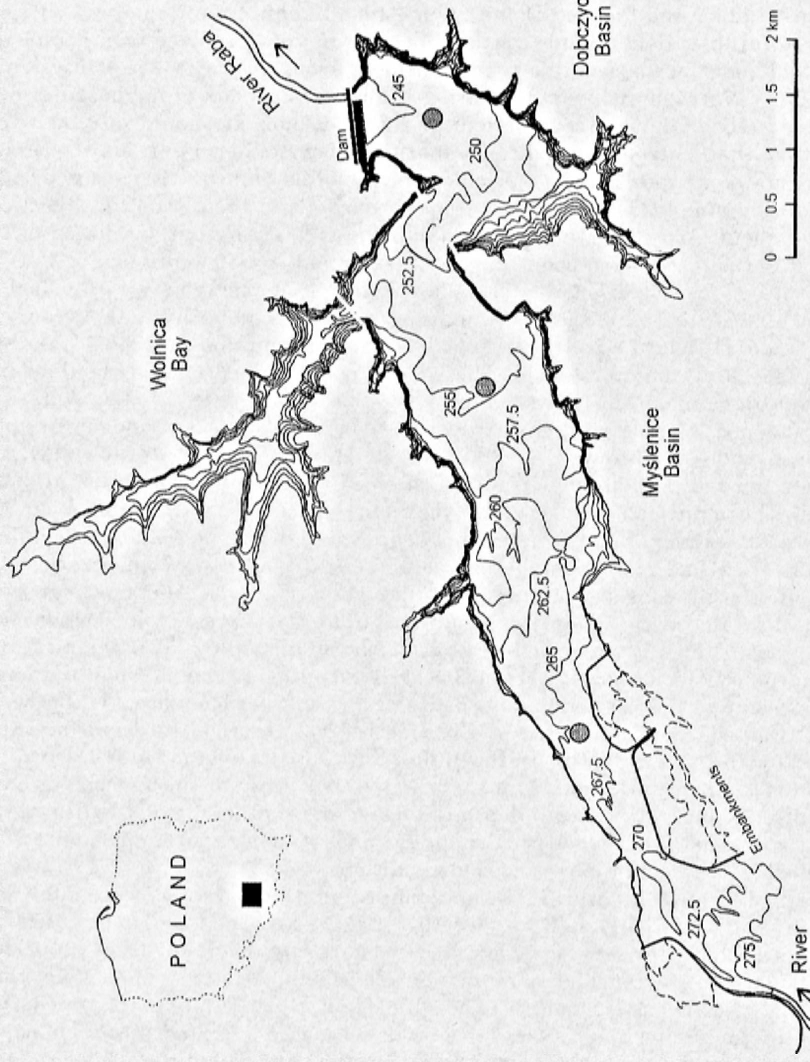

Fig. 1. Basin morphology of the Dobczyce Reservoir (at contour lines the altitudes are given). Circles indicate location of sampling points.

3. The lacustrine zone near the dam which has maximum depth and is characterized by long water residence time, low concentration of nutrients and deep photic layer.

The limits of these zones are not distinct and quite dynamic as they expand or contract in response to hydrologic events and reservoir operation schedules. Increases in basin width also cause the occurrence of lateral gradients between the main channel and coves.

On the other hand reservoirs with long water residence time can be considered as "semistagnant" water bodies with essential features exhibiting vertical gradients in the water column. The principal environmental factors are the light penetration and wind-induced water mixing (Moss 1988). These factors result in structuring the water mass in annual cycle. In temperate climate the main phases of that cycle are two periods of stagnation (with direct stratification of water column in summer and inverse stratification in winter) which are separated by periods of spring and autumn mixing. The vertical stratification in summer when the epilimnion and hypolimnion may remain separate for a long period, has large effects on the chemistry of water. The most important for fish is that hypolimnetic oxygen reserves cannot be restored until autumn overturn. However, even when the water column is mixed from top to bottom the vertical gradient in photic conditions results in division of the bottom area into the littoral where primary production can occur and the dark profundal.

To properly characterize the environmental conditions in a reservoir both the horizontal and vertical characteristics should be considered. To meet this requirement three points located in the headwater area, the possible transition zone, and near the dam were selected in the Dobczyce Reservoir (Fig. 1). Special attention was paid to vertical patterns in water column during summer stagnation. As it begins in May and lasts until September it was assumed that the clearest profiles occur in July and August. The study is based on the sets of data on Secchi depth, water temperature, and dissolved oxygen collected in 1988–1997 in fortnightly intervals by the Biology and Fisheries Station at Brzączowice during the long-term monitoring of main physico-chemical properties of water in the Dobczyce Reservoir. The daily records of water damming level were provided by the Regional Water Management Authority (ODGW) in Cracow. A topographical map in 1:10,000 scale was used to analyse the reservoir morphometry. The areas enclosed by the contour lines were measured using the polar planimeter PL 1 (PZO, Poland). The procedure of computation of morphologic characteristics of the reservoir basin is explained in Appendix A.

To estimate the euphotic depth, i.e. depth at which underwater light has decreased to 1% of the surface irradiance, Secchi disk readings were used following Tilzer (1988). On the basis of the results gathered in the meso-eutrophic Lake Constance with chlorophyll *a* concentration within range 0.3–35 μg L^{-1} the author found that euphotic depth (Z_p) can be related to Secchi depth (Z_S) according to a rough approximation expressed by $Z_p = 5\ (Z_S)^{1/2}$. The correlation calculated by Tilzer was significant ($P<0.001$) and relatively strong ($r^2=0.85$).

While summarizing the collected data sets the following characteristics of the recorded values were considered: (1) their distributions may be skewed and not unimodal, (2) they may be positively autocorrelated, and (3) they may depend on uncontrolled variables, seasonal patterns, and reservoir operation schedules. Therefore, to analyse correctly the collected data:

1. The median (M; central value of the distribution of data in an ordered array from smallest to largest) not the arithmetic mean (m) was used as the measure of location.

2. The interquartile range (IQR; the range between the 1st and 3rd quartile, Q_1 and Q_3, which comprise half of the data) and intersextile range (ISR; the range between the (1/6)th and (5/6)th quantile which comprise two thirds of the data sample and therefore may be regarded as an analogue to the m ±SD range in which fall 68.27% of the items in a normal frequency distribution) were used in place of the standard deviation (SD) as the measure of spread. To compute a quantile: (1) the data set was ranked from smallest to largest; (2) the position of the quantile was calculated according to Helsel and Hirsch (1992) as $Q(n+1)$ where Q is the quantile value (e.g. 1/2 for the median) and n is the sample size; and (3) if the obtained position was not an integer the average of the adjacent data was calculated, as by the Tukey's (1977) upper and lower hinges computation.

3. Results and discussion

In the Dobczyce Reservoir currently occurs a fish community consisting of 21 species (A. Amirowicz unpubl.). Prior to the reservoir origin twenty-three fish species were found on its territory in the Raba and tributaries in 1983–1985 (Jelonek and Starmach 1988). Among them the most abundant were chub, *Leuciscus cephalus* (L.), spotted barbel, *Barbus petenyi* Heckel, brown trout, *Salmo trutta* m. *fario* L., nase, *Chondrostoma nasus* (L.), minnow, *Phoxinus phoxinus* (L.), and stone loach, *Noemacheilus barbatulus* (L.), while less abundant but still common were also gudgeon, *Gobio gobio* (L.), and perch, *Perca fluviatilis* L. Only three of them, i.e. chub, nase and perch successfully colonized habitats offered by the newly constructed reservoir, however, only perch reached the rank of dominant species in the reservoir fish community. Other dominant reservoir species, i.e. bream, *Abramis brama* (L.), roach, *Rutilus rutilus* (L.), bleak, *Alburnus alburnus* (L.), and pikeperch, *Stizostedion lucioperca* (L.) were earlier uncommon or rare.

The new habitat complex for fish community which was created as the Dobczyce Reservoir basin filled is a water body which basic characteristics (surface area, volume, mean and maximum depth) depend on the damming ordinate (Table I). At the standard damming level, i.e. 269.9 m above sea level, the reservoir has a total area of 9.85 km^2 and a volume of 0.108 km^3. The mean depth is 11 m and the maximum depth about 27 m. The mean water residence time equals to 0.34 yr (the flushing rate: 2.92 yr^{-1}). Almost the whole water mass is divided between the Dobczyce Basin (39%) and the Myślenice Basin (56%), with the Wolnica Bay occupying the remaining 5%. The respective parts of the total surface area are 26%, 62%, and 12%. The mean depth of the Dobczyce Basin is 5.4 m greater than the mean depth of the whole reservoir. The mean depths of the Myślenice Basin and Wolnica Bay, on the contrary, are smaller (1.1 and 6.1 m, respectively). As the pool elevation is controlled according to the current and prognosed hydrological events and water supply schedule the raising and drawdown of the water level within the range of 13.2 m below and 2.7 m above the standard ordinate should be expected. This may result in the reduction of 61% or gain of 13% of the standard surface area. It shows how large areas may be alternately inundated or exposed. As concerns the volume these figures are 83% and 26%, while in the case of the mean depth 6.3 and 1.3 m, respectively. Reservoir biocoenosis, including fish populations must be resistant to all environmental consequences of such phenomena. In general relatively large and rapid fluctuation of water level is a common attribute of reservoirs.

In the Dobczyce Reservoir occurs another characteristic feature of the majority of reservoirs, that is the distinct downreservoir increase in Secchi depth (Kimmel

Table I. Morphologic characteristics of the Dobczyce Reservoir and its main parts according to a 1:10,000 scale topographical map: A – surface area, V – water mass volume, D – mean depth. The altitudes marked by contour lines on the map are indicated with bold type. At each contour line three measurements of the respective surface area were made with accuracy to at least 0.004 km^2. Therefore, their arithmetic means were assumed as being accurate to two decimal places. These averaged areas are also in bold type. All the remaining areas and volumes were calculated as explained in Appendix A. Volumes referring to the entire reservoir are the sums of the volumes of particular parts. Mean depths were obtained dividing volumes by areas.

Altitude (m)	Dobczyce Reservoir			Parts								
				Dobczyce Basin			Myślenice Basin			Wolnica Bay		
	A (km^2)	V (10^6 m^3)	D (m)	A (km^2)	V (10^6 m^3)	D (m)	A (km^2)	V (10^6 m^3)	D (m)	A (km^2)	V (10^6 m^3)	D (m)
243.3	0	0	0	0	0	0						
245	0.13	0.07	0.6	**0.13**	0.074	0.6						
247.6	0.52	0.86	1.7	0.520	0.86	1.7	0	0	0			
250	1.21	2.85	2.4	**1.11**	2.77	2.5	**0.10**	0.080	0.8			
252.5	1.78	6.56	3.7	**1.55**	6.08	3.9	**0.23**	0.48	2.1			
255	3.07	12.44	4.1	**1.76**	10.22	5.8	**1.31**	2.22	1.7			
256.2	3.62	16.44	4.5	1.812	12.36	6.8	1.805	4.08	2.3	0	0	0
256.7[a]	3.87	18.32	4.7	1.834	13.27	7.2	2.034	5.04	2.5	0.004	0.001	0.2
257.5	4.33	21.59	5.0	**1.87**	14.75	7.9	**2.43**	6.83	2.8	**0.03**	0.013	0.4
260	5.52	33.85	6.1	**2.01**	19.60	9.8	**3.36**	14.03	4.2	**0.15**	0.22	1.5
262.5	6.39	48.72	7.6	**2.16**	24.82	11.5	**3.94**	23.15	5.9	**0.29**	0.76	2.6
265	7.47	66.02	8.8	**2.29**	30.38	13.3	**4.67**	33.90	7.3	**0.51**	1.75	3.4
267.5	8.63	86.12	10.0	**2.41**	36.25	15.0	**5.40**	46.47	8.6	**0.82**	3.39	4.1
269.9[b]	9.85	108.27	11.0	2.573	42.23	16.4	6.090	60.25	9.9	1.183	5.78	4.9
270	9.90	109.25	11.0	**2.58**	42.49	16.5	**6.12**	60.86	9.9	**1.20**	5.90	4.9
272.5	11.07	135.44	12.2	**2.73**	49.12	18.0	**6.77**	76.96	11.4	**1.57**	9.35	6.0
272.6[c]	11.12	136.56	12.3	2.736	49.40	18.1	6.794	77.64	11.4	1.588	9.52	6.0
275				**2.89**			**7.39**			**2.05**		

[a] minimum reservoir operation level
[b] standard damming ordinate
[c] maximum pool elevation

et al. 1990). In summer 1988–1990 and 1994 Secchi depth in headwater area (0.5–1.2 m) was about 3 times smaller than in the Myślenice Basin and Dobczyce Basin where most of measurements ranged between 1.5 and 3 m (Fig. 2). The

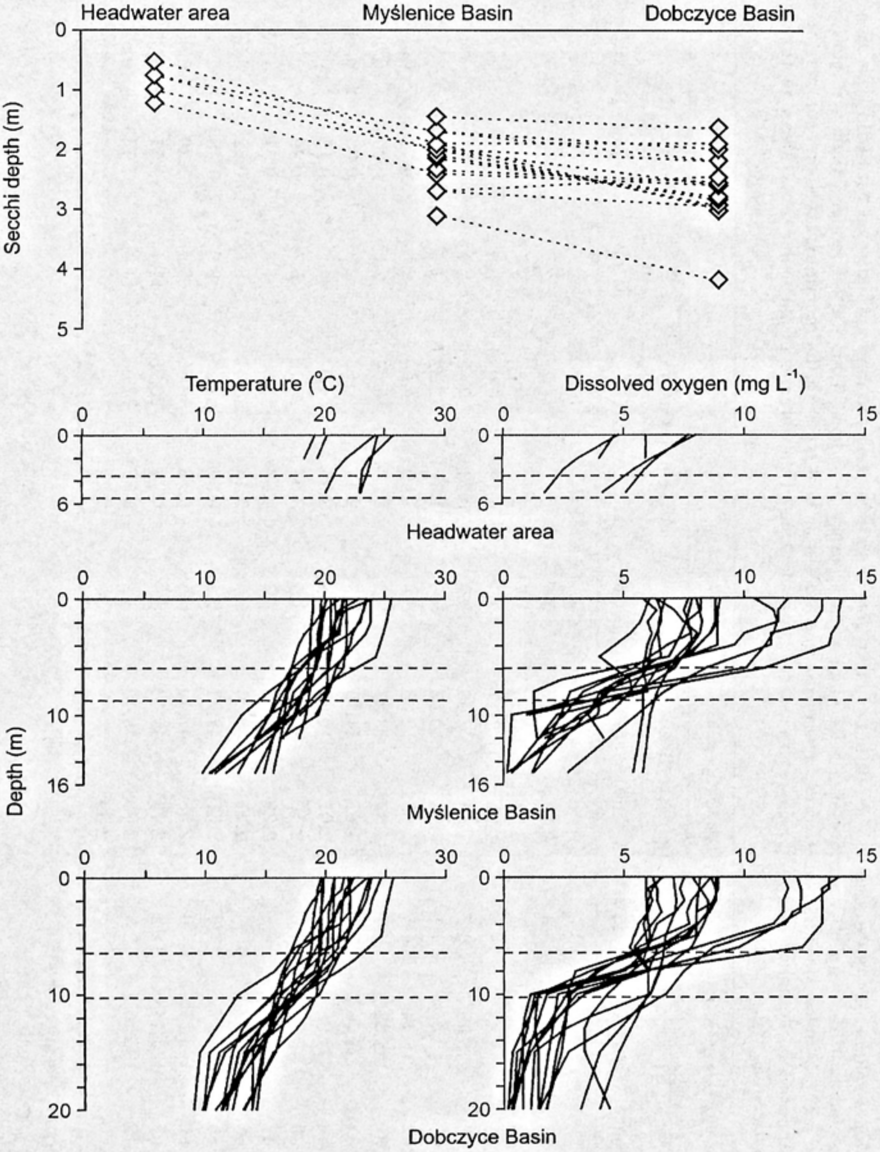

Fig. 2. Midsummer (July–August) Secchi depths and vertical patterns of water temperature and dissolved oxygen concentration at three sampling points along the longitudinal axis in the Dobczyce Reservoir in 1988–1990 (11 sampling dates) and 1994 (5 sampling dates). Dotted lines connect measurements collected on the same sampling date. Horizontal dashed lines in vertical pattern panels indicate minimum and maximum euphotic depth estimated according to Tilzer (1988).

respective lower boundaries of photic layer were estimated within 3.5–5.5 m depth range in the headwater zone, 6–8.8 m in the Myślenice Basin, and 6.4–10.2 m in the Dobczyce Basin. Contrary to this, the differences in temperature and dissolved oxygen profiles observed along the longitudinal axis of the reservoir were relatively small. General patterns of vertical profiles were uniform differing only in the vertical extent according to the depth at the sampling point (Fig. 2). Despite the possibly strongest horizontal gradient in habitat condition in the Dobczyce Reservoir (as the gradients between main pool and lateral coves are certainly weaker) the absolute differences in temperature or oxygen concentration measurements collected on the same day only rarely exceeded 2 °C or 3 mg L^{-1} (Table II). In addition, the probability that a value measured in headwater zone or

Table II. Difference ranges between records of water temperature and dissolved oxygen concentration at three sampling points along the longitudinal axis in the Dobczyce Reservoir in July–August 1988–1990 and 1994: H–DB – differences between the headwater area and the Dobczyce Basin (5 sampling dates), MB–DB – differences between the Myślenice Basin and Dobczyce Basin (16 sampling dates).

Depth (m)	Water temperature (°C)				Dissolved oxygen (mg L^{-1})			
	H–DB		MB–DB		H–DB		MB–DB	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
0	-0.5	0.8	-1.2	0.6	-3.04	0	-1.76	0.20
1	-0.9	0.4	-1.1	0.6	-3.74	-0.67	-1.12	1.12
2	-1.4	0.1	-1.1	1.0	-4.45	-0.54	-0.96	1.32
3	-1.7	0.3	-1.3	1.3	-4.86	-2.69	-1.60	2.06
4	-1.5	0.8	-1.7	0.5	-4.99	-2.62	-1.60	1.87
5	-1.3	1.4	-2.9	0.4	-5.12	-2.56	-2.08	1.31
6			-1.9	0.6			-2.20	1.12
7			-1.6	0.2			-2.53	1.87
8			-2.1	0.4			-2.34	2.62
9			-1.4	0.7			-2.30	1.86
10			-0.8	1.5			-2.56	3.20
11			-1.0	1.2			-2.30	2.05
12			-1.2	1.2			-2.05	1.38
13			-1.5	0.9			-1.47	1.08
14			-2.0	1.2			-1.21	1.44
15			-2.6	1.5			-1.50	1.80
Min.	-1.7		-2.9		-5.12		-2.56	
Max.		1.4		1.5		0		3.20

at the half of the reservoir length will be smaller or greater than that recorded at the same time and the same depth in lacustrine basin near the dam seems to be roughly equal. The only noticeable tendency occurred in oxygen concentration at the headwater sampling point where the collected measurements were smaller (2–5 mg L^{-1} in most cases) than those recorded downreservoir. Relative oxygen deficiency in headwater area of a reservoir in summer may be explained as the effect of increased oxygen demand due to river-borne organic matter load, and high temperature of shallow water (Cole and Hannan 1990).

Vertical differences in temperature and oxygen concentration seem to be more important to reservoir organisms than the horizontal ones. Vertical patterns of water temperature recorded in July and August 1988–1997 allow to distinguish the relatively warm surface water (18–25 °C), cold deep water (8–18 °C), and the middle layer with a considerable temperature gradient (Fig. 3). The vertical patterns of dissolved oxygen concentration show a similar picture. Also in this case the water column may be divided into three layers, the upper rich and even oversaturated with oxygen (6–14 mg L^{-1}), the lower with decreased oxygen content (<4 mg L^{-1} in most sampling dates), and a transitional one in which strong

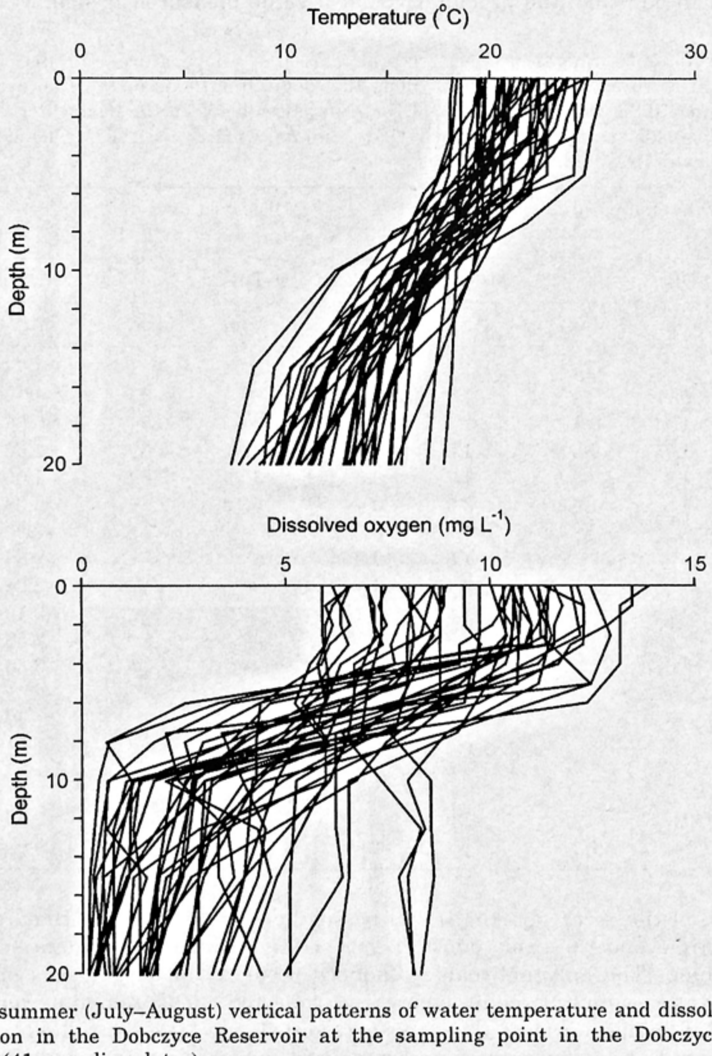

Fig. 3. Midsummer (July–August) vertical patterns of water temperature and dissolved oxygen concentration in the Dobczyce Reservoir at the sampling point in the Dobczyce Basin in 1988–1997 (41 sampling dates).

gradient in oxygen concentration is clearly visible. To analyse the observed gradients each of 41 vertical profiles was divided at 1-m depth intervals and within them particular gradients were calculated. This procedure gave two data sets of 820 items each. Particular vertical gradients in water temperature ranged from 0 to 2.44 °C m^{-1} and their frequency distribution was strongly skewed to the right (M: 0.40, Q_1: 0.16, Q_3: 0.72). Therefore, a sub-set of large gradient values was obtained by selecting all the greater than 3rd quartile, i.e. 0.72 °C m^{-1}. The vertical distribution of large gradients is normal-like with the median located within 8–9 m depth interval (IQR from 6–7 to 11–12 m; ISR from 5–6 to 12–13 m) (Fig. 4).

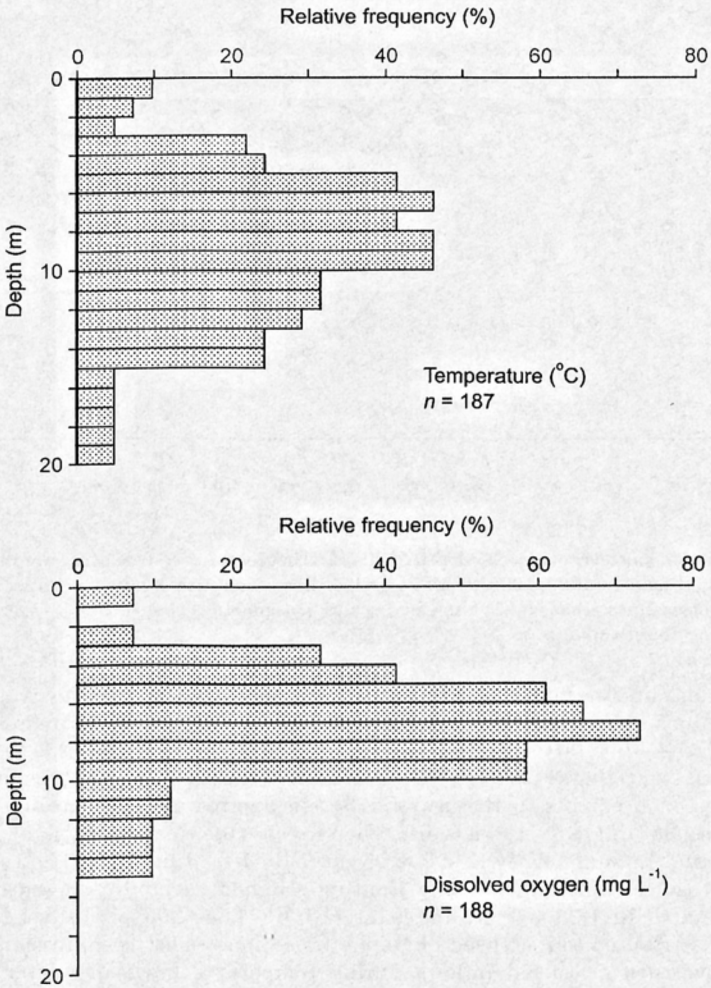

Fig. 4. Vertical distribution of relatively large gradient values in water temperature and dissolved oxygen concentration in the Dobczyce Reservoir at the sampling point in the Dobczyce Basin in 1988–1997. The relative frequency is calculated for each depth interval separately as the ratio of number of sampling dates with large gradient value to the total number of sampling dates (41).

Frequency distribution of particular vertical gradients in dissolved oxygen (ranging from 0 to 4.16 mg L^{-1} m^{-1}) was distinctly more skewed than that of temperature (*M*: 0.185, Q_1: 0.064, Q_3: 0.512), however, also in this case the vertical distribution of large gradient values (>0.512 mg L^{-1} m^{-1}) was roughly normal (*M*: 7–8 m; IQR from 5–6 to 8–9 m; ISR from 4–5 to 9–10 m).

At the same sampling point in the Dobczyce Basin Secchi depth varied from January 1988 to December 1996 within the range 0.5–5.7 m (Fig. 5). In annual

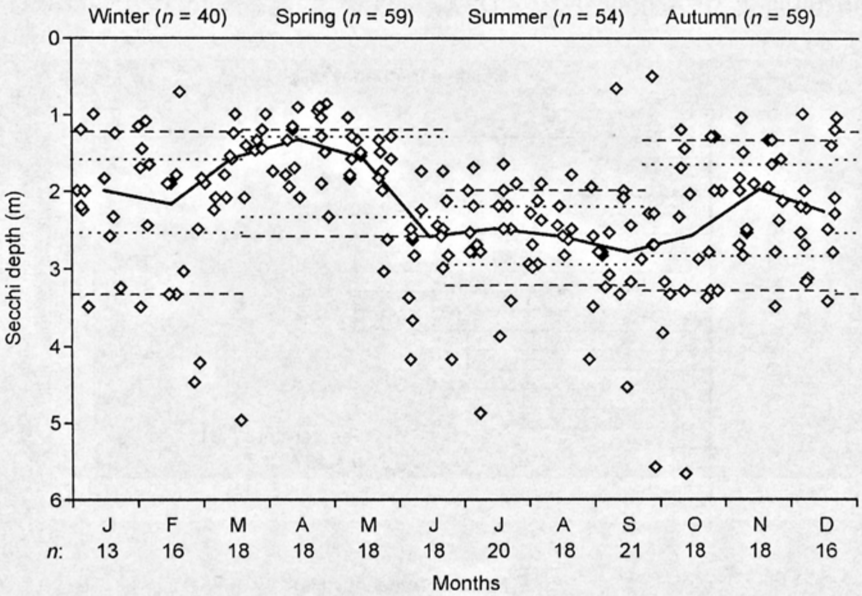

Fig. 5. Seasonal pattern of Secchi depth in the Dobczyce Reservoir at the sampling point in the Dobczyce Basin in 1988–1996 (n=212): broken line – monthly median (sample sizes at the abscissa), dotted lines – seasonal values of 1st and 3rd quartile, dashed lines – seasonal values of (1/6)th and (5/6)th quantile.

cycle this parameter followed a pattern that can be clearly demonstrated by the median values calculated for particular months. Average water transparency was low in March–May (*M*: 1.3–1.6 m), high in June–October (*M*: 2.5–2.8 m), and medium in November–February (*M*: 2–2.3 m). While comparing the distribution ranges of measurements in the seasons, Secchi depth was least variable in spring (IQR: 1.3–2.35 m; ISR: 1.2–2.6 m) when as a rule increased algal growth is observed, and in summer (IQR: 2.2–2.95 m; ISR: 2–3.23 m) when algal abundance decreases as the nutrients become limiting. Higher variability in autumn (IQR: 1.65–2.85 m; ISR: 1.35–3.3 m) and winter (IQR: 1.58–2.55 m; ISR: 1.23–3.35 m) should be attributed to increased phytoplankton biomass occurring irregularly after autumn overturn or turbid inflows during temporary thaws in winter. Euphotic depths respective to the collected Secchi depth measurements ranged from 3.5 to 11.9 m, with a median of 7.4 m and IQR of 6.3–8.4 m (Fig. 6). According to ISR calculated for these data it may be supposed, that in most cases photosynthesis may occur down to the depth of 5.8 m, and only rarely was possible in the portion of water column below 8.8 m.

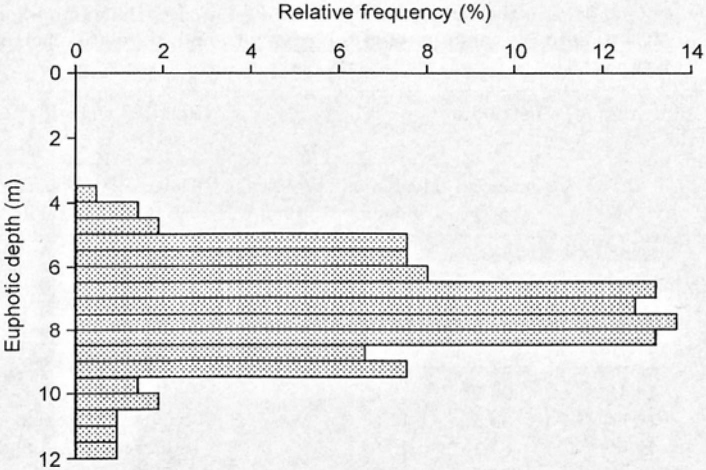

Fig. 6. Vertical distribution of the depths of euphotic zone in the Dobczyce Reservoir at the sampling point in the Dobczyce Basin in 1988–1996 (n=212; estimated according to Tilzer, 1988).

The lower boundary of the pelagial defined as a euphotic and mixing, and therefore warm and well-oxygenated upper layer of the water mass, may be regarded at a depth below which the water is cold and poor in oxygen. In the period of study the thermocline extended at most down to 12 m, the oxycline to 10 m, while the euphotic depth only rarely exceeded 8.8 m. Because the oxycline was more strongly marked than thermocline in vertical profiles and its estimate is quite close to the euphotic depth the pelagial zone was roughly defined as the open water layer within 0–10 m depth range (without adjoining shallower areas). As concerns littoral, its lower boundary is mostly determined by the permanent availability of sufficient photosynthetically active radiation to support photosynthesis in excess of respiration. These conditions occur in the middle of the reservoir down to 5.8 m, near shore, however, the light penetration may be decreased because of sediment particles resuspended by wave action and increased plankton biomass owing to continuous nutrient recycling from the bottom. According to this it may be supposed that in the Dobczyce Reservoir the littoral zone includes the part of the bottom and its overlying water between the shoreline and the approximate depth of 5 m.

Within the reservoir operation range (256.7–272.6 m a.s.l.) the volume of pelagial zone can magnify or reduce its value up to 18 times (Table III). At the standard damming level it contains 50.5% of the total water mass. The greatest part of this amount falls then to the Myślenice Basin. However, it is possible that in this part of reservoir pelagial may be absent. Contrary to this, the permanent presence of a considerable volume of this habitat is characteristic of the Dobczyce Basin. In that basin the relative share of pelagial decreases with the elevated water level owing to increasing share of the hypolimnetic water. In the Wolnica Bay pelagial zone comprises usually about a quarter of the local water mass but only a few percent of the reservoir total pelagic water.

It is noteworthy, that the Dobczyce Reservoir has a quite constant area of littoral zone (1.9–2.6 km^2) not depending directly on the water level (Table IV). This habitat is unequally distributed among parts of the reservoir. The most "littoral" part is the Wolnica Bay over 50% of which consists usually of this zone.

Table III. The pelagial zone in the Dobczyce Reservoir in relation to the damming ordinate: its total volume, distribution in the main parts of the reservoir, and its relative percentage share in volumes of these parts.

Altitude (m)	Total volume (10^6 m^3)	Distribution (%)			Relative share (%)		
		Dobczyce Basin	Myślenice Basin	Wolnica Bay	Dobczyce Basin	Myślenice Basin	Wolnica Bay
256.7[a]	3.55	100			26.8	0	0
257	4.06	100			29.4	0	0
258	6.05	99.5	0.5		38.4	0.4	0
259	8.69	96.2	3.8		47.4	3.0	0
260	12.04	92.0	8.0		56.5	6.8	0
261	14.18	90.1	9.9		59.0	8.1	0
262	16.54	88.1	11.9		61.4	9.2	0
263	19.65	81.1	18.9		61.5	14.8	0
264	24.45	68.5	31.5		59.5	26.3	0
265	30.71	57.2	42.8		57.8	38.8	0
266	35.24	51.2	48.8		55.1	44.5	0
267	40.42	45.8	54.0	0.2	52.8	49.8	3.3
268	45.50	41.8	57.3	0.9	50.7	53.0	11.3
269	50.15	39.0	59.2	1.8	49.0	54.1	18.4
269.9[b]	54.68	36.7	60.7	2.6	47.5	55.1	24.8
270	55.21	36.5	60.8	2.7	47.3	55.2	25.5
271	58.57	35.4	61.2	3.4	45.9	53.4	28.2
272	62.07	34.3	61.5	4.2	44.5	51.9	30.4
272.6[c]	64.29	33.7	61.7	4.7	43.8	51.1	31.7

[a] minimum reservoir operation level
[b] standard damming ordinate
[c] maximum pool elevation

However, despite the fact that littoral of the Myślenice Basin occupies considerably smaller relative portion of the bottom area, it is always the largest part of the total reservoir littoral zone. In the Dobczyce Basin the size of this habitat is small both in relative as in absolute units.

Fluctuation of water level in 1988–1996 was in range between -5.9 and 1.7 m, in relation to the standard damming ordinate. The respective ranges of the total surface area, volume and mean depth were 7.02–10.63 km^2, 58.8–125.7 10^6 m^3, and 8.4–11.8 m. Minimum volume of pelagial zone was 24.4 10^6 m^3 (42% of the total reservoir volume), while the maximum 60.6 10^6 m^3 (48%). The area of littoral was ranging from 2.01 km^2 (29% of the total area) to 2.43 km^2 (23%). Taking the mean annual discharge of the Raba (10 m^3 s^{-1}) the range of water residence time may be roughly approximated as 0.19–0.40 yr. These figures suggest that functioning of the reservoir ecosystem had been undergoing substantial changes during this period. As concerns pelagial probably the most important for fish assemblage were changes in trophic state and absolute size of this habitat, because they may effect the available food resources. An individual fish living in pelagial of the Dobczyce Reservoir may find zooplankton, terrestrial insects on water surface, or another fish (A. Pociecha and A. Amirowicz, unpubl.). For this reason the dominant species are bream, bleak, and pikeperch. Because vertical migrations down to the bottom

Table IV. The littoral zone in the Dobczyce Reservoir in relation to the damming ordinate: its total area, distribution in the main parts of the reservoir, and its relative percentage share in areas of these parts.

Altitude (m)	Total area (km^2)	Distribution (%)			Relative share (%)		
		Dobczyce Basin	Myślenice Basin	Wolnica Bay	Dobczyce Basin	Myślenice Basin	Wolnica Bay
256.7[a]	2.30	18.9	80.9	0.2	23.6	91.3	100
257	2.39	16.4	83.2	0.4	21.2	91.0	100
258	2.59	11.9	86.4	1.7	16.2	85.7	100
259	2.57	11.0	85.6	3.4	14.5	74.0	100
260	2.45	10.4	83.4	6.1	12.7	60.9	100
261	2.33	11.5	79.9	8.7	12.9	52.0	100
262	2.17	12.9	75.5	11.6	13.1	42.8	96.2
263	2.04	13.9	72.0	14.1	13.0	36.1	87.0
264	2.01	14.0	69.8	16.3	12.5	32.0	78.8
265	1.95	14.2	67.4	18.4	12.1	28.1	70.5
266	2.06	13.0	66.6	20.4	11.5	27.7	67.6
267	2.19	12.0	65.7	22.3	11.0	27.3	65.2
268	2.28	11.6	64.1	24.3	10.8	26.4	62.7
269	2.36	11.8	61.7	26.5	11.1	25.0	60.1
269.9[b]	2.42	12.0	59.7	28.4	11.3	23.7	57.9
270	2.43	12.0	59.4	28.6	11.3	23.6	57.7
271	2.43	12.3	58.1	29.5	11.4	22.2	53.6
272	2.43	12.6	56.9	30.5	11.4	20.9	49.7
272.6[c]	2.43	12.8	56.2	31.1	11.3	20.1	47.6

[a] minimum reservoir operation level
[b] standard damming ordinate
[c] maximum pool elevation

are impossible in the period of summer stagnation owing to deoxygenated hypolimnion the bottom-feeding species move to the shallow waters or migrate horizontally in diel cycle (e.g. roach). In unstable conditions of a reservoir these species which may temporarily change their diet composition are better adapted to exploit the pelagic food resources. One of them is undoubtedly bream which switches from zooplankton to bottom macrofauna and is well adapted to exploit both of these foods. This may explain its growing position in the fish community of the Dobczyce Reservoir.

Although the area of littoral zone did not change substantially in 1988–1996, the effect of water level fluctuations was even more important for this habitat than for pelagial. The reservoir operation makes the water level unpredictable in the annual cycle (Fig. 7). A regular pattern was observed only in May–July, when the water level approximated the standard damming ordinate. In remaining months the pool elevation varied substantially in the considered period. This precludes the development of aquatic vegetation characteristic of natural water bodies and destroys communities of bottom invertebrates by drying or freezing of exposed areas. In the Dobczyce Reservoir bare sandy, muddy and in places rocky bottom prevails in littoral, while rooted macrophytes form only sparse beds in coves. The main species are *Polygonum amphibium* L. which is adapted to both aquatic and

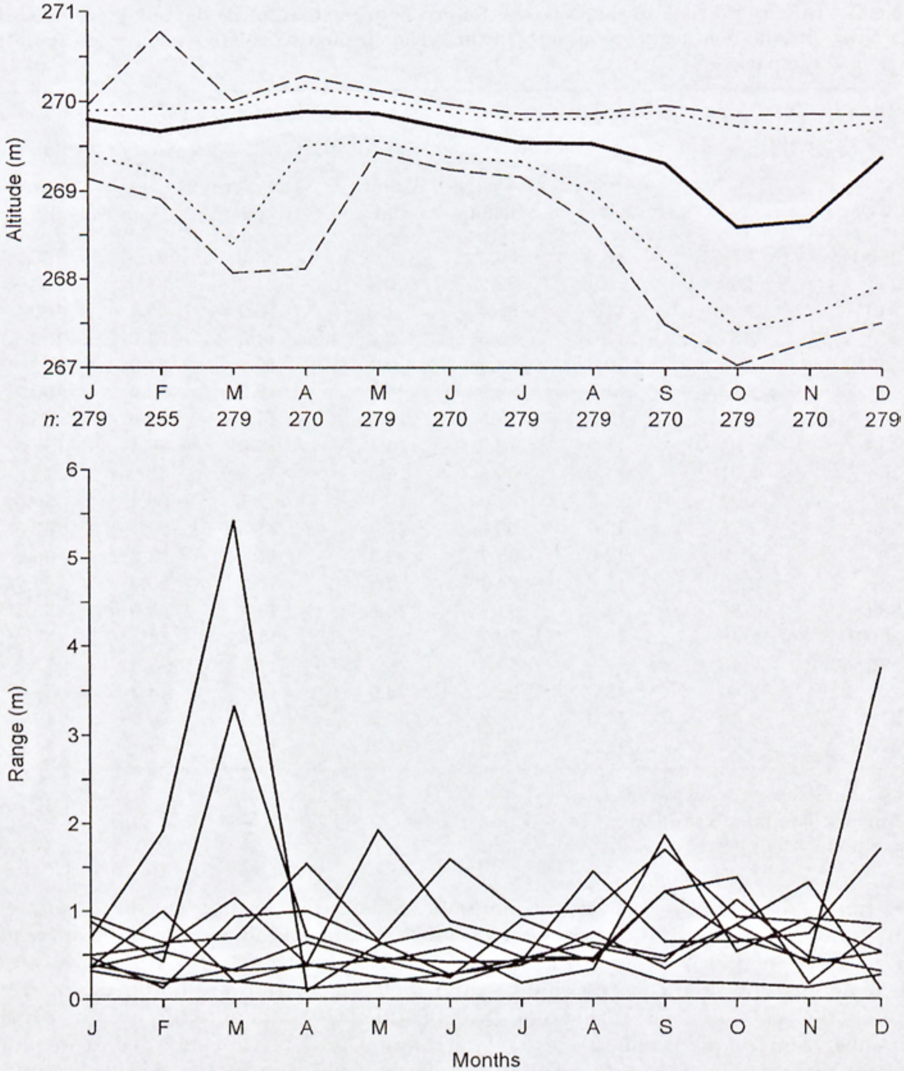

Fig. 7. Annual pattern of the damming level (upper panel) and maximum monthly range of water level fluctuation (lower panel) in the Dobczyce Reservoir in 1988–1996. In the upper panel: broken line – monthly median (sample sizes at the abscissa), dotted lines – values of 1st and 3rd quartile, dashed lines – values of (1/6)th and (5/6)th quantile. Note the same scale on the ordinates in both panels.

terrestrial conditions, *Myriophyllum* sp., *Potamogeton* sp., and some emergent plants (*Phragmites australis* (Cav.) Trin. ex Steud. and other swamp grasses, *Typha* sp., *Iris pseudoacorus* L.). Noticeable mats of filamentous algae also develop periodically on extensive portions of the bottom. Such a poor submerged vegetation results in the lack of spawning, nursery (i.e. offering a useable food resource and providing refuge from predation for early life stages), or living habitat that is necessary for many fish species. As a result, species depending upon vegetation, e.g. pike, *Esox lucius* L. or tench, *Tinca tinca* (L.), become rare after quite abundant occurrence in time of the reservoir basin filling. Recruitment of species spawning in the littoral zone is limited not only by the lack of suitable substrate but also by rapid spring and summer drawdowns which may decimate laid eggs, larvae and juveniles. In 1988–1996 in the Dobczyce Reservoir maximum monthly variations in water level did not exceed 1 m in most cases (*M*: 0.53 m; IQR: 0.36–0.88 m; ISR: 0.27–1.00 m) (Fig. 7). No clear seasonal pattern occurred during this period; therefore a change of water level may always be expected. In no case the water level remained unchanged within a month. Ecological effects of a drawdown depend on the bottom slope gradient. In flat areas even relatively low fluctuation of water level may be disastrous for the whole littoral community.

In addition to the presented cyclical events and processes a possible long-term temporal trend appeared in transparency as evidenced by comparison of midsummer records of Secchi depth. Two sets of measurements collected in July and August in 1988–1997 (for each month two sampling dates in every year, in the first and second half of the month were selected) yielded linear regressions indicating negative correlation between variables (Fig. 8). These relations are weak

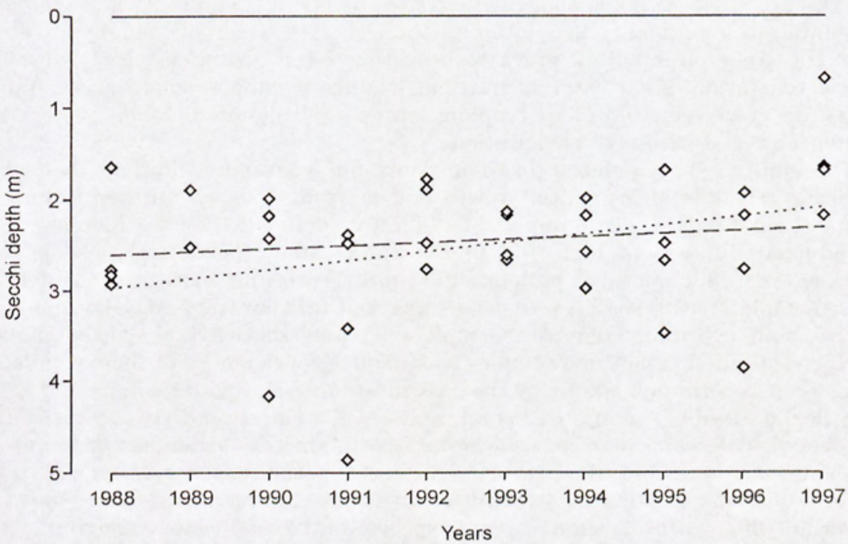

Fig. 8. Changes in midsummer (July–August) water transparency in the Dobczyce Reservoir at the sampling point in the Dobczyce Basin in 1988–1997: dashed line – July (Y = 69.2 – 0.0335 X; r^2=0.013, n=20), dotted line – August (Y = 198 – 0.0986 X; r^2=0.184, n=18).

and can neither be used to predict summer Secchi depths in particular years nor be extrapolated beyond the period from 1988 to 1997. However, within these ten years the water transparency in the Dobczyce Basin in summer (i.e. in the lacustrine zone characterized by nutrient-limited phytoplankton growth during summer stagnation) showed a tendency to decrease at a ratio of 3–10 cm of Secchi depth per year. This trend is noteworthy as a signal of warning that the reservoir is becoming eutrophicated. Decreased (to a limited extent) transparency in open water zone may be favourable to pikeperch. On the other hand, the greater epilimnetic production, the greater the supply of organic matter to the hypolimnion and hypolimnetic oxygen depletion. Therefore, in coming years the occurrence of the bottom-feeding fish may be more restricted to the shallower areas.

In conclusion, it should be stressed that a fish species may be able or unable to survive in a reservoir depending on the presence or lack of suitable: (1) water temperature, (2) dissolved oxygen, (3) diversity in habitat, (4) spawning sites, (5) sufficient prey for a particular stage in the life cycle, and (6) refuge from predators (O'Brien 1990). According to this it is obvious that summer conditions in the Dobczyce Reservoir exclude salmonids, e.g. lake trout, *Salmo trutta* m. *lacustris* L. which depends on a cool and well oxygenated habitat and cannot find it either in deoxygenated hypolimnion, too warm epilimnion, or in warm and oxygen-deficient headwater/transitional zone. Despite a stocking programme lake trout did not establish a self-sustaining population in the reservoir. On the contrary, typically riverine fish species may persist in reservoirs near river mouths. In the Dobczyce Reservoir a population of nase still occurs in the headwater area. This species preferring lotic habitats with stony bottom covered by attached algae probably found favourable feeding conditions in that part of reservoir where the sedimenting allochthonous organic matter and/or intensively growing bottom algae create rich food resource. It is possible that another riverine species, vimba, *Vimba vimba* (L.) will maintain a stationary population in the Dobczyce Reservoir. However, in most cases the reservoir habitats prove to be rather harsh owing to poorly developed littoral vegetation, great external nutrient loading causing eutrophication, reduced access to deoxygenated hypolimnion, large and unpredictable water level fluctuations, and excessive exploitation.

The ability of a population to compensate unfavourable conditions depends on a specific schedule of fecundity, growth and mortality, i.e. on an appropriate life-history strategy. Two main strategies are defined: (1) to increase early reproduction in case of high and unpredictable adult mortality rates, or (2) to decrease reproduction and prolong life time if juvenile mortality is high and unpredictable (Wootton 1991). In reservoirs, the first strategy may be applied by perch, some cyprinids and other small-sized and short-living species that are together classified as not marketable "trash fish". Development of their populations seems to be determined mainly by the spawning success, especially in case of species with flexible feeding habits (e.g. perch and roach). The second strategy is difficult to adopt in reservoir conditions, however, the life-history strategies of bream and pikeperch are possibly close to it. As concerns the latter species the proper protection seems to be crucial to its future in the Dobczyce Reservoir. The same concerns wels, *Silurus glanis* L., a species introduced into reservoir within a biomanipulation programme. Fish species that in reservoirs suffer high mortality both as juveniles and adults, i.e. pike, probably have no chance to establish their populations and, if regarded as necessary to maintain in the reservoir fish community, will depend in full on regular stocking.

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Appendix A

Method of computation of a reservoir volume

The volume of a water body can be estimated as the sum of volumes of layers of the whole water mass. The good approximations of these layers are two kinds of solid figures, a cone (for the deepest layer), and truncated cones (for the consecutive layers up to the surface) (Fig. 1). The volumes of these solids are calculated as

$$V = H_1 A_1/3 \qquad \text{(cone)} \qquad (1)$$

and

$$V = H (A_1 + (A_1 A_2)^{1/2} + A_2)/3 \qquad \text{(truncated cone)} \qquad (2)$$

where A, A_1, and A_2 are areas of bases, and H_1 and H are the respective heights. Formulae (1) and (2) allow to calculate the total volume of water body. Substituting heights with differences between depths at adjacent isobaths (or with the difference between the maximum depth and the depth at last isobath), and areas of bases with areas closed by these isobaths the volumes of all layers of the water mass of the studied water body can be computed. Respective areas may be obtained from precise bathymetric map by two methods, measuring them with a planimeter, or weighing their shapes drawn on paper and then cut off (Mastyński 1972). It should be taken into consideration that the volume of a truncated cone which bases are sums of base areas of a number of truncated cones is not equal to the sum of their volumes. The only exception is the case when the A_1/A_2 ratio is the same in all summed truncated cones. Therefore, the volume of a water layer calculated from areas measured in whole water body differs from that calculated as a sum of volumes of its parts.

When the layers of water mass are limited by depths not corresponding to isobaths presented in available bathymetric map some additional calculations are required. They can be reduced to two situations. The first case concerns the change of the area of base A_2 when the height of the cone changed from H_2 to H_1 (Fig. 1).

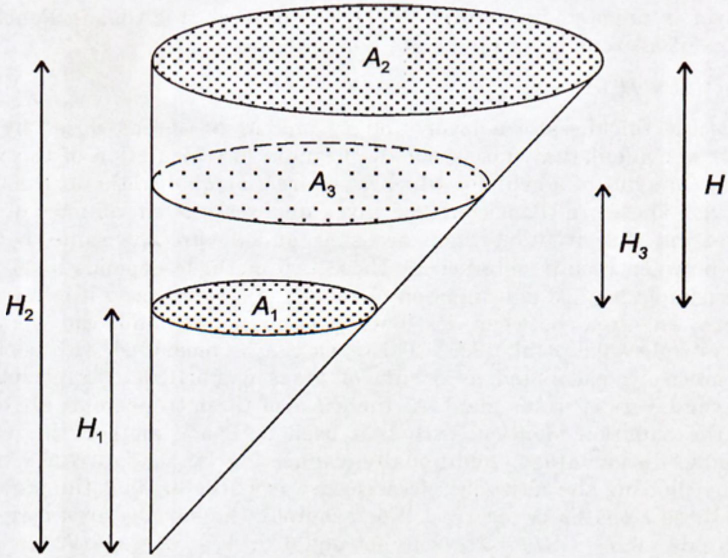

Fig. 1. General model of reservoir water mass.

Since the relation between base and height of a cone is

$$A = x\,H^2$$

therefore the following equation is obtained

$$A_1 = A_2\ (H_1/H_2)^2 \tag{3}$$

The second case concerns the change of the area of base A_2 when the height of truncated cone changed from H to H_3 (Fig. 1). The relation between bases A_1 and A_2 can be defined as

$$A_2 = A_1\ ((H + H_1)/H_1)^2$$

where H_1 is the height of truncated apex. This height is

$$H_1 = H/((A_2/A_1)^{1/2} - 1)$$

Similarly, the area of base A_3 at the height H_3 may be expressed as

$$A_3 = A_2\ ((H_3 + H_1)/(H + H_1))^2$$

After substituting H_1 this equation yields

$$A_3 = A_2\ [(H_3 + H/((A_2/A_1)^{1/2} - 1))/(H + H/((A_2/A_1)^{1/2} - 1))]^2$$

which can be written in simplified form as

$$A_3 = A_1\ [(H_3/H)\ ((A_2/A_1)^{1/2} - 1) + 1]^2 \tag{4}$$

It is obvious that formulae (3) and (4) can be used only for interpolation of an area closed by adjacent isobaths in the bathymetric map.

Presented procedure is very similar to Penck method of assessment of the volume of a water body (Mikulski 1977). According to that method the total volume is also considered as a sum of volumes of particular layers. The volume of the deepest layer is calculated according to (1). The difference is that in Penck method the volumes of all remaining layers are computed as

$$V = H\ (A_1 + A_2)/2$$

where H is the thickness of a layer, and A_1 and A_2 are areas closed by adjacent isobaths. It is evident that this is not the formula for calculation of the volume of a truncated cone but of a cylinder which base area is equal to the arithmetic mean of A_1 and A_2. Therefore, Penck method gives underestimated volumes of layers in all cases except the situation when areas A_1 and A_2 are the same, because the difference between results obtained by these two methods depends on A_1/A_2 ratio. As another simple method of estimation of volume of a water body it is recommended to measure an area between its bathygraphic curve and the vertical axis (Bajkiewicz-Grabowska et al. 1993). This area can be measured with a planimeter or, more precisely, calculated as a sum of areas of particular trapeziums which represent the layers of water mass. As the areas of these trapeziums are calculated following the equation identical with that used in Penck method this estimation has the same disadvantage. Additionally, connecting by straight lines the points obtained by plotting the altitudes of successive isobaths against the surface areas closed by these isobaths is incorrect. For example, the surface area corresponding to the altitude of $H_1 + (H_2 - H_1)/2$ is not equal to $A_1 + (A_2 - A_1)/2$ (it is smaller in fact). Although the differences in results obtained with above-mentioned methods are in most cases negligible, they should be taken into consideration when the computation procedure is selected.

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