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A COMPARISON OF ACCURACY AND EXTRAPOLATION RANGE OF THE VON BERTALANFFY EQUATION AND THE MODIFIED POWER FUNCTION

PORÓWNANIE MODELU VON BERTALAFFY`EGO I ZMODYFIKOWANEJ FUNKCJI POTĘGOWEJ POD WZGLĘDEM DOKŁADNOŚCI I ZAKRESU EKSTRAPOLACJI

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The paper presents results of a comparative analysis of two mathematical models of fish length growth: the von Bertalanffy equation and the modified power function. The accuracy of mathematical modelling of empirical data and a potential for extrapolation of theoretical growth range beyond the empirical data are compared. The data on accuracy and extrapolation potential, obtained with the two models tested and averaged for a species, were subject to the Student's t test. Additionally, an attempt was made to determine a relationship between accuracy and extrapolation potential of each model; linear regression was used to describe the relationship. The generalised (ignoring between-specific differences) description of the relationship involved exponential, logarithmic, and power regressions in addition to linear regression.

INTRODUCTION

The accuracy of mathematical models of fish length growth and their potential for extrapolation of the results beyond the range of empirical data are problems which have not attracted much attention. At the same time, these problems, once solved, may significantly contribute to the improvement of methodology of research on fish growth. The results of such studies may also have a practical application; for example, knowledge on the potential for extrapolation of results obtained with a model can verify back-read data for the oldest age groups (which are not fully representative due to a low, as a rule, sample size) and/or those for the first year of life of fish (poor legibility of the first annual ring).

Apart from testing the accuracy of two selected length growth models (the von Bertalanffy equation and the modified power function) and determining their extrapolation range, the present work was aimed also at describing the relationship between the two parameters with appropriate mathematical functions. Although it could be expected that a more accurate model would, as a rule, be capable of a wider extrapolation range, an attempt was made to describe the relationships as formally as possible, using linear regression and three different curvilinear regression analyses. An additional aspect of the work was a possibility to detect differences between the models and relationships as they pertain to different fish species analysed. It was assumed that by using two different models, it should be possible to lay foundations for a preliminary explanation of effects of a model used on its accuracy and extrapolation potential and for finding out if differences between results obtained with different models would be statistically significant.

MATERIALS AND METHODS

The calculations analysed in this work were made with data on length growth rate of 8 freshwater (blue bream, bream, roach, rudd, pike, perch, pikeperch, and cisco) and two marine (herring and cod) fish species. Each species yielded data on 21–30 cases. Each case consisted of mean lengths obtained in subsequent years of life, the means being calculated from growth rate analysis made on several tens to several hundred individuals. A total of 250 and 247 cases were studied for the model accuracy and extrapolation range analyses, respectively. The difference in the number of cases resulted from methodological reasons, discussed later on in this chapter.

The data on length growth rate of the species analysed were taken from reports by different authors, concerning different water bodies (seas of different salinity, lagoons, lakes, dam reservoirs, rivers); the author's own data on blue bream, perch, and pikeperch were made use of as well. The summary of catch sites and source of data is given below:

Blue bream: Lake Dąbie, Szczecin Lagoon, River Regalica (Filipiak et al. 1978; Kompowski 1991; Szypuła 1994a);

Bream: lakes of northern Poland, Lake Ladoga, Rybinski Reservoir, River Volga (Anon. 1949; Karpińska-Waluś 1961; Abdel-Baky 1983; Hanel 1992);

Roach: lakes of Finland and Northern Poland, Viatka River, Birket River, southern Baltic (Karpińska-Waluś 1961; Romański 1965);

Rudd: lakes of northern Poland, Finland, Denmark, Lake Ladoga (Zawisza and Żuromska 1961);

Pike: River Warta catchment, Lake Dąbie, lakes of northern Germany, Finland, Denmark, Sweden, North America (Antosiak 1961; Bauch 1966; Załachowski 1973; Do Cong Chinh 1977);

Perch: lakes of northern Poland, Goczałkowicki Reservoir, Lake Ladoga, Sala (Anon. 1949; Żuromska 1961; Bauch 1966; Rolik and Rembiszewski 1987; Szypuła 1994b);

Pikeperch: lakes Dąbie, Gopło, Jamno, Limen, Onega, lakes of northern Germany; Szczecin Lagoon, rivers: Regalica, Don, Kuban, Volga (Anon. 1949; Nagięć 1961; Bauch 1966; Filipiak et al. 1978; Krzykawski and Szypuła 1982; Rolik and Rembiszewski 1987);

Cisco: lakes of northern Poland and northern Germany, Ladoga, Narocz (Anon. 1949; Bernatowicz 1961; Marszałek 1961; Bauch 1966; Bernatowicz et al. 1975; Rolik and Rembiszewski 1987);

Herring: northern and southern Baltic, off southern Ireland, Faeroes Islands, Iceland (Sosiński 1969; Kompowski 1973; Anon. 1985);

Cod: Southern Baltic, North-West Atlantic, Labrador (Chrzan 1957; Stanek 1962; Rutkowicz 1963; Kosior 1971; Postolakij 1982).

To secure the maximum possible comparability of the data when calculating parameters of the growth models used, lengths attained by the fish species in their first eight years of life were included. The data set on cisco, due to the short life cycle of the species which made it impossible to collect length data on 8 years, was limited to the first 6 years.

The von Bertalanffy equation parameters were determined from empirical data using the Ford-Walford method. Parameters A, B, and C of the modified power function ($L_t = At^B + C$) were calculated as proposed by Szypuła (1991). Should the increment in the first year of life turn out to be substantially different from increments in subsequent years, it was disregarded when calculating L_∞ in the von Bertalanffy equation and exponent B in the modified power function, a procedure resulting in a higher accuracy of a model calculated.

Accuracy of the models tested was compared by calculating a mean absolute difference (Δ) between the empirical and theoretical (calculated from the model) results. As the species studied showed very diverse growth rates (from less than 20 cm in the sixth year of life, as in roach and rudd, to 60–70 cm in that year, as in cod, pike, and pikeperch), the mean absolute difference was also converted to percentage (Δ_W) of the mean length calculated across 8 (6 in cisco) years of life. Values of Δ and Δ_W were calculated separately for each case; the Tables contain averaged data calculated from all the differences obtained for a species. Szypuła (1987b) used an identical methodology to determine the accuracy of the model he was studying.

A potential for extrapolation of growth rate beyond the empirical data range was determined by calculating parameters of a model from a half of the real data; as a rule, lengths attained during the first 4 (3 in cisco) years of life were used. Subsequently, empirical data for years 5–8 (4–6 in cisco) were compared with those extrapolated with a model, assuming the extrapolation to be permissible within the range in which a difference between the empirical and extrapolated lengths did not exceed 5% of the first. The extrapolation range limit was determined in the following way: lengths, attained by a species in two consecutive years and selected so that the difference in the first year would be less than 5% and the difference in the second year would exceed 5% were compared and the extrapolation (with the difference of exactly 5%) range limit was determined by interpolation. The absolute value of extrapolation range ($Z_{0.05}$) was expressed in years and supplemented with a relative value (Z_W) of the range; the relative value, expressed as a percentage, was a ratio between $Z_{0.05}$ and the range of empirical data used for the growth model ($Z_M = Z_{E/2}$, where Z_E is the total range of empirical data). The method used was described in detail by Szypuła (1987a).

Relationships between the model's accuracy and its extrapolation range (both for the absolute and the relative values) were studied with the aid of the linear regression ($y = a + b\,x$), calculated with the least squares method. The relationships were described separately for each species from data on accuracy and extrapolation range of the cases analysed for the species. Due to a substantial scatter in the data (cf. Tabs. 1–4), the data were initially transformed by grouping the argument of the function (Δ or Δ_W) into classes at 0.1 cm intervals and calculating mean class values and mean values of the function ($Z_{0.05}$ or Z_W). The transformed data were used to calculate values of linear regression terms.

The final stage of the calculations was an attempt to generalise the nature of the relationships studied, regardless of the species-specific characteristics. At that stage, the relationships were described from mean values of and $Z_{0.05}$ (for absolute values) contained in Tables 1 and 3, and from Δ_W and Z_W (for percentages), given in Tables 2 and 4. In addition to the linear regression, the exponential ($y = a \cdot e^{b\,x}$), logarithmic ($y = a + b \cdot \ln x$) and power ($y = a \cdot x^b$) regression analyses were used.

Both the accuracy of each model and its extrapolation potential and regression parameters were determined separately for each growth model compared.

RESULTS

According to the theoretical assumptions of the modified power function, the exponent B describes the nature of growth of a species studied (asymptotic growth at $B<0$ and unlimited growth at $B>0$). Analysis of the detailed data on individual species, used to construct the modified power function in order to assess the accuracy of the model showed $B>0$ in all cases analysed for a species (blue bream, bream, roach, rudd, perch, and cod), which theoretically evidences the unlimited growth of those species. Out of 21 cases analysed for pike, $B<0$ was obtained in one case only (4.8%); out of 21 cases analysed for pikeperch, $B<0$ occurred in 5 cases (23.8%). Thus both species can also be regarded as having in most cases the unlimited growth. Cisco, on the other hand, can be regarded as a species whose growth is poorly determined ($B<0$ occurred in 10 out of 25 cases, or in 40.0%), while most cases of herring data (70.4%) pointed to the asymptotic growth.

Accuracy of the mathematical description of growth, as measured by a mean difference between empirical data and those calculated from the two models compared is presented in Table 1. The data show that the modified power function is a more accurate model for half of the species studied (roach, pike, cisco, herring, and cod); the two models had identical accuracy when applied to bream data, while a higher accuracy (i.e., lower) of description of growth of the remaining 4 species (blue bream, rudd, perch, and pikeperch) was obtained with the von Bertalanffy equation. Moreover, the weighted mean of values, calculated for all the species studies, turned out to be lower with the modified power function.

Table 1

Comparison of accuracy of von Bertalanffy equation (a) and modified power function (b) used for mathematical description of length growth in various fish species

Species	n	Δ (cm)							
		Range		$\overline{x}$		σ		ν	
		a	b	a	b	a	b	a	b
Blue bream	30	0.00–1.05	0.05–1.14	0.40	0.54	0.31	0.35	77.50	64.81
Bream	24	0.10–1.22	0.10–1.11	0.45	0.45	0.34	0.28	75.56	62.22
Roach	23	0.05–0.65	0.11–0.65	0.26	0.24	0.13	0.12	50.00	50.00
Rudd	25	0.07–0.50	0.05–0.52	0.23	0.24	0.12	0.12	52.17	50.00
Pike	21	0.19–3.60	0.21–2.90	1.01	0.97	0.81	0.67	80.20	69.07
Perch	26	0.02–0.70	0.05–0.60	0.17	0.19	0.17	0.18	100.00	94.74
Pikeperch	21	0.14–2.60	0.15–2.35	0.99	1.19	0.71	0.58	71.72	48.74
Cisco	25	0.10–0.77	0.10–1.07	0.47	0.41	0.24	0.23	51.06	56.10
Herring	27	0.07–1.15	0.10–1.27	0.33	0.29	0.25	0.28	75.76	96.55
Cod	28	0.27–5.41	0.39–2.25	1.95	0.87	1.62	0.39	83.08	44.83
Total	250	–	–	0.62	0.53	–	–	–	–

Δ—mean absolute difference (in cm) between empirical data and results calculated with growth model analysed.

Noteworthy is the extensive scatter of data obtained for different cases within a species. The coefficient of variation (v) was, as a rule, higher than 50%; in the extreme case (accuracy of the von Bertalanffy equation applied to perch) v was even 100%.

The data on accuracy of the models analysed are also given in Table 2; they are, however, expressed as percentages (Δ_W). The data were obtained by converting the values reported in Table 1 (Δ) to the mean length calculated from 8 (6 in cisco) empirical data used for construction of the models compared. A pattern reverse in relation to that in Table 1 is observed: the von Bertalanffy equation turned out to be more accurate for 5 species, the accuracy of the two models was identical in one species, and in the remaining 4 species lower values of Δ_W were obtained with the modified power function. However, the weighted mean Δ_W was lower in the modified power function as well. The scatter of the data obtained in different cases characterising growth of a species was very extensive, too, although not so as in the case of Δ.

Table 2

Comparison of relative accuracy of von Bertalanffy equation (a) and modified power function (b) used for mathematical description of length growth in various fish species

Species	n	Δ_W (%)							
		Range		$\bar{x}$		σ		v	
		a	b	a	b	a	b	a	b
Blue bream	30	0.06–5.45	0.30–5.56	1.96	2.63	1.56	1.67	79.59	63.50
Bream	24	0.56–6.30	0.67–5.73	2.30	2.34	1.53	1.32	66.52	56.41
Roach	23	0.29–4.98	0.63–4.98	2.07	1.87	1.14	0.95	55.07	50.80
Rudd	25	0.62–3.44	0.44–3.42	1.70	1.79	0.82	0.83	48.24	46.37
Pike	21	0.71–6.07	0.52–4.89	2.11	2.11	1.36	1.27	64.45	60.19
Perch	26	0.14–3.91	0.38–3.42	0.97	1.14	0.86	0.93	88.66	81.58
Pikeperch	21	0.47–5.78	0.34–5.50	2.15	2.65	1.39	1.24	64.65	46.79
Cisco	25	0.47–4.54	0.50–5.28	2.42	2.12	1.14	1.14	47.11	53.77
Herring	27	0.52–4.83	0.43–5.59	1.56	1.45	1.08	1.26	69.23	86.90
Cod	28	0.62–10.69	0.76–3.77	3.90	1.84	3.03	0.91	77.69	49.46
Total	250	–	–	2.12	1.98	–	–	–	–

Δ—mean relative difference (in %) between empirical data and results calculated with growth model analysed.

Although mean values of Δ and Δ_W calculated for the species studied differed between the two models compared, sometimes distinctly so, the differences within a species were, as a rule, non-significant (Student's t test, 0.99 confidence level). It was only in cod that the differences between values of Δ and Δ_W obtained with the von Bertalanffy equation and the modified power function differed significantly.

The extrapolation range of length growth rate in different fish species was determined (with 5% tolerance), as described in the previous chapter, by calculating the analysed growth models from lengths attained in the first 4 years of life and comparing, for the subsequent 4 years, results calculated from a model with the empirical data (the models for cisco were calculated for the first 3 years and compared for the subsequent 3 years). The number of cases analysed for roach, rudd, and pike was lower (by 1) than that used for model accuracy determination (Tabs. 1 and 2). The difference resulted from the fact that in some cases it was impossible to construct the von Bertalanffy model from data on the first 4 years (no decreasing trend in length increments, such trend being necessary to apply the model).

Table 3 summarises data on the absolute values of the extrapolation range ($Z_{0.05}$), broken down by fish species, model used, and basic statistical parameters (arithmetic mean, standard deviation, coefficient of variation).

The analysis of different cases used to calculate arithmetic means reported in Table 3 showed that the difference between the empirical and extrapolated lengths in the final, eighth (sixth in cisco) year was frequently (in 63 and 72 cases analysed with the von Bertalanffy equation and the modified power function, respectively, i.e., in 25.5 and 29.1% of all the 247 cases, respectively) lower (sometimes much lower) than the assumed 5% tolerance. The lowest number of such low differences (2 out of 28 cases, i.e., 7.1%) was observed in cod data, while the highest (15 out of 26 cases, i.e., 57.7%) was recorded in perch; these results concern both models tested. The results discussed are well correlated with species-specific mean values of $Z_{0.05}$: the highest values (3.0 and 3.26 for the von Bertalanffy equation and the modified power function, respectively) were recorded in the perch data as well. The lowest value obtained with the von Bertalanffy equation (1.40) was recorded in cod. The modified power function applied to the cod data resulted in a relatively low value (1.92), too; however, still lower values (1.90 and 1.69) were observed in pikeperch and cisco. Similarly to Δ and Δ_W, an extensive scatter of data was recorded as well (the coefficient of variation ranged from more than 30 to more than 70%). The weighted mean $Z_{0.05}$ values calculated for all the species studied demonstrated that the modified power function provides a slightly wider extrapolation range. In separate species-specific analyses, a higher range of $Z_{0.05}$ with the modified power function was found in 8 cases, while only two cases of the von Bertalanffy equation yielded higher range of $Z_{0.05}$.

Table 3

Extrapolation range ($Z_{0.05}$) of von Bertalanffy equation (a) and modified power function (b) calculated for fish species studied

Species	n	$Z_{0.05}$ (years)							
		Range		$\bar{x}$		σ		v	
		a	b	a	b	a	b	a	b
Blue bream	30	0.01–4.00	0.20–4.00	1.98	2.23	1.47	1.51	74.24	67.71
Bream	24	0.22–4.00	0.81–4.00	2.38	2.54	1.30	1.06	54.62	41.73
Roach	22	0.00–4.00	0.54–4.00	2.47	2.52	1.37	1.35	55.47	53.57
Rudd	24	0.33–4.00	0.42–4.00	2.12	2.39	1.35	1.30	63.68	54.39
Pike	20	0.17–4.00	0.33–4.00	1.67	2.29	1.01	1.34	60.48	58.52
Perch	26	0.41–4.00	0.58–4.00	3.10	3.26	1.31	1.20	42.26	36.81
Pikeperch	21	0.40–4.00	0.48–4.00	2.08	1.90	1.45	1.22	69.71	64.21
Cisco	25	0.43–3.00	0.25–3.00	1.76	1.69	0.94	1.00	53.41	59.17
Herring	27	0.72–4.00	0.72–4.00	2.64	2.97	1.12	1.17	42.42	39.39
Cod	28	0.00–4.00	0.45–4.00	1.40	1.92	0.96	1.10	68.57	57.29
Total	247	–	–	2.16	2.38	–	–	–	–

Table 4, arranged similarly to the previous one, shows values of the relative extrapolation range Z_W,obtained by converting $Z_{0.05}$ to the range of empirical data used to calculate the growth models compared (Z_M). The range of Z_M was 4 years (3 in cisco). Similarly to the $Z_{0.05}$ analysis, application of the von Bertalanffy equation yielded the highest values of Z_W for perch (77.59 and 81.42%), the lowest value (35.09%) being typical of cod. It was only in pikeperch that the modified power function resulted in a Z_W value slightly lower than that found for cod. On the other hand, Z_W of cisco, the species having the lowest $Z_{0.05}$ in the modified power function analysis, was clearly higher than that of cod and pikeperch. This happened because $Z_{0.05}$ was referred to 3 years rather than to 4, as was the case in the remaining species. Coefficients of variation varied within a range similar to those of $Z_{0.05}$. Weighted mean Z_W values were also slightly higher when the modified power function was used. Similarly to $Z_{0.05}$, the modified power function yielded better results in 8 species, while the von Bertalanffy equation supplied better results in 2 species only.

Table 4

Relative extrapolation range (Z_W) of von Bertalanffy equation (a) and modified power function (b) calculated for fish species studied

Species	n	Δ (cm)							
		Range		$\bar{x}$		σ		*v*	
		a	b	a	b	a	b	a	b
Blue bream	30	0.25–100.00	5.00–100.00	49.58	55.84	36.84	37.71	74.30	67.53
Bream	24	5.50–100.00	20.25–100.00	59.52	63.46	32.58	26.52	54.74	41.79
Roach	22	0.00–100.00	13.50–100.00	61.81	62.94	34.26	33.79	55.43	53.69
Rudd	24	8.25–100.00	10.50–100.00	53.09	59.76	33.73	32.51	63.53	54.40
Pike	20	4.25–100.00	8.25–100.00	41.70	57.36	25.22	33.59	60.48	58.56
Perch	26	10.25–100.00	14.50–100.00	77.59	81.42	32.64	30.08	42.07	36.94
Pikeperch	21	10.00–100.00	12.00–100.00	52.11	47.39	36.36	30.51	69.78	64.38
Cisco	25	14.33–100.00	8.33–100.00	58.63	56.17	31.21	33.48	53.23	59.60
Herring	27	18.00–100.00	18.00–100.00	65.91	74.34	28.01	29.10	42.50	39.14
Cod	28	0.00–100.00	11.25–100.00	35.09	47.97	23.95	24.75	68.25	51.59
Total	247	–	–	55.56	60.85	–	–	–	–

Differences between extrapolation ranges (with respect to both $Z_{0.05}$ and Z_W) determined with the two models were non-significant (Student's t test, 0.99 confidence level) for all the species.

Another problem tackled in this work involved relationship between extrapolation range and the accuracy of the growth model used. The problem was studied with respect to both the absolute ($Z_{0.05}$ and Δ) and percentage (Z_W and Δ_W) values. The relationships were described with linear regressions, separately for different fish species and growth models compared. Within a species, the relationships were studied based on the analysis of the cases included in calculations of Δ, Δ_W, and the corresponding $Z_{0.05}$ and Z_W. The linear regression terms along with correlation coefficients are reported in Table 5 (absolute values) and Table 6 (percentages).

All the relationships the terms of which are given in Tables 5 and 6, showed negative values of both the regression coefficient (*b*) and the correlation coefficient (*r*), which points to a reverse relationship between the variables compared. In other words, the less accurate a model (a larger difference between Δ or Δ_W), usually the narrower the extrapolation range with the 5% tolerance assumed ($Z_{0.05}$ or Z_W). The relationships are illustrated in Figs. 1 and 2.

Fig. 1, in which the real and extrapolated length growth rates of the Szczecin Lagoon perch are presented (based on data reported by Szypuła 1994b), shows that the extrapolated growth curve almost ideally fits the empirical data; the empirical and calculated lengths for the final year of life are identical, which suggests that the true extrapolation range is likely to be by a few years wider than that calculated with the model used. At the same time, the average difference between the empirical and model data was in this case minimal for the first 4 years of life (Δ = 0.02 cm; Δ_W = 0.14%). Fig. 2 shows a reverse pattern, found for the Szczecin Lagoon pikeperch (data reported by Nagięć 1961). The average differences in this case were large (Δ = 2.49 cm; Δ_W = 4.71%), the extrapolation range being relatively narrow ($Z_{0.05}$ = 0.97 yr). As of the fifth year of life, the extrapolated growth curve runs much higher than that based on the empirical data (particularly in the seventh and eighth years of life).

Table 5

Relationship between extrapolation range ($Z_{0.05}$) and accuracy (Δ) of model tested, described by linear regression ($Z_{0.05} = a + b \cdot \Delta$)

Species	Von Bertalanffy equation			Modified power function		
	a	*b*	*r*	*a*	*b*	*r*
Blue bream	3.2262	–3.1955	–0.8958	3.6352	–2.5349	–0.6316
Bream	3.3967	–1.9278	–0.7030	3.2565	–1.5968	–0.6647
Roach	3.5587	–3.3598	–0.8989	4.4319	–8.6531	–0.8441
Rudd	2.9154	–2.2224	–0.3872	3.3101	–4.6723	–0.8646
Pike	1.8241	–0.4364	–0.6392	3.4143	–1.2019	–0.6911
Perch	3.1215	–2.0328	–0.4064	3.5534	–2.5732	–0.4842
Pikeperch	3.4709	–1.0763	–0.6381	3.5421	–1.1609	–0.7598
Cisco	1.9200	–0.2664	–0.0963	2.0717	–0.6246	–0.2272
Herring	3.3121	–2.0641	–0.4629	3.6155	–2.1977	–0.5195
Cod	2.3448	–0.1785	–0.3549	2.5741	–0.6597	–0.4639
Total			–0.5483			–0.6151

Table 6

Relationship between relative extrapolation range (Z_W) and accuracy (Δ_W) of model tested, described by linear regression ($Z_W = a + b \cdot \Delta_W$)

Species	Von Bertalanffy equation			Modified power function		
	a	*b*	*r*	*a*	*b*	*r*
Blue bream	78.0794	–14.7888	–0.8970	98.5792	–15.9865	–0.9665
Bream	69.9338	–6.8253	–0.6727	88.0394	–8.8507	–0.8749
Roach	65.1119	–2.0041	–0.2524	79.0800	–15.4402	–0.7706
Rudd	55.7455	–2.6612	–0.1700	78.3618	–12.4594	–0.7776
Pike	57.7377	–9.2813	–0.9153	87.3420	–16.2197	–0.9264
Perch	91.3242	–13.5938	–0.8105	87.5264	–14.2092	–0.5404
Pikeperch	80.6993	–11.7930	–0.7950	80.7768	–10.2933	–0.8428
Cisco	87.8227	–10.6046	–0.6633	66.7802	–2.8391	–0.1907
Herring	74.5170	–6.4853	–0.4424	87.0988	–11.8742	–0.8497
Cod	54.3521	–4.5613	–0.7341	64.5383	–6.6376	–0.5776
Total			–0.6353			–0.7317

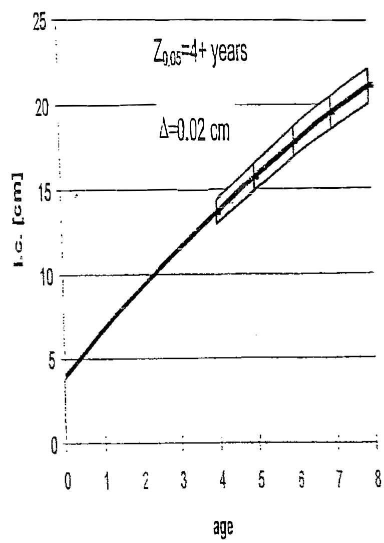

Fig. 1. Extrapolation of length growth in perch with the von Bertalanffy equation (points denote empirical data; stippled area represents 5% tolerance range)

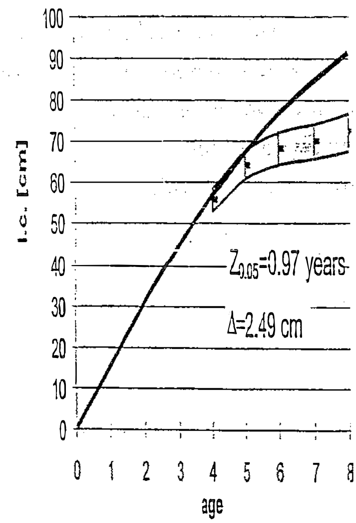

Fig. 2. Extrapolation of length growth in pikeperch with the von Bertalanffy equation (for explanations see Fig. 1)

Correlation coefficients concerning the von Bertalanffy equation, reported in Table 5, ranged from –0.0963 to –0.8989. In 5 species, the absolute values of r exceeded 0.6, evidencing a rather strong correlation of the variables analysed. In the remaining 5 species, the absolute values of r were lower than 0.5 (weaker correlation between model accuracy and its extrapolation range), virtually no correlation existing in cisco (r = –0.0963). As far as the modified power function is concerned, the range of variation in r was narrower (from –0.2272 to –0.8441); however, in as many as 6 species the absolute value of r exceeded 0.6. Usually (in 7 out of the 10 species studied), the absolute value of r was higher when the modified power function was used, compared to the correlation coefficient obtained when using the von Bertalanffy equation. The stronger correlations between the model accuracy and its extrapolation range, obtained for the modified power function, are evidenced also by the values of r, averaged across species separately for the von Bertalanffy equation (–0.5483) and the modified power function (–0.6151).

Very similar were the relationships determined for the percentages (Tab. 6): negative regression and correlation coefficients were obtained both for all the species and in both models compared. Similarly to the absolute values, in 7 out of 10 cases higher absolute values of correlation coefficients resulted from using the modified power function. Moreover, absolute values of correlation coefficients were, both in the von Bertalanffy equation and in the modified power function, slightly higher than those obtained when analysing the absolute values (–0.6353 and –0.7317 were the respective means for all the fish species used in the analysis).

Finally, an attempt was made to determine the general nature of relationships between the extrapolation range and the accuracy of the models compared, regardless of species. Data (arithmetic means) in Tables 1 and 3 (absolute data) and in Tables 2 and 4 (percentages) served as the material for the analyses. To determine the nature of the relationships studied as accurately as possible, the exponential, logarithmic, and power regressions were used in addition to the linear regression. Parameters of the relationships studied and the relevant correlation coefficients are summarised in Table 7.

The correlation coefficients were relatively high; as a rule, they exceeded 0.6 (except for the exponential regression calculated on absolute values obtained by using the modified power function). As a rule, curvilinear regressions (the logarithmic regression in particular), allowed to more accurately correlate the values analysed than did the linear regression. In contrast to linear regressions calculated for individual species (Tabs. 5 and 6), the data in Table 7 demonstrate that the von Bertalanffy equation provided a closer correlation between the extrapolation range and the model accuracy. The difference in favour of the von Bertalanffy model (higher absolute values of correlation coefficients) is particularly evident when comparing the relationships calculated on absolute values ($Z_{0.05}$ and Δ).

Table 7

General relationship between extrapolation range ($Z_{0.05}$, Z_W) and accuracy (Δ, Δ_W) of model tested, described by linear regression ($y = a + b \cdot x$), expoptential regression ($y = a \cdot e^{bx}$), logarithmic regression ($y = a + b \cdot \ln x$) and power regression ($y = a \cdot x^b$)

Relationship	Von Bertalanffy equation			Modified power function		
	a	*b*	*r*	*a*	*b*	*r*
absolute value ($x = \Delta$; $y = Z_{0.05}$)						
Linear regression	2.5797	–0.6705	–0.7336	2.8230	–0.8386	–0.6064
Expotential regression	2.6021	–0.3368	–0.7881	2.7998	–0.3429	–0.5926
Logarithmic regression	1.7605	–0.5327	–0.8061	1.9583	–0.5123	–0.6810
Power regression	1.7391	–0.2562	–0.8290	1.9678	–0.2084	–0.6620
percentages ($x = \Delta_W$; $y = Z_W$)						
Linear regression	81.9566	–12.5135	–0.7798	94.1231	–16.7794	–0.7583
Expotential regression	90.3506	–0.2412	–0.7996	100.4545	–0.2596	–0.7335
Logarithmic regression	74.8264	–27.8629	–0.8124	82.1830	–32.5521	–0.7999
Power regression	77.5195	–0.5143	–0.7976	83.3017	–0.4999	–0.7680

The differences in accuracy between different methods used for a general description of the extrapolation range vs. model accuracy relationship (differences between the means in Tables 3 and 4 and values calculated with regression equations given in Table 7) were slight only and, as a rule, ranged from 0.1 to 0.6 yr and within 2–8% for absolute values and percentages, respectively.

DISCUSSION

The results obtained when analysing accuracy of the models compared (Tabs. 1 and 2) point to a rather high accuracy of the mathematical description of length growth. The evidence is provided by the relatively low average across–species difference between empirical and calculated data (slightly exceeding 0.5 and about 2% for absolute values and percentages, respectively). The detailed analysis of results obtained for individuals species seems to demonstrate some advantage in using the modified power function (in 5 species, the results were lower than those obtained with the von Bertalanffy equation; the reverse was true in 4 species, while the two results were identical in 1 case). The weighted mean calculated for all species was, too, slightly lower when the modified power function was used. However, the difference between the weighted means was small and the differences between the two models in individual species were in 9 cases (except that of cod) non–significant. If, additionally, a wide scatter of individual data is taken into account (as evidenced by both the coefficients of variation and ranges of values), the two models can be regarded as having similar accuracies.

Results of earlier studies on the problem, obtained by Szypuła (1987b) are difficult to compare due to different assumptions when collecting the data. That study concerned, i.a., effects of the range of empirical data (Z_E) on a model's accuracy. For this reason, for each of the 50 species studied, only 1 case of length growth rate was analysed, but growth models were calculated from different Z_M ranges, starting from age group 3 up to—in some cases—several years of life. Additionally, apart from the von Bertalanffy equation, the Gompertz model, binomial, and the Ford-Walford formula were used. Out of the array of species studied by Szypuła (1987b), 4 only are included in the present study (bream, perch, pikeperch, and herring). A comparison of results concerning those 4 species showed that the earlier study resulted in clearly lower values of Δ and Δ_W, the difference being most conspicuous in pikeperch and the smallest in perch. Possibly, the discrepancies might have been caused by the fact that, as mentioned above, the von Bertalanffy equation (obviously this model only could be used for comparison) parameters were determined from different ranges of Z_E, while the range was – as a rule – 8 years in the present work. Somewhat more concordant results were obtained when the all–species average only, calculated with the use of the 8–yr range, was taken into account. In that case, the absolute value of the difference was 0.5 cm (0.63 cm in the present study), while the difference between percentages was quite substantial (1.09 % in the earlier work vs. 2.12% in this study).

Parenthetically, it is worth mentioning that when calculating the results for different cases, the concordance between the model and the empirical data was usually higher when the data were derived from a large and representative sample. It is suggested that the mathematical description of growth rate be based exclusively on such data and given up when they are not available, since results of theoretical calculations may then be very far from reality.

Results concerning extrapolation ranges ($Z_{0.05}$ and Z_W) obtained in this work are largely close to earlier data of Szypuła (1987a). With reservations analogous to those expressed when discussing the accuracy of the models compared, an average $Z_{0.05}$ of 2.16 yrs (2.30 in the earlier study) was obtained for the range equal to 8 yrs; Z_W was 55.6% in both works. Slightly higher differences occurred in individual species, compared to the data of Suryn (1990) who—using identical methodology—studied a potential for extrapolation of growth of roach, perch and herring. He used, i.a., the von Bertalanffy equation and the modified power function. His results are clearly lower (with respect to perch in particular) than those obtained in this study. Additionally, Suryn contended that clearly better results could have been obtained with the von Bertalanffy equation, while this study demonstrates a slight advantage of the modified power function over the von Bertalanffy model.

The negative regression (b) and correlation (r) coefficients obtained for all the species studied when using linear regression to analyse the relationships between and Δ_W on the one hand and $Z_{0.05}$ and Z_W on the other fully justify considering the relationships as reverse (although lower's in some case demonstrate poor correlations—or a virtual lack of correlation—between the values analysed). In other words, a more accurate model (lower Δ and Δ_W) allows, as a rule, for a wider extrapolation range (higher $Z_{0.05}$ and Z_W). This conclusion can be of a considerable practical importance when attempting to use the extrapolated lengths instead of tentative (few and non–representative) empirical values, particularly with respect to oldest age groups.

Finally, the various detailed descriptions of general relationships between the extrapolation range and the model accuracy (Tab. 7) confirm, on the one hand, the nature of the relationships, concerning individual species, as discussed above. On the other hand—as shown by the relatively high correlation coefficients in each case—the relationships can be regarded as rather highly correlated. It should be reminded that, when determining the relationships, species-specific means were used as the starting points (given in Tabs. 1–4); thus the relationships have a more general nature than those summarised in Tables 5 and 6. A somewhat closer correlation between the values, produced by the curvilinear regressions, was practically to be expected. It is of interest to note that the best results (highest absolute values of r) were, as a rule, obtained with the logarithmic regression. It has to be remembered, when assessing and comparing values of r yielded by different types of regression, that correlation coefficients of exponential and power regressions given in Table 7 concern the logarithmic forms of those regressions.

CONCLUSIONS

1. The average accuracy of the models tested slightly exceeded 0.5 cm (Δ) or was about 2% (Δ_W). The average extrapolation range exceeded 2 yrs ($Z_{0.05}$) or 55% (Z_W). Slightly better results in both cases were obtained with the modified power function; it should be stressed, however, that the differences between the two models were, as a rule, statistically non–significant.
2. Both the model accuracy and its extrapolation range varied extensively in different fish species studied (the coefficients of variation usually exceeded, sometimes substantially so, 55%).
3. A reverse relationship between an average difference between empirical and calculated data (Δ, Δ_W) on the one hand and the extrapolation range ($Z_{0.05}$; Z_W) on the other. Correlation coefficients were widely different in different species.
4. A more in-depth study of the relationship mentioned above (disregarding between-species differences) allowed to conclude that the relationship could be somewhat more accurately described with curvilinear regressions (particularly the logarithmic regression), when the von Bertalanffy equation was used to describe length growth rate.

REFERENCES

Abdel–Baky T.E., 1983: Some aspects on the biology of bream (*Abramis brama* L.) in Dąbie Lake. Ph.D. Thesis, AR Szczecin: 56–68.

Anonymous, 1949: Promyslovyje ryby SSSR [Commercial fish of USSR]. Piščepromizdat, Moskwa. (In Russian).

Anonymous, 1985: Report of the Working Group on assessment of pelagic stocks in the Baltic. ICES: 7–34.

Antosiak H., 1961: Wzrost szczupaka (*Esox lucius* L.) w jeziorach okolic Węgorzewa [The rate of growth of pike (*Esox lucius* L.) in Węgorzewo District Lakes]. Rocz. Nauk Rol., ser. B, 77, 2: 581–602. (In Polish).

Bauch G., 1966: Die einheimischen süsswasserfische. Neumann Verlag.

Bernatowicz S., 1961: Wpływ środowiska na populację sielawy [The influence of environment conditions on Coregonus albula L. population]. Rocz. Nauk Rol., ser. B, 77, 2: 641–679. (In Polish).

Bernatowicz S., W. Dembiński, J. Radziej, 1975: Sielawa [Cisco]. PWRiL, Warszawa: 111–112. (In Polish).

Chrzan F., 1957: Stan stada dorsza południowo–wschodniego Bałtyku w latach 1952–1954 [The state of cod stock in the South–Eastern Baltic in 1952–1954]. Prace MIR, 9: 7–43. (In Polish).

Do Cong Chinh, 1977: Wzrost szczupaka (*Esox lucius* L.) w jeziorze Dabie [The growth of pike (*Esox lucius* L.) in Dąbie Lake]. Manuscript, AR Szczecin: 16–18. (In Polish).

Filipiak J., A. Kompowski, I. Krzykawska, S. Krzykawski, J. Szypuła, R. Trzebiatowski, W. Załachowski, 1978: Wpływ wód podgrzanych elektrowni „Dolna Odra" na ichtiofaunę Odry Wschodniej i jeziora Dąbie w latach 1975–1977 [The influence of heated waters from "Dolna Odra" power station on ichthyofauna of the Eastern Odra River and Dąbie Lake in 1975–1977]. Manuscript, AR Szczecin: 9–16. (In Polish).

Hanel L., 1992 : Poznavame nase ryby. Zemedelske nakladatelstvi Brazda, Praha. (In Czech).

Karpińska–Waluś B., 1961: Wzrost płoci (*Rutilus rutilus* L.) w jeziorach okolic Węgorzewa [The Rate of Growth of Roach (*Rutilus rutilus* L.) in Lakes of Węgorzewo District]. Rocz. Nauk Rol., ser. B, 77, 2: 329–398. (In Polish).

Karpińska–Waluś B., 1961: Tempo wzrostu leszcza (*Abramis brama* L.) w jeziorach okolic Węgorzewa [The Rate of Growth of Bream (*Abramis brama* L.) in Lakes of Węgorzewo District]. Rocz. Nauk Rol., ser. B, 77, 2: 455–491. (In Polish).

Kompowski A., 1973: Wzrost śledzi południowobałtyckich o różnych typach otolitów [Growth of South Baltic herring with different types of otholiths]. Prace MIR, **17** A: 113–127. (In Polish).

Kompowski A., 1991: Catches and growth rate of *Abramis ballerus* (L., 1758) from Lake Dąbie and the Firth of Szczecin. Acta Ichth. Piscat., **21**, 2: 17–28.

Kosior M., 1971: Dorsz południowego Bałtyku w latach 1965–1967 [Cod of the southern Baltic in the years 1965–1967]. Prace MIR, **16** A: 143–168. (In Polish).

Krzykawski S., J. Szypuła, 1982: Charakterystyka wzrostu i odżywiania się sandacza w jeziorze Dąbie i Regalicy w latach 1974–1977 [Growth and feeding of pikeperch in the Lake Dąbie and Regalica River in 1974–1977]. Zesz. Nauk. AR Szczecin, **93**: 3–24. (In Polish).

Marszałek W., 1961: Wzrost sielawy w jeziorze Wdzydze [Growth of *Coregonus albula* L. in Wdzydze Lake]. Rocz. Nauk Rol., ser. D, **93** : 201–220. (In Polish).

Nagięć M., 1961: Wzrost sandacza (*Lucioperca lucioperca* L. w jeziorach północnej Polski [The growth of Pike-Perch (*Lucioperca lucioperca* L.) in North Polish Lakes]. Rocz. Nauk Rol., ser. B, 77, 2: 549–580. (In Polish).

Postolakij A., 1982: Žiznіennyj cykl i promysel treski Bolszoj Niufaundlandskoj Banki. Čislennost' i obraz žizni promyslovych ryb severno-zapadnoj Atlantiki [The life cycle and fishery of cod from Grand Newfoundland Bank. Number and biology of commercial fishes in the North-West Atlantic]. Sbornik naučnych rabot PINRO: 5–14. (In Russian).

Rolik M., J.M. Rembiszewski, 1987: Ryby i krągłouste [Fish and Cyclostomates]. PWN, Warszawa. (In Polish).

Romański J., 1965: Płoć (*Rutilus rutilus* L.) w polskich połowach z południowego Bałtyku, szczególnie z Zatoki Puckiej [Roach (*Rutilus rutilus* L.) in Polish catches in the Southern Baltic, particularly in Puck Bay]. Prace MIR, **13** A: 85–99. (In Polish).

Rutkowicz S., 1963: Wyniki badań nad stadem dorsza (*Gadus callarias* L.) południowo-wschodniego Bałtyku w latach 1946–1960 (dynamika stada na tle biologii i ekologii gatunku) [The results of investigations on the stock of cod (Gadus callarias L.) in south-eastern area of the Baltic Sea in the years 1946–1960 (dynamics of stock in view of biology and eoology of the species)]. Prace MIR, **12** A: 165–211. (In Polish).

Sosiński J., 1969: Charakter otolitów u śledzi z rejonu Dunmore (pd. Irlandia) [Character of otholiths in herring from the Dunmore Region (South Ireland)]. Prace MIR, **15** A: 193–209. (In Polish).

Suryn J., 1990: Próba zastosowania różnych modeli matematycznych do ekstrapolacji tempa wzrostu długości wybranych gatunków ryb poza zakres danych empirycznych [An attempt to use of various mathematical models to extrapolate growth rate of selected fish species beyond the range of empirical data]. Manuscript, AR Szczecin: 6–14. (In Polish).

Szypuła J., 1987 a: An attempt to use various mathematical models to extrapolate fish growth rate beyond the range of empirical data. Acta Ichth. Piscat., **17**, 2: 11–31. (In Polish).

Szypuła J., 1987 b: Comparison of accuracy of binomial, von Bertalanffy equation, Gompertz equation and Ford-Walford model used for mathematical description of length growth in various fish species. Acta Ichth. Piscat., **17**, 2: 33–47.

Szypuła J., 1991: Zmodyfikowana funkcja potęgowa jako uniwersalny model wzrostu długości ryb [A modified power function as a versatile fish length growth model]. Zesz. Nauk. AR Szczecin, **143**: 3–21. (In Polish).

Szypuła J., 1994 a: Tempo wzrostu rozpióra z jeziora Dąbie w roku 1992 [The rate of growth of blue bream in Lake Dąbie in 1992]. Zesz. Nauk. AR Szczecin, **164**: 61–71. (In Polish).

Szypuła J., 1994 b: Tempo wzrostu okonia z Zalewu Szczecińskiego i jeziora Dąbie [The rate of growth of perch in Firth of Szczecin and Dąbie Lake]. Zesz. Nauk. AR Szczecin, **164**: 73–84. (In Polish).
Załachowski W., 1973: Szczupak [Pike]. PWRiL, Warszawa: 120–125. (In Polish).
Zawisza J., H. Żuromska, 1961: Wzrost wzdręgi (*Scardinius erythrophthalmus* L.) w jeziorach okolic Węgorzewa [The growth of rudd (*Scardinius erythrophthalmus* L.) in lakes of Węgorzewo district]. Rocz. Nauk Rol., ser. B, 77, 2: 399–453. (In Polish).
Żuromska H., 1961: Wzrost okonia (*Perca fluviatilis* L.) w jeziorach okolic Węgorzewa [The growth of perch (*Perca fluviatilis* L.) in lakes of Węgorzewo district]. Rocz. Nauk Rol., ser. B, 77, 2: 603–639. (In Polish).

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PORÓWNANIE MODELU VON BERTALANFFY'EGO I ZMODYFIKOWANEJ FUNKCJI POTĘGOWEJ POD WZGLĘDEM DOKŁADNOŚCI I ZAKRESU EKSTRAPOLACJI

STRESZCZENIE

W niniejszej pracy przedstawiono porównanie dokładności dwóch wybranych matematycznych modeli wzrostu długości — równania von Bertalanffy'ego i zmodyfikowanej funkcji potęgowej. Następnym spośród badanych zagadnień było określenie zakresu ekstrapolacji wspomnianych modeli wzrostu (z dopuszczalną 5% tolerancją względem danych empirycznych) oraz — w końcowym etapie pracy — ustalenie charakteru zależności pomiędzy dokładnością modelu a zakresem ekstrapolacji.

Przedmiotem badań było tempo wzrostu długości (według danych różnych autorów) 10 gatunków ryb: rozpióra, leszcza, płoci, wzdręgi, szczupaka, okonia, sandacza, sielawy, śledzia i dorsza; w odniesieniu do każdego gatunku przeanalizowano od 21 do 30 przypadków.

Uzyskane wyniki wskazują, że przeciętna dokładność analizowanych modeli nieznacznie przekracza 0,5 cm (jest to wartość średniej różnicy wyników empirycznych i obliczonych z modelu), natomiast zakres ekstrapolacji wynosi około 2 lat. Zarówno w odniesieniu do poszczególnych przypadków, jak i do średnich wartości ustalonych dla badanych gatunków ryb odnotowano bardzo duże rozproszenie uzyskanych wyników.

Zależności pomiędzy dokładnością modelu a wielkością zakresu ekstrapolacji, określane dla poszczególnych gatunków metodą regresji prostoliniowej, miały we wszystkich badanych przypadkach charakter zależności odwrotnych (ujemne wartości współczynników regresji i współczynników korelacji). Przy podjęciu próby bardziej ogólnego określenia wspomnianych zależności, bez uwzględniania różnic gatunkowych, zastosowano dodatkowo regresję wykładniczą ($y = a \cdot e^{bx}$), logarytmiczną ($y = a + b \cdot \ln x$) i potęgową ($y = a \cdot x^b$). Okazało się, że regresje krzywoliniowe (szczególnie regresja logarytmiczna) pozwalają na nieco ściślejsze skorelowanie badanych wielkości niż regresja prostoliniowa.

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