APPLICATION OF PARKER-LARKIN EQUATION TO GROWTH OF FISHES AND OTHER AQUATIC ORGANISMS

by

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ABSTRACT

Any mathematical formulation for depicting the growth of organisms must yield an empirical fit that is reasonably good. Its validity is enhanced if the equation yields information of biological interest. This investigation is aimed at applying the Parker-Larkin (1959) growth equation to a number of aquatic organisms to describe the problems encountered in making use of this technique. The data are also analysed by the Von Bertalanffy growth equation to bring out the similarities of the constants of both the equations.

The data pertaining to three species of marine fish, brill, halibut and herring, four species of freshwater fish, rainbow trout, cutthroat trout and sturgeon and to a lamellibranch species scallops, have been analysed.

It is pointed out that the exponent of the length-weight relationship should not be taken as 3. It is shown that the length-weight relationship of rainbow trout varies depending on sex, maturity and size. In many species the Parker-Larkin growth equation predicted the lengths at various ages accurately. Von Bertalanffy's equation progressively overestimated the sizes.

In white sturgeon the growth increments decrease at first and then become equal. In such a situation it is suggested that the data be split into two stanzas for analysis since the analysis without splitting underestimates the sizes in the early years and overestimates in the older ages.

The anterior radius of the scale grows relatively slower than the length of the fish in herring. The regression equation of the body-scale relationship is used only to obtain the value of the intercept. The back calculation of lengths is made by keeping the intercept constant with variable slopes for the individual fish.

The Parker-Larkin equation gave an excellent fit for the data on halibut. This is because the observed values of halibut are actually calculated values from a linear logarithmic regression of weight on age - an algebraic equivalent of the Parker-Larkin equation in which the slope is the reciprocal of (1-x).

The range of values of z between 1.0 and 1.5, when the line of best fit on a Walford plot approaches the 45° diagonal, is true for salmonids only and in similar situations for other species a value as high as 3.6 for z is obtained.

The variability of z depending on the density of the population and/or availability or non-availability of food material is shown for rainbow trout. This dependence of z on the food available is similar to that of L_{∞} or W_{∞}

There is an inverse relationship between L_{∞} and z as that of L_{∞} and K. It is tentatively suggested that z might be a parameter of physiological importance in the Parker-Larkin equation.

Further work of an experimental nature is suggested to establish the physiological significance of the parameters of the Parker-Larkin equation.

ACKNOWLEDGMENTS

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The author also acknowledges Drs. K. S. Ketchen, F. H. C. Taylor, L. M. Dickie, Messrs. L. A. Sunde and C. E. Stenton for kindly providing the author with data on brill, herring, scallops, sturgeon and cutthroat trout respectively.

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INTRODUCTION

In the study of the dynamics of fish populations, there are a number of parameters that must be determined. In addition to the estimations of mortality rates, age composition etc., growth rates of fish are important since the growth of an organism is one of the basic determinants of yield.

It is a common practice to use age as a criterion of size and growth potential, even though this is a reliable index only under stable environmental conditions. Under changing environmental conditions age can no longer be considered as a criterion of size. Larkin, Terpenning and Parker (1957) suggest a method that relates growth to size independent of age. It is their contention that size gives a better indication of ecological opportunity for growth than does age. They also mention that many fish may change the "ultimate size" to which they are tending by changing their ecological niche. There may also be physiological changes in the life of a fish that are related to size. Thus fish growth may be considered as a series of cycles or growth stanzas each of which can be defined as a period during which the parameters used for describing growth processes can be considered constant, within reasonable limits.

Parker and Larkin (1959) suggested the use of the differential equation $\frac{dw}{dt} = kw^x$ in the description of growth of chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Salmo gairdneri). Essentially the use of this equation implies that growth can be treated like any other physiological function.

For instance, respiration rate is commonly related to weight by the differential equation.

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

where ΔO represents oxygen uptake

w represents weight

The respiration rate 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:

$$\log \left[\frac{\Delta w}{\Delta t}\right] = \log k + x \log w \qquad (1)$$

The question arises whether growth rate is related to initial weight, average weight or final weight during the period t. The classic solution to this kind of problem is to deal in instantaneous rates, integrating the expression

$$dw/dt = kw^x$$

to yield

$$w_t^{(1-x)} = kt(1-x) + w_0^{(1-x)} \qquad (2)$$

Using the expression $w = ql^y$ to denote the relationship between weight and length it can be demonstrated that growth in length can be depicted as:

$$l_{t+1}^z = \alpha + l_t^z \qquad (3)$$

where $z = y(1-x)$

$$\alpha = \frac{k(1-x)}{q^{(1-x)}}$$

Setting $l_{t=o} = 0$

The above equation can be written as

$$l^z_{t+1} = \alpha$$

and $$l^z_{t+2} = \alpha + l^z_{t+1}$$

since $$l^z_{t+1} = \alpha$$

$$l^z_{t+2} = 2\alpha$$

hence $$l^z_{t=n} = \alpha n$$

Taking logarithms and dividing by $\frac{1}{z}$

$$\log l_t = \frac{1}{z} \log \alpha + \frac{1}{z} \log n \qquad (4)$$

plotting log l against log t (i.e. n) yields a straight line with slope of $\frac{1}{z}$ analogous to (1) above, This is essentially a regression of length on age with the slope $b = \frac{1}{z}$. The solution is again made difficult, this time by the presence of z in both terms on the right had side, which would require iteration for an arbitrary estimate of z.

To obviate these difficulties Parker and Larkin suggested a solution using a technique based on a plot of l^z_{t+1} on l^z_t, using an appropriate valye of z that would minimize the relative variance of α. The solution is most conveniently handled by a computer (An ALWAC III-E computer was used. This program is on file at the Computing Centre, University of British Columbia).

An approximate solution can be obtained using the quadratic function

$$S_R = a + bz + cz^2$$

Three values of relative standard deviation (S_R) and their associated z values on simultaneous solution yield the best z value (the value of z giving minimum standard deviation) as

$$z = -\frac{b}{2c}$$

Approximate graphic methods for solution are also given by Parker and Larkin.

Carlander and Whitney (1961) mention that there is a different growth pattern for walleyes in Clear Lake which exceed 25.0 inches in length when the older fish beyond age VII are eliminated or 23.9 inches in length when only the fish which completed a given annual increment are considered. They made use of the Parker-Larkin growth equation to give a better fit.

The present work describes problems in applying these techniques of growth representation to data for various species of aquatic organisms including (1) brill (Eopsetta jordani), (2) halibut (Hippoglossus stenolepis), (3) lake sturgeon (Acipenser fulvescens), (4) white sturgeon (Acipenser transmontanous), (5) herring (Clupea pallasii), (6) cutthroat trout (Salmo clarkii), (7) rainbow trout (Salmo gairdnerii), and (8) scallops (Placopecten magellanicus).

Since the usefulness of any empirical equation is enhanced if its constants yield information of biological interest, the present work has tried to draw tentative conclusions on the significance of the constants included in the Parker-Larkin equation.

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

BRILL (Eopsetta jordani)

Back calculated lengths for brill were kindly provided by Dr. K. S. Ketchen of the Pacific Biological Station, Nanaimo.

Walford plots of l_{t+1} against l_t separately for the two sexes are shown in Figures 1 and 2. The data show a slight convergence towards the 45^{o} diagonal and indicate that an appropriate z value for the equation $l^{z}_{t+1} = \alpha + l^{z}_{t}$ would be more than 1. For convenience in computation, growth in the first five years only was considered. Using the quadratic method for estimating minimum relative variance the original length data, and sets of values for $l^{0.5}$ and $l^{0.65}$ yielded an estimate of z of 1.3. Using the ALWAC III E Computer the same value of z was obtained.

The plots of $l^{1.3}_{t+1}$ against $l^{1.3}_{t}$ are shown in Figures 3 and 4. The corresponding growth formulae are:-

Females $\quad l^{1.3}_{t+1} = 21.2837 + l^{1.3}_{t}$

Males $\quad l^{1.3}_{t+1} = 20.4991 + l^{1.3}_{t}$

Combined $\quad l^{1.3}_{t+1} = 20.8964 + l^{1.3}_{t}$

Mean growth increments between the various ages are given in Table I.

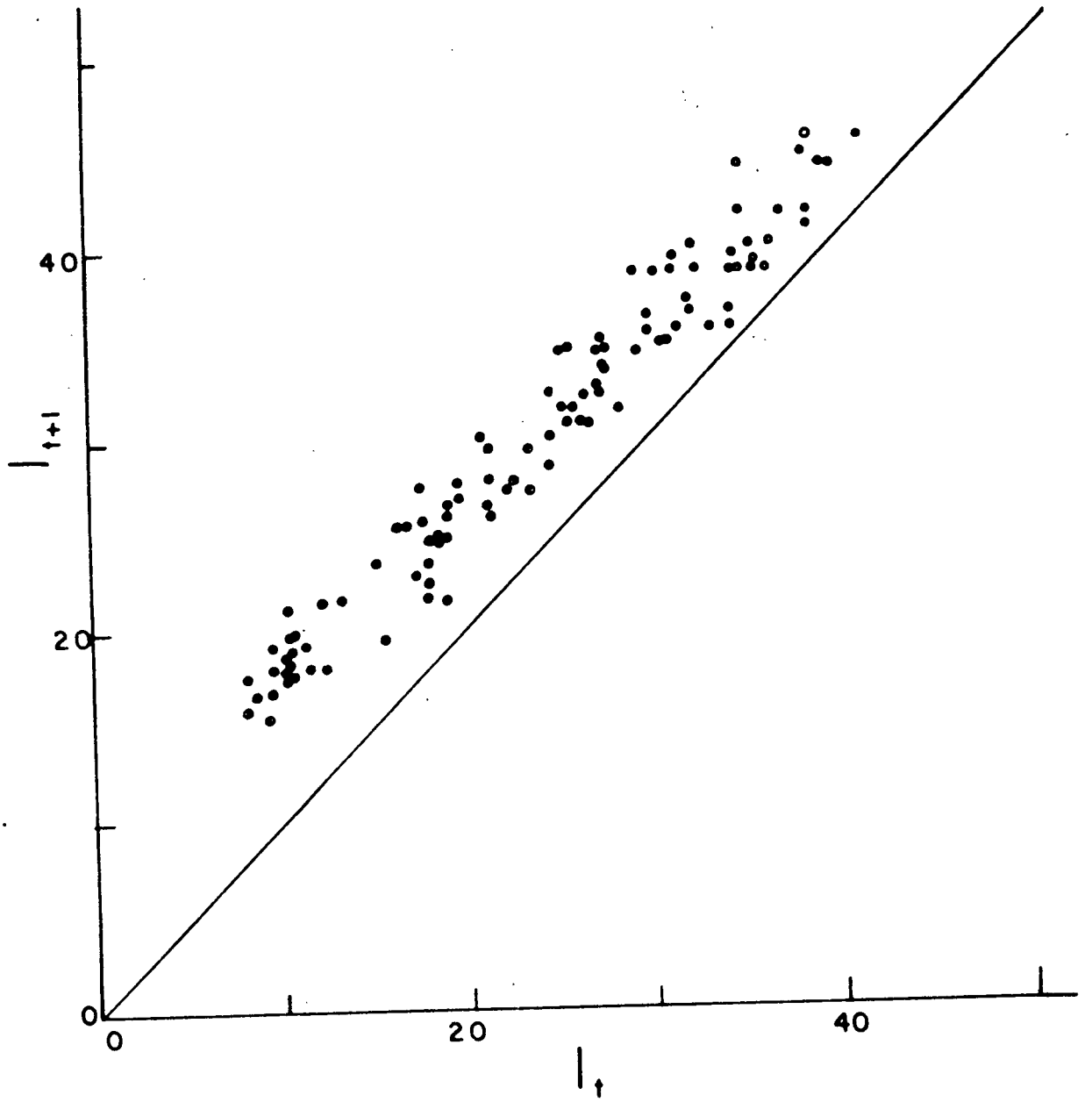

Figure 1. Plot of l_{t+1} on l_t for female brill.

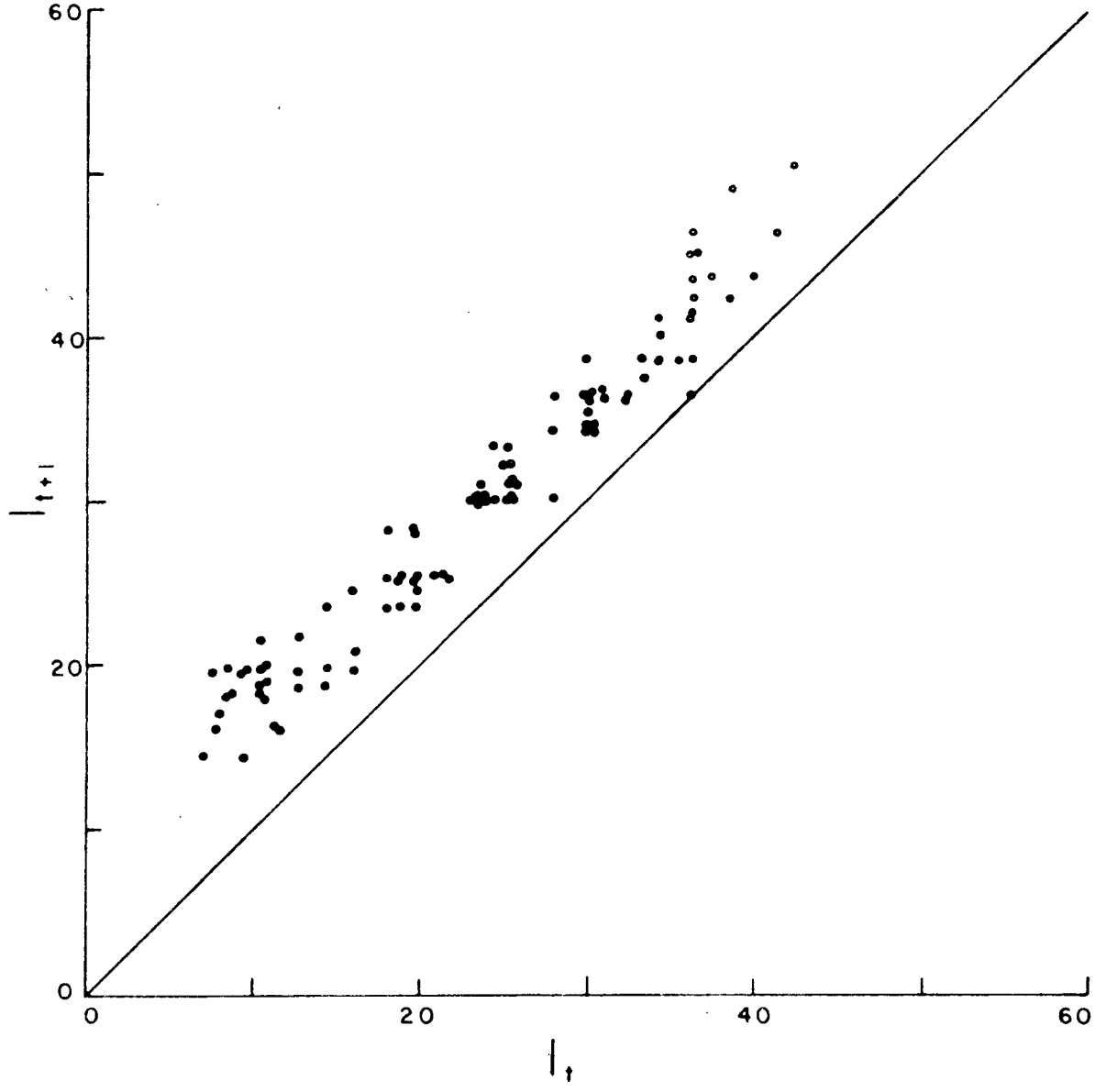

Figure 2. Plot of l_{t+1} on l_t for male brill.

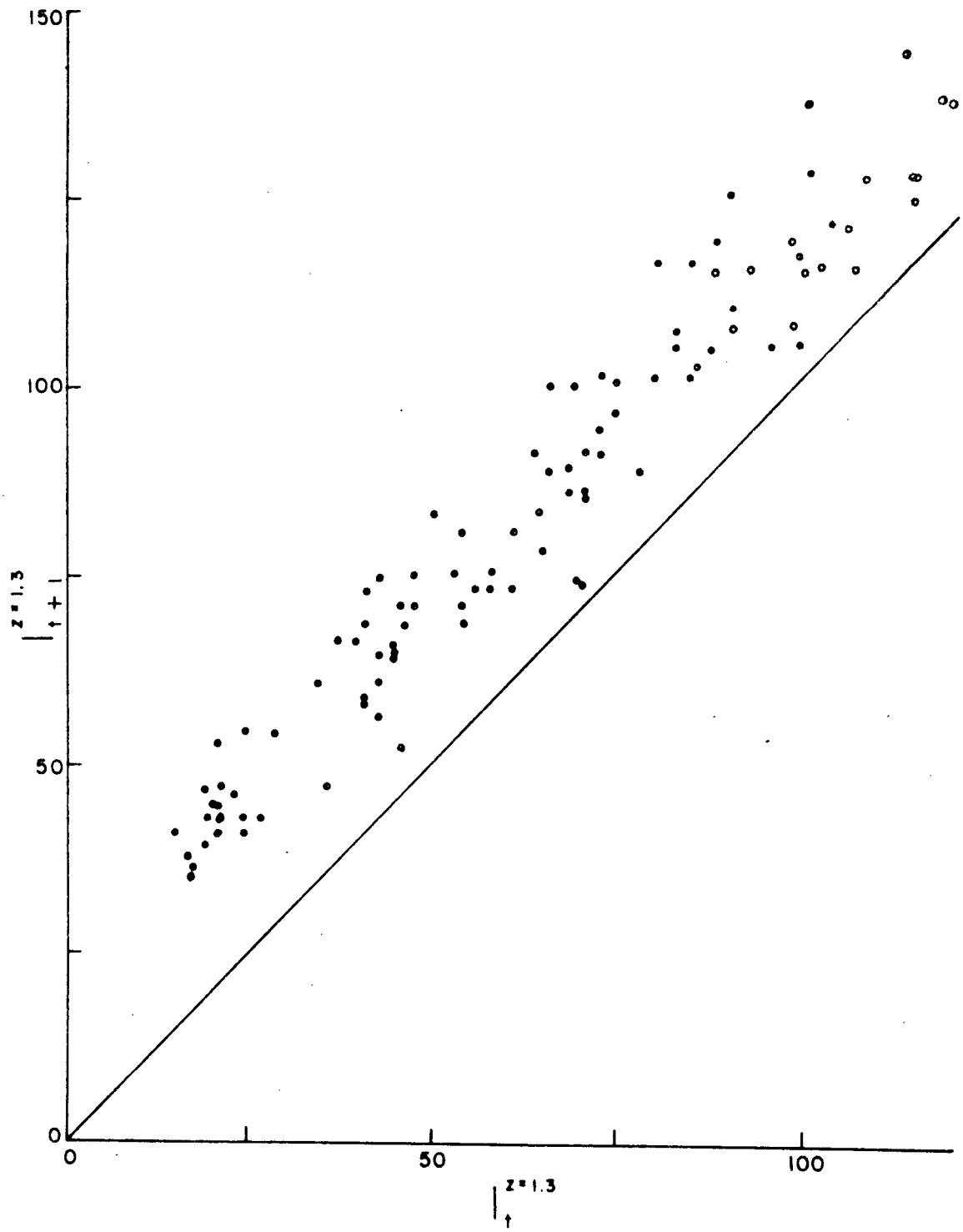

Figure 3. Plot of $l^{1.3}_{t+1}$ on $l^{1.3}_{t}$ for female brill.

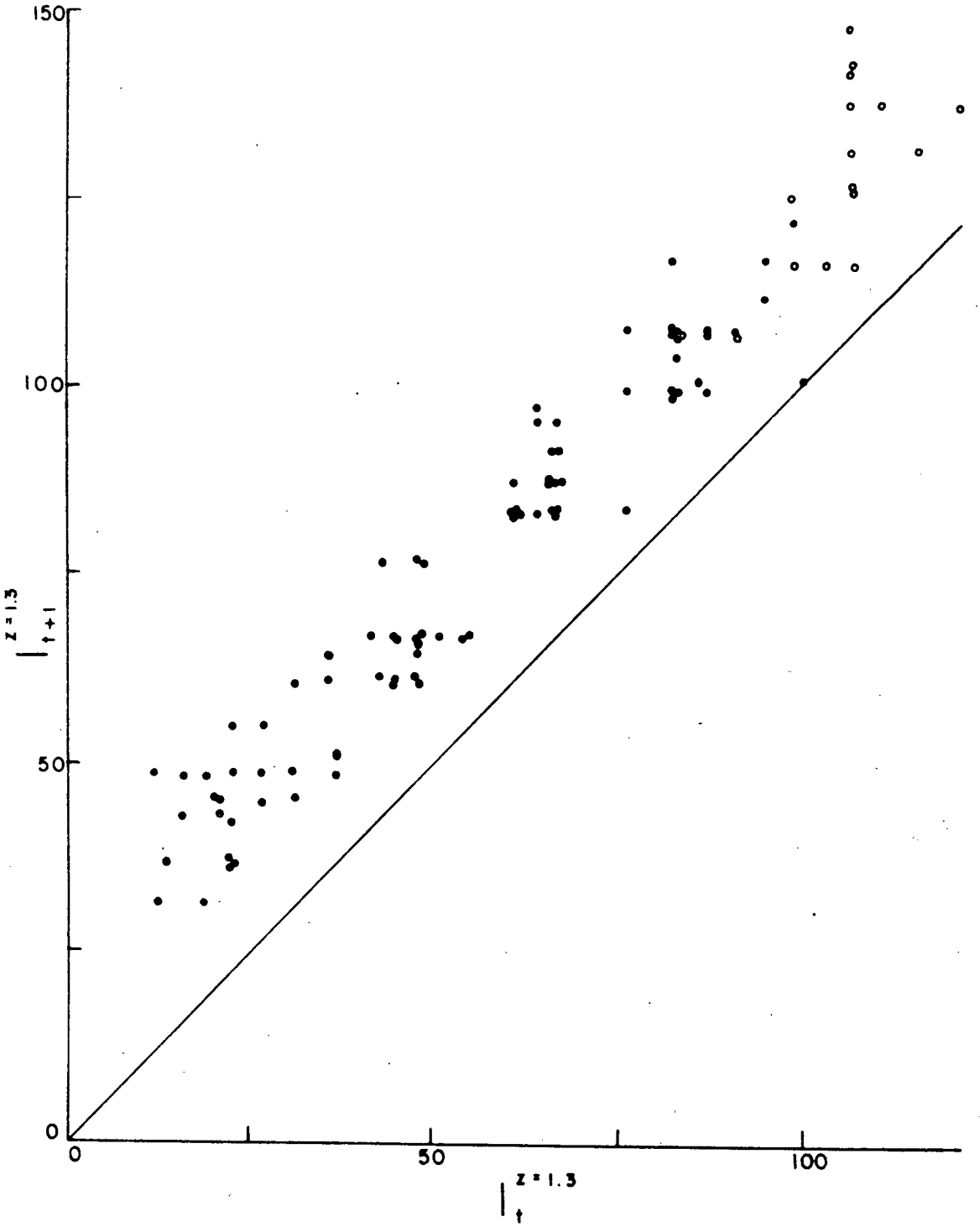

Figure 4. Plot of $l^{1.3}_{t+1}$ on $l^{1.3}_{t}$ for male brill.

Table I. Growth increments between various ages of brill

	α_{12}	α_{23}	α_{34}	α_{45}
Females	22.3030	22.0045	19.9550	20.9125
Males	22.4320	18.9295	21.6280	19.0070
Combined	22.3675	20.4670	20.7915	19.9597

Analysis of variance (Table II) indicates no significant differences between sexes or ages and no significant interaction, i.e. there is no significant departure from the average growth rate at various ages or for either sex or for any particular sex at any particular age.

Table II. Analysis of variance of growth increments at different ages of both sexes of brill.

Source of Variance	d.f.	Mean Square	F ratio	Probability
Total	159			
Means	7			
Individuals	152	41.3912		
Sexes	1	25.2571	0.610	> 0.25
Ages	3	43.1577	1.042	>0.25
Interaction	3	44.5880	1.077	>0.25

The analysis suggests that the equation $l^z_{t+1} = \alpha + l^z_t$ can usefully be applied to description of and comparison of growth rates of brill. However, the conversion from z to x should not be based on the assumption that y = 3. The length-

weigth relationship for male and female brill, provided by Dr. K. S. Ketchen are:

$$\text{Male} \quad \log W_{(0z)} = 3.1349 \log l_{(mm)} - 6.6982$$

$$\text{Female} \quad \log W_{(0z)} = 3.3523 \log l_{(mm)} - 7.2478$$

Substituting these regression coefficients for y in the relation $z = y(1-x)$ the values of the exponent x for males and females are 0.58 and 0.61 respectively.

The data were also analysed by using the von Bertalanffy equation according to the method described by Ricker (1958)*. Lengths at various ages could be calculated from the equations:

$$\text{Females} \quad l_{t+1} = 81(\cdot 104) + 0.8958\ l_t$$

$$\text{Males} \quad l_{t+1} = 85(\cdot 104) + 0.8958\ l_t$$

Observed and calculated lengths by Parker-Larkin and Von Bertalanffy equations are given in Table III.

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*The differential equation of von Bertalanffy, $\frac{dw}{dt} = HS - KW$ can be shown to yield the expression $l_{t+1} = l_{oo}(1-e^{-Kt}) + l_t e^{-Kt}$. By plotting l_{t+1} against l_t (Walford plot) the constants l_{oo} and K can be estimated. Alternatively, plotting $\log_e l_{oo} - \log_e(l_{oo} - l_t)$ against t gives a line of slope -K and y intercept (-Kto). Trial values of l_{oo} can be chosen to provide a best fit for the equation.

Table III. Observed and calculated lengths.

Age in years	Total length in centimeters					
	Observed		Parker-Larkin		Von Bertalanffy	
	Males	Females	Males	Females	Males	Females
1	10.5	10.8	10.68	10.73	10.50	10.80
2	18.3	18.3	17.80	18.17	18.14	18.54
3	24.0	25.0	24.14	24.63	25.09	25.04
4	30.4	30.6	30.00	30.69	31.32	30.87
5	35.5	36.2	35.53	36.40	36.90	36.09

Both equations do an adequate job of prediction although the Von Bertalanffy expression tends to progressively overestimate lengths.

HALIBUT (Hippoglossus stenolepis).

Halibut of Portlock-Albatross grounds are used for the present investigation. Growth rates estimated for 1926 and 1956 are obtained from Table5, page 15 of the 28th report of the International Pacific Halibut Commission. Average weights at each age given by the Commission's report were stated to have been obtained by converting the lengths to weight by using a length-weight table.

Average weight in pounds at each age of Portlock-Albatross halibut for 1926 and 1956 is shown in Figure 5. The plot of W_{t+1} against W_t for 1926 data of Figure 6 appear to diverge from the 45^0 diagonal line. When data on weights are used the minimum relative variance will yield an optimum value of (1-x) as is evident from the equation.

$$W_{t+1}^{(1-x)} = k(1-x) + W_t^{(1-x)}$$

Here for the sake of convenience k(1-x) is denoted as α^1 and thus we have

$$W_{t+1}^{(1-x)} = \alpha^1 + W_t^{(1-x)}$$

The optimum value of (1-x) obtained from 1926 data was 0.5 and the corresponding growth formula is:-

$$W_{t+1}^{0.5} = 0.276 + W_t^{0.5}$$

The plot of $W_{t+1}^{0.5}$ against $W_t^{0.5}$ is shown in Figure 7. Making use of the above growth formula, weights at various ages were computed and are shown in Table 4 along with the observed weights. Agreement between observed and calculated weights is good. This is hardly surprising since the observed values are

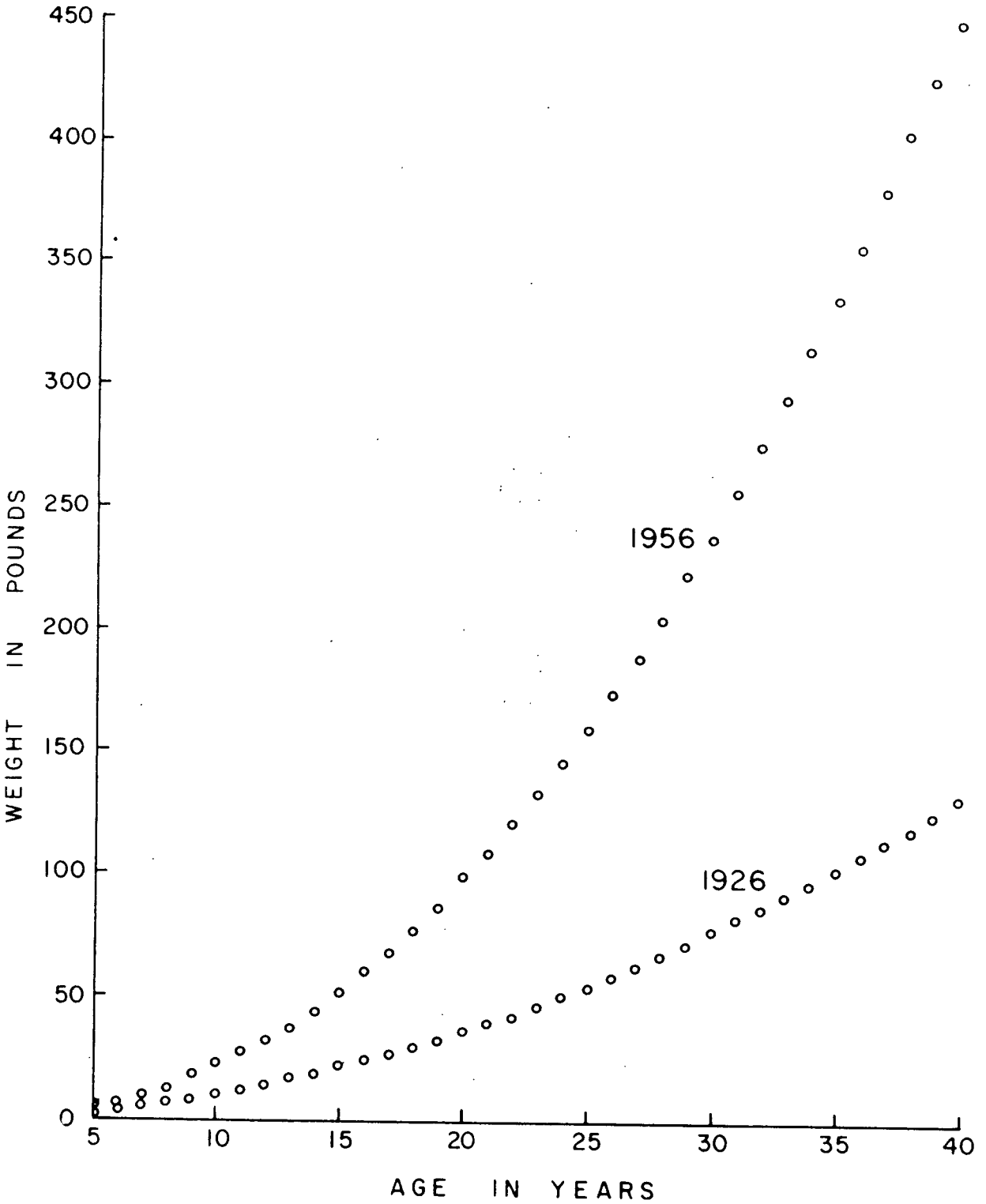

Figure 5. Growth curves showing age-weight relationship for Portlock-Albatross halibut.

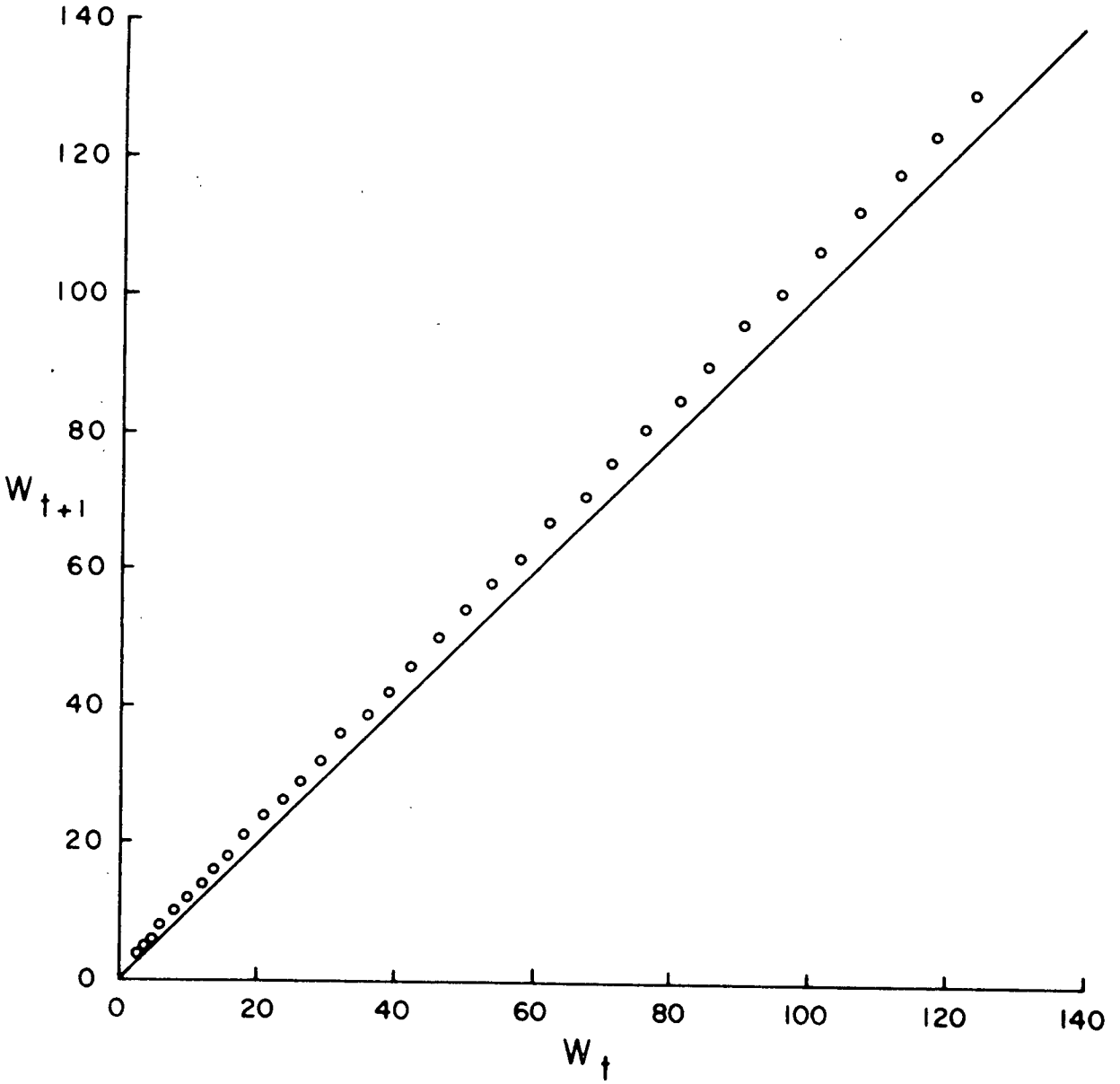

Figure 6. Plot of W_{t+1} on W_t for Portlock-Albatross halibut for 1926.

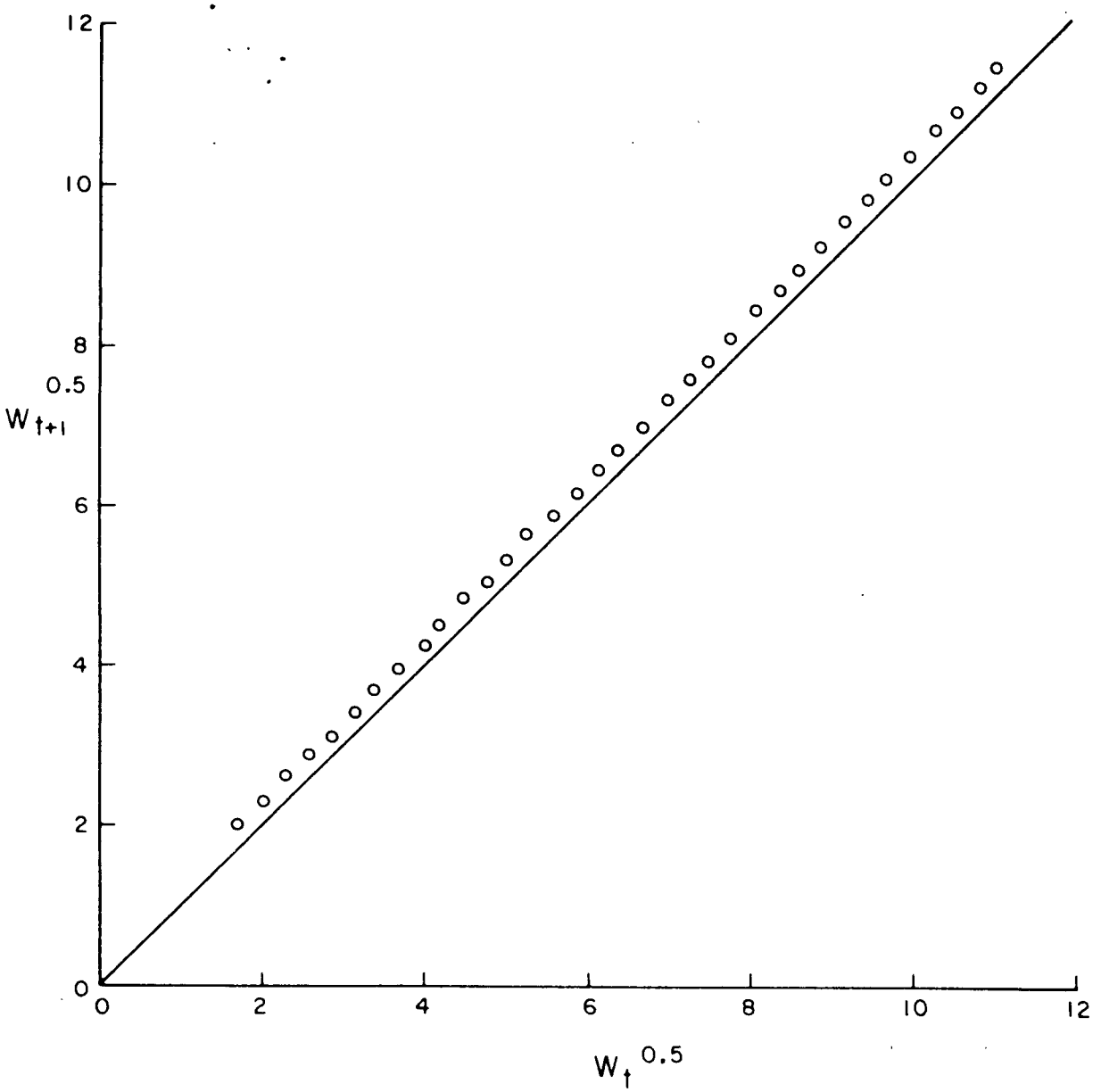

Figure 7. Plot of $W_{t+1}^{0.5}$ on $W_t^{0.5}$ for Portlock-Albatross halibut for 1926.

Table 4. Weight in pounds at ages 5 to 40 for Portlock-Albatross halibut in 1926

Age in years	Weight	
	Observed	Calculated
5	3	3.0
6	4	4.0
7	5	5.2
8	6	6.5
9	8	8.0
10	10	9.7
11	12	11.5
12	14	13.4
13	16	15.5
14	18	17.8
15	21	20.2
16	24	22.7
17	26	25.4
18	29	28.3
19	32	31.3
20	36	34.5
21	39	37.8
22	42	41.3
23	46	44.9
24	50	48.7
25	54	52.6
26	58	56.7
27	62	60.9
28	67	65.3
29	71	69.8
30	76	74.5
31	81	79.4
32	85	84.4
33	90	89.5
34	96	94.8
35	101	100.2
36	107	105.8
37	113	111.6
38	118	117.5
39	124	123.6
40	130	129.8

actually calculated values from a linear logarithmic regression of weight on age - an algebraic equivalent of the Parker-Larkin equation in which the slope is the reciprocal of (1-x). However the calculations confirm the usefulness of the Parker-Larkin equation in describing the growth of an average fish.

A plot of W_{t+1} against W_t for 1956 data is shown in Figure 8. In this data also the line of best fit diverges from the 45° diagonal. A value of 0.45 was obtained for (1-x). It would be noted that a change in 0.05 for the value of (1-x) would result in an enormous change in α'. For example, for 0.45 as (1-x) the mean value of α' was 0.385 whereas it was 0.539 for a value of 0.5 for (1-x). A plot of $W_{t+1}^{0.45}$ against $W_t^{0.45}$ is given in Figure 9. The formula for depicting weight is:-

$$W_{t+1}^{0.45} = 0.385 + W_t^{0.45}$$

Weights at various ages are tabulated in Table 5.

The average weights at each age for 1926 and 1956 were converted to lengths at age from a length-weight relationship expressed as:

$$\log W = 3.0417 \log L - 4.70054$$

This relationship was obtained by fitting a regression for average length in centimeters and average weight in pounds for ages from 4 to 25. The data made use of here are given in Table 4 of the 8th report of the International Pacific Halibut Commission 1934.

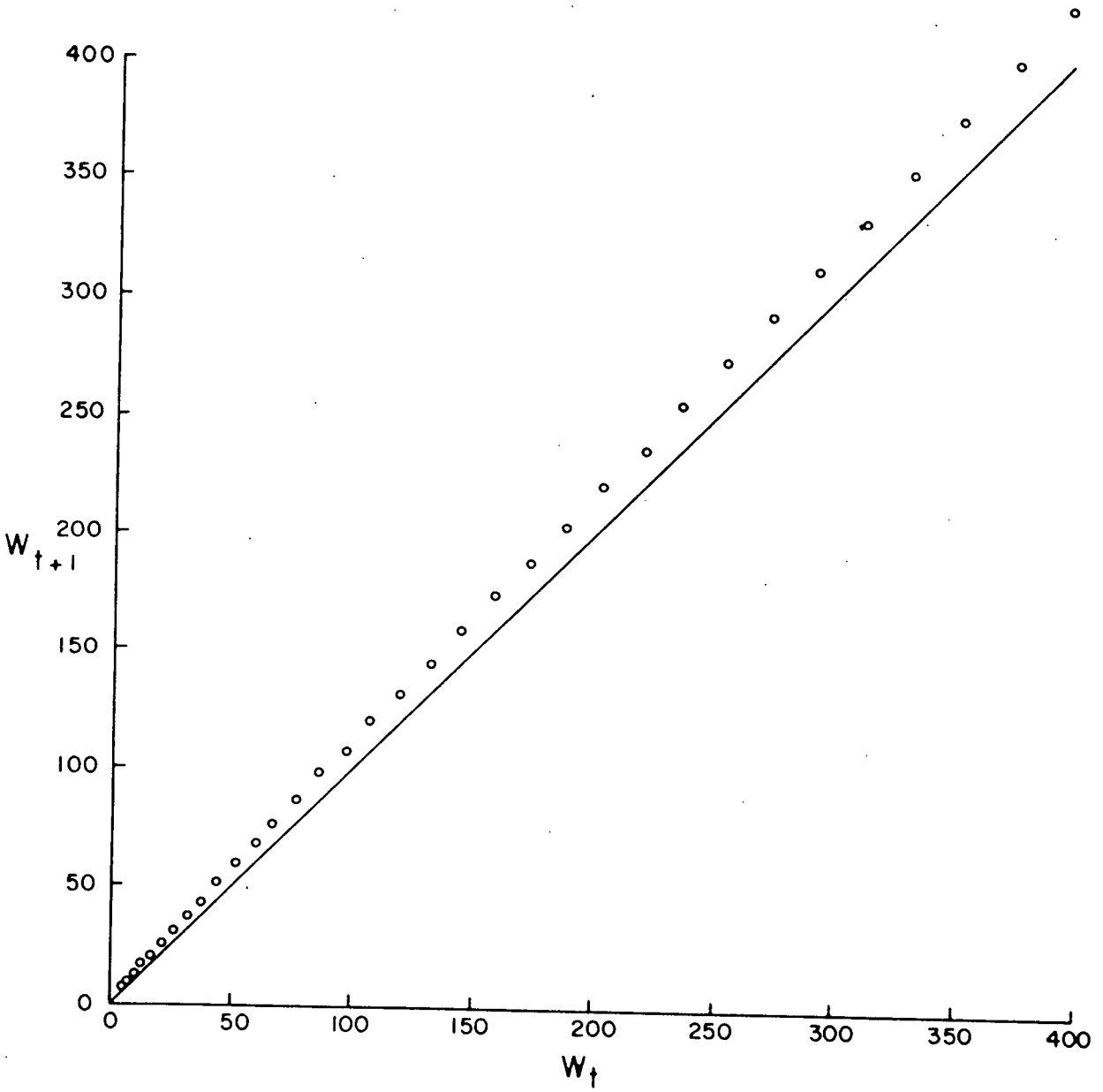

Figure 8. Plot of W_{t+1} on W_t for Portlock-Albatross halibut for 1956.

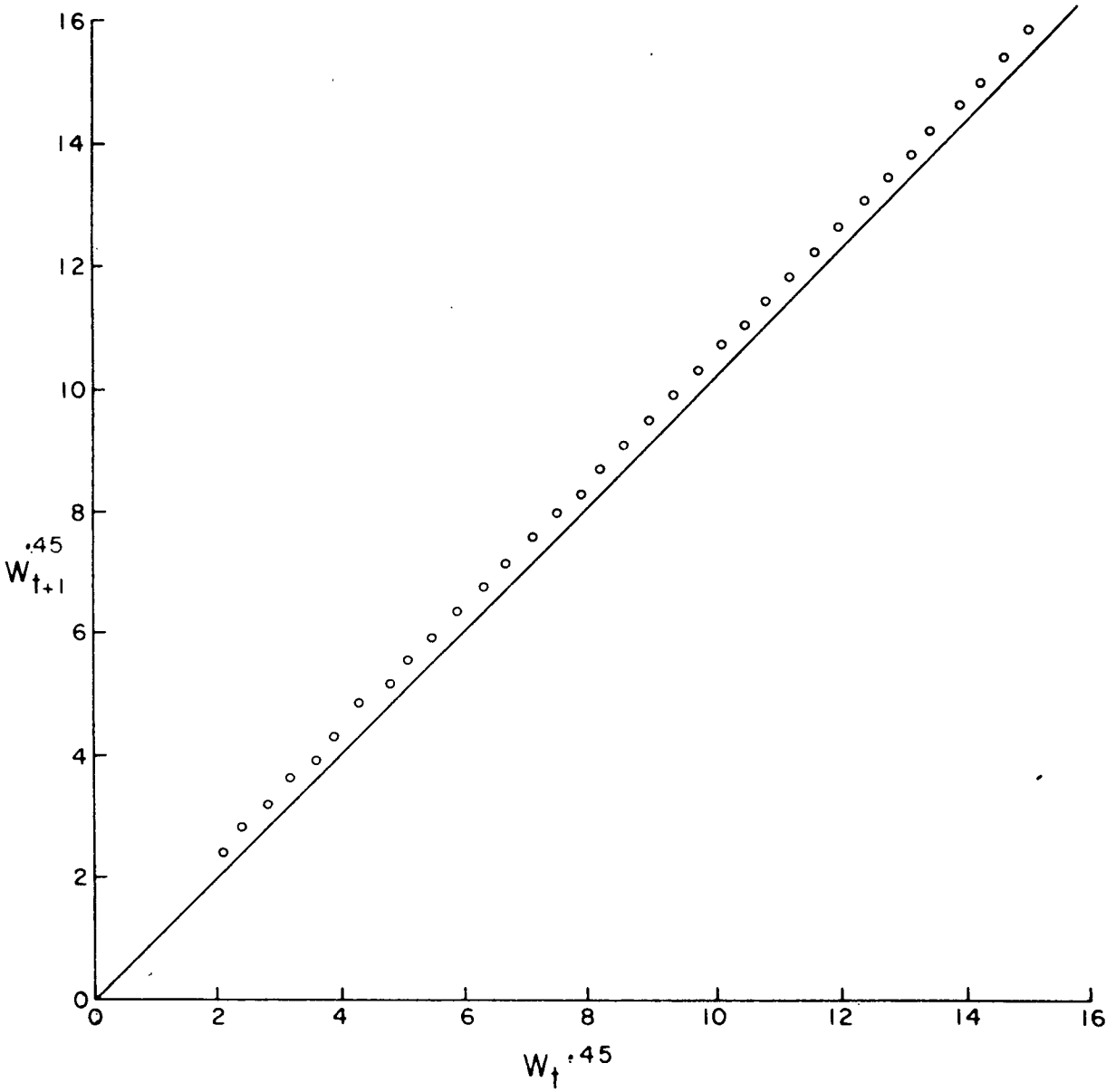

Figure 9. Plot of $W_{t+1}^{0.45}$ on $W_t^{0.45}$ for Portlock-Albatross halibut for 1956.

Table 5. Weight in pounds at ages 5 to 40 for Portlock-Albatross halibut in 1956

Age in years	Weight	
	Observed	Calculated
5	5	5.0
6	7	7.3
7	10	10.1
8	13	13.4
9	17	17.3
10	21	21.6
11	26	26.5
12	32	32.0
13	38	38.1
14	44	44.7
15	52	51.9
16	60	59.7
17	68	68.1
18	77	77.2
19	87	86.8
20	98	97.1
21	108	108.0
22	120	119.6
23	132	131.8
24	145	144.6
25	159	158.1
26	174	172.4
27	188	187.2
28	204	202.8
29	221	219.0
30	237	236.0
31	255	253.5
32	274	271.9
33	293	291.2
34	313	310.7
35	333	330.9
36	354	352.3
37	376	374.0
38	400	396.9
39	423	419.9
40	445	444.3

Walford plots of l_{t+1} against l_t are shown in Figures 10 and 11 for 1926 and 1956 respectively. In both plots the Walford line of best fit converges to the 45^{o} diagonal. The values of z estimated are 1.5 and 1.36 respectively. These estimates of z are obtained from the expression

$$y(1-x) = z$$

Transformed plots of $l_{t+1}^{1.5}$ against $l_t^{1.5}$ for 1926 and $l_{t+1}^{1.36}$ against $l_t^{1.36}$ for 1956 are given in Figures 12 and 13.

The formulae for depicting the growth rates are:

$$l_{t+1}^{1.5} = 55.31 + l_t^{1.5} \quad \ldots\ldots\ldots\ldots\ldots\ldots 1926$$

$$l_{t+1}^{1.36} = 47.76 + l_t^{1.36} \quad \ldots\ldots\ldots\ldots\ldots\ldots 1956$$

Observed and calculated lengths of Portlock-Albatross halibut for the years 1926 and 1956 are presented in Table 6. The agreement between the observed and calculated lengths is excellent.

The Von Bertalanffy equation could not be applied to the weight data as the line of best fit on the Walford plot diverges from the 45^{o} diagonal. It was used for the length data for both the years. Average sizes can be obtained by using the following equations.

$$l_{t+1} = 232(0.14) + l_t \; 0.8607 \ldots\ldots\ldots 1926$$

$$l_{t+1} = 400(0.21) + l_t \; 0.7866 \ldots\ldots\ldots 1956$$

These two equations give an overestimate of lengths.

Judging from Figures 5-9 and the values obtained for (1-x) it may be concluded that halibut grew faster in weight

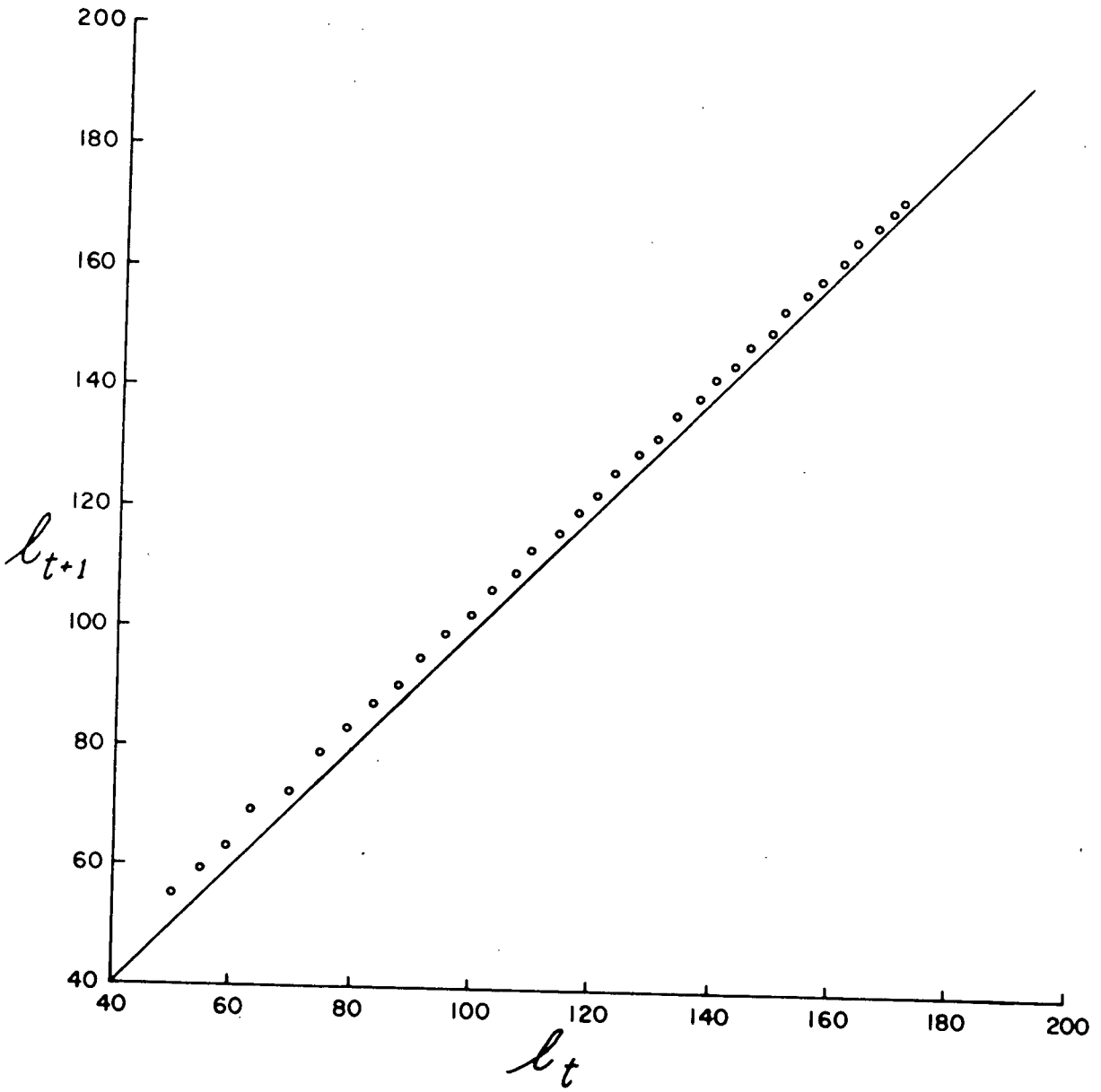

Figure 10. Plot of l_{t+1} on l_t for Portlock-Albatross halibut for 1926.

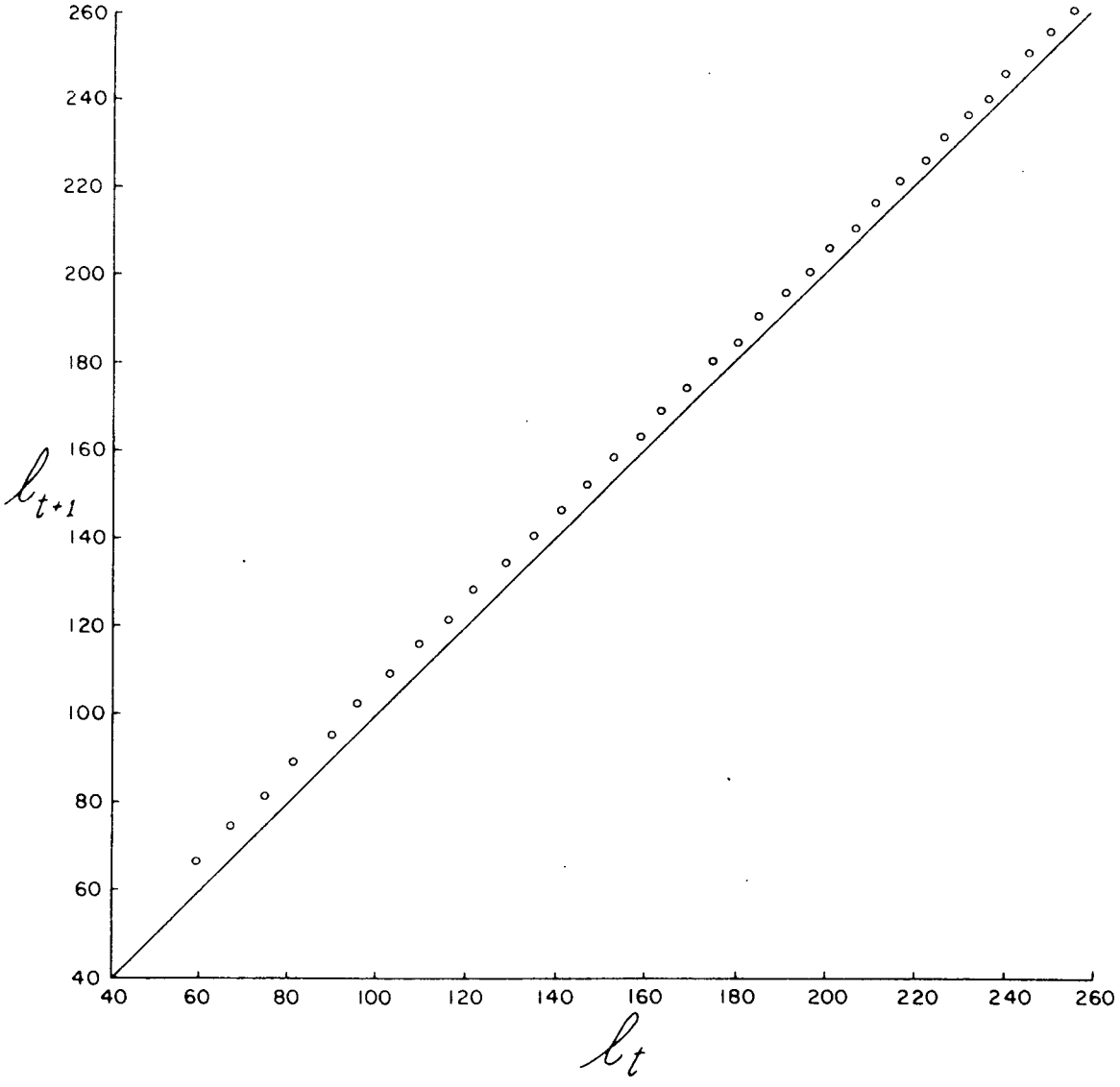

Figure 11. Plot of l_{t+1} on l_t for Portlock-Albatross halibut for 1956.

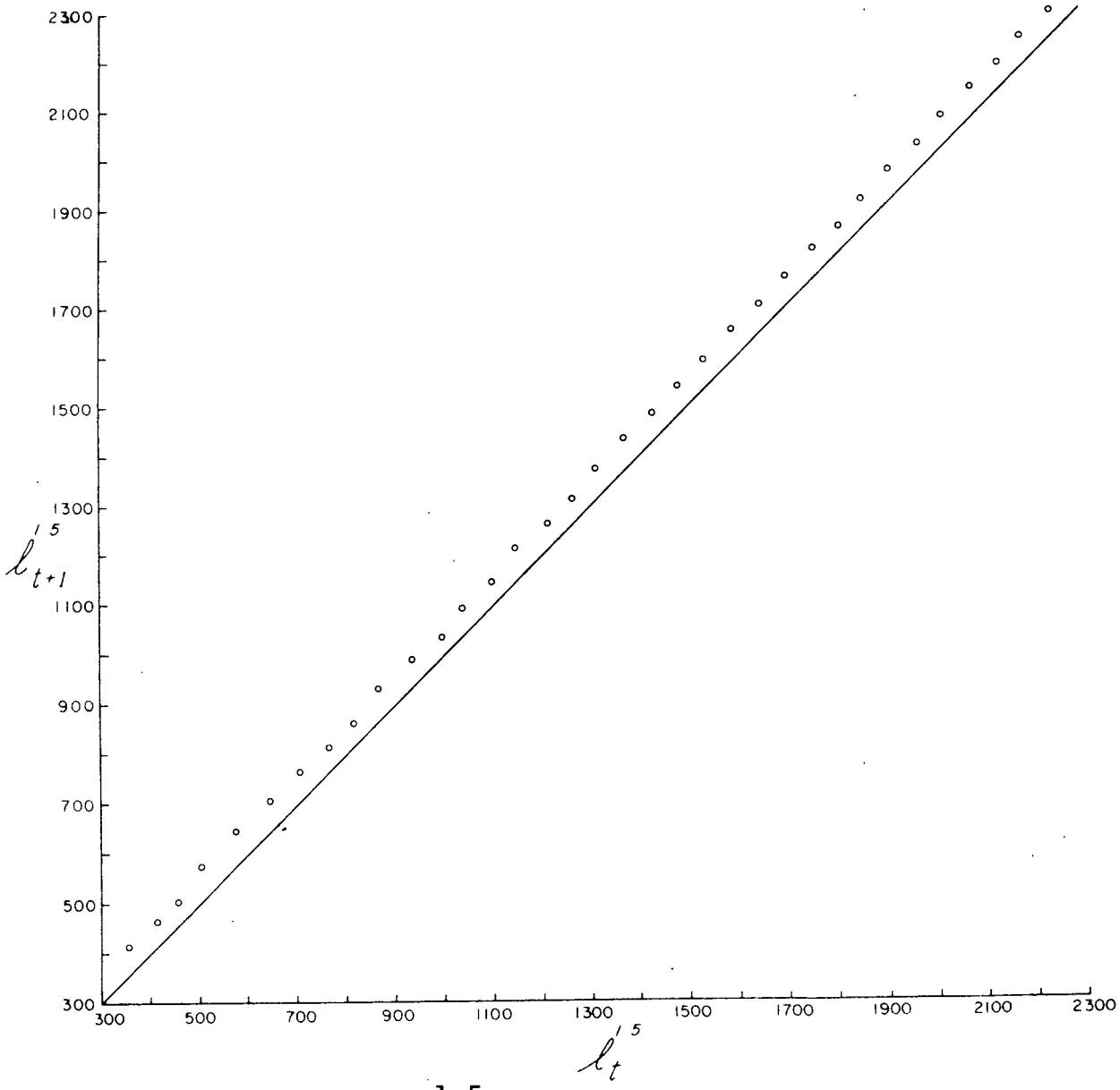

Figure 12. Plot of $l_{t+1}^{1.5}$ on $l_t^{1.5}$ for Portlock-Albatross halibut for 1926.

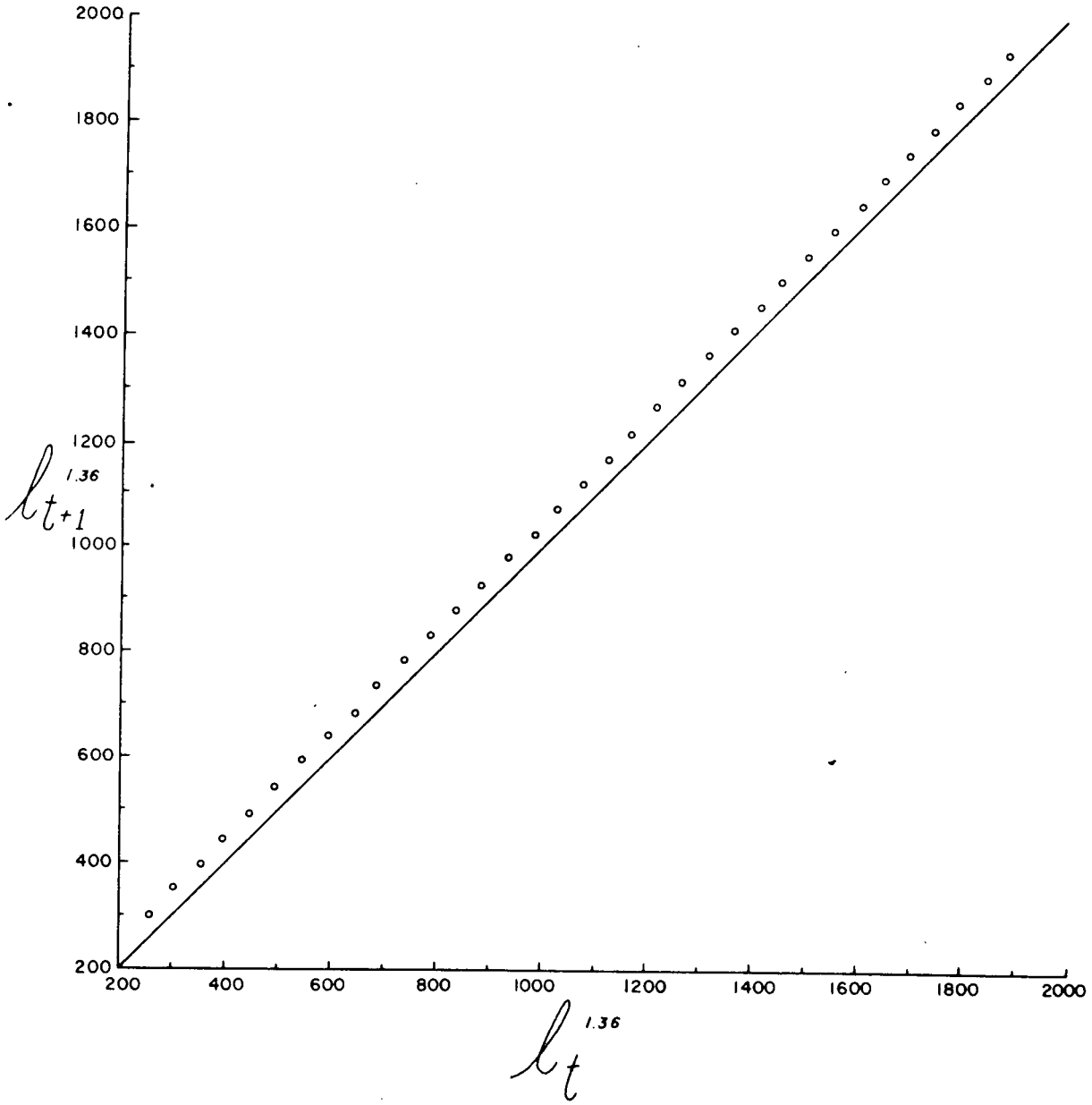

Figure 13. Plot of $l_{t+1}^{1.36}$ on $l_t^{1.36}$ for Portlock-Albatross halibut for 1956.

Table 6 . Length in centimeters at each age for 1926 and 1956 Portlock-Albatross halibut

Age in years	1926		1956	
	Observed	Calculated	Observed	Calculated
5	50.4	50.4	59.6	59.6
6	55.4	55.5	66.6	67.4
7	59.6	60.3	74.8	75.0
8	63.3	64.9	81.6	82.3
9	69.5	69.5	89.1	89.3
10	74.8	73.8	95.5	96.3
11	79.5	78.0	102.5	102.9
12	83.6	82.2	109.7	109.5
13	87.4	86.2	116.1	116.0
14	90.8	90.1	121.8	122.2
15	95.5	94.0	128.7	128.4
16	99.8	97.7	134.9	134.5
17	102.5	101.4	140.5	140.4
18	106.2	105.1	146.4	146.3
19	109.7	108.6	152.4	152.1
20	114.0	112.1	158.5	157.8
21	117.1	115.6	163.6	163.5
22	120.1	119.0	169.4	169.1
23	123.6	122.4	174.8	174.5
24	127.0	125.6	180.3	180.0
25	130.3	129.0	185.8	185.4
26	133.4	132.1	191.4	190.7
27	136.3	135.3	196.3	196.0
28	139.9	138.5	201.7	201.6
29	142.6	141.6	207.1	206.4
30	145.8	144.7	211.9	211.6
31	148.9	147.7	217.0	216.6
32	151.3	150.7	222.2	221.6
33	154.1	153.8	227.2	226.7
34	157.4	156.7	232.2	231.7
35	160.1	159.7	237.0	236.5
36	163.1	162.5	241.8	241.4
37	166.1	165.4	246.6	246.3
38	168.5	168.3	251.7	251.2
39	171.2	171.1	256.3	256.0
40	173.9	173.9	260.7	260.7

for the period of 1956 compared to that of 1926. The same is true for growth in length. Smaller values of (1-x) and z are the indications of fast growth rate.

LAKE STURGEON (Acipenser fulvescens)

Back calculated lengths of Nelson River lake sturgeon were kindly provided by Mr. L. A. Sunde of the Department of Mines and Natural Resources, Manitoba. The oldest fish from which back calculations were made was 55 years. For computational convenience only the first 21 years of back calculated growth were used. Sexes were treated separately. Walford plots of l_{t+1} on l_t for males and females are shown in Figures 14 and 15 respectively. In both cases the line of best fit approaches the 45° diagonal. The value of z for both males and females was 2.64. The transformed plot of $l_{t+1}^{2.64}$ against $l_t^{2.64}$ for males and females are shown in Figures 16 and 17 respectively.

Equations to express the growth rates are:-

$$\text{Males } l_{t+1}^{2.64} = 794.11 + l_t^{2.64}$$

$$\text{Females } l_{t+1}^{2.64} = 820.11 + l_t^{2.64}$$

Lengths at various ages were calculated using the above equations and are given in Tables 8 and 9. There was good agreement between observed and calculated lengths.

There were no significant differences in the growth rates of the sexes (Table 7).

Table 7. Analysis of variance on sturgeon for growth differences between sexes.

Source of Variance	d.f.	Sum of squares	Mean square	F ratio	Probability
Total	39	1702641.10			
Sexes	1	6733.20	6733.20	0.15	$\leq .01$
Individuals	38	1695907.90	44629.15		

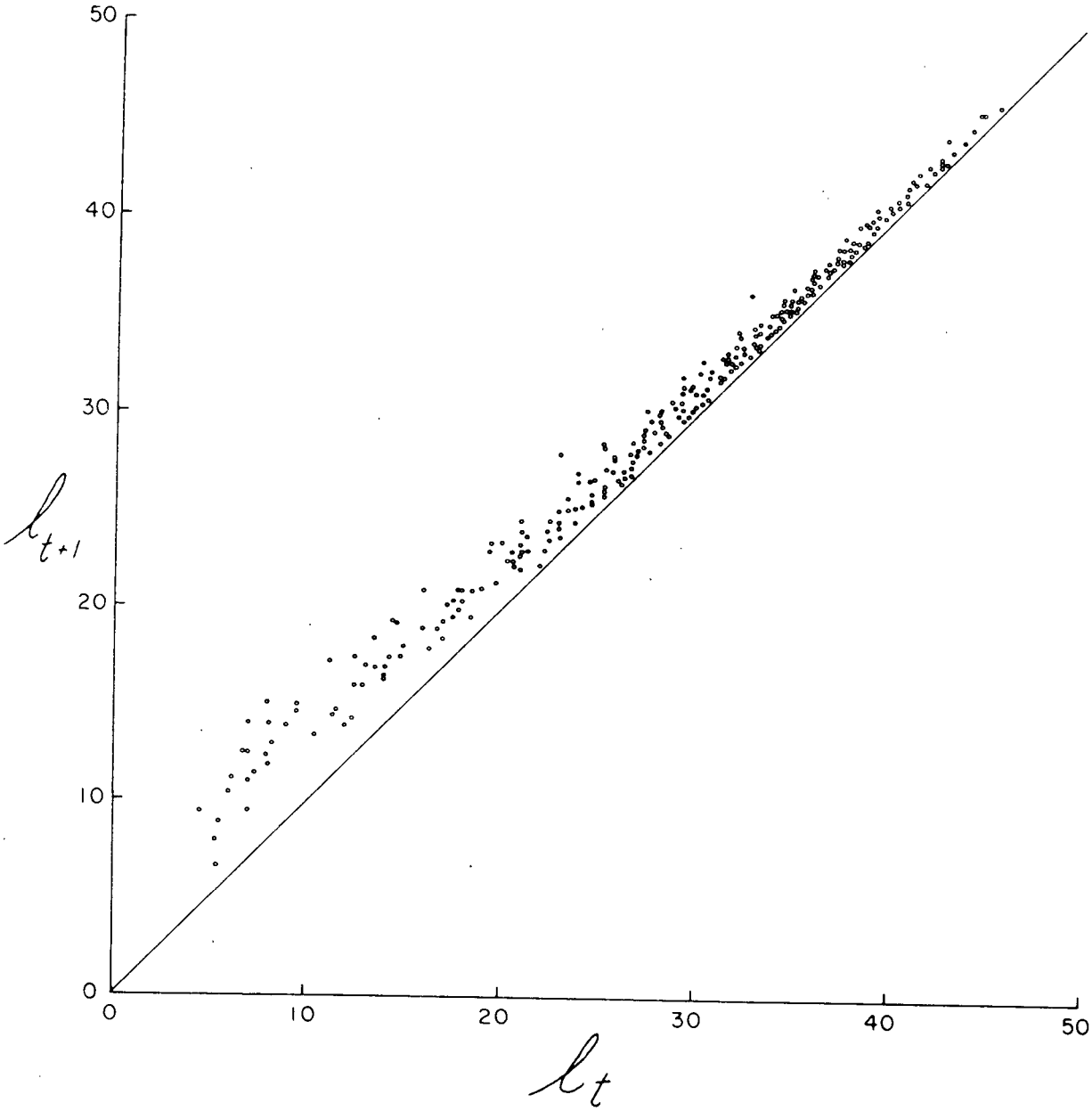

Figure 14. Plot of l_{t+1} on l_t for male lake sturgeon.

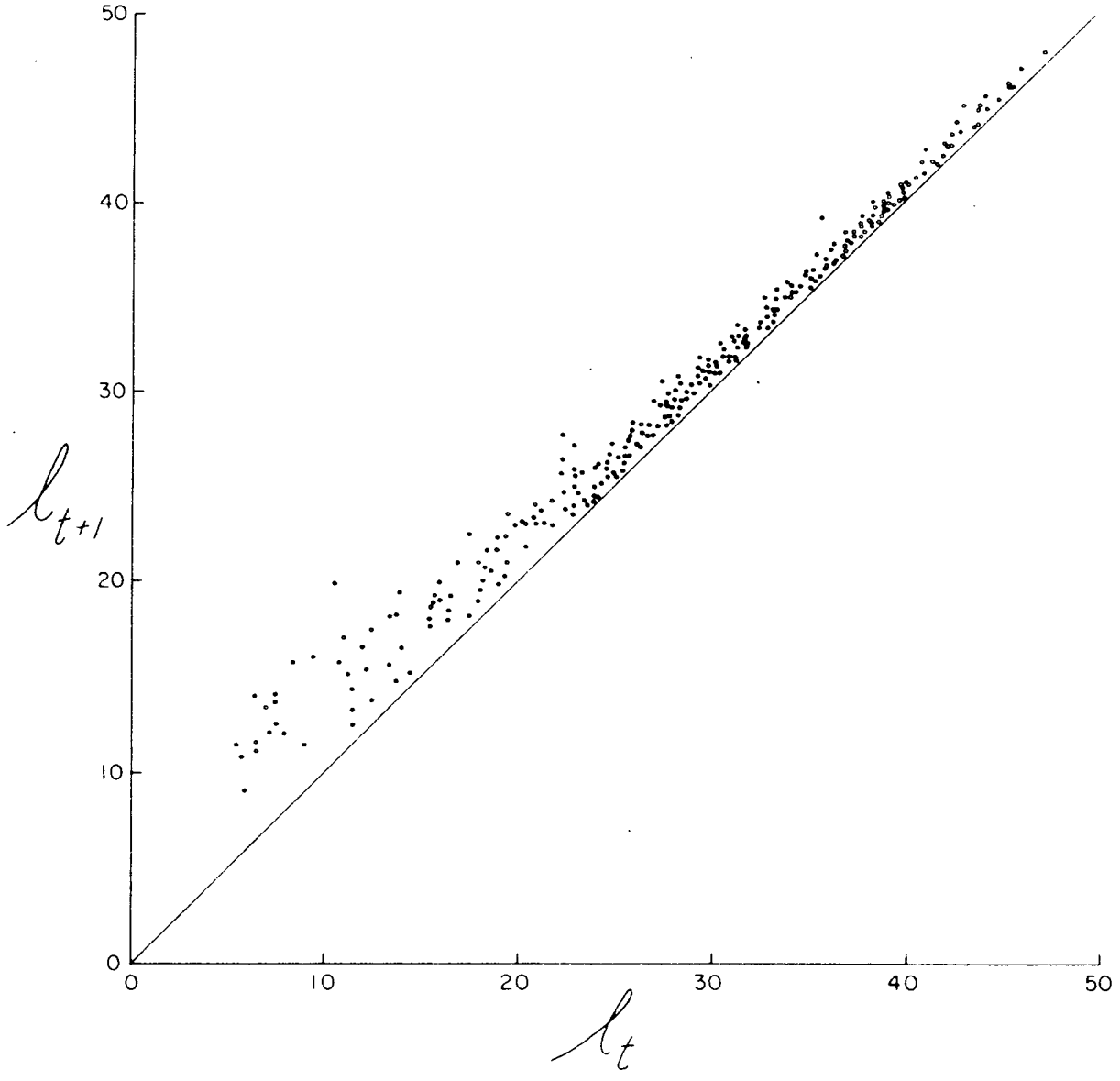

Figure 15. Plot of l_{t+1} on l_t for female lake sturgeon.

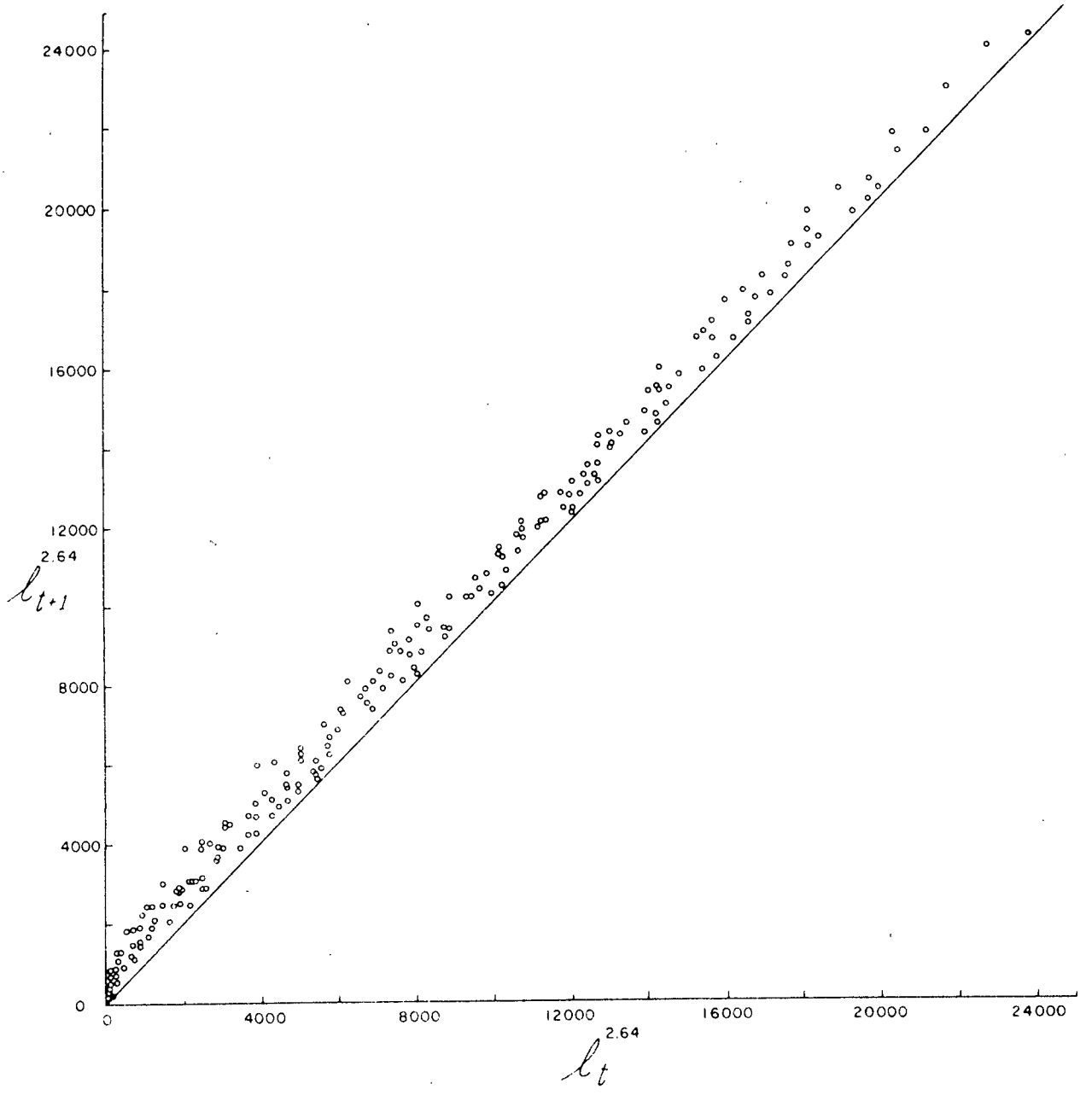

Figure 16. Plot of $l_{t+1}^{2.64}$ on $l_t^{2.64}$ for male lake sturgeon.

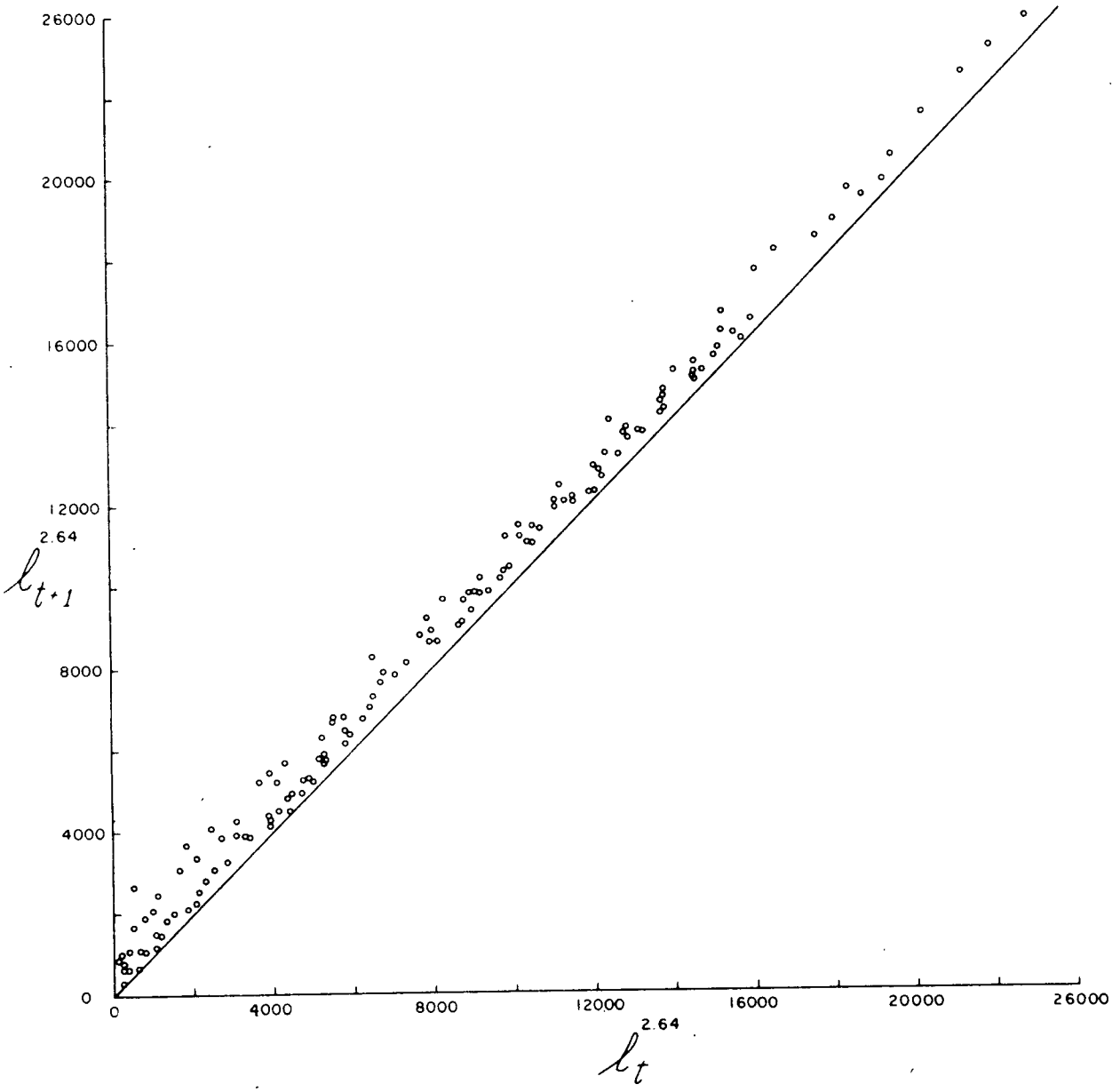

Figure 17. Plot of $l_{t+1}^{2.64}$ on $l_t^{2.64}$ for female lake sturgeon.

Growth in length was apparently rapid during the first year and decreased steadily to the age of 9 in females and 8 in males. Classen (1944) observed marked changes in growth of Acipenser sturio at the ages of 8 and 9 years and attributed the occurrence to alteration of the general metabolism, due to development of gonads. Cuerrier and Rowssow (1951) reported that male lake sturgeon matured sexually at approximately 14 years of age and females in about 25 years. Probst and Cooper (1954) observed irregularity in growth between 14 and 19 years of age. The irregularity in growth beyond the 9th year of age in Nelson River lake sturgeon cannot be explained because of the lack of information either on the environment or on the gonad development.

Since the lines of best fit on a Walford plot tend to converge to the 45° diagonal, the data were analyzed by using the Von Bertalanffy equation. The formulae obtained were

Males $l_{t+1} = 84(0.020) + 0.980\ l_t$

Females $l_{t+1} = 76(0.023) + 0.977\ l_t$

The predicted lengths at various ages by Von Bertalanffy equation for both the sexes are given in Tables 8 and 9. It can be seen from the tables that the lengths are overestimated progressively by the equation.

Table 8. Observed and calculated lengths for male sturgeon

Fork length in inches

Age in years	Observed	Calculated	
		Parker-Larkin	Von 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	24.2
6	23.43	23.43	25.4
7	25.19	25.04	26.6
8	26.70	26.50	27.7
9	28.29	27.84	28.8
10	29.89	29.08	29.9
11	31.21	30.24	31.0
12	32.41	31.33	32.1
13	33.94	32.36	33.1
14	34.29	33.34	34.1
15	35.13	34.27	35.1
16	35.89	35.17	36.1
17	36.61	36.03	37.0
18	37.32	36.85	37.9
19	37.88	37.66	38.9
20	38.39	38.41	39.8
21	38.85	39.17	40.6

Table 9. Observed calculated lengths for female sturgeon
Fork length in inches.

Age in years	Observed	Calculated	
		Parker-Larkin	Von 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	24.5
6	24.29	23.85	25.7
7	26.23	25.46	26.9
8	28.01	26.93	27.9
9	29.02	28.28	29.1
10	30.20	29.52	30.1
11	31.26	30.69	31.2
12	32.20	31.79	32.2
13	33.06	32.88	33.2
14	33.98	33.82	34.1
15	34.86	34.77	35.1
16	35.72	35.67	36.0
17	36.53	36.53	36.9
18	37.33	37.37	37.8
19	38.01	38.17	38.6
20	38.63	38.95	39.5
21	39.33	39.70	40.3

WHITE STURGEON (Acipenser transmontanous)

Data for this study was procured from Pycha's (1956) publication on white sturgeon. Total lengths in inches at capture of the various age groups were used to express growth rather than back calculated lengths. A plot of l_{t+1} on l_t is shown in Figure 18. It can be seen from the Walford plot that white sturgeon puts on large annual increments for the first 6 years and thereafter there are relatively constant increments, i.e. the line of best fit almost runs parallel to the 45° diagonal. In an analysis using lengths at ages from 0-30 years z was estimated as 1.45. But the estimated lengths were under-estimated for the early ages and overestimated for the older ages. Since the line of best fit on Walford plot runs parallel to the 45° line from a length of 38.5 inches (corresponding to 6 years of age) the data was split at this size and analysed separately. The Parker-Larkin equations for depicting lengths up to the 6th year and from the 6th year onward were respectively:

$$l_{t+1}^{1.89} = 151.15 + l_t^{1.89}$$

and

$$l_{t+1}^{0.9} = 1.4037 + l_t^{0.9}$$

Transformed plots of $l_{t+1}^{1.89}$ against $l_t^{1.89}$ and $l_{t+1}^{0.9}$ against $l_t^{0.9}$ are shown in Figures 19 and 20 respectively. Lengths at various ages estimated by the above equations are tabulated in Table 10. This example has provided an excellent agreement between observed and calculated lengths. The analysis underlines the fact that the data should be split at a length of 38.5 inches as the white sturgeon follows a different growth pattern above

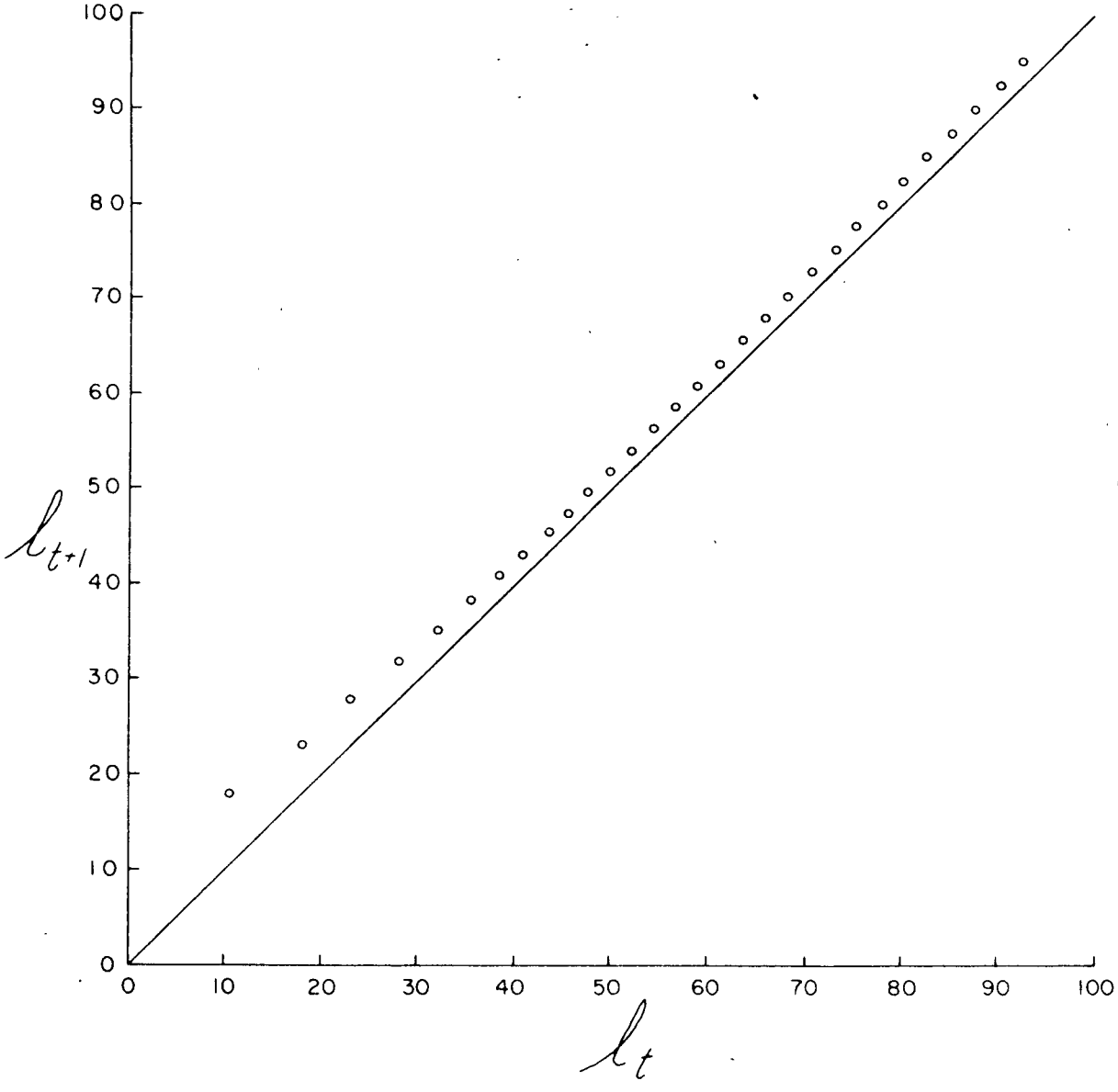

Figure 18. Plot of l_{t+1} on l_t for white sturgeon.

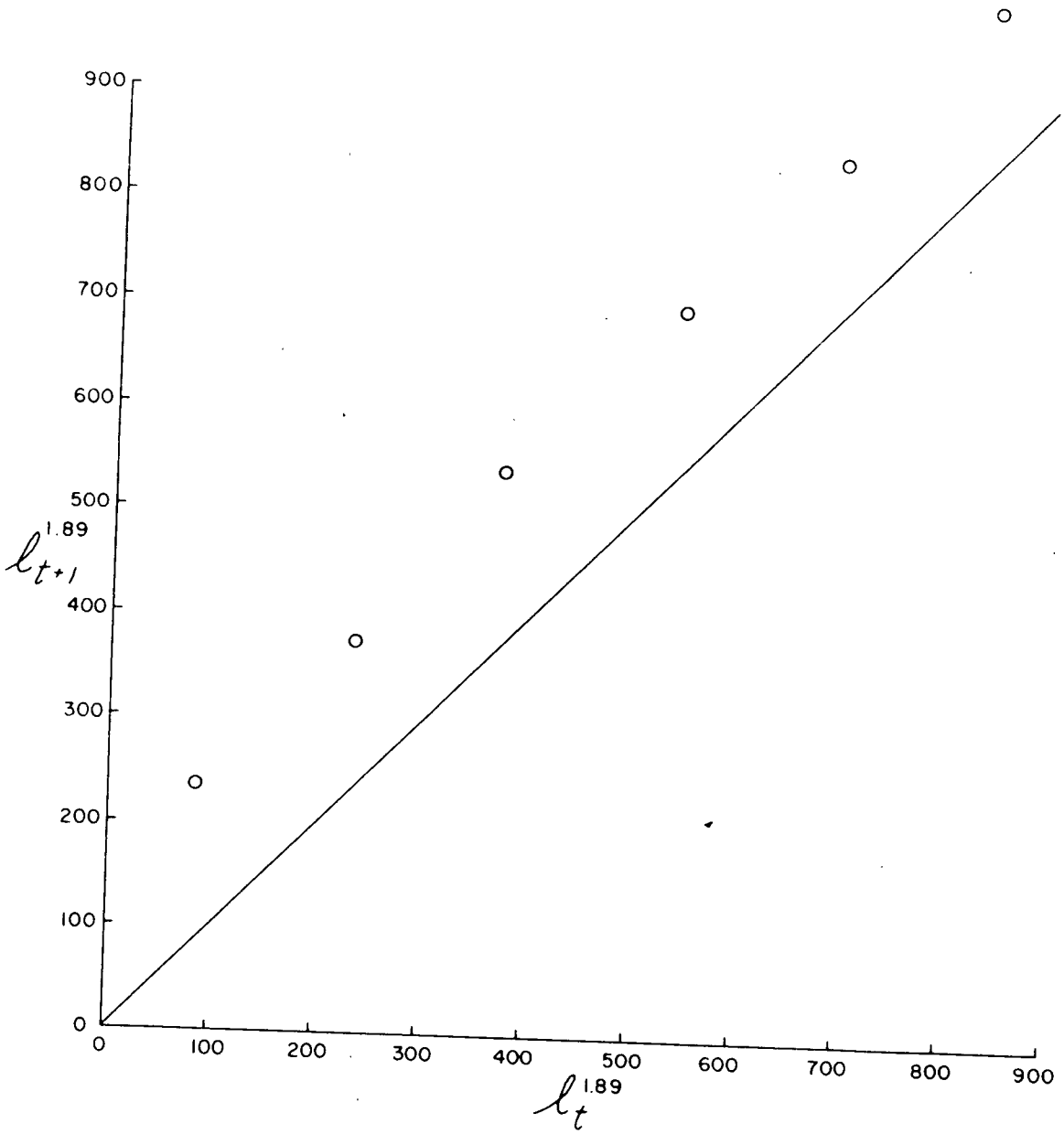

Figure 19. Plot of $l_{t+1}^{1.89}$ on $l_t^{1.89}$ for white sturgeon from 0-6 years.

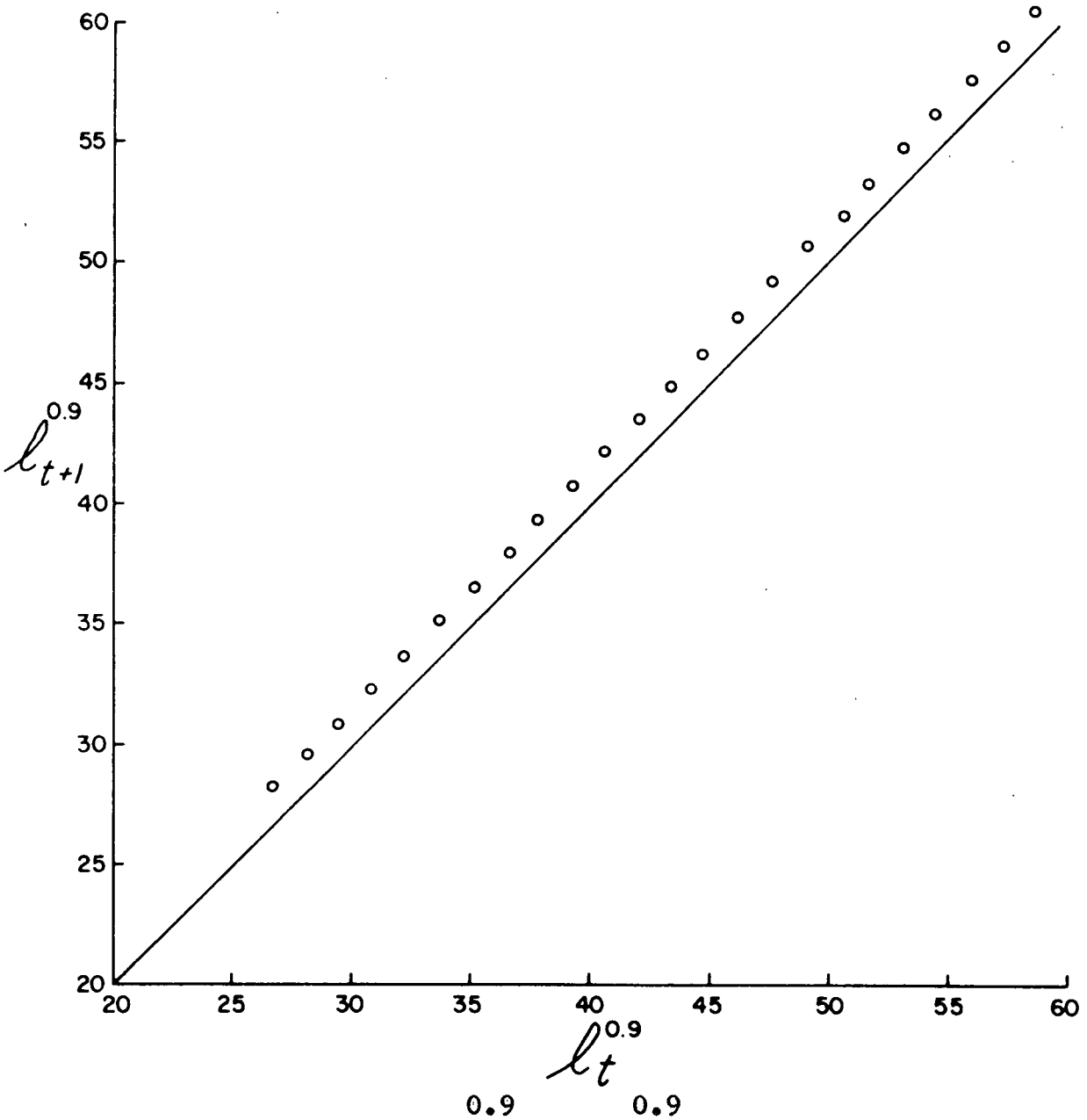

Figure 20. Plot of $l_{t+1}^{0.9}$ on $l_t^{0.9}$ for white sturgeon from 6-30 years.

Table 10. Observed and calculated lengths of white sturgeon from California waters

Age in years	Observed	Calculated	
		Parker-Larkin	Von 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

this size.

Since the line of best fit on a Walford plot for sturgeon above 6 years of age lies approximately parallel to the 45^{o} diagonal, the application of the Bertalanffy equation is not possible. Beverton and Holt (1959) tabulated the values of K and L_{∞} as 0.06 and 300 centimeters (120 inches) respectively. This could only be possible if the data on the older fish was ignored. The Von Bertalanffy equation for estimating growth with these constants is:-

$$l_{t+1} = 120(0.0582) + l_{t}(0.9418)$$

Lengths at various ages predicted by this equation are given in Table 10. It is evident from the table that the lengths are grossly overestimated at all ages above 4 years.

HERRING (Clupea pallasii).

Scales of herring from the Bella Bella area were kindly provided by Dr. F. H. C. Taylor of the Pacific Biological Station at Nanaimo. Scales were read and the back calculated lengths were used for the present investigation. Fish used in this study were five years of age caught in 1955 from the Bella Bella region.

Body-scale - relationship

Measurements of 290 scales from herring ranging in fork length from 112 to 244 millimeters were recorded. A regression line to show the relationship of fork length to the anterior radius of the magnified scale image was constructed and the appropriate formula is:

$$\log L = 0.88380 + 0.705 \log S$$

The correlation coefficient for this data is 0.93 which is highly significant. The slope 0.705 is significantly different from unity ($t = 17.56$); hence the use of direct proportion in back calculation would not be valid. Apparently the anterior radius of the scale grows relatively slower than length. These observations are partly explained by the work of Guyn (1939) who observed on Pacific herring that the growth rate of the anterior field of the scale is greater than that of body length up to a body length of about 40-50 mm. Thereafter it decreases to become less than body length growth rate. After the sixth year the scale again grows faster than the body length. The most convenient means of calculating the annual growth of the body from the growth of the scales would appear to be to construct a nomograph which took cognizance of the changing

scale to body length relationship.

However, if one is dealing only with the central period of growth as in the present case back calculations to lengths above 5 cm. should be accurate. There are two possible ways of back calculating the lengths at previous ages. (1) By assuming the slope is constant and the intercept is variable and (2) by keeping the intercept constant on the assumption that individual fish have a different slope from the other. The first method is obviously ridiculous in such variable data, for in back calculation the ranges in sizes at the end of the first year would be enormous. Accordingly, all the back calculations are made by the second method, keeping the intercept constant and assuming variable slopes.

Growth Rate.

Back calculated fork lengths in millimeters of the 5 year old herring are used. The sexes are treated separately. Walford plots of l_{t+1} against l_t for females and males are shown in Figures 21 and 22. In both the figures the points could yield a line of best fit that would intersect the 45^{o} diagonal. The values of z for the sexes were estimated and the corresponding equations are:-

$$\text{Females} \quad {}^{3.5}l_{t+1} = 8856.22 + {}^{3.5}l_t$$

$$\text{Males} \quad {}^{3.1}l_{t+1} = 2021.48 + {}^{3.1}l_t$$

Corresponding plots of ${}^{z}l_{t+1}$ on ${}^{z}l_t$ are shown in Figures 23 and 24. The data were analysed using the Von Bertalanffy equation

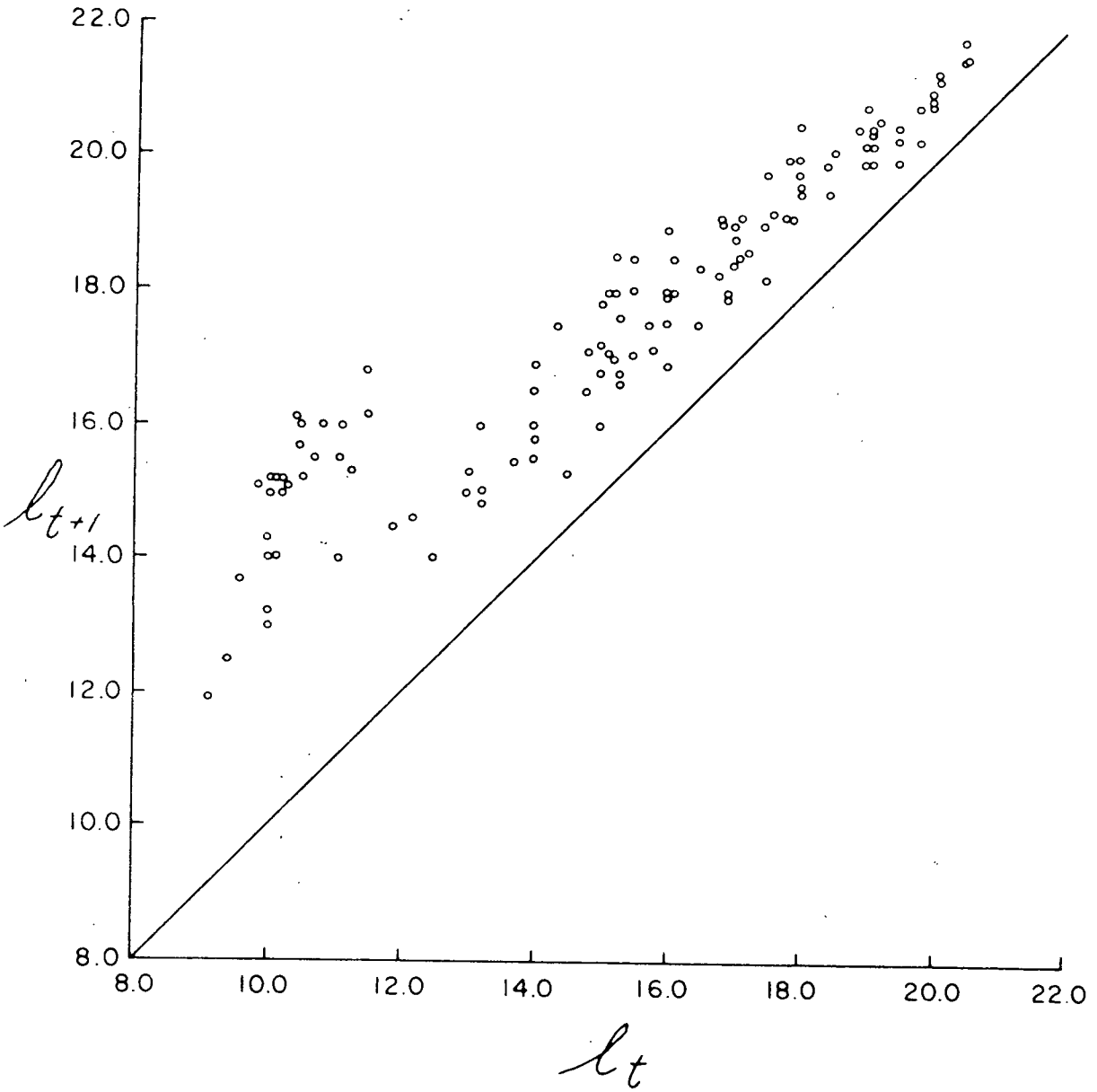

Figure 21. Plot of l_{t+1} on l_t for female herring from Bella Bella region.

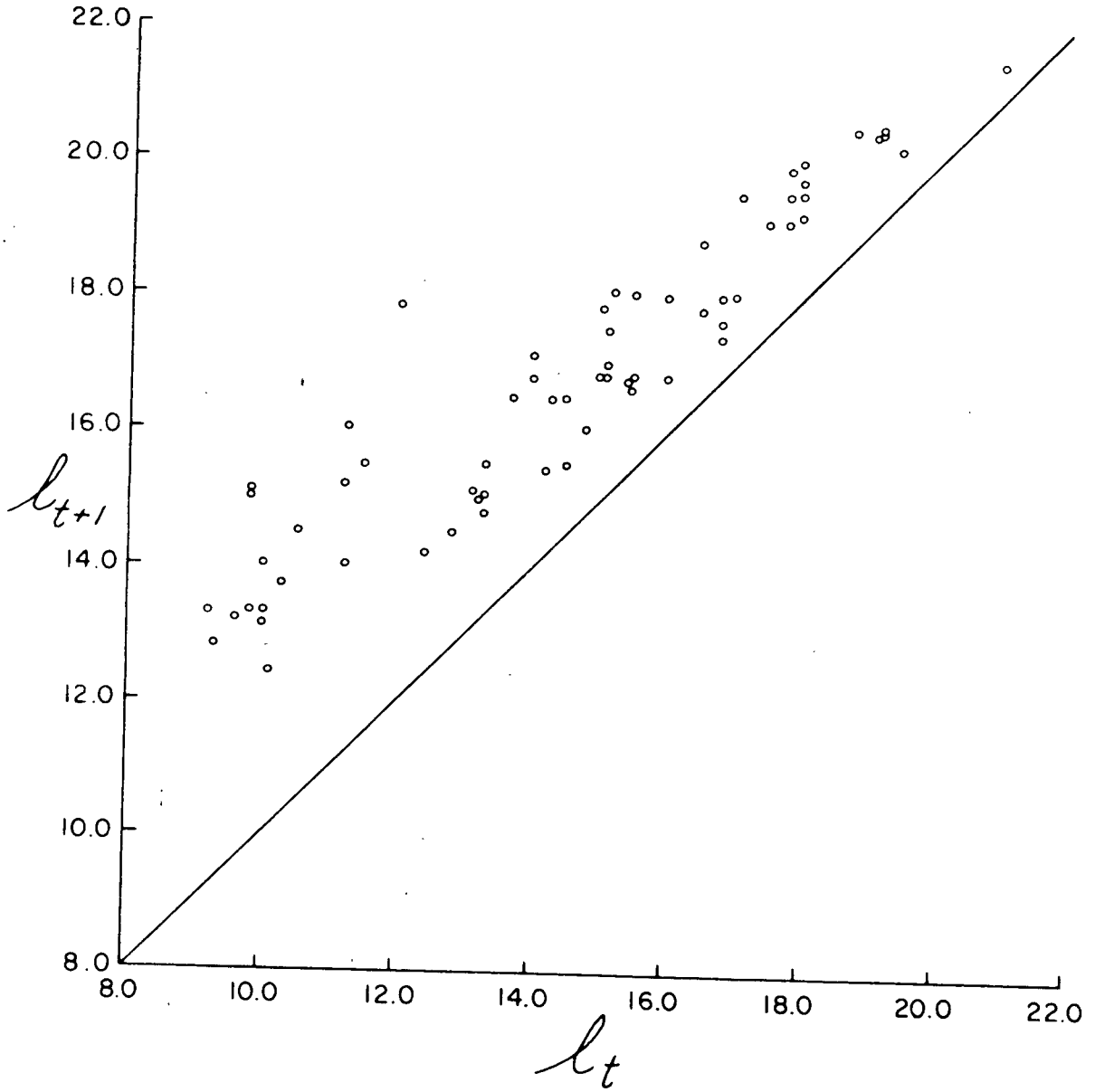

Figure 22. Plot of l_{t+1} on l_t for male herring from Bella Bella region.

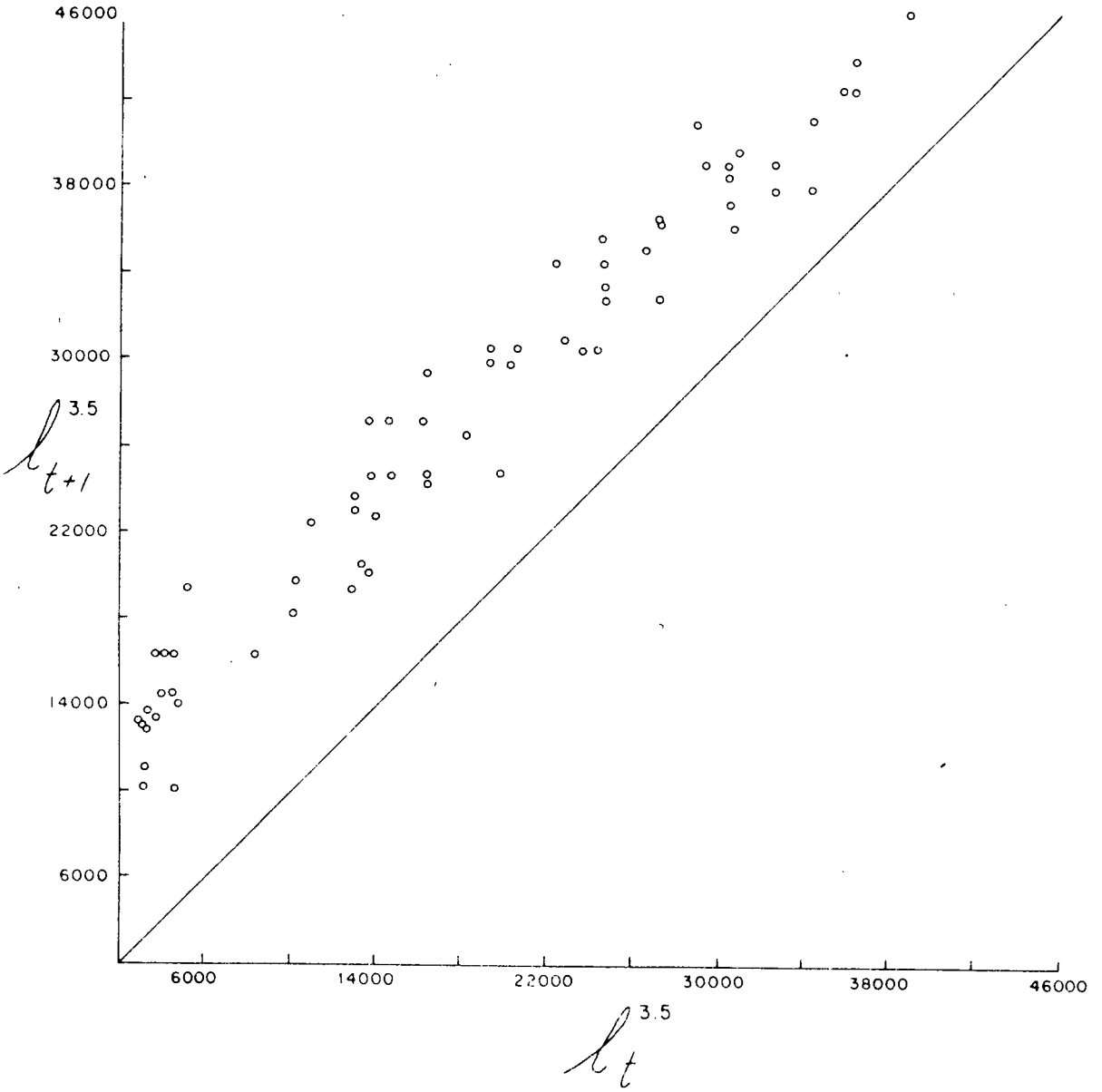

Figure 23. Plot of $l^{3.5}_{t+1}$ on $l^{3.5}_{t}$ for female herring from Bella Bella region.

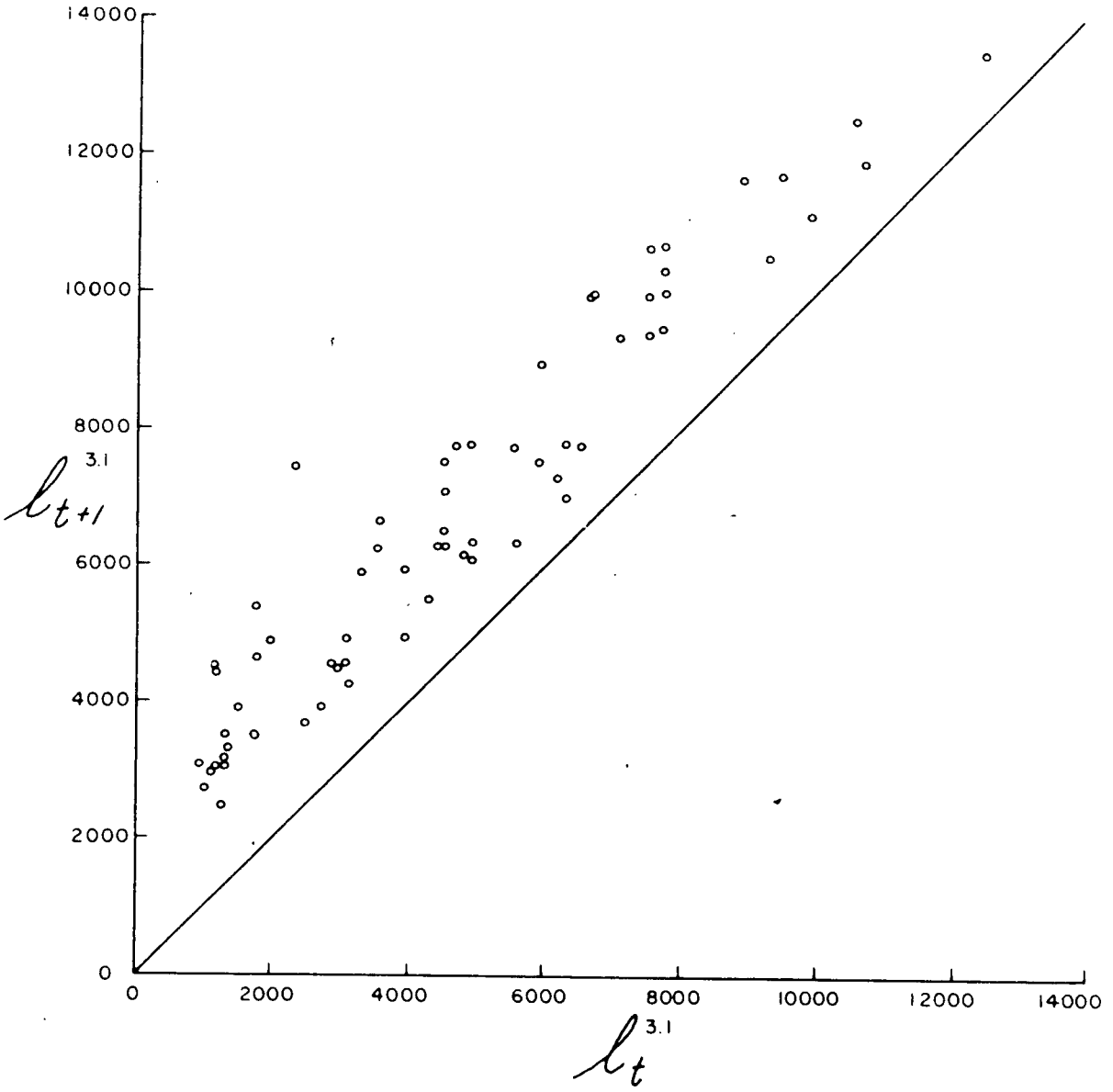

Figure 24. Plot of $l_{t+1}^{3.1}$ on $l_t^{3.1}$ for male herring from Bella Bella region.

and the growth rates can be depicted from the following formulae:

Females $l_{t+1} = 25.4(.190) + 0.810\ l_t$

Males $l_{t+1} = 27.6(.122) + 0.878\ l_t$

Lengths at higher ages calculated by Parker-Larkin and Von Bertalanffy's equations are given in Tables 11 and 12. Both the growth equations seem to predict the lengths equally well. By using the Parker-Larkin method lengths at earlier ages which do not lie on a straight line on the Walford plot could also be predicted, whereas application of the Von Bertalanffy' method is confined to the last three years of life of the 5 year old herring.

Table 11. Back calculated and calculated fork lengths for female herring.

Age in years	Back calculated	Calculated	
		Parker - Larkin	Von 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 12. Back calculated and calculated fork lengths for male herring.

Age in years	Back calculated	Calculated	
		Parker - Larkin	Von Bertalanffy
1	10.32	10.31	
2	14.24	15.09	
3	16.48	16.06	16.06
4	18.04	17.77	17.61
5	19.05	19.19	18.99

CUTTHROAT TROUT (Salmo clarkii)

Back calculated lengths of 5 year old cutthroat trout caught in 1958 from Kiakho Lake, B. C. were kindly provided by Mr. C. E. Stenton, Fish and Game Branch of B. C. A Walford plot of l_{t+1} on l_t is given in Figure 25. The general trend of points for cutthroat trout is parallel to the 45° diagonal suggesting that z = 1. The quadratic solution for z yields the value of 1.01; the computer solution was 0.94. The plot of $l_{t+1}^{0.94}$ on $l_t^{0.94}$ is shown in Figure 26.

While the use of the Parker-Larkin equation would permit more accurate prediction of growth than a Von Bertalanffy line fitted on the Walford transformation, it is obvious that the Parker-Larkin equation does not eliminate the "hump" in the scatter of points which occurs between the lengths of 10 to 20 centimeters. Table 13 gives the analysis of variance of values for various age intervals, the significant F value reflecting the real existence of the "hump". Two explanations could be offered for this hump: (1) there is an inflection in growth rate at about 15 cm in which case the data should be split at the inflection and the two parts treated separately or (2) because different environmental conditions may have prevailed in different years, the year of growth which largely corresponds to the hump may have been particularly favourable of the other years of growth unfavourable.

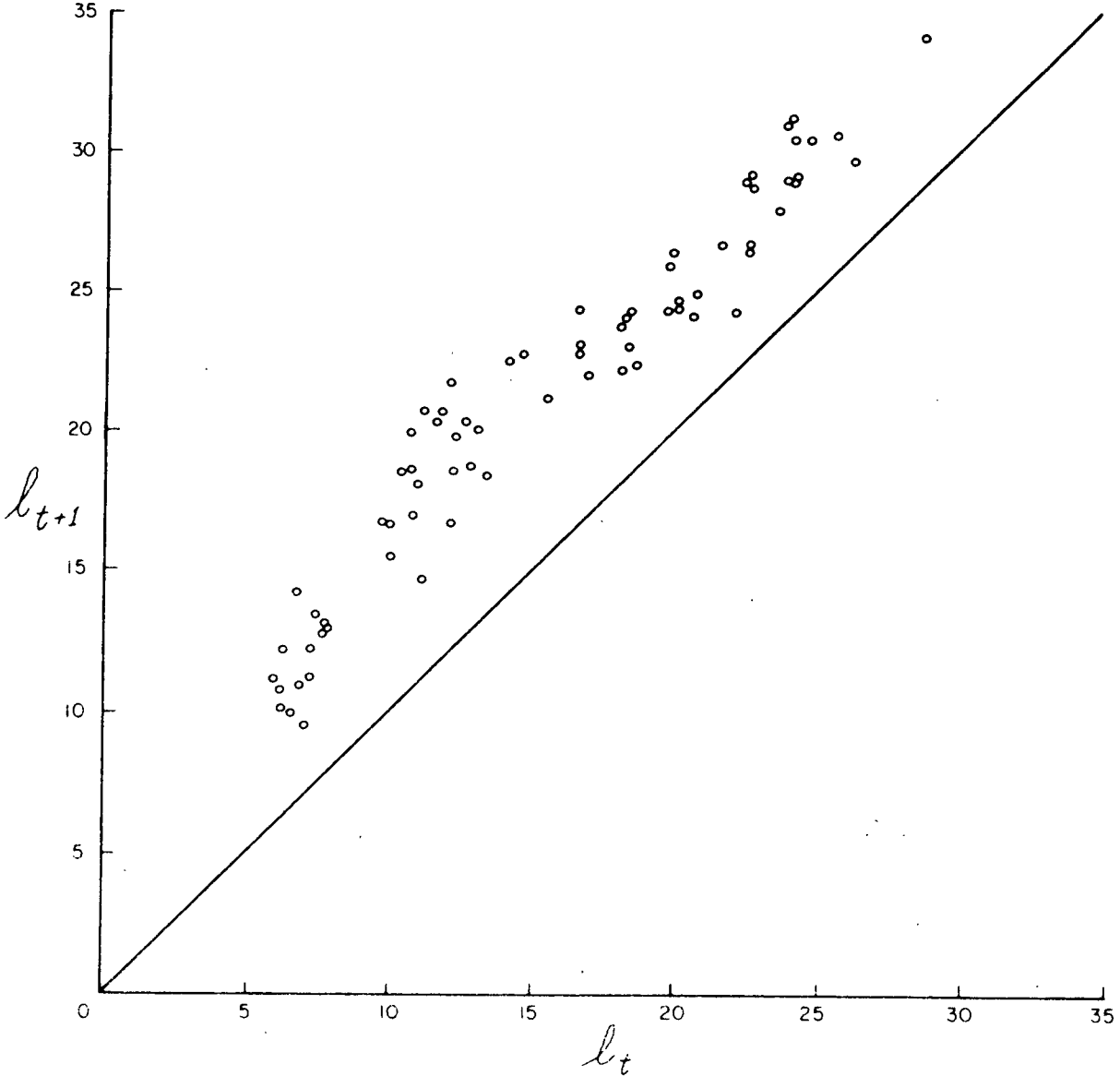

Figure 25. Plot of l_{t+1} on l_t for cutthroat trout from Kiakho Lake, B. C.

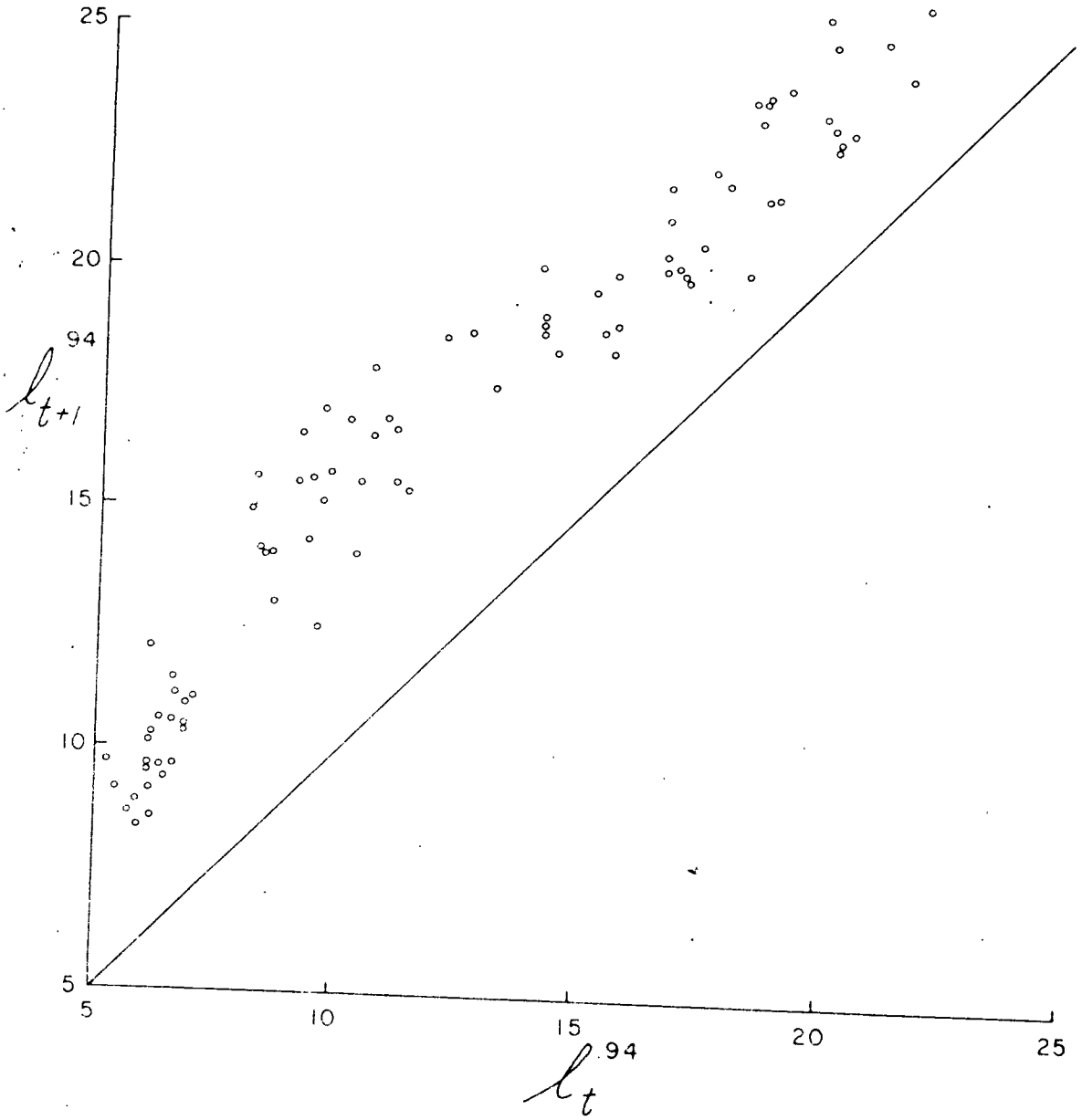

Figure 26. Plot of $l_{t+1}^{0.94}$ on $l_t^{0.94}$ for cutthroat trout from Kiakho Lake, B. C.

Table 13 . Analysis of variance on α values of cutthroat trout in different age intervals.

Source of variance	d.f.	Sum of squares	Mean square
Total	91	168.3548	
Mean	3	61.4352	20.4784
Individual	88	106.9196	1.2149

$$F = \frac{20.4784}{1.2149} = 16.8 \quad P = \quad < .01$$

Both explanations find support in field data. In their first year, Kiakho Lake fish reside in an outlet stream, migrating as yearlings between 10 and 15 centimeters into the lake. Hence there would be some justification for splitting the data as representative of the two environments, just as Parker and Larkin (1959) did for steelhead trout. On the other hand, the stream environment is strikingly variable from year to year in its favourability for growth and survival of young cutthroat. Accordingly, different year classes enter the lake at different sizes and strikingly different densities. Each year class then would show a pattern of growth reflecting the particular conditions that prevailed in the environment during its life. This is apparently true because 4 year old cutthroat caught in 1958 show no hump at 10 to 20 centimeters. Moreover, they yield an estimate of 0.7 for z (Stenton 1960) which would reflect good growth conditions for larger fish combined with poor growth conditions for smaller fish.

The analysis underlines that adequate estimation of z

hinges upon uniformity of environment. When the environment is variable, z could be calculated from observed increments in growth in the same year of fish of various sizes. In the Kiakho Lake situation the added precaution might be taken of splitting the growth in stream and lake environments. Having estimated z in this way, α values for a particular year are indices of environmental conditions (as they should be according to Parker and Larkin). This procedure runs the risk of bias from selection of fast growing fish by the fishery but it seems a lesser evil than spurious estimation of z from fluctuating environmental conditions. It is also consistent with the contention that z is a physiological constant and that differences in observed growth rate are caused by changes in environment.

Lengths at various ages are calculated according to the equation

$$l_{t+1}^{0.94} = 4.32 + l_t^{0.94}$$

The observed and calculated lengths are shown in Table 14.

Table 14. Observed and calculated lengths of cutthroat trout

Age in years	Fork length in centimeters	
	Observed	Calculated
I	7.01	7.07
II	11.54	12.34
III	18.71	17.74
IV	23.98	23.25
V	28.99	28.83

RAINBOW TROUT (Salmo gairdnerii)

Suitability of an environment for fish is reflected in the growth of the fish. For this purpose growth of rainbow trout from three lakes in British Columbia was investigated. The lakes chosen for study were Paul Lake, Loon Lake and Beaver Lake.

Paul Lake

The growth of rainbow trout in various years in Paul Lake has been described in several publications (Larkin et al. 1950, Larkin and Smith 1954, Crossman and Larkin 1958). To avoid complications arising from changes in growth rate during the period of an explosive increase of redside shiners (Richardsonius balteatus) the data selected for the present study apply to the 1946 year class, caught from 1946-49 as three year olds.

A Walford plot of l_{t+1} against l_t for three year old rainbow trout is shown in Figure 27. These points could yield a line of best fit that would intersect the 45° diagonal and hence the value of z could be expected to be more than one. By quadratic approximation z was estimated as 1.1, and by computer 1.3. Figure 28 shows $l_{t+1}^{1.3}$ plotted against $l_t^{1.3}$. The general equation for Paul Lake trout in terms of length is

$$l_{t+1}^{1.3} = 39.5609 + l_t^{1.3}$$

Mean growth increments between ages are

$$\alpha_{12} = 43.7436$$

$$\alpha_{23} = 35.3792$$

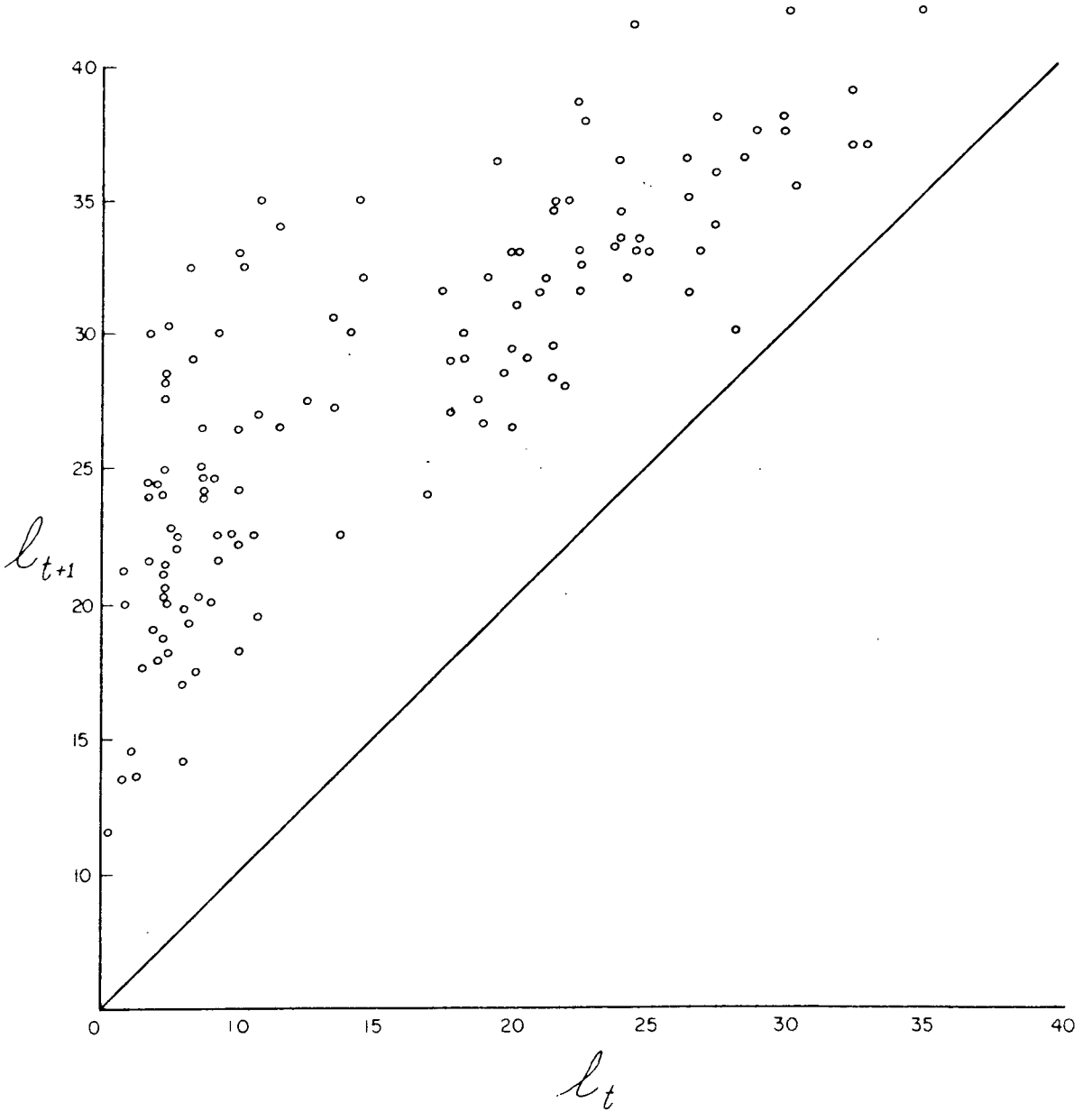

Figure 27. Plot of l_{t+1} on l_t for rainbow trout from Paul Lake, B. C.

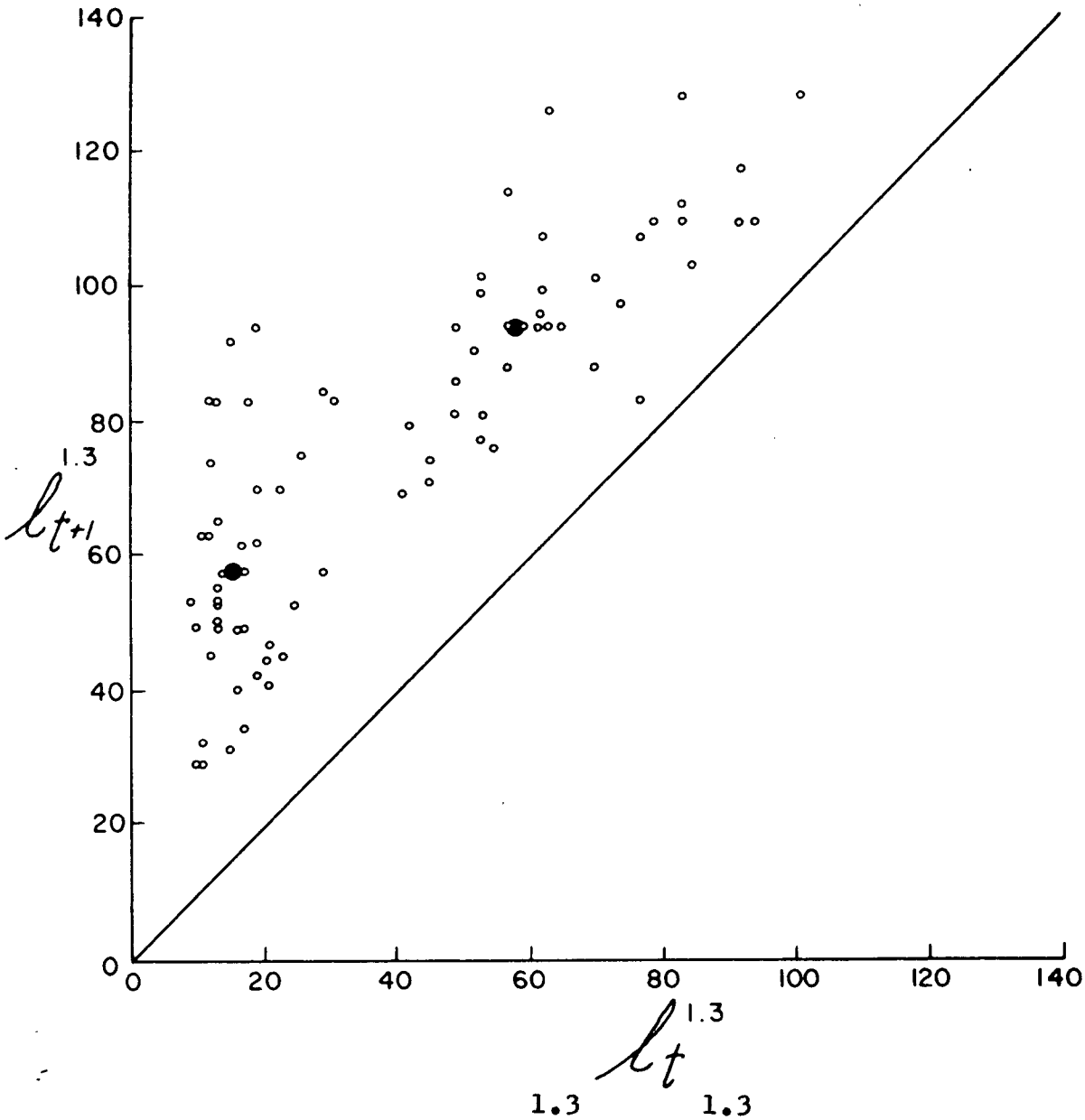

Figure 28. Plot of $l_{t+1}^{1.3}$ on $l_t^{1.3}$ for rainbow trout from Paul Lake, B. C.

Analysis of variance (Table 15) on α values show significant differences between ages.

Table 15. Analysis of Variance of Growth Increments Between Ages.

Source of Variance	d.f.	Mean square	F ratio	Probability
Total	133			
Means	1	2343.2247		
Individuals	132	216.3224	10.8	$<.01$

From this it may be inferred that 3 year Paul Lake trout grow faster in their second year of life than is predicted (see Table 16 below). Thus the Parker-Larkin equation is not a good fit to the data - i.e. the rate of change of increments is not describable by only two parameters. The data is analyzed by the Von Bertalanffy equation as

$$l_{t+1} = 55(.323) + 0.677\ l_t$$

and the calculated lengths are shown in Table 16.

Table 16. Comparison of observed and calculated lengths of Paul Lake rainbow trout.

Age in years	Observed Fork Length in centimeters	Calculated Fork Length in centimeters	
		Parker-Larkin	Von Bertalanffy
1	8.17	8.17	-
2	22.91	21.78	22.93
3	33.04	33.07	33.04

Analysis of rainbow trout growth data after the establishment of shiners in Paul Lake indicates another possible source of error in estimating z values. Back calculated growth data for three year old trout caught in 1955 and 1956 yield a z of 0.27, suggesting rapidly increasing increments which on extrapolation

to the fourth and fifth year would produce enormous trout of 51.0 cm and 91.17 cm respectively. The spurious z value can be explained from the work of Larkin and Smith (1954) on the growth of rainbow trout in Paul Lake. Small trout eat plankton and bottom organisms for which there is intensive competition by shiners. At lengths ranging from 15 to 25 centimeters trout switch to a diet of shiners during the summer months, their growth rate responding accordingly. Parker and Larkin (1959) denote this type of change as an "ecological growth stanza" and the data should obviously be split into two groups - fish below 15 cm and fish above 25 cm. For rainbow trout from Paul Lake this is an impractical procedure because many fish mature at age 3. In consequence there are only two growth increments (1 to 2 and 2 to 3) available for z estimations. Splitting the fish into two size groups results in size hierarchy effects within each group, - which can cause underestimation of z values. The best procedure would seem to be calculation of z from pre-shiner data and using this value, to estimate for small and large fish separately, any changes in α occasioned by the shiner introduction. The assumption would be made that z is a "physiological constant," an assumption consistent with the contentions of Parker and Larkin.

Paul Lake rainbow trout offer still another complication in growth analysis, because of variation in the length-weight relationship. The relation between growth in length and growth in weight was calculated for data collected before and after the introduction of shiners into Paul Lake. Fish were separated

according to size, stage of maturity and sex.

The measurements of lengths and weights were converted to logarithms and regressions were calculated by the method of least squares. The length-weight relationship for the periods 1947 and 1959 were

$$\log W = -1.47528 + 2.75216 \log L \quad \text{(1947)}$$

$$\log W = -1.81648 + 2.91714 \log L \quad \text{(1959)}$$

where W = weight in grams

L = fork length in centimetres.

Analysis of covariance was applied to test differences in the length-weight relationship among the years 1947 and 1959. The relationship was found to differ significantly at $P < .01$ with respect to the regression coefficient and the adjusted means.

For each period separately, the relationships for the fish below and above 25 cm. in length are

1947

<25 cm.

$$\log W = -1.57847 + 2.82398 \log L$$

>25 cm.

$$\log W = -1.04865 + 2.47248 \log L$$

1959

<25 cm.

$$\log W = -1.86505 + 2.95497 \log L$$

>25 cm.

$$\log W = -2.06575 + 3.07974 \log L$$

A comparison of slopes for fish below 25 cm. in size for

the periods 1947 and 1959 was not significant but for fish above 25 cm in size the slopes were significantly different at the 1% level. For 1947 the slopes for fish below and above 25 cm in size were significantly different at the 1% level whereas they were not different for the period 1959.

In 1947 trout below 25 cm size were relatively heavier than the larger fish, whereas the reverse was true in 1959. The explanation for this phenomenon would appear to be available from the history of the lake.

For the period 1946-49 there were no significant differences in the diet of trout of various sizes (Larkin and Smith 1953). In contrast to 39.8% amphipods in the diet during 1931, in 1947-49 Daphnia formed the major food item for all sizes (Larkin et al. 1950).

Presumably, the scarcity of Gammarus did not affect growth rates of trout of less than 25 cm size because of the abundance of Daphnia. But for trout above 25 cm in size Daphnia were perhaps an inadequate source of food, and with competition for Gammarus, growth rates were low. Moreover, it would be expected that during the 1946-47 period, trout of smaller size would be in relatively better condition than large trout. This was evident in the slopes of 2.47 and 2.82 for large and small trout respectively.

From 1952 onward trout over 25 cm started preying on shiners, while fish of small size were adversely affected by competition with shiners for plankton and bottom organisms. As a result, trout regression coefficients for 1959 indicate relatively

better condition of the larger fish. Moreover for trout above 25 cm. the regression coefficients were significantly different for the years 1947 and 1959 i.e. before and after the introduction of shiners and large trout of 1959 were heavier than those of 1947. The competition for food between shiners and small trout was not reflected in a lower condition of small trout as compared to the pre-shiner priod.

There were also changes in the length-weight relationships with regard to sexes, and maturity (see Table 17).

Table 17. Log length log weight relation of rainbow trout of various sizes, sexes and stages of maturity from Paul Lake, B. C.

	Slope		Intercept	
	1946-47	1957-59	1946-47	1957-59
$<$25 cm.	2.82398	2.95497	-1.57847	-1.86505
$\geq$25 cm	2.47248	3.07974	-1.04865	-2.06575
Females	2.71613	2.91285	-1.42076	-1.80537
Immature	2.70832	2.90824	-1.42002	-1.79895
Maturing	2.27125	3.02107	-0.73438	-1.97916
Males	2.78928	2.92746	-1.53017	-1.84281
Immature	2.96087	2.79529	-1.76698	-1.67601
Maturing	2.46134	3.49777	-1.03361	-2.72078
Total	2.75216	2.91714	-1.47528	-1.81648

Length measurements are thus inadequate indications of the weight increments and basically growth comprises weight increments.

Considering all of the above observations, the Parker-Larkin growth equation would appear to be inadequate for description of the growth of rainbow trout in Paul Lake. The short life cycle, change in food habits and changes in length-weight relation seem to militate against the use of any theoretical system of orderly related increments.

Loon Lake

Back calculated lengths of 3 year old rainbow trout caught in 1952 were used. A Walford plot of l_{t+1} against l_t is shown in Figure 29. These points tend to converge to the 45^{o} diagonal. Analysis of the data yielded a z value of 1.3. The plots of $l_{t+1}^{1.3}$ against $l_t^{1.3}$ is shown in Figure 30. The Parker-Larkin growth equation for rainbow trout of Loon Lake is

$$l_{t+1}^{1.3} = 24.46 + l_t^{1.3}$$

The agreement between the observed and calculated lengths was very satisfactory. (Table 18).

Table 18. Comparison of observed and calculated lengths of Loon Lake rainbow trout.

Age in years	Fork length in centimeters		
	Observed	Calculated	
		Parker-Larkin	Von Bertalanffy
1	7.08	7.06	-
2	15.97	15.81	15.99
3	23.17	23.18	23.60

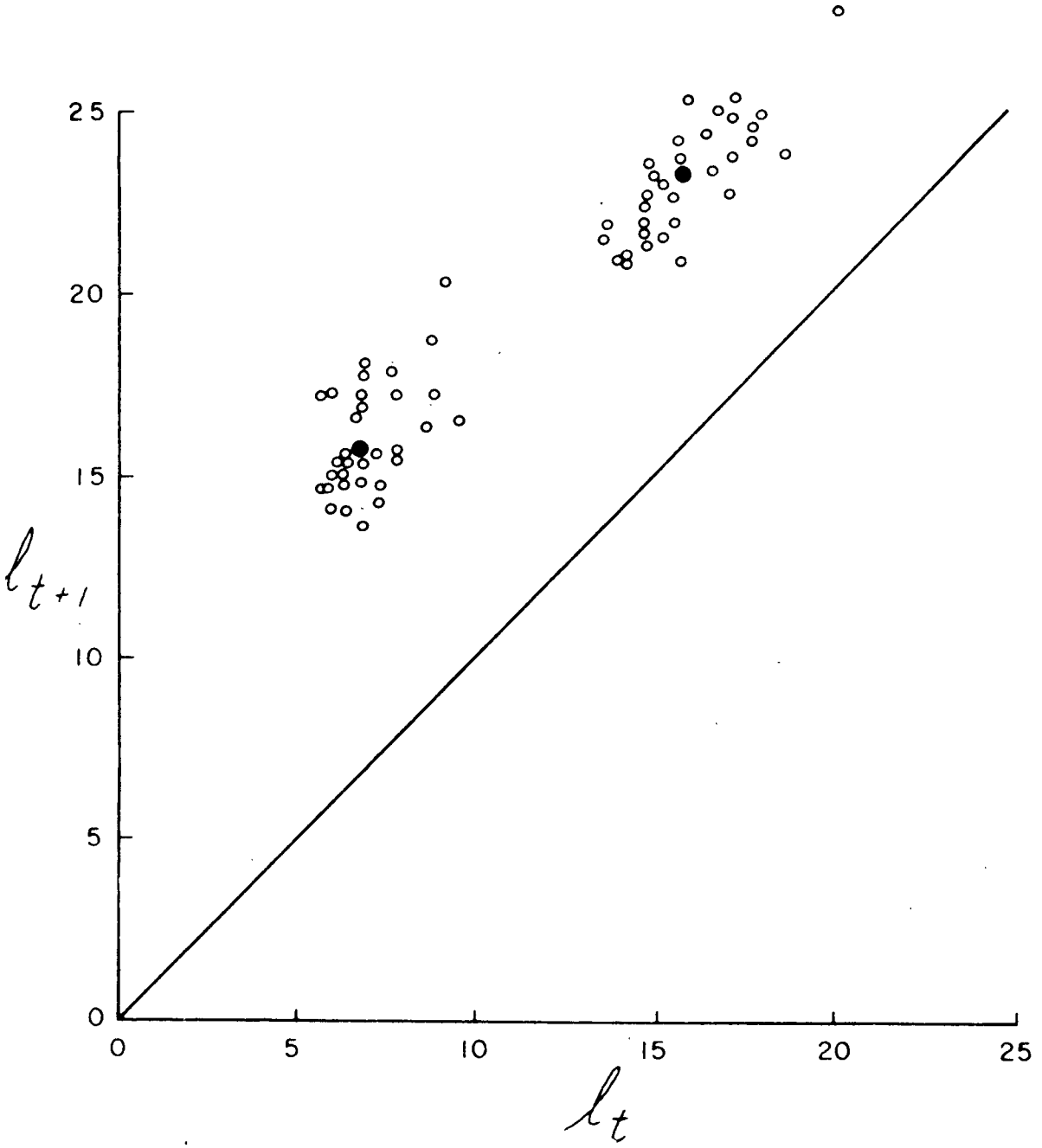

Figure 29. Plot l_{t+1} on l_t for rainbow trout from Loon Lake, B. C.

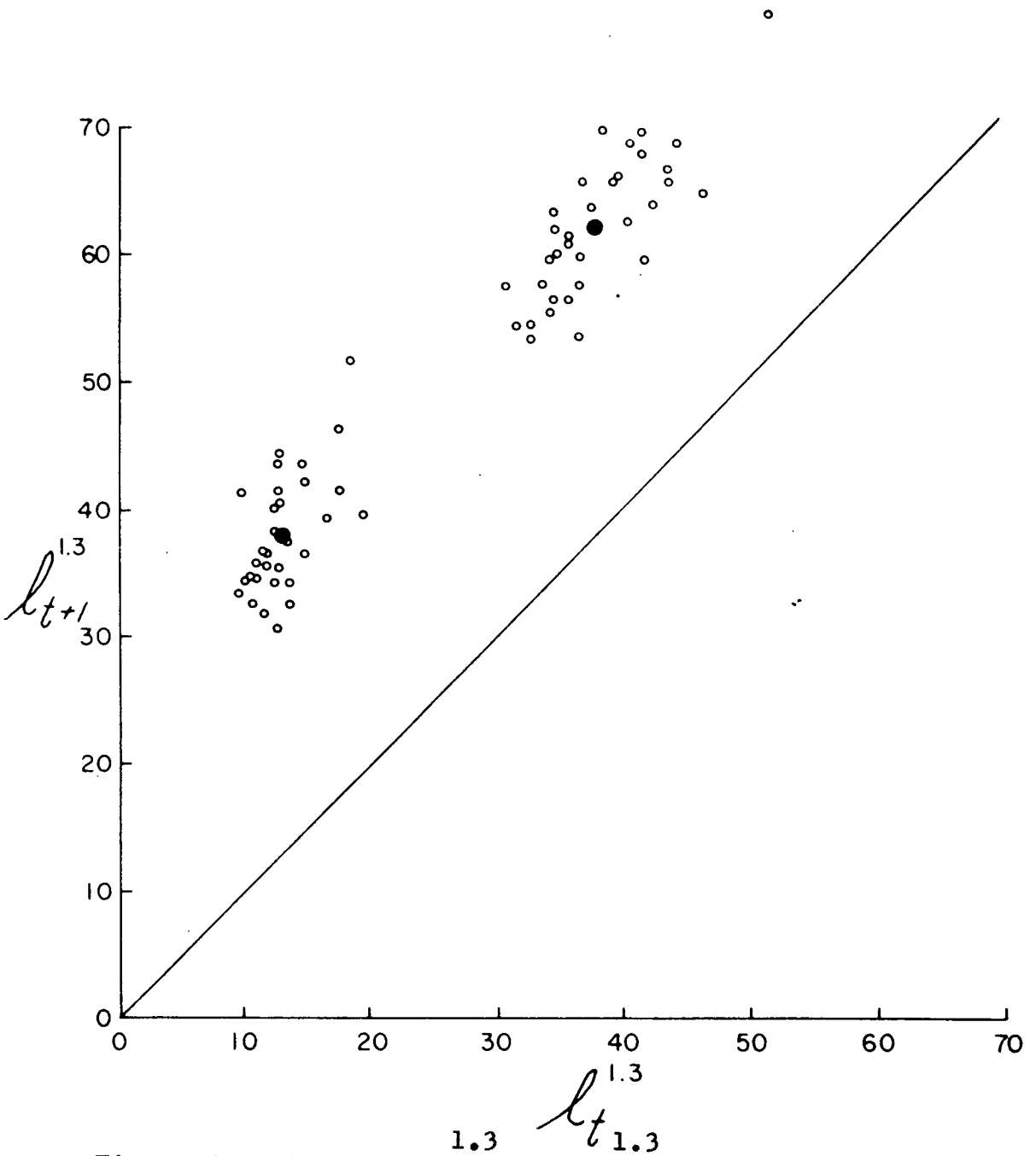

Figure 30. Plot of $l_{t+1}^{1.3}$ on $l_t^{1.3}$ for rainbow trout from Loon Lake, B. C.

In Loon Lake where there are only rainbow trout, the decline in growth rate follows a definite trend with increasing length (Larkin et al. 1950). As a result the estimate of exponent z in the Parker-Larkin equation is a reliable measure to express growth rate of rainbow trout in Loon Lake. The data were analysed by the Von Bertalanffy equation as the line of best fit of the Walford plot coverges to the 45° diagonal. The estimated equation is

$$l_{t+1} = 60(.173) + l_t\ 0.8270$$

The agreement between observed and calculated lengths is as good as that of Parker-Larkin equation (Table 18).

Beaver Lake

Back calculated lengths of three year old rainbow trout of the year classes 1952 and 1953 caught in 1955 and 1956 respectively are plotted to give the Walford line represented in Figures 31 and 32. For the 1952 year class the line of best fit would intersect the 45° diagonal and the value of z was estimated as 1.14. Figure 33 shows the transformed data raised to the power 1.14. Analysis of data for the 1953 year class gave a z of 0.65 which indicates that the growth increments get bigger as the fish grow older. The plot of $l_{t+1}^{.65}$ against $l_t^{.65}$ is shown in Figure 34. These two different values of z might be due to the varying growth rates of the year classes responding accordingly to the strength of the year classes.

A similar situation can be demonstrated in the data from Paul Lake, where z values from 0.8 to 1.4 were obtained for different individual year classes from 1946 to 1949. It may be summarized on the basis of these observations that the application of the Parker-Larkin equation is made difficult for rainbow trout due to short life span and variations in year class strength.

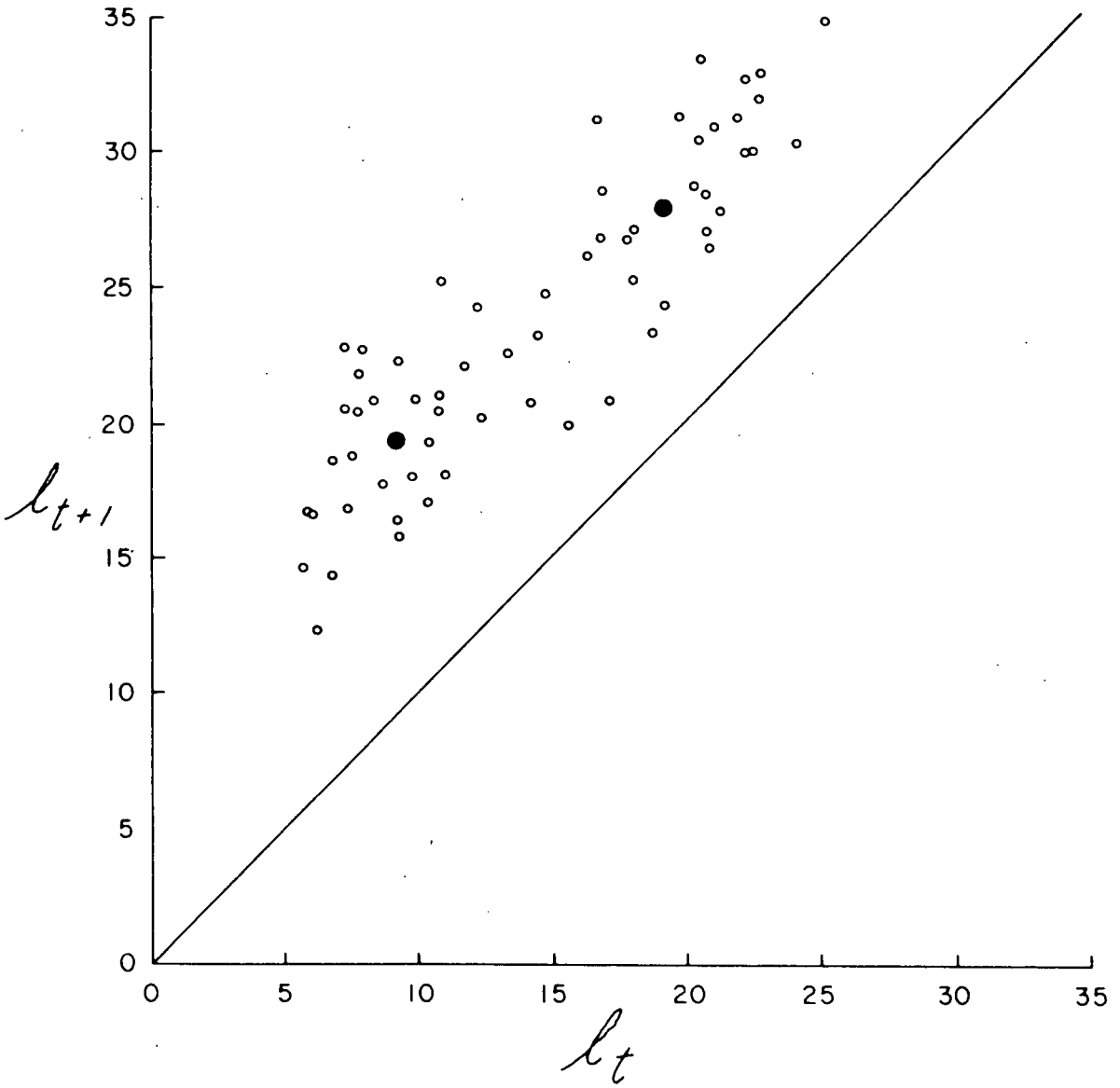

Figure 31. Plot of l_{t+1} on l_t for 1952 year class rainbow trout from Beaver Lake, B. C.

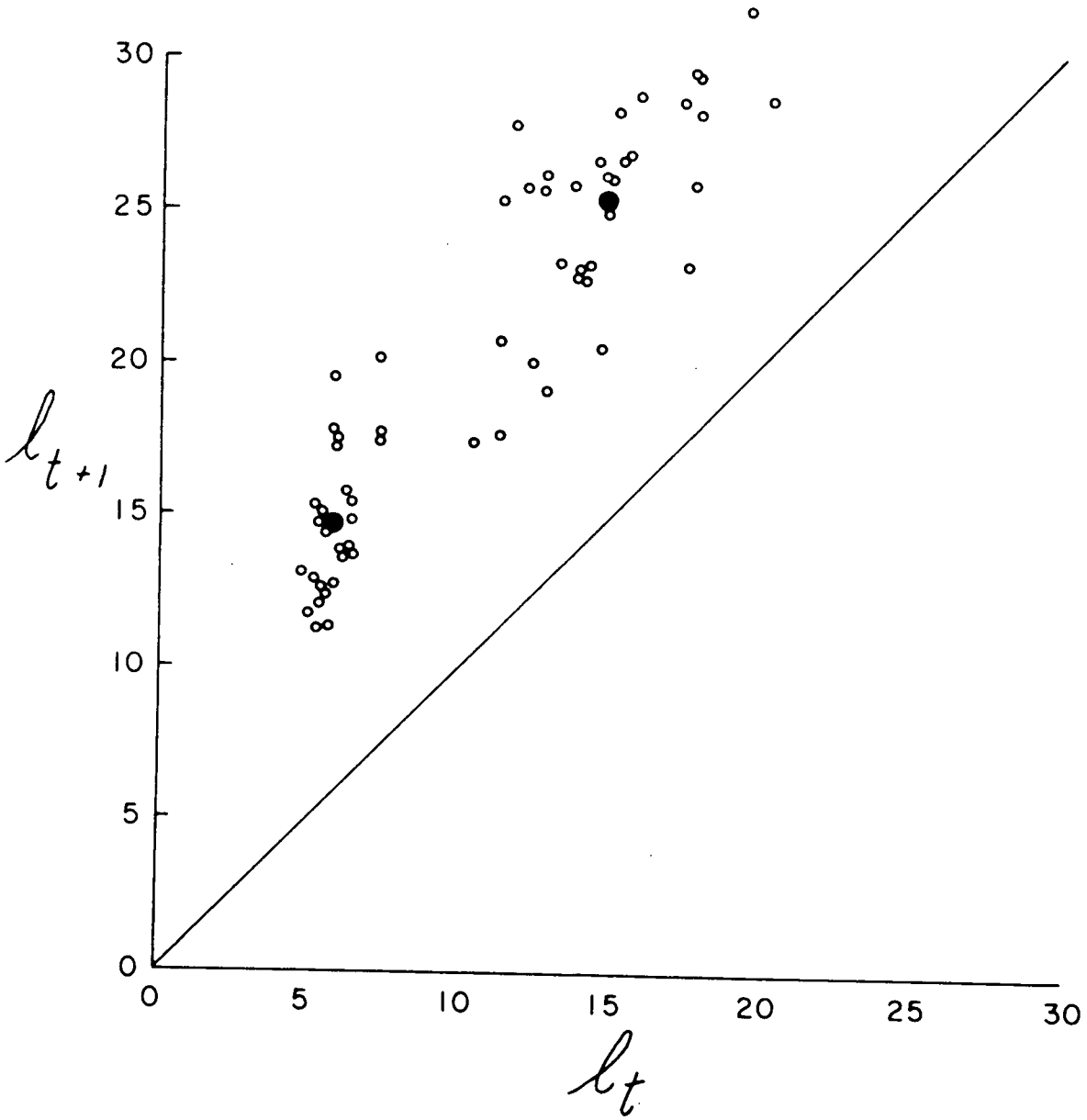

Figure 32. Plot of l_{t+1} on l_t for 1953 year class rainbow trout from Beaver Lake, B. C.

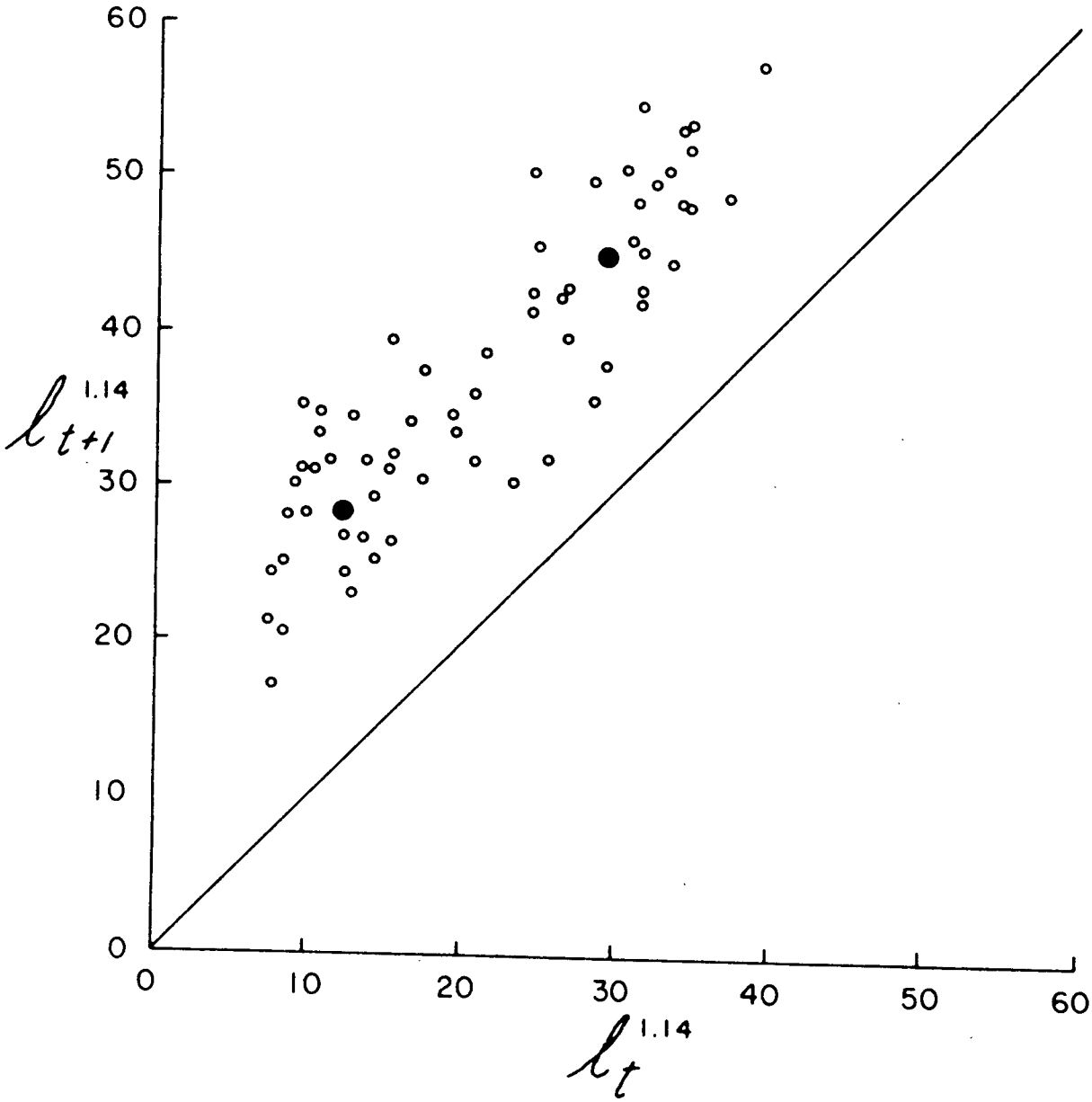

Figure 33. Plot of $l_{t+1}^{1.14}$ on $l_t^{1.14}$ for 1952 year class rainbow trout from Beaver Lake, B. C.

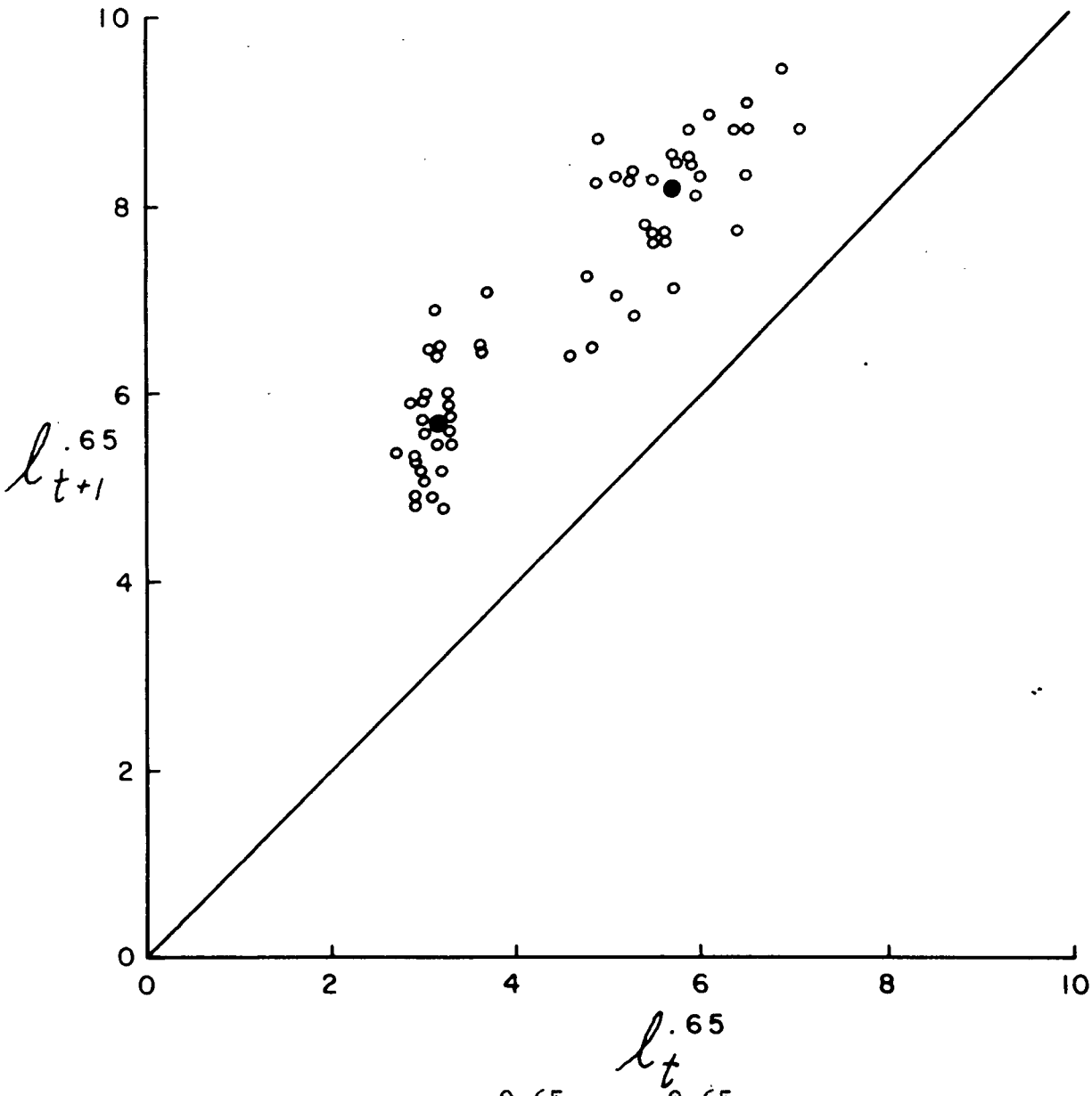

Figure 34. Plot of $l_{t+1}^{0.65}$ on $l_t^{0.65}$ for 1953 year class rainbow trout from Beaver Lake, B. C.

SCALLOPS (Placopecten magellanicus)

Dr. L. Dickie of the Atlantic Biological Station, St. Andrews, New Brunswick, kindly provided back calculated shell heights of scallops (Placopecten magellanicus) which were used in his study of this species on various Atlantic seaboard grounds (Dickie 1954, 1955). Scallops from Hour ground and Buoy ground are used for the present study.

The Walford plot of l_{t+1} on l_t is shown in Figure 35 for scallops from the Hour ground. Growth is sigmoid, so that the points first diverge from the 45° diagonal up to a shell height of 70 to 80 mm, corresponding to an age of approximately six years. Beyond this shell height the line of best fit approaches the 45° diagonal, thus showing an accelerating growth and then a decelerating growth. For this reason the Von Bertalanffy formula can only be applied to the older specimens. For the Parker-Larkin method the data must be split at the point of inflexion i.e. approximately at the age of six years. For the first six years of growth, analysis of the data yielded a z value of 0.625. The Parker-Larkin transformation of $l_{t+1}^{0.625}$ on $l_t^{0.625}$ is shown in Figure 36. The formula for expressing the growth during the accelerating growth phase is:-

$$l_{t+1}^{0.625} = 2.798 + l_t^{0.625}$$

Calculated and observed shell heights are shown in Table 19. The decelerating phase of growth from six to nine years yielded a z of 3.6. The equation for the decelerating phase of growth is:-

$$l_{T+1}^{3.6} = 674.469 + l_t^{3.6}$$

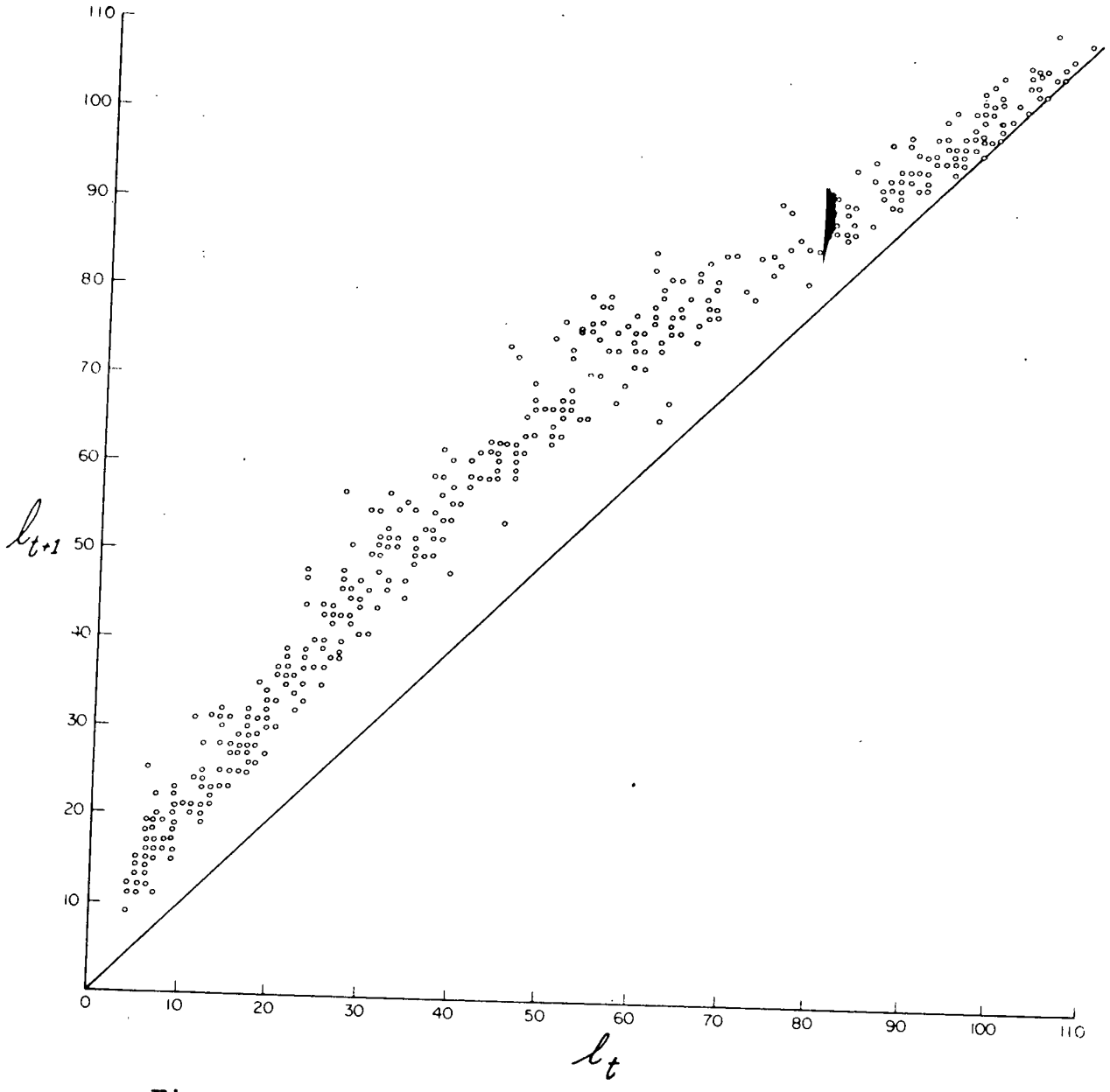

Figure 35. Plot of l_{t+1} on l_t for scallops from the Hour ground.

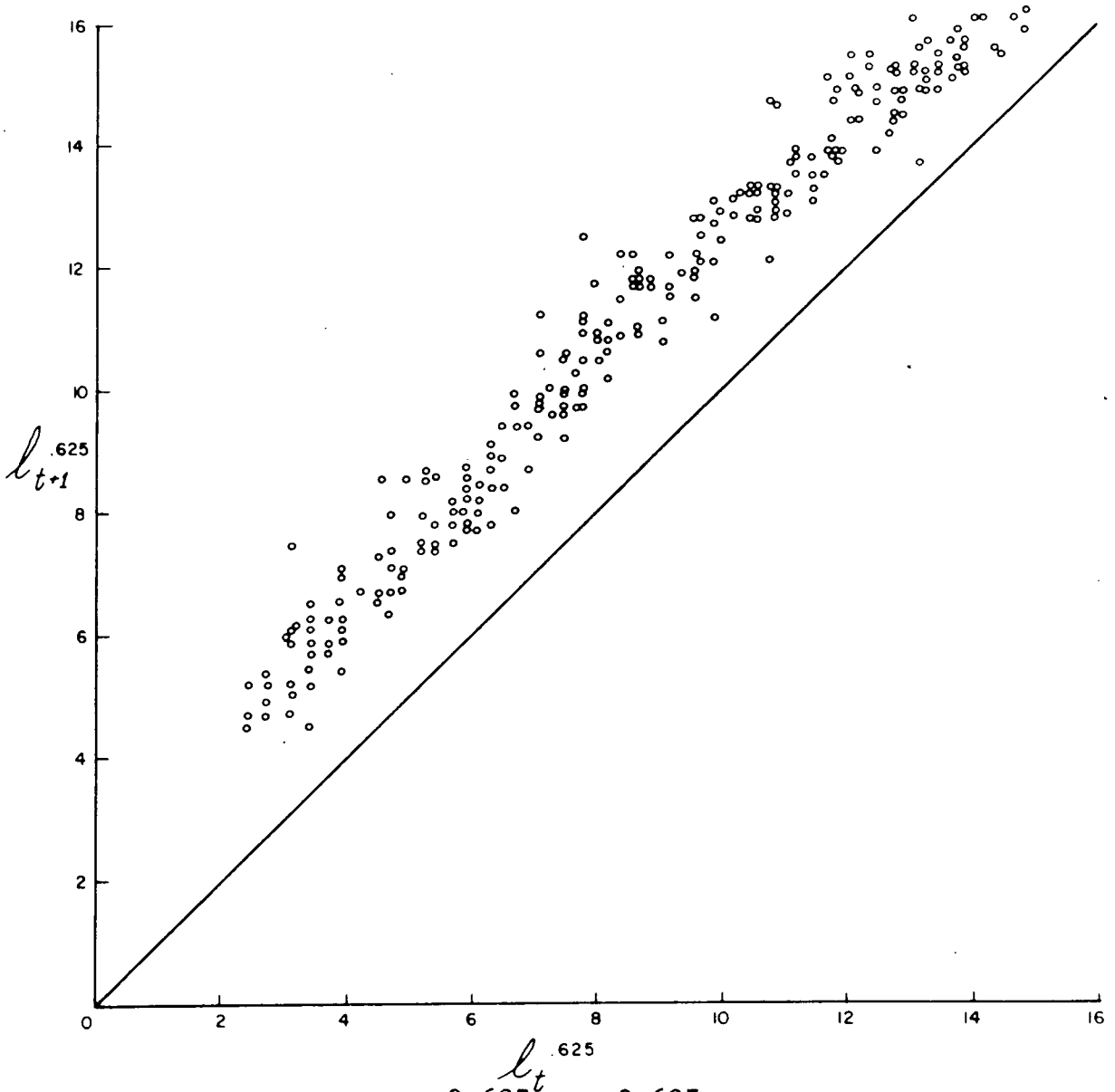

Figure 36. Plot of $l_{t+1}^{0.625}$ on $l_t^{0.625}$ for scallops of 1-6 years from Hour ground.

Table 19. Comparison of observed and calculated shell heights of scallops in millimeters from Hour ground.

Age in years	Observed	Calculated	
		Parker - Larkin	Von Bertalanffy
1	6.7	6.7	
2	16.2	17.9	
3	31.3	32.9	
4	53.0	51.0	
5	72.0	71.9	
6	83.4	83.8	
7	90.9	90.3	91.6
8	96.6	95.6	95.7
9	99.9	100.3	99.3
10	103.6		102.4
11	105.0		105.2

For the sake of convenience of computations the heights are expressed in centimeters and thus the above equation depicts the growth in centimeters. The calculated values from six to nine years are given in Table 19, and the plot of $l^{3.6}_{t+1}$ against $l^{3.6}_{t}$ is shown in Figure 37.

Since the line of best fit for the decelerating growth period approaches the 45^{o} diagonal on Walford graph, the data were also analysed by the Von Bertalanffy method. Lengths at various ages could be obtained from the equation:-

$$l_{t+1} = 126(.122) + 0.878\ l_{t}$$

The calculated lengths are shown in Table 19.

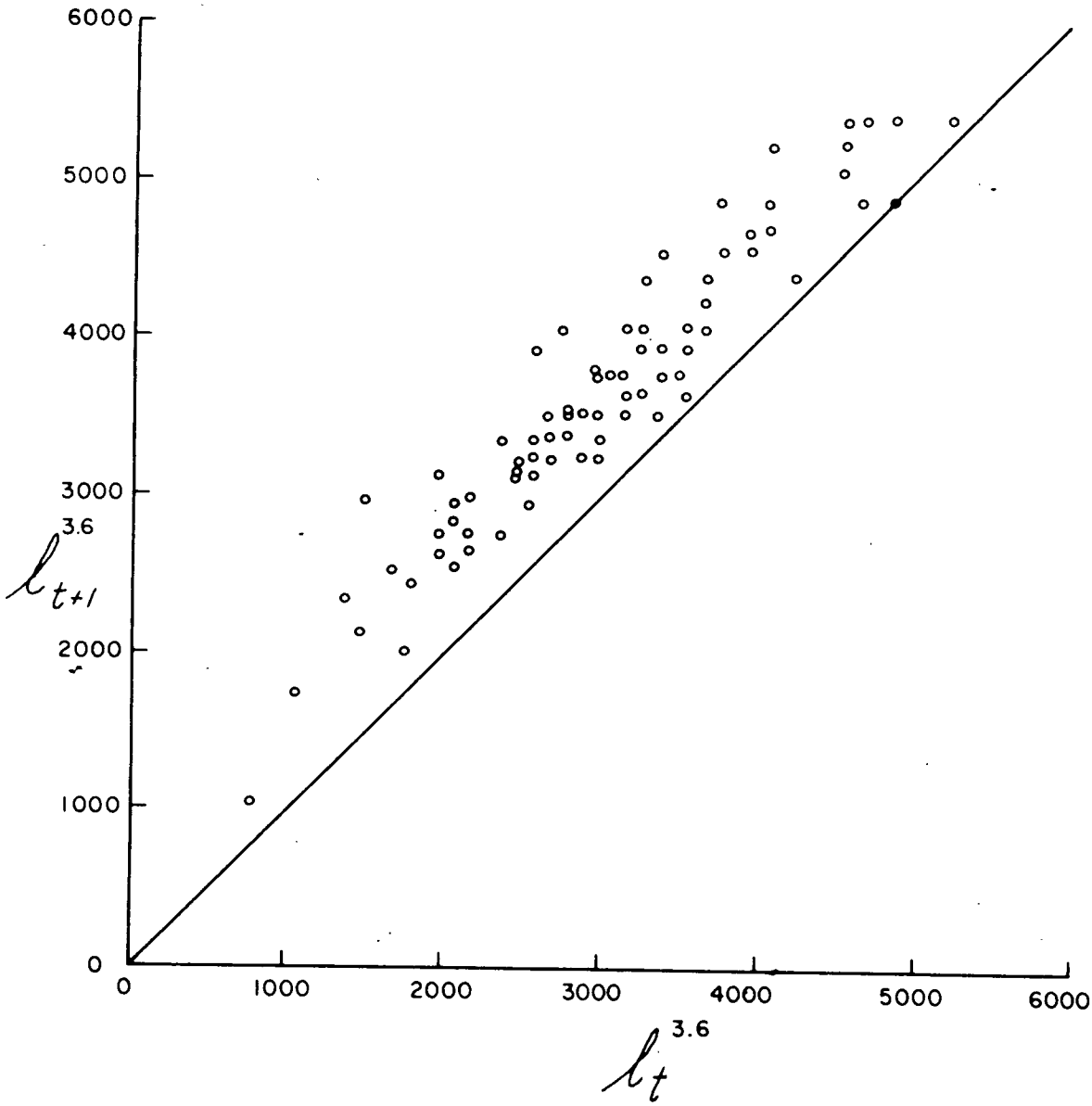

Figure 37. Plot of $l_{t+1}^{3.6}$ on $l_t^{3.6}$ for scallops of 6-9 years from the Hour ground.

Scallops from Buoy ground from one to six years of age were also analysed. The plot of l_{t+1} against l_t is shown in Figure 38. It is clear from the figure that there is a change in the growth pattern beyond the 6th year of life or between 60-80 mm of shell height. The line of best fit has a diverging trend from the 45^{o} diagonal. A value of 0.375 for z has been estimated. The transformed plot of $l_{t+1}^{0.375}$ on $l_t^{0.375}$ is shown in Figure 39. The Parker-Larkin equation to predict the shell heights during the accelerating growth phase is:-

$$l_{t+1}^{0.375} = 0.6562 + l_t^{0.375}$$

Observed and predicted values are given in Table 20.

Table 20. Comparison of observed and calculated shell heights of scallops from Buoy ground.

Age in years	Observed	Calculated
1	5.55	5.55
2	12.06	12.24
3	21.50	22.50
4	36.25	36.92
5	56.56	56.05
6	80.44	80.44

The Parker-Larkin equation is satisfactorily applied to the scallops of Hour ground and Buoy ground which is evident from the agreement between observed and calculated values.

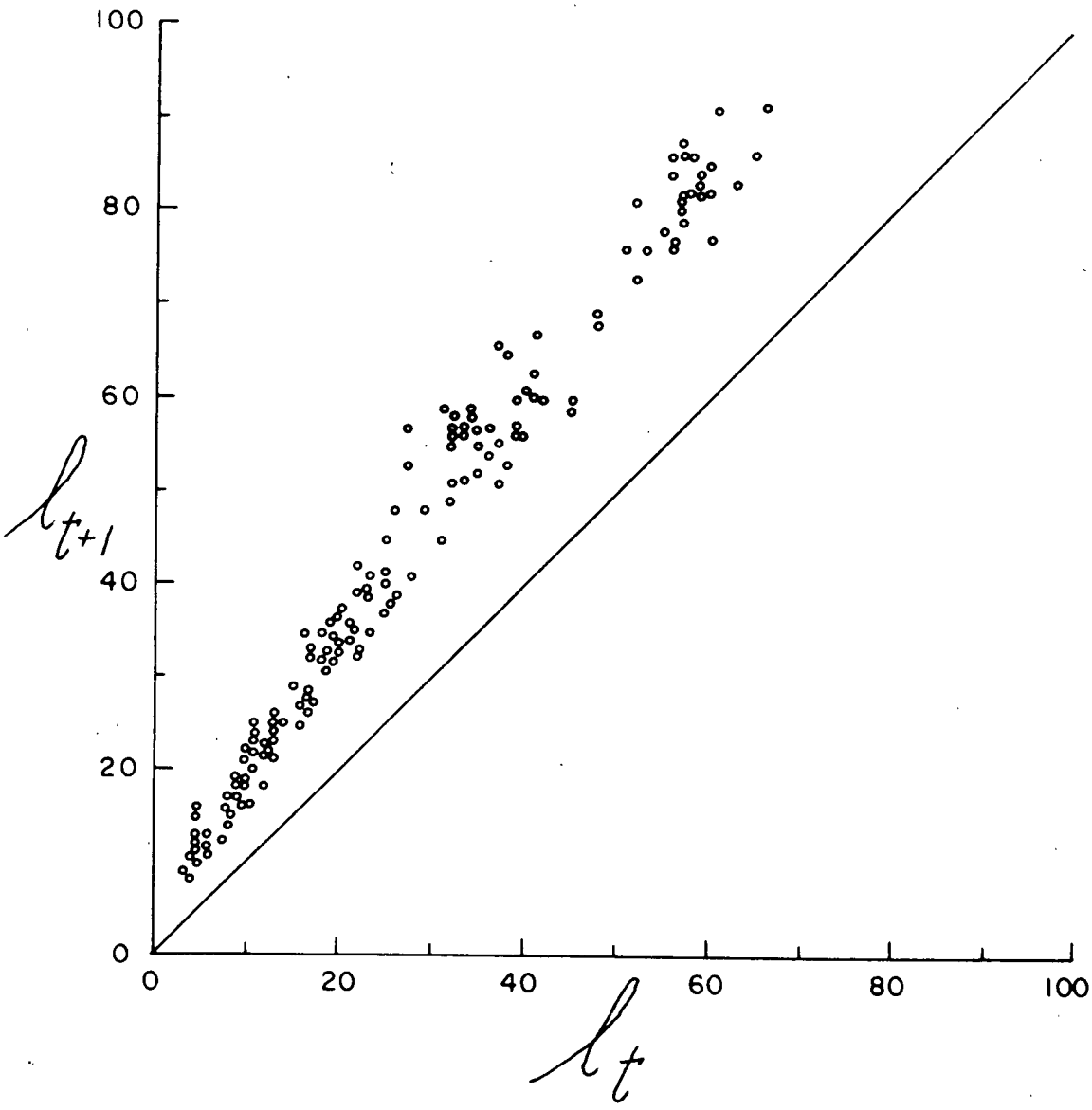

Figure 38. Plot of l_{t+1} on l_t for scallops from the Buoy ground.

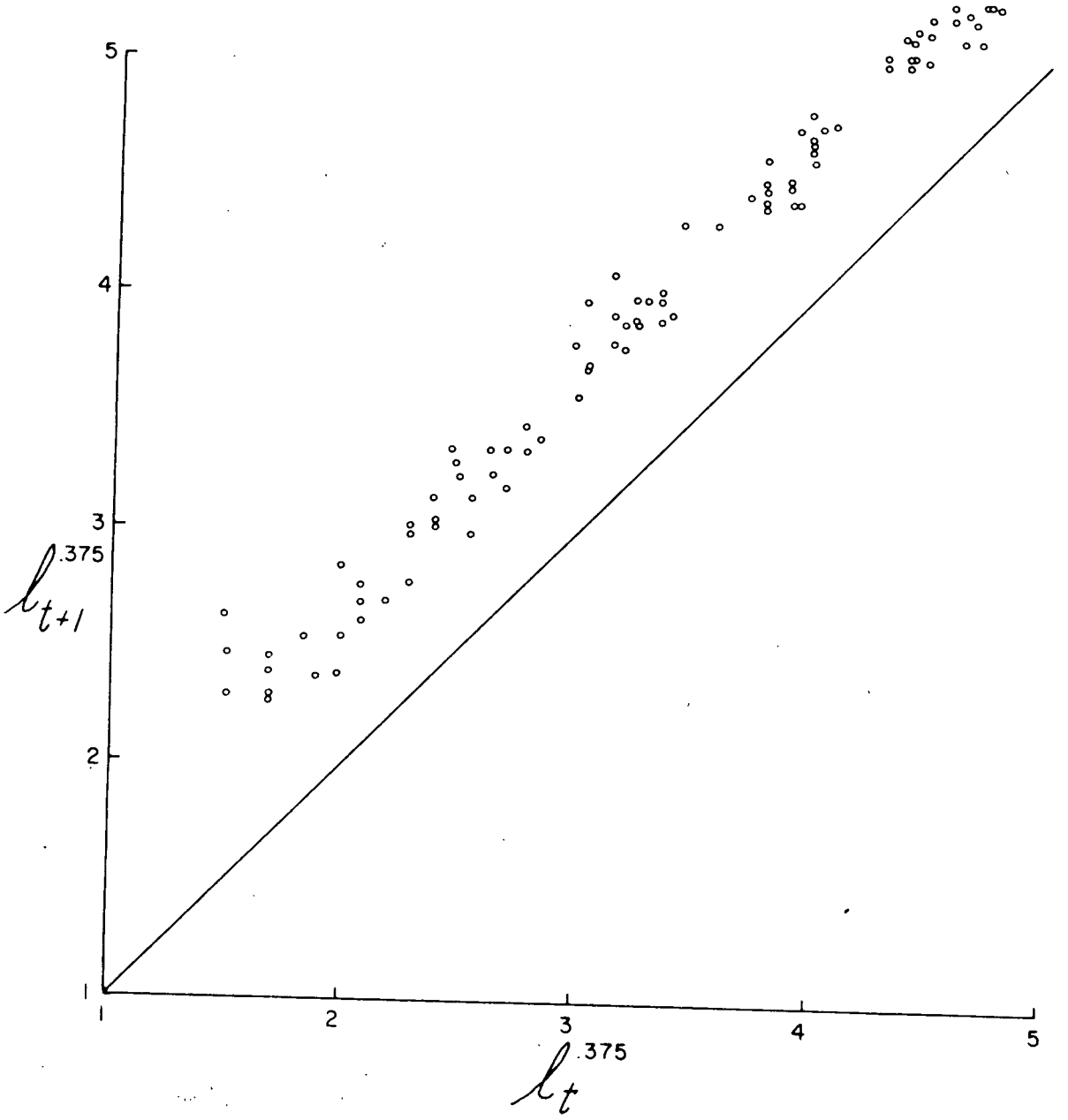

Figure 39. Plot of $l^{0.375}_{t+1}$ on $l^{0.375}_{t}$ for scallops from the Buoy ground.

DISCUSSION AND CONCLUSIONS

The usefulness of an empirical equation is enhanced if its constants yield easily information of biological interest. It is solely on this basis that the Von Bertalanffy equation has had a wide and varied use in fisheries biology. The parameter K of Von Bertalanffy's equation is supposed to be proportional to the coefficient of catabolism i.e. it is the rate at which the animal attains the asymptotic size. Intra and inter species growth comparisons nearly always show that K is high when L_{∞} is low and vice versa (Holt 1960). Taylor (1959) showed that changes in the value of K are temperature dependent. He also showed (1959 and 1960) the inverse relationship existing between K and L_{∞} for cod and razor clam. The values of K and L_{∞} of Von Bertalanffy and z of Parker-Larkin equation obtained in the present investigations are given in Table 21.

Table 21. Growth parameter of Von Bertalanffy and Parker-Larkin equations.

Species	Sex	L_{∞}	K	z
Eopsetta jordani	M	85 cm.	0.11	1.3
	F	81 cm.	0.11	1.3
Clupea pallasii	M	27.6 cm.	0.13	3.1
	F	25.4 cm.	0.21	3.5
Salmo gairdnerii	Paul Lake	55 cm.	0.39	1.3
	Loon Lake	60 cm.	0.19	1.3
Hippoglossus stenolepis	1926	232 cm.	0.16	1.5
	1956	400 cm.	0.24	1.36
Acipenser fulvescens	M	210 cm.	0.02	2.64
	F	180 cm.	0.023	2.64

It can be seen from the table that there is an inverse relationship between L_∞ and z in the same way as between L_∞ and K. From this it may tentatively be concluded that the parameter z of the Parker-Larkin growth equation is an index of the physiological activity. Parker and Larkin (1959) suggested that x or z of their growth equation may be derived from a comparative study of metabolic rate over a range of size. The values of z can also be explained in terms of the factors that affect L_∞. Due to its plasticity, growth is affected by the availability of food material. The availability of food is dependent not only on the physico-chemical factors of the environment but also on the density of the population. In terms of the Von Bertalanffy equation it is the parameter L_∞ or W_∞ that is affected by variations in the food consumption (Beverton and Holt 1957). From the present investigation on trout from Paul Lake and Beaver Lake it is evident that the values of the parameter z were variable which was explainable by varying year class strength and ensuing competition for food. When there is no sufficient food there is a lessening of L_∞ and higher L_∞ where there is sufficient food. In order to make the empirical growth data linear it requires a high z value in the former case and a low z in the latter instance. It is too early to attribute any physiological interpretation to the parameter z. Assuming that fish growth is isometric the exponent x of $\frac{dw}{dt} = kw^x$, appears to serve as a measure of the complex of physiological processes.

Parker and Larkin (1959 p. 726, Fig. 1) mentioned that the value of z is likely to lie between 1.0 and 1.5, if the

data appear to approach the 45° diagonal. This is true for the chinook salmon they worked on. In the present series of observations the value of z is more than 1.0 and a value as high as 3.6 was obtained. For trout the value of z was between 1.0 and 1.5. From this it may be concluded that this range of values is true for salmonids only.

It is evident from this study that the Parker-Larkin growth equation can be applied to many aquatic organisms and in many instances the agreement between the observed and calculated values is good. However, to evaluate the usefulness of the various constants as tools of physiological and/or ecological events of the growth pattern, further work is suggested, probably in the experimental field.

SUMMARY

The Parker-Larkin equation $dw/dt = kw^x$ has been fitted to observed data on lengths, weights of fishes and heights of scallops. The following is the summary of the findings.

(1) Conversion of z to values of x should not assume that the exponent relating to length to weight is necessarily 3.

(2) Back calculated lengths may reflect bad and good growth years and may give a spurious estimation of a z value appropriate for comparisons. In a variable environment z should be calculated from increments in growth for fish of various sizes in the same year even though this procedure may be biased by selection of fast growing fish by the fishery.

(3) In short lived species with highly variable growth rates combinations of complications make the estimation of z from field data highly unreliable. In rainbow trout from Paul Lake it is necessary to recognize ecological growth stanzas. However the component "stanzas" are then inadequate for z estimation because of the great variability in growth rate and selection of fast growing fish by the fishery. Early maturity and differing length-weight relationships for both sexes and stages of maturity etc. further confound the analysis.

(4) Separation of ecological growth stanzas should be based on a size rather than on age criterion to avoid bias from extremely fast or slow growing individuals.

(5) The Von Bertalanffy equation was found to overestimate the size in the older ages in many species.

(6) Fish from fresh water as well as from the marine environment are described adequately by the Parker-Larkin equation.

(7) When the growth increments decrease at first and then become equal as in white sturgeon it is suggested that the data be split into two stanzas for analysis.

(8) When the line of best fit on Walford plots tends to approach the 45^{o} diagonal the value of z lies between 1.0 and 1.5 in the case of salmonids. In other species a value as high as 3.6 is obtained.

(9) Tentative biological interpretation is attempted to explain the parameter z of the Parker-Larkin equation by drawing a comparison with the parameters of the Von Bertalanffy equation.

(10) The regression equation of the body-scale relationship is used only to obtain the value of the intercept. All the back calculations are made by keeping the intercept constant with variable slopes for the individual fish.

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