

Allometric Growth Formula & Yield Estimation in Fish Populations

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Variations in the yield estimates, when the length-weight relation is fitted by (i) allometric growth formula and (ii) isometric growth formula, are examined using the Beverton-Holt yield equation. When the length-weight data cover only a narrow size range, minor deviations in the data and especially 'extrapolation errors can seriously bias the yield estimates. In such cases it is suggested that an yield equation based on the isometric growth formula be used. When the length-weight exponent is not very different from three, the error in yield estimates based on the cubic equation may not be much and can often be ignored. But the use of the allometric growth formula in yield estimations may become necessary if the length-weight exponent is considerably different from three even when the length-weight data are extensive and cover a wide size range.

THE length-weight relation of most of the commercially important fishes are generally examined by means of the allometric growth formula :

$$w = cL^n \quad \dots(1)$$

This is partly because the measurements are often made on whole-fish and hence length-weight exponent need not be always three. Since the fishes are also sold in the market with the gut and the gonad intact, the question arises whether the estimation of yield and optimum conditions of exploitation should also be made from an yield equation based on the allometric growth formula. Beverton and Holt¹ have used an isometric growth formula in their yield equation partly because fishes in general grow isometrically and there are many limitations in the allometric growth formula. Although this has helped them to go beyond their simple steady state population model, most of the current studies on exploited populations are done only with the help of their simple yield equation and is due to difficulties in collecting all the required data necessary for detailed analysis. Hence, if the aim is only to examine the optimum conditions of exploitation under steady state conditions, as it is often the case, should the assumption of isometric growth be upheld in yield estimations instead of using the allometric growth formula which gives a better fit to the data than the cubic equation? Although fishes in general grow isometrically, the growth of the viscera and especially the gonads do not follow this pattern and the length-weight relation based on the whole-fish often gives an exponent which is considerably different from three. Beverton and Holt¹ have pointed out that the two constants in the allometric formula will vary widely even for small changes in the length-weight data and hence, if not adequately sampled, will introduce serious errors in the yield estimates especially if extrapolation beyond the size range of the data is done for calculating the yield. No studies on the magnitude of the error in such yield calculations are known. Hence, possible errors in yield estimations are examined in this paper using both allometric and

isometric growth equations. This study is also necessary because there are other yield equations like that of Ricker^{2,3} which also uses the length-weight relation for estimating the yield. Similarly Jones⁴ and Paulik and Gales⁵ have published methods of estimating the yield by applying the simple Beverton-Holt model when the growth of fish is not isometric. Krishnan Kutty⁶⁻⁹ and Krishnan Kutty and Qasim¹⁰ have also discussed the methods of arriving at the optimum conditions of exploitation by rewriting the simple Beverton-Holt model so as to accommodate both isometric and allometric growth conditions.

Materials and Methods

The present study is made using the length-weight data of butter sole (*Isopsetta isolepis*) population collected by the author off the west coast of Canada during 1961. Length-weight data were collected on whole-fish by sex and by season. During February 1961, 324 measurements were taken of which 89 were mature females in the size range 30-38 cm. (Females, sampled in winter, are from the spawning ground and only mature females belonging mostly to the size range 30-38 cm occur here during this time. The summer samples are from the feeding ground.) The rest were mature males and belong to the size range 13-36 cm. In July 1961, 536 measurements were made; of these 200 were males with a size range of 10-36 cm and the remaining females were of the size range 10-39 cm. The estimated length-weight relation by sex and season are:

$$\left. \begin{aligned} \text{Male (summer)} &: W(g) = 0.009260 L(\text{cm})^{3.023} \\ \text{Male (winter)} &: W(g) = 0.007236 L(\text{cm})^{3.103} \\ \text{Female (summer)} &: W(g) = 0.007344 L(\text{cm})^{3.094} \\ \text{Female (winter)} &: W(g) = 0.027896 L(\text{cm})^{2.746} \end{aligned} \right\} \dots(2)$$

Information on growth data is based on 762 otolith readings. The fitted von Bertalanffy growth equations for the two sexes are:

$$\left. \begin{aligned} \text{Males} &: l_t(\text{cm}) = 36.64[1 - e^{-0.2814(t-0.43230)}] \\ \text{Females} &: l_t(\text{cm}) = 41.71[1 - e^{-0.2437(t-0.39087)}] \end{aligned} \right\} \dots(3)$$

where t is the age in years.

The effect of different values of the length-weight exponent on the yield per recruit (YW/R), were studied for natural mortality rates (M) of 0.1 and 0.4 and by changing the rate of attaining the asymptotic length or K from their actual values of 0.2814 and 0.2437 respectively to 0.1. By keeping the age of recruitment (t_p) steady at 4 yr, the age of exploitation (t_e) was altered from 4 to 6 yr and the yield calculated as above for females. The effect of extrapolation on yield is studied by fitting both the allometric and the isometric growth formula to the length-weight data on females of 32 cm and above, collected during summer. The fitted equations are:

$$\left. \begin{aligned} W(g) &= 0.3218946 L(\text{cm})^{2.015492} \\ W(g) &= 0.0098705 L(\text{cm})^3 \end{aligned} \right\} \dots(4)$$

The cubic equation is of the form $y=bX$ where $X=L^3$ and is like-fitting a straight line with the restriction that it should pass through the 'origin'. Scarborough¹¹ has explained the theory of fitting any equation which is linear in the constants by the method of least squares.

Since the length-weight exponent of female (winter) is considerably different from three, the isometric growth formula was also fitted to these data and the yield calculated for comparison. The fitted length-weight equation for the female (winter) data is:

$$W(g) = 0.0113768 L(\text{cm})^3 \dots(5)$$

Although **Beverton-Holt** method of estimating the yield and notation was followed throughout, the actual calculation is done by approximate integration¹² using Simpson's rule of integration when t_p is 4 yr and

males are mature while the summer males are not. The yield per recruit for females vary considerably among themselves and when compared with those of males. The sexual difference in the yield based on the summer data is not due to significant difference in the length-weight relation but is mainly because of the differences in the growth rates. The asymptotic length of the females is 41.71 cm while that of males is only 36.64 cm. Within females also there is considerable difference in the yield values. This can be ascribed to the following reasons. Although the length-weight exponent for female (winter) is only 2.746 all are mature at this time and for all lengths the observed weight is more on the average when compared to the female (summer) data (Fig. 1A) which, therefore, raise the yield. The reason why the exponent is much lower than three is because, at the lower length range, i.e. around 30-32 cm, the weight seems to be considerably more for its length when compared to the higher size groups. This raises the intercept but lowers the slope or the value of the length-weight exponent. The asymptotic weight for female (winter) is 784.7 g while for female (summer) it is 756.5 g. This is because the two regression lines cross each other only beyond a length of 41.71 cm which is the asymptotic length of the females (Fig. 1A). The larger fish was found to weigh less probably because they are partly spawned and may also be due to the lack of sensitivity of the balance used at higher weights.

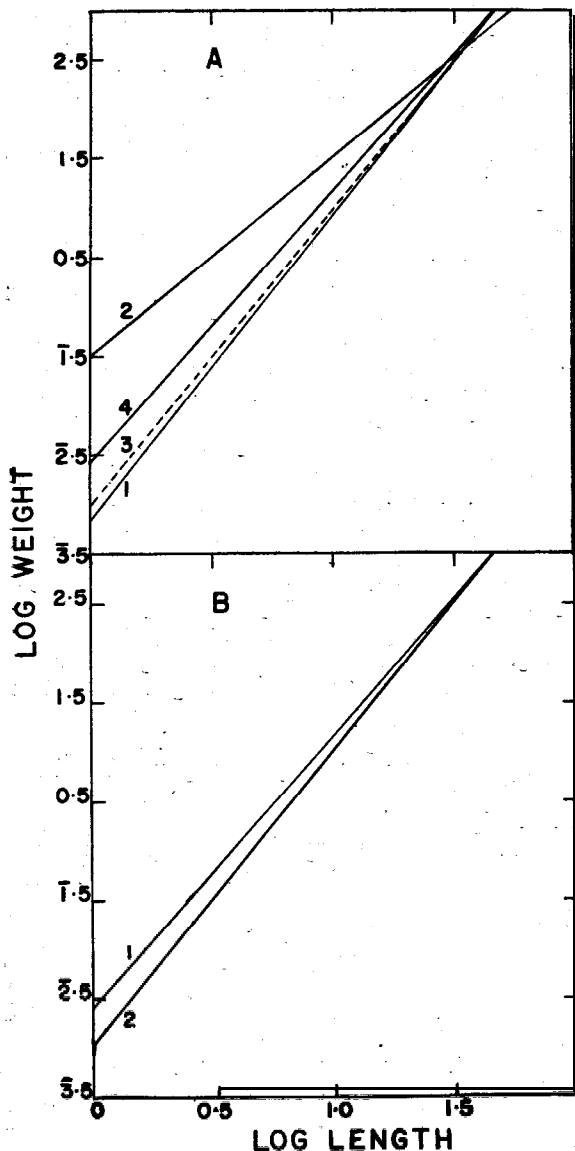


Fig. 1 — Length-weight relation in female butter sole [A: 1, summer — entire data; 2, summer — 32 cm and above; 3, summer — 32 cm and above; 4, winter data. B: 1, winter data, $W = cL^2$; and 2, winter data, $W = cL^3$]

is fairly high but the slope is low. Hence it cuts the regression line of female (summer — entire data) before the asymptotic length, i.e. at a length of approximately 33.3 cm and hence the calculated asymptotic weight based on the length-weight data of female (summer — 32 cm and above) is much lower than that based on the length-weight relation

of female (summer — entire data). The weight estimated from the two regression lines are nearly equal at 7 yr of age, i.e. at a length of 33.4 cm and further estimates based on the length-weight relation of female (summer — 32 cm and above) get progressively reduced at higher ages. Hence the yield values based on this length-weight relation for $K = 0.2437$ are all underestimates although this error is much less when M is increased to 0.4. At high values of M such errors are less evident because the contribution from older year classes is much less than when M is low. This difference in the yield estimates when compared to that of female (summer — entire data) is caused by minor deviations in the length-weight data at the size range 32-39 cm. The length-weight relation of female (summer — 32 cm and above) seems to be affected by two factors. The weight of the individuals in the neighbourhood of 32 cm seems to be comparatively high while that of the higher length groups quite low. Since the size range is quite narrow, the fitted regression line is significantly different from the line based on the entire data in both the slope and the intercept. Hence the length-weight exponent is as low as 2.015 and the other constant as high as 0.3219. This is seen from Fig. 1A also. While the slope of the line is least in this case the intercept is the highest. Since the exploited size range lies between 31 and 39.3 cm corresponding to t_p of 6 yr and t_λ of 12 yr, much of the yield is from fish of age above 7 yr which considerably lowers the total yield. The W_∞ or the asymptotic weight for female (summer — 32 cm and above) is only 593.3 g while that based on female (summer — entire data) is 756.5 g.

Another source of error in the yield estimations is also evident from Table 2. When K is changed from 0.2437 to 0.1, the yield values based on female (summer — 32 cm and above) are all over-estimates when compared to the yield values based on the length-weight relation of female [summer — entire data]. When K is as low as 0.1, the estimated lengths of the exploited fish at different ages between 6 and 12 yr range only from 17.9 to 28.7 cm. Hence, when calculating the yield this in essence introduces a serious error due to extrapolation. Because the length-weight relation is based on data 32 cm and above and since the intercept is very high, the estimated weight and hence the yield from lower length groups will be higher than those based on the length-weight relation of female (summer — entire data). Thus, when K is low and the length-weight relation is based on a narrow size range like that of female (summer — 32 cm and above), serious errors can at times be introduced in the yield estimations when the latter is based on the

TABLE 2 — YIELD PER RECRUIT VALUES USING THE LENGTH-WEIGHT EQUATIONS BASED ON FEMALE (SUMMER — ENTIRE DATA), FEMALE (SUMMER — 32 CM AND ABOVE) AND FEMALE (WINTER)

($t_p = 4$ yr, $t_p' = 6$ yr, $t_\lambda = 12$ yr, $F = 0.3$)

M	Female (summer)				Female (winter)			
	Entire data		32 cm and above		Entire data		32 cm and above	
	0.1	0.2437	0.1	0.2437	0.1	0.2437	0.1	0.2437
K	0.1	0.2437	0.1	0.2437	0.1	0.2437	0.1	0.2437
YW/R (g)	240.20	60.03	75.25	17.250	91.23	228.27	73.62	264.94
	2437			2437				2437

TABLE 3 -YIELD PER RECRUIT VALUES BASED ON ALLOMETRIC AND ISOMETRIC GROWTH FORMULAE FITTED TO FEMALE (SUMMER — 32 CM AND ABOVE)

$$(t_p = 4 \text{ yr}, t_\lambda = 12 \text{ yr}, F = 0.3)$$

	Allometric growth formula				Isometric growth formula									
	$t_p = 4 \text{ yr}$		$t_p = 6 \text{ yr}$		$t_p = 4 \text{ yr}$		$t_p = 6 \text{ yr}$		$t_p = 4 \text{ yr}$		$t_p = 6 \text{ yr}$			
M	0.2437	0.1	0.1	0.2437	0.4	0.1	0.2437	0.1	0.1	0.2437	0.1	0.1	0.2437	0.4
K	232.14	81.62	121.98	39.14	213.53	47.22	105.21	20.09	231.20	60.16	72.61	1	%	

allometric formula. Similarly if the length-weight data are restricted to smaller size groups and K is high extrapolation errors may again seriously affect the yield estimates.

The difference in the yield values between female (summer — entire data) and female (winter) in Table 2 is mainly because the females are all mature in winter and hence their weights are higher. However, when K is reduced to 0.1 the YW/R values also become slightly biased due to extrapolation errors.

Yield per recruit values using allometric and isometric formulae fitted to length-weight data on female (summer — 32 cm and above) are presented in Table 3. The yield per recruit values based on the allometric growth formula fitted to the entire data are treated as the standard for comparison. These values are reliable because there is no extrapolation error as the data are extensive, covering a wide size range and since an allometric equation with two constants gives a better fit to the data than the cubic equation with only one constant. Comparing the YW/R values in the first four columns of Tables 1 and 3, the yield values in Table 3 are all over-estimates and the error is considerable when K is reduced from the actual value to 0.1 due to extrapolation errors as discussed above. In Table 2 when t_p is 6 yr and K is 0.2437 we find that the yield values based on the length-weight data of female (summer — 32 cm and above) are all under-estimates. This is because exploitation begins only at 6 yr of age and hence the exploited size range was quite high. In Table 3, the t_p is 4 yr and hence when K is 0.2437 fish of size 24.4 cm and above are all exploited. Since at lower size range the weight is over-estimated by the regression line based on the length-weight data of female (summer — 32 cm and above) the yield obtained from the early age groups are all over-estimates and hence the overall yield is also higher. When K is reduced to 0.1 this error is further increased because the exploited size range is now 12.6 to 28.7 cm.

When isometric growth formula is used the estimated YW/R values (the middle four columns in Table 3) are very close to the comparable figures in Table 1 and the similarity is more striking for low K values. This is especially interesting because isometric growth formula is fitted to a narrow length range of 32-39 cm. While YW/R values in Table 3, when allometric growth formula is used, are subjected to serious extrapolation errors, such errors are minimum when the length-weight data are limited to a narrow size range. Since the growth of fish in general is isometric, the errors involved in the yield values based on a cubic equation fitted to the whole-fish data may not be

TABLE 4 — YIELD PER RECRUIT VALUES BASED ON ISOMETRIC GROWTH FORMULA FITTED TO FEMALE (WINTER) DATA

$$(t_p = 4 \text{ yr}, t_p' = 6 \text{ yr}, t_\lambda = 12 \text{ yr}, F = 0.3)$$

M	0	1	0.4	
K	0.2437	0.1	0.2437	0.1
YW/R (g)	266.48	69.34	83.69	20.03

significant. In fact the results here even suggest that when the length-weight data are limited to a narrow size range it is even better to fit an isometric growth formula for purposes of calculating the yield especially when the exploited size range lies much beyond that of the length-weight data. In Fig. 1A, the regression line based on the cubic equation (line 3) is very close to the regression line based on the length-weight data of female (summer — entire data) while line 2 based on allometric growth equation is very much off from line 1. Allometric growth formula appears to be necessary in yield estimation only if the length-weight exponent is considerably different from three even when the size range of the data fitted is extensive.

The above conclusions can also be made by comparing the YW/R value; in the last four columns of Table 3, i.e. when t_p is altered to 6 yr, with those in the first and middle four columns in Table 2. The extrapolation error caused by a change in the value of K to 0.1 is almost negligible when the isometric formula is employed although there is some difference in the estimated YW/R when the original K is used. But this yield (231.20) is slightly better than the estimate (228.27) obtained using the allometric formula. It appears, therefore, that even when the exploited size range is within the limits of the length-weight data, if the latter belongs to a narrow size range errors from deviations in the data may be more when allometric equation is used. Since the growth of fish in general is isometric, use of the cubic equation evidently reduces such errors in the yield estimates. If the data are not biased, the yield estimation based on the allometric formula should give a better estimate of the yield since the anisometric formula gives a closer fit to the data. But, when the size range is restricted, such errors in the data can easily influence the fitted line. The YW/R values in Table 4 also substantiate the above conclusions.

In Table 4 YW/R values are calculated by fitting a cubic equation to the female (winter) data. On comparing these estimates with those in the last four columns in Table 2, it is found that they are very close when the original K values are used although they are slightly off when K is reduced

to 0.1. When the length-weight exponent is assumed to be three instead of 2.746, the intercept is somewhat lowered. When K is reduced to 0.1 the exploited size range between the ages $t_p = 6$ and $t_h = 12$ yr become, as already indicated, 17.9 to 28.7 cm. At these lower lengths (Fig. 1B) the corresponding weights and hence the yield values are lower than when the allometric equation is used. But these yield values are likely to be more accurate. YW/R values based on the allometric growth formula may be subjected to extrapolation errors because the length-weight data comprise mature females belonging to a narrow size range of 30-38 cm and since females below 30 cm are largely immature.

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References

1. BEVERTON, R. J. H. & HOLT, S. J., *On the dynamics of exploited fish populations*, U.K. Min. Agr. Fish., Fish. Invest. Ser. 2, 19 (1957).
2. RICKER, W. E., *Bull. Fish. Res. Bd Can.*, No. 119, 1958.
3. RICKER, W. E., *Copeia*, (1945), 84.
4. JONES, R., *Lisbon joint meeting of ICNAF/ICES/FAO Document No. P. 21, 1957*.
5. PAULIK, G. J. & GALES, L. E., *Trans. Am. Fish. Soc.*, 93 (1964), 369.
6. KRISHNAN KUTTY, M., *J. Fish. Res. Bd Can.*, 25 (1968), 1291.
7. KRISHNAN KUTTY, M., *Proc. natn. Inst. Sci. India*, 34 (1968), 293.
8. KRISHNAN KUTTY, M., *Proc. Indian natn. Sci. Acad.*, 36 (1970), 21.
9. KRISHNAN KUTTY, M., *Proc. Indian natn. Sci. Acad.* (in press).
10. KRISHNAN KUTTY, M. & QASIM, S. Z., *J. Cons. int. Explor. mer.*, 32 (1968), 249.
11. SCARBOROUGH, J. B., *Numerical mathematical analysis* (Oxford & IBH Publishing Co., New Delhi), 1966.