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External morphology and growth rate of white-eye bream *Ballerus sapa* (Cyprinidae, Teleostei) in a lowland dam reservoir on the lower Vistula River (Włocławek Reservoir, central Poland)

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Abstract. To address the dearth of information on the biology of white-eye bream in its novel range of Europe, we examined the morphology and growth rate of specimens inhabiting a dam reservoir on the lower Vistula River and compared the results with those from other waters of native and non-native regions of this species. Altogether, 24 mensural and 15 qualitative characters of 93 individuals (45 females and 48 males) as well as age of 108 specimens were determined. Body length (*l*) of the fish ranged from 142 to 277 mm. To examine the patterns of relative growth, relationships between 21 mensural characters (raw data) and *l* were tested using a non-linear regression analysis: 5 characters were best described by a linear function, 5 by a power one, 10 by a quadratic and 1 by a split-linear regression. There were significant differences in morphometric characters among the studied population and those from the Zegrze Reservoir (Vistula River catchment) and the Dnieper River, suggesting substantial morphological plasticity of white-eye bream. Meristic characters (the basic characters are expressed by the following formula: l.l. 50-57; D II-III 7-8; A III-IV 36-43; P I-III 15-18; V I-III 8-9; C IV-VII 16-18; sp.br. 18-25; 5-5) showed considerable overlap with the literature data except the number of unbranched fin rays, which revealed greater variability. The growth rate of the white-bream from the Włocławek Reservoir was moderate in the first year of life, and then it was faster than in many waters from its native range. This marked increase of growth rate seemed to be site-specific rather than region-specific, and associated with particularly rich feeding resources (abundant bottom fauna) of the eutrophic and strongly flowing dam reservoir.

Key words: feeding resources, mensural characters, meristic characters, non-native fish

Introduction

White-eye bream *Ballerus sapa* (Pallas, 1814) occurs naturally in the Ponto-Caspian (Black, Caspian, Azov seas) and Aral Sea basins. It inhabits coastal marine waters, mainly brackish (estuaries), and fresh waters of large rivers systems, such as Amu-Daria, Boh, Danube, Dnieper, Dniestr, Don, Kuban, Prut, Syr-Daria, Terek, Ural, Volga. Within these systems, it avoids small tributaries (Berg 1949, Nikolski 1970, Blank et al. 1971, Lelek 1987, Zhukov 1988, Holčík 2003). White-eye bream has been reported as a rheophilic species associated mainly with typical riverine, main channel habitats. It is a rather rare species and its documented share in commercial fish stocks has been low, especially in dam reservoirs (on average < 2 % of total catches) (Kozhevnikow 1965, Chikova 1966, Ilina 1966, Kozhevnikov et al. 1978, Gorokhov 1978). Two subspecies

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of *Ballerus* (formerly *Abramis,* see Freyhof & Huckstorf 2006) *sapa* have been described: south white-eye bream *A. sapa bergi*, which occurs in the middle and southern parts of the Caspian Sea basin and *A. sapa bergi* natio *aralensis*, which is typical for the Aral Sea basin (Berg 1949, Maksunov 1972).

White-eye bream has established populations outside its native geographic range. Reports of white-eye bream in the Baltic Sea basin began in the 1860s when, as Zhukov (1988) stated, this species penetrated the Volkov River from the Volga River. In the 1980s, Terlecki (1990) documented the first occurrence of white-eye bream population in Poland in the Zegrze Reservoir on the Bug and Narev Rivers. Probably, it moved there via the man-made Bug-Prypyat Canal, connecting the Vistula River catchment (Baltic basin) with the Dnieper River catchment (Black Sea basin). Several years later, white-eye bream was reported in the Włocławek Reservoir on the lower Vistula where it established a rather abundant population (Brylińska 2000, Kakareko – unpubl. data). In the 1990s, white-eye bream was unintentionally introduced into the Rhine catchment of Germany, most likely from the Weser and Danube Rivers (Freyhoff 2003). In Russia, it moved outside its native geographic range of inland waters and become locally a non-indigenous species, but its range expansion is relatively slow (Bogutskaya & Naseka 2002).

Although white-eye bream has extended its distribution beyond its native range, and this process seems to be accelerated in the last decades, little is known about biological characteristics of this species in newly established areas. In the latest literature there are only mentions about the presence of white-eye bream in European rivers, especially in the native range within the Danube catchment area, e.g. in the Drava River (Majer & Biro 2001), Morava River (Reichard et al. 2002), Morava and Dyje Rivers (Lusk et al. 2004) and Danube (Spindler 1997, Şindilariu 2002, Holčík 2003). Detailed studies on morphological characteristics and growth rate of white-eye bream have only been undertaken in the Zegrze Reservoir (Terlecki 1990). However, they were based on a sample of 14 individuals only. We found three papers dealing with external morphology of white-eye bream from its native range (Berg 1949, Zhukov 1965, 1988). They provide species descriptions and include general data of its main morphological characters. Zhukov (1965) also presents more detailed data (with basic statistics) of various mensural characters of specimens from the Dnieper River, suitable for further inter-population comparisons.

The morphological and biological characteristics of fish are known to be strongly influenced by environmental conditions (Norton et al. 1995, Kováč & Copp 1996). Phenotypic plasticity between native and introduced populations, which can be demonstrated in the variability of body shape and growth, is an important cue for explanation of phenomenon of successful establishing some species in novel environment (Tomeček et al. 2005). In the case of white-eye bream in introduced areas, such comparative morphological, as well as other biological investigations, at any ontogenetic stage (larvae, juveniles, adults), are still missing.

To address the lack of information on phenotypic characteristics of white-eye bream in novel environments, we studied the patterns of external morphology and qualitative morphological characters as well as growth rate of specimens from the Włocławek Reservoir, located on the lower Vistula River in central Poland. This water body is a part of one of the main corridors used by Ponto-Caspian organisms to migrate in Europe (Bij de Vaate et al. 2002). We also intended to compare our findings with published data from native range of this species. Our specific objective was to describe the morphology of white-eye bream in a standard manner to allow inter-population comparisons with past and future studies.

Materials and Methods

Fish were sampled from the Włocławek Reservoir, constructed in 1970 in the lower course of the Vistula River (Głogowska 2000). It is the largest dam reservoir in Poland with respect to surface area (75 km^2), characterized by a short retention time (4–5 days), high water trophy and extremely rich benthic fauna (Giziński et al. 1989, Żbikowski 2000). White-eye bream were fished in 2001 from the central part of the reservoir (52°37-38'N, 019°18-20'E) by commercial fishermen using gill nets. The examined individuals were divided into two groups: one was used in the growth analysis (n = 108) and the other in the analysis of external morphology and meristic characteristics (n = 93). The specimens to be used in the growth analysis were sampled gradually from March till October, while those destined for the morphological study were collected and examined later, from 23 till 28 November. The fish were frozen shortly after capture and transported to the laboratory where they were defrosted and further analysed.

Age determination was based on the annual ring structure of scales. Scales (4–8 from each specimen) were taken from the left side of the body, from the first row above the lateral line and below the insertion of the dorsal fin. The scales were examined using a microfilm projector (magnification: 14.5; 24.5; 48.0 x), and under a stereomicroscope. Caudal radii of the scales were measured to the nearest 0.04 mm. The growth rate was back-calculated from the scale measurements, based on the assumption that it was isometric (Bagenal & Tesch 1978). In order to evaluate the between-sex differences in growth, body lengths of males and females were compared using a Mann–Whitney *U*-test, (separately for 1+ and 2+ age groups). The von Bertalanffy growth model was used (Ricker 1975) to describe the fish growth in terms of length and weight. For all fish (n=201) the body length-weight power relationship, as well as the length frequency distribution were established.

In order to examine external morphology, 24 mensural characters were measured using vernier callipers to the nearest 0.1 mm, according to Pravdin (1931, 1966), Holčík (1989) and Brylińska (2000) (Fig. 1). Most of 24 morphometric characters were measured according to Pravdin's scheme. Only 2 characters (head width, X6 and preanal distance, X13) were taken following Holčík (1989). Additionally, 15 meristic characters were also counted. All measurements and counts were made on the left side of the fish. Fin rays and gill rakers were counted using a fine dissecting needle under a binocular stereoscopic microscope. The position of the first unbranched rays was determined by the needle during careful examination of the origins of fins. The two last branched rays of the dorsal and anal fins were counted as one. In the case of the caudal fin, only the principal (dorsal) unbranched rays were counted. All gill rakers on the first arch were counted, without distinction between the upper and lower limbs. Fish sex was determined by visual examination of gonads after dissection.

All mensural characters except X7-X9 were expressed in % body length (*l*) and their basic statistics (mean, standard deviation SD, standard error SE, Min-Max, coefficient of variation (CV) were provided. The coefficient of variation was assumed to indicate low variability of characters at CV<3 or high variability at CV>10 (Ruszczyc 1982). Relationships between each of the 21 mensural characters and body length (*l*) were estimated by means of non-linear regression methods (Kováč et al. 1999, 2002). Raw data of mensural characters were used in the analysis instead of relative values (in % *l*) to avoid spurious curvilinear trends in the absence of allometry, following Kováč et al. (1999). Initially, a power function (allometric equation) was fitted to the data. A t-test was applied

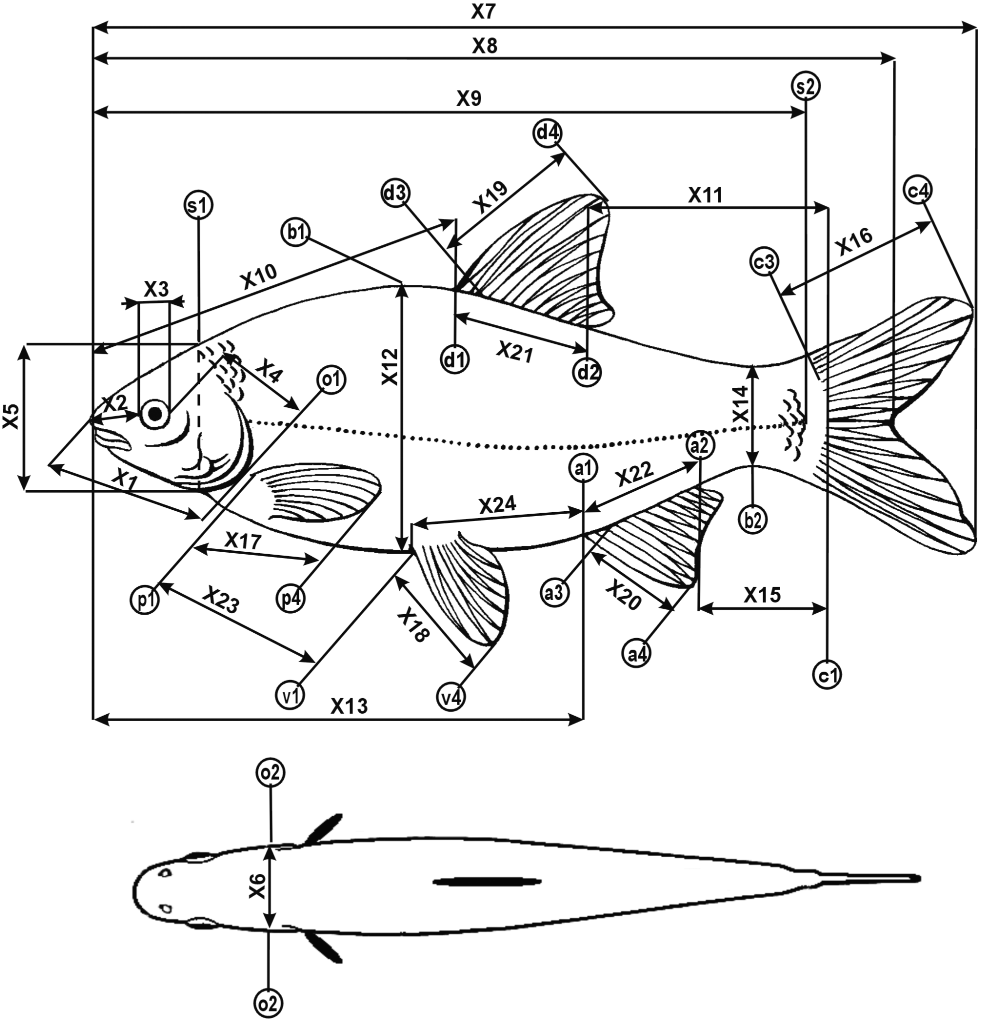

Fig. 1. Linear measurements (X1-X24) with reference points (a1-v4) of a cyprinid fish (according to Pravdin 1931, 1966, Holčík 1989, Brylińska 2000), which were used for the white-eye bream from the Włocławek Reservoir (Vistula River) (see description of mensural characters in Table 1). Reference points, a1: the origin of the anal fin, a2: the rear end of the anal fin, a3: the base of the longest ray of the anal fin, a4: the tip of the longest ray of the anal fin, b1 and b2: the maximum and minimum body depth, respectively, c1: the base of the middle ray of the caudal fin, c3: the base of the longest ray in the upper lobe of the caudal fin, c4: the tip of the longest ray in the upper lobe of the caudal fin, d1: the origin of the dorsal fin, d2: the rear end of the dorsal fin, d3: the base of the longest ray of the dorsal fin, d4: the tip of the longest ray of the dorsal fin, o1: the posteriormost end of the opercular bone, o2: the upper origin of the operculum, p1: the base of the first ray of the pectoral fin, p4: the tip of the longest ray of the pectoral fin, s1: the beginning of the scale cover, s2: the end of the scale cover, v1: the base of the first ray of the pelvic fin, v4: the tip of the longest ray of the pelvic fin.

to check whether an exponent in the power equation is different than 1 (after linearising it by logarithmic transformation). If not, a linear function was used. A quadratic function (second order polynomial) and a split regression (indicating that there is an abrupt change in the relationship between the variables) were then fitted to the data. These functions would produce slightly “better” results (in terms of the higher R^2) simply due to the higher number of parameters (respectively 3 and 4 versus 2 in the linear and power functions). Therefore, to find the best fitted model, various equations were compared by means of the Akaike's Information Criterion (AIC) (Motulsky & Christopoulos 2003). Briefly, it consists in calculating the AIC coefficient for each of the compared models, according to the formula:

$$AIC = N \ln(SS / N) + 2(K + 1)$$

Where N is the number of data points, SS is the sum of squared vertical distances of the points to the curve, K is the number of parameters in the model.

If the difference between the AIC coefficients for the more complicated model (B) and the simpler one (A):

$$\Delta AIC = N \ln(SS_B / SS_A) + 2(K_B - K_A))$$

is negative, one can assume that the former is more likely to be correct. The probability (p) that the correct model was chosen can be calculated by the following equation:

$$p = e^{-0.5\Delta AIC} / (1 + e^{-0.5\Delta AIC})$$

One should note that this method does not involve hypothesis testing, but indicates which model is more likely to be correct, and, additionally, shows how much likely it is.

The significance of between-sex differences in mensural characters was tested using a logistic regression, conducted on the data expressed in *% l*. The variables that were strongly correlated with other variables in the data set (with the multiple correlation coefficients > 0.7) were removed from the analysis (lateral head length, postorbital distance, total length, preanal distance, caudal fin length) to reduce redundancy. To control for the high number of variables in the model, sequential Bonferroni correction was applied to the statistical significances obtained for the particular variables. As the females in our study reached much larger sizes than males, we repeated the above-described analysis after excluding those females, which were larger than any of the caught male individuals. In this analysis, 32 females were used, so that the mean lengths of both sexes were similar. It allowed to distinguish sex-related differences from those caused by various fish sizes and allometric growth.

Between-catchment (Vistula River vs. Dnieper River) comparisons of mensural characters were carried out using one-way analyses of variance, separately for each character. We compared morphological characters of white-eye bream from the non-native, newly established sites of the Vistula River catchment in Poland (Włocławek Reservoir – present data; Zegrze Reservoir – Terlecki 1990) with those from its native range (Dnieper River – two data sets provided by Zhukov 1965 – DR1 and DR2 respectively). The above-mentioned literature data contain arithmetic means, numbers of individuals and standard deviations of various mensural characters and therefore are suitable for comparative analysis using parametric tests. Altogether, 13 characters expressed in % of body length and 4 characters expressed in % of lateral head length, measured in the present study and by all the mentioned authors according to the Pravdin's scheme (Pravdin 1931), were used for the comparisons. Sequential Bonferroni correction was applied to the results to control for multiple analyses.

Meristic characters of white-eye bream, due to the lack of appropriate data with basic statistics from its native range, were only roughly compared with the available general data, provided by Berg (1949) and Zhukov (1965, 1988).

Table 1. Mean, standard deviation (SD), standard error (SE), range, coefficient of variation (CV) and number of specimens (n) for 24 morphometric characters (all characters except X7-X9 are expressed in % of body length) of white-eye bream collected from the Włocławek Reservoir. Four size-classes of white-eye bream were considered (in mm): **A** (121–160, 161–200) and **B** (201–240, 241–280).

A Character	Mean	SD	SE	min.	max.	CV	Mean	SD	SE	min.	max.	CV
Size-class (mm)	121–160 (n=49)						161–200 (n=12)					
X7 Total length (mm)	190.5	4.8	0.69	180.0	201.0	2.52	226.5	19.0	5.73	199.0	246.0	8.39
X8 Fork length (mm)	166.5	4.5	0.64	156.0	176.0	2.71	200.4	18.2	5.47	176.0	220.0	9.06
X9 Body length (mm)	152.7	3.8	0.54	142.0	158.0	2.49	183.0	15.6	4.70	162.0	200.0	8.51
Weight (g)	59.6	5.2	0.75	46.7	69.2	8.79	107.3	33.2	9.57	68.3	144.4	30.91
X1 Lateral head length	20.7	0.8	0.12	18.6	23.9	3.96	20.5	0.6	0.18	19.2	21.4	3.12
X2 Preorbital distance	4.4	0.4	0.05	3.5	5.3	8.59	4.2	0.3	0.09	3.8	4.7	7.63
X3 Eye diameter	6.9	0.3	0.04	6.4	7.6	4.14	6.7	0.4	0.11	6.2	7.5	5.87
X4 Postorbital distance	9.7	0.4	0.06	9.0	11.5	4.16	9.8	0.4	0.13	9.2	10.7	4.49
X5 Head depth	17.5	0.9	0.13	14.4	19.4	5.27	17.6	0.5	0.13	16.6	18.4	2.65
X6 Head width	11.5	0.3	0.05	10.5	12.4	3.00	11.7	0.5	0.13	11.0	12.3	3.92
X10 Predorsal distance	47.1	9.8	1.40	10.1	55.1	20.89	48.3	1.7	0.48	45.7	52.0	3.42
X11 Postdorsal distance	41.6	1.7	0.25	35.4	43.9	4.17	42.2	1.6	0.46	39.8	45.7	3.74
X12 Body depth	33.4	1.0	0.14	31.6	35.9	2.87	33.3	0.8	0.24	31.4	34.5	2.54
X13 Preanal distance	57.3	2.2	0.32	51.6	68.1	3.87	56.6	1.4	0.41	54.4	58.6	2.51
X14 Minimum body depth	9.2	0.6	0.09	8.1	11.2	6.90	9.0	0.4	0.12	8.5	9.7	4.61
X15 Caudal peduncle length	10.1	1.0	0.14	7.7	12.3	9.93	10.0	1.3	0.37	7.9	12.1	12.80
X16 Caudal fin length	24.1	1.8	0.25	20.2	28.0	7.27	23.5	2.0	0.59	20.4	26.7	8.65
X17 Pectoral fin length	18.7	0.9	0.12	15.5	20.1	4.66	18.7	0.8	0.22	17.3	20.2	4.15
X18 Ventral fin length	14.8	1.1	0.16	12.2	19.9	7.40	14.9	0.5	0.15	14.0	15.5	3.41
X19 Dorsal fin height	24.6	1.8	0.25	18.1	27.8	7.22	24.2	1.3	0.37	21.8	25.8	5.29
X20 Anal fin height	15.3	1.1	0.16	12.1	18.8	7.44	14.4	1.1	0.32	12.5	15.8	7.59
X21 Dorsal fin length	9.6	0.5	0.07	8.9	12.2	5.26	10.1	0.5	0.16	9.3	10.9	5.43
X22 Anal fin length	34.8	4.3	0.62	9.3	39.2	12.45	35.0	2.3	0.66	30.8	38.7	6.55
X23 Distance P-V	20.1	2.8	0.40	17.7	37.4	13.91	19.8	1.1	0.31	18.3	22.7	5.45
X24 Distance V-A	18.0	1.3	0.19	15.2	21.9	7.42	17.4	2.0	0.57	13.0	21.3	11.28

Table 1 – continuation.

B Character	Mean	SD	SE	min.	max.	CV	Mean	SD	SE	min.	max.	CV
Size-class (mm *l*)	201–240 (n=20)						241–280 (n=12)					
X7 Total length (mm)	261.4	11.0	2.46	242.0	288.0	4.22	314.8	13.0	3.7	292.0	333.0	4.13
X8 Fork length (mm)	233.9	9.8	2.20	220.0	262.0	4.21	281.5	10.9	3.1	263.0	295.0	3.87
X9 Body length (mm)	214.1	7.7	1.72	202.0	230.0	3.59	258.5	11.2	3.2	243.0	277.0	4.34
Weight (g)	182.9	33.7	7.53	136.9	256.4	18.42	329.8	39.0	11.2	263.0	397.8	11.81
X1 Lateral head length	20.2	1.0	0.22	17.4	21.7	4.84	19.6	0.6	0.2	18.2	20.5	3.23
X2 Preorbital distance	4.8	0.5	0.10	4.1	5.6	9.63	4.5	0.4	0.1	4.0	5.4	9.83
X3 Eye diameter	6.3	0.3	0.07	5.8	6.7	4.65	6.0	0.3	0.1	5.2	6.3	5.00
X4 Postorbital distance	9.9	0.4	0.09	9.3	10.6	3.88	9.8	0.5	0.1	8.9	10.7	4.86
X5 Head depth	17.0	1.4	0.32	12.0	19.5	8.36	16.6	1.0	0.3	15.0	17.7	5.80
X6 Head width	11.8	1.2	0.26	11.2	16.6	9.90	11.9	1.3	0.4	10.6	15.4	11.30
X10 Predorsal distance	48.1	2.0	0.44	43.7	52.7	4.09	49.3	1.9	0.5	46.7	53.9	3.83
X11 Postdorsal distance	42.0	1.1	0.24	39.4	44.1	2.54	41.9	1.3	0.4	39.9	43.8	3.09
X12 Body depth	32.8	5.6	1.26	9.2	36.4	17.22	34.4	1.3	0.4	31.4	36.7	3.87
X13 Preanal distance	57.2	1.6	0.36	54.9	60.4	2.80	57.9	1.5	0.4	55.9	60.7	2.55
X14 Minimum body depth	9.1	0.3	0.07	8.4	9.6	3.23	8.9	0.4	0.1	8.1	9.5	4.21
X15 Caudal peduncle length	10.0	0.6	0.13	9.1	11.0	5.90	9.7	0.8	0.2	8.5	11.3	8.38
X16 Caudal fin length	21.8	1.4	0.32	18.7	23.5	6.63	20.5	1.5	0.4	16.7	22.8	7.31
X17 Pectoral fin length	18.0	0.6	0.14	16.5	19.1	3.35	17.2	0.5	0.2	16.0	18.0	3.15
X18 Ventral fin length	14.6	0.6	0.13	13.6	15.6	4.08	13.6	1.4	0.4	9.6	15.1	10.14
X19 Dorsal fin height	24.1	1.2	0.27	20.4	25.9	5.07	22.6	1.2	0.3	19.2	24.0	5.32
X20 Anal fin height	14.4	1.0	0.22	12.4	15.9	6.77	14.0	0.9	0.3	12.9	15.4	6.23
X21 Dorsal fin length	10.1	0.6	0.13	8.6	11.5	5.68	9.9	0.6	0.2	9.1	11.0	5.85
X22 Anal fin length	34.5	2.9	0.66	25.8	38.3	8.51	34.4	1.6	0.4	30.5	35.7	4.51
X23 Distance P-V	20.2	1.0	0.22	17.8	22.2	4.84	21.8	1.3	0.4	19.4	24.4	5.88
X24 Distance V-A	17.9	1.0	0.23	15.2	19.7	5.85	18.6	1.1	0.3	17.2	20.5	5.86

Results

External morphology

Most of the 21 mensural characters expressed in % *l* showed limited variation. The most and the least variable characters were different in particular size-classes of fish (Table 1). Meristic characters did not reveal high variability except numbers of pectoral, pelvic and caudal unbranched rays (Table 2). Five mensural characters were best described by a power function, five by a linear function, ten by a quadratic function and one by a split linear regression (Table 3). However, only in three cases (distance P-V, dorsal fin length and postorbital distance) was a quadratic model much more likely (>90 %) than a respective linear or power function.

Between-sex differences

In our samples, females were significantly larger than males (Mann–Whitney U-test, n=93: l: z=1.99, p=0.046; weight: z=1.98, p=0.048). The mean body length and weight of females (n=45) reached 19.2 mm and 153 g, whereas the values obtained for males (n=48) were 17.4 cm and 99.9 g, respectively. The logistic regression revealed that between-sex differences in mensural characters were highly significant ($\chi^2 = 51.19$, df = 17, $p < 0.001$). The variables that had the highest influence upon the model were postdorsal distance, dorsal fin length, eye diameter and caudal peduncle length. However, only for the first two characters were the results statistically significant after applying the Bonferroni correction for multiple comparisons (Table 4). The model correctly predicted the sex of 80 % of females and 83 % of males used in this study. The results of the analysis carried out on the reduced data set (without the largest females) were similar ($\chi^2 = 35.72$, df = 17, $p = 0.0050$), but, apart from postdorsal distance and dorsal fin length, the effect of eye diameter was also significant. This model correctly predicted the sex of 72 % of females and 85 % of males. Dorsal fin length and eye diameter were relatively larger in males, while postdorsal distance was relatively longer in females.

Between-catchment comparisons

Specimens from the Dnieper River differed significantly ($p < 0.001$) with regard to nine and eleven (DR1 and DR2, respectively) mensural characters from those from the Włocławek Reservoir (Table 5). Such differences between the Włocławek and Zegrze reservoirs, both from the Vistula River catchment, occurred in the case of five characters only. In comparisons of the two combined groups: (1) fish from the Dnieper River (both DR1 and DR2) vs. (2) fish from the Vistula River catchment (Włocławek and Zegrze reservoirs), four characters (X1, X3, X4, X17) revealed significant differences (Table 5).

Growth rate

The age of fish used in the growth rate analysis (n=108) ranged from 1+ to 3+ years, with the majority (59.3%) belonging to the 2+ years group. The percentage of 1+ and 3+ age classes were 6.5 and 34.3, respectively. A linear relationship between the body length (l) and the length of the caudal radius of scales (S) was found:

$$l = 1.5602 * \mathrm{S} + 4.1002,\ \mathrm{R}^2 = 0.792,\ \mathrm{n} = 108,\ p < 0.001$$

Table 2. Mean, standard deviation (SD), standard error (SE), range, coefficient of variation (CV) and number of specimens (n) for 15 meristic characters of white-eye bream collected from the Włocławek Reservoir (Vistula River).

Character	Mean	SD	SE	min.	max.	CV	n
Scales on lateral line	51.7	1.27	0.15	50	57	2.45	70
Scales above lateral line	51.9	1.10	0.13	50	55	2.13	68
Scales below lateral line	51.7	1.07	0.14	50	55	2.07	62
Dorsal branched rays	7.1	0.30	0.03	7	8	4.19	93
Dorsal unbranched rays	2.9	0.23	0.02	2	3	7.70	93
Pectoral branched rays	16.7	0.54	0.06	15	18	3.25	93
Pectoral unbranched rays	1.2	0.42	0.04	1	3	35.50	93
Pelvic branched rays	8.0	0.10	0.01	8	9	1.29	93
Pelvic unbranched rays	2.0	0.25	0.03	1	3	12.86	93
Caudal branched rays	17.0	0.23	0.02	16	18	1.37	93
Caudal unbranched rays	5.6	0.73	0.08	4	7	13.03	93
Anal branched rays	39.4	1.38	0.14	36	43	3.51	93
Anal unbranched rays	3.0	0.18	0.02	3	4	5.86	93
Pharyngeal teeth count	5.0	-	-	5	5	-	93
Gill rakers	21.3	1.44	0.16	18	25	6.77	83

Table 3. Statistics of linear (L), quadratic (Q), power (P) and split linear (S) (only if the breaking point was inside the range of the fish length) regressions and best fitted model equations for mensural characters in white-eye bream from the Włocławek Reservoir (the Vistula River). **A.** Coefficients of determinations. **B.** Model comparisons. L_b – fish length; t, p – the results of the t-test verifying the hypothesis that the exponent in the power equation is equal to 1 (* 0.05>p>0.01, ** 0.01>p>0.001; *** 0.001>p); ΔAIC – the difference between AIC coefficients; p2 – probability that a more complicated model is correct; $ indicates that a more complicated model is more likely to be correct.

A Character	R^2 (P)	R^2 (Q)	R^2 (L)	R^2 (S)
X1 Lateral head length	0.9577	0.9583	0.9572	
X2 Preorbital distance	0.8459	0.8495	0.8465	
X3 Eye diameter	0.9128	0.9128	0.9126	
X4 Postorbital distance	0.9611	0.9639	0.9613	
X5 Head depth	0.9000	0.9040	0.8988	
X6 Head width	0.8839	0.8880	0.8843	0.8850
X10 Predorsal distance	0.9558	0.9582	0.9560	0.9600
X11 Postdorsal distance	0.9745	0.9751	0.9746	
X12 Body depth	0.9789	0.9790	0.9790	
X13 Preanal distance	0.9789	0.9794	0.9788	
X14 Minimum body depth	0.9377	0.9388	0.9375	
X15 Caudal peduncle length	0.8260	0.8274	0.8256	
X16 Caudal fin length	0.8066	0.8073	0.8073	0.8078
X17 Pectoral fin length	0.9518	0.9547	0.9505	
X18 Ventral fin length	0.8671	0.8720	0.8657	
X19 Dorsal fin height	0.9098	0.9125	0.9085	
X20 Anal fin height	0.8613	0.8632	0.8624	
X21 Dorsal fin length	0.9395	0.9445	0.9401	
X22 Anal fin length	0.9043	0.9042	0.9042	
X23 Distance P-V	0.9429	0.9520	0.9403	
X24 Distance V-A	0.8995	0.9065	0.8989	

Table 3 – continuation.

B	t-test		Model comparison with Akaike's Information Criterion										Best fitted model	Equation
	P/L		Q/P		Q/L		S/P		S/L		S/Q			
	t(91)	p	ΔAIC	p2	ΔAIC	p2	ΔAIC	p2	ΔAIC	p2	ΔAIC	p2		
X1	4.62	<0.001***	0.7	0.42	$-0.3^{\$}$	0.54							P	$0.345L_b^{0.899}$
X2	1.98	0.051	$-0.2^{\$}$	0.52	0.2	0.47							L	$0.049L_b-0.764$
X3	11.78	<0.001***	2.0	0.27	1.8	0.29							P	$0.283L_b^{0.721}$
X4	1.73	0.087	$-4.9^{\$}$	0.92	$-4.5^{\$}$	0.90							Q	$-6.786+0.166L_b-0.0002L_b^2$
X5	3.32	0.001**	$-1.9^{\$}$	0.72	$-2.9^{\$}$	0.81							Q	$-9.793+0.294L_b-0.0004L_b^2$
X6	1.33	0.186	$-1.3^{\$}$	0.66	$-1.1^{\$}$	0.63	3.2	0.17	3.4	0.15	4.5	0.09	Q	$-10.306+0.220L_b-0.0002L_b^2$
X10	1.39	0.168	$-3.1^{\$}$	0.82	$-2.7^{\$}$	0.79	$-5.2^{\$}$	0.93	$-4.9^{\$}$	0.92	$-2.1^{\$}$	0.75	S	$L_b<166.5$: $0.221L_b+45.241$ $L_b\geq165.5$: $0.521L_b-7.833$
X11	0.96	0.339	0.0	0.50	0.1	0.48							L	$0.424L_b-1.012$
X12	3.00	0.003**	1.9	0.28	2.0	0.27							P	$0.262L_b^{1.049}$
X13	0.36	0.717	$-0.4^{\$}$	0.55	$-0.6^{\$}$	0.58							Q	$-3.747+0.146L_b-0.0001L_b^2$
X14	1.14	0.256	0.4	0.45	0.1	0.49							L	$0.087L_b+0.716$
X15	1.12	0.264	1.3	0.35	1.1	0.37							L	$0.093L_b+1.302$
X16	8.20	<0.001***	1.7	0.30	2.0	0.27	3.4	0.15	3.8	0.13	1.8	0.29	P	$1.137L_b^{0.692}$
X17	6.02	<0.001***	$-3.7^{\$}$	0.86	$-6.2^{\$}$	0.96							Q	$-8.601+0.367L_b-0.0004L_b^2$
X18	3.43	0.001***	$-1.5^{\$}$	0.68	$-2.5^{\$}$	0.78							Q	$9.361+0.074L_b+0.0001L_b^2$
X19	4.88	<0.001***	$-0.9^{\$}$	0.61	$-2.2^{\$}$	0.75							Q	$-9.677+0.194L_b-0.0002L_b^2$
X20	4.83	<0.001***	0.7	0.41	1.4	0.33							P	$0.360L_b^{0.829}$
X21	2.72	0.008**	$-6.0^{\$}$	0.95	$-5.1^{\$}$	0.93							Q	$24.925-0.090L_b+0.0008L_b^2$
X22	0.91	0.363	2.0	0.27	2.0	0.27							L	$0.336L_b+2.428$
X23	4.31	<0.001***	$-14.1^{\$}$	1.00	$-18.1^{\$}$	1.00							Q	$-3.209+0.257L_b-0.0002L_b^2$
X24	0.49	0.625	$-4.7^{\$}$	0.91	$-5.3^{\$}$	0.93							Q	$-4.187+0.085L_b-0.0005L_b^2$

Table 4. Results of the logistic regression indicating between-sex differences in mensural characters. Asterisks show statistically significant ($p < 0.05$) coefficients after applying the sequential Bonferroni correction. The variables that were strongly correlated with the other data (multiple correlation coefficients >0.7) were removed from the data set.

	Standardized regression coefficients	Regression coefficients	SE	t(75)	p
Intercept	0.009	16.322	20.595	0.79	0.4306
X2 Preorbital distance	0.822	191.304	89.751	2.13	0.0363
X3 Eye diameter	1.580	336.390	111.108	3.03	0.0034
X5 Head depth	-0.541	-50.858	33.221	-1.53	0.1300
X6 Head width	0.252	32.427	52.978	0.61	0.5423
X10 Predorsal distance	-0.779	-34.411	16.545	-2.08	0.0410
X11 Postdorsal distance	-1.506	-98.299	32.086	-3.06	0.0030*
X12 Body depth	-0.757	-70.685	34.735	-2.04	0.0454
X14 Minimum body depth	0.664	127.573	73.748	1.73	0.0878
X15 Caudal peduncle length	1.000	105.612	45.484	2.32	0.0230
X17 Pectoral fin length	-0.093	-10.063	45.573	-0.22	0.8258
X18 Ventral fin length	0.849	79.639	43.413	1.83	0.0706
X19 Dorsal fin height	-0.386	-25.131	24.111	-1.04	0.3006
X20 Anal fin height	-0.101	-8.550	32.481	-0.26	0.7931
X21 Dorsal fin length	1.505	268.633	84.495	3.18	0.0021*
X22 Anal fin length	0.009	0.372	14.347	0.03	0.9794
X23 Distance P-V	0.043	3.253	27.638	0.12	0.9066
X24 Distance V-A	-0.932	-68.278	32.303	-2.11	0.0379

There was no significant difference between the growth of 1 and 2-year old females and males (Mann–Whitney U-test: 1-year old fish: n=75, z=-0.11, *p*=0.909; 2-year old fish: n=48, z=1.61, *p*=0.107). The 3-year-old fish were excluded from the analysis because almost all of them were females. The back-calculated lengths-at-age of the white-eye bream in the Włocławek Reservoir are given in Table 6.

The parameters of the von Bertalanffy's growth model are as follows: $L_\infty=37.79$, $W_\infty=1125.75$, $K=0.29$, $t_0=0.23$. The theoretical values of body length (L) and weight (W) calculated with the von Bertalanffy's equation were well-fitted with the empirical data (L: $R^2=0.9977$; W: $R^2=0.9999$).

The weight-length relationship (Fig. 2), as well as the length-frequency distribution (Fig. 3) revealed three distinct size groups of fish from the examined sample. There was a clear overlap between the peak lengths of fish from the first two size groups and the mean lengths at the ages of 1 and 2 years (Table 6). The size composition by length of males and females differed (Fig. 3), with the largest individuals (23–28 cm *l*) being females only.

Discussion

External morphology

We investigated mensural and qualitative characters of specimens ranging from 142 to 277 mm *l*. This is the size range of white-eye bream usually recorded in commercial net catches and equal to that which has often been used in morphological investigations

Table 5. The comparison of morphometric characters of white-eye bream from the Włocławek Reservoir (Vistula River) with those from the Dnieper River (two data sets provided by Zhukov 1965: Dnieper1, Dnieper2) and from the Zegrze Reservoir (Bug and Narev River) (Terlecki 1990), by use of one-way ANOVA. Mean and standard deviation (SD) were included. Asterisks show statistically significant coefficients after applying the sequential Bonferroni correction. Areas labelled with the same superscript letter did not differ significantly from one another with respect to a given character (Tukey test).

	Włocławek		Dnieper1		Dnieper2		Zegrze Reservoir				
Character/sites compared	Mean±SD	n	Mean±SD	n	Mean±SD	n	Mean±SD	n	*F*	d.f.	*P*
in % of body length											
X1 Lateral head length	20.43±0.89^{a}	93	22.2±0.90^{b}	37	22.2±1.05^{b}	47	20.9±0.81^{a}	14	54.13	3.187	<0.001*
X10 Predorsal distance	47.74±7.25^{a}	93	52.4±1.44^{b}	37	52.7±1.60^{b}	35	52.5±1.29^{b}	14	11.85	3.175	<0.001*
X11 Postdorsal distance	41.8±1.53^{a}	93	41.1±1.77^{a}	37	39.9±1.56^{b}	35	41.8±1.36^{a}	14	13.74	3.175	<0.001*
X12 Body depth	33.41±2.75	93	33.4±1.24	37	33.3±1.36	47	34.1±1.91	14	0.53	3.187	0.661
X14 Minimum body depth	9.09±0.52^{ab}	93	8.9±0.58^{a}	37	8.6±0.54^{c}	47	9.4±0.23^{b}	14	13.00	3.187	<0.001*
X17 Pectoral fin length	18.37±0.92^{a}	93	19.1±0.8^{b}	37	19.5±0.88^{b}	35	18.3±0.76^{a}	14	20.75	3.185	<0.001*
X18 Ventral fin length	14.63±1.07	93	15.1±0.87	37	15.0±0.91	35	14.9±0.68	14	2.03	3.175	0.111
X19 Dorsal fin height	24.18±1.66^{a}	93	21.8±1.2^{b}	37	22.4±1.70^{b}	47	22.9±1.14^{b}	14	25.57	3.175	<0.001*
X20 Anal fin height	14.85±1.18^{a}	93	13.4±1.15^{bc}	37	14.3±1.51^{a}	35	14.1±0.74^{ac}	14	12.35	3.175	<0.001*
X21 Dorsal fin length	9.82±0.56	93	10.1±0.7	37	10.0±0.69	47	9.7±0.62	14	1.82	3.175	0.146
X22 Anal fin length	34.69±3.54^{a}	93	36.4±1.38^{b}	37	36.2±1.89^{b}	35	35.3±1.82^{ab}	14	4.41	3.175	0.005*
X23 Distance P-V	20.32±2.23	93	19.6±1.43	37	20.5±1.48	35	20.2±0.89	14	1.79	3.175	0.150
X24 Distance V-A	17.99±1.36	93	17.3±1.14	37	17.9±1.30	35	18.0±1.08	14	2.89	3.175	0.037
in % of Lateral head length											
X2 Preorbital distance	21.96±2.08^{a}	93	27.3±2.15^{b}	37	28.8±1.57^{c}	35	28.2±1.47^{bc}	14	146.88	3.175	<0.001*
X3 Eye diameter	32.56±2.25^{a}	93	29.5±2.12^{b}	37	29.7±1.6^{b}	35	27.5±1.99^{c}	14	41.47	3.175	<0.001*
X4 Postorbital dostance	47.95±2.47^{a}	93	43.7±2.78^{b}	36	42.4±1.99^{b}	35	48.7±2.53^{a}	14	61.98	3.176	<0.001*
X5 Head depth	84.69±4.77^{a}	93	84.0±0.76^{ac}	37	79.9±0.72^{b}	35	81.6±3.42^{bc}	14	16.52	3.175	<0.001*

Table 6. Mean back-calculated body lengths at age of white-eye bream from several waters of Eurasia including those from the Włocławek Reservoir.

Study site	Back-calculated length at age (cm)						Author
	1	2	3	4	5	6	
Aral Sea	8.2	12.2	16.3	19.4	23.1	26.2	Berg 1949
Amu-Daria River	7.8	12.0	16.1	19.9			Maksunov 1972
Dnieper River	5.2	10.6	15.7	20.2	24.0		Zhukov 1965
Farkhadskoe Reservoir	8.1	13.1	16.2	17.6			Maksunov 1972
Kajrak-Kumskoe Reservoir	9.0	14.0	16.8	18.6			Maksunov 1972
Zegrze Reservoir (Bug and Narev Rivers)	7.0	13.8	19.2	24.4	26.0		Terlecki 1990
Włocławek Reservoir (Vistula River)	7.6	15.2	20.9				present study

(Zhukov 1965, Terlecki 1990). However, in this length range of white-eye bream most of the mensural characters exhibited considerable size-related variability. These characters grew allometrically and were best described by a power or quadratic function (Table 3). Thus, in order to avoid bias caused by ontogenetic variability, it is necessary to consider the size of the individuals investigated in any interspecific and/or interpopulation morphological comparisons. Therefore, to allow such comparisons in the future, we presented the basic statistics of the mensural characters in four size classes (Table 1).

Five of the 21 characters demonstrated isometric growth and a linear regression provided the best model for them (Table 3). Split-linear regression revealed the best model for predorsal distance only. This pattern of growth represents two different isometric stages

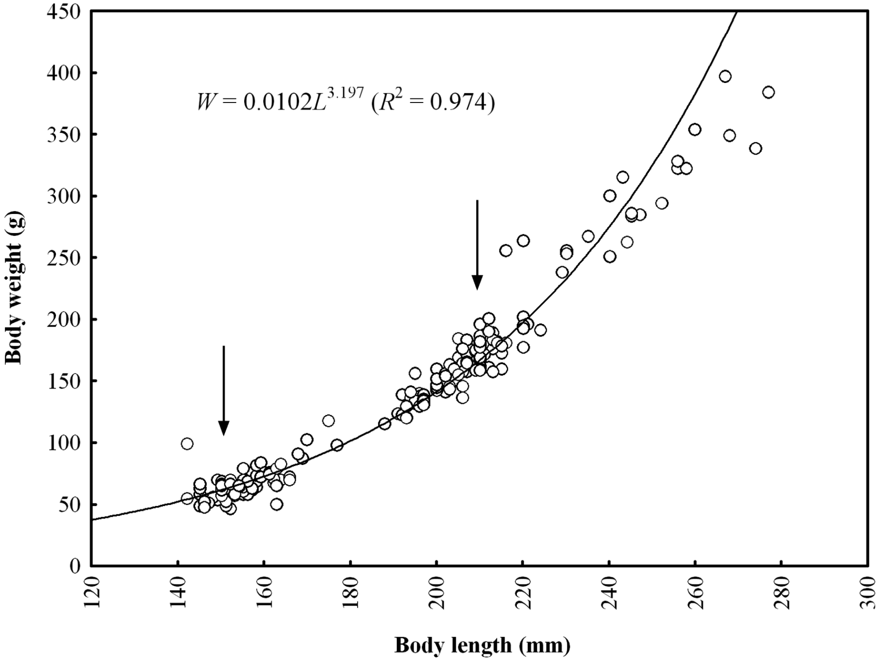

Fig. 2. Relationship between body weight and body length of white-eye bream (n=201) collected from the Włocławek Reservoir (Vistula River). Arrows indicate mean back-calculated lengths of fish achieved at age of 2 (152 mm) and 3 (209 mm) years, respectively.

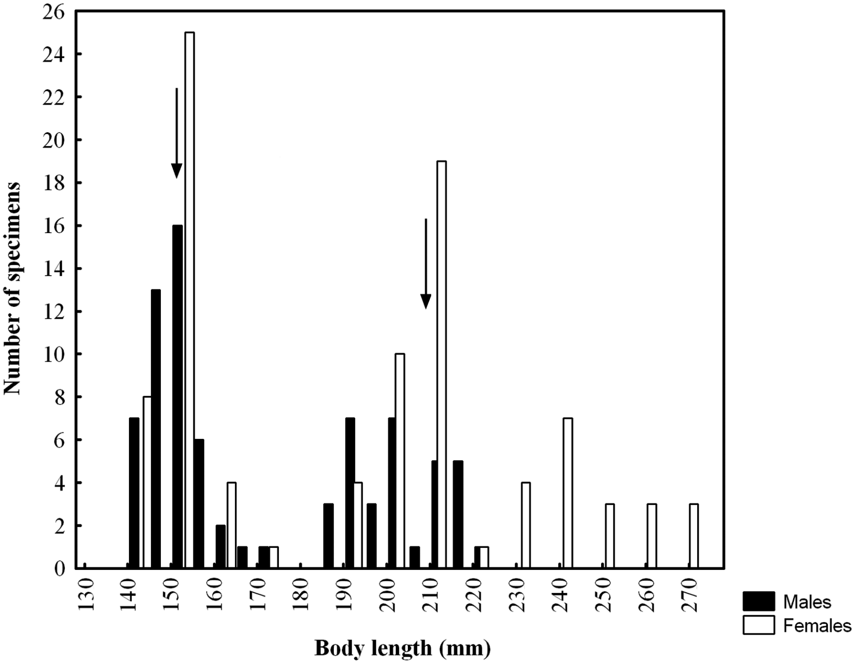

Fig. 3. Length-frequency distribution of white-eye bream (n=201) caught in the Włocławek Reservoir (Vistula River). Arrows indicate mean back-calculated lengths of fish achieved at 2 (152 mm) and 3 (209 mm) years of age, respectively.

with an abrupt shift in proportional growth occurring at a specific body length. The lack of characters changing according to this model in our sample seems to result from too large size of the available fish ($l > 142$ mm). Abrupt changes in isometric growth occur in early life stages of fish (Kováč et al. 1999), which were not covered by our study.

Between-sex differences

Berg (1949) stated that white-eye bream did not reveal sexual dimorphism. Contrary to these results, in our study we detected significant between-sex differences using logistic regression. It showed statistically significant differences between males and females in two mensural characters: postdorsal distance and dorsal fin length (Table 4). These differences could result from real morphological differences between sexes or from allometric growth of fish. In our study, females were significantly larger than males, with the largest group of fish (192–277 m *l*) consisting of females only (Fig. 3). The results of the analysis carried out after excluding the largest females from the data set suggest that the former hypothesis was more probable. However, the latter possibility cannot be undoubtedly excluded using our data, thus further studies are needed to resolve this problem.

Between-catchment comparisons

The results of comparisons of non-native white-eye bream populations from the River Vistula catchment (Włocławek Reservoir and Zegrze Reservoir) and the native fish from the Dnieper

River catchment revealed morphological discrepancies between these groups. However, the observed variations of non-linear characters could be size-related. Although there is a considerable overlap between size ranges of compared specimens from different regions (Włocławek Reservoir: 142–277 mm; Zegrze Reservoir: 200–300 mm; Dnieper River: 126–255 mm and 128–285 mm, respectively in DR1 and DR2), the length-frequency distributions of the fish samples from the literature data are unknown. Thus, they may differ substantially between one another. On the other hand, all four isometrically increasing characters (Table 3), in which size effect was eliminated, also showed statistically significant differences in our analysis (Table 5). These results indicate that white-eye bream from the compared regions were not morphologically uniform. At present, it is difficult to define the influence of habitat divergence on the observed morphological differences. It is possible that white-eye bream exhibit substantial morphological plasticity and, similarly to some other European fish species, considerable differences can be observed even within very restricted geographic areas (Baker et al. 1998).

Meristic characters showed considerable overlap with the data provided by Berg (1949) and Zhukov (1965, 1988) except the number of unbranched fin rays, which revealed greater variability. The numbers of dorsal and anal unbranched fin rays provided by the mentioned authors were constant (3), whereas we found that these values were variable (Table 2). In addition, the numbers of unbranched pectoral and pelvic fin rays showed greater variability than in other studies (2 and 1, respectively) (Terlecki 1990), suggesting substantial morphological plasticity of white-eye bream (Table 2).

Growth rate

Length-frequency distribution of white-eye bream (Fig. 3) at the end of the growing season evidently corresponded to the growth rate pattern of these fish (Table 6). The length–frequency diagram revealed a multimodal distribution with at least three size groups. The mean lengths of the first two groups (155 and 206 mm *l*) very strictly corresponded to the back-calculated mean lengths of fish at age of 2 and 3 years (155 and 211 mm *l*, respectively), which suggests that recorded size distribution strongly coincided with age composition of white-eye bream population in the reservoir. However, fish were collected by commercial fishermen using gill nets, which are size-selective tools. Although the set of appropriately coupled gill nets could give a non-selective sample of fish population (Backiel & Korycki 1972), the details of the nets used (e.g. mesh size) to collect white-eye bream are unknown and it is not possible to speculate how strongly they might affect the size composition. Nevertheless, the growth increments of most of the age groups of white-eye bream in the Włocławek Reservoir appeared to be quite rapid. The growth rate showed a similar pattern to that in the Zegrze reservoir (Terlecki 1990), which is also a strongly lotic dam reservoir from the non-native Vistula River catchment. The growth was moderate in the first year of life and then faster compared with that occurring in many waters within the native range of this species (Table 6). This marked increase of growth seems to be site-related, rather than region-specific, depending on the quantity of food resources. In both riverine reservoirs enormously high abundances of bottom fauna (Dusoge 1989, Żbikowski 2000) compared with other waters (Kajak et al. 1980) was noticed. Thus, they provide feeding conditions favoring older fish, which become benthivorous. In the Włocławek Reservoir, the mean abundance of zoobenthos can exceed 100 thousand ind. m^{-2} and the mean biomass ca 0.5 kg m^{-2} (Żbikowski 2000). Biomass of chironomid larvae, a major source of food for fish (Kakareko 2001, 2002, Kakareko et al. 2005), demonstrated considerable temporal and spatial variability but often attained very high values: approximately 70–100 g m^{-2} (Żbikowski 2000). The fast growth rate of a closely related species, common bream *Abramis brama* (L.), was also observed in the reservoir and it was clearly supported by the high abundance of benthic prey (Kakareko 2001).

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