

SOME ASPECTS OF GROWTH IN THE FAMILY SALMONIDAE

by

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B.S. in Zoology, University of Washington, 1946

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

in the Department
of
ZOOLOGY

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
May, 1957

ABSTRACT

Mathematical descriptions of the growth of animals are reviewed in the light of applicability to two species of the Family Salmonidae. No generalized growth equation is found to accurately depict growth for the material discussed. Theoretical and practical limitations of the use of age as a classification for relating growth rates are given. An hypothesis that relative growth rate declines with increase in size but is independent of age is offered and explored. Data on steelhead from Chilliwack River, British Columbia, are analysed with the use of size-specific instantaneous growth rate regressions. Factors leading to observed variation and life history events are discussed and the literature reviewed. In all cases, size is determined to be a more reliable criterion of physiological development than age.

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ACKNOWLEDGEMENTS

The author takes sincere pleasure in acknowledging the guidance of Dr. P.A. Larkin on the investigation of growth and development of the hypothesis of size-specific instantaneous growth rates. Dr. C.C. Lindsey critically reviewed the manuscript and contributed materially to the query. Virginia E. Parker, wife of the author, carried out typing of the manuscript in its many drafts as well as assisting in processing the raw data. The British Columbia Game Commission, for use of steelhead and rainbow trout data, and the Alaska Department of Fisheries for providing data on chinook salmon as well as research funds, are gratefully acknowledged.

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SOME ASPECTS OF GROWTH IN THE FAMILY SALMONIDAE

INTRODUCTION

Growth of fishes is an important vital statistic, yet in wild populations the opportunity to directly measure growth of an individual is seldom obtained. It thus becomes necessary both to measure and to predict growth by statistical inference. The problem has been approached both theoretically and empirically. Theorists have attempted general growth formulae that, given a series of observations at some stage of life, will accurately extrapolate the series to predict growth at some future time. Other scientists, working with empirical observations, have transformed the data by various methods to allow statistical analysis. Predictions of size have been made on the basis of consistency of past observations. Both approaches are essential to understanding growth.

Where growth is measured, either directly or indirectly, a problem arises when a comparison is made between individuals or groups or a prediction of growth is the objective. Most commonly, growth is compared between groups of the same age, which implies that age is considered to be a significant determinant of growth. Similarly, estimates

of future size are based on growth with age.

This thesis is concerned with reviewing the important concepts of growth and discussing their application to representative species of Salmonidae. The concept of age as a determinant of growth is examined and the use of size as an alternate explored.

THE PHENOMENON OF GROWTH

Definitions

The term growth may have a broad connotation to many workers, i.e. it may include differentiation as well as size increment (Hammett, 1943). For the purposes of this discussion growth is restricted by definition to mean increase in size. While growth of a fish is in three dimensions, and relative growth of parts may not be isometric, these attributes may all be computed from length by appropriate empirical formulae (Huxley, 1932; Martin, 1949). Increment of fork length, then, is representative of growth of the whole animal and is used throughout this thesis.

Huxley (1932) lists three essential attributes of growth: (a) it is a process of self multiplication, (b) the relative rate is retarded with increase in size or age, and (c) growth rate is affected by external environment. Fry (1947) considers growth as one of the many "activities" of an animal and therefore dependent upon energies available

in excess of that required for sustenance. The sustenance requirement for any particular size is modified by physical, chemical, and biological factors of the environment. Thus, growth is a result of many complex, interacting factors, few of which may be predictable or forecast except under laboratory conditions.

Mathematical Attempts at Growth Formulae

Many workers have attempted to describe growth mathematically, i.e. to formulate an equation that describes the course of growth throughout life. Minot (1891), working on the guinea pig (Cavia cobaya), observed that absolute increment (total increase in weight per unit time) was related to the size of the animal. Relative increment, expressed as a percentage of initial size for any short period of time, decreased with increase in size. He interpreted this observation as implying a progressive loss of power of growth, beginning close to birth. Growth during a finite period of time was described by a percentage growth rate,

$$K = 100 \frac{W_2 - W_1}{W_1} \quad . . . \quad (1)$$

where W_1 denotes weight at time 1,

W_2 denotes weight at time 2, and

K is the percentage growth rate.

Minot also suggested that average size during the time period should replace W_1 in the denominator, i.e.

assuming linear growth,

$$K = 100 \frac{W_2 - W_1}{(W_1 + W_2) / 2} \quad . . . \quad (2)$$

This modification, while suggested, was not used as it made little improvement to the description.

Robertson (1908) considered the course of growth throughout the life of an animal to be like a monomolecular, autocatalytic reaction in which instantaneous velocity of growth is proportional not only to size attained, but also to size yet to be attained. His formula, in differential form, is

$$\frac{d W}{d t} = k W (A - W) \quad . . . \quad (3)$$

where W denotes size at any instant,

A denotes adult or final size, and

k is a velocity constant.

This equation, while intended to provide a theoretical description of the whole course of growth, has been criticized by Brody (1945), Crozier (1926), and other workers as having little similarity to empirically derived growth curves.

Robertson's equation describes a sigmoid curve with the point of inflection occurring at the center, i.e. the curve is, by definition, symmetrical. Observations, principally on homiotherms, have not shown such symmetry to be usual.

Robertson's equation does establish a fundamental aspect of growth in that it identifies two simultaneously

acting, opposing forces: (a) the capacity for growth as a function of size, i.e. instantaneous "compound interest" at a constant rate, and (b) a decrease in growth rate proportional to increase in size, reflecting a progressive decrease in metabolic efficiency.

Attempts to modify Robertson's equation (3) (see Brody, 1945) have led to practical difficulties. To make a curve descriptive of a process dependent upon many variables necessitates the use of several constants. The resultant curve thus becomes a multi-inflected line, fitted to particular empirical data. Such a formula has little theoretical significance unless the constants are meaningful and identifiable with biological processes.

Brody (1927a,b) was able to describe the course of growth for homiotherms by considering Robertson's growth curve as encompassing two phases of growth. Accepting the hypothesis that the general growth curve is sigmoid, Brody pointed to the difficulty in placing the point of inflection. His solution was to write two equations, one for the "self-accelerating" phase where growth rate is proportional to size attained and the other for the "self-inhibiting" phase where growth rate is proportional to the growth yet to be made. These formulae are: for the self-accelerating phase in differential form,

$$\frac{d W}{d t} = k_1 W \quad . . . \quad (4)$$

and for the self-inhibiting phase, in differential form,

$$\frac{dW}{dt} = k_2 (A - W) \quad . . . (5)$$

The separation of the growth curve into two component parts would seem to imply that during the self-accelerating phase growth is unrestricted except by size^{*}; at the point of inflection a second force (or sum of forces) begins to apply. Since in fish it is generally conceded that the point of inflection occurs close to or within the embryonic stage, the self-accelerating phase may not be observable under field conditions.

Ford (1933) observed that in herring (Clupea harengus) increment in length measured between succeeding scale annuli, i.e. $L_{t+1} - L_t$, was inversely correlated with L_t . He determined a regression equation of the type

$$L_{t+1} = a + KL_t \quad . . . (6)$$

It can be shown that a series of lengths calculated by equation (6) form a geometric progression when K is greater or less than unity, and form an arithmetic progression when K equals unity. As noted above, the usual case observed is $K < 1$, i.e. the self-inhibiting phase of Brody (equation 5).

Von Bertalanffy (1938) approached the problem

* Although empirical data may be observed to comply with a growth form $dW/dt = k_1 W$, this cannot be distinguished from a growth form described by $dW/dt = (k_1 - k_2)W$, where k_2 is negative and less than k_1 . Hence, growth retarding processes may act during the self-accelerating phase and not be detected (see Gray, 1929).

of growth from a physiological point of view, stating that relative energy available for growth could be calculated from the relationship between surface and volume of a growing sphere. Since maintenance requirement is related to mass, and the ability to exceed this requirement is related to absorptive area, growth rate of an organism (in three dimensions) will necessarily decline with increase in size. His formula for the growth curve is equivalent to Brody's equation for the self-inhibiting phase and needs no further consideration here. His formula was shown to accurately describe the growth of the guppy (Lebistes reticulatus (Peters)) under laboratory conditions.

Walford (1946) has provided a graphic solution of a geometric progression where $K < 1$ by plotting L_{t+1} against L_t and has pointed out that the resulting straight line intersects a 45° diagonal passing through the origin. The intersection represents a statistical adult size of the animal, i.e. the average size where growth ceases (see Figure 1.).

Walford's growth transformation, Ford's regression (6), von Bertalanffy's equation, and Brody's equation (5) for the self-inhibiting phase are in reality equivalent solutions of a general growth curve where deceleration of relative growth rate is constant and terminates at zero. Walford's graphic solution has the advantage of being much easier to use, but has a disadvantage of yielding $n - 1$

points on the plot where n denotes age in whole years. Implicit in all of these growth formulae is the concept that the animal grows to a genetically predetermined ultimate size.

Ultimate Size of Fish

Ultimate size, in the case of the higher vertebrates, may be reached at maturity, past which point the animal may live for several years (Brody, 1945). Fish, however, usually grow throughout life (Jordan, 1905). Thus, in fishes, a progression of lengths can hardly be extrapolated to the point where growth ceases and retain any real meaning. This criticism is illustrated as follows.

If size increment in unit time is a constant proportion of growth yet to be made, a series of lengths will form a geometric progression having a common ratio of less than unity. Ultimate size may be solved graphically by either a Walford (1946) graph or a Brody (1927a, 1945) graph. Examples of these are provided in Figures 1 and 2. Data for chinook salmon (Oncorhynchus tshawytscha) are taken from Parker and Kirkness (1956); for rainbow trout (Salmo gairdneri) from Larkin, et.al. (1957).

It is immediately apparent from the Walford growth transformation (Figure 1) that the coefficient of regression is close to unity. This means that an extrapolation of the transformation line either will not intersect the 45° di-

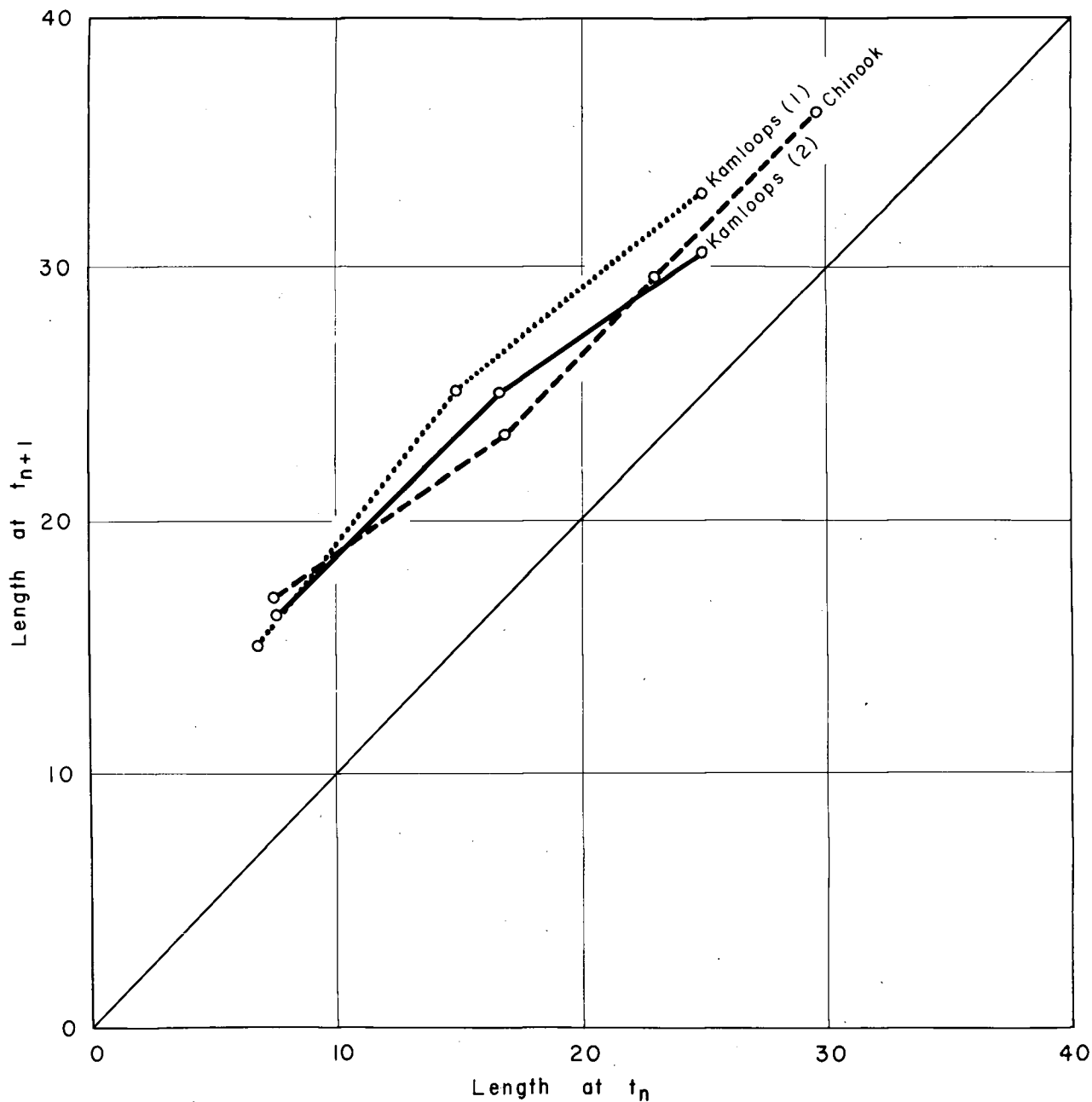


Figure 1. Walford transformation for Kamloops trout and Chinook salmon. (1) Kamloops Lake, (2) Paul Lake, British Columbia. (Larkin, *et al.* in press.) Chinook salmon from Parker and Kirkness, (1956).

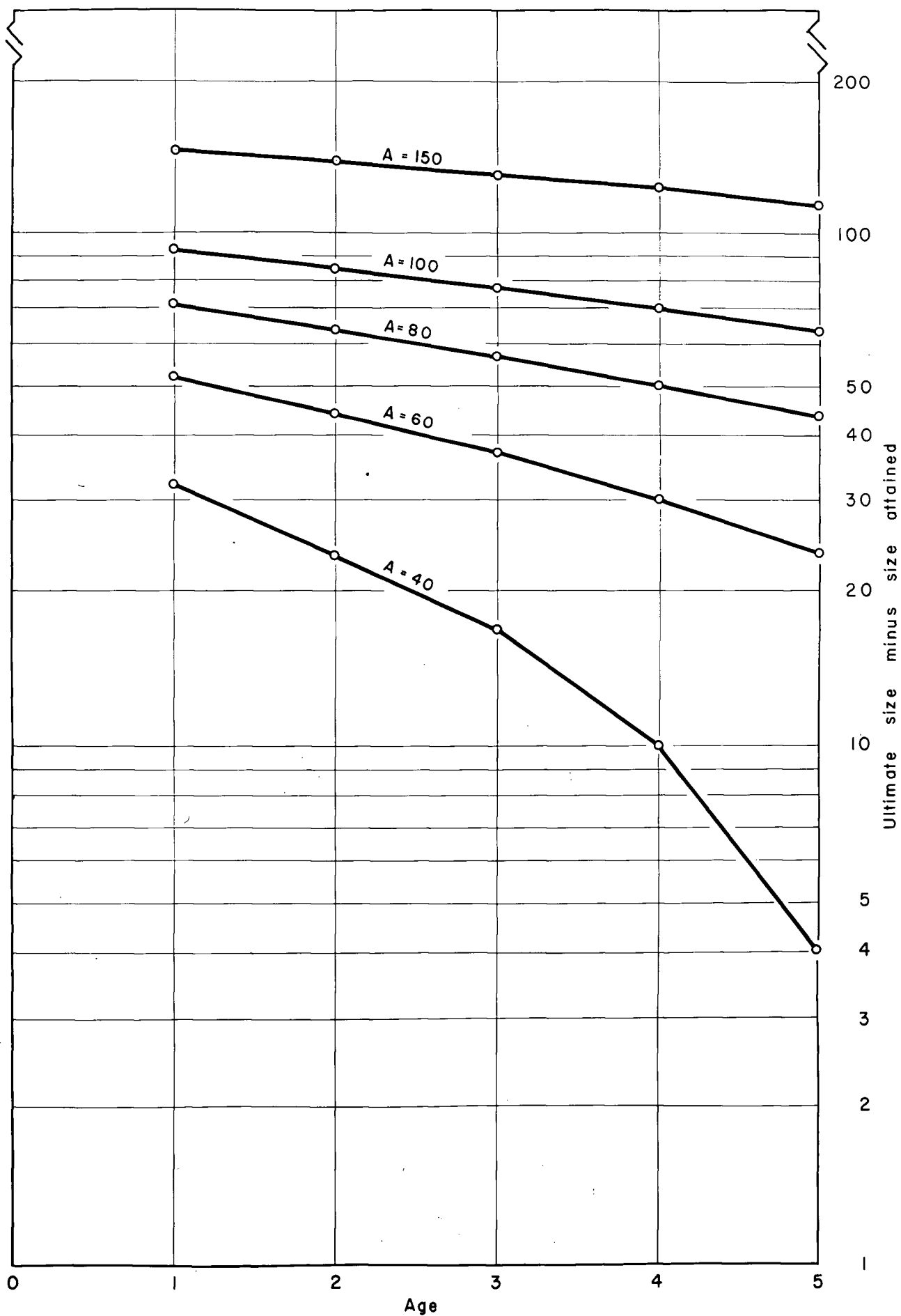


Figure 2. A Brody graphic solution of ultimate size, Chinook salmon.

diagonal or will do so only at some completely unrealistic "ultimate" size. Figure 2 again illustrates this point. A series of trial ultimate sizes are used to achieve a straight line in a semi-logarithmic plot of $A - L$ (for complete discussion, see Brody, 1945). It is seen that the higher the value of A chosen, the straighter the series of points becomes and the more horizontal the slope, indicating a very large ultimate size. It must be concluded that for fish of these species and perhaps many others the concept of ultimate size has no real meaning.

The Validity of a General Growth Curve

Gray (1929) proposed that growth rate of an embryo (fish) is proportional to weight of the embryo (x) and concentration or amount of growth promoting substance (y); thus,

$$\frac{d x}{d t} = k (x) y \quad . . . (7)$$

Gray states (p. 270):

"If y decreases from a finite value to zero, it follows that the integrated growth curve will be sigmoidal quite independent of the manner in which the decrease in y occurs."

Equation (7) becomes Robertson's basic formula under conditions where growth is constantly proportional to size, but modified by a constant decrease in "growth promoting" substance. However, as Gray pointed out, there is no a priori basis nor experimental evidence for the precise manner in which growth is limited; thus, there is no justi-

fication for Robertson's derivation. Gray's summation of this argument is worthy of quotation (p. 271):

"The known facts of growth in vivo and in vitro seem to indicate quite clearly that as an organism increases in size or age, the environment for growth becomes less favourable for those tissues still capable of growth. Until the cause of this phenomenon has been subjected to direct quantitative study, it is unlikely that we shall find an equation for any particular growth curve which is more than an empirical representation of observed data."

Other discussions on this theme include that of Wilson (1934), Bernstein (1934), and Davenport (1934).

The general shape of an absolute growth curve for fish need not necessarily be sigmoid, although this is a generally accepted rule. From the data already presented graphically (Figure 1) absolute annual increment might be described as a constant, in which case the series is arithmetic and a series of relative growth rates becomes a harmonic progression without limit. Ricker (personal communication) has observed that for several long-lived northern fishes a Walford line tends to parallel the diagonal, and suggests that while the general growth curve may be sigmoidal, the "point" of inflection is greatly protracted, occupying the greater portion of the life span. In the light of von Bertalanffy's (1938, 1949) and Robertson's (1923) arguments, this would necessitate an increase in metabolic efficiency with increase in mass. This has been experimentally shown to occur by Brown (1946b), who noted that maintenance requirement of food per unit weight

of fish (Salmo trutta) decreased with increase in weight.

It appears that a general mathematical equation has not been conceived that, through its constants, depicts the interaction of the many factors affecting rate of growth. Attempts, such as Robertson's, while valuable for theoretical comprehension, imply a single governing reaction, i.e. Liebig's Law of the Minimum (Odum, 1953). That a limiting reaction governs the rate of growth is not contested, but that a particular reaction is at all times throughout life the limiting factor has not been demonstrated. A mathematical equation, used to express growth rate, must be considered as an empirical device, without general theoretical validity at the present level of knowledge. That rate of growth is resultant from the interaction of two opposing forces, (a) the size-specific capacity for growth, which is progressively suppressed by (b) the effects of growth, appears to be the only clearly established, general concept at this time.

Practical Difficulties Encountered with Fish

The opportunity to directly measure growth of fishes is seldom obtained. This is especially true where data on growth in a natural environment are desired as opposed to growth data obtained under laboratory conditions. As a result of this difficulty, growth studies are often based on the method of back-calculating the size of a fish

at some previous stage of life history as indicated by markings on scales or other bony parts. Usually the end of the winter annulus or check is taken as a reference point. This method precludes information on growth rate during the very early (first year) and sometimes very late (ultimate) years of life. The actual course of a growth curve obtained within any one year would reflect the annual cyclic variation of seasonal changes in the surrounding environment. A growth curve related to some recurring event, i.e. the formation of the annulus, uses the sum of seasonal increment and the unit of time in all cases is taken as one year. Prior to and after the formation of the first and last annuli, respectively, absolute time cannot usually be computed. Thus, comparative growth rates for these periods are not obtainable.

The Use of Age-specific Rates of Growth

Age, as measured by solar time, is not necessarily a causative factor of decrease in growth rate. Brody (1945) considered time only as a reference point and criticized growth equations of Glaser (1938) and other workers as being functions of time and, therefore, unrealistic.

Brown (1946a), on the other hand, explicitly states that for brown trout (Salmo trutta) fry, age is a significant factor determining the deceleration of specific growth rate. She found no correlation between body weight and specific growth rate. Her conclusions were derived

from controlled laboratory experiments in which physical and chemical environmental fluctuations were held to a minimum. Under these conditions the inherent physiological efficiency of individuals would be primarily affected only by biological stresses such as a social hierarchy interacting with a limited food supply. The fact that fish of the same absolute age but of different sizes grew at approximately the same rates, if they occupied the same relative positions in different peck orders, does not necessarily preclude a size-specific growth rate. Miss Brown's fish were fed but once a day, a practice that would tend to favour growth in larger individuals. Fish of different absolute ages were not compared. The experiment did, however, isolate some of the factors which cause the wide variation observed between growth rates of individuals.

For field data, the classification of fish according to age groups involves three averages. (1) Since fish do not all hatch out at the same time, absolute age at completion of the first annulus is variable. (2) The completion of the annulus and commencement of spring growth does not take place at precisely the same time for all individuals; thus, another averaging procedure is involved. (3) The capacity to grow is quite variable between individuals, even between progeny of the same parents (Brown, 1946a,b) and a third averaging procedure is involved in age-specific growth rates of fish derived in this manner.

For fishes with a long life span, living in a fairly constant environment, age-specific growth rates may yield fairly reliable growth curves with sufficient points to indicate an average relationship and trend. With fishes such as the salmon (Oncorhynchus) and trout (Salmo) of the Pacific Coast, the life span is relatively short and environmental changes may occur either in fresh water or as a consequence of anadromous habits.

The chinook salmon provide an example typical of this situation. Individuals of this species may spend from a few months to two years in fresh water residence and then migrate to sea. After a period from a few months to six years in the ocean, they return to spawn and die. Depending upon the ultimate life history, different average sizes may be calculated for the end of each growth year. Starting with data collected from a spawning run and lacking knowledge of mortality rates, it is quite impossible to correctly weight the obtained samples into an average age-specific growth curve that is representative of the population at any one time, or over any span of years (Parker and Kirkness, 1956). This lack of age-size relationship is borne out by the inability to determine accurately year classes from a length frequency distribution.

This problem has been encountered by several workers. Larkin, et.al. (1957), suggested that an erroneous interpretation was made of the effects of a known environ-

mental change on the growth rate of Kamloops trout (S. gairdneri) in using age-specific growth rates. They suggested that size-specific, rather than age-specific, growth rates be used. In this case a change of growth rate was shown to be the effect of a change in food habits at a critical size. Ford (1933) in his herring studies at Plymouth, noted the large error attached to average lengths at each annulus and also a large variation of absolute age at such a specific reference point. His procedure was to group the fishes of each age into cells of length at the beginning of each growth year and use this size-within-age-specific reference point for predicting or characterizing annual increment.

Moore (1934) working on the barnacle, Balanus balanoides, plotted the average growth rate (average percent increase in sample population volume per ten days) against size to show the effects of different environments upon the size-specific growth rate. MacKay and Weymouth (1935) in their studies of the crab, Cancer magister, were forced to relate growth at ecdysis to size in describing the rate of growth as they were without any reliable method for determining age. They obtained a size-age relationship independent of the growth data and synthesized the two sets of data into an average age-specific growth curve.

HYPOTHESIS ON GROWTH OF FISH

The foregoing discussion leads to the following

hypothesis:

In fish, relative growth rate declines with increase in size independent of age. Age is simply a necessary event as growth takes place in time. Passage of time in itself exerts no limit on the rate of growth. Environmental or biological changes which cause a change in metabolic efficiency will be reflected as a point of inflection in a growth curve. This concept implies that, for the species studied, size is a much more reliable indicator of physiological development than age. This hypothesis is presently limited to that period of life susceptible to calculation by scale analysis.

THE TEST OF THE HYPOTHESIS

Methods and Materials

The hypothesis was tested in detail, using a collection of data made available by the British Columbia Game Commission. Steelhead trout (S. gairdneri) were chosen as a species for study, primarily for two reasons. First, steelhead trout are anadromous and, therefore, a sudden and profound change occurs in the environment. Second, a fairly large collection of data, obtained from angler's catches, were available that had been analyzed (Maher and Larkin, 1955). Dorsal-ventral diameters of annuli, marked on cards from projected scale images, were made available to the author. For each fish considered, the size at the com-

pletion of each annulus was estimated by back-calculation, using a direct proportion ratio between size of fish and size of scale. This method and its validity has been discussed by Smith (1955) for rainbow trout and the present study assumes the method has validity for the same species of anadromous habits. The entire conversion of dorsal-ventral diameters to length, and to \log_{10} length, was obtained in one operation on a ten inch arith-log slide rule, yielding three significant places in the logarithm of size. All tests of statistical significance were made by methods given by Snedecor (1946). A growth year is defined as the period of life between the completion of an annulus at $t = n$ to the completion of the subsequent annulus at $t = n+1$. This roughly coincides with the period from April to April for steelhead in fresh water. The growth year is designated by the calendar year during which most of the growth occurs. Thus, growth year 1950 refers to the period approximately corresponding to April 1950 to March 1951, inclusive.

From the material available on Chilliwack River steelhead a sample of 152 individuals was drawn which conformed to the following criteria.

1. Individuals were all maturing for the first time. This criterion eliminates any possible changes or displacement of an annulus because of resorption during a previous spawning migration. About five percent of the

available total were discarded because they were repeat spawners.

2. Scale margins were sharply defined without apparent resorption at the site of measurement. Resorption would cause an apparent greater length at each annulus than had actually been realized. While the extent of error from this source has been minimized, it has probably not been completely eliminated.

3. Only individuals that were early spring out-migrants were considered, i.e. the entrance into salt water was accomplished during or immediately after the completion of the winter annulus. Error may be inherent in the placement of the edge of this annulus, as fish that entered salt water before normal completion of the winter zone may show an immediate increase in growth rate which would be interpreted as the point of annulus completion.

4. The material considered was restricted to those individuals that completed the ultimate annulus in the 1949 or 1950 growth year. This restriction was imposed because of the possibility that environmental differences might exist between growth years. A substantial error might be introduced into the study by including small groups that could not be analyzed separately.

With these criteria the material cannot be considered as an unbiased sample of the entire population; however, this is not the objective of the study. Rather, the data were

chosen to avoid systematic error affecting the apparent growth rate. For the groups that are represented, the data presented are without known bias.

All material used is presented in Table I, compiled by life history and growth year groups. The terminology used is descriptive of life history events; 2/2/50 denoting a group or an individual that completed two annuli in fresh water, two annuli in salt water, and the last annulus was completed at the close of the 1950 growth year. Thus, the animal was a member of the 1947 year class and returned to fresh water to spawn in 1951. It was captured in the Chilliwack River in the 1951 growth year. The "50" of the symbol, referring to the penultimate year of life, is the last growth year bounded by completed annuli.

While the exponential growth curve does not accurately describe the course of growth in a time period, it may be used as a convenient standard of comparison. The instantaneous growth rate k is calculated as the difference between \log_{10} fork length at the beginning and end of the time period. Thus:

$$k = \frac{\log_{10} L_{t+1} - \log_{10} L_t}{t} \quad \dots (8)$$

In all cases t is unity, representing an entire growth year. This instantaneous growth rate, k , is not to be confused with the constant of Brody's equation (5) for the self-

Table I. Life history composition of samples of Chilliwack River steelhead used for growth analysis. (C) = year of hatching; (FW) = fresh water; (SW) = salt water; (Sp) = year of spawning.

Life history	Number		Growth year					
	♂♂	♀♀	1946	1947	1948	1949	1950	1951
2/1/50	7	12			C	FW	SW	Sp
2/1/49	13	9		C	FW	SW	Sp	
2/2/50	10	22		C	FW	SW	SW	Sp
2/2/49	11	9	C	FW	SW	SW	Sp	
3/1/50	15	15		C	FW	FW	SW	Sp
3/1/49	7	10	C	FW	FW	SW	Sp	
3/2/50	4	8	C	FW	FW	SW	SW	Sp

inhibiting phase, but is identical with the constant k of formula (4) for the self-accelerating phase where growth is calculated separately for each time period. The successive values of k , the instantaneous growth rate, are observed to decrease with increase in both t and L .

Individual k values were plotted against \log_{10} of the length at the beginning of that growth year. These are presented as a scatter diagram in Figure 3. Particular notice should be made of the axes. Each circle represents the instantaneous growth rate observed during an entire growth year for a fish of a particular size at the beginning of that time period. Three relationships are immediately apparent.

1. The scatter forms two distinct clouds, one for growth in fresh water, one for growth in salt water. The clouds overlap considerably on the abscissa, illustrating the variation in size of seaward migrants.

2. Each cloud forms an approximately linear regression typical for each environment. Regression lines were fitted to the scatter of points for each environment by the method of least squares. These are graphically demonstrated in Figure 3. Further analysis of growth rate is discussed relative to each environment.

3. There is a well defined proportional decline in instantaneous growth rate k as the length increases. It should be borne in mind that the data shown in Figure 3

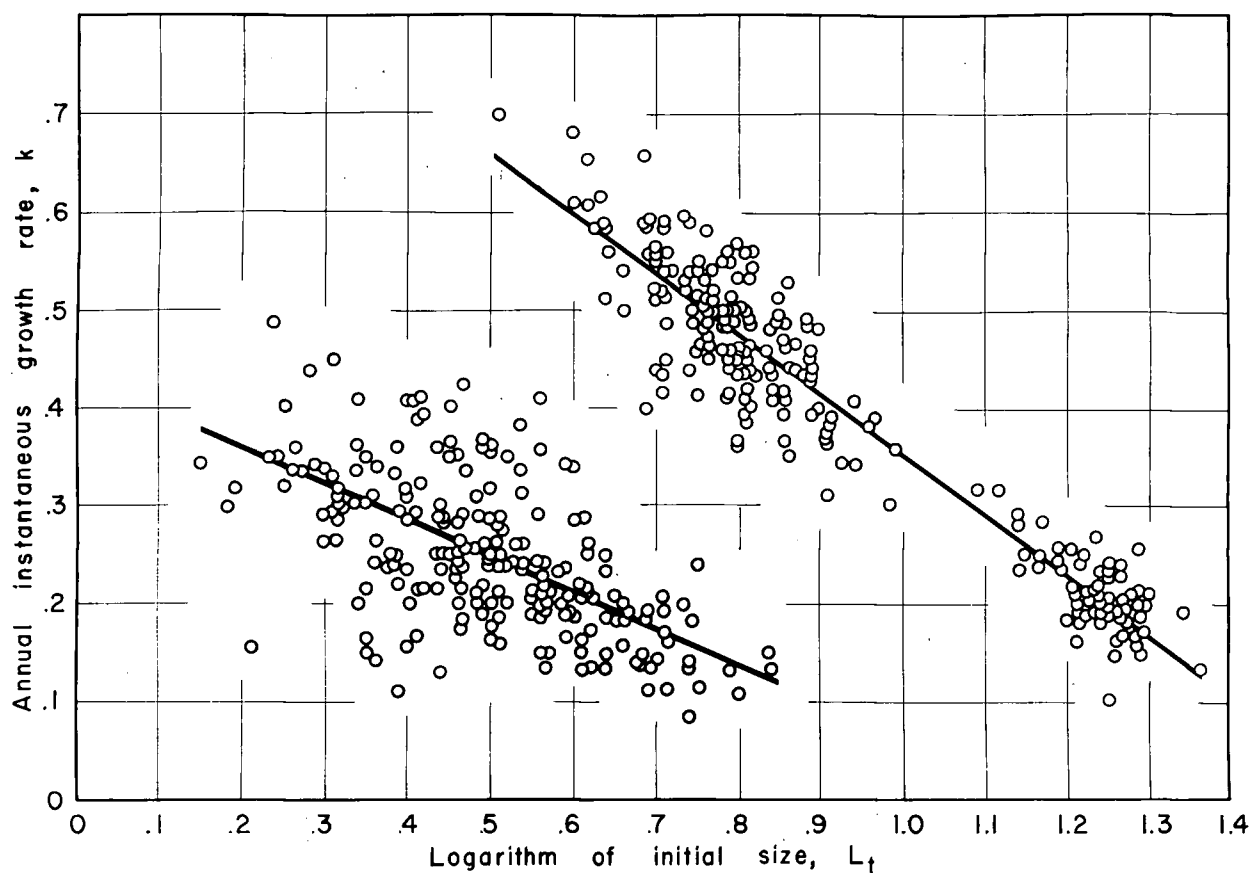


Figure 3. Scatter diagram of k on length, Chillwack River steelhead.

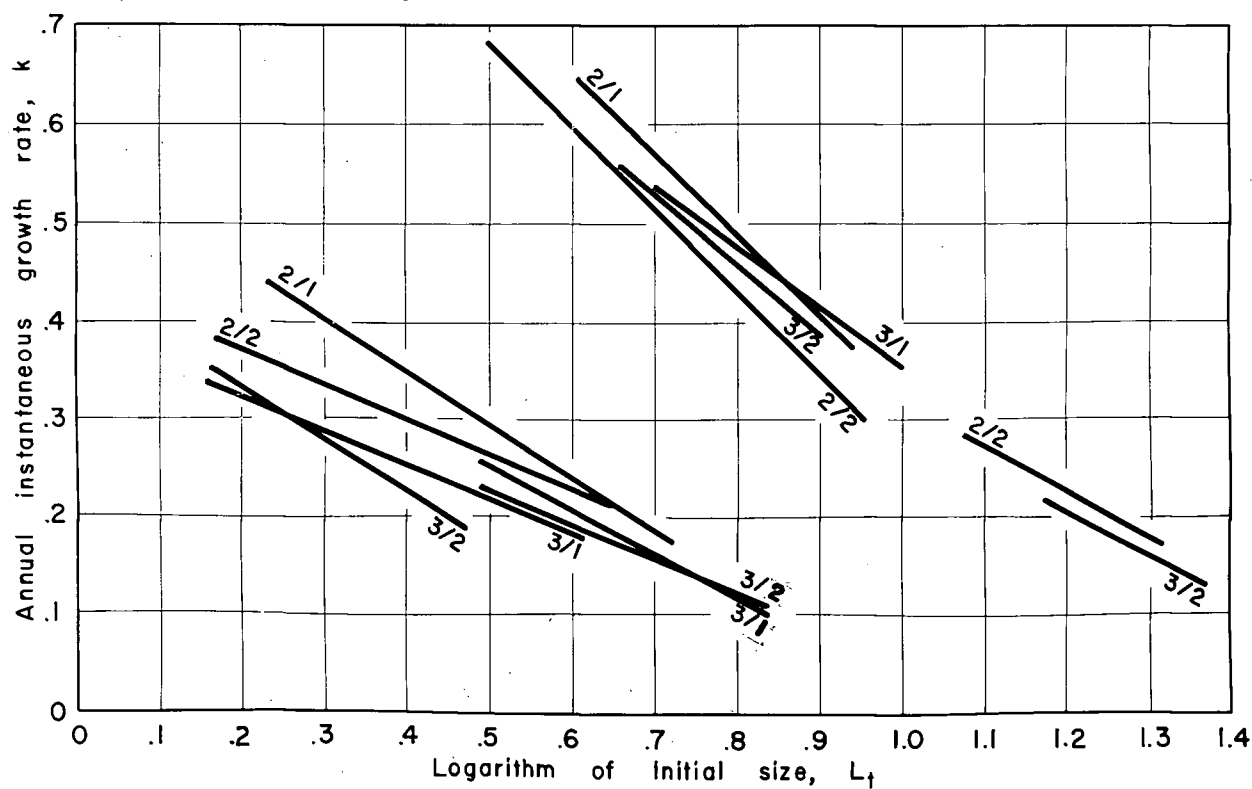


Figure 4. Regression lines of k on length for each life history group.

comprise a mixture of fish of different lengths, life histories, sex, and growth years. The contribution of each of these groups is discussed below.

Fresh Water Environment

The regression line fitted to the scatter of points for all fish in the fresh water environment is described by the formula, $\hat{Y} = 0.4308 - 0.3637 X$, where \hat{Y} is the predicted value of k for any X , the \log_{10} of initial size, L_n . While the regression is obviously significant, the standard deviation from regression is 0.9064, indicating a wide variation between individuals. There is the possibility of measurable differences between several groupings of these data. Groupings that may be tested for contribution to the total variance are: (1) life history types, (2) ages, (3) sexes, and (4) growth years. Two or more of these groups may be correlated in effecting the variation. For example, if the 1948 growth year offered a much better opportunity for growth than the 1949 growth year, and the 1948 sample contained largely males, a single test by covariance would show a significant difference between the sexes in respect to growth rate. Accordingly, the significance of differences between sexes should be determined within each group. The plan followed in the present analysis has been to proceed from the simple to the complex.

Sex Differences

Using covariance, each life history group in each growth year was tested for statistical differences in growth between the sexes. "F" ratios were all less than significant at the 0.05 probability level (Table II.). The conclusion is, that the sexes are not differentially contributing to the variation of the total sample and need not be considered separately.

Differences Between Growth Years

There is no reason to assume that every growth year presents equal opportunity for growth to the population of fishes. Differences can be visualized, stemming from either climatic or biological variation. Consequently, these data were tested for differences in growth rate that could be ascribed to variation between growth years. The comparison of growth years for similar life history types and ages is given in Table III. No significant differences were found between growth rates obtained between years 1947 and 1948 nor between 1948 and 1949. The years 1947 and 1949 cannot be directly compared, but certainly no differences are suggested. The conclusion is reached that there are no significant differences apparent in these data and the groups need not be considered separately.

Life History Groups

Growth rates of different life history groups

Table II. Tests of significance of differences in growth rate between sexes.
Chilliwack River steelhead, fresh water.

Life history	Age	Growth year	d.f.(1)	"F" ratio	Significance(2)
2/1/50	2	1949	1,16	0.45	$P > 0.25$
2/1/49	2	1948	1,19	1.60	$0.25 > P > 0.10$
2/2/50	2	1948	1,29	3.20	$0.10 > P > 0.05$
2/2/49	2	1947	1,17	2.80	$0.25 > P > 0.10$
3/1/50	3	1949	1,27	3.70	$0.10 > P > 0.05$
3/1/50	2	1948	1,27	0.23	$P > 0.25$
3/1/49	3	1948	1,14	2.80	$0.25 > P > 0.10$
3/1/49	2	1947	1,14	0.47	$P > 0.25$
3/2/50	3	1948	1,9	0.37	$P > 0.25$
3/2/50	2	1947	1,9	0.02	$P > 0.25$

(1) Degrees of freedom.

(2) In all tables, significance will be given as the probability of obtaining a larger "F" ratio by chance.

Table III. Tests of significance of differences in growth rate between growth years. Chilliwack River steelhead, fresh water.

Growth years compared	Life history groups	Age	d.f.	"F" ratio	Significance
1948 : 1949	2/1/49 : 2/1/50	2	1,38	.67	P > 0.25
1948 : 1949	3/1/49 : 3/1/50	3	1,44	.26	P > 0.25
1947 : 1948	2/2/49 : 2/2/50	2	1,49	.86	P > 0.25
1947 : 1948	3/1/49 : 3/1/50	2	1,49	.76	P > 0.25

were compared, yielding a highly significant "F" ratio of 15.1, d.f. 3, 147. Apparently growth rate is significantly associated with the eventual type of life history pattern achieved. The test used (covariance) does not distinguish between individual life history groups; however, the relationship is shown graphically in Figure 4. Equations for the regression lines shown are given in Table IV. In no case are the regression lines extrapolated beyond the range of each life history group.

Three phenomena are clearly shown by these data.

(1). growth rate declines with increase in size, independent of age. Each regression line represents fish of identical age and life history. (2) Growth velocity and time to maturity are inversely correlated. The regression line for the group maturing as 3's (i.e. 2/1) is above those of groups maturing as 4's (2/2/ and 3/1) which are in turn above that group maturing as 5's (3/2). (3) Older fish of the same life history group have higher size-specific instantaneous growth rates than the younger ones in the same environment. This is most clearly shown in the two regression lines depicting size-specific instantaneous growth rate of the 3/2 group for the second and third growth years in fresh water. This increase in growth velocity appears to occur suddenly and is associated with the time of seaward migration of other members of the population. A more complete explanation of this observation will be given

Table IV. Regression equations for life history groups. Chilliwack River steelhead, fresh water.

Life history group	Age	Number	Regression equation	$S_{y \cdot x(1)}$
2/1	2	41	$\hat{Y} = .5582 - .5251 X$.0562
2/2	2	52	$\hat{Y} = .4413 - .3535 X$.0606
3/1	2	47	$\hat{Y} = .3971 - .3601 X$.0642
3/2	2	12	$\hat{Y} = .4384 - .5278 X$.0381
3/1	3	47	$\hat{Y} = .4745 - .4429 X$.0437
3/2	3	12	$\hat{Y} = .3930 - .3450 X$.0383

(1) Standard deviation from regression.

in the following section.

Table V presents a compilation of average size at the completion of each fresh water annulus for individual life history groups. Variation between individuals of each group is large, as shown by standard deviation. What is of special interest is the apparent critical size fish must attain to respond to stimuli that trigger out-migration. This size level is approximately five inches, fork length, regardless of age, i.e. size is a more reliable indicator of physiological development than age.

Discussion of Causative Factors

The rate of growth of fish is dependent upon two types of factors. (1) A genetic capacity for growth peculiar to individuals that together form a variable population in any one area and (2) environmental opportunity which determines the degree of growth rate potential attained. Genetic variation between individuals is a well established fact and needs no further discussion. The environmental effects upon growth are aptly demonstrated in these data. A discussion on some of these factors will clarify the observed phenomena.

The work of Gray (1928a,b) has shown that the size of a trout (S. fario) at the end of the embryonic stage is largely dependent upon two factors: (a) the amount of yolk the egg contained and (b) the temperature at which

Table V. Mean size and standard deviation of life history groups at completion of fresh water annuli. Size given as fork length in inches.

Group	Number	Size at completion of annulus			
		1	2	3	4
2/1/49	22	3.31 \pm .788	6.41 \pm 0.736	migrated	
2/1/50	19	3.01 \pm .549	6.13 \pm 1.066	migrated	
2/2/49	20	3.06 \pm .772	5.56 \pm 1.260	migrated	
2/2/50	32	2.83 \pm .611	5.57 \pm 1.222	migrated	
3/1/49	17	2.45 \pm .412	4.36 \pm 0.696	6.47 \pm 1.138	migrated
3/1/50	30	2.61 \pm .626	4.71 \pm 1.029	7.22 \pm 1.150	migrated
3/2/50	12	2.30 \pm .454	3.99 \pm 0.589	6.08 \pm 0.669	migrated

development took place. Under identical incubating temperatures eggs having larger yolk content will produce larger fry than smaller eggs. Under higher temperatures development will be faster, but the resulting embryo will be smaller due to a greater proportion of the available food supply (yolk) being used for sustenance. This means that under wild conditions, eggs of the same size, fertilized at the same time but in different parts of the stream, may produce different sized fry. Add to these, variation between egg size, variation in time of actual egg fertilization, and the genetic variability in capacity for growth, and it is not surprising that a population of steelhead fry exhibits considerable variation in individual size.

Brown (1946a) raised brown trout (S. trutta) fry from hatching to eight months under experimental conditions where fluctuations in temperature, light, food, etc. were held to a minimum. She found that growth rate was highest during the first three weeks after beginning of feeding and declined thereafter. Although the experimental individuals were from a single pair of parents, and were incubated under identical conditions, a large amount of variation was reported in size and in growth rate. After initial feeding a social hierarchy was established in each tank. The largest fish dominated the feeding habits and, therefore, the growth of the smaller individuals, so that the largest fish of each experimental lot grew the fastest. In studying

the growth of two year old brown trout under constant temperature Brown (1946b) again showed the existence of a social hierarchy. Hoar (1953, p. 477) states:

"Prolonged residence of juvenile salmon and trout in stream beds depends primarily on their territorial behavior. This behavior of occupying and defending territories is associated with migration into shallow water and settling to the bottom to remain inactive at night."

Newman (1956) observed social structure (Salvelinus fontinalis, Salmo gairdneri) under wild conditions as well as in aquaria. Two observations are especially significant. (1) The frequency of nipping was higher in smaller, confined tanks than in large ones, which leads to the observation that confinement, such as produced by low water conditions or by dense populations, may intensify social behavior. This condition would suppress growth rates of the dominated individuals. In a natural environment the dominated individuals may be either younger or slower growing or both. (2) A rotation in the peck order of a stream when dominant fish were absent from the area. This situation would, under conditions of low population density, allow feeding of the smaller individuals; however, in a high population density the smallest individuals might starve or succumb to other forms of mortality from a weakened condition .

In steelhead the mass out-migration of the largest individuals in the spring would be expected to result in an

improved environment for the residual inhabitants, i.e. a sudden upward shift in a curve describing the size-specific growth rate. Referring to Figure 3, the observed discontinuity in the size-specific growth curves between the second and third fresh water growth years has a rational explanation.

Salt Water Environment

The migration of steelhead from fresh to salt water offers a striking example of the effects of an environmental change upon growth rate. The total scatter of points of size-specific growth rates has been presented in Figure 3. A regression line for salt water growth is described by the equation $\hat{Y} = 0.9592 - 0.6070 X$. Standard deviation from regression is 0.0499 which, compared with 0.9064 obtained in fresh water, reflects considerably less variation in the growth rates of the individuals. The individuals, however, were not of the same age group, nor was the duration of salt water residence the same. Treatment of these data follows the pattern used for comparison of groups in the fresh water environment.

Sex Differences

While no differences between growth rates of sexes were apparent in fresh water, the possibility of a difference as the fish approach maturity was not overlooked. Each life history group was tested by covariance. The results are

presented in Table VI. There is no reason to suspect differential growth between the sexes during that period of life history studied.

Differences Between Growth Years

It is a common belief among fisheries biologists that the salt water environment may be considered as relatively constant in affecting the vital statistics of anadromous fish (Neave, 1953). This postulate has not been fully investigated, however, and is still open to question. Growth years of steelhead in the marine environment have been compared, using size-specific growth rates from groups having identical life histories. The results of covariance tests are presented in Table VII. The consistency of growth opportunity within the three years tested is well demonstrated, provided only fish during their first salt water growth year are compared. Differences between the 1949 and 1950 growth years are significant at the five percent level when fish in their second marine growth years are compared. There are several alternative explanations, one of which is that those fish spending more time at sea wandered farther, thus encountering more diverse environmental opportunity.

Differences Between Life History Groups

Differences in growth during the first year of marine environment between life history groups were tested.

Table VI. Tests of significance of differences in growth rate between sexes.
Chilliwack River steelhead, salt water.

Life history	Age	Growth year	d.f.	"F" ratio	Significance
2/1/50	3	1950	1,16	0.90	P > 0.25
2/1/49	3	1949	1,19	4.30	0.10 > P > 0.05
2/2/50	3	1949	1,29	0.29	P > 0.25
2/2/49	3	1948	1,17	3.80	0.10 > P > 0.05
2/2/50	4	1950	1,29	3.20	0.10 > P > 0.05
2/2/49	4	1949	1,17	2.30	0.25 > P > 0.10
3/1/50	4	1950	1,27	1.10	P > 0.25
3/1/49	4	1949	1,14	0.00+	P > 0.25
3/2/50	4	1948	1,9	0.72	P > 0.25
3/2/50	5	1949	1,9	3.30	0.25 > P > 0.10

Table VII. Tests of significance of differences in growth rate between growth years. Chilliwack River steelhead, salt water.

Growth years compared	Life history groups	Age	d.f.	"F" ratio	Significance
1949 : 1950	2/1/49 : 2/1/50	3	1,38	0.18	$P > 0.25$
1949 : 1950	3/1/49 : 3/1/50	4	1,44	0.01	$P > 0.25$
1949 : 1950	2/2/49 : 2/2/50	4	1,49	5.20	$0.05 > P > 0.025$
1948 : 1949	2/2/49 : 2/2/50	3	1,49	0.06	$P > 0.25$

An "F" value of 11.4, d.f. 3, 147 is significant at .005; thus, there is little chance that the life history groups were growing at the same rate. A further test was carried out comparing groups with the same marine history. These data are presented in Table VIII. Differences significant at the five percent probability level are noted between the 2/1 and 3/1 groups. The comparisons between the 2/2 and 3/2 groups show no differences in either the antipenultimate or penultimate years. Further, this comparison shows fish of different ages to be growing at the same size-specific growth rate.

Noting that in one case a difference significant at the five percent level exists, the growth years were nevertheless combined. Regression lines were fitted to the data for each year of marine residence and are presented in Table IX. These data are graphically presented in Figure 4. As was noted for fish in fresh water, continued residence in salt water appears to increase the relative opportunity for growth with further increase in size. Rather than an abrupt change in position between regression lines for first and second growth years, (2/2/ and 3/2) the process is more gradual as indicated by a change in slope, i.e. the rate of deceleration of k on $\log_{10} L$ is less. This could indicate several factors, including a size-specific change in environmental opportunity, perhaps a change from planktivorous to piscivorous habits, or a different

Table VIII. Tests of significance of differences between life history groups of the same marine history. Chilliwack River steelhead.

Life history groups	Age	Marine year	d.f.	"F" ratio	Significance
2/1 3/1	3 4	first	1,85	4.3	0.050 > P > 0.025
4/2 3/2	3 4	first	1,61	1.7	0.25 > P > 0.10
2/2 3/2	4 5	second	1,61	2.3	0.25 > P > 0.10

Table IX. Regression equations for life history groups. Chilliwack River steelhead, salt water.

Life history group	Age	Number	Regression equation	$S_{y.x}$
2/1	3	41	$\hat{Y} = 1.0765 - .7215 X$.0456
3/1	4	47	$\hat{Y} = 0.9562 - .5988 X$.0321
2/2	3	52	$\hat{Y} = 1.0753 - .7950 X$.0481
3/2	4	12	$\hat{Y} = 1.0293 - .7110 X$.0404
2/2	4	52	$\hat{Y} = 0.8202 - .4916 X$.0372
3/2	5	12	$\hat{Y} = 0.7982 - .4855 X$.0390

environment encountered by wandering farther from the natal stream, or perhaps that the growth year containing migration from fresh water is not completely in salt water. These postulates are pure speculation; however, the fact remains that differences exist and the changes occurred in an opposite direction to that expected if growth declines with age.

The acts of maturing, leaving the sea, and spawning are, like the out-migration from fresh water, functions of physiological development. Again size is a more reliable indication of physiological development than age. The relationship between size, age, and maturity is presented in Table X. Two groups of fish entered the sea from fresh water, those in their third and fourth growth years of life. Each group may be split into slow and fast growing components. On the average, if a fish grew to a size of more than nineteen inches at the end of the first marine growth year, it matured and returned to spawn the following year. On the average, if a size of nineteen inches was not attained, the fish remained in the sea another year, returning to spawn at a much larger size than its fast growing, but younger, counterpart. This is not to say that size in itself is a causative factor of maturity. Size is, however, a fairly reliable measurement of physiological development for these fish. The size at the end of a growth year has no significance other than a point that can be measured conveniently, and reflects or predicts the physiological

Table X. Mean size and standard deviation of life history groups at the completion of salt water annuli. Size given as fork length in inches.

Group	Number	Size in inches, at end of marine growth years					
		Age	first year $\bar{x} \pm S_x$	Age	second year $\bar{x} \pm S_x$	Age	third year
2/1	41	3	19.8 \pm 2.112	4	spawned		
3/1	47	4	19.8 \pm 2.171	5	spawned		
2/2	52	3	16.9 \pm 1.982	4	27.6 \pm 2.745	5	spawned
3/2	12	4	18.2 \pm 1.842	5	28.4 \pm 2.008	6	spawned

threshold of development that fish must attain to respond to migratory stimuli.

The foregoing discussion would appear to place an evolutionary advantage on rapid growth. However, rapid growth is also associated with early maturity at a smaller ultimate size. Scott (1956) has shown that egg number is, in part, a function of size of the adult; thus, an evolutionary advantage could also be ascribed to a slow growth rate. However, while large individuals produce many eggs, they also suffer a greater total mortality with advanced age and selective advantage is not tenable on the basis of growth rate alone. Evolutionary advantage is apparent in a system that insures against permanent damage from a catastrophe to any one year's spawning population. This is accomplished by the diversity of life histories, including some second spawning of steelhead. This diversity, however, is dependent on variation of growth rate. Age in itself cannot logically be considered as an independent factor.

The complete life history and several factors determining the course of events of any brood year of steelhead may be recapitulated as follows. From any given year's seeding the resulting emergent fry will exhibit variation from a mean in respect to (1) inherited capacity for growth, (2) size, and (3) time of emergence. This variation, coupled with a social hierarchy, results in a

wide variation between individual sizes and growth rates calculated for the time corresponding to the second growth year. At the start of the third growth year, those individuals that have attained a physiological stage receptive to migratory stimuli will respond and leave fresh water. The residual population then assumes a position of dominance formerly occupied by the larger individuals that migrated. The residual group grows at an improved average growth rate during the third growth year and responds to migratory stimuli at the start of the fourth growth year.

In salt water those individuals, composing the early migrants (at the start of the third growth year) have variable capacities for growth. Those that grow fast will begin maturing and respond to migratory stimuli. The slower growing individuals remain in the sea, attaining maturity the following year. Identical marine life histories are followed by the group that remained in fresh water an additional year. The final product, in terms of size of spawners, is a heterogeneous size distribution. The whole course of life history is seen to be best describable in terms of size. Age is not a reliable indicator of either size or physiological development under these natural conditions.

The course of growth during the first and ultimate growth years cannot be approached through scale analysis, and these periods constitute a gap in available

knowledge of steelhead and salmon. Existing growth curves are not sufficiently descriptive of the growth of these fishes, even under conditions of an unchanging environment, and much remains to be done on this problem. It is doubtful, however, that the growth of fishes under changing environmental conditions can be described, hence predicted, by other than empirical formulations.

SUMMARY

The ability to predict the size of a fish is considered essential to fisheries management. The accuracy of a prediction necessitates knowledge of the causative factors of growth. Many attempts have been made to write general equations that describe the entire course of growth throughout life; yet, in final analysis, growth is the result of many interacting factors, many of which are not predictable. In the absence of a valid general growth equation, the exponential growth formula is used as a convenient means of describing average annual growth rates for a comparison between individuals or groups.

Instantaneous growth rates, calculated as the differences in logarithms of size at yearly intervals, are shown to decline with increase in size and age. Thus, a comparison of growth rate between individuals or groups must be made at some point or level common to both groups. Age has been widely used by fishery workers, i.e. average

age-specific instantaneous growth rates are compared. The classification of individuals by age, however, lacks precision and may lead to considerable anomaly unless a constant environmental opportunity can be postulated.

An hypothesis is advanced that growth rate, while necessarily occurring in time, is independent of absolute age, at least during juvenile stages of development. Rather growth rate appears to be a function of size. Steelhead (because of anadromous habits) provide an exceptional opportunity to explore the general hypothesis. Individuals are subject to a wide variety of environmental stresses and stimuli, each of which may contribute individually or through interaction in altering the growth rate.

The inference of size at previous times in the life history through the use of scales or other bony parts provides growth data only for the juvenile stages. At maturity the deceleration of growth may well be a function of time. This relationship may also be true during early life history, i.e. the embryo and alvin, however these data do not apply to those stages. During the juvenile stages, growth rate appears to be associated with size and independent of age. The use of size-specific instantaneous growth rates offers considerable increase in precision of a comparative growth study during that period of life history of prime interest to the fisheries manager.

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