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UTILIZATION OF PACIFIC HALIBUT STOCKS: STUDY OF BERTALANFFY'S GROWTH EQUATION

by

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and

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FOREWORD

The Convention of 1953 between Canada and the United States for the Preservation of the Halibut Fishery of the Northern Pacific Ocean and Bering Sea continued the conservation objectives of the three previous conventions, specifically requiring that the stocks of halibut be developed to levels which will permit maximum sustained yield and that the stocks be maintained at those levels.

Maximum sustained yield can be determined on a theoretical basis provided certain measures of the stocks are known, one of which is the rate of growth.

The Commission, in its continuing study of the dynamics of halibut in the northern Pacific Ocean and Bering Sea, has used various measures of growth; this report presents a further analysis of the growth function.

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INTRODUCTION

Determination of maximum sustainable yield of a population of fish on a theoretical basis requires a measure of the rate of growth that can be introduced into yield equations. The rate of growth may be determined empirically or represented by an equation in which the parameters may be functions of population density. Thompson and Bell (1934) introduced growth empirically in their calculations as average weight at each age. In the Commission's report on Yield Per Recruitment (IPHC No. 28, 1960) growth rate was estimated from the linear regression of the logarithm of weight on the logarithm of age. Such a procedure was also used for growth rate estimates necessary for the studies on utilization of halibut reported by Chapman, Myhre and Southward (1962) and by Dunlop et al (1964).

Beverton and Holt (1957) formulated a model by utilizing a growth equation derived by Bertalanffy (1934, 1938). In the Bertalanffy equation growth was regarded as the net result of two opposing processes, catabolism, or the destructive process, and anabolism, the building-up process. The former was considered to be proportional to the weight of the organism and the latter to its surface area. It was further assumed that the weight and surface area were proportional to the cube and square respectively of the length of the organism.

The following growth equation relating length to age was thus obtained:

$$L_t = L_\infty - (L_\infty - L_o)\, e^{-Kt} \qquad (1)$$

where L_t = length at (age) t
L_∞ = maximum length attained by the animal
L_o = length at time o
K = growth rate

This equation, which has been widely used to describe growth in fishes, had been derived earlier in other fields of research; it has been used to describe the effects of fertilizer on crop yields (Mitscherlich, 1930).

It is observed in fish, however, that the relationship between weight or surface area and length in many instances differs from the respective cubic or quadratic power laws. However, most of these observations have been based not on the relationship with respect to the individual or a single age group but to composite data from a group of individuals. For example, the average exponent of the power law expressing the weight-length relationship in the halibut population has been observed to be about 3.2. However, individually, members of such a population could have an exponent differing materially from this value.

If it is assumed that the exponents in the power law relationship between weight or surface area and length of the individual fish differ from the cubic or quadratic laws respectively but remain constant over time, a more generalized four-parameter Bertalanffy equation is obtained (Chapman, 1960; Richard, 1959). It is as follows:

$$L_t^{1-m} = L_\infty^{1-m} - (L_\infty^{1-m} - L_o^{1-m})\ e^{-K(1-m)t} \qquad (2)$$

where m is the rate of change between metabolic rate and weight and the other constants are as defined for equation (1).

As shown by Richards (1959) the constant m governs the proportion of L_∞ attained by the individual at the time the inflection point in the growth curve occurs; K/m is the actual relative growth rate at the point of inflection of the curve; K/2m+2 is the weighted mean growth rate on a proportional basis; the difference (L_∞ $-L_o$) has no biological meaning and if the proper point in time were known it could be eliminated by adjustment of the time scale.

Prior to the development of the extended equation (2) attempts were made to apply equation (1) to halibut data in spite of the non-cubic relationship between weight and length that was observed in grouped data of that species.

Reasonable parametric values were obtained only if large amounts of data covering the growth of several year classes over a period of years were averaged and fitted by the equation. In such cases it was difficult to ascertain to which portion of the time period the growth parameters applied. However, when the lengths at each age were obtained from fish of different year classes, i.e. fitting data from a catch curve, the estimation procedure would frequently not converge; and when it did converge the values of the parameters were often unreasonable, such as negative L_∞'s. If average lengths obtained at each age throughout the life of a year class were used, there was usually convergence. However, in many instances the estimated L_∞'s were out of reason either by being much less than observed lengths or by being excessively high. Since the weight of halibut does increase at a greater rate than the cube of the length these results were not unexpected. The extended Bertalanffy equation was expected to eliminate these problems. The availability of high speed computing equipment made the application of the extended equation feasible not only to averages but indeed to fitting growth curves of individual fish.

This report examines some of the problems encountered in describing growth of halibut by the extended Bertalanffy growth equation (2) as well as considers their effect on estimating maximum sustainable yield. In particular, it is shown that the estimation of L_∞ and weighted mean growth rate, K/2m+2, depends on the age of the fish used in the estimation and that this effect causes substantial bias in the estimation of maximum sustainable yield.

ESTIMATION OF PARAMETERS

One method of estimating K and L_∞ for the simple Bertalanffy model (equation 1) is by regressing L_{t+1} on L_t. This is of course the Ford-Walford plot (Ricker, 1958, p. 194), which was developed much earlier than the application of the Bertalanffy equation to yield models and growth studies in general. In recent years the Ford-Walford plot and the Bertalanffy equation have been widely used to fit growth data of fish and shellfish (C. C. Taylor, 1958, 1959).

These equations have been fitted to averaged data, i.e. average lengths or weights of a number of individuals or to averages where different fish are involved at each age, such as in the case of a catch curve. Yet the growth equation (1) as derived by Bertalanffy and the extended form (2) applies to an individual animal and the parameters are defined in such terms if they are to have biological meaning. Whether the average of a number of Bertalanffy growth curves is itself a Bertalanffy growth curve has not been shown. However, if the growth rates of every fish were identical, the summation of different Bertalanffy curves of the form (1) will still be a Bertalanffy curve of the same form. If this is not the case it is not at all clear whether the parameters L_∞ and K, determined from average lengths or weights, are related in any meaningful way to the average of the L_∞'s and K's that would be obtained by averaging parameters determined for individual fish. Obviously with the extended Bertalanffy equation, if the parameter m as well as K differs within a group of fish, the relationship of the composite curve to the average of individual curves is even more complex.

As noted earlier, equation (2) is fitted to data of individual fish in this study to avoid these problems. Various methods are available to fit equation (1) in addition to the Ford-Walford plot. Tables have been prepared for the determination of maximum likelihood and least squares estimates (Stevens 1951, Gomes 1953) and computer programs (Abramson 1963) are also available to further facilitate the estimation of the three parameters. Less attention has been given to the estimation of the parameters in the newer and more complicated equation (2) though Richards (1959) did consider the problem. Taylor (1962) used a graphical or trial and error method of estimating m. Once m is estimated it is possible to estimate the remaining three parameters as in the simpler model of equation (1). Thus Taylor regressed L_{t+1}^{1-m} on L_t^{1-m}, that is used a modified Ford-Walford plot.

Since the point of inflection is in part governed by m, it might be thought that this would serve as an aid in the estimation of m. Unfortunately, the point of inflection is frequently very difficult to determine, and this cannot be regarded as a reliable tool. In the present study equation (2) was fitted by the method of least squares using a program for the IBM 7094 computer.* This program varies all four parameters so as to obtain those values which minimize

$$\left\{L_t - \left[L_\infty^{1-m} - (L_\infty^{1-m} - L_0^{1-m})e^{-K(1-m)t}\right]^{\frac{1}{1-m}}\right\}^2$$

It is to be noted that different estimates are obtained if

$$\left\{L_t^{1-m} - \left[L_\infty^{1-m} - (L_\infty^{1-m} - L_0^{1-m})e^{-K(1-m)t}\right]\right\}^2$$

is minimized. Unfortunately, it is difficult to compare the residual variances in the latter case since they vary widely with 1—m.

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* Developed by K. Turnbull, College of Forestry, University of Washington. Recent versions of this program contain additional modifications and features that were not present when the program was used for this study.

ANALYSIS OF HALIBUT AGE-LENGTH DATA

Samples from five year classes (1941-1946) from the Portlock-Albatross grounds were selected for the study to minimize density dependent effects as these five year classes lived through a period of relatively stable stock conditions (Chapman, Myhre and Southward, 1963). Otoliths of five fish of age 8, five of age 12 and five of age 16 from each year class were randomly selected from the otolith collection of the Commission. Unfortunately, the lengths could not be selected according to the sex of the individual fish. It is assumed in this study that the ages were determined without error. Lengths of each fish at earlier ages (Table 1) were obtained through back-calculations of otolith radii measurements (Southward, 1962).

Average values of the individually estimated parameters L_∞, m, K/m, and K/2m+2 for the age 8-, 12- and 16-year-old fish for each year class are given in Table 2. It is obvious that the estimate of L_∞, the maximum length, and K/2m+2, the weighted mean growth rate, depend very strongly on the span of ages used in the estimation. L_∞ increases and K/2m+2 decreases as the span of ages increases.

To test the statistical significance of this dependency the estimates were subjected to analysis of variance (Table 3). The change of L_∞ with age is highly significant, as are the changes in K/2m+2. On the other hand, the changes in m or K/m are not significant. Also, none of the foregoing estimates show any significant effect due to year class or any interaction between year class and age effects. Inasmuch as the sex composition of the different age composition used here is unknown, the effects of estimating average growth parameters from such data would be to increase the error term of the analysis of variance. However, the extent of the increase is not regarded as large on the basis of samples of known sex compositions taken on the Portlock-Albatross grounds in 1964 where females comprised 62, 71 and 79 percent of the 8-, 12- and 16-year-old fish respectively.

The procedure of estimating and comparing growth parameters for fish of different ages of a year class, i.e., fish taken by the fishery when they were 8, 12 and 16 years of age, is open to some question because of possible effect of gear selectivity. The 16-year-old fish could represent a different component of the year class than the 8- or 12-year-olds and, therefore, the growth parameters could be different. In order to examine this question the parameters (L_∞, m, K/m and K/2m+2) were estimated using only the first 8 years and also the first 12 years of the 16-year-old fish (Table 4). The same pronounced increase of L_∞ and decrease of K/2m+2 with increasing age is evident. These estimates were also tested using analysis of variance (Table 5). As was the case with the independent samples significant differences exist between estimates of L_∞ and K/2m+2 according to the span of ages used in the estimation. Again there is no observable year class or interaction effect.

Table 1. Back calculated lengths (in centimeters) of halibut for age groups eight, twelve and sixteen years of age of the 1941 through 1946 year classes taken on Portlock-Albatross grounds.

	AGE															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1941 Year Class																
Fish No. 1	9	22	31	46	54	61	68	74	—	—	—	—	—	—	—	—
2	12	26	33	43	58	64	69	74	—	—	—	—	—	—	—	—
3	10	28	38	47	59	67	76	81	—	—	—	—	—	—	—	—
4	8	18	32	45	59	67	76	85	—	—	—	—	—	—	—	—
5	8	17	26	45	57	72	86	99	—	—	—	—	—	—	—	—
Average	9.4	22.2	32.0	45.2	57.4	66.2	75.0	82.6	—	—	—	—	—	—	—	—
1942 Year Class																
Fish No. 1	9	18	33	45	53	65	73	82	—	—	—	—	—	—	—	—
2	8	18	33	50	67	78	88	100	—	—	—	—	—	—	—	—
3	7	15	30	40	47	60	70	81	—	—	—	—	—	—	—	—
4	8	16	32	45	57	67	77	88	—	—	—	—	—	—	—	—
5	10	20	34	45	50	57	64	69	—	—	—	—	—	—	—	—
Average	8.4	17.4	32.4	45.0	54.8	65.4	74.4	84.0	—	—	—	—	—	—	—	—
1943 Year Class																
Fish No. 1	10	24	33	46	54	63	69	73	—	—	—	—	—	—	—	—
2	11	27	35	43	50	56	64	74	—	—	—	—	—	—	—	—
3	9	21	29	38	43	50	60	69	—	—	—	—	—	—	—	—
4	9	23	38	44	49	61	72	82	—	—	—	—	—	—	—	—
5	8	20	26	35	41	48	54	60	—	—	—	—	—	—	—	—
Average	9.4	23.0	32.2	41.2	47.4	55.6	63.8	71.6	—	—	—	—	—	—	—	—
1944 Year Class																
Fish No. 1	8	21	32	40	46	55	64	68	—	—	—	—	—	—	—	—
2	12	21	31	38	44	52	61	69	—	—	—	—	—	—	—	—
3	11	21	35	50	61	76	89	98	—	—	—	—	—	—	—	—
4	7	23	35	43	52	59	69	74	—	—	—	—	—	—	—	—
5	9	20	29	37	45	50	60	68	—	—	—	—	—	—	—	—
Average	9.4	21.2	32.4	41.6	49.6	58.4	68.6	75.4								
1945 Year Class																
Fish No. 1	5	17	34	42	50	58	68	72	—	—	—	—	—	—	—	—
2	7	18	31	41	50	63	68	80	—	—	—	—	—	—	—	—
3	7	17	28	45	57	65	72	80	—	—	—	—	—	—	—	—
4	9	17	32	41	48	57	65	73	—	—	—	—	—	—	—	—
5	8	16	30	45	54	67	89	106	—	—	—	—	—	—	—	—
Average	7.2	17.0	31.0	42.8	51.8	62.0	72.4	82.2	—	—	—	—	—	—	—	—
1946 Year Class																
Fish No. 1	9	15	24	37	47	59	67	74	—	—	—	—	—	—	—	—
2	5	16	28	45	59	73	89	103	—	—	—	—	—	—	—	—
3	11	22	30	40	48	57	69	82	—	—	—	—	—	—	—	—
4	11	23	32	43	55	60	65	70	—	—	—	—	—	—	—	—
5	12	20	35	44	53	64	71	73	—	—	—	—	—	—	—	—
Average	9.6	19.2	29.8	41.8	52.4	62.6	72.2	80.4	—	—	—	—	—	—	—	—

Table 1 (continued)

							AGE									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1941 Year Class																
Fish No. 1	5	17	31	41	50	60	65	72	88	93	102	109	—	—	—	—
2	8	18	33	39	50	58	65	76	81	86	90	97	—	—	—	—
3	9	18	26	39	52	63	80	89	100	106	116	128	—	—	—	—
4	4	11	23	33	45	53	58	68	77	86	95	102	—	—	—	—
5	9	18	32	40	45	52	57	63	68	76	78	81	—	—	—	—
Average	7.0	16.4	29.0	38.4	48.4	57.2	65.0	73.6	82.8	89.4	96.2	103.4	—	—	—	—
1942 Year Class																
Fish No. 1	10	15	22	33	47	49	59	64	72	82	89	96	—	—	—	—
2	7	14	25	39	48	55	63	70	77	92	97	100	—	—	—	—
3	9	19	30	41	49	56	63	69	76	88	96	104	—	—	—	—
4	7	14	31	43	49	55	63	74	82	90	96	106	—	—	—	—
5	10	19	29	42	48	63	68	76	85	92	102	106	—	—	—	—
Average	8.6	16.2	27.4	39.6	48.2	55.6	63.2	70.6	78.4	88.8	96.0	102.4	—	—	—	—
1943 Year Class																
Fish No. 1	7	18	28	38	46	52	56	63	67	70	73	76	—	—	—	—
2	6	16	30	40	56	65	70	78	86	95	102	109	—	—	—	—
3	8	16	29	38	50	58	64	70	78	82	106	110	—	—	—	—
4	7	15	30	47	56	69	77	90	104	118	125	135	—	—	—	—
5	7	14	29	47	54	61	68	73	82	86	93	100	—	—	—	—
Average	7.0	15.8	29.2	42.0	52.4	61.0	67.0	74.8	83.4	90.2	99.8	106.0	—	—	—	—
1944 Year Class																
Fish No. 1	8	18	28	33	42	52	55	70	84	93	99	106	—	—	—	—
2	7	20	32	41	48	55	63	70	77	84	92	98	—	—	—	—
3	6	16	28	38	43	52	60	69	80	89	96	99	—	—	—	—
4	7	14	30	43	53	65	76	86	97	106	110	117	—	—	—	—
5	9	20	31	39	46	53	63	68	76	86	96	100	—	—	—	—
Average	7.4	17.6	29.8	38.8	46.4	55.4	63.4	72.6	82.8	91.6	98.6	104.0	—	—	—	—
1945 Year Class																
Fish No. 1	7	31	42	53	68	77	93	110	117	126	134	144	—	—	—	—
2	7	20	28	41	47	55	67	77	82	90	98	106	—	—	—	—
3	5	15	22	31	41	53	65	74	80	86	92	99	—	—	—	—
4	6	12	25	37	52	60	76	86	97	103	111	119	—	—	—	—
5	9	27	38	50	58	69	78	85	90	92	96	100	—	—	—	—
Average	6.8	21.0	31.0	42.4	53.2	62.8	75.8	86.4	93.2	99.4	106.2	113.6	—	—	—	—
1946 Year Class																
Fish No. 1	8	18	28	35	45	52	64	69	76	88	93	99	—	—	—	—
2	6	17	29	39	47	55	64	76	81	89	95	99	—	—	—	—
3	10	21	27	38	54	73	86	98	104	116	120	125	—	—	—	—
4	6	18	29	42	53	63	72	80	86	92	96	100	—	—	—	—
5	8	18	29	42	47	58	69	82	96	103	107	111	—	—	—	—
Average	7.6	18.4	28.4	39.2	49.2	60.2	71.0	81.0	88.6	97.6	102.2	106.8	—	—	—	—

Table 1 (continued)

	AGE															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1941 Year Class																
Fish No. 1	7	17	33	48	54	59	67	73	78	88	92	103	106	110	123	128
2	8	20	39	46	53	58	63	67	72	76	80	84	89	86	99	102
3	8	20	30	35	41	46	50	55	59	65	76	82	85	88	90	99
4	7	15	29	42	50	59	69	78	89	96	108	111	119	122	131	143
5	7	15	25	42	55	61	69	77	88	96	102	105	111	118	122	125
Average	7.4	17.4	31.2	42.6	50.6	56.6	63.6	70.0	77.2	84.2	91.6	97.0	102.0	104.8	113.0	119.4
1942 Year Class																
Fish No. 1	7	20	40	45	52	65	74	86	93	100	108	117	132	140	146	155
2	7	23	33	45	53	63	69	77	84	89	95	98	108	113	120	131
3	7	20	34	46	61	72	77	82	86	93	98	108	111	117	125	132
4	8	15	26	33	40	48	53	58	63	69	76	80	85	90	95	102
5	8	19	33	44	52	56	63	69	73	81	88	93	98	104	108	113
Average	7.4	19.4	33.2	42.6	51.6	60.8	67.2	74.4	79.8	86.4	93.0	99.2	106.8	112.8	118.8	126.6
1943 Year Class																
Fish No. 1	11	26	34	39	47	53	60	67	73	80	88	99	104	109	113	117
2	9	18	30	39	45	49	55	63	76	84	90	96	102	106	113	119
3	6	13	33	50	56	63	69	76	82	89	93	98	104	108	111	116
4	9	18	30	39	44	49	54	63	74	82	89	95	100	106	113	118
5	9	23	33	44	52	58	64	70	77	85	92	98	108	116	128	137
Average	8.8	19.6	32.0	42.2	48.8	54.4	60.4	67.8	76.4	84.0	90.4	97.2	103.6	109.0	115.6	121.4
1944 Year Class																
Fish No. 1	5	16	31	45	58	67	73	81	88	96	108	115	119	129	135	138
2	8	20	29	40	53	63	74	84	96	99	103	108	113	119	125	131
3	5	16	26	40	49	55	61	68	74	80	84	89	95	100	106	110
4	9	20	34	50	65	82	96	102	113	125	140	149	155	165	171	174
5	9	20	32	43	49	53	59	70	84	92	102	110	115	120	128	137
Average	7.2	18.4	30.4	43.6	54.8	64.0	72.6	81.0	91.0	98.4	107.4	114.2	119.4	126.6	133.0	138.0
1945 Year Class																
Fish No. 1	13	23	33	45	52	64	78	89	104	116	125	132	140	144	149	154
2	6	18	33	42	49	60	70	76	80	85	90	102	108	113	116	120
3	8	16	28	42	52	60	73	82	92	102	109	115	119	123	129	134
4	9	23	31	42	48	54	56	63	69	76	86	92	96	103	110	117
5	7	18	32	42	49	56	67	76	82	90	104	113	125	133	140	146
Average	8.6	19.6	31.4	42.6	50.0	58.8	68.8	77.2	85.4	93.8	102.8	110.8	117.6	123.2	128.8	134.2
1946 Year Class																
Fish No. 1	5	14	29	41	53	69	82	98	110	120	128	135	144	154	160	168
2	7	16	28	39	50	58	70	84	93	103	113	122	131	141	151	163
3	4	11	18	29	40	46	49	54	56	64	69	74	78	82	85	88
4	5	18	37	48	60	70	78	86	95	103	110	120	131	140	147	155
5	9	23	35	44	50	56	63	69	76	88	98	110	118	125	137	146
Average	6.0	16.4	29.4	40.2	50.6	59.8	68.4	78.2	86.0	95.6	103.6	112.2	120.4	128.4	136.0	144.0

Inasmuch as the estimates of m, the slope of the line relating metabolic rate and weight, were found from the above analyses not to differ significantly either with respect to age or year class, an average m (0.67) was substituted in the extended Bertalanffy equation and the values of the other parameters were computed by the method of Stevens (1951) and are shown in Table 6. This represents an intermediate level of generality between the Bertalanffy equation (1) and the extended or more general equation (2). Again, on the average the estimated maximum length L_∞ increases and K decreases as the span of ages of the fish used in the estimation increases.

In order to compare parameters determined from averaged lengths with averages of parameters determined from individual fish, the lengths of five fish of each year class were averaged and the growth parameters were determined from the averaged data (Table 7). Several differences between these growth parameters and those obtained by averaging growth parameters obtained from individual fish (Table 2) are apparent. The estimated L_∞ based on averaged length data is lower at each age than the average of the five individually estimated L_∞'s. However, the estimated L_∞'s again increase as the span of ages used to estimate them is increased. The values of m estimated from fitting a growth curve to average lengths are generally more variable than the averaged values of m determined from individually fitted curves. The two measures of growth rate (K/m and K/2m+2) are also usually higher and more variable when determined from averaged length data than when the corresponding rates for individual fish are averaged.

Table 2. Average growth parameters for the 1941 through 1946 classes, individually estimated from back-calculated lengths of fish eight, twelve and sixteen years of age.

Parameter	L_∞			m			K/m			K/(2m+2)		
Age	8	12	16	8	12	16	8	12	16	8	12	16
Year Class												
1941	114.5	118.5	140.1	0.62	0.73	0.56	0.54	0.46	0.36	0.08	0.06	0.03
1942	171.9	142.8	141.8	0.45	0.75	0.69	0.85	0.24	0.29	0.06	0.05	0.04
1943	90.8	151.1	319.1	1.10	0.58	0.21	0.32	0.55	0.70	0.08	0.06	0.03
1944	111.4	179.1	177.2	0.65	0.46	0.46	0.46	0.26	0.34	0.07	0.04	0.04
1945	128.9	145.4	204.8	0.84	0.76	0.62	0.56	0.43	0.18	0.08	0.06	0.05
1946	118.7	144.0	188.2	1.00	0.70	1.09	0.32	0.32	0.19	0.08	0.06	0.04
Average	122.7	146.8	195.2	0.78	0.66	0.60	0.51	0.38	0.35	0.08	0.06	0.04

The phenomena observed here for data from different fish, from the same fish and for averaged data, viz., that the estimated L_∞ and K/2m+2 are dependent on the age of fish used in the study, greatly complicates the problem of estimating growth parameters. Since most of the calculated lengths were extremely close to the observed lengths, the extended Bertalanffy equation cannot be regarded as wholly inappropriate for halibut data. Some examples of the fits are shown in

Figure 1. The curves for the sixteen-year-olds were subjectively classified as A, B or C according to which of these three fits they most closely resembled; 43 percent fell into the A category, an equal proportion into B, and 13 percent into C. In a few cases the fitted line did not describe the observed data well or the estimation process did not converge. An example of such an unaccptable fit is shown by D in Figure 1. Data of this type were not included in this study.

Although the change of the estimates of L_∞ and K/2m+2 with increasing age is of importance in the management of halibut stocks, it is also of interest to determine if it occurs with fish other than halibut. Back-calculated lengths of walleye and bass, reported upon by Smith and Pycha (1961) and Mraz and Threinen (1955) respectively, were fitted with equation (2). In the case of walleye data

Table 3. Analysis of variance of the estimated growth parameters (L_∞, m, K/m and K/(2m+2)), based on eight, twelve and sixteen-year-old individual halibut.

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	F[1]
L_∞: Maximum Length				
Variation due to year class	30221.6	5	6044.3	0.84
Variation due to age	76760.3	2	38380.1	5.33**
Variation due to interactions	111154.8	10	11115.5	1.67
Error	478829.4	72	6650.4	
Pooled error	589984.2	82	7194.9	
m: Rate of Change between Metabolic Rate and Weight				
Variation due to year class	0.97	5	0.19	0.95
Variation due to age	0.47	2	0.24	1.20
Variation due to interactions	2.33	10	0.23	1.15
Error	14.24	72	0.20	
Pooled error	16.57	84	0.20	
K/m: Relative Growth Rate				
Variation due to year class	63.1	5	12.6	0.85
Variation due to age	43.7	2	21.8	1.47
Variation due to interactions	164.6	10	16.5	1.13
Error	1030.8	70	14.6	
Pooled error	1185.4	80	14.8	
K/(2m+2): Weighted Mean Growth Rate				
Variation due to year class	0.13	5	0.026	0.67
Variation due to age	1.57	2	0.785	20.13**
Variation due to interactions	0.61	10	0.061	1.69
Error	2.56	72	0.036	
Pooled error	3.17	82	0.039	

[1] The significance of the F ratios are indicated in the customary manner, a single asterisk denoting significance at the five percent level and a double asterisk at the one percent level.

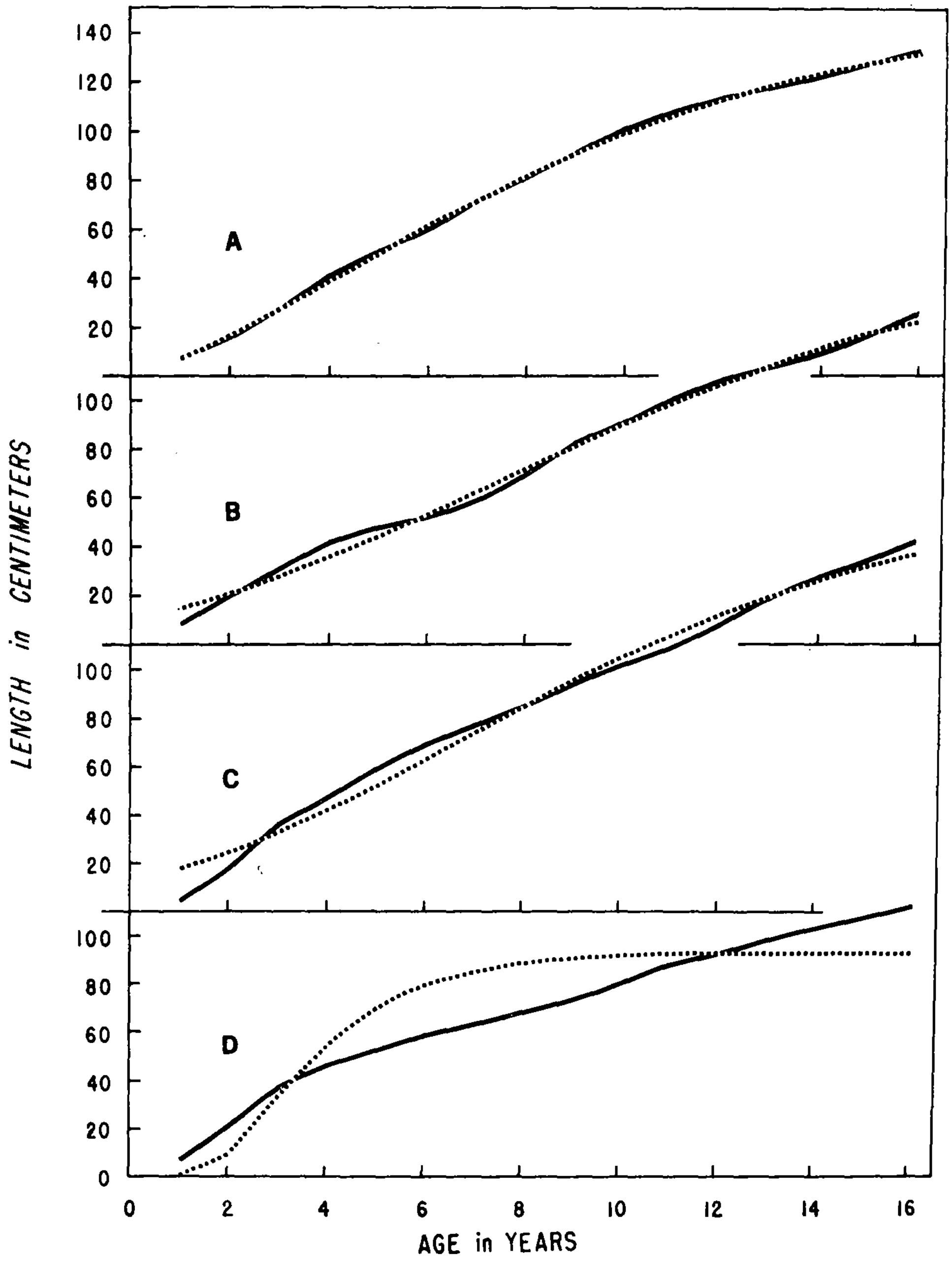


Figure 1. Observed and calculated length at each age. Examples of an excellent fit, A; a good fit, B; a less satisfactory fit, C; and an unacceptable fit, D.

the lengths at the first five of the nine ages as well as the lengths at all nine ages of the June sample of the respective reference were used to estimate the growth parameters. The dual analyses of the bass data were based upon the lengths at the first seven and at all thirteen ages given in Table 4 of the respective reference.

The estimated growth parameters are as follows:

		L_∞	m	K/m	K/(2m+2)
Walleye	age 5	15.8	0.54	0.80	0.140
	age 9	17.7	0.38	0.82	0.113
Bass	age 7	14.3	1.20	0.55	0.15
	age 13	21.5	0.59	0.32	0.069

Table 4. Average growth parameters for the 1941 through 1946 year classes using lengths at the first eight and the first twelve years of sixteen-year-old halibut.

Parameter	L_∞			m			K/m			K/(2m+2)		
Age	8	12	16	8	12	16	8	12	16	8	12	16
Year Class												
1941	79.2	114.8	140.1	0.72	0.71	0.56	0.62	0.49	0.36	0.11	0.08	0.03
1942	79.0	114.1	141.8	0.60	0.70	0.69	0.96	0.50	0.29	0.17	0.07	0.04
1943	82.6	114.7	319.1	0.70	0.63	0.21	0.54	0.23	0.70	0.11	0.08	0.03
1944	120.9	139.4	177.2	0.64	0.84	0.46	0.49	0.41	0.34	0.08	0.08	0.04
1945	108.0	144.7	204.8	0.67	0.71	0.62	0.95	0.37	0.18	0.12	0.06	0.05
1946	110.0	160.1	188.2	0.65	0.84	1.09	0.92	0.25	0.19	0.11	0.05	0.04
Average	96.6	131.3	195.2	0.66	0.74	0.61	0.75	0.38	0.34	0.12	0.07	0.04

Table 5. Analysis of variance of estimated growth parameters based on the first eight and twelve years of the sixteen-year-old fish.

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	F
L_∞: Maximum Length				
Variation due to year class	46680.1	5	9336.0	1.44
Variation due to age	134998.3	2	67499.1	10.4**
Variation due to interactions	93050.1	10	9305.0	1.53
Error	430653.2	71	6065.5	
Pooled error	523703.3	81	6465.4	
m: Rate of Change Between Metabolic Rate and Weight				
Variation due to year class	0.65	5	0.13	0.72
Variation due to age	0.27	2	0.14	0.78
Variation due to interactions	0.79	10	0.079	0.41
Error	13.60	71	0.191	
Pooled error	14.39	81	0.18	
K/m: Relative Growth Rate				
Variation due to year class	31.9	5	6.4	0.29
Variation due to age	115.8	2	57.9	2.66
Variation due to interactions	339.7	10	34.0	1.69
Error	1364.8	68	20.1	
Pooled error	1704.5	78	21.8	
K/(2m+2): Weighted Mean Growth Rate				
Variation due to year class	0.67	5	0.13	0.32
Variation due to age	7.16	2	3.58	8.95**
Variation due to interactions	3.97	10	0.40	1.74
Error	16.37	71	0.23	

The absence of data for individual fish precludes statistical tests of the differences in the above estimated parameters, such as made in the analysis of the halibut data. Notwithstanding, it is apparent from the above table that the estimate of L_∞ increases and that of $K/2m+2$ decreases with age for both walleye and bass. Hence these phenomena are not restricted to halibut data alone and may be inherent in the Bertalanffy equations.

In summary the estimation of L_∞ and growth rate, $K/2m+2$, from equation (2) cannot be relied upon and their changes with age thus impose a limitation on comparative growth studies. On the other hand, the extended Bartalanffy equation (2) describes well the growth of halibut within the range of ages used. Whether Bertalanffy's physiological interpretations of the parameters are incorrect with respect to halibut cannot be resolved at this time. Some alternative explanations for the change are now considered.

Table 6. Average growth parameters L_∞ and K for year classes 1941 through 1946 from the extended Bertalanffy equation (2) with $m=0.67$.

Age	8		12		16	
Parameter	L_∞	K	L_∞	K	L_∞	K
Year Class						
1941	117.7	0.28	122.0	0.22	122.9	0.20
1942	113.5	0.26	127.0	0.19	129.2	0.19
1943	82.4	0.30	120.4	0.24	140.0	0.16
1944	98.9	0.29	133.2	0.19	150.9	0.19
1945	138.5	0.24	132.1	0.23	156.8	0.16
1946	121.0	0.24	134.2	0.20	165.8	0.17

Table 7. Growth parameters for the 1941 through 1946 year classes estimated from averaged length data of halibut eight, twelve and sixteen years of age.

Parameter	L_∞			m			K/m			K/(2m+2)		
Age	8	12	16	8	12	16	8	12	16	8	12	16
Year Class												
1941	96.6	115.6	130.8	0.70	1.40	0.90	0.47	0.21	0.30	0.10	0.06	0.07
1942	98.4	123.8	136.0	1.19	1.19	1.50	0.33	0.20	0.15	0.09	0.05	0.04
1943	69.5	82.1	90.1	0.39	1.40	1.22	1.43	0.14	0.32	0.20	0.14	0.09
1944	191.6	188.9	212.0	0.01	0.33	0.09	6.50	0.27	0.80	0.03	0.03	0.03
1945	107.2	176.5	203.7	0.91	0.21	0.30	0.33	0.49	0.28	0.08	0.04	0.03
1946	126.8	135.6	161.0	0.60	0.70	1.50	0.32	0.28	0.15	0.06	0.06	0.04
Average	115.0	137.1	155.6	0.63	0.87	0.91	1.56	0.26	0.33	0.09	0.06	0.05

EXAMINATION OF WEIGHT-LENGTH RELATIONSHIP

The Bertalanffy growth models require the assumption that the relationship between weight and length ($W_t = q L_t^B$) remains constant throughout the age span involved in the estimation procedure. The change of the estimates of L_∞ and K/2m+2 with age and the occasional wide divergence between the observed and expected lengths could be caused by a changing weight-length relationship.

To study this possibility the weight-length relationships of male and female halibut taken in 1926 and 1929 were calculated. The exponents of the weight-length relationship for each age group are shown in Figure 2, Table 8. There appears to be a slight increase in the value of the exponent as age increases. Analysis of covariance was used to determine if the trends of the exponents with age differed due to sex or between samples (Table 9). This analysis suggested that

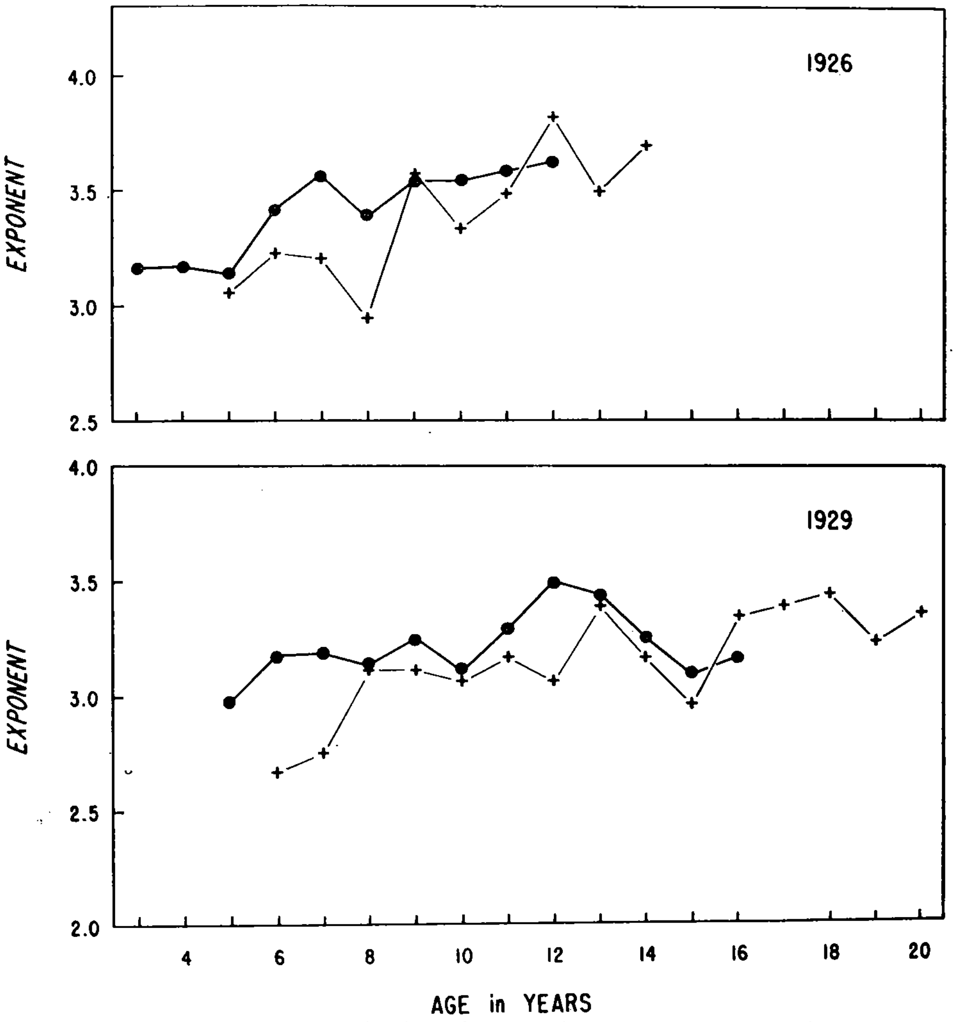


Figure 2. Exponent of the weight-length relationship at each age for males (+——+) and females (•——•) of the 1926 and 1929 samples.

Table 8. Values of the exponent B for the relation $W=qL^B$ for two samples of male and female halibut.

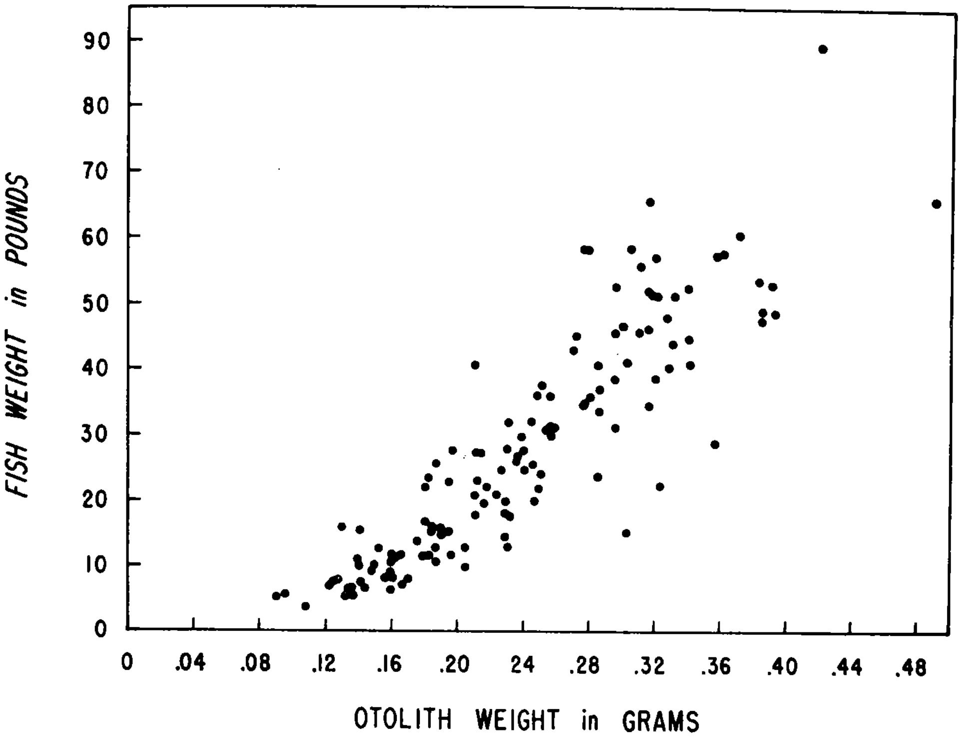
Age	1926 Sample		1929 Sample	
	Males	Females	Males	Females
3		3.17		
4		3.17		
5	3.05	3.13		2.97
6	3.22	3.42	2.66	3.18
7	3.20	3.57	2.74	3.18
8	2.95	3.38	3.11	3.13
9	3.57	3.55	3.11	3.25
10	3.33	3.54	3.06	3.10
11	3.49	3.58	3.17	3.29
12	3.82	3.62	3.06	3.50
13	3.50		3.39	3.44
14	3.70		3.16	3.25
15			2.95	3.08
16			3.34	3.17
17			3.38	
18			3.44	
19			3.23	
20			3.36	

the points could be fitted neither by a common line nor by parallel lines. A t-test to determine whether the slope of trend lines for both sexes in each sample was different from zero resulted in rejection of the hypothesis of a zero slope ($t = 2.13$ with 46 degrees of freedom). Thus there is an indication of an increase in the exponent of the weight-length relationship as the age of the fish increases. However, since the foregoing data are not of a single year class the tests do not answer the question as to whether or not the same weight-length relationship applies at each age within a year class but they do raise some doubt.

While halibut weights and lengths for each age within a year class over at least the ages represented in the commercial setline fishery are not available, an alternative analysis is possible because there is a high correlation ($r > .90$) between logarithm of fish weight and logarithm of otolith weight as well as a high correlation ($r > 0.90$) between logarithm of fish length and logarithm of otolith radius.

Using a sample of otoliths collected in 1954 the relationship between fish weight and otolith weight was calculated after both variables had been transformed to logarithms. Both original and transformed data points are shown in Figure 3 for fish six years of age and older. The line fitted to the transformed data is $\ln (Y) = 5.99924 + 1.96451 \ln (X)$, where Y is fish weight in pounds and X is otolith weight in grams.

Two samples of approximately 10 otoliths from each of the ages 9 through 14 from fish of the 1945 and 1946 year classes taken on the Portlock-Albatross



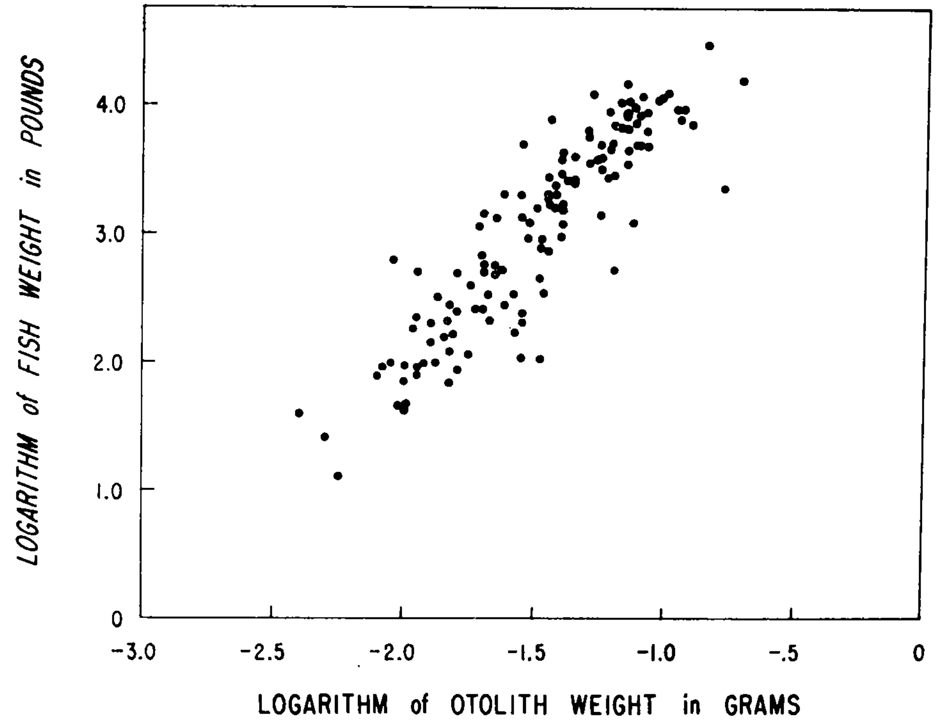


Figure 3. Scatter diagram of original and transformed fish weights in pounds and otolith weights in grams.

grounds were weighed. The otolith weights were converted into fish weights using the above relationship. The slope of the regression of body weight on body length (computed from otolith weights and lengths) for each age in the samples as well as the standard error of the slope are given in Table 10.

A transformed weight-length relationship was determined for each age and each sample and year class. Whether the relationship could be represented by a common line for the two samples and the two year classes at each age was tested by analysis of covariance (Table 11). This analysis indicates that the weight-length relationship for samples and year classes cannot be represented by a single line at each age nor even by parallel lines. Furthermore, from one age group to another the pattern of rejection shows that the heterogeneity of the samples is not affected by the age of the fish in the samples.

A regression of slopes on age was calculated for each sample and each year class. In three cases the regression is non-significant; only sample 2 of the 1945 year class is significantly different from zero ($t = -6.53$, $P < 0.01$). The data and regressions are shown in Figure 4 and Table 12.

While this relationship needs further investigation, at the present time any change with age in the weight-length relationship in halibut does not seem to contribute materially to explaining the changes observed in the estimates of L_∞ and $K/2m+2$.

Table 9. Analyses of covariance of the four series of exponents of the weight-length relationship of male and female halibut taken in 1926 and in 1929.

Hypothesis 1[1]:

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square
Deviations about common line	2.4020		
Deviations from individual lines	0.8533	42	0.0203
Due to fitting common line	1.5487	6	0.2581

$F=12.71$:** reject hypothesis that the data can be fitted by a single common line.

Hypothesis 2[2]:

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square
Deviations about parallel lines	1.0603		
Deviations from individual lines	0.8533	42	0.0203
Due to fitting parallel lines	0.2070	3	0.0690

$F=3.399$*: reject hypothesis that the data can be fitted by parallel lines.

[1] Hypothesis 1 tests whether a single line can be fitted to all groups.

[2] Hypothesis 2 tests whether parallel lines can be fitted to all groups.

CONSIDERATION OF CATABOLIC AND ANABOLIC COEFFICIENTS

Another possible cause of changes in the estimates of L_∞ and $K/2m+2$ with the increase in the number of ages used in the estimation may be that the basic

Table 10. Slope of regression of body weight on body length, standard error of the slope and sample size by age for halibut of the 1945 and 1946 year classes taken on Portlock-Albatross grounds.

1945 Year Class	Age	Slope	Standard Error	Sample Size
Sample 1	9	3.92	0.80	9
	10	2.51	0.40	10
	11	5.50	0.57	8
	12	2.71	0.70	10
	13	3.10	0.47	10
	14	2.58	0.63	10
Sample 2	9	3.16	0.27	10
	10	2.88	0.73	10
	11	2.45	0.51	10
	12	1.54	0.98	10
	13	1.74	1.06	10
	14	0.69	0.30	10
1946 Year Class				
Sample 1	9	0.27	0.53	10
	10	2.32	0.41	10
	11	2.78	0.68	10
	12	3.45	0.58	10
	13	1.48	0.61	10
	14	3.05	0.85	10
Sample 2	9	1.16	0.55	10
	10	2.89	0.36	10
	11	3.17	0.31	10
	12	2.98	0.69	10
	13	2.03	0.46	10
	14	2.06	0.70	10

Table 11. Analysis of covariance of samples 1 and 2 for ages 9 through 14 of the 1945 and 1946 year classes.

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	F
Age 9 H_1^1				
Deviations about common line	0.1048	37		
Deviations from individual lines	0.0684	31	0.0022	2.77*
Due to fitting common line	0.0364	6	0.0061	
H_2^2				
Deviations about parallel lines	0.1025	34		
Deviations from individual lines	0.0684	31	0.0022	5.18*
Due to fitting parallel lines	0.0341	3	0.0114	
Age 10 H_1				
Deviations about common line	0.0792	38		
Deviations from individual lines	0.0606	32	0.0019	1.63
Due to fitting common line	0.0186	6	0.0031	
H_2^3				
Age 11 H_1				
Deviations about common line	0.1220	36	0.0023	2.83*
Deviations from individual lines	0.0828	30	0.0065	

(Cont'd on page 22)

Table 11 (Continued)

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	F
Due to fitting common line	0.0392	6		
H_2				
Deviations about parallel lines	0.1062	33		
Deviations from individual lines	0.0828	30	0.0023	3.39*
Due to fitting parallel lines	0.0234	3	0.0078	
Age 12 H_1				
Deviations about common line	2.2306	38		
Deviations from individual lines	1.8349	32	0.0573	1.16
Due to fitting common line	0.3957	6	0.0662	
H_2[3]				
Age 13 H_1				
Deviations about common line	0.1256	38		
Deviations from individual lines	0.0687	32	0.0021	4.52*
Due to fitting common line	0.0509	6	0.0095	
H_2				
Deviations about parallel lines	0.0837	35		
Deviations from individual lines	0.0687	32	0.0021	2.39
Due to fitting parallel lines	0.0150	3	0.0050	
Age 14 H_1				
Deviations about common line	0.0997	38		
Deviations from individual lines	0.0529	32	0.0017	4.59*
Due to fitting common line	0.0468	6	0.0078	
H_2				
Deviations about parallel lines	0.0715	35		
Deviations from individual lines	0.0529	32	0.0017	2.90*
Due to fitting parallel lines	0.0186	3	0.0062	

1. Hypothesis 1, H_1: tests whether a single line can be fitted to all groups.
2. Hypothesis 2, H_2: tests whether parallel lines can be fitted to all groups.
3. Acceptance of H_1 automatically implies acceptance of H_2.

Table 12. Slopes of otolith-weight otolith-length, ages 9 through 14, for samples 1 and 2 of the 1945 and 1946 year classes.

	1945 Year Class		1946 Year Class	
Age	Sample 1	Sample 2	Sample 1	Sample 2
9	2.65	2.01	1.64	0.78
10	1.69	1.93	1.54	1.95
11	3.61	1.59	1.84	2.12
12	1.79	1.01	2.29	1.98
13	2.15	1.16	0.99	1.38
14	1.73	0.46	2.06	1.37

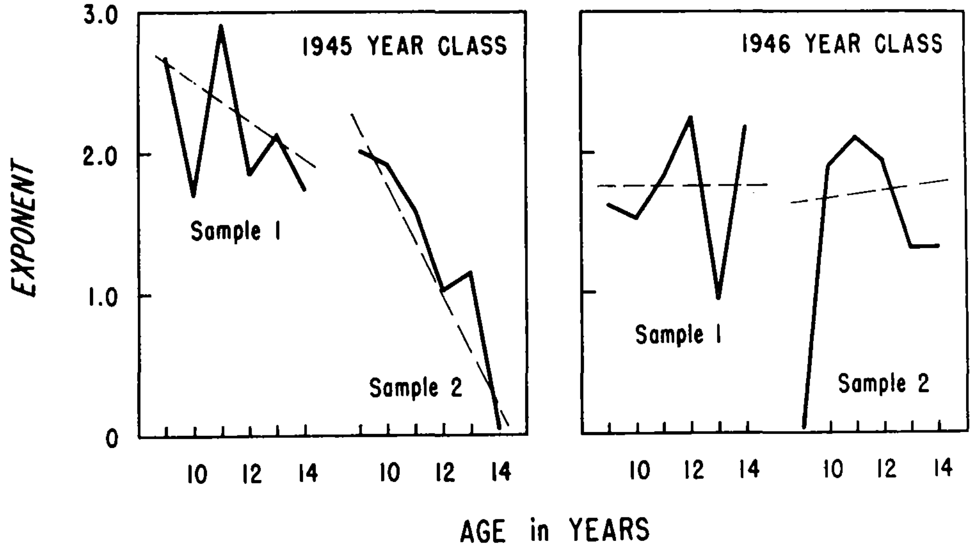


Figure 4. Regression of the exponent of the weight-length relationship (— — —) for ages 9 through 14 for samples 1 and 2 from the 1945 and 1946 year classes.

parameters H, k, the coefficients in the catabolism and anabolism processes, vary over the life of the fish. If this is the case, a single equation either of the forms (1) or (2) has no biological significance. However, an equation may have no biological significance but still may serve empirically, that is, fit the observed data well, particularly if enough parameters are introduced — as for example, the modified logistic of Pearl and Reed (1923), where in the denominator an nth degree polynomial is introduced in the exponent. To determine whether or not the catabolic and anabolic processes vary throughout the life of halibut is beyond the scope of this report.

EFFECT OF METHOD OF ESTIMATION

The least squares or maximum likelihood estimation procedure to obtain the parameters of a regression equation are based upon the assumption that the errors in the model are uncorrelated. Formally, this says that the variables (X, Y) have some structure

$$Y = f(X) + e_i$$

where f is a function such as (1) or (2) and the e_i are normally and independently distributed "errors" with mean zero and variance δ^2. The assumption of independent errors is reasonable when the equation is fitted to different animals but not necessarily so when fitted to data from the same animal at different ages.

This problem has been investigated in part for equation (1) by Finney (1958) and by Patterson (1958). Finney suggests that a more realistic model of the error structure for a biological growth curve is one that assumes an increasing variance of the errors with time as well as auto-correlation between successive errors. He and Patterson studied one such model and the latter author concluded that "the

Table 13. Mean, standard deviation and correlation coefficients of residual errors of estimate by age.

Mean Error of Estimate by Age:

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Means	3.9667	1.2667	−1.7333	−3.3667	−2.4333	−0.9333	0.5000	1.3667	1.9000	1.9667	1.2667	1.1333	0.7667	0.1667	1.1333	−3.0000

Standard Deviation of Error of Estimate by Age:

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Std. Dev.	4.4759	3.0050	2.7535	2.4280	3.3064	2.9117	2.9798	2.3560	3.0889	2.8221	2.7908	2.3302	1.8696	2.5337	2.4598	3.9479

Correlation Matrix of Errors of Estimate by Age:

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	1.0000															
2	0.4314	1.0000														
3	0.0119	0.3078	1.0000													
4	−0.6643*	−0.5769*	0.0254	1.0000												
5	−0.7115*	−0.6143*	−0.4641*	0.6091*	1.0000											
6	−0.5978*	−0.5499*	−0.4410	0.2621	0.7717*	1.0000										
7	−0.4718*	−0.4852*	−0.5001*	0.0786	0.5431*	0.7909	1.0000									
8	−0.3683	−0.1507	−0.4834*	−0.0480	0.3170	0.4437	0.6950*	1.0000								
9	−0.0451	−0.0639	−0.4630*	−0.1108	0.0430	−0.0414	0.2079	0.5975*	1.0000							
10	−0.0329	−0.2063	−0.5757*	0.0384	0.1793	−0.0249	0.1620	0.4272	0.8580*	1.0000						
11	0.0946	−0.0293	−0.3327	0.0302	0.1199	−0.0532	0.0041	0.0213	0.4472	0.5922*	1.0000					
12	0.0335	−0.0200	−0.1293	0.0394	0.1010	−0.0166	0.0546	−0.1034	0.0211	0.2576	0.5723*	1.0000				
13	0.4111	0.3061	0.6221*	−0.2094	−0.6319*	−0.5545*	−0.4921	−0.5671*	−0.4162	−0.3740	−0.1529	0.1261	1.0000			
14	0.4931*	0.2974	0.4630*	−0.4325	−0.5147*	−0.3054	−0.3311	−0.4381	−0.5353*	−0.5683*	−0.4308	−0.2492	0.6127*	1.0000		
15	0.1781	0.1449	0.3567	−0.0431	−0.2758	−0.2298	−0.3717	−0.4851*	−0.5827*	−0.6067*	−0.7230*	−0.5082	0.2929	0.6178*	1.0000	
16	0.0078	0.2267	0.3870	0.0144	−0.2359	−0.1800	−0.3752	−0.2966	−0.4100	−0.5447*	−0.6948*	−0.7122*	0.0234	0.2482	0.7421*	1.0000

method of Stevens (least squares) can be safely recommended for most biological applications."

The studies cited refer only to equation (1) and not to its extended form (2). Even if the error structure were known for equation (2), a theoretical study of the behavior of the estimates of this model would be much more difficult and perhaps not possible at the present time, though some results could be obtained by numerical methods using a high speed computer. As a partial answer to this question the pattern of the estimated error-of-estimate of the thirty 16-year-old fish has been investigated. More precisely if $\hat{Y}_i$ is the estimated length at age i as fitted by equation (2), Y_i the observed length, the error-of-estimate is $(Y_i - \hat{Y}_i)$ denoted by $\hat{e}_i$. The means, standard deviations and correlations of these $\hat{e}_i$ are shown in Table 13. From the table of standard deviations it is observed that no trend in the magnitude of the errors is evident. On the other hand, the correlation pattern is less clearcut. Forty-one of the 120 intercorrelations are significant at the one percent level (those marked with an asterisk). Yet, except for the number of adjacent significant r's in the first three columns, the other significant intercorrelations seem to be scattered randomly. Consequently, there is no strong reason to suggest that the least squares estimation method should fail.

THE YIELD EQUATION AND EUMETRIC FISHING

The yield from a stock is found by multiplying fishing rate by biomass (number times average weight) at any age and summing over all ages past the age of entry. In symbols this is:

$$Y_w = \int_{t_{p'}}^{\infty} F R' N(t) W(t) \, dt, \qquad (3)$$

where Y_w = yield in weight,
$t_{p'}$ = age of entry,
F = fishing mortality coefficient,
R' = recruitment surviving to age $t_{p'}$,
$N(t)$ = population size at time t,
$W(t)$ = average weight of fish in the population at time t.

Assuming equilibrium conditions, N(t), W(t), and R' may refer to a year class over its life span or to all age classes in the stable population in one year.

To establish a theoretical model for yield it is necessary to express N(t), W(t) in some functional form and to determine the interrelationships of the parameters. Thus inserting

$$N(t) = R' e^{-(M+F)(t-t_{p'})} \qquad (4)$$

$$W(t) = W_\infty (1 - e^{-K(t-t_0)})^3$$

in (3) leads to the yield model developed by Beverton-Holt (1957)[1].

---

[1] The equation for W(t) corresponds to Bertalanffy's equation (1). Usually W_∞ is determined from L_∞ by the relationship $W_\infty = qL_\infty^B$.

It is to be noted that there is a related equation to (3)

$$\overline{P} = \int_{t_{p'}}^{\infty} R' \, N(t) \, W(t) \, dt \qquad (5)$$

where $\overline{P}$ = biomass of the fished population, i.e. those of age $t_{p'}$ or more

and hence $Y_w = F \overline{P}$ (6)

Beverton and Holt further assumed that L_∞ is a decreasing linear function of $\overline{P}$, i.e.

$$L_\infty = a - b \overline{P} \qquad (7)$$

where a and b are the usual regression parameters.

They also assumed that K, the growth rate, is independent of stock density ($\overline{P}$) though it was noted that this may not apply generally.

The adjustment of the fishing mortality coefficient F and the age of entry $t_{p'}$ so that maximum yield is obtained has been termed eumetric fishing by Beverton and Holt (1957, p. 373). Determination of such optimum F and $t_{p'}$ and the corresponding maximum yield depends on correct formulation of the functional form of N(t), correct estimation of the parameters of the equation and also of the interrelationship of the parameters.

EFFECT OF GROWTH PARAMETERS ON YIELD EQUATIONS

Since management of a fishery may be based upon a theoretical yield model, it is important to inquire how incorrect estimation of any of the parameters of the model affect determination of maximum yield, and in particular how the apparent dependence of the estimate of L_∞ (and hence W_∞) and $K/2m+2$ on age of the fish in the sample could bias the estimation of yield. A related study is that of Paulik and Gales (1964). They considered the effect of using the relationship $W = q L^3$ in the Beverton and Holt yield model when in fact $W = q' L^B$ for $B \neq 3$.

Since the average population size depends in a rather complex way upon fishing mortality as well as on the other parameters, it is therefore very difficult to solve analytically for the coefficient of fishing mortality which maximizes yield in the yield equation (3).

It is even more difficult to evaluate the effect of bias in the estimation of W_∞ and $K/2m+2$ on the determination of maximum yield or on the estimation of the fishing mortality rate which should provide maximum yield. On the other hand, it can be shown that such bias will exist when these parameters are incorrectly estimated with data only from young fish.

Consider initially the effect on yield of underestimating L_∞ (and hence W_∞) without taking into account changes in growth rate. In the event that the composition of the stock were mainly young fish, say 8 years and younger, the estimated W_∞ will be too low. On the contrary, when the stock is composed of older fish, the estimated W_∞ should approximate the true value. This is illustrated schematically in Figure 5. As this suggests, the true regression of W_∞ on average population size might be quite different from the estimated regression. However, when growth rate is considered, the decreasing trend in the estimation of K/2m+2 that occurs with increasing age of the fish produces an opposite effect.

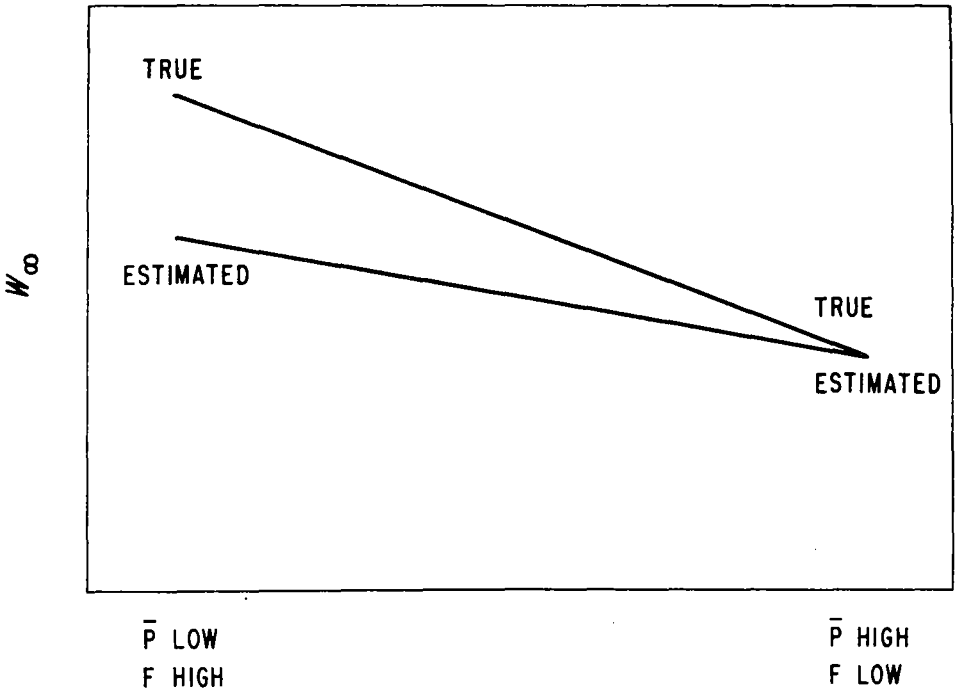


Figure 5. Schematic representation of maximum weight, W_∞, on average population size $\bar{P}$.

One method of investigating the possibilities in this situation is by calculation of yield per recruit for several different values of W_∞, i.e. those estimated from 8-year-old fish, 12-year-old fish and 16-year-old fish. This is illustrated with plaice data given by Beverton and Holt (1957, p. 310). The maximum weight (W_∞,) and growth rate (K) given by these authors for plaice (estimated from postwar data) are 2867 grams and 0.095 respectively. For the present evaluation yield has been calculated with these values and also with two different sets of W_∞ and K, the latter parameters were determined from the given set by making proportionally the same changes as the observed changes in the same parameters for halibut from 8 to 12 and from 8 to 16 years of age. These are the changes shown in Table 2, with L_∞ now converted to W_∞ by a length-weight table. The bias due to estimation errors is well illustrated by these calculations. With an age of entry of 4.7 years the maximum yield appears to be obtained at a fishing mortality coefficient of 0.3 when the parameters are estimated from age 8 fish while the maximum yield is actually obtained at a fishing mortality coefficient of 0.2. (W_∞ and K determined from age 16 fish). These data are used rather than the yield curves in Report No. 28 of the Commission since in that report growth was described on an empirical basis (Ricker, 1958) and W_∞ was not estimated.

It is apparent from examination of Table 14 that the yield per recruit is related to the growth parameters in an involved manner. The yields corresponding to age 12 fish are intermediate to those of age 8 and age 16 fish. It is also apparent that at higher ages of entry the yields are nearly the same so the problem then becomes one of the relative economic significance of small or of large fish, provided that if the fishery were to operate at younger ages enough fish must be left to provide adequate spawning. However, economic considerations are outside the scope of this paper.

Another method of achieving the maximum sustainable yield is through controlling age of entry, such as either by mesh size regulations or by minimum

Table 14. Yields per recruit for plaice when W_∞ and K have been altered in proportion to the changes observed in the growth parameters of halibut, estimated from eight, twelve, or sixteen-year-old fish.

Age of Entry	Coefficient of Fishing Mortality 0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2
Parameters estimated from eight-year-old fish												
3.7	215	257	252	236	221	208	197	189	182	176	172	168
4.7	222	281	288	280	268	258	249	241	235	230	226	222
5.7	224	298	317	317	311	303	296	290	285	280	276	273
6.7	220	307	339	347	346	342	338	333	329	325	322	320
7.7	211	307	350	367	373	373	371	369	366	363	361	359
8.7	196	298	350	377	389	394	396	396	395	393	392	391
9.7	177	280	339	374	393	404	410	413	414	414	414	414
10.7	152	251	315	356	383	400	411	418	423	425	427	428
11.7	123	212	276	321	355	378	395	408	416	423	427	430
Parameters estimated from twelve-year-old fish												
3.7	153	176	167	152	139	128	120	113	108	104	101	98
4.7	160	197	196	185	174	165	157	151	146	142	138	135
5.7	164	213	222	217	209	201	194	188	184	180	177	174
6.7	164	225	243	245	241	236	230	225	221	218	214	212
7.7	161	231	259	268	269	266	263	259	256	253	250	248
8.7	153	229	266	283	290	291	291	289	287	284	282	281
9.7	140	220	265	290	303	309	312	312	312	311	310	309
10.7	123	202	252	284	304	316	323	328	330	331	331	331
11.7	102	174	226	263	289	308	321	330	336	341	343	345
Parameters estimated from sixteen-year-old fish												
3.7	244	278	260	235	213	195	182	172	163	157	151	147
4.7	256	312	308	289	270	254	241	230	222	215	210	205
5.7	264	340	351	341	327	313	302	292	284	277	272	267
6.7	266	361	388	389	381	371	361	353	346	340	334	330
7.7	261	373	416	429	429	424	417	411	405	399	395	391
8.7	249	373	433	458	468	469	467	463	459	454	451	448
9.7	230	361	434	473	493	503	506	506	505	503	501	498
10.7	204	334	416	468	500	519	531	537	540	541	541	541
11.7	169	290	376	436	480	510	531	546	556	563	567	570

size limits. This can be seen from the above table where for a fixed coefficient of fishing mortality optimum age of entry is consistently underestimated when the parameters are estimated from 8 year old fish. A more general treatment can be based on the following theoretical considerations. If fishing pressure may be made arbitrarily large and selection is knife-edged (Beverton and Holt, 1957, pg. 30) then the optimum age of entry should be that age where growth rate and natural mortality rate are exactly in balance. In practice there is a limit to the possible increase in fishing pressure and hence of F. Additionally, selection is almost always spread over a range of sizes rather than being knife-edged. These considerations will tend to reduce the optimum age of entry from the theoretical ideal where growth rate and natural mortality rate are equal. In the actual situation it may also be necessary to take into account other considerations, e.g. age of spawning, limitations of the gear, etc. Disregarding such considerations, the ideal age of entry is the age at which $\frac{dW}{dt}$ equals M, where M is the coefficient of natural mortality. The growth equation for weight analogous to (2) can be written in the form:

$$W_t = W_\infty \left[1 - e^{-Km\ (t - t_o)} \right]^{\frac{B}{m}} \qquad (8)$$

where K, m and B are as defined before. Since

$$\frac{dW}{dt} = BKW_\infty \left[1 - e^{-Km\ (t - t_o)} \right]^{\frac{B}{m} - 1} e^{-Km\ (t - t_o)},$$

the optimum age of entry, t_{pl}, is the solution of the equation

$n^{\frac{B}{m} - 1} (1 - u) = \frac{M}{BKW_\infty}$ where $u = 1 - e^{-Km\ (t_{pl} - t_o)}$. This equation has two solutions, if there are any. This arises from the fact that the Bertalanffy growth curve is sigmoid—the rate of growth is zero when t equals t_o, increases slowly to a maximum at the point of inflection and thereafter decreases again. It is this second, i.e. the larger solution, that is relevant here.

Two parameters of the growth equation, K and W_∞, enter into the determination of this optimum age of entry in the form of the product (BKW_∞). While W_∞ may be underestimated when estimation is based on young fish, it appears that K is overestimated, and fortunately these errors are compensating. Table 15 shows the products $BKL_\infty^{3.24}$ as derived from the earlier estimates (Table 2).

The effect of overestimating BKW_∞ is shown in the following diagram. If BKW_∞ is overestimated then $\frac{M}{BKW_\infty}$ is too small and the solution for u and hence for t_{pl} is moved to the right. If BKW_∞ is underestimated, the estimate of t_{pl} is biased in the opposite direction. Thus in a stock where fishing pressure has greatly reduced the older age groups, the estimates based on growth curves from the young fish available to the fishery could lead to erroneous estimates of the optimum age of entry. It should be pointed out that if the error is one of overestimating the correct age of entry this will in time be detected as additional data become available.

Table 15. Average products* (BKW_∞) for the 1941 through 1946 year classes, indvidually estimated from growth parameters of fish eight, twelve and sixteen years of age.

Year Class	8	12	16
1941	17.47	27.49	53.55
1942	66.14 (43.17)	38.92	38.50
1943	19.44	57.73	165.30 (36.49)
1944	47.46	58.08	67.92
1945	68.42	54.07	92.22 (60.54)
1946	41.74	47.94	124.08
Average	43.44 (39.62)	47.37	90.26 (63.51)

*Three fish had L_∞'s of 335, 826 and 347. The values in ( ) exclude these; however, it is seen that the trend of the product (BKW_∞) is the same with respect to age of estimation whether these are included or excluded.

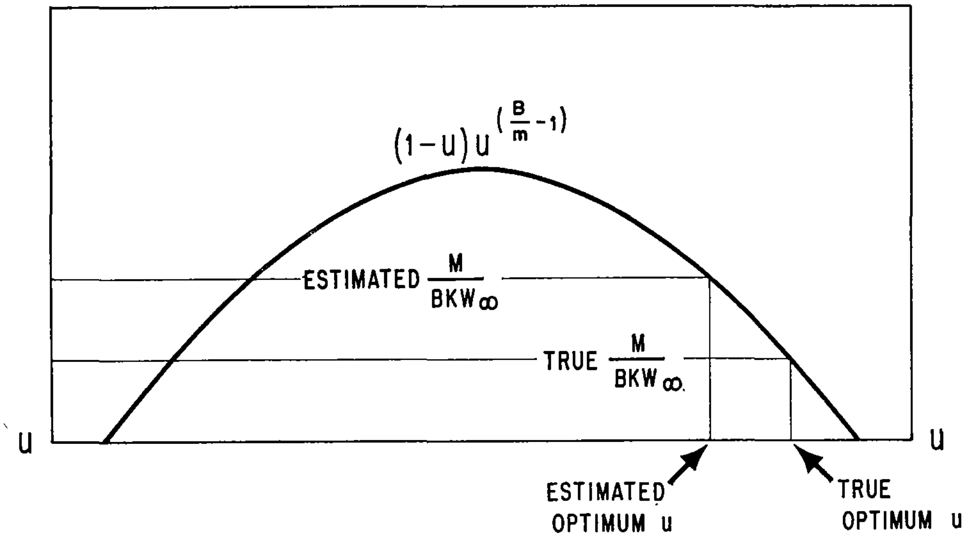


Figure 6. Diagram illustrating the bias introduced in estimating u, when BKW_∞ is underestimated.

SUMMARY

The applicability of the Bertalanffy growth equation and an extension thereof to individual fish or to groups of fish is discussed.

To study various aspects of the problem, back-calculated lengths based on measurements of otoliths of 90 halibut, five from age 8, five from age 12, and five from age 16 from each of six year classes were fitted by the use of an extended Bertalanffy growth equation.

It was shown that the maximum length L_∞ and the weighted mean growth rate $K/2m+2$ are dependent upon the span of ages used and that the rate of change between metabolic rate and weight, m, as well as the relative growth rate, K/m, are not dependent upon age.

The foregoing changes in L_∞ and $K/2m+2$ do not appear to be restricted to halibut as limited data for walleye and bass indicated the same results.

Statistical tests indicated that any changes in the weight-length relationship associated with the age of the halibut do not contribute significantly to the change in L_∞ and $K/2m+2$.

Errors-of-estimate of the fitting procedure were determined, and the magnitudes and conformity of the means, the sizes of the standard deviations and the pattern of the significant correlation coefficients do not suggest that the least squares method of estimation would fail and thereby cause the change noted in the parameters.

It was also shown that if growth rate or optimum age of entry were determined from a stock composed mainly of young fish the growth parameters estimated from such data might result in a management decision which would cause the harvesting of the population below the optimum age of entry and thereby reduce rather than increase the yield from such a stock.

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