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SCALE RADIUS GROWTH VERSUS STANDARD LENGTH GROWTH IN SOME FISH SPECIES

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ABSTRACT. The growth of the scale radius was followed in seven fish species (roach, bream, rudd, humped rockcod, perch, halibut, and zander). The results obtained by analyzing a total of 11304 individuals were compared with corresponding data on the standard length growth of each species. The mathematical description of growth was done with the following six models: the von Bertalanffy equation, the Ford-Walford formula, the second order polynomial, the Gompertz model, the power function, and the modified power function. Data on length growth and length growth versus scale radius growth, which were used to determine the scale radius growth of each species, were taken from the literature. The growth of both the scale radius and body length of the species analyzed was fairly uniform: the increment ratios, averaged for the entire growth period, were close to 0.9. However, slightly higher values, hence more uniform growth, were recorded in radius growth (0.93) than in fish length growth (0.90). The fish length increments in the first two years of life were lower than the scale radius increments during the same time.

Key words: SCALE RADIUS, BODY LENGTH, GROWTH, MATHEMATICAL GROWTH MODELS

INTRODUCTION

Contemporary studies on fish length growth usually employ back calculations. This is a technique based on the relationship between body length (L) and scale radius length (R), or the L/R ratio, which permits reproducing the lengths attained by a fish in the consecutive years of its life from measurements of distances between individual annual rings on the scale (scale radius measurements). The Dahl-Lea version of back calculations, which assumes proportionality in the L/R ratio, has been abandoned because it underestimates length increments in the early years of life. The versions used most frequently, *i.e.*, those of Rosa Lee and Vovk, assume the L/R ratio to deviate from proportionality, hence the rates of body length and scale radius growth in a species are different.

Whereas the problem of fish length growth determined by back calculations has received thorough and comprehensive treatment in the literature, the available

ichthyological literature lacks publications on scale radius growth. This prompted the author to undertake the study described in this paper.

The aim of the study was to track the growth of scale radius in some fish species and compare it with body length growth and to verify whether the growth models used can also be applied to describe scale radius growth.

MATERIAL AND METHODS

This study utilizes various authors' calculations of the length growth of seven fish species: roach, *Rutilus rutilus* (L.), bream, *Abramis brama* (L.), rudd, *Scardinius erythrophthalmus* (L.), humped rockcod, *Notothenia gibberifrons* (Lönnberg), European perch, *Perca fluviatilis* L., halibut, *Reinhardtius hippoglossoides* (Walb.), and zander, *Sander lucioperca* (L.). Data from a total of 93 samples numbering from six (halibut) to 25 (roach) were analyzed; the total number of individuals examined was 11304. Detailed data on the origin of the fish, the authors, and sample sizes are given in Table 1.

TABLE 1

Summary of the materials analyzed

Species	Area	Author	N	n
1. Roach	Węgorzewo lakes	Karpińska-Waluś (1961)	19	879
2. Roach	Lake Dąbie	Załachowski and Krzykawska (1995)	3	192
3. Roach	Pomeranian Bay	Załachowski et al. (1997)	3	200
4. Bream	Węgorzewo lakes	Karpińska-Waluś (1961)	6	261
5. Bream	Lake Dąbie	Abdel-Baky (1983)	3	1306
6. Rudd	Węgorzewo lakes	Zawisza and Żuromska (1961)	11	300
7. Humped rockcod	South Atlantic	Skóra (1985)	8	5135
8. Perch	Węgorzewo lakes	Żuromska (1961)	15	623
9. Perch	Oder estuary	Szypuła and Rybczyk (2001)	4	822
10. Halibut	Labrador	Krzykawski (1988)	3	154
11. Halibut	Barents Sea	Krzykawski (1988)	3	127
12. Zander	lakes of northern Poland	Nagięć (1961)	9	380
13. Zander	Oder estuary	Szypuła (2002)	4	633
14. Zander	Lake Dąbie and Regalica	Krzykawski and Szypuła (1982)	2	292
Total			93	11304

N - number of samples

n - number of individuals examined

The fish growth rate was explored with back calculations based most often on the Rosa Lee method. The L-R relationship was curvilinear only for the Oder estuary zander, which is why the Vovk method with scale radius correction was applied. The author of the source publication on the Węgorzewo Lakeland zander (Nagięć 1961) found the L-R relationship

to be curvilinear and used the Segerstråle method of back calculations. However, because this author provided no data-based equation to describe the L-R relationship, which was presented as a graph (Nagięć 1961), a linear relationship was assumed for the Węgorzewo Lakeland zander. The relationship differed from that obtained with the Segerstråle method only slightly, so the Rosa Lee method was used to calculate the scale radius from body length data in the consecutive years of life. The scale radius growth was reconstructed from the L-R equations for individual species and areas presented by each author.

Both length growth (back calculations) and scale radius growth (calculated from the L-R relationship) are also presented in the form of most frequently used mathematical growth models:

A. von Bertalanffy model: $L_t = L_\infty [1 - e^{-K(t-t_0)}]$

B. Ford-Walford model: $L_t = L_1 \frac{1 - k^t}{1 - k}$

C. second order polynomial: $L_t = a + bt + ct^2$

D. Gompertz model: $L_t = a \cdot b^{c^t}$

E. power function: $L_t = kt^n$

F. modified power function: $L_t = At^B + C$

To avoid possible discrepancies (frequent in older years of life due to the small number of individuals) between model-derived results and those produced by back calculations, it was decided that, as a matter of principle, the models would be based only on the data from the examination of at least ten individuals. Therefore, the age ranges used for comparing the growth rate of fish length and that of the scale radius of various species are, in this study, usually narrower than the ranges used in the source publications.

The average absolute difference (AAD), *i.e.*, the mean of differences between values computed with a model and those supplied by back calculations (or by an appropriate L-R relationship) for individual years of life, was used to assess the accuracy of individual growth models. As the differences were expressed in different units (cm for the length and mm for the scale radius), they were also converted to percentages (AAD relative to the mean length or the mean radius used to construct an appropriate growth model) for the purpose of comparisons.

For a general characterization of fish length and scale radius growth histories, mean ratios of increments in consecutive years of life ($\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$ and $\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$) as well as the ratio between increments in the first and the second year of life ($\frac{\Delta r_2}{\Delta r_1}$ and $\frac{\Delta l_2}{\Delta l_1}$) were calculated.

Student's t test for two means (at the significance level of $P = 0.05$) was applied to test for statistical significance of differences between selected terms of the fish length and scale radius growth models used as well as between increment ratios.

RESULTS

A) SCALE RADIUS GROWTH VERSUS FISH LENGTH GROWTH

Scale radius growth and the results of its comparison with fish length growth are shown in Figures 1, 2, 3, and 4. Figure 1 shows the radius growth of the species whose age and growth rate were assessed from measurements of the oral part of the scale (humped rockcod, perch, halibut, zander). The figure shows that scale radius growth

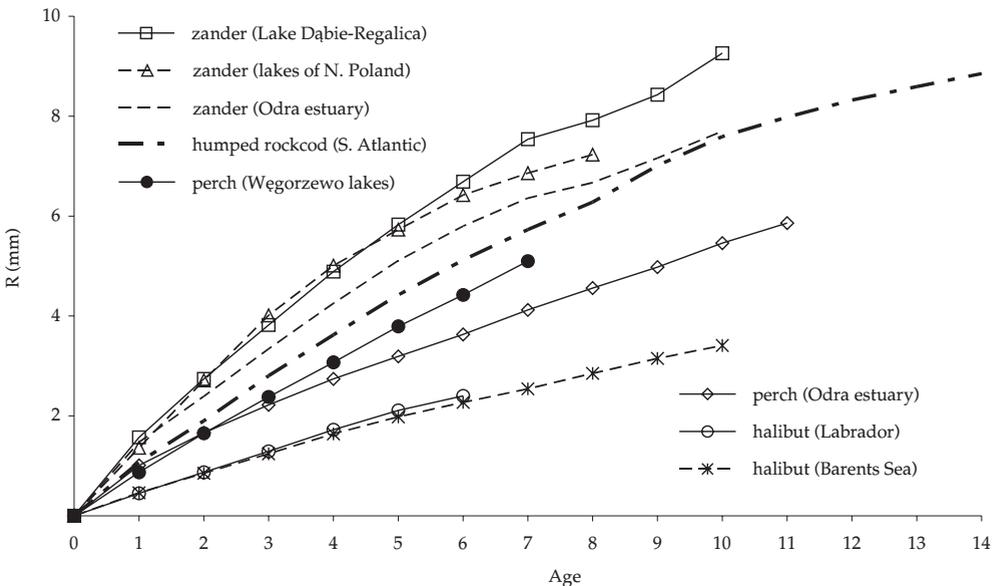


Fig. 1. Scale radius growth (R) in the species in which age and growth are determined on the oral part of the scale.

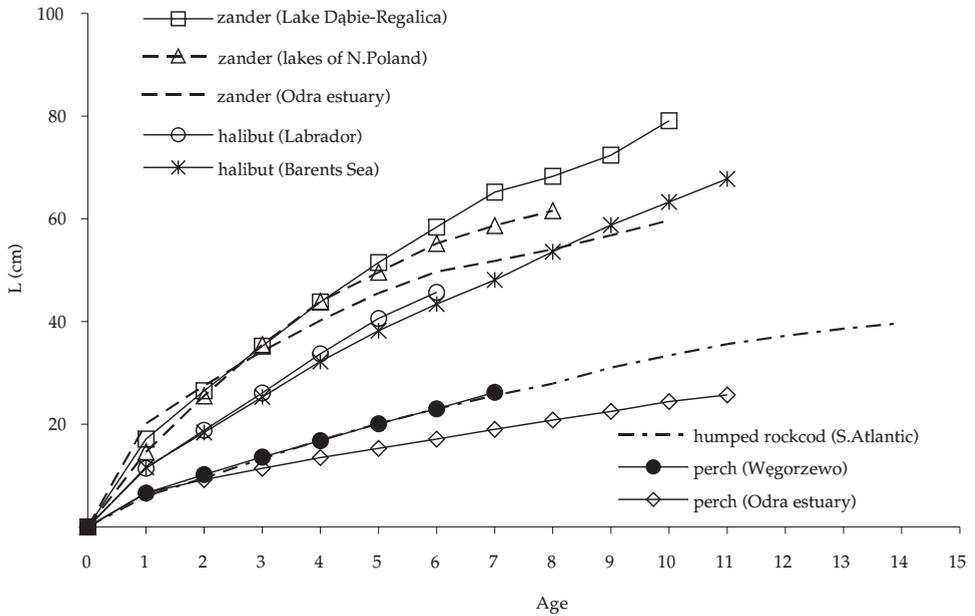


Fig. 2. Standard length growth (L) of the species in Fig. 1.

differs widely among species. The slowest growth was typical of Barents Sea halibut, while the fastest-growing scales belonged to zander from Lake Dąbie and Regalica River (in 10-year-old individuals, the oral scale radius was as low as 3.5 mm and was more than 9 mm in halibut and zander, respectively). Similarly, considerable variability was seen in length growth (Fig. 2), but here the slowest growth rate was noted in Oder estuary perch (24.4 cm in year 10), while the fastest was exhibited by Lake Dąbie and Regalica River zander (79.1 cm in year 10).

The comparison of scale radius and body length growth in years 4 and 5 showed that the former was almost uniform while the latter was clearly inhibited after year 1. The increment in year 1 was markedly higher than individual increments in subsequent years.

Figures 3 and 4 show the scale radius and body length growth of the species in which the caudal part of the scale is used for determinations (roach, bream, and rudd). Here, both scale radius and body length growth were much less variable. The fastest growth in the caudal scale radius (Fig. 3) was observed in Lake Dąbie bream (more than 6.5 mm in year 9), while the slowest was detected in Węgorzewo Lakeland roach

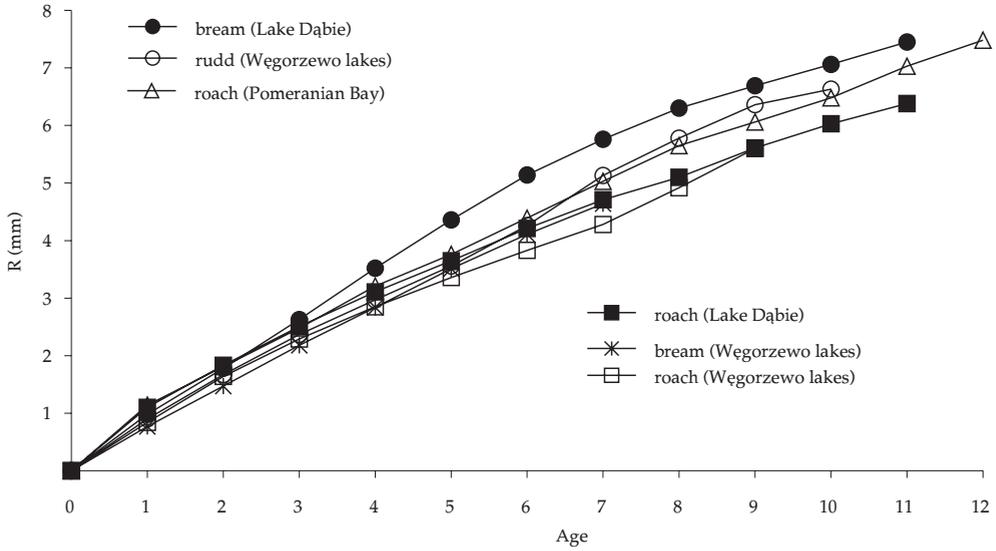


Fig. 3. Scale radius growth (R) in the species in which age and growth is determined on the caudal part of the scale.

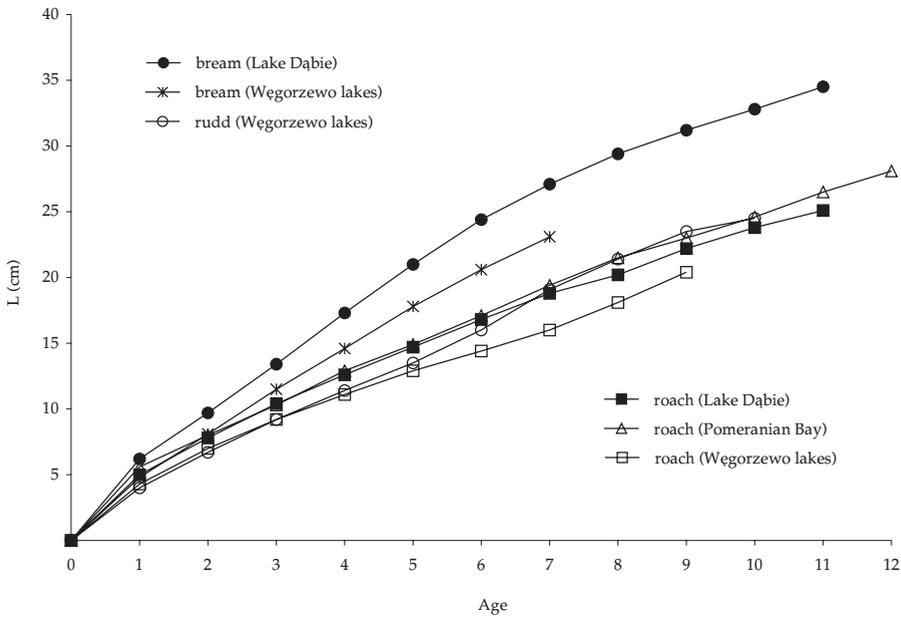


Fig. 4. Standard length growth (L) of the species in Fig. 3.

(slightly more than 5.5 mm in year 9). A similar scale of variability was observed in body length growth (Fig. 4). Here, too, the fastest growth was noted in Lake Dąbie bream (32.8 cm in year 9), while the slowest was displayed by Węgorzewo Lakeland roach (20.4 cm in year 9). Additionally, there was a difference between the scale radius and body length growth exhibited by these species that was analogous to that described above - almost uniform scale radius growth versus a more or less pronounced reduction of length increments beginning in year 2.

In order to quantify the history of the scale radius and body length growth of the species studied, the ratios of increments of both scale radius and body length were averaged over time ($\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$ and $\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$). The results are shown in Table 2.

TABLE 2

Ratios of scale radius increments ($\frac{\overline{\Delta r_n}, \Delta r_2}{\Delta r_{n-1}, \Delta r_1}$) and length increments ($\frac{\overline{\Delta l_n}, \Delta l_2}{\Delta l_{n-1}, \Delta l_1}$) in the species studied

Species	$\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$	$\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$	$\frac{\Delta r_2}{\Delta r_1}$	$\frac{\Delta l_2}{\Delta l_1}$
Roach	0.94	0.92	0.73	0.54
Bream	0.93	0.90	0.86	0.62
Rudd	0.91	0.89	0.86	0.67
Humped rockcod	0.91	0.89	0.76	0.58
Perch	0.94	0.89	0.77	0.47
Halibut	0.94	0.90	0.89	0.62
Zander	0.93	0.88	0.79	0.56
Mean	0.93	0.90	0.81	0.58

The mean ratios of scale radius increments, $\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$, had similar values in the species studied (from 0.91 in rudd and humped rockcod to 0.94 in roach, perch, and halibut; the overall mean was 0.93). These can be regarded as the expression of the growth increment in one year as a proportion of the previous year's increment. The values obtained are evidence of the very slight reduction in scale radius increments with age; therefore, scale radius growth can be regarded as almost uniform.

The mean ratios of fish body length increments ($\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$) were only slightly lower. It has to be stressed that the mean length increment ratio was somewhat lower than the mean

scale radius increment in each species (differences ranged from 0.02 to 0.05). The mean length increment ratio ranged from 0.88 in zander to 0.92 in roach (the overall mean was 0.90). Differences between the mean ratios of scale radius increments and the mean ratios of body length increments were non-significant at $P = 0.05$.

The ratios between scale radius increments in the second and first years of life ($\frac{\Delta r_2}{\Delta r_1}$) were clearly lower than the ratios averaged over all years and ranged from 0.73 in roach to 0.89 in halibut (the mean ratio was 0.81). Such values are evidence of a somewhat higher scale increment in the first year of life than in the second. An even larger difference was observed between the fish length increments in the first two years of life ($\frac{\Delta l_2}{\Delta l_1}$) and the averaged length increment ratios. The value of $\frac{\Delta l_2}{\Delta l_1}$ ranged from 0.47 in perch to 0.67 in rudd (the mean ratio was 0.58). So, while the mean difference between the averaged ratios of scale radius and fish length increment was 0.03, the corresponding difference between the ratios calculated for the first two years of life was as high as 0.23. The latter difference and that calculated for individual species were significant at $P = 0.05$.

B) MATHEMATICAL MODELING OF SCALE RADIUS AND FISH LENGTH GROWTH IN THE SPECIES STUDIED

The following mathematical models, which are most commonly used for fish growth, were tested to see whether they could be applied to describe scale radius growth: the von Bertalanffy equation, the Ford-Walford formula, the second order polynomial, the Gompertz model, the power function, the modified power function. The mean values of the terms of each model were calculated and compared with values of the corresponding terms of individual models used to describe fish length growth. The results are summarized in Table 3.

TABLE 3

Mathematical description of scale radius (R) growth and standard length (L) growth in the species studied (model symbols as in Material and Methods; □ differences significant at $P = 0.05$, ■ differences non-significant at $P = 0.05$)

		Species													
Model		Roach		Bream		Rudd		Humped rockcod		Perch		Halibut		Zander	
		term		term		term		term		term		term		term	
A	R	L_{∞}	11.96	L_{∞}	41.83	L_{∞}	17.06	L_{∞}	11.94	L_{∞}	77.87	L_{∞}	18.28	L_{∞}	14.64
		K_{\blacksquare}	0.1241	K_{\blacksquare}	0.0557	K_{\blacksquare}	0.1170	K_{\blacksquare}	0.1025	K_{\blacksquare}	0.0670	K_{\blacksquare}	0.0576	K_{\blacksquare}	0.1247
		$t_{0\blacksquare}$	-0.0910	$t_{0\blacksquare}$	0.0154	$t_{0\blacksquare}$	-0.0293	$t_{0\blacksquare}$	0.0538	$t_{0\blacksquare}$	-0.1590	$t_{0\blacksquare}$	0.0447	$t_{0\blacksquare}$	-0.0095
	L	L_{∞}	42.62	L_{∞}	204.35	L_{∞}	62.46	L_{∞}	51.60	L_{∞}	117.27	L_{∞}	216.61	L_{∞}	106.96
		K_{\blacksquare}	0.1237	K_{\blacksquare}	0.0529	K_{\blacksquare}	0.1167	K_{\blacksquare}	0.1023	K_{\blacksquare}	0.0678	K_{\blacksquare}	0.0584	K_{\blacksquare}	0.1406
		$t_{0\blacksquare}$	-0.5451	$t_{0\blacksquare}$	-0.3486	$t_{0\blacksquare}$	-0.2767	$t_{0\blacksquare}$	-0.2545	$t_{0\blacksquare}$	-0.8506	$t_{0\blacksquare}$	-0.4112	$t_{0\blacksquare}$	-0.4375
B	R	L_1	0.8682	L_1	0.8454	L_1	0.8906	L_1	1.0796	L_1	0.8480	L_1	0.4514	L_1	1.4155
		k_{\square}	0.8909	k_{\blacksquare}	0.9458	k_{\blacksquare}	0.8843	k_{\blacksquare}	0.9048	k_{\square}	0.9229	k_{\square}	0.9437	k_{\square}	0.8916
		k_{\square}	0.8179	k_{\blacksquare}	0.9114	k_{\blacksquare}	0.8420	k_{\blacksquare}	0.8863	k_{\square}	0.8067	k_{\square}	0.8881	k_{\square}	0.7935
	L	L_1	3.9158	L_1	4.5813	L_1	3.6880	L_1	5.1742	L_1	5.5839	L_1	9.9012	L_1	15.0357
		k_{\square}	0.8179	k_{\blacksquare}	0.9114	k_{\blacksquare}	0.8420	k_{\blacksquare}	0.8863	k_{\square}	0.8067	k_{\square}	0.8881	k_{\square}	0.7935
		k_{\square}	0.8179	k_{\blacksquare}	0.9114	k_{\blacksquare}	0.8420	k_{\blacksquare}	0.8863	k_{\square}	0.8067	k_{\square}	0.8881	k_{\square}	0.7935
C	R	a	0.1161	a	-0.0497	a	0.1078	a	-0.0329	a	0.1322	a	0.0170	a	0.0380
		b	0.8449	b	0.8639	b	0.8932	b	1.0553	b	0.8007	b	0.4463	b	1.4304
		c	-0.0362	c	-0.0195	c	-0.0300	c	-0.0325	c	-0.0215	c	-0.0090	c	-0.0602
	L	a	1.8529	a	1.2223	a	1.0867	a	1.4774	a	3.0735	a	2.9502	a	5.5737
		b	2.8975	b	3.9399	b	3.0330	b	4.3953	b	3.6413	b	8.2109	b	11.4232
		c	-0.1215	c	-0.0848	c	-0.1095	c	-0.1335	c	-0.0988	c	-0.1913	c	-0.5239
D	R	a	5.9909	a	7.5671	a	5.7573	a	9.6612	a	6.4801	a	3.7211	a	8.2408
		b	0.0806	b	0.0596	b	0.0795	b	0.0693	b	0.0744	b	0.0604	b	0.0793
		c_{\blacksquare}	0.7030	c_{\blacksquare}	0.7484	c_{\blacksquare}	0.6829	c_{\blacksquare}	0.7834	c_{\blacksquare}	0.7223	c_{\blacksquare}	0.7305	c_{\blacksquare}	0.6661
	L	a	23.0612	a	37.6564	a	21.9634	a	42.4373	a	35.2230	a	72.0578	a	68.3174
		b	0.1243	b	0.0829	b	0.1026	b	0.0926	b	0.1236	b	0.0921	b	0.1319
		c_{\blacksquare}	0.7306	c_{\blacksquare}	0.7681	c_{\blacksquare}	0.6998	c_{\blacksquare}	0.7923	c_{\blacksquare}	0.7620	c_{\blacksquare}	0.7569	c_{\blacksquare}	0.6802
E	R	k	0.9284	k	0.8542	k	0.9189	k	1.1526	k	0.9011	k	0.4613	k	1.4460
		n_{\square}	0.8260	n_{\square}	0.9161	n_{\square}	0.8424	n_{\square}	0.7995	n_{\square}	0.8701	n_{\square}	0.9125	n_{\square}	0.8575
		k	4.5327	k	5.1781	k	3.9988	k	6.1508	k	6.4062	k	11.2648	k	16.4989
	L	n_{\square}	0.6750	n_{\square}	0.7644	n_{\square}	0.7546	n_{\square}	0.7146	n_{\square}	0.6846	n_{\square}	0.7670	n_{\square}	0.6885
		k	4.5327	k	5.1781	k	3.9988	k	6.1508	k	6.4062	k	11.2648	k	16.4989
		n_{\square}	0.6750	n_{\square}	0.7644	n_{\square}	0.7546	n_{\square}	0.7146	n_{\square}	0.6846	n_{\square}	0.7670	n_{\square}	0.6885
F	R	A	2.7443	A	1.7779	A	1.0856	A	3.3848	A	1.2444	A	0.6920	A	65.2305
		B_{\blacksquare}	0.5406	B_{\blacksquare}	0.7297	B_{\blacksquare}	0.5995	B_{\blacksquare}	0.2605	B_{\blacksquare}	0.7613	B_{\blacksquare}	0.7587	B_{\blacksquare}	0.5345
		C	-1.8873	C	-1.0000	C	-0.2235	C	-2.9920	C	-0.3711	C	-0.2690	C	-66.5244
	L	A	9.4998	A	7.6868	A	3.7902	A	15.1458	A	5.6479	A	12.1909	A	160.7748
		B_{\blacksquare}	0.5442	B_{\blacksquare}	0.7392	B_{\blacksquare}	0.5997	B_{\blacksquare}	0.2576	B_{\blacksquare}	0.7645	B_{\blacksquare}	0.7547	B_{\blacksquare}	0.4565
		C	-5.1102	C	-2.9108	C	0.0601	C	-11.9850	C	0.8107	C	-1.2526	C	-176.1965

Since scale radius growth was expressed in mm and fish body length growth in cm, not all the terms were comparable. Those amenable to comparisons were the terms expressed in units other than length (e.g., t_0 in the von Bertalanffy equation), as were terms that were power exponents and bases. Finally, the terms compared were K and t_0 of the von Bertalanffy equation, k of the Ford-Walford formula, c of the Gompertz model, n of the power function, and B of the modified power function (all the terms of the second order polynomial were considered non-comparable). The comparisons also consisted of tests of significance of the differences between mean values of the terms contained in the models applied to scale radius and to body length growth.

Term K of the von Bertalanffy equation applied in the description of scale radius growth was almost identical to its counterpart used to describe fish growth. The differences were non-significant in all the species studied. The slightly higher values of K were somewhat more frequent with respect to the scale radius in roach, bream, rudd, and humped rockcod; higher K in the remaining three species was found in the mathematical description of length growth. On the other hand, rather pronounced differences were observed in the values of t_0 . It should be mentioned here that, whereas t_0 was always negative in length growth, positive values were obtained in the scale radius growth description in bream, humped rockcod, and halibut. The absolute values of t_0 were higher in length growth by a factor ranging from 4.7 (in humped rockcod) to 46.1 (in zander). The differences in t_0 values between the equations describing scale radius growth and fish length were significant in all the species studied.

Term k of the Ford-Walford formula, which corresponds approximately to the mean ratio of increments of scale radius or fish length, was always higher in the scale radius growth description. This indicates that scale radius growth is closer to linear than is fish body length growth. It should be stressed that the difference in the values of k between the scale radius and fish length growth was non-significant only in bream, rudd, and humped rockcod; the remaining species exhibited significant differences.

Exponent c from the Gompertz model was compared, and the values of it in the equations describing scale radius growth were very similar to those used to characterize fork length growth. Although the differences were non-significant, slightly higher values of this term were always observed in the fish length growth models.

Exponent n was the power function term compared, and values of it were much higher in all species in the equations describing scale radius growth, with all differences significant.

Exponent B from the modified power function was compared, and there were only minimal differences between its values in the two applications of the model. Somewhat more marked differences were observed only with respect to zander, and in neither case was the difference significant. As with von Bertalanffy equation term K , the modified power function exponent was slightly higher in some equations describing scale radius growth and in others applied to model fish length growth (in roach, bream, rudd, and perch).

C) THE ACCURACY OF MATHEMATICAL DESCRIPTIONS OF SCALE RADIUS AND FISH LENGTH GROWTH

Another problem analyzed in this work was the comparison of the accuracy achieved when different mathematical models were used to describe scale radius growth calculated from the L-R relationship and fish length growth determined with back calculations. Comparisons among species and models were conducted and the results are summarized in Table 4.

TABLE 4

The accuracy of scale radius (R) and fish length (L) prediction in relation to the mathematical growth models used and the fish species

Species	AAD (R) (mm)	AAD (R) %	AAD (L) (cm)	AAD (L) %
Roach	0.049	1.67	0.18	1.52
Bream	0.070	1.87	0.28	1.70
Rudd	0.036	1.32	0.13	1.24
Humped rockcod	0.166	2.82	0.63	2.37
Perch	0.035	1.27	0.22	1.52
Halibut	0.022	1.29	0.45	1.34
Zander	0.078	1.80	0.61	1.59
Mean	0.065	1.72	0.36	1.61
Model	AAD (R) (mm)	AAD (R) %	AAD (L) (cm)	AAD (L) %
A	0.046	1.23	0.24	1.03
B	0.060	1.67	0.54	2.52
C	0.041	1.15	0.24	1.03
D	0.064	1.79	0.31	1.42
E	0.107	2.67	0.47	2.07
F	0.073	1.82	0.36	1.61
Mean	0.065	1.72	0.36	1.61

AAD (R) – average absolute difference in scale radius; AAD (R) % – average percentage difference in scale radius; AAD (L) – average absolute difference in fish length; AAD (L) % – average percentage difference in scale radius; Model symbols as in Material and Methods

As the data show, the average absolute differences between scale radius growth rates ranged from 0.02 mm (halibut) to 0.166 mm (humped rockcod). When expressed as percentages, the differences followed a somewhat different pattern; the lowest difference (1.27%) was observed in perch, while the highest (2.82%) was again in humped rockcod. With respect to fish length growth, the AAD(L) ranged from 0.13 cm in rudd to 0.63 cm in humped rockcod. The same species produced AAD(L)% values ranging from 1.24% in rudd to 2.37% in humped rockcod.

The accuracy of individual scale radius and fish length growth models also differed. The most accurate description of scale radius growth was achieved with the second order polynomial [AAD(R) = 0.041 mm; AAD(R)% = 1.15%], while the power function

was the least accurate [AAD(R) = 0.107 mm; AAD(R)% = 2.67%]. The most accurate descriptions of fish length growth were from the von Bertalanffy and the second order polynomial equations [in both cases AAD(L) = 0.24 cm; AAD(L)% = 1.03%], while the Ford-Walford formula was the least accurate [AAD(L) = 0.54 cm; AAD(L)% = 2.52%].

DISCUSSION

Within each species, scale radius and fish length growth proceeded similarly, as is evidenced, for example, by the very similar mean ratios of radius and length increments in consecutive years of life. In addition, the species studied showed relatively uniform growth in both scale radius and fish length, as is evidenced by the values of $\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$ and $\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$ that are close to 1 (0.93 and 0.90, respectively). Although the differences between the mean ratios of scale radius increments and length increments were non-significant, the higher values of the first in all the species may suggest that it was closer to being linear than fish length growth was.

The usually slight differences between the values of the mean ratios of scale radius and length increments ($\frac{\overline{\Delta r_n}}{\Delta r_{n-1}}$ and $\frac{\overline{\Delta l_n}}{\Delta l_{n-1}}$) and the corresponding values of term k from the Ford-Walford formula resulted from the different ways the values were calculated. The reader should also be reminded that the theoretical growth curve described by the Ford-Walford equation passes through the coordinate origin, while true fish length growth is almost always higher in year 1 than in subsequent years. For this reason, the true growth curve extrapolated back will most often intercept the length axis (y axis) at a lower or higher positive value.

Much more pronounced differences were observed when the ratios between scale radius and fish length increments in the first and second years of life were compared. Firstly, the values of both $\frac{\Delta r_2}{\Delta r_1}$ and $\frac{\Delta l_2}{\Delta l_1}$ were much lower than the mean ratios of increments, discussed above, which demonstrates a clearly higher increment in the first than in the second year of life. Secondly, differences between $\frac{\Delta r_2}{\Delta r_1}$ and $\frac{\Delta l_2}{\Delta l_1}$ were larger

and significant in all cases. Much higher values were attained by the scale radius increment ratios. This pattern provides evidence of much stronger inhibition, past the first year of life, in fish length increments than in scale radius increments. Identical conclusions can be drawn from the analysis of the scale radius and length growth of the species studied, as is illustrated in Figs. 1, 2, 3, and 4.

On the other hand, the results on average values of growth model terms suggest a relatively close similarity between the mathematically described growths of the scale radius and body length in the species studied. Similarity is particularly clear in von Bertalanffy equation term K and in the modified power function term B . Differences in the values of these terms applied to describe the growth of the scale radius and fish body were always non-significant in a given species. Moreover, the terms in question assumed values that, in some species, were higher in the scale radius growth description than in that of fish growth; the opposite pattern was observed in other species.

The other term (t_0) of the von Bertalanffy equation produced pronounced differences between the values used in the description of scale radius and length growth: much higher t_0 values were typical of the length growth models and the differences were significant in all the species studied. This pattern of K and t_0 values suggests that, although the shapes of the theoretical growth curves were very similar in scale radius and length growth (as evidenced by the very close values of K), the radius growth curves intercepted the time axis (x axis) much closer to the origin (clearly lower t_0 values) than the fish length growth curve did.

In the remaining models, the differences between the values of the Ford-Walford term k , the Gompertz model term c , and the power function term n were clearly indicative of the more uniform growth of scales compared to the more "curvilinear" growth of body length in the species studied.

Finally, the last problem addressed in the previous section was that of the accuracy of the mathematical reconstruction of scale radius and body length growth with the growth models used. It should be stressed that the models used so far to describe fish growth allowed describing scale radius growth equally well. The AAD(R)% value, averaged across species, was 1.72% and was only slightly higher than the similarly averaged AAD(L)% (1.61%). The absolute values of the average differences were relatively low as well at AAD(R) = 0.065 mm and AAD(L) = 0.36 cm. In conclusion, it can be said that slightly higher accuracy was attained when modeling length growth, but in some cases (perch and

halibut in interspecific comparisons, the Ford-Walford formula in comparisons among models; see Table 4), scale radius growth was modeled with higher accuracy.

CONCLUSIONS

1. Scale radius growth proceeded in a manner similar to that of fish body length. Essentially, the differences were the much more pronounced growth inhibition between the first and the second year of life that were visible in the length as compared to scale radius growth. Additionally, the latter was somewhat more uniform over time compared to body length growth.
2. Mathematical growth models applied to describe fish length growth can be used successfully in the mathematical description of scale radius growth.
3. The comparison between the terms of the growth models applied to describe fish body length and scale radius growth in a given species showed the most pronounced differences (significant in all the species studied) in von Bertalanffy equation term t_0 and power function term n . Significant differences in some species only (4 out of 7) were revealed in the Ford-Walford formula term k . The remaining terms compared, specifically the von Bertalanffy equation K , Gompertz model c , and modified power function B , only differed minimally and in none of the species were the differences significant at $P = 0.05$.
4. The models tested in this study allowed describing, with sufficient accuracy, the growth of both scale radius and fish length. However, slightly higher accuracy (a lower average absolute difference, AAD) was typical of fish length growth descriptions. The AAD(R) averaged across species was 0.065 mm [or 1.72% as AAD(R)%] and the corresponding averaged AAD(L) was 0.36 cm [or 1.61% as AAD(L)%].

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STRESZCZENIE

PORÓWNANIE WZROSTU PROMIENIA ŁUSKI ZE WZROSTEM DŁUGOŚCI WYBRANYCH GATUNKÓW RYB

Celem niniejszej pracy było zbadanie przebiegu wzrostu promienia łuski różnych gatunków ryb i jego porównanie ze wzrostem długości. Materiałem były dane o wzroście długości 7 gatunków: płoci, leszcza, wzdręgi, nototeni, okonia, halibuta i sandacza (tab. 1), uzyskane przez różnych autorów metodą odczytów wstecznych. Na podstawie przytaczanych zależności L/R określano wielkości promienia łuski w kolejnych latach życia. Wzrost zarówno promienia łuski, jak i długości ciała (rys. 1, 2, 3, 4) scharakteryzowano matematycznie przy zastosowaniu 6 modeli wzrostu: równania von Bertalanffy'ego, formuły Forda-Walforda, wielomianu 2 stopnia, modelu Gompertza, funkcji potęgowej i zmodyfikowanej funkcji potęgowej (tab. 3). Określono również dokładność matematycznego opisu wzrostu za pomocą różnych modeli, a także różnice wartości parametrów poszczególnych modeli powstające przy matematycznej charakterystyce wzrostu promienia łuski i długości ciała.

Uzyskane wyniki wskazują na dość duże podobieństwo wzrostu promienia łuski i długości ciała tego samego gatunku. Różnice sprowadzały się do nieco bardziej równomiernego wzrostu promienia łuski w porównaniu ze wzrostem długości ciała. Również spadek przyrostów promienia łuski w 1 i 2 roku życia był wyraźnie mniejszy, niż spadek przyrostów długości (tab. 2). Stosowane modele opisują wzrost długości nieco dokładniej, niż wzrost promienia łuski (tab. 4), ale różnica dokładności jest nieznaczna (przeciętna procentowa różnica wyniosła 1,72% w przypadku wzrostu promienia łuski i 1,61% w odniesieniu do wzrostu długości).