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COMPARISON OF ACCURACY OF BINOMIAL, VON BERTALANFFY
EQUATION, GOMPERTZ EQUATION AND FORD-WALFORD MODEL
USED FOR MATHEMATIC DESCRIPTION OF LENGTH GROWTH
IN VARIOUS FISH SPECIES

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The paper presents results of studies comparing empirical lengths of 50 fish species with lengths calculated by means of 4 most common mathematic growth models (binomial, von Bertalanffy equation, Gompertz equation and Ford-Walford model). From 5 to 19 versions of each model were calculated for every species, both for the whole range of empirical data and for its initial or terminal part. A total of 1920 mathematic length growth models were calculated, and mean difference between empirical and calculated results was computed for each model. The binomial was found to yield the best results (smallest mean differences), the worst results being obtained with the Ford-Walford model.

INTRODUCTION

Fish growth is commonly described at present by means of mathematic models. Models offer a number of advantages, like brevity (a relatively simple, short equation instead of a complex table containing lengths attained in various years of life); they better

reflect the general trend of growth by levelling off deviations, sometimes very substantial, produced by non-typical, sporadic effects of environmental factors or poor reliability of some data; finally, models allow to extrapolate growth beyond the range of empirical data. Moreover, fish growth models are indispensable in stock assessment and in prediction of changes in the dynamics of fish resources.

In order to find out which of the most commonly used growth models yields the best results (smallest differences between empirical and calculated data), a comparison is made between results obtained by using each of the models and the empirical data. Abundant and representative material in the form of about 2 thousand growth models calculated for 50 fish species served as a basis for the comparison. The results obtained are statistically treated by calculating means and commonly used dispersion measures; significance of differences occurring when using various growth models is evaluated as well.

MATERIALS AND METHODS

The materials for the present work consist of mathematical length growth models (the binomial, von Bertalanffy equation, Gompertz equation and Ford-Walford model) calculated for 50 fish species (Anon., 1949; Cięglewicz and Draganik, 1969; Krzykowski, 1976; Nikolski, 1956, Svetovidov, 1964) with no possibility for extrapolation of model data beyond the empirical range (Szypuła, in press). As the models mentioned had been calculated for a part of the empirical data only (for various ranges covering early or late years of fish life), they were supplemented with models computed for the entire range of empirical data. A total of 1920 mathematic length growth models were calculated (482 binomials, 482 von Bertalanffy equations, 472 Gompertz equations, and 484 Ford-Walford models). For each model, a mean difference between empirical and calculated results was computed. The difference is expressed as both an absolute value and in per cent of mean empirical length calculated from the data range analysed. Fig. 1 presents examples of such differences for the 4 growth models applied to the Black Sea Hake (*Merluccius merluccius*) (the empirical data covered 10 years). As can be seen, the least variability in absolute values of differences (0.2 to 2.6 cm) and the lowest mean difference (1.08 cm) were found when using the binomial, while the greatest variability (0.2 to 6.5 cm) and the highest mean difference (2.71 cm) were observed with the Ford-Walford model.

Tables present the statistical characteristics of the results, such as the arithmetic mean, standard deviation, coefficient of variation, and range. Parameters of linear relationship between the differences and the range of empirical data (with reference to a model used) were determined. Furthermore, differences between mean results obtained with various models were tested for significance by means of Student's *t* test at 0.95 confidence level.

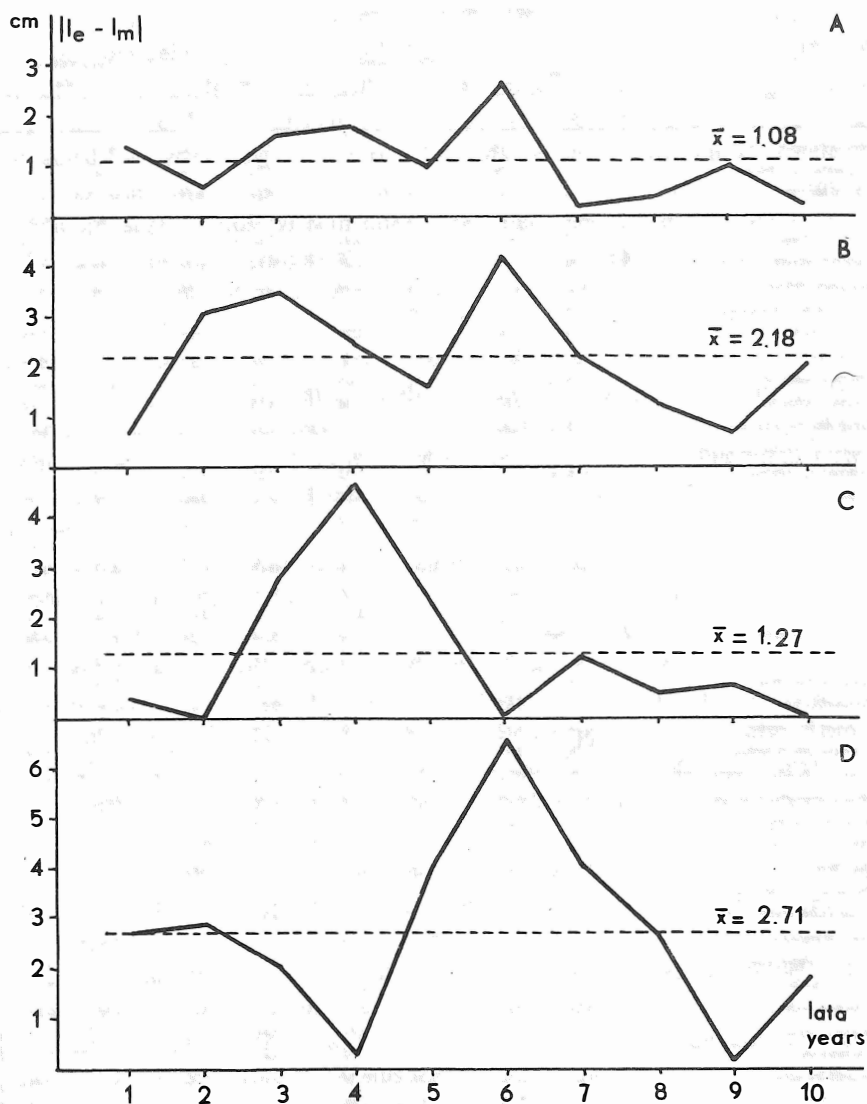


Fig. 1. Differences between empirical data and model results ($l_e - l_m$) calculated with various growth models for successive years of life of the Black Sea hake (*Merluccius merluccius*)

(A = binomial; B = von Bertalanffy equation; C = Gompertz equation; D = Ford-Walford model)

Table 1

Mean differences (cm) between empirical data and results calculated with growth models analysed
(a = absolute difference; b = difference expressed as % of empirical data; x = smallest difference in a species;
o = largest difference in a species)

No.	Species	Binomial		von Bertalanffy equation		Gomertz equation		Ford-Walford model	
		a	b	a	b	a	b	a	b
1.	<i>Sardinops sagax</i>	0.47	2.58	0.53	3.05	0.71	o 4.00	0.37	x 2.12
2.	<i>Caspialosa saposhnikovii</i>	0.17	0.89	0.16	x 0.79	0.24	1.26	0.30	o 1.52
3.	<i>Clupea harengus</i>	0.15	0.83	0.16	0.98	0.11	x 0.59	0.27	o 1.65
4.	<i>Oncorhynchus keta</i>	0.50	0.80	0.90	o 1.59	0.17	x 0.27	0.49	0.85
5.	<i>Pelecus cultratus</i>	0.67	2.67	1.20	o 4.91	0.66	x 2.50	1.01	4.18
6.	<i>Callionymus lyra</i>	0.18	1.46	0.21	2.04	0.12	x 1.04	0.38	o 3.34
7.	<i>Scorpaena porcus</i>	0.13	1.08	0.06	0.44	0.06	x 0.41	0.16	o 1.41
8.	<i>Plagiognathops microlepis</i>	0.38	x 1.58	0.49	o 1.93	0.46	1.97	0.48	1.93
9.	<i>Culter alburnus</i>	0.24	1.00	0.32	1.29	0.22	x 0.86	0.47	o 2.15
10.	<i>Aspius aspius</i>	0.33	x 1.13	0.53	1.73	0.48	1.67	0.57	o 1.82
11.	<i>Leuciscus waleckii</i>	0.06	x 0.37	0.10	0.66	0.11	0.71	0.15	o 1.01
12.	<i>Leuciscus schmidtii</i>	0.13	0.67	0.07	x 0.38	0.15	o 0.83	0.15	0.69
13.	<i>Coregonus lavaretus baeri</i>	0.33	x 1.02	0.42	1.26	0.34	1.08	0.49	o 1.47
14.	<i>Thymallus arcticus baicalensis</i>	0.21	0.77	0.21	x 0.76	0.33	o 1.25	0.29	1.05
15.	<i>Parabramis pekinensis</i>	0.18	x 0.73	0.23	1.02	0.25	o 1.14	0.22	1.04
16.	<i>Elopichthys bambusa</i>	0.29	0.51	0.31	0.55	0.23	x 0.40	0.72	o 1.46
17.	<i>Siniperca chuatsi</i>	0.31	1.06	0.26	x 0.79	0.42	1.49	0.46	o 1.61
18.	<i>Ophiocephalus argus</i>	0.39	0.75	0.30	x 0.59	0.52	1.04	0.95	o 1.97
19.	<i>Hemibarbus maculatus</i>	0.08	0.41	0.06	x 0.31	0.11	0.62	0.17	o 0.92
20.	<i>Osmerus eperlanus dentex</i>	0.14	x 0.73	0.17	1.13	0.19	1.12	0.27	o 1.66
21.	<i>Lucioperca lucioperca</i>	0.28	0.60	0.28	0.58	0.27	x 0.60	0.48	o 1.12
22.	<i>Brachymystax lenok</i>	0.16	x 0.64	0.27	1.24	0.31	o 1.29	0.18	0.71
23.	<i>Merluccius merluccius</i>	0.64	x 1.04	0.88	1.45	0.66	1.20	1.12	o 1.72
24.	<i>Liocassis ussuriensis</i>	0.31	x 1.29	0.31	1.31	0.36	1.44	1.28	o 5.03
25.	<i>Hemibarbus labeo</i>	0.15	x 0.63	0.21	0.93	0.23	1.02	0.26	o 1.16
26.	<i>Acipenser nudiiventris</i>	1.28	x 1.62	1.65	2.15	1.76	2.33	1.98	o 2.53
27.	<i>Acipenser güldenstaedtii</i>	0.78	0.97	0.76	x 0.99	0.91	1.16	0.93	o 1.19
28.	<i>Coregonus autumnalis migratorius</i>	0.25	0.72	0.22	0.63	0.15	x 0.43	1.26	o 4.32
29.	<i>Coregonus lavaretus widegreni</i>	0.21	x 0.96	0.24	1.08	0.30	1.32	0.32	o 1.40
30.	<i>Lucioperca marina</i>	0.39	x 1.23	0.42	1.31	0.43	1.37	0.43	o 1.38
31.	<i>Thynnus thynnus</i>	0.52	x 0.37	1.59	1.46	0.85	0.66	2.34	o 2.04
32.	<i>Mugil auratus</i>	0.19	0.70	0.19	x 0.69	0.25	0.97	0.67	o 2.78
33.	<i>Trachurus mediterraneus ponticus</i>	0.32	1.02	0.38	1.17	0.29	x 0.97	0.85	o 3.39
34.	<i>Erythroculter erythropterus</i>	0.46	x 1.13	0.52	1.24	0.57	1.45	1.22	o 3.39
35.	<i>Mylopharyngodon piceus</i>	0.25	x 0.54	0.34	0.83	0.56	o 1.32	0.52	1.40
36.	<i>Clupea harengus pallasi</i>	0.21	x 1.08	0.30	1.69	0.23	1.25	0.37	o 1.94
37.	<i>Perca fluviatilis</i>	0.11	x 0.57	0.13	0.65	0.15	0.75	0.21	o 1.10
38.	<i>Pollachius virens</i>	0.35	x 0.55	0.45	0.74	0.42	0.77	0.49	o 0.81
39.	<i>Cyprinus carpio</i>	0.32	x 0.84	0.37	0.99	0.44	1.25	0.49	o 1.27
40.	<i>Leuciscus idus</i>	0.31	x 1.33	0.32	1.29	0.41	o 1.83	0.34	1.42
41.	<i>Abramis brama</i>	0.23	o 0.82	0.20	0.79	0.16	x 0.56	0.22	0.84
42.	<i>Mugil cephalus</i>	0.15	0.50	0.15	x 0.48	0.21	0.76	0.63	o 2.38
43.	<i>Hucho taimen</i>	0.63	0.93	0.57	x 0.80	0.87	o 1.37	0.64	0.90
44.	<i>Ctenopharyngodon idella</i>	0.22	x 0.54	0.26	0.67	0.39	o 1.09	0.36	0.87
45.	<i>Melanogrammus aeglefinus</i>	0.39	0.83	0.45	0.94	0.34	x 0.74	1.16	o 2.76
46.	<i>Huso huso</i>	3.12	x 2.61	3.36	2.75	3.67	3.13	4.39	o 3.47
47.	<i>Coregonus lavaretus baicalensis</i>	0.31	x 0.67	0.32	0.72	0.39	0.88	1.32	o 3.60
48.	<i>Atheresthes evermanni</i>	0.34	x 0.82	0.39	0.95	0.59	o 1.49	0.50	1.28
49.	<i>Reinhardtius hippoglossoides</i>	0.49	x 0.92	0.68	1.43	0.53	0.96	0.76	o 1.60
50.	<i>Acipenser stellatus</i>	1.72	1.87	2.43	o 2.62	1.71	x 1.83	2.37	2.46

Note: Mean differences were calculated as weighted means (considering the range of empirical data) for all versions of a given model, computed for each fish species.

RESULTS

First of all, differences between the empirical data and calculated values for the fish species considered were calculated. For each species, a mean value of the difference resulting from using the 4 models listed in "Materials and methods" was calculated as: (a) absolute value (cm), and (b) relative value expressed as per cent of the mean length obtained for a given range of empirical data. Mathematical growth models were calculated from various data ranges; the results in Table 1 are mean values (for species, such as *Sardinops sagax*, whose growth rates were determined empirically within 6 years, the difference between the empirical and model values is a mean of models calculated for 3, 4 and 6 years; empirical data for *Acipenser stellatus* covered 16 years, and models were calculated for 3–12 and 16 years). The table indicates the model yielding the best (lowest mean difference) and the worst results for each species.

Table 1 shows clearly that application of the binomial produced most frequently the smallest mean differences between the empirical and model values, the highest differences being obtained with the Ford-Walford model. The two remaining models give similar results, worse than those of the binomial and much better than those of the Ford-Walford model.

In most cases, absolute values of mean differences calculated with each of the four models are less than 1 cm. Differences exceeding 1 cm were found when using the binomial and Gompertz equation in 3 out of 50 cases; application of the von Bertalanffy equation produced differences higher than 1 cm in 5 cases, while in 11 cases the Ford-Walford model resulted in such differences. The maximum mean difference (4.39 cm) was obtained for the Ford-Walford model applied to *Huso huso*. Relative values of differences exceeded 2% in 3 cases of using the binomial, in 6 cases for the von Bertalanffy equation, in 4 cases for the Gompertz equation, and in 16 cases of using the Ford-Walford model. The maximum relative difference (5.03%) was obtained with the Ford-Walford model for *Liocassis ussuriensis*. These results demonstrate once again that the binomial fits the empirical data best, while the Ford-Walford model is least suited for the purpose.

Subsequent tables (2–5) present mean differences between the model and empirical data relative to the range of the latter (Z_E), and their detailed statistical characteristics (standard deviation, coefficient of variation, and range). Similarly to Table 1, the differences are presented as (a) absolute values, and (b) per cent value relative to the empirical data. Each table (in its row "Total") shows also mean differences obtained with a given growth model for every species and every empirical range.

Generalised results presented in Tables 2–5 indicate again the binomial as a model yielding the best results (the lowest mean differences), the Ford-Walford model being identified as the one producing the least acceptable results. The variability range of detailed data was clearly wider in the latter case than in the other three models. On the other hand, the overall coefficient of variation was at its lowest in the Ford-Walford model, which is associated with the highest mean difference between the model and empirical data: the difference is almost twice that obtained with the binomial.

Table 2

Mean differences between empirical data and results calculated
with the binomial, arranged in order of increasing range of empirical data Z_E
(a = absolute difference; b = difference expressed
as % of empirical data)

Z_E		\bar{x} (cm)	σ	v	Variability range	n
3	a	0.00	0.00	0.00	0.00	76
	b	0.00	0.00	0.00	0.00	
4	a	0.26	0.41	157.69	0.00 – 3.30	92
	b	0.69	0.81	117.39	0.00 – 6.14	
5	a	0.26	0.25	96.15	0.00 – 1.20	76
	b	0.68	0.55	80.88	0.00 – 2.76	
6	a	0.41	0.44	107.32	0.05 – 3.15	82
	b	1.09	0.96	88.07	0.18 – 4.75	
7	a	0.46	0.45	97.83	0.09 – 2.04	54
	b	0.99	0.65	65.66	0.27 – 3.06	
8	a	0.48	0.50	104.17	0.09 – 2.86	40
	b	1.05	0.61	58.10	0.27 – 2.81	
9	a	0.72	0.75	104.17	0.12 – 2.92	17
	b	1.23	0.79	64.23	0.35 – 2.72	
10	a	0.85	0.81	95.29	0.14 – 2.75	18
	b	1.33	0.73	54.89	0.38 – 2.59	
11	a	0.59	0.58	98.31	0.12 – 2.31	12
	b	1.17	0.73	62.39	0.35 – 2.52	
12	a	0.81	0.78	96.30	0.31 – 2.55	7
	b	1.44	0.74	51.39	0.48 – 2.67	
13	a	0.54	0.19	35.19	0.35 – 0.72	3
	b	0.95	0.16	16.84	0.78 – 1.08	
14	a	7.25	—	—	7.25	1
	b	5.14	—	—	5.14	
15	a	0.61	0.02	3.28	0.60 – 0.63	3
	b	1.31	0.13	9.92	1.17 – 1.41	
16	a	3.24	—	—	3.24	1
	b	2.97	—	—	2.97	
Total	a	0.36	0.58	161.11	0.00 – 7.25	482
	b	0.80	0.82	102.50	0.00 – 6.14	

Table 3

Mean differences between empirical data and results calculated
with the von Bertalanffy equation, arranged in order of increasing
range of empirical data

Z_E		\bar{x} (cm)	σ	v	Variability range	n
3	a	0.26	0.48	184.62	0.00 – 3.33	76
	b	0.79	1.31	165.82	0.00 – 8.52	
4	a	0.30	0.41	136.67	0.02 – 2.50	90
	b	0.91	1.02	112.09	0.08 – 6.14	
5	a	0.36	0.39	108.33	0.00 – 2.80	77
	b	0.94	0.82	87.23	0.00 – 4.54	
6	a	0.40	0.42	105.00	0.05 – 2.88	83
	b	1.05	0.93	88.57	0.18 – 6.60	
7	a	0.56	0.58	103.57	0.11 – 2.87	54
	b	1.21	0.91	75.21	0.35 – 4.94	
8	a	0.50	0.53	106.00	0.09 – 2.82	39
	b	1.09	0.67	61.47	0.33 – 2.85	
9	a	0.78	1.03	132.05	0.17 – 3.86	17
	b	1.23	0.95	77.24	0.42 – 3.59	
10	a	1.01	1.16	114.85	0.21 – 3.91	19
	b	1.51	1.13	74.83	0.35 – 4.43	
11	a	0.85	1.27	149.41	0.20 – 4.81	12
	b	1.51	1.34	88.74	0.41 – 5.23	
12	a	1.33	2.04	153.38	0.30 – 5.92	7
	b	1.94	1.92	98.97	0.56 – 6.20	
13	a	0.83	0.26	31.33	0.55 – 1.07	3
	b	1.51	0.48	31.79	1.23 – 2.06	
14	a	7.79	—	—	7.79	1
	b	5.53	—	—	5.53	
15	a	0.62	0.12	19.35	0.49 – 0.73	3
	b	1.33	0.21	15.79	1.09 – 1.47	
16	a	3.60	—	—	3.60	1
	b	3.30	—	—	3.30	
Total	a	0.47	0.73	155.32	0.00 – 7.79	482
	b	1.05	1.05	100.00	0.00 – 8.52	

Table 4

Mean differences between empirical data and results calculated
with the Gompertz equation, arranged in order of increasing
range of empirical data

Z_E		\bar{x} (cm)	σ	v	Variability range	n
3	a	0.00	0.00	0.00	0.00	71
	b	0.00	0.00	0.00	0.00	
4	a	0.34	0.35	102.94	0.00 – 1.95	85
	b	1.24	1.29	104.03	0.00 – 8.56	
5	a	0.24	0.23	95.83	0.00 – 1.10	74
	b	0.68	0.53	77.94	0.00 – 2.27	
6	a	0.44	0.41	93.18	0.02 – 2.07	83
	b	1.19	1.04	87.39	0.07 – 6.67	
7	a	0.53	0.50	94.34	0.07 – 2.50	55
	b	1.18	0.86	72.88	0.25 – 3.75	
8	a	0.53	0.57	107.55	0.09 – 3.34	40
	b	1.20	0.81	67.50	0.26 – 3.28	
9	a	0.80	0.97	121.25	0.17 – 3.98	18
	b	1.40	1.04	74.29	0.27 – 3.62	
10	a	1.00	0.94	94.00	0.19 – 3.27	19
	b	1.58	0.91	57.59	0.39 – 3.59	
11	a	0.90	0.85	94.44	0.22 – 3.34	12
	b	1.79	1.04	58.10	0.49 – 3.64	
12	a	0.92	0.80	86.96	0.44 – 2.71	7
	b	1.72	0.86	50.00	0.65 – 2.84	
13	a	1.19	0.85	71.43	0.50 – 2.14	3
	b	2.00	1.01	50.50	0.96 – 2.98	
14	a	8.18	—	—	8.18	1
	b	5.81	—	—	5.81	
15	a	1.43	0.49	34.27	1.12 – 1.99	3
	b	3.09	1.18	38.19	2.29 – 4.44	
16	a	3.86	—	—	3.86	1
	b	3.54	—	—	3.54	
Total	a	0.43	0.66	153.49	0.00 – 8.18	472
	b	1.02	1.06	103.92	0.00 – 8.56	

Table 5

Mean differences between empirical data and results calculated
with the Ford-Walford model, arranged in order of increasing range
of empirical data

Z_E		\bar{x} (cm)	σ	v	Variability range	n
3	a	0.35	0.52	148.57	0.00 – 3.77	77
	b	1.19	1.31	110.08	0.00 – 8.23	
4	a	0.39	0.40	102.56	0.00 – 2.62	92
	b	1.41	1.40	99.29	0.00 – 6.23	
5	a	0.54	0.53	98.15	0.08 – 3.20	77
	b	1.55	1.46	94.19	0.23 – 6.68	
6	a	0.60	0.54	90.00	0.08 – 3.57	83
	b	1.77	1.49	84.18	0.30 – 6.83	
7	a	0.81	0.73	90.12	0.16 – 3.74	53
	b	2.01	1.64	81.59	0.30 – 7.04	
8	a	0.76	0.66	86.84	0.12 – 3.21	39
	b	1.81	1.36	75.14	0.33 – 6.38	
9	a	0.94	0.87	92.55	0.26 – 3.43	17
	b	1.73	1.25	72.25	0.60 – 4.78	
10	a	1.59	1.17	73.58	0.37 – 3.54	19
	b	2.86	1.96	68.53	0.38 – 7.39	
11	a	1.21	0.84	69.42	0.49 – 3.21	12
	b	2.64	1.53	61.74	0.82 – 5.78	
12	a	1.33	1.18	88.72	0.32 – 3.87	7
	b	2.38	1.39	58.40	0.91 – 4.45	
13	a	1.09	0.28	25.69	0.86 – 1.40	3
	b	2.01	0.64	31.84	1.41 – 2.69	
14	a	13.14	—	—	13.14	1
	b	9.33	—	—	9.33	
15	a	1.24	0.51	41.13	0.94 – 1.83	3
	b	2.70	1.24	45.93	1.87 – 4.13	
61	a	6.31	—	—	6.31	1
	b	5.79	—	—	5.79	
Total	a	0.67	0.92	137.31	0.00 – 13.14	484
	b	1.71	1.55	90.64	0.00 – 9.33	

Table 6

Correlation coefficients and parameters of relationship between differences studied and range of empirical data ($|l_e - l_m| = a_0 + a_1 Z_E$)

Model		r	a_0	a_1
A	a	0.7695	0.0668	0.0504
	b	0.7506	0.3211	0.0784
B	a	0.7296	0.1142	0.0624
	a	0.8087	0.6470	0.0704
C	a	0.9747	-0.2374	0.1084
	b	0.9059	-0.1246	0.1802
D	a	0.8531	0.1324	0.0899
	b	0.8152	1.0069	0.1163

Note l_e = empirical length; l_m = length calculated with a growth model; A,B,C,D,a,b as in Table 7.

Table 7

Significance of differences found for mean results obtained with various growth models (data from "Total" rows of Tables 2-5) as tested with Student's t test at 0.95 confidence level

Difference		Degrees of freedom	t	t_M	Significance of differences
A - B	a	962	2.588	1.960	+
	b		4.116	1.960	+
A - C	a	952	1.739	1.960	-
	b		3.586	1.960	+
A - D	a	964	6.255	1.960	+
	b		11.387	1.960	+
B - C	a	952	0.886	1.960	-
	b		0.439	1.960	-
B - D	a	964	3.738	1.960	+
	b		7.737	1.960	+
C - D	a	954	4.620	1.960	+
	b		8.006	1.960	+

Note: A = binomial; B = von Bertalanffy equation; C = Gompertz equation; D = Ford-Walford model
 + = difference statistically significant; - = difference statistically non-significant; a,b = as in Table 1.

Mean differences between the empirical and model data, typical of each empirical range, are relatively small, which shows that each model renders a relatively good description of fish growth. When using the binomial, differences exceeding (quite substantially, to be frank) 1 cm were found in 2 ranges (14 and 16 years) only. It should be, however, mentioned that the two ranges were represented by a single fish species each, *Huso huso* and *Acipenser stellatus*, respectively, which may cast some doubt on the reliability of the results. With the von Bertalanffy equation, differences exceeding 1 cm were found in 4 ranges. The Gompertz equation and Ford-Walford model produced such differences in 5 and 7 cases, respectively (Tables 2–5).

The analysis of trends in changes of mean differences and their measures of dispersion reveals an increase in differences and standard deviations with increasing range of empirical data. However, changes in mean differences are much more pronounced than changes in standard deviations, which results in the relative dispersion index, i.e. the coefficient of variation, being subject to a reverse trend: its values decrease with increasing empirical ranges. Such pattern was found for all the four models used in both the absolute and relative values.

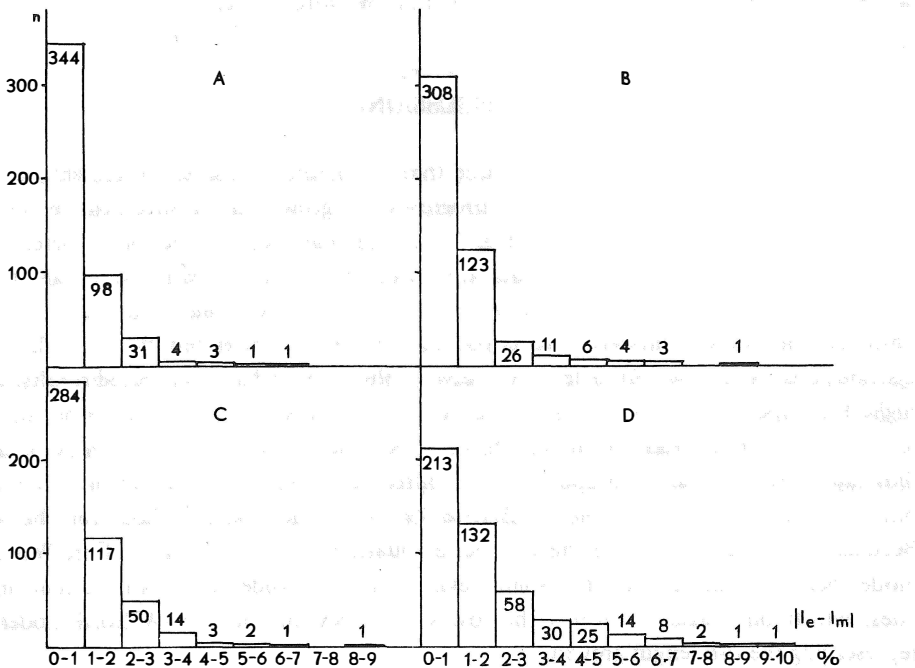


Fig. 2. Distribution of numbers of relative (%) mean differences between empirical and model data, calculated for the entire set of data examined

(A, B, C and D as in Fig. 1)

Table 6 presents parameters of linear relationships between the differences analysed and ranges of empirical data. Correlation coefficients, given in the table, are high (and positive in all cases), evidencing a significant association between the data. The highest correlation coefficients were found when using the Gompertz equation, the lowest coefficients being obtained with the binomial and von Bertalanffy equation. Similar was the pattern of the direction coefficient (a_1) indicating the magnitude of changes in the differences studied, accompanying a 1-yr increase in the empirical data range.

To compare the differences obtained with the growth models analysed, significance of differences between mean values ("Total" in Tables 2–5) was tested with Student's *t* test at 0.95 confidence level (Table 7). Both the absolute (a) and per cent (b) mean values were tested. Nonsignificant differences were found in only 3 out of 12 cases tested, the non-significant differences being the absolute ones between the binomial and Gompertz equation and both types of differences between the von Bertalanffy and Gompertz equations. The results show that it is not without meaning which growth model is being employed in a study; in order to arrive at the best possible representation of empirical data, a case on hand should be tested with several growth models. The results discussed point out that the binomial offers the greatest potential for obtaining optimal results, while the smallest chance is presented by the Ford-Walford model.

DISCUSSION

The results obtained allow to conclude that the mathematical length growth models analysed represent fairly accurately the progression of growth in fish species under study. Data contained in Tables 1–5 and Fig. 2 indicate that most of the mean differences between the empirical and model data are lower than 1 cm or 2% (relative value of a difference). On the other hand, there are clear differences in the accuracy of results obtained with various models. This is particularly clearly illustrated by Fig. 2 showing distributions of relative (%) differences between the empirical and computed results. The highest number of small relative differences (0–2%) was found for the binomial, the lowest for the Ford-Walford model. Differing accuracy of various models may be also illustrated by comparing proportions of differences exceeding 2%. When using the binomial, such differences amounted to 8.3% of all the results, 10.6% for the von Bertalanffy equation; 15% for the Gompertz equation; and 27.7% for the Ford-Walford model being obtained. The latter value deviates rather considerably from the remaining ones, which once again confirms the lowest accuracy of the Ford-Walford model in representing the fish length growth.

It should be borne in mind that, in spite of using four models to mathematically characterise growth of the same 50 fish species, the number of definite models is not equal in each case (see "Materials and methods"). The differences stem from differing theoretical assumptions and computation methods of each model, which – when

confronted with certain species and some ranges of empirical data – results in the fact that some ranges lend themselves to 3 mathematical growth models only.

The next problem which requires a detailed discussion is whether Student's *t* test is an appropriate one to test for significance of differences between mean results obtained for the models studied. As it is well known, Student's *t* test requires a normal, or close to normal, distribution of data serving to calculate the means compared. However, the distributions presented in Fig. 2 clearly deviate from the normal distribution. It should be remembered that a well-marked preponderance of small (0–1%) differences, evident in all the four models, results most probably from the fact that the largest amount of models calculated was based on small empirical data sets (see “*n*” in Tables 2–5) and narrow ranges of empirical data. On the other hand, results in Table 6 point to a clear-cut relationship between the differences studied and the range of empirical data, the relationship being direct (the larger the data range, the higher the difference) and relatively well-defined, as indicated by the high positive correlation coefficients. Thus, considering the small, medium, and large data ranges and their effect on the magnitude of differences, one can assume that the distribution would be presumably normal, should the number of models calculated for various ranges of empirical data be approximately equal.

A further comment on mean results obtained from using different models concerns effects of the method for equation parameter calculation on the results obtained. The two models yielding the best results (the binomial and the Gompertz equation) allow to obtain, for the smallest data range used (3 years), calculated results always identical with the empirical data (as seen in Tables 2 and 4), similar results being frequently (but not always) arrived at in the two subsequent data ranges (4 and 5 years). On the other hand, when using the von Bertalanffy equation and Ford-Walford model, it was only sporadically that calculated results were identical with the empirical data (also in the case of the smallest empirical data ranges).

Finally, one should consider the reliability of the results reported in the present work. It may be assumed with a high degree of probability that to use 50 fish species differing in their growth characteristics and to calculate almost five hundred versions of each model analysed render the results obtained reliable, both in terms of the accuracy of mathematical representation of fish length growth and in relation to the usually significant differences appearing when various models are applied.

Conclusions

- 1) Mathematical description of fish growth with the binomial, von Bertalanffy equation, Gompertz equation and Ford-Walford model allows to obtain fairly accurate results, differing in most cases by less than 1 cm (2% of empirical length) from the empirical data.
- 2) The best results were obtained with the binomial, while the Ford-Walford model

- yielded the least reliable results. The two remaining models produced close results, slightly worse than those obtained with the binomial, but clearly superior to those given by the Ford-Walford model.
- 3) The analysed differences between empirical data and calculated (model) results were observed to be markedly and significantly dependent on the empirical range used to calculate growth models. The relationships were direct (high positive correlation coefficients) in every model analysed.
 - 4) Differences between mean results obtained with various growth models are statistically significant in most cases.

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PORÓWNANIE DOKŁADNOŚCI MATEMATYCZNEJ CHARAKTERYSTYKI WZROSTU RÓŻNYCH GATUNKÓW RYB DOKONYWANEJ PRZY ZASTOSOWANIU WIELOMIANU 2-GO STOPNIA, RÓWNANIA VON BERTALANFFY'EGO, RÓWNANIA GOMPERTZA I MODELU FORDA – WALFORDA

STRESZCZENIE

W pracy przedstawiono wyniki porównania empirycznego przebiegu wzrostu długości różnych gatunków ryb z jego matematyczną charakterystyką, przeprowadzoną przy zastosowaniu 4 najczęściej używanych modeli: wielomianu 2-go stopnia, równania von Bertalanffy'ego, równania Gomperta i

modelu Forda-Walforda. Ogółem obliczono 1920 modeli (odpowiednio 482, 482 i 484) dla 50 gatunków ryb (dla każdego gatunku obliczano od 5 do 19 wersji danego modelu, z różnych zakresów danych empirycznych). Otrzymane z porównania różnice przedstawiono jako wartości bezwzględne (w cm) oraz w procentach w stosunku do długości empirycznych. Wyniki zestawiono w dwu wersjach: dla badanych gatunków ryb (tabela 1) oraz dla różnych zakresów danych empirycznych (tabele 2–5).

Uzyskane wyniki wskazują, że znaczna większość stwierdzonych różnic nie przekracza 1 cm lub 2% (w przypadku różnic względnych). Najdokładniejsze matematyczne odwzorowanie wzrostu długości badanych gatunków uzyskano stosując wielomian 2-go stopnia, najmniej dokładne – przy użyciu modelu Forda-Walforda. Różnice pomiędzy ogólnymi średnimi wartościami, określonymi przy zastosowaniu różnych modeli wzrostu były w większości przypadków statystycznie istotne.

Zanotowano wysokie dodatnie wartości współczynników korelacji prostoliniowej pomiędzy wielkością różnic wyników empirycznych i modelowych a zakresem danych empirycznych – co świadczy o tym, że badane zależności miały charakter zależności prostych (im większy zakres danych empirycznych, tym większa średnia różnica pomiędzy wynikami empirycznymi a modelowymi).

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