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Standaryzacja wzrostu ryb i ocena zasobności ich środowiska w oparciu o temperaturę wody na przykładzie trzech populacji okonia w zbiornikach zaporowych południowej Polski

The standardization of fish growth and evaluation of the quality of habitat with data on water temperature: An example of Eurasian perch populations in three dam reservoirs in southern Poland

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Summary

In contrary to other vertebrates the growth of fishes is not limited by a determined size of an adult individual. This property results in quite wide and variable range of the upper limit of body size recorded in natural populations of each species. Also the individual growth patterns are flexible in response to environmental changes. The achieved size has important consequences for the survival and fecundity of an individual fish, because (1) larger individuals are more successful in avoidance of predators and sequestering resources than smaller ones, and (2) in Teleostei the egg production is closely related to fish size. As the lifetime growth pattern of an individual affects significantly the possibility of the transfer of its genes to the gene pool of next generation, the ability to accomplish a pattern which turns out to be "proper" at a given place and time is very important adaptation.

An individual fish is properly adapted when it successfully maximises the number and quality of offspring during its life. To achieve this aim an individual should accurately allocate energy and materials among (1) current cost of maintenance, (2) synthesis of new tissue of its body, and (3) production of gametes. All these tasks usually compete for energy and nutrient reserves stored in the organism which are acquired by fish from food containing proteins, fat, carbohydrates and minerals. Therefore, in natural conditions the growth of an individual is permanently constrained by the current food supply, considering both its amount and nutritional quality, and also by the state of other environmental features, especially those limiting metabolic rate, such as oxygen concentration, or those generating additional energetic expenditures. The final amount of food and of all other environmental benefits strongly depends on individual tolerances and responses, both physiological and behavioural. The realised growth pattern is then the result of an interplay between the internal potential of an individual and the actual habitat conditions, including both the physical and biotic components of the environment. Among the external physical factors the temperature plays a special role in the growth of poikilotherm fish, because temperature controls rates of all biochemical reactions of its physiological processes, both anabolic (synthesis of tissue) and catabolic (breakdown of tissue).

Achieved growth is described in terms of fish size (weight in most cases) as the absolute change in a definite period, or as a coefficient relating that change to the initial size. If such measures are related to an interval of time they become growth rates. Another method to describe growth of a fish consists in fitting a general model to its lifetime growth pattern. Among several models, von Bertalanffy growth model is the most commonly used. However, besides many advantages these measures and models have an important drawback that their values say directly nothing about the strength of the above mentioned external constraints. It is certainly true, that such results may be related to selected factors which are controlled in laboratory or aquaculture, but in natural waters the whole complex of all environmental conditions which significantly influence growth of the given individual or population is much more difficult to define, and even harder to monitor and study. Additionally, the methods of assessment of fish growth ignore the temperature.

The current progress in macroecology (Brown & Maurer 1989; Smith *et al*. 2008) allows to solve this problem. The results concerning two general relations, *i.e.* (1) between the individual size and biomass production (Niklas & Enquist 2001), and (2) between the individual size and population density (Belgrano *et al*. 2002), when considered jointly justify the supposition that the production of a population, expressed in g m^{-2} y^{-1}, does not depend on the average individual biomass, but remains a constant corresponding to the possible density of individuals

of average size. Also the total consumption of a population may be regarded as independent of average individual mass (Ernest *et al*. 2003). Thus, the rates of both total consumption and production of a population depend on these environmental factors which limit the number and/or the body mass of individuals, and are crucial for their metabolic processes. Additionally, the number of individuals, their average size, and the rate of environmental resource supply remain related within a population (Marquet *et al*. 2005). Therefore, every change in the population density will result in respective change of average body mass, assuming the constant "quality" of the environment.

The production of individual biomass, which results in its current body mass, is related to the rate of respiration (McNeill & Lawton 1970) while the individual respiration depends on both body mass and temperature, accordingly to the equation of *universal temperature dependence* (Gillooly *et al*. 2001; Brown *et al*. 2004). Assuming this with the above, the general metabolic equation was proposed which relates the metabolic rate of an individual with its body mass, temperature, and the state of available resources (Marquet *et al*. 2004). As a result, the following equation relating production to body mass, temperature and resources may be formulated:

$$P_{ind} = a\,M^{3/4}\,e^{-E_a/k_BT_a}\,f(R)$$

where: P_{ind} – production rate of individual body mass, *i.e.* the increment of its size expressed in g ind.$^{-1}$ y^{-1}, a – a normalisation constant, M – initial body mass in grams, e^{-E_a/k_BT_a} – Boltzmann factor in Arrhenius equation, E_a – activation energy of metabolism, k_B – Boltzmann's constant, T_a – absolute temperature in K, $f(R)$ – a function of amount and quality of available resources. In general, the output of this function controls the increment of body mass, or in other words the individual growth which is rapid when the available resources are plentiful or slow when they are scarce. The function of available resources remains unknown, but it can be now replaced by the quotient P_{ind}/P_{max}, where P_{max} is an extreme biomass production in comfortable environment, *i.e.* depending only on the initial body mass and temperature.

The value of P_{max} may be reliably approximated under two general assumptions. Firstly, according to existing data on fish growth in Central European inland waters, the weight increment which is ten times larger than initial body mass of 10 g ($P_{max}/M = 10$ y^{-1}), and is achieved in the average temperature of 20 °C can be assumed as a standard of very rapid growth. Secondly, an average value of activation energy fitted to a wide variety of organisms from unicellular algae through invertebrates, fishes, and birds to large vascular plants and mammals equals to 0.63 eV (Brown *et al*. 2004). After substituting all above values the equation for P_{max} can be solved for a. The final version of this equation is then the following:

$$P_{max} = 1{,}205\ 10^{12}\ M^{0{,}75} / e^{7311/(T+273{,}15)}$$

where T is the mean temperature of water in °C during the season of fish growth, which lasts from May to September in Central Europe. The P_{max} values estimated with use of this equation correspond well to published results concerning two exemplary species, the wild one regarded as relatively slow growing, and the other reared in fish ponds and growing very fast (Figure 12). Thus, the quotient P_{ind}/P_{max} may be introduced as an **index of environmental quality**:

$$Q_E = e^{7311/(T+273{,}15)\,-\,27{,}82}\ P_{ind}/M^{0{,}75}$$

The proposed Q_E index standardises the increment in body mass in relation to theoretical capacity for increase in the body size, and refers to the whole pool of resources and benefits available in all the habitats which compose the whole real life environment of a fish, in the sense of Greek term *οίκος*, which has been included into the word 'ecology'.

The application of the index of environmental quality Q_E to assessment of fish growth was demonstrated on examples of natural populations of Eurasian perch, *Perca fluviatilis* L., 1758, in three dam reservoirs. The selected species is known as very adaptive to habitat conditions, and occurs in a wide range of freshwater ecosystems, mainly in rivers and lakes, and also in coastal brackish lagoons. Perch is an opportunistic carnivore feeding on zooplankton, benthic invertebrates and fishes. The life-history patterns are flexible in this species, and the growth in perch populations is very variable. The variability is also the feature of environmental conditions in dam reservoirs. Despite their similarity to lakes, reservoir ecosystems are greatly affected by rivers flowing through them, especially as concerns the flushing rate, input of nutrients, and sediment load. Therefore, the habitat conditions in a reservoir change not only between littoral, pelagial, and profundal but also along the longitudinal axis from river inflow to the dam. Additionally, in contrary to lakes, reservoir ecosystems are permanently manipulated according to the current needs of their users, which effects in rapid and broad fluctuations of water level, surface area and water volume, and results in scarcity of submerged vegetation. The fish communities are most abundant and relatively rich in species in littoral near the inflows of tributaries, and most scarce in limnetic zone near the dam and in profundal. In general, a reservoir offers to the population of a fish species a set of habitats where the conditions are relatively variable both spatially and temporally, and also unpredictable due to dam operation.

The material for study on perch growth was collected in three reservoirs in the Vistula basin in S Poland in 1981–2005 (Tables 2, and 6–9). The climatic conditions in these reservoirs are very similar, while their different morphologies determine the differences in the functioning of their ecosystems and in interactions within their food webs. Collected individuals were measured to the nearest mm (TL, FL and SL were recorded; Figure 14) and weighed (body mass was approximated to three significant digits). The FL may be regarded as the best predictive variable of body mass in the length-weight relationship, however, the quality of two remaining measures does not differ significantly (Table 3).

The age of perch may be read from scales, otoliths and opercular bones. Annual rings are most distinct on thin slides cut from otoliths while these on scales are most dubious. The scales, however, are most easy to collect and prepare. Therefore, they still are, and undoubtedly will remain an useful source of information on perch age also in the future. Annual rings on scales are distinguished by a more or less visible band of concentrated narrow sclerites, mostly with a hyaline edge at the outer border of the zone of retarded growth (Figure 17). The accuracy of perch age readings does not require verification, because the number of annuli is equal to the true age, as it was confirmed in a lot of previous studies. In contrary to that, the correctness of annuli identification in perch scales should be verified. It was done by the comparison of lengths back-calculated on the basis of scales and opercula collected from the same specimens (Figures 20, 22, and 23). The length of perch was back-calculated with Fraser–Lee equation under assumption that the standard length at the scale formation is equal to 2.5 cm (Tables 6–9). The values of body mass at age were estimated using length-weight relationships (Tables 11 and 12). Condition was determined with Fulton's condition factor and standard weight (Table 13).

Both mean growth and condition in perch populations in three dam reservoirs were similar to these recorded in natural lakes in Poland. Exceptionally rapid growth was recorded in the newly created Dobczyce Reservoir during the first two years of its existence (1986–1987). New reservoirs provide perch with comfortable living conditions – low density of colonising population resulting in lack of competition in that time, high primary production feeding dense zooplankton, abundant benthic invertebrates developing on decomposing inundated terrestrial vegetation, rich spawning substrate for phytophilous fish which results in high density of YOY forage fish, relatively high oxygen concentration in whole water column, and low energetic expenditures in stagnant water, in comparison to the submontane river before impoundment. The ranges of standard length achieved in consecutive seasons were relatively wide in all reservoirs (Figure 27), which make purposeless the calculation of mean growth trajectories. Also the attempt to calculate respective formulae of von Bertalanffy growth model failed. The main cause was a two-stage pattern of individual growth resulting from the switch to piscivory at the length between 10–20 cm (Figure 28). Therefore, the growth trajectories in perch should be described by two von Bertalanffy formulae, as a rule (Figure 29). During the first stage an individual quickly approaches small asymptotic length, and next it may change its growth pattern into slower approaching a relatively large size. The unusual simultaneous change of growth patterns in all age classes of the population was observed only in the newly created Dobczyce Reservoir (Figures 30–32). This feature may be attributed to the possibility to colonise a variety of "empty" lacustrine habitats rich in all kinds of "free" resources.

Taking into consideration that the principal habitat of the population of perch in a reservoir is the photic depth layer, and especially the littoral zone, the weighted mean temperature of water within a 0–5 m depth layer from the start of May till end of September was adopted as an approximation of the thermal conditions of the process of fish growth (Figure 25). The mean temperatures of water during the seasons of fish growth in the studied reservoirs were obtained from the published results of investigations of water temperature in the fish ponds in Gołysz and from the data collected in the long-term monitoring of selected environmental parameters in the Dobczyce Reservoir conducted by the Institute of Nature Conservation, Polish Academy of Sciences, Cracow (Tables 5 and 14–16, Figure 24).

The perch populations living in mature reservoir ecosystems, *i.e.* those existing ten years at least, were characterised by relatively low medians of Q_E index (0.20–0.27; Tables 17–18), while the maximal values ranged within 0.54–1.19. It is worth of note, that in every population a small number of individuals with $Q_E < 0.10$ was found, which may be explained by probable effects of diseases, parasites or predator-caused injuries. Extremely high values of Q_E index were recorded in the Dobczyce Reservoir in first two years of its existence (median: 0.62, max.: 1.73). The distribution of results obtained there in 1986–1987 is distinctly right-skewed and 90% of Q_E values are <1.25 (Figure 33) what evidences the proper calibration of this index. These findings should be regarded as unique records of extremely rapid growth of Eurasian perch in Central European climatic conditions. Such growth was achieved in a water body, which, although artificially created, consists exclusively of natural habitats, and is managed without any attempts to improve fish growth.

The index of environmental quality was used to compare the conditions for growth of individuals of the same age classes in two reservoirs. The significance of differences were tested with Mann–Whitney *U* test because the true distribution of Q_E values in a population should be regarded as unknown yet. The average volume of resources available to perch population and allocated to individual growth was always greater and allowed perches in the Goczałkowice

Reservoir to achieve body mass increment in range of 131–270% of that in the Rożnów Reservoir in 1980–1982 (Figure 34). Certain chosen years were compared in a similar way. In this case, however, the differences were mostly insignificant (Table 20). It seems possible that perch is able to compensate to some extent the fluctuations in availability of resources in consecutive years even in such a labile ecosystem as a dam reservoir, probably due to the ability of this species to use relatively broad range of habitats and food categories. Especially noteworthy are significant differences which occurred in the Dobczyce Reservoir between the first year of its existence and two growth seasons 16–17 years later. They may be attributed much more to the effects of succession of reservoir ecosystem than to the conditions fluctuating from year to year, and therefore these cases should be considered rather as examples for comparison of two different environments. Another mode of application of Q_E index is the comparison of conditions for growth of individuals of different age in given years. The significant differences were not frequent – occurred only in about 1/3 of cases – and always in the same growth season the resources were relatively poorer for older than younger perches in the studied reservoirs (Table 19). It may probably be explained by the increasing with age proportion of resources allocated to reproduction. Additional analysis revealed that Q_E index does not duplicate results obtained with using other measures of growth, *i.e.* the absolute growth and the relative growth (Table 21). Despite the significantly correlated values of relative growth and the Q_E index, this last does not measure the efficiency of initial body mass in production of an increment, but standardises the achieved increment in relation to mass possible to achieve.

In conclusion, it was demonstrated that the index of environmental quality Q_E can be applied to (1) comparisons between aquatic ecosystems or years considered as different places or times of the growth of individuals of the same age, as well as to (2) comparisons of the resource availability at the same sites and years to individuals of different age classes. The main advantage of this new measure of fish growth is that it summarises physiology of an individual and the gains and losses arising from habitat conditions of its real place of life. Therefore, the Q_E index seems to be a prospective tool in fish growth studies, both ecological investigations focusing on relations between a species and its environment, and those in the field of fishery management focusing on assessment of fisheries and stocks.

Appendix: Tables, figures and bibliography cited in the summary

Table 2. Principal characteristics of dam reservoirs where the material for study on Eurasian perch growth was collected (the presented data concern the standard water level).

	Rożnów Reservoir	Goczałkowice Reservoir	Dobczyce Reservoir
Created in	1941	1955	1986
Main tributary	Dunajec	Vistula	Raba
Coordinates	49°45′ N 20°42′ E	49°56′ N 18°52′ E	49°52′ N 20°03′ E
Altitude (m)	264 [a]	255.5 [b]	269.9
Area (ha)	958 [a]	2990 [b]	985 [d]
Volume (hm^3)	78.4 [a]	120.2 [b]	108.3 [d]
Average depth (m)	8.2	4.0	11.0
Catchment (km^2)	4864 [a]	523 [b]	763 [e]
Catchment per reservoir area ratio	507.7	17.5	77.5
Average discharge ($m^3\ s^{-1}$)	70 [a]	7.3 [c]	10 [f]
Flushing rate (y^{-1})	28.2	1.91	2.9

Sources: [a] data provided by TAURON Ekoserwis Ltd. in Rożnów, [b] GPW 2012, [c] Tuszko 1984, [d] Amirowicz 1998, [e] Pasternak 1980, [f] Punzet 1969.

Table 3. Correlation coefficients (r) between logarithms of length and mass of perch in sample of 301 individuals >10 cm TL collected in the Dobczyce Reservoir in periods June–September in 2000–2010 (TL – total length, SL – standard length, FL – fork length; CL – confidence limits; $P < 10^{-6}$ in all cases).

Measure of length	r	95% CL	
		Range	Width
TL	0.994690	0.993341–0.995766	0.002426
SL	0.994695	0.993347–0.995771	0.002423
FL	0.994933	0.993645–0.995960	0.002315

Table 5. Mean temperature of water during the growth season (May–September) in fish ponds in Gołysz (S Poland, 49°52′ N, 18°48′ E; altitude 270 m) and in surface layer (0–5 m) of the Dobczyce Reservoir (49°52′ N, 20°03′ E, altitude 269.9 m).

Year	Dobczyce Reservoir [a]	Fish ponds in Gołysz						
		May	June	July	Aug	Sept	Mean	Source
1988	18.6	16.9	20.0	23.7	22.2	16.1	19.8	Szumiec 1989
1989	17.0	17.4	19.3	22.1	21.2	17.4	19.5	data from ZIGR PAN [b]
1990	17.8	18.3	20.5	21.3	21.7	14.6	19.3	data from ZIGR PAN [b]
1991	17.6	13.5	19.7	23.3	21.6	17.4	19.1	data from ZIGR PAN [b]
1992	19.3	16.6	21.8	24.1	24.0	16.1	20.5	Augustyn 1993
1993	18.5	18.3	20.7	20.2	21.9	16.4	19.5	Augustyn 1994
1994	18.9	17.7	20.2	25.8	22.9	18.3	21.0	Augustyn 1995
1995	18.3	16.0	20.9	24.8	22.1	15.4	19.8	Augustyn 1996
1996	17.4	16.2	21.5	20.4	21.6	13.2	18.6	Szumiec & Augustyn 1997
1997	17.6	17.5	20.5	21.1	22.5	17.3	19.8	Augustyn 1998
1998	17.0	17.9	21.6	21.5	21.9	15.9	19.8	Augustyn 1999
1999	19.8	16.6	20.9	23.8	21.9	19.7	20.6	Augustyn 2000
2000	19.5	19.6	21.9	19.4	22.0	16.0	19.8	Augustyn 2001
2001	17.9	18.7	18.6	22.0	23.7	15.1	19.6	Augustyn 2002
2002	19.9	20.2	22.7	23.7	23.5	17.4	21.5	Augustyn 2003
2003	18.9	19.8	23.6	22.8	23.8	18.3	21.7	Augustyn 2004
2004	18.8	15.9	20.1	21.9	22.1	17.4	19.5	Augustyn 2005
2005	18.2	17.1	21.0	22.9	21.3	18.7	20.4	Augustyn 2006
2006	18.9	16.9	21.0	25.2	22.0	20.2	21.1	Augustyn 2007
2007	18.7	20.1	23.7	23.3	23.1	15.7	21.2	Augustyn 2008
2008	20.4	17.8	23.4	22.8	22.4	16.5	20.6	Szumiec 2009
2009	19.6	18.5	24.4	23.8	23.4	17.5	21.5	data from ZIGR PAN [b]
Mean	18.6						20.2	

[a] Mean temperature in the period May–September was calculated from the data base of the long-term monitoring of the Dobczyce Reservoir ecosystem. The unpublished source data were kindly provided by Associate Professor Grażyna Mazurkiewicz-Boroń, Institute of Nature Conservation, Polish Academy of Sciences, Cracow.

[b] Unpublished data kindly provided by Professor Maria Szumiec, Institute of Ichthyobiology and Aquaculture, Polish Academy of Sciences, Gołysz.

Table 6. Mean standard length (cm; back-calculated with using Fraser–Lee equation) achieved by Eurasian perch in age 1–7 in the Rożnów Reservoir in growth seasons 1975–1984 (the growth seasons run diagonally across the table to the top right). Below the extreme individual lengths are given. In parentheses are presented sample sizes, *i.e.* numbers of individuals belonging to respective cohorts and age classes collected in 1981–1985.

Cohort	Age class													
	1		2		3		4		5		6		7	
1975	7.1	(2)	10.3	(1)	13.9	(2)	17.2	(2)	22.1	(2)	25.9	(2)	28.3	(2)
1976	6.5	(8)	9.5	(8)	12.5	(8)	15.5	(8)	19.3	(8)	23.1	(6)		
1977	6.2	(15)	9.5	(16)	13.1	(15)	17.2	(16)	22.4	(5)				
1978	6.0	(11)	9.1	(11)	12.1	(10)	15.4	(7)	18.2	(3)	19.9	(2)		
1979	6.9	(12)	9.7	(11)	13.0	(12)	16.0	(11)	19.1	(10)	24.9	(3)		
1980	6.8	(14)	9.8	(14)	13.1	(11)	17.6	(11)	23.5	(5)				
1981	7.1	(6)	10.8	(5)	12.6	(3)								
1982	7.1	(3)	11.6	(3)										
Min	5.5		7.9		10.3		12.3		14.7		19.0		27.2	
Max	8.6		13.8		17.2		20.6		24.9		28.4		29.4	
n		71		69		61		55		33		13		2

Table 7. Mean standard length (cm; back-calculated with using Fraser–Lee equation) achieved by Eurasian perch in age 1–7 in the Goczałkowice Reservoir in growth seasons 1976–1983 (the growth seasons run diagonally across the table to the top right). Below the extreme individual lengths are given. In parentheses are presented sample sizes, *i.e.* numbers of individuals belonging to respective cohorts and age classes collected in 1982–1984.

Cohort	Age class													
	1		2		3		4		5		6		7	
1976	6.5	(1)	10.8	(1)	16.2	(1)	24.1	(1)	28.3	(1)	31.3	(1)	33.4	(1)
1977	7.2	(2)	11.6	(2)	15.7	(2)	20.8	(2)	25.1	(2)	28.3	(2)	29.5	(1)
1978	7.0	(4)	11.8	(4)	15.8	(4)	19.6	(4)	22.8	(4)	29.5	(1)		
1979	7.0	(24)	11.2	(24)	15.5	(24)	20.1	(23)	24.1	(3)				
1980	6.9	(34)	10.8	(34)	18.3	(26)	24.8	(5)						
1981	9.0	(4)	14.5	(4)	15.7	(1)								
1982	7.9	(11)	15.1	(1)										
Min	5.2		9.1		12.2		16.1		19.3		27.4		29.5	
Max	10.0		17.0		22.2		28.0		28.3		31.3		33.4	
n		80		70		58		35		10		4		2

Table 8. Mean standard length (cm; back-calculated with using Fraser–Lee equation) achieved by Eurasian perch in age 1–7 in the Dobczyce Reservoir in growth seasons 1997–2005 (the growth seasons run diagonally across the table to the top right). The growth season 2005 is represented by five individuals collected on 28 October and 25 November 2005. Below the extreme individual lengths are given. In parentheses are presented sample sizes, *i.e.* numbers of individuals belonging to respective cohorts and age classes collected in 2004–2005.

Cohort	Age class													
	1		2		3		4		5		6		7	
1997	8.2	(1)	11.2	(2)	15.5	(3)	21.6	(3)	26.2	(3)	28.9	(3)	31.6	(3)
1998	6.8	(1)	11.7	(2)	18.7	(2)	22.5	(2)	26.5	(2)	28.9	(2)		
1999	7.8	(10)	12.1	(8)	17.1	(12)	22.9	(12)	26.8	(12)	29.7	(2)	30.8	(2)
2000	7.6	(8)	11.4	(7)	16.3	(9)	20.5	(9)	27.1	(3)	28.4	(2)		
2001	7.2	(14)	11.6	(11)	17.3	(17)	25.4	(5)	27.9	(1)				
2002	7.8	(4)	14.0	(7)	24.9	(3)								
2003	7.4	(3)	12.0	(5)										
Min	4.7		7.5		12.4		14.9		19.6		25.5		27.9	
Max	8.7		18.4		25.8		26.7		31.4		32.6		33.7	
n		41		42		46		31		21		9		5

Table 9. Mean standard length (cm; back-calculated with using Fraser–Lee equation) achieved by Eurasian perch in age 1–7 in the newly created Dobczyce Reservoir in growth seasons 1986–1987 (the growth seasons run diagonally across the table to the top right). The growth after the origin of reservoir is typed in bold. Below the extreme individual lengths are given. In parentheses are presented sample sizes, *i.e.* numbers of individuals belonging to respective cohorts and age classes collected in 1986–1988.

Cohort	Age class													
	1		2		3		4		5		6		7	
1981	6.3	(2)	8.8	(2)	12.1	(3)	14.6	(3)	17.4	(3)	**23.9**	(3)	**33.0**	(2)
1982	7.0	(2)	8.7	(2)	12.7	(4)	17.0	(5)	**26.1**	(4)	**32.3**	(3)		
1983	7.3	(7)	10.2	(8)	14.2	(8)	**23.4**	(6)	**31.0**	(4)				
1984	6.8	(23)	10.0	(23)	**18.8**	(15)	**27.0**	(4)						
1985	6.9	(14)	**14.5**	(14)	**18.1**	(2)								
1986	**8.1**	(3)	**12.3**	(2)										
Min	5.3		8.0		9.6		11.7		14.0		18.0		30.6	
Max	9.3		18.4		22.1		27.9		32.7		33.4		35.3	
n		51		51		32		18		11		6		2

Table 11. Body mass (g; estimated using regressions of weight on length) corresponding to the mean and extreme standard length (cm; Tables 6 and 7) achieved by Eurasian perch in age 1–7 in the Rożnów Reservoir and the Goczałkowice Reservoir in consecutive age classes (the growth seasons run diagonally across the table to the top right).

Cohort	Age class						
	1	2	3	4	5	6	7
Rożnów Reservoir 1981–1985: $W = 1.1503\ 10^{-2}\ SL^{3.1740}$							
1975	5.8	18.9	48.7	96.0	212.5	350.7	465.6
1976	4.5	14.6	34.6	69.6	138.8	243.7	
1977	3.8	14.4	40.2	96.8	222.7		
1978	3.4	12.7	31.8	67.4	114.0	153.3	
1979	5.2	15.8	40.0	76.1	133.2	311.2	
1980	5.1	16.0	40.0	103.7	260.0		
1981	5.9	21.7	36.0				
1982	5.9	27.5					
Min	2.6	8.1	18.7	32.9	58.3	130.8	411.5
Max	10.6	47.5	96.6	170.3	311.4	473.2	524.3
Goczałkowice Reservoir 1982–1984: $W = 1.8086\ 10^{-2}\ SL^{3.0568}$							
1976	5.6	26.4	89.6	304.2	496.7	672.8	825.0
1977	7.6	32.4	82.0	192.0	342.3	496.4	562.7
1978	6.9	34.2	83.0	161.6	256.8	562.7	
1979	7.0	29.1	78.3	173.7	302.2		
1980	6.6	26.0	131.6	330.2			
1981	15.1	64.8	81.6				
1982	10.1	72.1					
Min	2.8	15.6	37.9	88.7	154.8	447.7	562.7
Max	20.6	104.4	234.8	479.7	496.7	672.8	825.0

Table 12. Body mass (g; estimated using regressions of weight on length) corresponding to the mean and extreme standard length (cm; Tables 8 and 9) achieved by Eurasian perch in age 1–7 in the Dobczyce Reservoir in consecutive age classes (the growth seasons run diagonally across the table to the top right). In cohorts of 1981–1986 growth after the origin of reservoir is typed in bold.

Cohort	Age class						
	1	2	3	4	5	6	7
1986–1988: $W = 0.9428\ 10^{-2}\ SL^{3.2549}$							
1981	3.9	11.0	31.9	57.7	102.3	**290.2**	**823.1**
1982	5.3	10.9	37.0	94.6	**385.8**	**767.5**	
1983	6.1	18.1	52.6	**271.5**	**676.4**		
1984	4.9	17.0	**132.2**	**430.8**			
1985	5.0	**56.9**	**117.1**				
1986	**8.5**	**33.2**					
Min	2.2	8.2	14.8	28.4	50.5	114.9	645.9
Max	13.5	122.7	222.9	477.1	798.6	855.4	1031.5
2004–2005: $W = 0.8749\ 10^{-2}\ SL^{3.2602}$							
1997	8.3	23.4	65.9	196.2	369.7	506.6	680.4
1998	4.6	26.7	121.9	223.4	379.9	506.8	
1999	6.9	29.9	92.1	238.9	397.3	553.2	623.7
2000	6.5	24.6	78.0	164.9	412.9	476.0	
2001	5.5	25.7	95.5	334.1	451.8		
2002	7.2	47.2	310.3				
2003	6.1	28.6					
Min	1.4	6.2	31.9	58.5	142.9	337.0	451.8
Max	10.1	116.0	347.9	391.5	663.1	747.9	836.3

Table 13. Average condition corresponding to the standard lengths 10 and 30 cm which were defined as the standard size of small and large Eurasian perch in three dam reservoirs in S Poland: $TL_{SL\ 10}$, $W_{SL\ 10}$ – total length and body mass corresponding to the standard length 10 cm, K – Fulton's condition factor, W_s – standard weight (Giannetto *et al*. 2012)*, W_r – relative weight.

	$TL_{SL\ 10}$	$TL_{SL\ 30}$	$W_{SL\ 10}$	$W_{SL\ 30}$	$K_{SL\ 10}$	$K_{SL\ 30}$	$W_{s\ SL\ 10}$	$W_{s\ SL\ 30}$	$W_{r\ SL\ 10}$	$W_{r\ SL\ 30}$
Rożnów Reservoir 1981–1985	11.85	34.25	17.2	561.3	1.72	2.08	21.0	657.8	81.9	85.3
Goczałkowice Reservoir 1982–1984	11.73	33.86	20.6	592.4	2.06	2.19	20.4	632.4	101.0	93.7
Dobczyce Reservoir 1986–1988	11.77	34.09	17.0	605.7	1.70	2.24	20.6	647.3	82.5	93.6
Dobczyce Reservoir 2004–2005	12.05	35.10	15.9	572.4	1.59	2.12	22.1	715.8	71.9	80.0

* The published equation for calculation the standard weight of Eurasian perch is adapted for common logarithms of total length expressed in mm. After conversion for natural logarithms of total length expressed in cm it takes the form $\ln (W_s) = -3.3454 + 2.1245 \ln (TL) + 0.18636 (\ln (TL))^2$, which was used to obtain the presented results.

Table 14. Mean and extreme annual increments of individual body mass (g ind.$^{-1}$ y^{-1}) in Eurasian perch population in the Rożnów Reservoir. Average water temperature in the growth season (May–September) was estimated from the published records of temperature in fish ponds in Gołysz as 0.7366 T_G + 3.7080. Cohorts of the years 1975–1982 run diagonally across the table to the down right.

Year	Mean temperature		Age class						
	Fish ponds in Gołysz (T_G)	Rożnów Reservoir	1	2	3	4	5	6	7
1975	19.6 [a]	18.2	5.9						
1976	18.6 [b]	17.4	4.5	11.7					
1977	18.7 [c]	17.4	3.9	10.7	42.1				
1978	17.2 [d]	16.4	3.5	10.4	20.9	46.5			
1979	19.3 [e]	17.9	5.3	9.4	27.0	36.4	116.7		
1980	17.4 [f]	16.5	5.3	10.9	20.0	59.3	72.6	139.3	
1981	19.3 [g]	17.9	6.1	11.2	25.4	38.0	118.6	109.9	115.9
1982	20.2 [h]	18.6	6.0	17.3	26.1	37.9	56.8		
1983	20.2 [i]	18.6		21.8	20.7	61.1	57.6	53.3	
1984	17.8 [j]	16.8					126.9	142.8	
Min			2.6	4.4	9.7	14.3	16.7	46.3	97.1
Max			10.6	36.9	70.2	99.8	157.7	214.8	134.6

Sources: [a] Szumiec 1976; [b] Szumiec 1977; [c] Szumiec 1978; [d] Szumiec 1979; [e] Szumiec 1980; [f] Szumiec 1981*a*; [g] Szumiec 1982; [h] Szumiec 1983; [i] Szumiec 1984*b*; [j] Szumiec 1985*b*.

Table 15. Mean and extreme annual increments of individual body mass (g ind.$^{-1}$ y^{-1}) in Eurasian perch population in the Goczałkowice Reservoir. Average water temperature in the growth season (May–September) was assumed as equal to the published records of temperature in fish ponds in Gołysz. Cohorts of the years 1976–1982 run diagonally across the table to the down right.

Year	Mean temperature	Age class						
		1	2	3	4	5	6	7
1976	18.6 [a]	5.6						
1977	18.7 [b]	7.8	20.8					
1978	17.2 [c]	7.4	24.6	63.3				
1979	19.3 [d]	7.1	30.9	50.1	214.5			
1980	17.4 [e]	6.8	22.4	50.3	113.9	192.5		
1981	19.3 [f]	15.7	19.9	50.7	87.4	150.4	176.1	
1982	20.2 [g]	9.0	54.4	107.2	93.2	100.7	151.3	152.2
1983	20.2 [h]		63.1	56.4	176.7	90.4	96.6	115.0
Min		2.8	9.4	13.8	37.9	59.4	96.6	115.0
Max		20.6	85.2	194.8	244.9	195.3	176.1	152.2

Sources: [a] Szumiec 1977; [b] Szumiec 1978; [c] Szumiec 1979; [d] Szumiec 1980; [e] Szumiec 1981*a*; [f] Szumiec 1982; [g] Szumiec 1983; [h] Szumiec 1984*b*.

Table 16. Mean and extreme annual increments of individual body mass (g ind.$^{-1}$ y^{-1}) in Eurasian perch population in the Dobczyce Reservoir. Cohorts run diagonally across the table to the down right. The mass increments achieved by individuals of the cohorts of 1981–1986 after the origin of reservoir are typed in bold.

Year	Mean temperature	Age class						
		1	2	3	4	5	6	7
1981		3.9						
1982		5.3	7.5					
1983		6.3	5.7	10.6				
1984		5.0	14.3	13.4	30.0			
1985		5.1	13.2	39.6	42.6	50.3		
1986	18.7	**8.9**	**56.2**	**122.2**	**226.3**	**274.5**	**219.5**	
1987	17.9		**24.0**	**83.2**	**302.3**	**325.3**	**354.2**	**392.4**
Min		2.2	4.4	6.6	13.6	22.1	31.7	364.2
Max		13.5	114.5	172.3	400.4	368.7	406.3	420.7
1997	17.7	8.3						
1998	17.0	4.6	20.0					
1999	19.8	7.1	10.9	41.3				
2000	19.5	6.7	26.9	108.7	136.1			
2001	18.0	5.9	18.6	60.2	113.5	173.5		
2002	19.9	7.4	22.8	48.4	153.7	160.5	136.4	
2003	18.9	6.1	66.4	88.6	99.6	166.4	120.9	170.6
2004	18.8		42.1	221.0	230.0	183.7	102.7	
2005	18.2					146.5	119.8	71.7
Min		1.4	4.8	15.6	19.6	65.5	84.8	55.1
Max		10.1	106.4	249.5	294.1	334.8	156.5	200.9

Table 17. Index of environmental quality Q_E for age classes of Eurasian perch in the Rożnów Reservoir and the Goczałkowice Reservoir (mean values in cohorts and extreme values in age classes). Cohorts run diagonally across the table to the down right.

Year	Age class						
	1	2	3	4	5	6	7
				Rożnów Reservoir			
1975	–						
1976	–	0.19					
1977	–	0.24	0.33				
1978	–	0.30	0.22	0.20			
1979	–	0.26	0.25	0.17	0.26		
1980	–	0.24	0.23	0.28	0.22	0.19	
1981	–	0.22	0.21	0.19	0.24	0.18	0.10
1982	–	0.27	0.19	0.15	0.17		
1983	–	0.38	0.17	0.24	0.14	0.11	
1984					0.24	0.22	
Min		0.12	0.10	0.06	0.06	0.10	0.09
Max		0.54	0.46	0.47	0.35	0.26	0.10
				Goczałkowice Reservoir			
1976	–						
1977	–	0.36					
1978	–	0.39	0.39				
1979	–	0.40	0.22	0.44			
1980	–	0.37	0.25	0.29	0.19		
1981	–	0.29	0.24	0.17	0.17	0.10	
1982	–	0.36	0.52	0.19	0.12	0.11	0.06
1983		0.67	0.28	0.22	0.09	0.05	0.07
Min		0.12	0.08	0.10	0.06	0.05	0.06
Max		0.70	0.71	0.44	0.19	0.14	0.07

Table 18. Index of environmental quality Q_E for age classes of Eurasian perch in the Dobczyce Reservoir (mean values in cohorts and extreme values in age classes). Cohorts run diagonally across the table to the down right.

Year	Age class						
	1	2	3	4	5	6	7
1981	–						
1982	–	–					
1983	–	–	–				
1984	–	–	–	–			
1985	–	–	–	–	–		
1986	–	1.07	0.85	0.66	0.51	0.43	
1987		0.32	0.26	0.65	0.28	0.26	0.29
Min		0.26	0.21	0.27	0.21	0.07	0.23
Max		1.73	1.13	1.20	0.62	0.76	0.36
1997	–						
1998	–	0.30					
1999	–	0.20	0.23				
2000	–	0.38	0.47	0.34			
2001	–	0.32	0.30	0.18	0.22		
2002	–	0.38	0.23	0.29	0.16	0.09	
2003	–	0.86	0.43	0.21	0.16	0.09	0.10
2004		0.66	0.48	0.45	0.19	0.08	
2005					0.13	0.10	0.04
Min		0.15	0.08	0.07	0.10	0.04	0.04
Max		1.19	0.73	0.67	0.27	0.12	0.14

Table 19. The significance of differences between values of the index of environmental quality Q_E for age classes of Eurasian perch in three dam reservoirs in S Poland (mean values in age classes; *ns* – not significant).

Growth season	Age class						
	2		3		4		5
			Rożnów Reservoir				
1979	0.26	*ns*	0.25				
1980	0.24	*ns*	0.23	*ns*	0.28		
1980	0.24	*ns*	→		0.28		
1981	0.22	*ns*	0.21				
1982			0.19	*ns*	0.15		
1983					0.24	<0.01	0.14
			Goczałkowice Reservoir				
1981	0.29	<0.01	0.24				
1982			0.52	<0.001	0.19		
			Dobczyce Reservoir				
1986	1.07	*ns*	0.85				
2002	0.38	*ns*	→		0.29		
2003			0.43	<0.002	→		0.16

Table 20. The significance of differences between values of the index of environmental quality Q_E for growth seasons of Eurasian perch in three dam reservoirs in S Poland (mean values in age classes; *ns* – not significant).

Age class	Growth season						
			Rożnów Reservoir				
	1978		1979		1980		1981
2	0.30	*ns*	0.26	*ns*	0.24	*ns*	0.22
2	0.30	*ns*	→		0.24		
2	0.30	<0.02	→		→		0.22
2			0.26	*ns*	→		0.22
	1979		1980		1981		1982
3	0.25	*ns*	0.23	*ns*	0.21	*ns*	0.19
3	0.25	*ns*	→		0.21		
3	0.25	*ns*	→		→		0.19
3			0.23	*ns*	→		0.19
	1980		1981		1982		1983
4	0.28	<0.002	→		0.15	<0.02	0.24
4	0.28	*ns*	→		→		0.24
			Goczałkowice Reservoir				
	1980		1981		1982		
2	0.37	<0.01	0.29				
3			0.24	<0.002	0.52		
			Dobczyce Reservoir				
	1986		...		2002		2003
2	1.07	<0.002			0.38		
3	0.85	<0.002			→		0.43

Table 21. Characteristics of distributions of the values of absolute and relative growth recorded in Eurasian perch populations in three dam reservoirs in S Poland and the relationships of these measures of body mass increment to the index of environmental quality Q_E (*ns* – not significant).

Data set	Characteristics of the distributions of results					Correlation with the index of environmental quality Q_E	
	Median	Q_1	Q_3	Min	Max	*r*	*P*
			Absolute growth (g) [a]				
Rożnów Reservoir 1976–1984	25.2	12.6	59.4	4.4	214.8	0.122	*ns*
Goczałkowice Reservoir 1977–1983	54.2	22.7	96.4	9.4	244.9	0.081	*ns*
Dobczyce Reservoir 1986–1987	141.3	71.1	290.3	17.2	420.7	−0.343	0.0085
Dobczyce Reservoir 1998–2005	89.5	32.8	151.8	4.8	334.8	0.070	*ns*
			Relative growth [b]				
Rożnów Reservoir 1976–1984	1.46	0.99	2.18	0.31	5.74	0.833	<0.0001
Goczałkowice Reservoir 1977–1983	2.26	1.25	3.65	0.21	6.99	0.942	<0.0001
Dobczyce Reservoir 1986–1987	4.01	1.84	7.75	0.38	20.31	0.947	<0.0001
Dobczyce Reservoir 1998–2005	1.72	0.84	3.05	0.12	10.99	0.921	<0.0001

[a] As the mass increment was achieved during the whole growth season. its value may be related to the time period of one year. Therefore. the absolute growth (g) equals to absolute growth rate ($g\ y^{-1}$).

[b] = relative growth rate (relative growth/year; y^{-1})

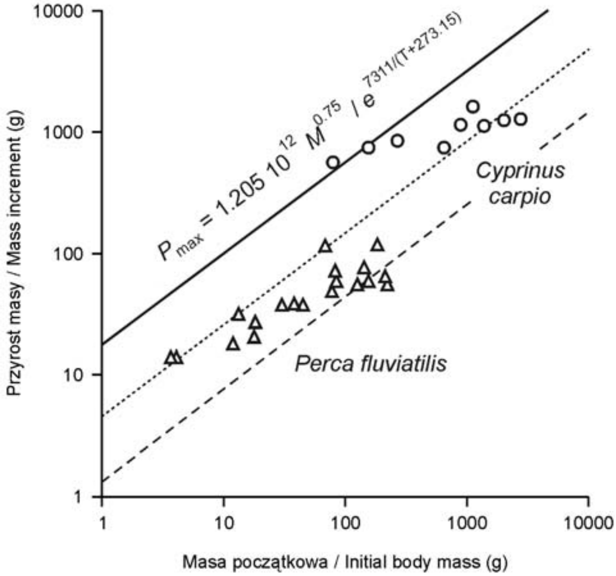

Figure 12. Individual increments of body mass in natural populations of Eurasian perch in Poland (triangles; Zawisza 1953, Zawisza & Karpińska-Waluś 1961, Skóra 1964, Krawczak 1965) and in stocks of common carp reared in ponds (circles; Kempińska 1970) compared with the maximal limit of possible annual growth at 20 °C defined by two equations of P_{MTE} (dotted line – Ernest *et al*. 2003, dashed line – Brown *et al*. 2004) and by the equation of P_{max} presented in this study (solid line).

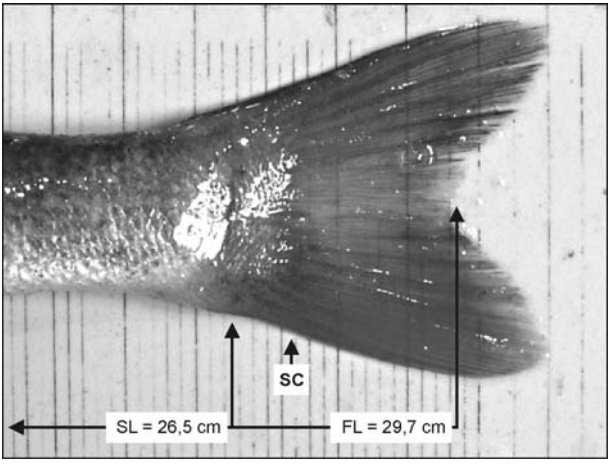

Figure 14. Definition of measurements of the standard length (SL) and fork length (FL) of Eurasian perch (SC – posterior edge of scale cover extending over caudal fin).

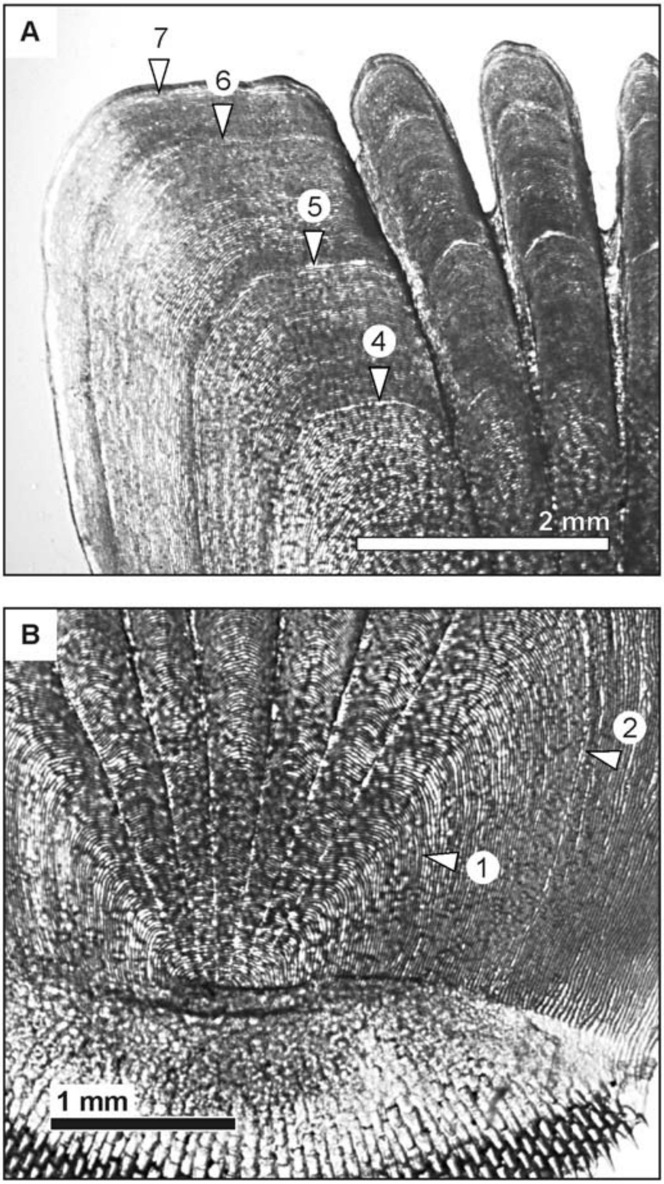

Figure 17. Annual rings identified on scales of Eurasian perch.

A. Scale of perch collected in the Goczałkowice Reservoir on 15 May 1984 (cohort of 1977, age read 7+). The beginning increment of 8th growth season (1984) is visible at the scale margin.

B. Edges of the 1st and 2nd growth zones on the scale of perch collected in the Goczałkowice Reservoir on 5 November 1982 (cohort of 1979, age read 3+).

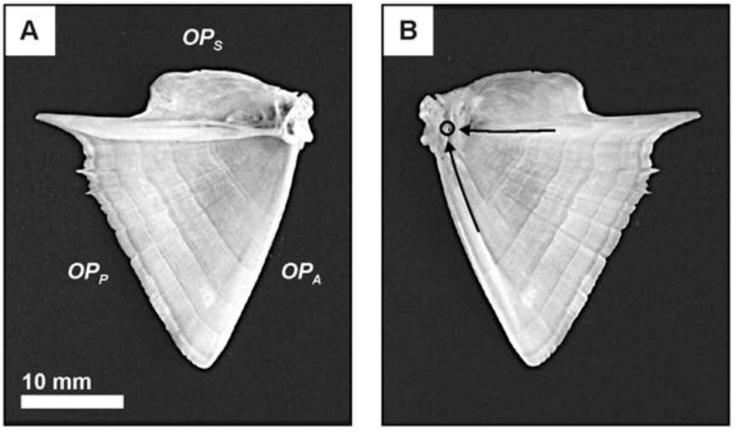

Figure 20. Left opercular bone of Eurasian perch collected in the Dobczyce Reservoir on 26 August 2010 (SL: 29.7 cm; W: 572 g): OP_A – anterior edge, OP_P – posterior edge, OP_S– superior edge. Location of the point used for measure of radii of annual rings is shown on external side of bone.

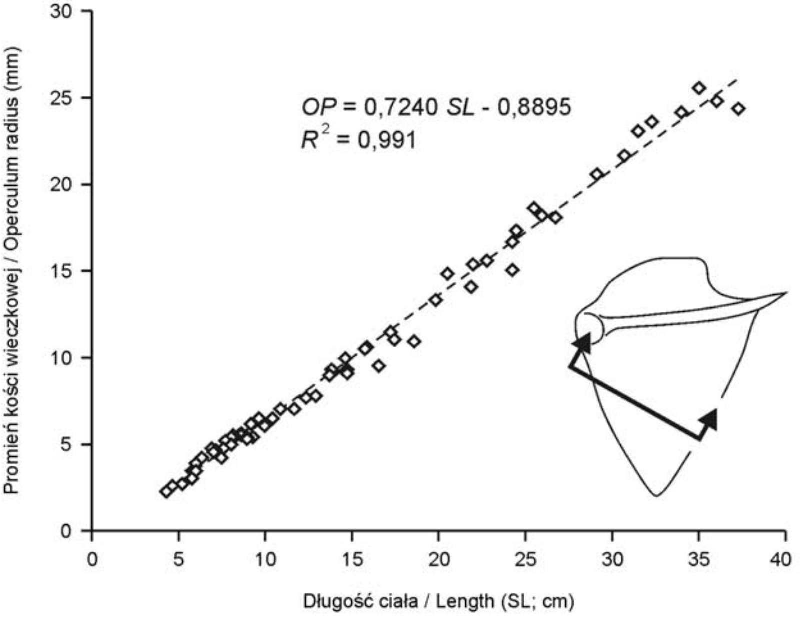

Figure 22. Relationship between radius of the opercular bone (*OP*) and standard length (*SL*) in Eurasian perch collected in the Dobczyce Reservoir in 1990–2010 ($n = 62$).

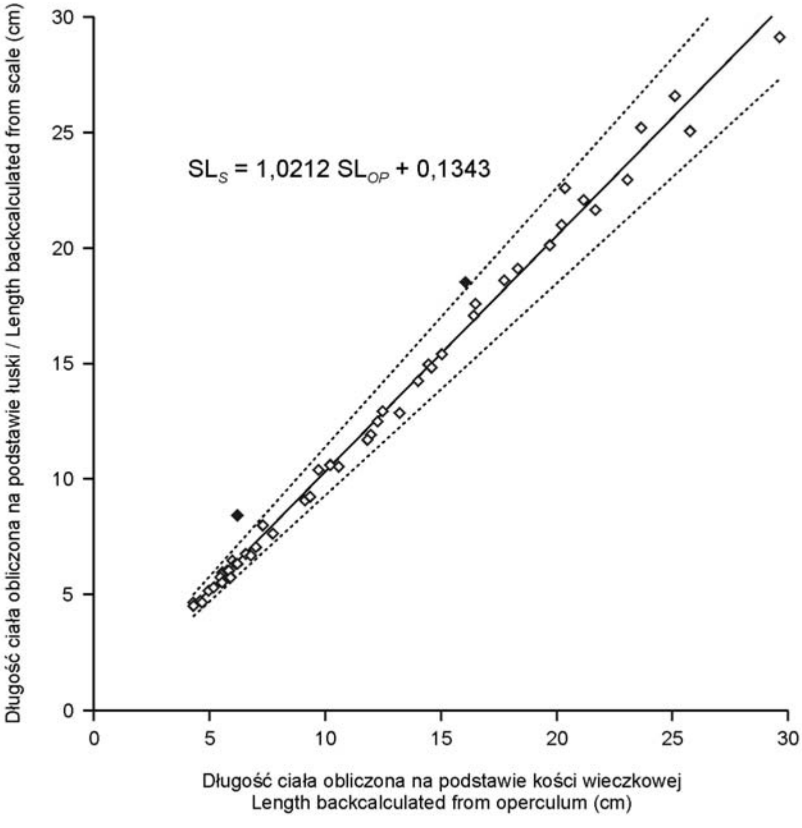

Figure 23. Relationship between lengths at age back-calculated from scale (SL_S) and opercular bone (SL_{OP}) of the same individual. Solid diamonds indicate points out of the 10%-range of the average estimate of SL_S from SL_{OP} (the range is limited by dotted lines).

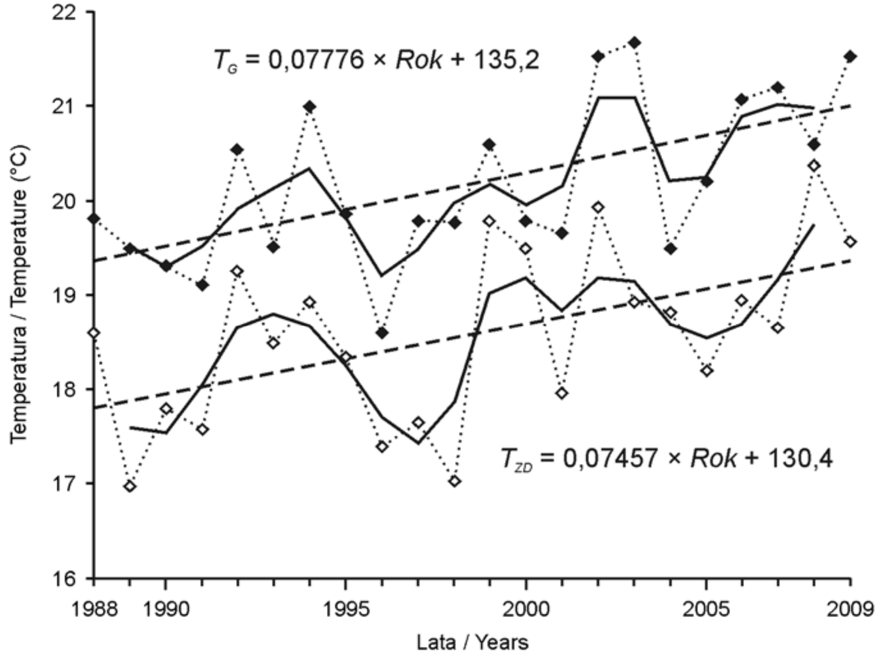

Figure 24. Comparison of the mean temperature of water in fish growth seasons (May–September) in 1988–2009: full diamonds – fish ponds in Gołysz (49°52′ N, 18°48′ E, elevation 270 m), open diamonds – epilimnion (0–5 m) of the Dobczyce Reservoir (49°52′ N, 20°03′ E, elevation 269.9 m), solid lines – trends obtained by using central weighted moving averages, dashed lines – fitted regressions of mean temperature on years (T_G – temperature in Gołysz, T_{ZD} – temperature in Dobczyce Reservoir, *Rok* – year; sources of data are presented in Table 5).

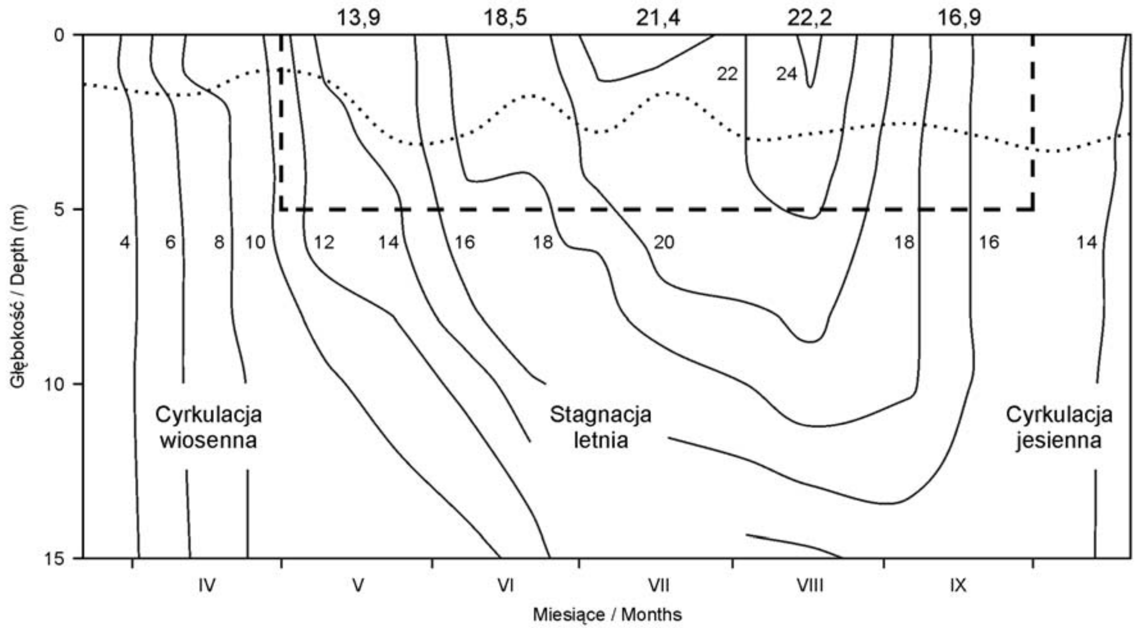

Figure 25. Location of the 0–5 m depth layer (indicated by the dashed-line rectangle) within which the average water temperature in the fish growth season (May–September) has been calculated, presented on the temperature profile of the Dobczyce Reservoir in 1988. Dotted line shows Secchi depth. Monthly mean values of temperature are given above the plot.

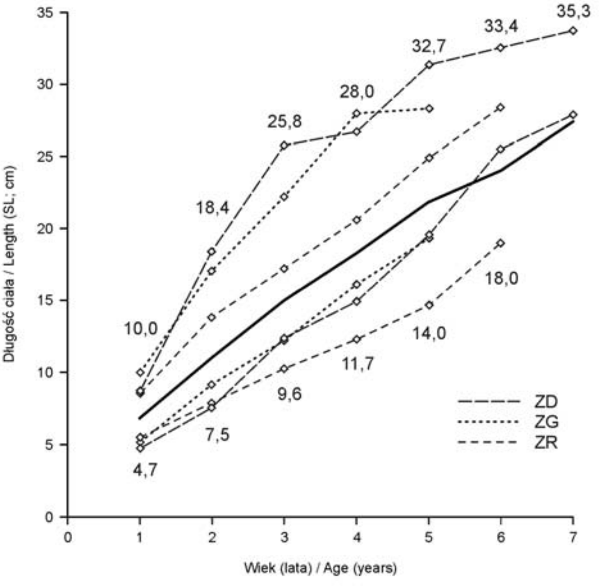

Figure 27. Ranges of standard length of Eurasian perch in three dam reservoirs in S Poland (ZD – Dobczyce Reservoir, ZG – Goczałkowice Reservoir, ZR – Rożnów Reservoir) and the extreme values recorded in age classes compared with mean length in Lake Węgielsztyńskie (solid line; Żuromska 1961).

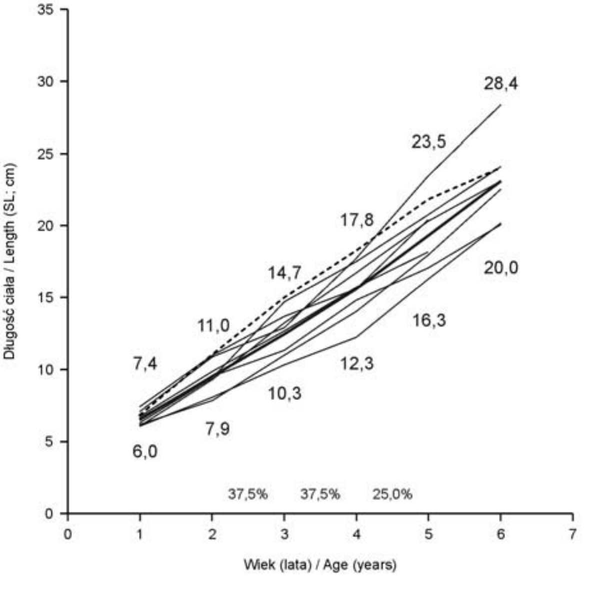

Figure 28. Individual growth trajectories of Eurasian perch belonging to the cohort of 1976 in the Rożnów Reservoir, the averaged growth pattern (thick line), and extreme length values in age classes compared with mean length in Lake Węgielsztyńskie (dashed line; Żuromska 1961). Above abscissa the percent of individuals accelerating growth during the respective season is given.

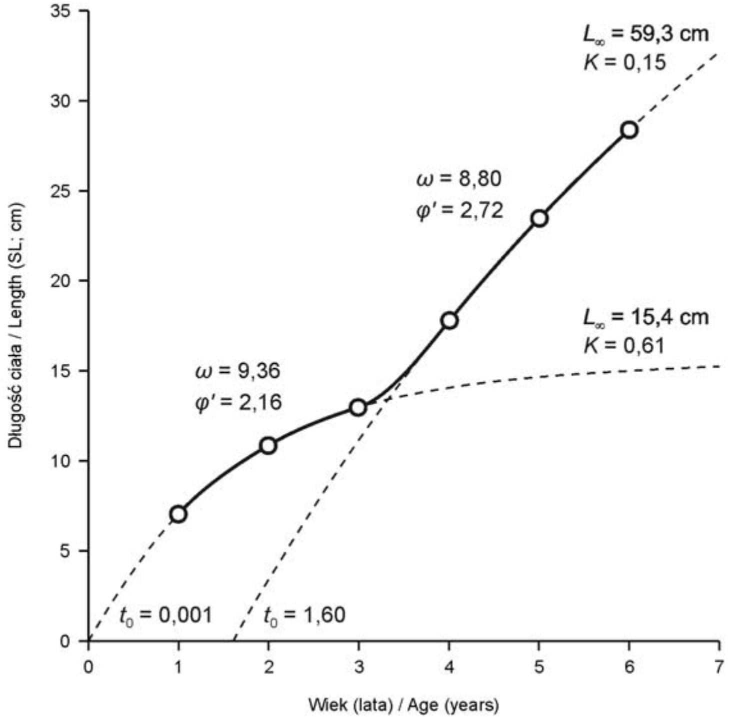

Figure 29. Two-stage growth trajectory of Eurasian perch belonging to the cohort of 1976 collected at age 6+ in the Rożnów Reservoir on 15 October 1982 described with two equations von Bertalanffy growth function (VBGF).

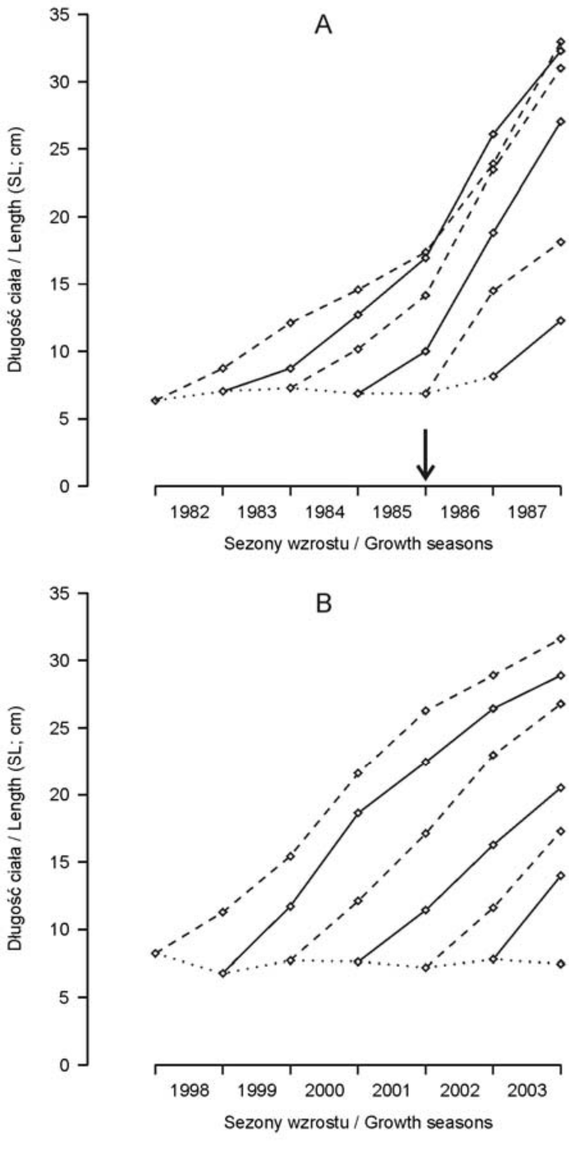

Figure 30. Average growth patterns in cohorts of Eurasian perch in the Dobczyce Reservoir (dashed line – cohorts of odd years, solid line – cohorts of even years, dotted line – mean standard length achieved during first growth season).

A. Acceleration of growth in the population colonising newly created reservoir (vertical arrow indicates the origin of reservoir).

B. Growth patterns in the reservoir in the second decade of its existence.

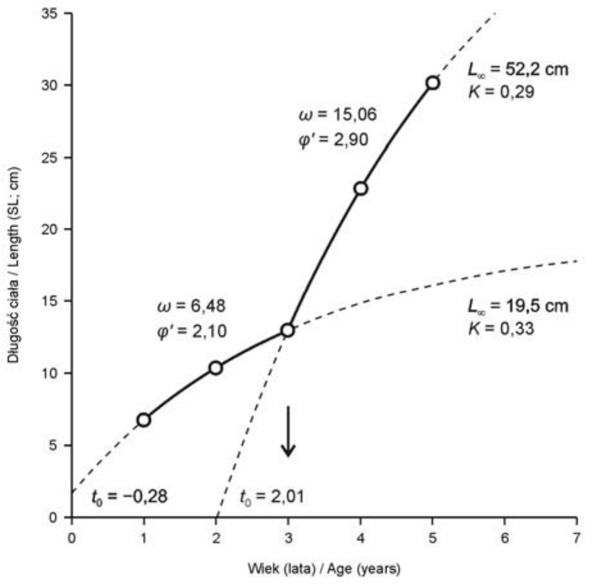

Figure 31. Acceleration of growth of Eurasian perch belonging to the cohort of 1983 collected at age 5+ in the Dobczyce Reservoir on 7 July 1988. Vertical arrow indicates the origin of reservoir. Growth trajectory is described with two VBGF equations.

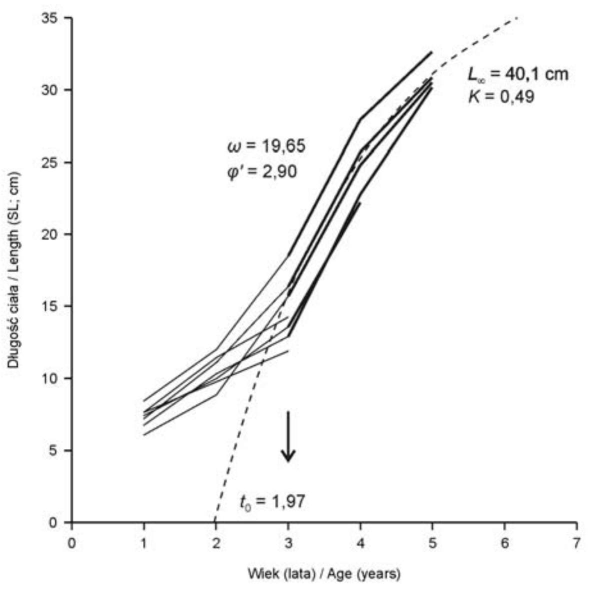

Figure 32. Individual growth trajectories of Eurasian perch belonging to the cohort of 1983 in the Dobczyce Reservoir (thick lines), and the averaged pattern of accelerated growth in newly created reservoir described with VBGF equation (dashed line). Vertical arrow indicates the origin of reservoir.

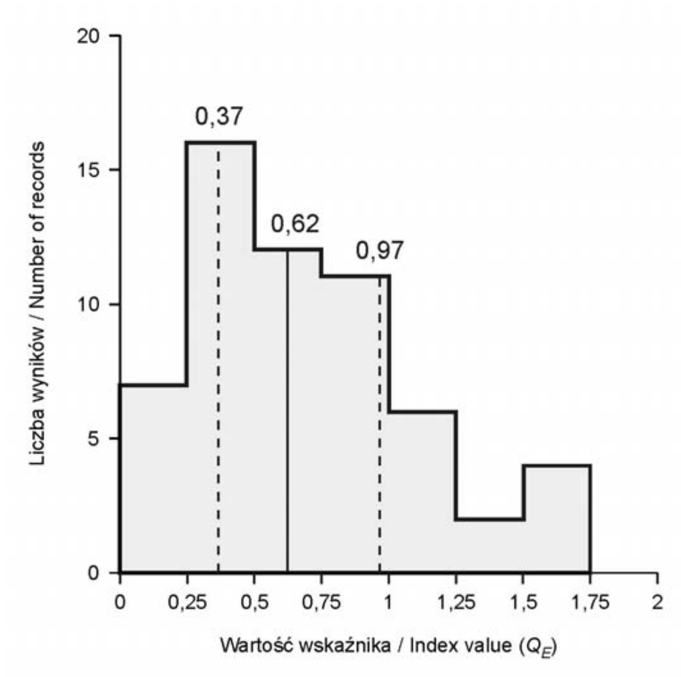

Figure 33. Distribution of the values of index of environmental quality Q_E recorded in the population of Eurasian perch in the newly created Dobczyce Reservoir in 1986–1987 (n = 58). The values of median (vertical solid line), and the first and third quartile (dashed lines) are given.

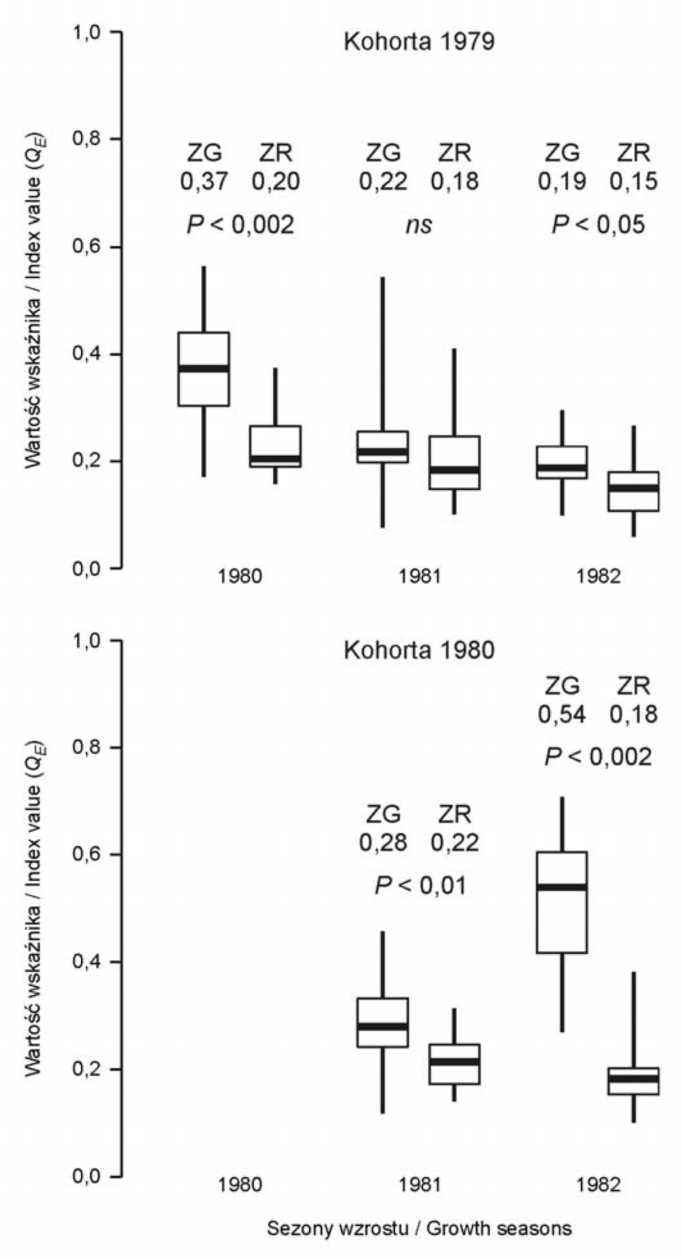

Figure 34. Comparison of environmental quality of the Goczałkowice Reservoir (ZG) and the Rożnów Reservoir (ZR) for age classes 2–3 of Eurasian perch estimated with index Q_E (significance of differences was tested with Mann–Whitney U test; *ns* – not significant). The distributions of recorded values are presented as boxplots: horizontal line – median, box – interquartile range, whiskers – range of extreme values. The mean values of compared groups are presented above.

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