the name of the species or taxonomic code in addition to the results of the analysis performed on the data.

Using an off or on-line sort to arrange the taxonomic codes in numerical order, automatically places the specimens in a semi-phylogenetic order.

The implementation of this code in the handling of the various data has eliminated many time-consuming steps in progressing from raw data to the final comprehensive interpretation of the processed results. Future applications of such codes will be valuable in storage and retrieval of literature relating to the respective coded specimen.

LITERATURE CITED

Rivas, Luis Rene. 1964. A Proposed Code System for Storage and Retrieval of Information in Systematic Zoology. Systematic Zoology; Vol. 14, No. 2, June 1965. pp. 131-132.

FAO Fisheries Biology Branch. 1965. Volume Taxonomic Index 8-01001 to 8-12523 and 8-001me to 8-143me. Current Bibliography for the Aquatic Sciences and Fisheries. Vol. 8, Sec. 2; parts 8 to 12. Taylor & Francis Ltd., London, E.C.4. 8:T1 to T30.

AN ANALYSIS OF THE GROWTH OF PACIFIC HERRING *(CLUPEA PALLASII)*, LAKE STURGEON *(ACIPENSER FULVESCENS)* AND WHITE STURGEON *(ACIPENSER TRANSMONTANOUS)*

BY THE PARKER-LARKIN AND VON BERTALANFFY METHODS[1]

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ABSTRACT

The growth of the Pacific herring (*Clupea pallasii*), lake sturgeon (*Acipenser fulvescens*) and white sturgeon (*Acipenser transmontanous*) is analyzed by the application of Parker-Larkin and Von Bertalanffy equations. The physiological significance of the parameters of the two equations is discussed.

ACKNOWLEDGMENTS

The author sincerely expresses his gratitude to Dr. P. A. Larkin for suggestions and criticism during the investigation. The author also acknowledges Dr. F. H. C. Taylor of the Fisheries Research Board of Canada, Nanaimo, and Mr. L. A. Sunde, of the Department of Mines and Natural Resources, Manitoba, for providing data on Pacific Herring and Lake Sturgeon, respectively.

INTRODUCTION

Of the parameters in the dynamics of fish populations, the measure of the rate of growth is of primary importance since growth is a basic determinant of productivity. In Fishery Science the growth equation of Von Bertalanffy is most commonly used (Beverton and Holt, 1957). The equation assumes asymptotic growth, and the difference between size and an "ultimate attainable size" determines growth rate. A linear

[1] Based on a thesis submitted to the University of British Columbia in partial fulfillment of the requirements for the degree of Master of Science.

function relating length at age t to length at age t+1 is $l_{t+1} = l_{\infty}(1-e^{-K}) + l_t e^{-K}$.

Some fish, however, may not be growing to and never attain an ultimate size. Many species may change their ultimate size to which they are tending in adapting to a different ecological niche (Larkin, Terpenning, and Parker, 1957). Size is also related to physiological changes during the life of a fish. Fish growth may thus be considered as a series of cycles or growth stanzas, in which each of the parameters of the growth processes are reasonably constant. Parker and Larkin (1959) proposed the parabolic function $dw/_{dt} = kw^x$. Essentially the use of this equation implied that growth can be treated like any physiological function. For instance the relationship between the respiration rate and the weight of the organism is expressed by the following differential equation.

$$\frac{\Delta o}{\Delta t} = kw^x$$

where Δo = oxygen uptake
w = weight

This equation is usually expressed algebraically as:

$$\log\left[\frac{\Delta o}{\Delta t}\right] = \log k + x \log w$$

Treating the growth equation in the same way would yield:

$$\log\left[\frac{\Delta w}{\Delta t}\right] = \log k + x \log w$$

The question arises whether growth rate is related to initial weight, average weight or final weight during the period t. This can be overcome by dealing in instantaneous rates. Integration of the expression $dw/_{dt} = kw^x$ yields.

$$w_t^{(1-x)} = kt(1-x) + w_o^{(1-x)}.$$

Denoting the relationship between weight and length as $w = ql^y$, it can be demonstrated that growth in length can be expressed as:

$$l^z_{t+1} = \infty + l^z_t$$

where $z = y(1-x)$
$\infty = \dfrac{k(1-x)}{q^{(1-x)}}$

The constants ∞ and z are to be derived from the empirical data (for details see Parker and Larkin, 1959; Larkin and Ayyangar, 1961).

The Parker-Larkin equation takes into account the fact that size is an important criterion of physiological opportunity for growth. By the selection of a proper power of length, the growth increments can be made independent of length and a plot of l^z_{t+1} on l^z_t will parallel the 45-degree diagonal.

In this study the growth of herring (*Clupea pallasii*) lake sturgeon (*Acipenser fulvescens*), and white sturgeon (*Acipenser transmontanous*) were described by the Parker-Larkin and Bertalanffy equations. Conclusions were reached concerning the significance of the constants.

MATERIALS AND METHODS

The backcalculated fork lengths of herring from the Bella Bella area (British Columbia, Canada) from scale readings and of the lake sturgeon from the Nelson River (Manitoba, Canada) from pectoral fin rays and the total lengths of white sturgeon from San Pablo Bay, California, U. S. A. (Pycha, 1956) were used in the study. In the Parker-Larkin equation, an approximate solution for the optimum value of the exponent z was obtained from the quadratic function $S_R = a+bz+cz^2$. Three values of the relative standard deviation $S_R = \left[\frac{S^2}{\alpha^2}\right]^{1/2}$ of the constant α and their associated z values on simultaneous solution yielded the best z value (the value of z giving the minimum standard deviation), $z = -\frac{b}{2c}$. In the present investigation the computer program ALWAC III E was used to compute optimum z. The program is on file at the Computing Center, University of British Columbia.

The constants l_α and k of the Bertalanffy equation can be estimated by plotting l_{t+1} on l_t (Walford plot). Alternatively, plotting $\log_e (l_\alpha - l_t)$ against t gives a line of slope K and the intercept $\log_e l_\alpha + Kt_0$. Trial values of l_α were chosen to provide a best fit for the equation.

Raw data pertaining to the species studied and the input and output tapes of the computer work are stored in the Institute of Fisheries, University of British Columbia.

RESULTS

Herring (*Clupea pallasii*)

The herring were five years of age when caught in 1955. Walford plots of l_{t+1} on l_t for the female and male herring are shown in Figures 1 and 2, respectively. For fitting the Parker-Larkin equation, the values of z for the sexes were estimated and the corresponding equations were: for the females, $l_{t+1}^{3.5} = 8856.22 + l_t^{3.5}$; for the males, $l_{t+1}^{3.1} = 2021.48 + l_t^{3.1}$. Plots of l_{t+1}^z on l_t^z were parallel to the 45-degree diagonal (Figures 3 and 4), so that the annual increments were independent of length.

Since points on the Walford plot yielded a line of best fit that intersected the 45-degree diagonal, the data were analyzed by the Bertalanffy method. For all age groups the asymptotic lengths for females and males were 22.0 and 20.5 centimeters, respectively. Several of the herring examined for scale-length relationship, however, exceeded the theoretical maximum lengths for the sexes. Since the points for ages one and two did not line up with the points for the rest of the ages, only the data for ages three to five were analyzed. The growth rates were depicted by the following formulae: for the females, $l_{t+1} = 25.4\ (0.190) + 0.810\ l_t$; for the males, $l_{t+1} = 27.6\ (0.122) + 0.878\ l_t$.

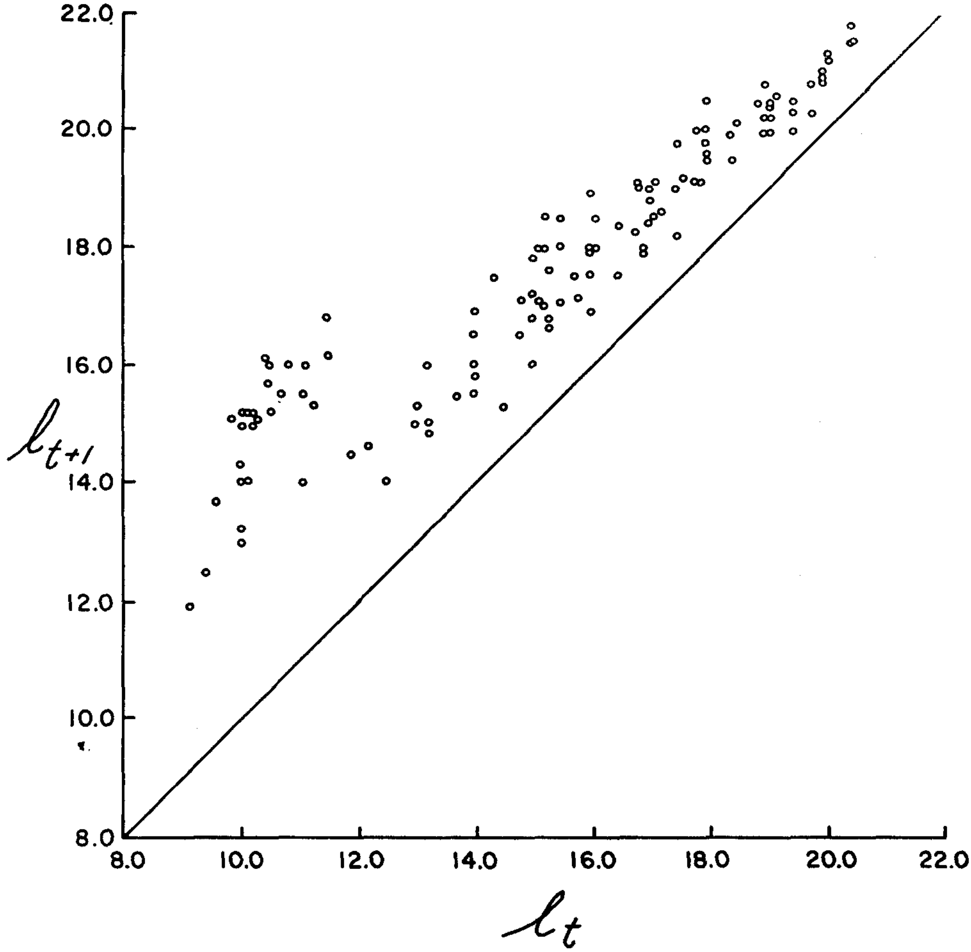

Figure 1 — Plot of 1_{t+1} and 1_t for female herring from the Bella Bella region (British Columbia, Canada).

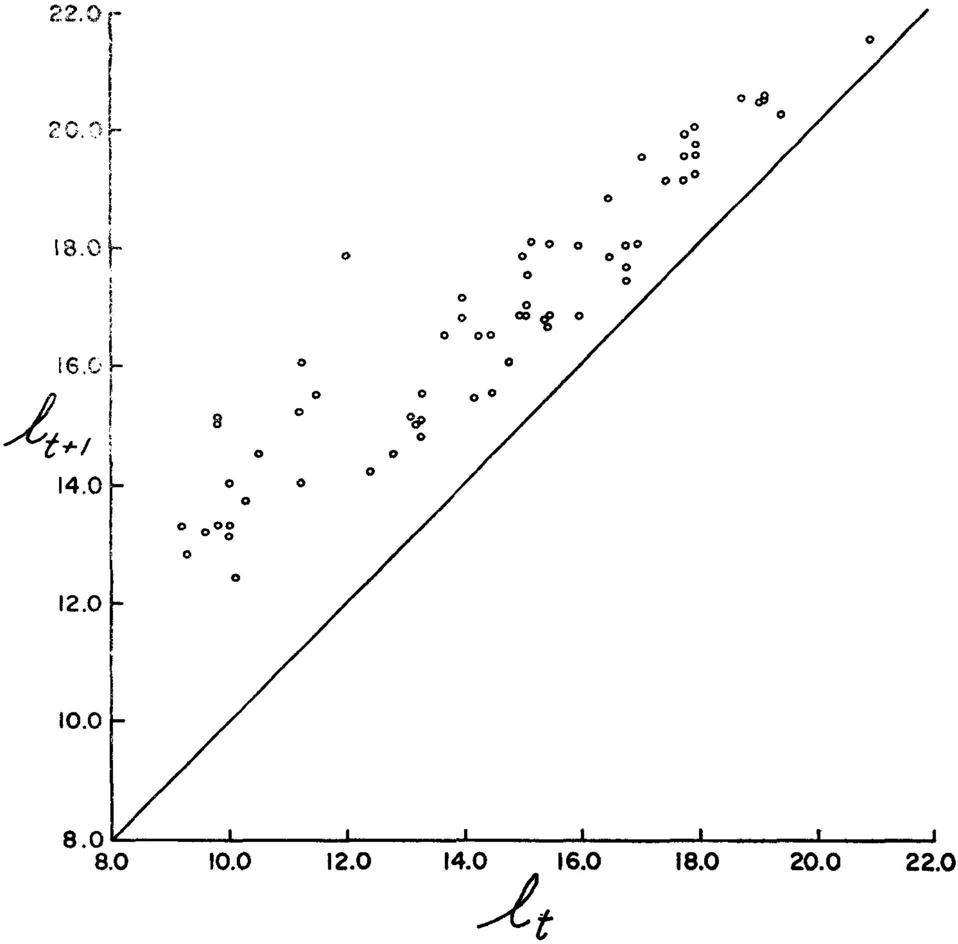

Figure 2 — Plot of 1_{t+1} on 1_t for male herring from the Bella Bella region.

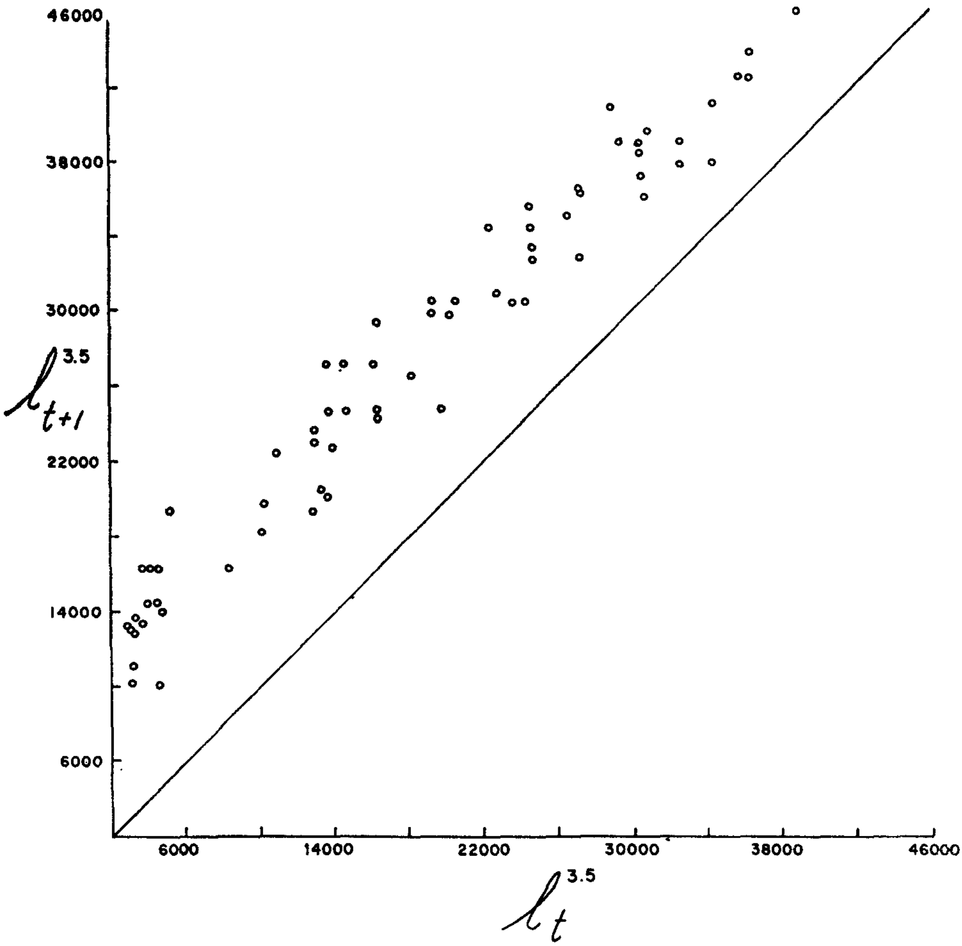

Figure 3 — Plot of $l_{t+1}^{3.5}$ on $l_t^{3.5}$ for female herring from the Bella Bella region.

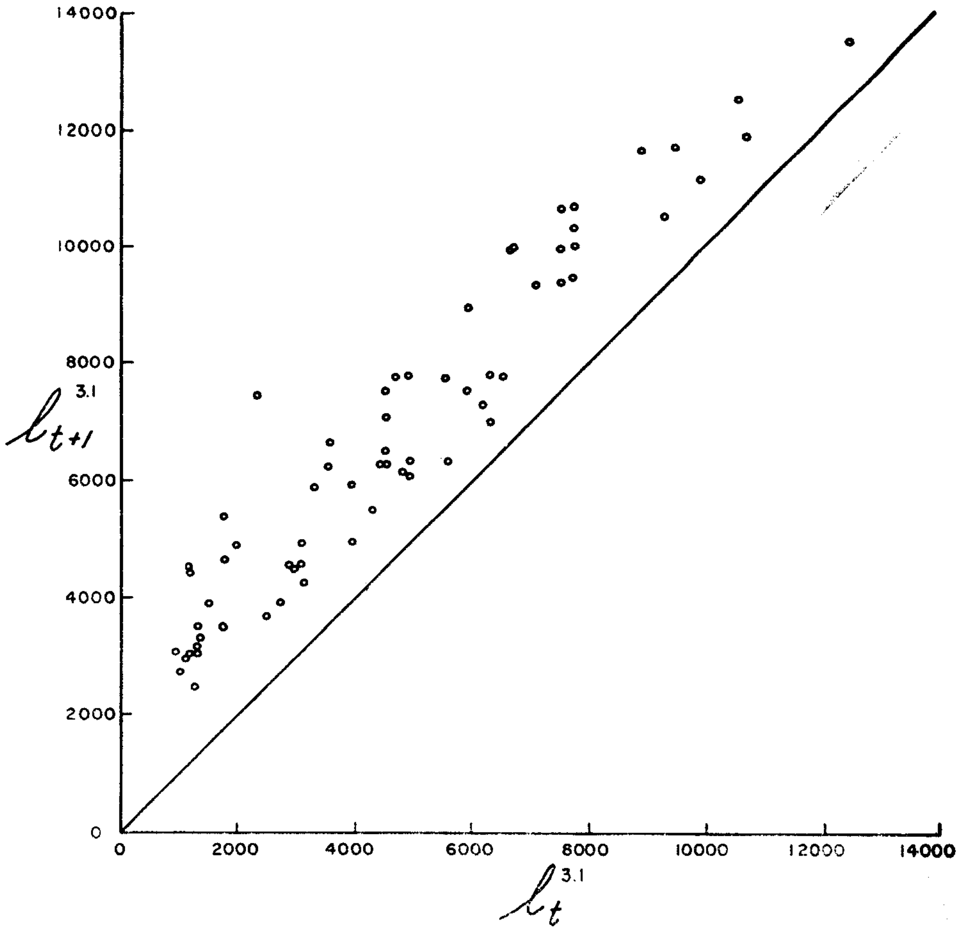

Figure 4 — Plot of $l^{3.1}_{t+1}$ on $l^{3.1}_{t}$ for male herring from Bella Bella region.

Observed and predicted lengths of herring are given in Tables 1 and 2. Both growth equations predict lengths equally well. Lengths in the

TABLE 1—BACK-CALCULATED AND ESTIMATED FORK LENGTHS IN CENTIMETERS FOR FEMALE HERRING

Age in years	Back Calculated lengths	Estimated lengths Parker-Larkin	Bertalanffy
1	10.71	10.80	
2	15.29	14.98	
3	17.77	17.37	17.77
4	19.41	19.15	19.26
5	20.56	20.58	20.41

TABLE 2—BACK-CALCULATED AND ESTIMATED FORK LENGTHS IN CENTIMETERS FOR MALE HERRING

Age in years	Back Calculated lengths	Estimated lengths Parker-Larkin	Bertalanffy
1	10.32	10.32	
2	14.24	15.09	
3	16.48	16.06	16.48
4	18.04	17.77	17.84
5	19.05	19.19	19.03

last three years of age of five-year-old herring were computed by the application of the Bertalanffy equation, whereas lengths at earlier ages were predicted by the Parker-Larkin method.

Lake sturgeon (*Acipenser fulvescens*)

The oldest fish was 55 years old. Only the length measurements for the first 21 years were used and the sexes were treated separately. The Walford plots for females and males are shown in Figures 5 and 6, respectively. The value of z for both sexes was 2.64. The trans-

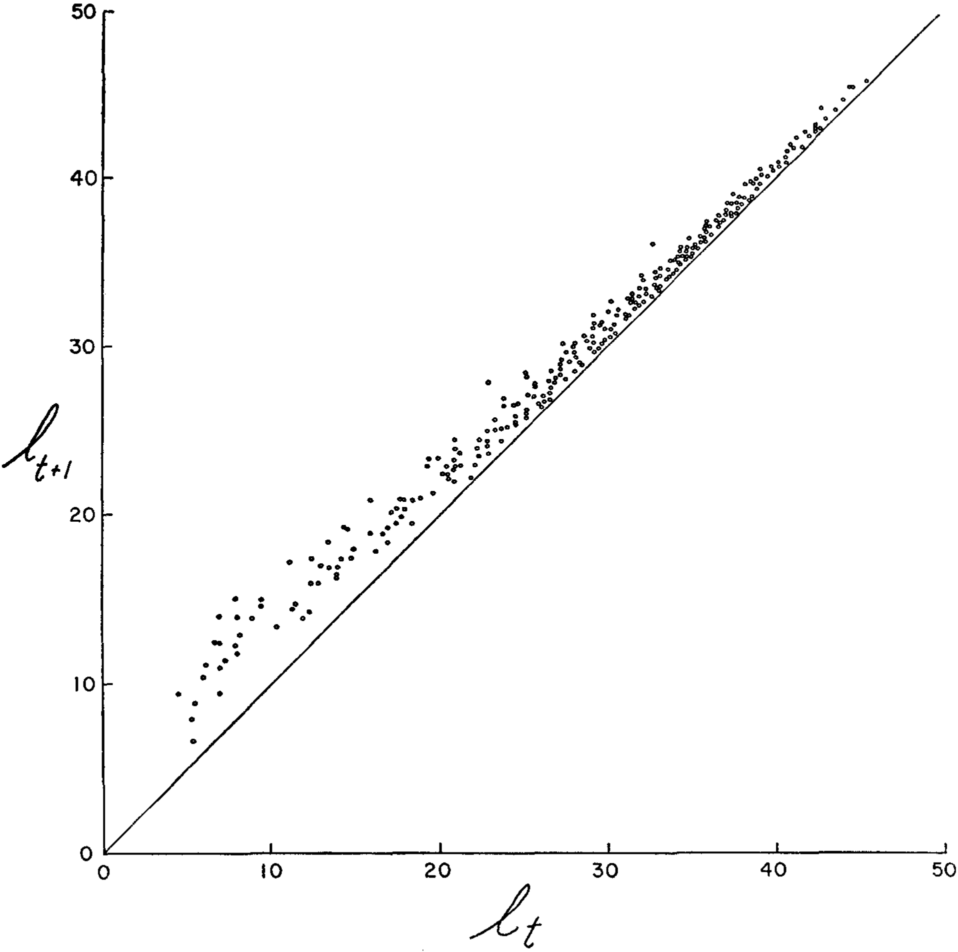

Figure 5 — Plot of 1_{t+1} on 1_t for female lake sturgeon from Manitoba.

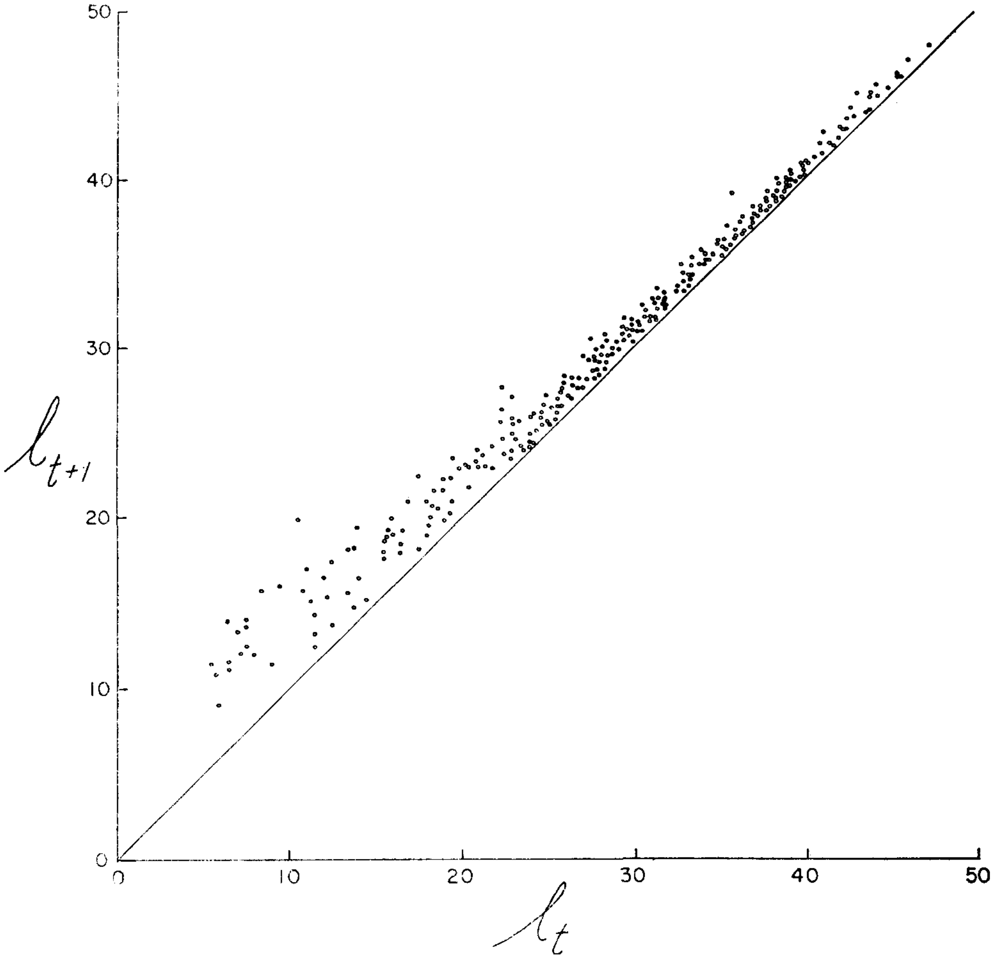

Figure 6 — Plot of l_{t+1} on l_t for male lake sturgeon from Manitoba.

formed plots of $l_{t+1}^{2.64}$ on $l_t^{2.64}$ for females and males are shown in Figures 7 and 8, respectively. The growth rates were expressed as follows: for the females, $l^{2.64} = 820.11 + l_t^{2.64}$; for the males, $l_{t+1}^{2.64} = 794.11 + l_t^{2.64}$. The differences in the growth rates ($\overline{\alpha}$ values) between the sexes were not significantly different ($F_{1.38} = 0.15$). Thus the female and male lake sturgeon grow at the same rate and adapt similarly to ecological opportunity for growth.

When data were fitted by the Bertalanffy method, these formulae were obtained: for the females, $l_{t+1} = 76\ (0.023) + 0.977\ l_t$; for the males, $l_{t+1} = 84\ (0.020) + 0.980\ l_t$.

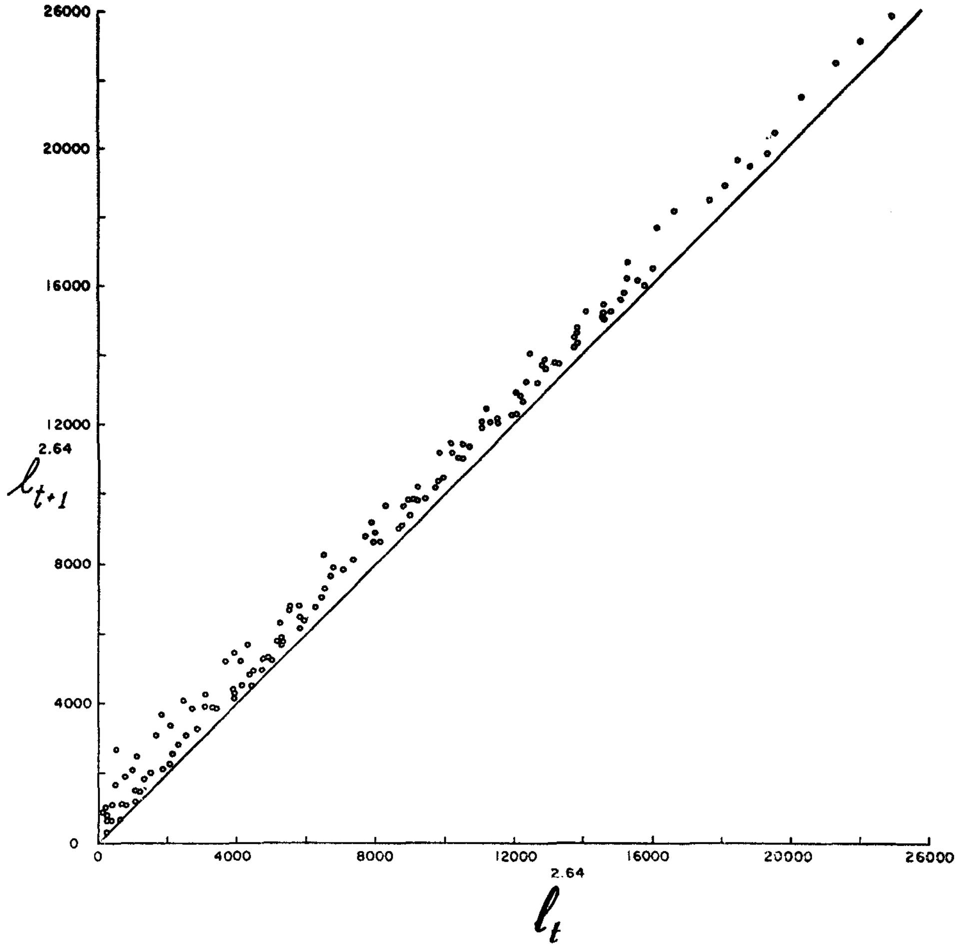

Figure 7 — Plot of $l_{t+1}^{2.64}$ on $l_t^{2.64}$ for female lake sturgeon from Manitoba.

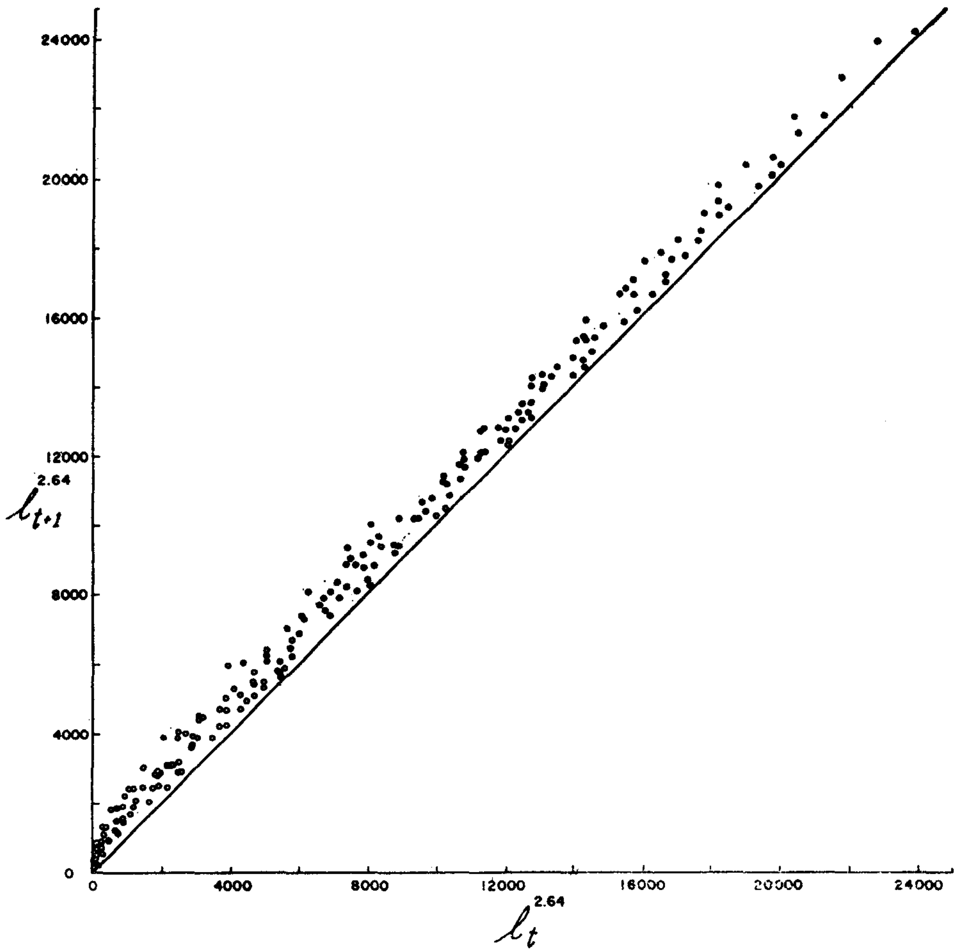

Figure 8 — Plot of $l_{t+1}^{2.64}$ on $l_t^{2.64}$ for male lake sturgeon from Manitoba.

Observed and predicted lengths at various ages by the Parker-Larkin and Bertalanffy methods for females and males are shown in Tables 3 and 4, respectively. Observed and predicted lengths agree well by the Parker-Larkin method, whereas lengths were underestimated by the Bertalanffy method.

TABLE 3—BACK-CALCULATED AND ESTIMATED FORK LENGTHS IN INCHES FOR FEMALE LAKE STURGEON

Age in years	Back Calculated lengths	Estimated lengths Parker-Larkin	Bertalanffy
1	7.53	8.53	
2	13.40	13.90	
3	17.21	17.35	
4	20.01	19.91	
5	22.34	22.02	22.34
6	24.29	23.85	23.58
7	26.23	25.46	24.79
8	28.01	26.93	25.98
9	29.02	28.28	27.13
10	30.20	29.52	28.26
11	31.26	30.69	29.37
12	32.20	31.79	30.45
13	33.06	32.83	31.51
14	33.98	33.82	32.54
15	34.86	34.77	33.55
16	35.72	35.67	34.54
17	36.53	36.53	35.50
18	37.33	37.37	36.44
19	38.01	38.17	37.36
20	38.63	38.95	38.25
21	39.33	39.70	39.12

TABLE 4—BACK-CALCULATED AND ESTIMATED FORK LENGTHS IN INCHES FOR MALE LAKE STURGEON

Age in years	Back Calculated lengths	Estimated lengths Parker-Larkin	Bertalanffy
1	6.70	6.85	
2	11.16	13.45	
3	15.29	16.92	
4	18.49	19.49	
5	21.21	21.64	21.21
6	23.43	23.43	22.47
7	25.19	25.04	23.70
8	26.70	26.50	24.91
9	28.29	27.84	26.09
10	29.89	29.08	27.24
11	31.21	30.24	28.38
12	32.41	31.33	29.49
13	33.94	32.36	30.58
14	34.29	33.34	31.65
15	35.13	34.27	32.69
16	35.89	35.17	33.72
17	36.61	36.03	34.73
18	37.32	36.85	35.72
19	37.88	37.66	36.69
20	38.39	38.41	37.64
21	38.85	39.17	38.57

White sturgeon (*Acipenser transmontanous*)

Mean total lengths for each age group (Pycha, 1956), were used to express growth. The plot of 1_{t+1} on 1_t is shown in Figure 9. It is

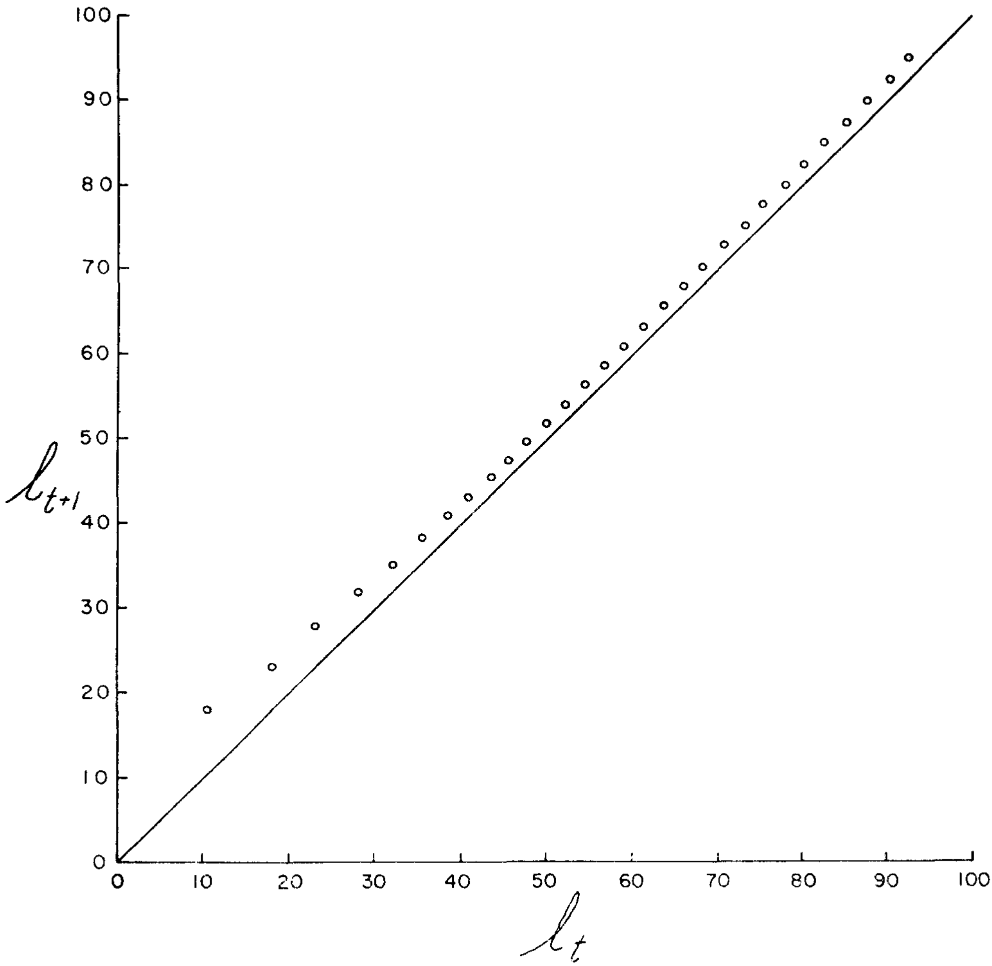

Figure 9 — Plot of 1_{t+1} on 1_t for white sturgeon from California.

evident that there are large annual size increments in the first six years and relatively constant increments thereafter, i.e., the line of best fit runs almost parallel to the 45-degree diagonal. A value of 1.45 for z was estimated from the lengths at ages 0 to 30 years, but the lengths were underestimated for the early ages (less than six years) and overestimated for the older ages (more than six years). Since the line of best fit on the Walford plot ran parallel to the 45-degree line from a length of 38.5 inches (corresponding to six years of age), the data were separated at this size and the two segments were analyzed individually. The Parker-Larkin equations for depicting lengths for the first six years and for the years thereafter were respectively,

$l^{1.89}_{t+1} = 151.15 + l^{1.89}_{t}$ and $l^{0.9}_{t+1} = 1.40 + l^{0.9}_{t}$. Transformed plots using appropriate z values are shown in Figures 10 and 11. The observed and estimated lengths agreed excellently (Table 5). The analysis confirmed separation of the data at 38.5 inches, beyond which size the white sturgeon follows a different growth pattern.

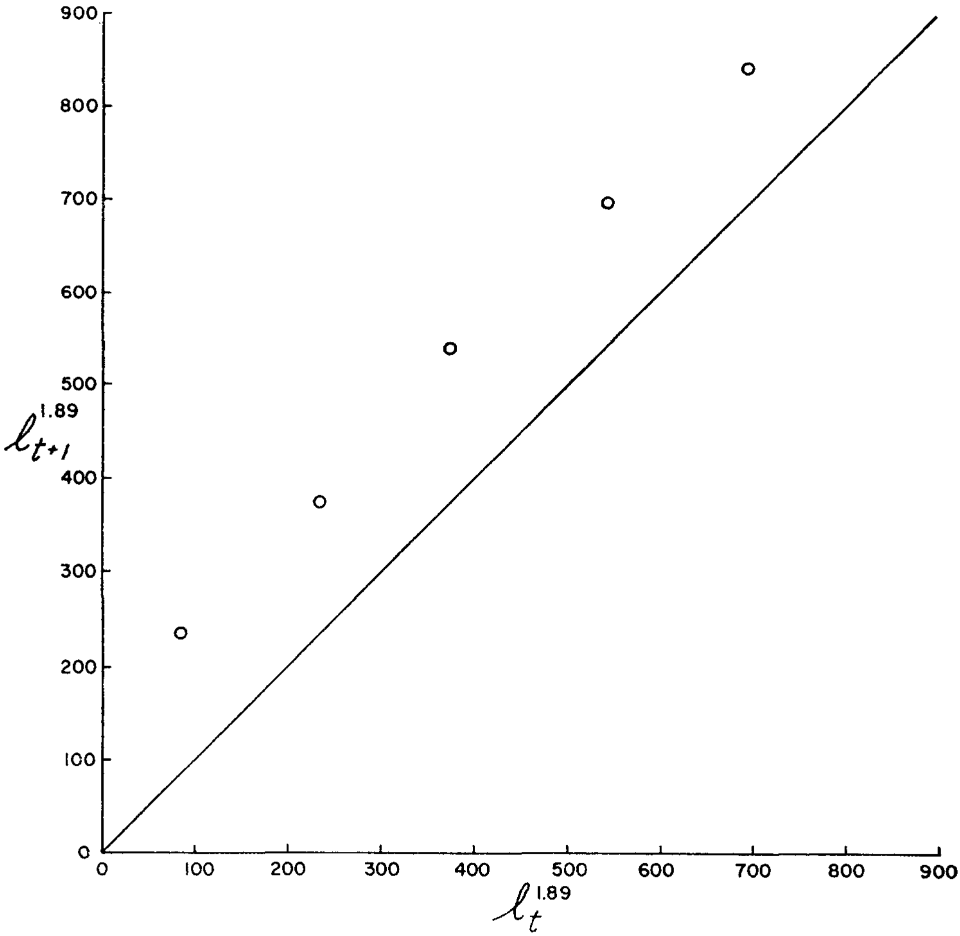

Figure 10 — Plot of $l^{1.89}_{t+1}$ on $l^{1.89}_{t}$ for white sturgeon from 0-6 years.

Since the line of best fit above six years of age did not intersect the 45-degree diagonal line, the data could not be fitted by the Bertalanffy method. However, Beverton and Holt (1959) tabulated the values of K and l_{∞} for this species as 0.06 and 300 centimeters (120 inches), respectively. The Bertalanffy equation for estimating the growth of white sturgeon with these constants was $l_{t+1} = 120\ (0.058) + (0.942) l_{t}$. The lengths were grossly overestimated at all ages above four years (Table 5).

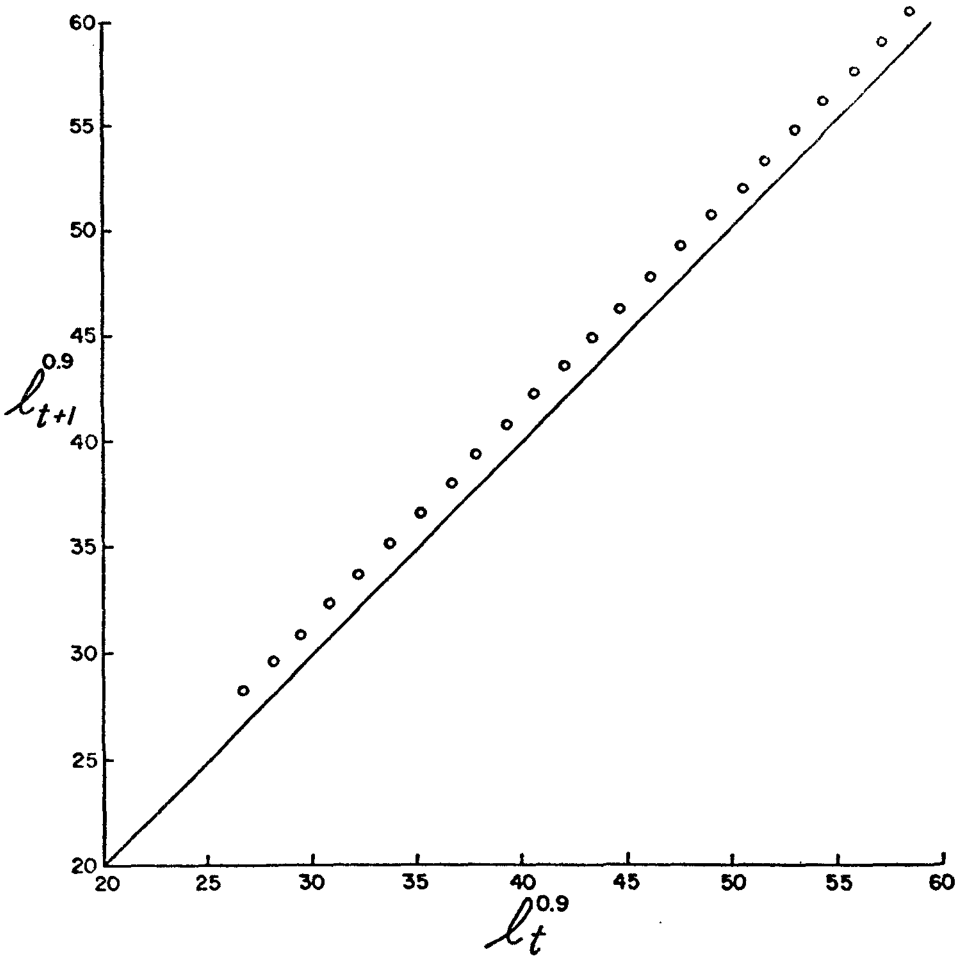

Figure 11 — Plot of $l_{t+1}^{0.9}$ on $l_t^{0.9}$ for white sturgeon from 6-30 years.

TABLE 5—BACK-CALCULATED AND ESTIMATED TOTAL LENGTHS IN INCHES FOR WHITE STURGEON FROM CALIFORNIA WATERS (PYCHA, 1956).

Age in years	Back Calculated lengths	Estimated lengths Parker-Larkin	Bertalanffy
0	10.5	10.5	10.5
1	18.0	18.0	16.9
2	23.0	23.4	22.9
3	28.0	27.9	28.5
4	32.0	31.8	33.8
5	35.3	35.3	38.9
6	38.5	38.5	43.6
7	41.0	40.6	48.0
8	43.6	43.0	52.2
9	45.8	45.3	56.1
10	47.9	47.6	59.9
11	50.0	49.9	63.4
12	52.2	52.2	66.7
13	54.5	54.5	69.8
14	56.8	56.8	72.7
15	59.0	59.1	75.4
16	61.2	61.5	78.0
17	63.6	63.8	80.5
18	66.0	66.2	82.8
19	68.3	68.6	84.9
20	70.7	70.9	86.9
21	73.1	73.3	88.9
22	75.5	75.7	90.7
23	78.0	78.1	92.4
24	80.4	80.5	93.9
25	82.8	82.9	95.5
26	85.2	85.4	96.9
27	87.7	87.8	98.3
28	90.2	90.2	99.5
29	92.8	92.7	100.7
30	95.3	95.1	101.8

DISCUSSION

The growth of an animal is the result of interaction of many processes. There is no simple way of expressing the growth pattern. Mathematical models of various degrees of complexity are available that simulated the growth curves of teleost fishes.

The usefullness of an empirical equation is enhanced if its constants easily yield information of biological interest. It is solely on this basis that the Bertalanffy equation has had a wide and varied use in fishery investigations. The parameter K of Bertalanffy is supposed to be proportional to the coefficient of catabolism, i.e., it is the rate at which the fish attains its asymptotic size. Intra- and interspecies growth comparisons nearly always show that K and 1 $\propto$ are inversely related (Beverton and Holt, 1959). Taylor (1958 and 1959) showed that changes in the value of K are dependent on temperatures. He also reported (1958, 1959 and 1960) the existing inverse relationship between K and 1 $\propto$ for the cod, *Gadus callarias*; the Pacific razor clam, *Siliqua patula*; and the Pacific cockle, *Cardium corbis*. The values of K and 1 $\propto$ of Bertalanffy and z of Parker-Larkin obtained for various species of fish are given in Table 6.

The relationship between 1 $\propto$ and z appears to be the same as between 1 $\propto$ and K. From the available data, it may be concluded tentatively that the parameter z of the Parker-Larkin growth equa-

TABLE 6 — GROWTH PARAMETERS OF THE VON BERTALANFFY AND PARKER-LARKIN EQUATIONS

Species	Sex	1α	K	Z
Eopsetta jordani (Kilambi, 1961)	f	81 cm	0.11	1.3
	m	85 cm	0.11	1.3
Clupea pallasii	f	25.4 cm	0.21	3.5
	m	27.6 cm	0.13	3.1
Acipenser fulvescens	f	76 inches	0.023	2.64
	m	84 inches	0.020	2.64

tion is as much an index of physiological activity as the parameter K of the Bertalanffy equation. Parker and Larkin (1959) suggested the possibility of deriving the values for x or z of their equation from a comparative study of metabolic rate over a range of size. They also thought that the parameter z may be determined by an inherited enzyme system. Cooper (1961), in his analysis of the growth of wild and hatchery strains of brook trout, *Salvelinus fontinalis,* obtained z values of 1.5 for the randomly bred groups and 1.2 for inbred groups. He concluded that the concept of Parker-Larkin was useful in measuring difference due to genetic factors.

Parker and Larkin (1959) mentioned that the value of z is likely to lie between 1.0 and 1.5 if the line of the Walford plot approaches the 45-degree diagonal. This held true for the steelhead trout (*Salmo gairdneri*) and chinook salmon (*Oncorhynchus tshawytscha*) they used as examples. The same applies to rainbow trout from Paul, Loon and Beaver Lakes, British Columbia (Kilambi, 1961; Larkin and Ayyangar, 1961). For brook trout (*Salvelinus fontinalis*) Cooper (1961) reported z values of 1.20 to 1.53. Carlander and Whitney (1961) obtained z values of 2.3 on age groups I to VII and 3.1 for all age groups for walleye (*Stizostedion vitreum vitreum*), in Clear Lake. Larkin and Ayyangar (1961) estimated 3.625 for scallops (*Placopecten magellanicus*). In this study the values of z ranged from 1.89 to 3.5. The evidence thus far available suggests that the value of z lies between 1.0 and 1.5 only for salmonids and closely related species.

This study and the available literature show that the Parker-Larkin equation can be applied to nearly any type of growth curve, since growth is depicted in various stanzas of different growth patterns, whereas the Bertalanffy equation is of limited application because it assumes asymptotic growth.

LITERATURE CITED

Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Ministry of Agr. and Fish. Fish, Invest. Series 2, 19·533 p.

————. 1959. A review of the lifespans and mortality values of fish in nature and their relation to growth and other physiological characteristics, p. 142-180. In the lifespan of animals. Vol. 5. CIBA Foundations colloquia on ageing. Boston. Little, Brown and Co.

Carlander, K. D. and R. R. Whitney. 1961. Age and growth of walleyes in Clear Lake, Iowa. 1935-1957. Amer. Fish. Soc. Trans., *90* (2): 130-138.

Cooper, E. L. 1961. Growth of wild and hatchery strains of brook trout. Amer. Fish. Soc. Trans., *90* (4): 424-438.

Kilambi, R. V. 1961. Application of Parker-Larkin equation to growth of fishes and other aquatic organisms. Master of Science Thesis, University of British Columbia, Vancouver, 87 p.

Larkin, P. A., J. C. Terpenning, and R. R. Parker. 1956. Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. Amer. Fish. Soc. Trans., *86*: 84-96.

Larkin, P. A. and K. V. Ayyangar. 1961. Applications of the Parker equation to growth of aquatic organisms. Proc. 11th Alaska Sci. Congr.: 103-124.

Parker, R. R. and P. A. Larkin. 1959. A concept of growth in fishes. Fish. Res. Bo. Can. *16* (5): 721-745.

Pycha, R. L. 1956. Progress report on white sturgeon studies. Calif. Fish and Game, *44* (1): 23-35.

Taylor, C. C. 1958. Cod growth and temperature. J. du Conseil., *23* (3) 366-370.

————. 1959. Temperature and growth—The Pacific razor clam. J. du Conseil., *25* (1): 93-101.

————. 1960. Temperature, growth, and mortality—The Pacific cockle. J. du Conseil., *26* (19): 117-124.

NOTES ON THE LIFE HISTORIES OF THE SILVERSIDES, *MENIDIA BERYLLINA* (COPE) AND *MEMBRAS MARTINICA* (VALENCIENNES) IN MISSISSIPPI SOUND AND ADJACENT WATER[1]

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ABSTRACT

During the process of a biological sampling program for Mississippi's Estuarine Inventory, data on the spawning season and influx of young were compiled for the two species of silversides found in Mississippi estuarine waters, *Menidia beryllina* (Cope) and *Membras martinica* (Valenciennes). Silversides taken from collections made with seines, beam trawls, plankton nets and dip nets were measured and the condition of the gonads noted. These data, when combined with associated field observations, first revealed ripe male and female *Menidia beryllina* (68 mm to 98 mm) in late March (water temperature 23.9°C) and *Membras martinica* (66 mm to 79 mm) in early April. *M. beryllina* in spawning condition were collected in salinities ranging from 3.6°/oo to 31.5°/oo and water temperatures ranging from 23.9°C to 32.7°C throughout the spring and summer months. Spawning *M. martinica* were collected in salinities from 9.4°/oo to 31.1°oo and in water temperatures from 21.2°C to 30.7°C.

Postlarval atherinids (4.5 mm to 9 mm) were taken in plankton tows in late March and early April. Juvenile *Menidia beryllina* (14 mm) first appeared in early April. Juvenile *Membras martinica* (26-31 mm) were first collected in early May.

These observations from the Mississippi coast parallel those of other workers reporting on atherinid spawning elsewhere along the Gulf and Atlantic coasts of the United States.

INTRODUCTION

Since January, 1966, a research project has been underway at the Gulf Coast Research Laboratory to gather as much information as time, personnel, funds and all other variable factors will permit, concerning the ecology of the estuaries of the Mississippi Gulf Coast. This project is

[1] Conducted in cooperation with the United States Department of Interior, Bureau of Commercial Fisheries, under Public Law 88-309. (Project 2-25-R)