# The 解utursitg of Thatish Columbia <br> Faculty of Graduate Studies 



PROGRAMME OF THE

## FINAL ORAL EXAMINATION

FOR THE DEGREE OF

## DOCTOR OF PHILOSOPHY

## of

## ROBERT RAY PARKER

B. S. University of Washington, 1946
M. A. University of British Columbia, 1957

IN ROOM 187A, BIOLOGICAL SCIENCES BUILDING
TUESDAY, APRIL 14, 1959 at 3:30 p.m.

## COMMITTEE IN CHARGE

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External Examiner: Dr. W. E. RICKER<br>Fisheries Research Board of Canada

# GROWTH AND MORTALITY IN RELATION TO MAXIMUM YIELD IN POUNDS OF CHINOOK SALMON (Oncorhynchus tshawytscha) 


#### Abstract

Life history events of chinook salmon preclude determination of a critical size for this species by established methods. The use of size, rather than age, as a basic correlate of growth rate is discussed and compared to analagous treatment of physiological rates described in literature. Ecological opportunity and physiological opportunity are visualized as the two interacting components that determine growth, both of which are related to size attained. Growth opportunity occurs in stanzas which are entered at 'threshold' sizes.


The function, $\mathrm{dw} / \mathrm{dt}=\mathrm{kw}$ is developed into a growth equation for linear dimensions, $l_{t}+1=a+1_{\mathrm{t}}^{\mathrm{z}}$, and three methods of fitting this equation to growth data are demonstrated. Application is explored and discussed using steelhead trout and chinook salmon as examples. Significant differences in growth rate were found between life history types and sexes. The chinook data were then treated on a $1_{t}+1,1_{t}$ plot and it was shown how an apparent fit of the von Bertalanffy type growth equation can result from selectively fishing for the larger fish of any brood year. Accordingly, life history subgroups of a year class must either be treated separately or weighted according to relative abundance in determining critical size. The former alternative is followed in lieu of necessary weighting data.

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The growth equation was then transformed to a length-specific average annual instantaneous growth (weight) rate and critical size was observed to occur at maturity for each life history type. Since fishing is presently allowed on the immature stock, a size limit protecting the older life history types causes a loss in yield from the younger life history types. This loss might be offset, depending on the relative abundance of life history types in the stock, providing mortality due to hooking and releasing is negligible.

Capture by trolling was found to subject feeding coho and chinook salmon to hyperactivity which may lead to a distressed condition or death,
and death cannot be predicted from examination of individual fish at time of capture. Mortality of coho was estimated to be in the 0.95 confidence interval of 34 percent and 52 percent; of chinook in the 0.95 confidence interval of 40 percent and 71 percent. Time of maximum death rate is shown to coincide with the period of maximum blood lactate response. Survival occurred either when blood lactate did not reach critical levels (above $125 \mathrm{mg} \%$ ) or reached critical levels and subsequently subsided. Holding salmon in a live box for $8-14$ hours before release did not improve tag recovery, suggesting additional indiscriminate stress was caused at release. Adult coho in freshwater did not appear capable of lethal hyperactivity. This led to the hypothesis that cessation of feeding during spawn ing migration has adaptive significance for survival of P acific salmon.

The combination of natural mortality, mortality from hooking injur and delayed mortality from fatigue gave a total instantaneous first year mortality rate (exclusive of fishing) greater than 1.0 and possibly as high as 2.5. This mortality rate results in a critical size of not more than 22.5 inches and most likely about 15.0 inches fork length.

It is thus concluded that for maximum yield in pounds (1) fishing for chinook should be restricted to their ultimate year (maturity) and (2) the use of non-selective gear should be encouraged. These recommendations are opposite to present practices. If fishing is to be allowed on the immature stock, size limits should be abolished.

## GRADUATE STUDIES

Field of Study: Zoology

> Population Dynamics . . . . . . . . . . . . . . . . . . P. P. Larkin
> Marine Field Course. . . . . . . . . . . . . . . . . . A. Dehnel
> Biology of Fishes. . . . . . . . . . . . . . .

Other Studies:
Fisheries Hydraulics . . . . . . . . . . . . . . . . . . . .E. S. Pretious
Fisheries Anthropology. . . . . . . . . . . . . . . . H. B. Hawthorn Introduction to Dynamic Oceanography. ....G. L. Pickard Introduction to Synoptic Oceanography . . . . .G. L. Pickard Advanced Synoptic Oceanography. . . . . . . . . .G. L. Pickard Chemical Oceanography............... J.D. H. Strickland

## PUBLICATIONS

Larkin, P.A., J.G. Terpenning and R.R. Parker. 1957. Size as a determinant of growth rate in rainbow trout, Salmo gairdneri. Trans. Am. Fish. Soc., 86: 84-96.

Parker, Robert R. 1955. Two proposed methods of estimatıng animal populations. Proc. 7th Alaska Science Conference.

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GROWTH AND MORTALITY IN RELATION TO MAXIMUM YIELD IN POUNDS OF CHINOOK SALMON (Oncorhynchus tshawytscha)

by<br>Robert Ray Parker<br>B.S. in Zool., University of Washington, 1946 M.A., University of British Columbia, 1957<br>A THESIS SUBMITMED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF<br>Doctor of Philosophy<br>, in the Department<br>of Zoology<br>We accept this thesis as conforming to the required standard

## ABSTRACT

Life history events of chinook salmon preclude determination of a critical size for this species by established methods. The use of size, rather than age, as a basic correlate of growth rate is discussed and compared to analagous treatment of physiological rates described in literature. Ecological opportunity and physiological opportunity are visualized as the two interacting components that determine growth, both of which are related to size attained. Growth opportunity occurs in stanzas which are entered at "threshold" sizes.

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Robert Ray Parker

Department of Zoology

The University of British Columbia, Vancouver 8, Canada.

Date March 20, 1959

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GROWTH AND MORTALITY IN RELATION TO MAXIMUM YIELD IN POUNDS OF CHINOOK SALMON (Oncorhynchus tshawytscha)

## INTRODUCTION

The theory of size limits has been discussed by Allen (1953, 1954), Ricker (1945), and Beverton and Holt (1957) and applications of this theory by regulation to maximize the yield of various populations of fishes have been explored. The population models used portray a population structure in which a year class, fully recruited to the fishable stock, is subjected to an approximately constant natural mortality rate while growth rate is a declining function of age....It,is shown that a critical size results from these two rates, defined by Ricker (1958, p.209) as ": . . the size at which the instantaneous rates of growth and natural mortality are equal. At that time and size the year class has its maximum bulk". Ricker (1945, 1958) presents arguments for maximising yield by a minimum size regulation consistent with a given rate of fishing where fishing starts prior to attainment of critical size in lieu of the ability of a fishery to crop a year class instantaneously. Life history events of chinook salmon, however, exclude this species from such a simple model. Chinook are anadromous, and any particular race is widely distributed in the marine environment (Milne, 1957; Parker and Kirkness,

1956; Kauffman, 1951; Fry and Hughes, 1951; Neave, 1951). During the immature stage some fraction of the population is susceptible to present fishing methods. Year classes are recruited annually, thus fish of all sizes and ages may be present. With approaching maturity members of each particular race migrate from oceanic feeding grounds to the ancestral river and thus become increasingly concentrated and vulnerable to fishing, particularly by troll gear along migration routes and by gill net fisheries in the river estuaries or within the river itself. Individuals die after spawning and consequently do not re-enter the fishable stock.

Other features of chinook life history further complicate their populations dynamics. Maturity may occur within any given year class at several ages. For example, entering adult runs of Taku River chinook contained fish of ages $1+$ to $5+$ years (l to 5 scale annuli) and of length groups from 10.0 to 47.5 inches (Anon., 1951). A size restriction, or gear restriction designed to accomplish a maximum yield should consider the spawning loss of small but mature fish from the fishable stock.

A chinook year class, then, at first is susceptible while immature to protracted fishing (both spatial and temporal) and then finally to highly intensive fishing during a short period of approaching maturity. Each life history type
is subject to natural mortality from disease, predation, etc. while immature and then to complete mortality after spawning. Thus a population model must either consider life history types separately or include appropriate methods of weighting.

While all elements necessary to construct a population model are not at present known, certain questions can be discussed and answered from somewhat less complete information. Critical size for each life history type may be determined from natural mortality and growth rates, and, from knowledge of critical size, methods of fishing to produce maximum yield may be deduced.

While chinook are used in the present study, other species of Oncorhynchus show similarity to varying degrees in respect to life history events. Any general conclusions regarding management principles gained from a study of chinook may be of value in considering these other related types. The questions of critical size and maximum yield are in themselves important in view of present oceanic salmon fisheries (Anon., 1957) and the desire to enter these fisheries expressed by North American fishermen. The determination of critical size and its application in management constitutes the main objective of this thesis. Material for each phase of the study has been organized and presented separately.

## A. A CONCEPT OF GROWTH IN FISHES ${ }^{1}$

## INTRODUCTION

Prediction of growth in natural populations of fishes is an important facet of many applied problems of fisheries management. It might be expected that age would be an adequate criterion of size and growth potential. However, it is well known that growth rates of fishes are influenced by environmental conditions such as food abundance and population. Age is thus only a reliable index of size or growth rate in relatively constant environments. However, even under a given set of physical conditions opportunity for growth of the individual fish may not be. related to age. Brown (1946), Stringer and Hoar (1955), Newman (1956), and Kalleberg (1958) describe size hiérarchies in groups of fishes which might influence their growth rates. Larkin, Terpenning and Parker (1957) suggest that size, rather than age, gives a better indication of ecological opportunity for growth in rainbow trout (Salmo gairdnerii). They also suggest size "thresholds" which, when crossed, provide the individual with new growth opportunities.
$1_{\text {Parker, R.R. and P.A.Larkin. 1959. A concept of growth }}$ in fishes. Submitted to J. Fish. Res. Bd. Canada. Feb. 1959.

Physiologists have long recognized that size is the better criterion of physiological opportunity for growth. Brody (1937, 1945) indicates that chronological age may not reflect physiological age. Putter (1920), Brody (1945) and von Bertalanffy (1938) developed growth equations in which size and the difference between size and an "ultimate size" determines the growth rate.

These equations have been applied to studies of natural populations of fish (Beverton and Holt, 1957). However, there are instances in which growth of fishes is not adequately described by these systems (Ricker, 1958). Some fish do not appear to be growing to an "ultimate size". Many species may change their ecological niche as they grow larger, thus revising the "ultimate size" to which they are growing (Larkin, Terpenning and Parker, 1957). Many species of salmonoids undergo marked physiological transformations (Hoar, 1939, 1957; Hoar and Bell, 1950; Green, 1926; Mislin, 1941) at different periods of their life history and these transformations may also be related to a size "threshold" (Alm, 1949; Elson, 1957; Parry, 1958). Growth of fish may thus be visualized as a series of growth stanzas (Brody, 1945) which are entered by ecological and physiological size thresholds, and within which size is the basic determinant of both ecological and physiological opportunity for growth.

The question of mathematical technique for describing growth is highly controversial. Arbitrary curve fitting may result in growth equations which combine dissimilar growth stanzas, thus "smooth out" important aspects of growth processes. Within each growth stanza, curves of "best fit" may result in growth equations in which the constants have no biological meaning or at best are of vague and complex significance (Gray, 1929). Alternatively, if equations are used which have been derived from physiological premises (and for which presumably the constants have physiological meaning) there is the risk that empirically determined values of these constants will reflect the combination of physiological processes with other factors influencing growth in natural environments, hence will not actually describe accurately the physiological processes from which they were deduced. Under such circumstances it would seem appropriate to choose a method of depicting growth which (1) summarizes the complex of interacting factors in each stage of growth into a minimum number of constants which reflect the combined effects of both ecological and physiological factors, (2) chooses as a basic premise the widely accepted view that size is the major correlate of growth.

Assuming that size is the basic correlate of growth the simplest mathematical expression to describe growth would be:
where growth rate (weight/time) is some function of weight attained.

A widely used first approximation containing one variable is:

$$
d w / d t=k w \text {. . . . . . . . . . . . . . . . . . . (A.2) }
$$

i.e., exponential growth as derived from Minot's (1891) growth equation by Brody (1927). Since growth in weight is rarely observed to be exponential, a modified function involving two variables is:

$$
d w / d t=k w^{x} \text {. . . . . . . . . . . . . . . . . . . (A.3) }
$$

where $k$ establishes the coordinates, of the system and $x$ is a fractional exponent of weight less than unity.

This type of equation appears a particularly suitable choice because it parallels empirical description of the relationship between weight and various physiological processes. In these instances also, the mechanisms involved may be complex and incompletely understood but the mathematical expression adequately describes the end result. For example, it has been abundantly demonstrated (Brody, 1945; Adolph, 1949) for mammals that standardized physiological rates are size-specific and can be adequately represented by the parabolic equation:

$$
d R / d t=A w X
$$

where $d R / d t$ denotes a physiological rate and $A$ is a proportion constant. Why equation (A.3a) should adequately
represent so many body functions is not understood (Weymouth, Field and Kleiber, 1942; Pirozynski and von Bertalanffy, 1951; von Bertalanffy and Pirozynski, 1953; von Bertalanffy and Estwick, 1953, 1954) but is well established as empirical fact through many observations. As far as is known, equation (A.3a) describes physiological rates for fish, viz. oxygen uptake at standard resting and active conditions (Fry, 1957; Job, 1955), oxygen uptake being interpreted to indicate metabolic rate.

The present study has as a main objective the description of growth of fishes, using the theoretical premise that growth rate may also be described by a parabolic equation. This possibility has apparently not been previously explored.

MATERIALS

Steelhead trout (Salmo gairdnerii), the anadromous form of rainbow trout, and chinook salmon (Oncorhynchus tshawytscha), offer an opportunity for study of the growth problem. They have highly variable life histories (Maher and Larkin, 1955; Parker and Kirkness, 1956; see Wilimovsky and Freihofer, 1957, for entrance to literature on chinook), and show greatly differing growth rates in their freshwater and marine environments. Accordingly, fish of several ages and life history patterns but of the same size can be compared in similar environments at the same time.

Material for this study was selected from data described for Chilliwack River ${ }^{2}$ steelhead by Maher and Larkin (1955) and for chinook salmon ${ }^{3}$ by Parker and Kirkness (1956). It is noted that steelhead used were all mature. The chinook sample contained some immature specimens; however, the sample as a whole was calculated to include more than 80 percent of fish in their ultimate year of life (Parker and Kirkness, 1956), and were of mixed racial origin. All original measurements were in inches fork length.

Length at previous age was estimated from scale measurements by direct proportion. For steelhead dorsoventral diameters of scale and scale annuli were used. The use of direct proportion back calculation seemed justified for this species from the findings of Smith (1955) and of Mottley (1942). Direct proportion between fork length and anterior radii of scale and scale annuli was assumed for chinook. Preliminary examination of this assumption was made using a sample of 93 chinook selected to provide maximum range in size (18.5 to 41.0 inches). The equation $Y=a x^{b}$ was fitted to the regression of anterior scale radius ( $Y$ ) on the fork length (x). In log form the regression was obviously linear, with

[^0]slope $b=0.9731, S_{b}^{2}=18.0863 \times 10^{-4}$. If $b$ is tested against unity, $t=0.63$, d.f. $91,0.6>P>0.5$. Accordingly, the use of direct proportion for back calculating length at age of chinook cannot introduce serious error.

All data were selected to conform to the following criteria:

1. Scale margins were clearly defined, showing no apparent resorption associated with sexual maturity.
2. Steelhead used were "first spawners", eliminating any error in back calculation from scale resorption of a previous spawning.
3. Steelhead had gone to sea during the early spring. The "fall migrants" of Maher and Larkin were eliminated. Freshwater growth of chinook was not considered in the present analysis.
4. Scales used were regularly shaped and without apparent previous damage or regenerated parts.
5. All individuals completed the last annulus in the 1949 or 1950 growth year. A growth year is here defined as that portion of life history bounded by the completion . of two adjoining annuli.
6. Growth in the year of maturity is not considered in the present analysis.
7. Chinook used were restricted to the "ocean type". (Fraser, 1917; Rich, 1925), i.e. those fish that migrated to the
sea before the formation of the first annulus.

The "life history type" or combination of freshwater and salt water annuli on the scales of each fish is indicated as, for example, $1 / 3$, which denotes one annulus in freshwater and three in salt water, etc.

Table I presents the data used in the present study grouped according to sex (steelhead) and life history types. MATHEMATICAL DERIVATION

The basic relationship describing growth in mass is taken as:

## Integrating:

$$
\int_{0}^{w} t w^{-x} d w=k \int_{0}^{t} d t
$$

and:

$$
w_{t}^{(1-x)}=(1-x) k t+w_{0}^{(1-x)} \cdot . \cdot \cdot \cdot \cdot \cdot \cdot \cdot(\mathbb{A} .4)
$$

Since there is no knowledge of size except at the completion of each annulus, $t$ must be considered in whole units of one year each. If we set $t=1$, i.e., only consider growth

Table I. Life history of steelhead and chinook used in growth analysis.
$\left.\begin{array}{cccc}\hline \text { Life history } \\ \text { type } & \text { Sex } & \begin{array}{c}\text { Total number } \\ \text { of fish }\end{array} \\ \text { Steelhead } & 2 / 1 & 0 & 9\end{array}\right]$
from time to to l, the relationship becomes a regression of $w_{t+1}^{(1-x)}$ on $w_{t}^{(1-x)}$, with intercept $k(1-x)$ and slope always equal to unity, thus:

$$
\begin{equation*}
w_{t+1}^{(1-x)}=k(1-x)+w_{t}^{(1-x)} \tag{A.5}
\end{equation*}
$$

Equation (A.5) holds for all values of $w_{t}$ without regard to absolute age.

Assuming the weight length relationship to be adequately described by the expression:

$$
\mathrm{w}=\mathrm{q} I^{\mathrm{y}} \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot(A \cdot 6)
$$

and substituting for $w$ in (A.5) the general equation in terms of length becomes:

$$
\begin{equation*}
1_{t+1}^{y(1-x)}=\frac{k(1-x)}{q^{(1-x)}}+1_{t}^{y(1-x)} \tag{A.7}
\end{equation*}
$$

which may be further simplified to:

$$
\begin{equation*}
I_{t+1}^{2}=a+I_{t}^{2} \tag{A.8}
\end{equation*}
$$

where, for convenience:
$\alpha=\frac{k(1-x)}{q^{(1-x)}}$
and:

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

Thus $\alpha$ is an abstract constant unit expressing annual growth in length when the length axes are adjusted by the exponent z .

Graphically, if $1_{t+1}^{2}$ is plotted on the ordinate and $l_{t}^{Z}$ on the abscissa, points formed from a length progression $l_{1}, l_{2}, l_{3}$, etc. will lie $\alpha$ distance above a $45^{\circ}$ diagonal originating at 0,0. Thus, a expresses length increment in a manner which is comparable regardless of size or age. It has the same utility as instantaneous relative growth rate would have in the case of an animal growing exponentially ${ }^{4}$ (equation (A.2)).

Some characteristic curves (for relationships characterized by values of $z=0.5,1.0,1.5$ ) are plotted on unmodified axes in Figure 1. Two of the curves, $1^{.5}$ and $1^{1.5}$ represent extremes that have been met with. Thus, in plotting $l_{t+1}$ against $l_{t}$, if the trend appears to diverge from the $45^{\circ}$ diagonal, the value of $z$ probably lies between 0.5 and 1.0. Conversely, if the data appear to approach the $45^{\circ}$ diagonal, $z$ is likely to lie between 1.0 and 1.5. If the data appear linear and parallel to the diagonal, the value of z will be close to l. Assuming no progressive change in shape

[^1]

Figure 1. Plot of $l_{t+1}$ on $l_{t}$ for hypothetical fish growing from 2 to 30 units (length) in four years, using different exponents ( z ). 1. represents exponential growth.
(isometry) weight may be described by the equation:

$$
w=q 13.0
$$

and the corresponding differentials for growth are as follows:

$$
\begin{aligned}
& z=0.5, \mathrm{dw} / \mathrm{dt}=\mathrm{kw} / 6 \\
& \mathrm{z}=1.0, \mathrm{dw} / \mathrm{dt}=\mathrm{kw} w^{2 / 3} \\
& \mathrm{z}=1.5, \mathrm{dw} / \mathrm{dt}=\mathrm{kw} w^{1 / 2} .
\end{aligned}
$$

Since in (A.8) both $\alpha$ and $z$ are presumably unknown, $z$ is found using trial values and seeking a minimum relative variance of $\alpha .5$ If a computer is unavailable the tedium of determining $z$ may be considerably reduced in the following manner. Length at previous age data ( $1_{1}, 1_{2}, 1_{3}$, etc.) are transformed to $1_{1}^{\circ}, 1_{2}^{5}, 1_{3}^{.5}$, etc. and $1_{1}^{1.5}, 1 \frac{1}{2} \cdot 5,1_{3}^{1} \cdot 5$, etc., giving three sets with $z$ values of $0.5,1.0$, and 1.5 , respectively. For each set compute mean $\alpha(\bar{\alpha})$ and the variance $\left(S_{\alpha}^{2}\right)$. The square root of the relative variance $\left[\frac{s_{\alpha}^{2}}{\bar{a}^{2}}\right]^{1 / 2}$ or relative standard deviation, $S_{r}$, was found
$5_{\text {An Alwac IIIE computer was used. The program is on file }}$ at the Computing Centre, University of British Columbia, Canada. Copies may be obtained upon request.
to be related to $\mathbf{z}$ approximately as a quadratic function:

$$
\mathrm{S}_{\mathrm{R}} \approx a+\mathrm{bz}+\mathrm{cz} \mathbf{z}^{2} \ldots . . . . . . . . . . . .(\mathrm{A} \cdot 9)
$$

Having three sets of values of $S_{R}^{\prime}$ and $z$, (A.9) can be solved using simultaneous equations. Optimum $z$ (the value of $z$ giving minimum relative variance) is obtained when the derivative of (A.9) is zero, thus:

$$
\begin{aligned}
& 2 c z-b=0 \text { and } \\
& z=\frac{b}{2 c} \ldots \ldots \ldots \ldots(A .10) .
\end{aligned}
$$

This method has given values of optimum $z$ accurate to two places.

A graphic approximation can also yield usable estimates of both $z$ and $\alpha$. As stated by Brody (1945) the eye is quite sensitive to deviations from a straight line and if data are rectified by suitable alteration of the axis linearity will be apparent. Scales for converting axis for $z$ values of 0.1 to 2.0 are presented in Figure 2. Graph paper can be made using these scales, length data converted to a hundred unit scale (so all length values are more than one and less than 100) and plotted directly as $l_{t+1}$ on $l_{t}$. A straight line fitted by "eye" to the data and with a slope of $45^{\circ}$ can be used to judge goodness of fit.

For best accuracy, in lieu of a computer, it is sug-


Figure 2. Nomograph for establishing axis in making graph paper with $1^{2}$ scales.
gested that the treatment of data be first approached graphically, then solved by use of the quadratic method, choosing two values to bracket and a third to approximate the desired optimum.

With an optimum value of $z$ the length at age data are then converted to $I_{1}^{2}, 1_{2}^{2}, 1_{3}^{2}$, etc. Significance of differences in growth between any desired grouping or populations can then be decided using analysis of variance on the $o$ values for individual fish.

Certain precautions are necessary when determifing z for any group of data. When $I_{t+1}$ is plotted against $1_{t}$ a single point, representing growth as distance above the $45^{\circ}$ diagonal is obtained. At optimum $z$ growth is given as $\bar{\alpha}_{\text {: }}$, an abstract unit, which is an appropriate statistic for all sizes and/or ages provided the assumption of constant environmental and physiological conditions is approximated. However, natural variation in ability to grow. (genotypic) as well as variation in growth dictated by environmental opportunity and social interaction (phenotypic) is typical of fish populations. To some degree fast growing individuals and slow growing individuals maintain their relative status throughout life. For any group of fish in which all $l_{t}$ values are close, i.e., in the same order of magnitude, the plot of points with coordinates $I_{t}, I_{t+l}$ will be biased
if the relative size position of fish in a population tends to remain stationary. Under these conditions a fast growing member is always larger, and the resulting line will have a steeper slope than the average growth of the group warrants. This error may be visualized from a consideration of Figures 4,5,8, and 10. For this reason $z$ has been determined only from series of lengths containing three or more successive values for each fish (two or more complete growth years).

In the foregoing treatment, all of the variation in a sample has been ascribed to $\alpha$. $z$ was treated as an independent variable, determined without error, thus facilitating direct comparison of growth rates without regard to size or age, provided average growth in the compared groups is adequately described by the same $z$ value. The variability of $z$ values is further explored in the following section.

APPLICATION

Optimum z was determined for the freshwater phase of life history for the $3 / 1$ steelhead group (Fig. 6). The $2 / 2$ group was used to compute $z$ for steelhead in salt water (Fig. 9). For chinook, z was independently computed for the $0 / 3$, $0 / 4$, and $0 / 5$ groups (Fig. 11-13). Table II summarizes the statistical results.

To gain some appreciation of the variability of $z$, two

Table II. Summary of statistics relative to optimum $z$ as found by iteration.

| Species | Life history type | Number of fish | $z$ | "Mean" difference $\bar{\alpha}$ | $\begin{gathered} \text { Variance } \\ s_{\alpha}^{2} \end{gathered}$ | Relative variance $s^{2} / \bar{a}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Steelhead | 3/1 | 47 | 0.59 | 0.69536 | 0.03749 | 0.07752 |
|  | 2/2 | 52 | 1.00 | 11.14231 | 3.59302 | 0.02894 |
| Chinook | $0 / 3$ | 150 | 1.32 | 31.64658 | 30.59787 | 0.03055 |
|  | $0 / 4$ | 60 | 1.30 | 27.57002 | 28.54040 | 0.03755 |
|  | 0/5 | 8 | 1.11 | 12.56085 | 8.58274 | 0.05440 |

of the chinook groups were subdivided. For the $0 / 4$ group (60 fish) the first and last 30 were treated separately. For the $0 / 3$ group ( 150 fish) the first 30 , second 31 , third 43 , and remaining 46 fish were treated separately. The pertinent statistics are presented in Table III. $z$ is observed to vary between 1.25 to 1.46 when calculated from sub-groups of apparently random classification.

The parabolic relationship between values of $z$ and the relative standard deviation of $\alpha$ are demonstrated in Figure 3, the $0 / 4$ chinook group was used in this example (Table IV). Optimum z lies close to 1.3. A parabolic solution gave $z=1.33$. From Figure 3, a change of .05 in either direction from optimum $z$ is seen to effect a change of only approximately 0.001 in relative standard deviation. Thus the attachment of significance beyond the first decimal place in $z$ is unarranted.

Accordingly, the entire data (Table I) were treated as follows:

$$
\begin{array}{ll}
\text { Steelhead, freshwater, } & I_{t+1}^{.6}=\alpha+1_{t}^{.6} \\
\text { Steelhead, marine, } & I_{t+1}=\alpha+1_{t} \\
\text { Chinook, marine, } & I_{t+1}^{1.3}=\alpha+1_{t}^{1.3}
\end{array}
$$

Values of $1^{z}, 1^{z}, 1^{z}$, etc. and $\alpha_{12}, \alpha_{23}$, etc. were computed for each individual. These transformations are presented.

Table III. Values of $z$ and accompanying statistics found for sub-group of chinook.

| Sub-group | Number of <br> fish | $z$ | $\bar{\alpha}$ | $s_{\alpha}^{2}$ | $s^{2} / \bar{\alpha}{ }_{\alpha}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $0 / 4$ | 30 | 1.36 | 36.14174 | 33.35864 | 0.02550 |
|  | 30 | 1.26 | 24.17668 | 27.27589 | 0.04666 |
|  | 43 | 1.42 | 43.60381 | 52.53047 | 0.02763 |
| $0 / 3$ | 46 | 1.25 | 24.26675 | 16.95653 | 0.02879 |
|  | 30 | 1.30 | 31.19169 | 35.49098 | 0.03648 |
|  | 31 | 1.46 | 53.29454 | 78.56134 | 0.02766 |

Table IV. Statistics leading to solution (by Alwac IIIE computer) of optimum $z$ for the $0 / 4$ group of chinook, $I_{t+1}^{2}=a+I_{t}^{z}$.
z
$\bar{\alpha} \quad s_{\alpha}^{2}$
$(s / \bar{\alpha})^{2}$
$s / \bar{\alpha}$

| 1.00000 | 8.75056 | 4.15228 | 0.05423 | 0.23287 |
| ---: | ---: | ---: | ---: | ---: |
| 0.50000 | 1.04882 | 0.18507 | 0.16824 | 0.41017 |
| 1.50000 | 57.65691 | 145.35886 | 0.04373 | 0.20912 |
| 1.25000 | 22.79004 | 19.75700 | 0.03804 | 0.19504 |
| 1.37500 | 36.34871 | 50.71640 | 0.03839 | 0.19593 |
| 1.31250 | 28.80405 | 31.16188 | 0.03756 | 0.19380 |
| 1.28125 | 25.62648 | 24.71367 | 0.03763 | 0.19398 |
| 1.29688 | 27.17020 | 27.72342 | 0.03755 | 0.19378 |
| 1.30469 | 27.97554 | 29.38511 | 0.03755 | 0.19378 |
| 1.30078 | 27.50020 | 28.54040 | 0.03755 | 0.19378 |



Figure 3. Plot of relationship between relative standard deviation of $\alpha$ and trial value of $z$ for 0/4 chinook data.
graphically for each major grouping of fish in Figures 4 - 13. Differences between a values for life history groups and sexes were tested by analysis of variance, with appropriate correction for disproportionality in sample size (Snedecor, 1946). Results are presented in Tables V and VI.

From these results the following conclusions for steelhead may be drawn:

1. In freshwater, male and female steelhead grow at approximately the same rate. In salt water males grow significantly faster than females.
2. Growth rate is inversely related to eventual life history events in both fresh and salt water. Slow-growing steelhead failed to become smolts at completion of the second growth year and remained an additional year in freshwater. Fast-growing individuals migrated at the completion of the second growth year.
3. In salt water, the two freshwater growth groups further subdivided into fast and slow-growing fractions. The faster-growing fraction of the former slow-growing group matured following the first ocean growth year. The slowgrowing fraction matured after two ocean growth years. The same subdivision took place in the freshwater fastgrowing group. These results are in part substantiated by observations of Alm (1949) and by Elson (1957) for Salmo salar, and of Parry (1958) for S. salar, S. trutta, and S. gairdnerii.


Figure 4. Plot of $I_{t+1}$ on $I_{t}$ and $I_{t+1}^{0.6}$ on $I_{t}^{0.6,}$ 2/1 life history group of steelhead in freshwater.


Figure 5. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{0.6}$ on $1_{t}^{0.6,}$ 2/2 lifịe history group of steelhead in freshwater.


Figure 6. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{0.6}$ on $1_{t}^{0.6}$ $3 / 1$ life history group of steelhead in freshwater.


Figure 7. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{0.6}$ on $1_{t}^{0.6}$, $3 / 2$ life history group of steelhead, in freshwater.



Figure 8. Plot of $1_{t+1}$ on $1_{t}$ for $2 / 1$ and $3 / 1$ life history groups of steelhead in salt water.



Figure 9. Plot of $1_{t+1}$ on $1_{t}$ for $2 / 2$ and $3 / 2$ life history groups of steelhead in salt water.

29


Figure 10. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{1.3}$ on $1_{t}^{1.3}$ for $0 / 2$ life history group of chinook in salt water.


Figure 11. Plot of $I_{t+1}$ on $I_{t}$ and $I_{t+1}^{1} 3$ on $I_{t} \frac{1}{} 3$ for $0 / 3$ life history group of chinook in salt water.


Figure 12. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{1.3}$ on ${ }^{l_{t}^{\prime 3}} 1_{t} .3$ for $0 / 4$ life history groups of chinook in salt water.


Figure 13. Plot of $1_{t+1}$ on $1_{t}$ and $1_{t+1}^{1.3}$ on $1_{t}^{1.3}$ for $0 / 5$ life history groups of chinook in salt water.

Table V. Analysis of variance on steelhead and chinook for growth differences between life history groups and sexes.


Table VI. Average growth (measured by $\alpha$ ) for groupings of steelhead and chinook, showing significant differences.


For chinook salmon, both sexes were lumped. As in the steelhead in salt water, the fastest growing fish matured at the earliest age.

## DISCUSSION

Growth of steelhead and chinook has been described using the basic premise that ghowth rate ( $d w / d t$ ) increases proportionally to weight raised to a power ( $w^{x}$, where $x$ varies between 0.5 and 1.5 approximately). No experimental evidence has been offered to justify the use of this relationship, however empirical growth data for those species considered were approximately linear after transformation by a suitable choice of the length exponent 2 . In thìs manner these data are adequately described by the hypothesis. Equation (A.3) has analogy with empirical expressions of other physiological rates, summarized as equation (A.4). Adolph (1949) listed 33 physiological rates ( $\mathrm{O}_{2}$ uptake, $\mathrm{H}_{2}$ excretion, ventilation, etc.) that appear (for mammals) adequately described by the general equation (A.4), i.e. that the rates are proportional to $\mathrm{w}^{\mathrm{x}}$. Zeuthen (1953) and Weymouth, et al. (1942) extended these observations to respiration of various individual organs. This parallelism underlines the coordinated aspect of a living system (Haldane, 1936). Various physiological rates are not independent but correlated. That growth rate is also part of the correlated system appears to be a tenable hypothesis. Barrett (Fry, 1957) demonstrated for rainbow trout (5-75
grammes) in freshwater and under standard conditions that the rate of $\mathrm{O}_{2}$ consumption increases in proportion to $\mathrm{w}=0.8$. It was shown in a previous section that juvenile steelhead in freshwater grew proportional to $i^{z=0.6}$. Assuming that weight is proportional to $1^{3}$, then growth rate in terms of weight ${ }^{6}$ was proportional to $\mathrm{w}^{\mathrm{x}=0.8}$. This similarity of exponents suggests the possibility that values of $x$ or $z$ for growth equations may be derived from a comparative study of standard metabolic rate over a range of sizes. Data are not at present available to make such a comparison.

The phenomenon of "btanzas" is characteristic both of metabolic rates and growth rates. Anadromous salmon and trout experience at least two rather abrupt physiological transformations (Hoar, 1939, 1957; Hoar and Bell, 1950; Green, 1926), one at parr-smolt transformation, the other at maturity. While published data have not been found describing the relation of standard metabolic rate to weight for fish in each stage of life history, certain analogies may be drawn from other groups of animals. For mammals, Brody (1945) has described discontinuities or "breaks" in weight-specific metabolic rate curves and he directed attention to similar breaks in growth curves. He has suggested a direct connection between metabolic rate and growth rate. Zeuthen (1953, 1955)

$$
\sigma_{x}=1-\frac{z}{\bar{y}}=1-\frac{.6}{3}=.8 .
$$

extended these observations to include several poikilotherms. Martin (1949) has demonstrated sharp breaks in relative growth lines for several species of fish and related these discontinuities to ossification and maturity. Hiatt (1947) demonstrated a sharp break in relative growth of gut length of Chanos chanos occurring at approximately 100 mm body length. Available data suggest that increase in growth rate is proportional to increase in standard metabolic rate as measured by $\mathrm{O}_{2}$ consumption. The exponent x may be primarily established for each growth stanza by the endocrine control system and the proportion constant $k$ perhaps has meaning as environmental opportunity. The analogy has the limitation that growth stanzas may be delimited by ecological as well as physiological thresholds. Thus within any physiological growth stanza (within which $x$ may be constant) there may be more than one ecological growth stanza, each characterized by a particular $k$, or perhaps progressive shift of $k$ from a low to a high value or vice versa.

A growth equation currently popular in fisheries science is that of von Bertalanffy (1938, 1949, 1957). It is equivalent to the "self-inhibiting" growth equation of Brody (1945) which is_much used on mamals; to the modified exponential of Croxton and Cowdan (1946) and to the graphic transformation presented by Walford (1946). Bentalanffy considers growth to be the net result of an open system of supply and demand of resources which can be metabolized. Since material
must enter the organism through a surface, and maintenance demand is proportional to mass, given isometric growth the organism will eventually reach a size where supply and maintenance demand are in equilibrium. Bertalanffy's basic equation is therefore:

$$
\begin{equation*}
d w / d t=H S-k w \tag{A.11}
\end{equation*}
$$

where $S$ denotes surface of some limiting membrane,
w denotes mass, and
$H$ and $k$ are proportion constants.

With isometric growth and constant density a surface is proportional to the square of the length while mass is proportional to length cubed. Introducing equation (A.6) for mass, and letting:

$$
\mathrm{s}=\mathrm{p} 1^{2}
$$

equation (A.11) takes the form:
where $\alpha=\frac{H P}{3 q}$ and $\beta=\frac{k}{3}$.

Integrated, equation (A.12) depicts growth as a process in which first differences of a length series $l_{1}, I_{2}, I_{3}$, etc. decrease by a constant percentage, i.e. on a arithmetic plot of $I_{t+1}$ against $I_{t}$, points fall on a line which intercepts a $45^{\circ}$ diagonal with origin 0,0 (Walford, 1946). Bertalanffy's equation has found practical application in yield equations by Beverton and Holt (1957).

There are several assumptions inherent in von Bertalanffy's growth equation that need to be examined. Firstly, emphasis is placed on the "two-thirds" rule or surface rule (see Brody, 1945) which states that standard metabolism, as measured by rate of $\mathrm{O}_{2}$ consumption, increases as the $2 / 3$ power of weight. Brody,(1945), Adolph (1949), Prosser (1950), Zeuthen (1953), von Bertalanffy (1957), and others have indicated that, more accurately, metabolic rate increases approximately as the 0.73 power of weight. Further, these obser-si. vations have been based on interspecific comparisons of adult animals (mouse to elephant) and do not reflect the weight specific metabolic rate of any single organism throughout life.

Secondly, as pointed out by Cohn and Murray (1927), there is no reason for growth of internal surfaces to be isometric. Szarski et al. (1956) have found the absorptive area of the gut of Abramis brama to grow approximately proportionally to the weight by means of infolding. Klust $(1939,1940)$ and Al Hussaini (1949) have demonstrated ontogenetic increase in relative gut length and/or relative absorptive surface in cyprinids. Hiatt (1947) demonstrated a relationship between allometric growth of the gut of Chanos chanos and a sizespecific change in dietary habit. Price (1931) demonstrated positive allometry in growth of gill surfaces ( $G=8.65 w^{0.785 \text { ) }}$ of Micropterus dolomieui. It would appear to be the unusual case where a surface membrane restricts growth in the manner
of equation (A.11).

The apparent fit of a von Bertalanffy equation or Walford line to growth data may in some cases be forced as a result of the method of sampling or combining the data. Average lengths at the completion of an annulus for the several groups of chinook are used as an example.(Table VII). In Figure 14 these data are graphically transposed from an average size at age plot (right side) to a $I_{t+1}$ on $I_{t}$ plot (left side). Two treatments have been used. The first represented by solid lines in both sides of the figure, considers the life history groups separately. The dashed line in both sides of the figure represents the case where only fish captured in their fourth growth year are used to compute average size at age III, etc. This latter method reflects "Lee's phenomenon" (Lee, 1920) which can be accounted for by the growth rate-life history relationship previously demonstrated (Table V), by selectivity of the fishing gear for larger fish, and by shoaling of chinook according to stage of maturity (Neave, 1951; Parker and Kirkness, 1956) or by a direct correlation between growth rate and mortality rate (Gerking, 1957). These two methods of treatment lead to diverse conclusions. By considering each life history group separately growth is seen to approach parallelism with the $45^{\circ}$ diagonal. The second treatment depicts growth rate as gradually decreasing and forms an approximately linear plot (Walford line) which will inter-

Table VII. Average size at age for life history groups of chinook salmon, as estimated by direct proportion back calculation.

| Life history |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| type | Number of <br> fish |  | Size at end of annulus |  |  |  |
|  |  | 1 | 2 | 3 | 4 | 5 |
|  |  |  |  |  |  |  |
| $0 / 1$ | 4 | 10.9 |  |  |  |  |
| $0 / 2$ | 27 | 9.0 | 20.8 |  |  |  |
| $0 / 3$ | 150 | 7.5 | 19.1 | 27.7 |  |  |
| $0 / 4$ | 60 | 7.0 | 17.4 | 25.5 | 33.3 |  |
| $0 / 5$ | 8 | 5.0 | 15.1 | 22.5 | 29.9 | 37.6 |

a Sample of four fish captured in their second year of life, not included in Table $I$ or previously considered.


Figure 14. Two treatments of data by "Walford transformation" leading to different conclusions. Chinook, salt water. See text for explanation.
cept the $45^{\circ}$ diagonal. Thus the latter treatment depicts growth as a von Bertalanffy equation. In the present case the latter method leads to a serious underestimation when predicting future increment to the stock from growth.

Thus far, growth of the average individual of subgroups of the population has been presented. For chinook, the von Bertalanffy equation is shown to oversimplify and underestimate the growth of a hypothetical "average" fish in the entire population. Each component group should be weighted according to its actual abundance in the population, a proposition necessitating a schedule of mortality rates which are related to growth rates.

Considering that approximately 95 percent of steelhead (Maher and Larkin, 1956) and substantially all chinook (for possible exceptions see Robertson, 1957) die at first spawning, and considering selectivity of fishing gear for larger fish, the relative magnitudes of growth rate and total mortality rate in these populations are undoubtedly directly correlated (see Gerking, 1957, for comment on other species). This aspect of populations dynamics has been little explored and presents a necessary field for study before the average growth of a population can be depicted from a consideration of growth of individuals.

## SUMMARY AND CONCLUSION

Growth in fishes has here been visualized as a series of stanzas within each of which the growth rate is proportional to a constant multiplied by a fractional power of weight, i.e.

$$
d w / d t=k w^{x} .
$$

This approach implies that in each growth stanza the increment of weight can be related to the weight in the same way as various physiological rates are related to weight. In both of these instances a complex of processes may be involved which are best summarized mathematically in the relatively simple parabolic equation. However, the interpretation attached to the constants $k$ and $x$ is complicated in the case of growth rate because both ecological and physiological factors act as determinants.

The similarity in $x$, the exponent of weight for metabolic rate and growth rate suggests that x measures the complex of physiological processes while $k$ measures ecological opportunities. Whether or not this is true does not alter the usefulness of the equation in describing growth processes. This equation can be considered as an example of General Systems Theory approach of von Bertalanffy (1950, 1951). In addition growth stanzas may be delimited both by ecological and by physiological thresholds. Finally growth of the indi-
vidual or of a group of individuals may be characterized by different values of the constants $k$ and $x$, necessitating separation of a population into "life history" groups, etc. These groups may be characterized by mortality rates associated with their respective growth rates.

The prediction of growth increment in a population thus requires:

1. Separation into life history groups (and possibly sex), each characterized by particular growth rates.
2. Determination for each group and for each growth stanza of appropriate value of the constant $k$ for an average exponent x .
3. Determination for each group and each growth stanza of appropriate total mortality rate.
4. Summation of the increments to each group with correction for mortality.

Sampling data of a population obtained through a selective fishery cannot be used per se to depict "average individual", and detailed mortality studies, as related to size and growth rate are needed. A relationship between growth rate and metabolic rate is suggested as a means of independently establishing one basic parameter of the growth equation. These two approaches constitute profitable fields of research for agencies engaged in fisheries management.

## B. NATURAL MORTALITY OF CHINOOK SALMON

The rate of natural mortality is perhaps the most elusive parameter to determine. A widely used approach is by the analysis of catch curves (Ricker, 1958), but the peculiarities of the chinook life history omit this method from consideration. It is, however, possible to compute natural mortality of a chinook population using data from tagging. This method was summarily published by the author (Parker and Kirkness, 1956), but is included here in expanded form.

A population of $N$ tagged fish are released during the year 0. As long as these fish remain immature they are subject to a negligable fishing rate. $N_{0}, N_{1}, N_{2}$, etc. denotes the number of fish tagged belonging to groups which will mature during years $0,1,2$, respectively, and $R_{0}, R_{1}, R_{2}$, etc. denote the number of tags recovered and turned in during the subscript years.

It has been assumed that:

1. The annual expectation of death from fishing (u) is constant,
2. annual mortality rate from natural causes (n) is constant, and natural survival rate, denoted by $s$, is $s=(1-n)$,
3. that loss of tags from structural failure is not progressive,
4. that the numbers of tags turned in is a constant fraction (X) of those tagged fish recaptured,
5. that mortality due to tagging is complete within a short time of tagging. $J$ denotes the fraction surviving this mortality,
6. that natural mortality rate is the same for tagged and untagged fish.

The basic relationship between the tagged population and recovery of tags is defined by the equation:

$$
\begin{equation*}
R_{i}=N_{i} J X u s^{i} \cdot \ldots . . . . . . . . . . . . . . \tag{B.1}
\end{equation*}
$$

where $i$ denotes any year of maturity after tagging. For the year of tagging (B.1) becomes:

$$
\begin{equation*}
R_{0}=N_{0} \text { OXus }^{0} \cdot . . . . . . . . . . . . . . . \tag{B.2}
\end{equation*}
$$

and the survival term becomes 1 . When the stock matures over a series of years,

$$
\begin{equation*}
\varepsilon N_{i \mathrm{i}} \mathrm{JXu}=\varepsilon \frac{R_{i}}{s^{i}} . \tag{B.3}
\end{equation*}
$$

and where tag recovery extends over $j$ years,

$$
N J X u=R_{0}+\frac{R_{1}}{s^{1}}+\frac{R_{2}}{s^{2}}+\ldots \cdot \frac{R_{j}}{s^{j}} \ldots . . . . . . .(B .4)
$$

also:

$$
\left[N J X u-R_{0}\right]^{j}=R_{1} s^{(j-1)}+R_{2} s^{(j-2)}+\ldots \cdot R_{j} s^{0} \cdot .(B \cdot 5)
$$

and:

$$
\left[N J X u-R_{0}\right] s^{j}-R_{1} s^{(j-1)}-R_{2} s^{(j-2)}-\ldots R_{j}=0 \quad .(B \cdot \sigma)
$$

JXu can be estimated from the recovery during year 0 of fish known to be mature.

Appropriate data presented by Parker and Kirkness (1956) from tagging studies conducted along the coast of Southeastern Alaska are:

$$
\begin{aligned}
& \mathrm{N}=918 \\
& \mathrm{R}_{0}=110 \\
& \mathrm{R}_{1}=35 \\
& \mathrm{R}_{2}=11 \\
& \mathrm{R}_{3}=1
\end{aligned}
$$

JXu was estimated from the recovery of fish tagged and released in their 5th and 6th years of life. From 215 of these fish tagged, 44 were recovered ( 42 during year 0 ). Thus:

$$
J X u=\frac{44}{215}=.205
$$

and substituting the above data in equation (B.6) the relationship becomes:

$$
\begin{aligned}
& {[918(.205)-110] s^{3}-35 s^{2}-11 s-1=0} \\
& 78 s^{3}-35 s^{2}-11 s-1=0
\end{aligned}
$$

the approximate solution of which gives: $s=0.681$.

Since not all the 4+ and 5+ year old fish were mature, further consideration of JXu is necessary. Following above reasoning:

$$
J X u=\frac{I}{N} \cdot \frac{R_{1}}{s}+R_{0}
$$

and $J X u=\frac{1}{215} \cdot \frac{2}{0.681}+42=0.209$
which value is substituted into equation (B.6) and the second estimate of $s$ is: $s=0.659$. Further iteration does not affect the third decimal place of $s$.

The problem of variance of $s$ has not been considered. It is appreciated that a difference of one unit in the second decimal place of JXu causes a change of approximately five units in the second decimal place of $s$; thus, $s$ is critically affected by error in estimating JXu.

The assumptions given are also not completely satisfied. A small number of fish tagged were recaptured while yet immature. Fishing mortality rate may vary from year to year. Annual natural mortality may not be constant. No evidence of progressive tag loss has been found in the Alaskan experiment, yet Calhoun, et al. (1951) report high incidence of progressive tag failure (the same type tags were used) in the California studies. As will be shown in a later section and from observations reported by Milne (1956) mortality from tagging would appear to be over or negligible
within a few days. Perhaps the most critical assumption of $a l l$ is that tagged fish are representative of the untagged population. It is at present impossible to establish the validity of this assumption. All assumptions appear to be reasonable satisfied in the population studied (Parker and Kirkness, 1956); however, no significance is placed beyond the first decimal place. The best available estimate of annual natural mortality rate is then given as in the magnitude of 0.3 to 0.4 . The instantaneous natural mortality rate (q) is estimated to be of the magnitude 0.36 to 0.51 .

## C. CRITICAL SIZE

For any particular life history group the average size specific annual growth (length) rate is described by the equation:

$$
\begin{equation*}
1_{t+1}^{z}=a+1_{t}^{z} \tag{A.8}
\end{equation*}
$$

and the relationship:

$$
\begin{equation*}
w=q 1^{y} \tag{A.6}
\end{equation*}
$$

also defines 1 as a function of $w$, thus:

$$
\begin{equation*}
I=\left[\frac{\mathbf{w}}{q}\right]^{\frac{1}{\bar{y}}} \tag{C.1}
\end{equation*}
$$

Substituting (C.1) into (A.8):

$$
\begin{align*}
& {\left[\frac{w_{t+1}}{q}\right]^{\frac{z}{y}}=a+1_{t}^{z},} \\
& \frac{z}{w_{t+1}^{y}}=q^{\frac{z}{\bar{y}}}\left(a+1_{t}^{z}\right), \text { and } \\
& w_{t+1}=q\left(a+1_{t}^{z}\right)^{\frac{y}{z}} \tag{c.2}
\end{align*}
$$

For a specific size subclass of a life history group, the annual instantaneous relative growth rate (g) is:

$$
g=\ln \left[\frac{w_{t+1}}{w_{t}}\right] \cdots \cdots \cdots \cdots \cdots \cdots(C .3)
$$

and:

$$
g=\ln \left[\frac{q\left(a+1_{t}^{Z}\right)^{\frac{Z}{2}}}{q 1_{t}^{Y}}\right]
$$

or:

$$
\begin{equation*}
g=\frac{Y}{z} \ln \left(a+I_{t}^{z}\right)-J \ln I_{t} \tag{C.4}
\end{equation*}
$$

Thus $g$ is a function of $\bar{J}, z, a$, and $I_{t}$. Since $y, z$, and a are constants at any size during a particular physiological phase, within a particular life history group g changes only with change in $l_{t}$, ie. the relationship is an "average size-
specific instantaneous relative growth rate" as proposed by Larkin, Terpenning and Parker (1957).

Average size at the ultimate annulus, mean $\alpha$ and the fiducial interval of $\vec{a}$ for each life history type of chinook are presented in Table VIII. Table IX presents size-specific empirical average values of $g$, and the 0.95 fiducial intervals. Figure 15 graphically presents the empirical average annual instantaneous relative growth rate of each life. history type as a function of size. Also included in Figure 15 is the zone of instantaneous natural mortality. Clearly, the total mass of each life history group gains weight until the ultimate year, the only exception being the largest members of the slow-growing $0 / 5$ group. The $0 / 2,0 / 3$, and $0 / 4$ groups mature and leave the marine environment before the instantaneous growth rate decreases to equality with the instantaneous mortality rate. If maximum yield, in pounds of fish, from the sotck is desired, fishing should be restricted to the maturing individuals in their ultimate year.

If fishing is allowed on the immature stock a dilemma arises in choosing a size limit. It is impractical, if not impossible, to separate the life history groups while immature. Yet a size limit which would allow cropping, say the $0 / 2$ group, would be wasteful of the potential growth

Table VIII. Average size at ultimate annulus, mean $\alpha$ ( $z=1.3$ ) and fiducial intervals for chinook life history groups. Data from Tables VI and VII.

| Life <br> history <br> group | No. of fish | Average size at ultimate annulus | $\begin{gathered} \text { Mean } \\ \alpha \end{gathered}$ | $\begin{gathered} \text { Fiducial interval }{ }^{\text {a }} \\ \bar{\alpha} \pm t \\ \text { Lower }{ }^{.05^{S}} \bar{\alpha} \\ \text { Upper } \end{gathered}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 0/2 | 27 | 20.8 | 34.10 | 32.06 | 36.14 |
| $0 / 3$ | 150 | 27.7 | 29.82 | 28.98 | 30.66 |
| 0/4 | 60 | 33.3 | 27.49 | 26.11 | 28.87 |
| $0 / 5$ | 8 | 37.6 | 25.89 | 20.34 | 31.44 |

${ }^{2}$ While the variance of $\alpha$ was calculated using the number of observations (i.e. number of fish times number of observations per fish less one), standard error was calculated using above variance and number of fish.

Table IX. Average annual size specific instantaneous growth rates and 0.95 fiducial intervals for each life history type.

${ }^{2} I, U$ denote lower and upper fiducial intervals.


Figure 15. Length-specific average annual instantaneous growth (weight) rates of life history groups of chinook salmon compared with zone of instantaneous natural mortality rate.
obtainable from the older life history types. The biological answer appears to be the restriction of fishing to areas which do not contain appreciable quantities of immature fish.

At present, management agencies of the Pacific Coast have size limit restrictions which in effect, prevent the landing of fish less than 25.0 inches fork length. It is seen from Figure 15 that fish maturing at earlier ages than $2+$ and some portion of the $0 / 3$ group are excluded entirely from the catch. This loss might be offset by the gain in weight of the older life history types, depending upon their relative strength within the year class. This, of course, is dependent upon the validity of the assumption of no release mortality. The following section deals with the evaluation of this mortality.
D. MUSCULAR FATIGUE AND MORTALITY

IN TROIU CAUGHT PACIFIC SAIMON 7

INTRODUCTION

That fish die in captivity following strenuous muscular exertion has been demonstrated by several authors. Among these are von Buddenbrock (1938) working with cod (Gadus

Parker, R.R., E.C.Black, and P.A.Larkin, 1959. Fatigue and mortality in troll caught Pacific salmon (Oncorhynchus). In press. J. Fish. Res. Bd. Canada.
morrhua) and dab (Platessa limanda); Secondat and Diaz (1942) with tench (Tinca tinca); Milne and Ball (1956) with coho salmon (Oncorhynchus kisutch) and later (1958) with both coho and chinook (ㅇ. tshawytscha); Black (1957c) with sockeye (ㅇ. nerka); Bates and Vinsonhaler (1957) with smolt chinook, striped bass (Roccus saxatalis), and shad (Alosa sapidissima); Fry (1958) with coho and chinook; and Parker and Black (1959) with chinook. In every case severe muscular activity was followed by significant mortality.

Other authors have subjected these and other species to severe fatigue and have not observed significant ensuing mortality. Included here are Black (1957a,b) working with rainbow trout (Salmo gairdnerii) and lake trout (Salvelinus namaycush). Paulik, DeLacy and Stacy (1957) working with coho, and Paulik and DeLacy (1958) with sockeye repeatedly subjected their animals to exhaustion without resulting significant mortality. Jensen (1958) hooked and released salt-water-pond-reared chinook without significant mortality. Black (1958b) has reviewed the subject of hyperactivity and death. The specific causes of mortality have not been determined. Why fatigue should in one case lead to mortality, and in another case, not, remains a mystery.

It has been suggested by colleagues that mortality in live boxes of fatigued fish reported by Parker and Black
(1959) was caused by factors other than fatigue, viz. unrecognized injury, psychosis from enclosure in a small space or from handling, breaking the mucous coat, etc. Perhaps a summation (Brett, 1958) of these stresses ${ }^{8}$ is responsible. The validity of extrapolating mortality observations in holding experiment's to apply to fish caught and released after tagging, or released because of a size limit restriction, is thus open to question. However, investigators have repeatedly shown tag recoveries of less than 30 percent for troll-caught salmon (Milne, 1957) released in the face of a fishery known to be much more intensive.

For example, Parker and Kirkness (1956) tagged selected chinook salmon, apparently unharmed and predominantly of Columbia River origin. For fish in their ultimate year recoveries were only 21 percent, yet from data of Silliman (1948, 1950) it can be estimated that a total fishing mortality of Columbia River chinook averaged 86 per cent per annum over the 11 years 1935 to 1945. A total nonfishing mortality (or tag loss which was known to be minimal) of over 70 percent is necessary to account for this difference. Parker and Kirkness (1956) estimated average annual natural mortality to be approximately 34 percent. Thus, a

[^2]mortality in excess of 45 percent remains unaccounted for by this rough approximation.

Sedondat and Diaz (1942) reported that blood lactate concentrations of tench increased following forced activity but usually subsided by the end of six hours. They also observed that some fish died and blood lactate levels of these had failed to decrease. Black (1955, 1957a,b,c) demonstrated a similar response for several species of salmonids; in gener al, blood lactate levels continued to increase during postexercise rest periods, and peak values were attained during the second or third hour of post-exercise rest. Blood lactate levels then decreased at a decelerating rate. Resting levels were not attained before 12 hours. This sequence is termed "typical response". Black (1957c) suspected a correlation between death and concentration of blood lactate, but lacked sufficient data for a conclusive demonstration. Parker and Black (1959), working with troll-caught chinook, demonstrated a positive association between blood lactate levels and death. While high blood lactate levels have not been shown to be a primary cause of death, they are a significant correlate of death following hyperactivity.

It is the purpose of this experiment to extend these observations to include coho salmon, to further explore the signficance of death as related to hyperactivity, and to
examine the problem in both salt and freshwater environments. METHODS AND MATERIALS

Ocean Study

Fish were obtained aboard a commercial troller operating in the Gulf of Alaska in 1958. During July fishing was in the vicinity of the coast at Cross Sound (Lat. $58^{\circ} \mathrm{N}$ ) and in August in the vicinity of Middleton Island (Lat. $60^{\circ} \mathrm{N}$, Long. $147^{\circ}$ W). Either four or six lines were used (depending upon the distance off shore) and from eight to twelve lures per line. Lures were changed often and no general statement can be made of make and type. Hook size ranged from No. 6 to No. 8. Time, place and manner of fishing were at the discretion of the Captain.

Captured fish were lifted aboard by the lure and placed in a preliminary bath of sea water where the hook was carefully removed. Fish showing damage to vital parts or heavy bleeding were excluded from further consideration except to obtain blood samples from specimens without postexercise rest. All non-critically damaged fish were tagged at the origin of the dorsal fin, using standard Petersen type tags with $5 / 8$ inch red baffles and pure nickel pins.

Fish to be retained in captivity were transferred to a live box measuring 28 l/4 by $441 / 4$ inches ( $72 \times 112 \mathrm{~cm}$ )
inside horizontally and $231 / 2$ inches ( 60 cm ) between top and bottom. Access to the inside was through a 12 by 12 inch ( 30 cm square) chimney, eight inches ( 20 cm ) high and fitted with a removable cover. Water was introduced under pressure at the bottom and expelled through holes drilled in the top panel. The water level was approximately four inches ( 10 cm ) in the chimney, which prevented sloshing or surge in the main box. Two identical boxes were used, and each was supplied with fresh sea water at a rate of approximately ten U.S. gallons ( 39 litres) per minute. The top was fitted with a 12 by 12 inch plexiglass panel through which fish could be observed. A maximum of four fish or less than 40 pounds ( 18 kg ) of fish was held in a live box at any one time.

Fish which died in the live box were removed with a small gaff and a blood sample taken. Cessation of respiratory movement was used as a criterion of death. Fish were under more or less constant.observation and blood samples were obtained before rigor mortis. Survivors were liberated without taking a blood sample. To do this, the water supply to the live box was cut off and contents drawn down to approximately 50 U.S. gallons (190 litres). A sedative (Tricane methane sulfonate, MS222 Sandoz) was introduced into the water, and as soon as fish became disorientated they were removed by means of a polyethylene bucket and liberated. This method of release was unsatisfactory because (a) fish
were unable to orient themselves for some minutes until the effects of the sedative wore off and (b) fish in live boxes one-third full were subject to severe sloshing, depending upon the state of the sea (seldom smooth). With the equipment at hand, however, the alternative of subjecting them to chase and struggling in a dip net appeared to be even less satisfactory.

One millilitre or less of blood was drawn routinely from the caudal vein. In some instances samples were also drawn from the heart. Blood was drawn into a 2-ml Luer syringe coated with mineral oil and rinsed with heparin solution. The sample was immediately expelled into a polyethylene bottle containing 9 ml of $10 \%$ trichloracetic acid. This mixture was then filtered and the filtrate stored in a second polyethylene bottle until chemical analysis. These samples were taken to the laboratory at the University of British Columbia and analysed for lactic acid by the method of Barker and Summerson (Hawk, Oser and Summerson, 1949). Values of blood lactate are reported as milligrammes lactic acid per 100 millilitres of whole blood (mg\%) and expressed to three integers. The true value, as determined from analysis of several triplicated determinations, is considered to be within a range of plus or minus $10 \mathrm{mg} \%$.

Live box sea water was drawn from a depth of approxi-
mately 1.5 metres and was between $13^{\circ}$ and $15^{\circ} \mathrm{C}$. Fishing ranged over depths from 20 to 100 metres. Salmon were taken at all depths, but coho more frequently above a depth of 30 metres and in water ranging from $10^{\circ}$ upward, while chinook were more frequently below 30 metres and at $7-10^{\circ} \mathrm{C}$. Reliable temperature data could not be taken for individual fish and the significance of temperature changes cannot be evaluated.

Fish used were feeding coho and chinook. Coho were in their ultimate year but not showing sexual dimorphism typical of the species at maturity. Gonad examination showed signs of approaching maturity and tagging showed fairly rapid subsequent movement into inside waters. Chinook used were probably either in their ultimate or penultimate year of life.

Fish were disturbed as little as possible during the rest period: Design of the live boxes eliminated sloshing due to vessel motion, but vibration ffom the propulsion engine was present. When first placed in the live box, fish would generally swim about but quickly assumed and maintained a position. Some fish failed to maintain equilibrium and remained upside down either at the surface or bottom. This condition usually appeared after 15-30 minutes although a few individuals turned over when first placed in the live
box. Some fish righted themselves after varying amounts of rest, others failed entirely to do so. These observations are similar to those made by Brett et al.(1958) on fatigued juvenile sockeye and coho in freshwater, and by Parker and Black (1959) on sub-adult chinook in sea water.

An attempt was made to determine the amount of time each fish spent on the troll gear, but was largely unsuccessful, either because of failure to observe the strike or inability to discriminate between several fish caught on the same line. From the reliable data available, coho were on the gear for an approximate average of five minutes, and the time varied from less than two to more than 25 minutes. Coho were of a fairly uniform size, averaging eight pounds ( 3.6 kg ) and varying from six to ten pounds ( 2.7 to 4.5 kg ). Chinook used varied between eight and 20 pounds ( 3.6 to 9.1 kg )

## Freshwater Study

In September the live boxes and equipment were taken to the Canyon Island Research Station 17 miles above salt water on Taku River, Alaska. Upstream migrating adult coho were captured by a fish-wheel (Anon., 1953) and used as test animals. These fish were of the same size range as those used in the ocean study, were non-feeding, in an advanced stage of sexual dimorphism, and were in freshwater. The
live boxes were set up on the pontoons of the fish-wheel and river water pumped at approximately the same rate as in the previous experiment at sea. A pole was fixed to overhang the stream and standard troll gear with a 20 -pound ( 9.1 kg ) weight attached. This device was used to simulate the action of troll gear towed through the water. Stream velocity was approximately equivalent to trolling speed. Fish were dipnetted from holding tanks, a hook was inserted from inside the mouth through the membranes and tissue posterior to the maxillary, and the fish was then released into the river attached to the troll gear. After intervals from less than one and up to 30 minutes on the troll gear fish were landed by the lure and placed in a preliminary water bath containing sedative. Here the hook was removed, the fish tagged, and then placed in a live box. A maximum of six fish or 60 pounds ( 27 kg ) was placed in each box. Groups were anaesthetized and removed from the live boxes after post-exercise rest periods over a range of zero to 52 hours, and a blood sample was taken by caudal vein puncture. Sampled fish were further observed until recovery from the anaesthetic and then released into the river. A control group was dip-netted from the tanks directly into the sedative bath and sampled. Other aspects of the experiment were identical with the ocean study.

SUB-MATURE COHO IN SEA WATER

Comparison of Lactate of Blood of Heart and Caudal Vein

Blood was drawn from both the caudal vein and the heart of 11 coho to facilitate comparison between the present experiment and those of Black (1957c) and Parker and Black (1959). Three determinations were made on each sample and values of heart and caudal vein blood lactate compared. Table $X$ gives the results of the determinations. Caudal vein blood lactate levels were significantly lower than heart blood lactate levels in the seven fish sampled immediat.ely after catching ( $F=9.01$; d.f. 1,$6 ; 0.01>P>0.025$ ). In the four fish sampled after one to five hours of rest caudal levels were slightly higher than heart levels but differences were not significant ( $F=.2 .13$; d.f. 1, 3; 0.10〉P>0.25). Thus the degree of blood lactate response may appear greater in the coho than reported for sockeye and chinook, but the anomaly may be due to the anatomical sampling location.

## Blood Lactate Levels

Eleven coho were killed immediatley when landed to establish a post-exercise base level. One fish died in the live box in less than one-half hour and is included in the first group. Fish were held in live boxes up to 14 hours. During this time 48 additional fish died, 47 of which were sampled for blood. These are grouped into half-hour time

Table X. Repeated determinations of blood lactate levels from the caudal vein and heart of each of eleven coho caught by troll in salt water. Values in parentheses are dummy values for ease in computation.

periods including the time on the gear. Where this statistic is unknown (eight cases), average time spent on the gear is used ( 4.74 minute, $n=50$ ). Table XI gives average values and ranges for time and blood lactate values. These data are presented graphically in Figure 16. A typical delayed blood lactate response is depicted. Blood levels of lactate increased at least four-fold from pre-exercised levels. In this study lactate levels did not subside; however, these samples are from fish which died. Lactate in the blood of a single normal-appearing specimen deliberately killed in the fifth hour was $115 \mathrm{mg} \%$. While not by itself sufficient evidence, this relatively low value of blood lactate in a survivor is substantiated by previous work with chinook (Parker and Black, 1959).

## Mortality

During the course of the experiment 49 fish died. As 26 fish were released during the time periods when deaths occurred, the simple ratio, $49 / 115$, is not a valid estimate of mortality. Further, the problem of setting confidence limits is complicated by a decreasing sample size. Because the solution to this statistical problem has general applicability to a variety of similar problems it is presented in detail as an Appendix. The results, together with the original observations, are summarily presented in Table XII. Two points are of special interest. First, the highest rate of mortality

Table XI. Blood lactate levels of troll-caught coho salmon which died during post-exercise period.


[^3]Table XII. Mortality of coho salmon during post-exercise rest period.

| Time | Number of fish at start of time period <br> (n) | Number which died during time period <br> (y) | Number released during time period | Instantaneous mortality rate <br> (i) | Cumulat mort Point estimate Q | tive total ality Confidence interval $Q-\bar{Q}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| hours |  |  |  |  |  |  |
| 0-1 | 115 | 5 | 0 | 0.044 | 0.044 | 0.0060 .080 |
| 1-2 | 110 | 21 | 0 | 0.212 | 0.226 | 0.1460 .299 |
| 2-3 | 89 | 14 | 2 | 0.171 | 0.348 | 0.2550 .429 |
| 3-4 | 73 | 1 | 0 | 0.038 | 0.357 | 0.2630 .438 |
| 4-5 | 72 | 3 | 6 | 0.043 | 0.384 | 0.2880 .474 |
| $5-6$ | 63 | 4 | 7 | 0.066 | 0.423 | $0.330 \quad 0.507$ |
| 6-7 | 52 | 0 | 5 | 0 | do | do do |
| 7-8 | 47 | 0 | 6 | 0 | do | do do |
| 8-9 | 41 | 1 | 0 | 0.025 | 0.437 | 0.3360 .522 |
| 9-14 | 40 | 0 | 40 | 0 | 0.437 | 0.3360 .522 |
| Total |  | 49 | 66 |  |  |  |



Figure 16. Coho blood lactate (expressed as mg\% lactic acid) response in time from hooking. Open circles represent mean value for fish which died in salt water experiment. Dashed line drawn free-hand to indicate probable average. Solid circles represent mean value for fish in freshwater. Vertical lines through means indicate range of values.
took place in the second and third hours after hooking. Second, mortality was substantially complete (97\%) by the end of six hours.

## Recapture of Tagged Fish

If observed mortalities on troll caught salmon held in live tanks aboard the vessel are representative of mortality experienced by lots of fish released immediately after capture, then survivors of lots held past the mortality period should show a higher percentage recaptured than those released immediately. This hypothesis was explored by releasing 60 fish immediately after capture and 40 fish held nine hours or longer (Table XII). Recoveries were entirely from subsequent commercial fishing and while probably not completely reported at time of analysis (October, 1958) no substantial change can be expected. Twelve of the first group and seven of the second have been recaptured.

Comparison of the two ratios 60 to 12 and 40 to 7 requires certain precautions. The observed probability of recapture, $\hat{P}$, for the 60 fish released immediately after capture was $12 / 60=0.2000$. This probability is a product of the probability of surviving the hooking and tagging procedure and the "true" probability of recapture. The former can be estimated from the observed live box survival probability, $\hat{p}_{a}=0.5633$ (Appendix, Table B), i.e. of the 60 fish liber-
ate it is estimated that $0.5633 \times 60=33.8$ survived. The "true" probability of recapture $\hat{\mathrm{p}}_{\mathrm{bl}}$ is $12 / 33.8=0.3551$. The "true" probability of recapture for the second group $\hat{\mathrm{p}}_{\mathrm{b} 2}$ is simply $7 / 40=0.1750$. The ratio of 12 to 33.8 might be compared with the ratio of 7 to 40 by means of a chi-square test. However, this would involve only the assumption of sampling error and would ignore the variance associated with the estimate of survivors from the hooking and tagging procedure. To avoid this error the survival rates can be compared using a "t" test:

$$
t=\frac{\hat{p}_{\mathrm{b} 2}-\hat{p}_{\mathrm{b} 1}}{\left(\mathrm{~s}_{\overline{\mathrm{x}}_{\hat{p}_{\mathrm{b} 1}}}\right)^{2}+\left(\mathrm{s}_{\overline{\mathrm{x}}_{\hat{p}_{\mathrm{b}}}}\right)^{2}}
$$

The value $\mathrm{S}_{\overline{\mathrm{x}}_{\hat{p}_{b l}}}$ is given by combining the variance associated with $\hat{\mathrm{p}}_{\mathrm{a}}$ and the sampling variance of $\hat{\mathrm{p}}_{\mathrm{bl}}$. By the reasoning given in the Appendix this combined variance is given directly by the variance of the ratio 12 to 60 as estimated by the binomial theorem, $\mathrm{pq} / \mathrm{n}$. The value of $\mathrm{S}_{\overline{\mathrm{x}}_{\hat{p}_{\mathrm{b} 2}}}$ is given directly by the bionomial theorem.

The details of the particular test were therefore:

$$
t=\frac{0.3551-0.1750}{(0.00267+0.00361)^{1 / 2}}=2.28 ; \text { d.f. } 2,0.2<P<0.1
$$

The hypothesis that an improved tag recovery would result from releasing only survivors held in live boxes need not be rejected, but neither is it validated.

Although these data are homogeneous, many of the fish which recovered in the live boxes were disoriented for varying lengths of time and one might expect that fish which were released immediately would not only suffer the same mortality as those which were held but an additional mortality associated with disorientation, i.e. loss to predators. As stated in a previous section, there was reason to consider the releasing procedure unsatisfactory. Further studies are needed on proper techniques for testing the hypothesis.

## ADULT COHO IN FRESHWATER

This phase of the experiment was designed to test the significance of time spent on the gear in relation to levels attained by blood lactate and its associated mortality, and to compare these results for fish in freshwater which have undergone physiological changes of approaching maturity with those of fish feeding in the ocean. In this experiment it was possible to have relatively unexercised control fish which were not obtainable in the ocean study. Results are summarized in Table XIII.

Blood lactate increased from the control level two-

Table XIII. Blood lactate levels of coho salmon during post-exercise period in freshwater (exercise time, varying from less than one minute to 30 minutes, is included in the "post-exercise" period).

| Number of specimens | Time period |  |  | Lactic acid |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Average | Range |  | Average | Range |  |
|  | hours |  |  | mg\% |  |  |
| 25 | Control | (unexe | cised) | 20.20 | 8.2 | 37.5 |
| 27 | 0.427 | .05 | . 95 | 38.07 | 15.2 | 54.3 |
| 30 | 1.488 | 1.11 | 2.00 | 40.07 | 7.7 | 74.5 |
| 23 | 2.455 | 2.05 | 2.82 | 24.62 | 9.1 | 58.8 |
| 18 | 3.213 | 3.02 | 3.72 | 28.78 | 7.7 | 64.6 |
| 15 | 4.285 | 4.01 | 4.93 | 13.89 | 3.3 | 42.8 |
| 12 | 5.357 | 5.08 | 5.83 | 19.50 | 3.4 | 43.9 |
| 15 | 6.343 | 6.01 | 6.96 | 17.05 | 4.0 | 43.6 |
| 13 | 10.434 | 9.98 | 10.99 | 21.86 | 9.3 | 29.7 |
| 12 | 28 hours | and mo |  | 12.46 | 7.2 | 19.6 |

fold in the first two hours, then subsequently fell to a level below that of the controls in the fifth hour. This typical response is depicted in Figure 16 where it may be compared with the lactate response of coho in the ocean study. It is obvious that lactate concentrations at no time approached those of fish dying in the live boxes at sea. Equally apparent is the decrease in range of lactate values as fish were held for longer periods.

Multiple regression analysis was used to test the effect of time spent on the hook on the lactate response. Controls and fish held longer than five hours were excluded from the data; mean levels of blood lactate approximate a linear regression on time for the segment 0.05 to 5.0 hours of total time. The regression, in ordinary units, is:

$$
Y=43.855-6.297 X_{1}+2.396 x_{2}
$$

where $Y$ estimates the blood lactate level,
$X_{1}$ is the total time from start of exercise to sampling, $\mathrm{X}_{2}$ is the total time spent on hook.

The standard regression of $Y$ on $X_{1}$ independent of $X_{2}$ proved significant ( $t$ of $b_{Y l .2}=5.676$; d.f. 110; $P$ ( 0.01 ); however, the lactate response was not significantly influenced by the amount of time spent on the hook ( $t$ of $b_{Y 2.1}^{\prime}=0.269$; $P>0.5$ ). This observation is interpreted to mean that the initial struggle from hooking plus final struggle of unhooking
elicited maximum response of blood lactate that fish were capable of producing.

Blood lactate levels from 0.05 to 0.5 hours were tested against the control group by analysis of variance and found significantly higher ( $F=14.87$; d.f. 1,$39 ; P$ ( 0.01 ). Similar treatment shows blood lactate was significantly lower in fish held 28 hours or more than in the control group ( $F=$ 7.38; d.f. 1,$36 ; P(0.01)$. Thus the control group reflected blood lactate present from either work done in swimming against the river current or in initial excitement in the fish-wheel holding tanks.

While exposed to treatment similar to the salt water group, fish in these experiments did not respond with the same degree of violence on the gear. They appeared to be content to swim the same speed as the current and made few rushes against the gear. When landed they struggled less violently than their salt water counterparts. This was reflected in the blood lactate levels which in no case increased above $77.5 \mathrm{mg} \%$. Further, not one fish died during the experiment. The type of blood lactate response was the same for both groups, but the degree of response was much less for the freshwater group.

OCEAN CHINOOK

Secondat and Diaz (1942) followed the rise and fall of blood lactate of tench by taking three consecutive samples of blood from each fish; the first immediately after exercise, the second at two hours, and the third at six hours. Cardiac puncture was used. Subsequent workers have taken blood samples only from stunned, killed, or dying fish (Black, 1955, 1957a,b,c; Nakatani, 1957; Parker and Black, 1959), and from these data it has been deduced that blood lactate level of survivors has at first risen and then declined. While there is little doubt of the type of response, actual evidence that blood lactate has been at concentrations equal to those of fish which died is lacking. To examine this question 25 chinook salmon were landed and for 16 of them series of blood samples were taken by caudal vein puncture during the postexercise period. Individuals were tested from two .to nine times, depending upon their survival. Repeated handling undoubtedly contributed to fatigue and excessive mortality, hence this lot cannot be compared with other studies.

The results are summarized in Table XIV. Thirteen of the fish died, reflecting excessive handling. Two were considered very lively after three hours and were sampled and killed. Only one specimen survived repeated sampling and provided both a measure of high blood lactate three hours

Table XIV. Blood lactate ( $\mathrm{mg} \%$ ) of 16 troll-caught ocean chinook which were sampled. more than once.


[^4]after exercise and low blood lactate almost 14 hours after hooking. The serial samples confirm that death was associated with the attainment of high blood lactate concentration but indicate a wide range of variability in individuals. "In 10 of the 13 cases, death occurred when blood lactate exceeded $200 \mathrm{mg} \%$ and in two cases when it reached $174 \mathrm{mg} \%$. In contrast, the two specimens that were lively after three hours of rest showed blood lactate of over $260 \mathrm{mg} \%$ and blood lactate concentration of the survivor was at the same time $187 \mathrm{mg} \%$. These observations demonstrate the variability among fish in the association between death and high blood lactate concentration following hyperactivity.

## SUMMMARY OF RESULTS

1. Troll-caught coho showed a typical delayed blood lactate response after hooking.
2. Blood lactate levels of coho feeding in the ocean increased at least four-fold from pre-exercised levels in two hours.
3. For coho which died in the live box no significant decline in blood lactate level was evident.
4. Mortality was estimated to lie in the range 0.336 to 0.522 at the 95 percent level of confidence. The empirical estimate is 0.437 .
5. The mortality rate of coho reached a maximum in the second hour and then declined.
6. Mortality was substantially complete (97\%) by the end of six. hours.
7. The recapture of tagged fish was not shown to be erhanced by holding in live boxes past the period of mortality.
8. A typical delayed blood lactate response to exercise was obtained for non-feeding adult coho in freshwater.
9. Degree of lactate response in freshwater was much less than in (2) above.
10. No deaths occurred among fish tested in freshwater.
11. It was noted (but not measured) that fish did not struggle as violently in freshwater as in salt water.
12. For ocean-caught chinook salmon which died, blood lactate was shown to have increased until death; while for a single survivor blood lactate reached a peak of $187 \mathrm{mg} \%$ at approximately the third hour and subsequently subsided to $103 \mathrm{mg} \%$ in the 14th hour.

## DISCUSSION

The fact that blood lactate levels of coho increased following exertion on troll gear needs little discussion. Black (1957a:) has described adequately the typical delayed response and this has been subsequently confirmed for several salmonids by Black (1957b, c) and Parker and Black (1959). Blood lactate levels of other Pacific salmon which died following hyperactivity were higher than blood lactate levels
obtained from comparable living fish. The present study has confirmed this relationship for an additional species, the coho.

The fact that apparently uninjured fish died is not surprising. It is well known that severe muscular exertion may result in death of seteral species of animals. As early as 1938 Huntsman suggested that mortality in fish might result from severe muscular exertion. Subsequently several authors have reported instances of this occurring as outlined in the introduction to this section and reviewed by Black (1958b). That significant numbers of troll-caught salmon have died in post-exercise captivity has been reported several times. These observations are compared in Table XV. In each case significant mortality of fish captured by trolling occurred while being held aboard the fishing vessel in live tanks.

These experiments must be compared with caution. That of Milne and Ball(1956) includes only fish judged to be uninjured and fit for tagging, as were fish used by Fry (Fry and Hughes, 1951), by Parker and Black (1959), and in the present experiment. It is not known if such grading occurred in Milne and Ball's (1958) second experiment. Fry's experiments were carried past the term of maximum mortality rate, as were Parker and Black's and the present one. Milne and

Table XV. Comparison of delayed mortality observations on troll-caught salmon.

| Investigators | Species | $\begin{aligned} & \text { Number } \\ & \text { in } \\ & \text { sample } \end{aligned}$ | Reported mortality estimate | Total <br> time <br> observed | ```0.95 binomial confidence interval``` |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | \% | hours | \% |
| Milne and Ball (1954) | Coho | 55 | 20 | 1-6 | 10-30 |
| Milne and Ball (1958) | Coho | 289 | 18 | $1+$ | 13:-22 |
| " " . 1 | Chinook | 91 | 20 | $1+$ | 12-28 |
| Fry (1958) | Coho | 88 | 38 | 16-24 | 28-47 |
| " $\quad 1$ | Chinook | 96 | 44 | 16-24 | 34-54 |
| Parker and Black (1959) | Chinook | 66 | 71 | 8 | 40-86 |
| Present experiment | Coho | 115 | 44 | 8 | $34-52$ |

Ball liberated some fish prior to or during this period, either into a live pond or into the sea. All the experiments agree in the use of submature feeding fish in salt water. All investigators report that mortality is delayed and substantially complete within six hours.

Mortality rate is closely correlated with blood lactate level. In Parker and Black's experiments with chinook and in the present experiment with coho the rate of mortality (i) is relatively low in the first hour, increases to a maximum in the second or third hour and becomes negligible by the end of six hours (Table XII). This is the same type of delayed response described for blood lactate. Further, with a single exception in each of the above experiments, no fish died in which blood lactate levels were less than 125 mg \% (see Figure 16; :also Parker and Black, 1959, Appendix). This also true of Black's (1957c) sockeye experiment. Blood lactate levels above $125 \mathrm{mg} \%$ may, then, be considered as a danger zone for three species of Pacific salmon. This is not to say that when blood lactate levels rise above this point death will follow; rather, deaith may follow.

Several experimenters have subjected salmonids to hyperactivity but observed no ensuing mortality. Paulik DeLacy and Stacy (1957) repeatedly subjected coho, and

Paulik and DeLacy (1958) sockeye, to severe fatigue. Many of their test animals became so severely fatigued that equilibrium was lost, yet no significant mortality followed. In these experiments maturing adult fish were used in freshwater. Black (1957a,b) subjected rainbow trout and lake trout to hyperactivity without ensuing mortality. He noted a blood lactate response well above $125 \mathrm{mg} \%$ in these experiments. Jensen (1958) caught and released two and three-year-old chinook salmon reared in salt water ponds. These fish were not fed six days prior to the experiment. Fish actively fought the lure for one to two minutes and were then easily netted and released. A small mortality of 2.0 percent occurred during the first week following treatment.

In the freshwater experiment, adult coho were treated in a manner essentially the same as fish on the troll gear. Lactate response was significant and typical. Quantitatively it was much less than for the feeding, submature coho in the sea. Further, from subjective observations, fish ceased to struggle after less expenditure of effort than their salt water counterparts. Most significant: no deaths occurred. These observations appear to exclude psychosis from close confinement, hook injury, abrasion of the mucous coat, etc. as primary factors of death. Death appears to be a condition brought about by severe fatigue of fish in a particular physiological state.

A greater recovery of tags was not realized by Fry and Hughes (1951) when only survivors held past the critical mortality period were released. These authors report a 1.63 percent recovery of tags from 123 chinook held overnight in live tanks after catching. A control group of 179 chinook gave 18 percent tag recovery. It is perhaps significant that tagging occurred at release, i.e. the survivors in the tanks were subjected to additional stresses of capture, tagging, and releasing after the recovery period, while the controls were tagged and released after capture, at a time when further handling could have had little effect in producing fatigue.

Milne and Ball (1958) obtained 27 percent recovery of 118 coho, tagged at capture, and held not less than one hour. In their earlier experiment (1956) 32 percent of 28 tagged coho were subsequently recovered after being held in a floating live pond for more than 30 days. While no control lots were liberated, these recovery rates are much higher than previously reported experiments on troll tagging (Milne, 1957).

In the present experiment fish were tagged when captured and survivors released and compared with a control group. Recoveries have suggested less chance of survival for experimental fish than controls, and as in the case of Fry and Hughes (1951), the treatment during liberation is
suspect. Survival from original fatigue is not the only consideration in these cases. A disoriented fish is easy prey to predators known to be present in the surface waters, i.e. mackerel shark (Isurus nasus) and northern sea lions (Eumetopias jubata). Further research is indicated along these lines. At present it is not possible to state methods by which mortality can be avoided; it can, however, be measured. It is suggested that fatigue is an indiscriminate stress acting in either a lethal manner or in an impairing manner (Brett, 1958) until full return to normal is achieved.

The mechanisms responsible for the differing susceptibility of salmon to effects of exercise in fresh and salt water may find explanation in the following arguments:

Most fish are chronically in oxygen distress because of low solubility of oxygen in water ( く $10 \mathrm{mg} / \mathrm{l}$ for sea water in most cases, Sverdrup et al., 1942 , and 〈 $15 \mathrm{mg} / \mathrm{l}$ for freshwater in most cases, Welch, 1935). The active rate of oxygen uptake is restricted to a few multiples of the standard rate, i.e. approximately four-fold (F.E.J.Fry, 1957). As in air-breathing animals, energy for activity in excess of the active rate (F.E.J.Fry, 1957) must be derived anaerobically, mainly by glycolysis. Job (1954) reported oxygen consumption at near the active rate for digestion of food alone, which indicates that further activity in a
glutted stage of feeding must be done anaerobically. The production of lactic acid and its diffusion into the blood must be considered as a regular physiological process for even moderate activity, and activity must be followed by rest. Loss of circulatory blood volume may result from severe muscular activity (Bainbridge, 1931). Black (1955) found a significant increase in blood hemoglobin following severe exercise in largemouth bass (Micropterus salmoides), and postulated an osmotic shift of water from the blood to the tissues in respose to a greatly increased number of osmotically active particles present from hydrolysis of the large glycogen molecule. It is, of course, possible that increased blood hemoglobin results from introduction of stored erythrocytes into the circulating blood. If there is a significant increase in osmotically active particles within the muscle cells, it is possible that, in some situations, so much water may be drawn from the effective circulating blood that circulatory shock may ensue. Further, upon diffusion of hydrogen ions and (or) lactate ions into the blood, the blood fluid may become severly hypertonic to the erythrocytes which may explain the observations of von Buddenbrock (1938) that the red blood cells appeared to be collapsed and misshapen when blood lactate levels were high. This condition could further aggravate the situation by reducing oxygen transport ability of the circulating blood. Fish insea water obtain water from either oxidation of food or by drinking sea water
and excreting the salts, a process which involves cellular work (see V.S.Black, 1957). Thus an osmotic imbalance caused by excessive production of lactate ions could lead to a distressed condition of suffocation.

Sub-adult Pacific salmon, susceptible to trolling, are in a feeding stage. Large quantities of food are consumed, fat is being stored and protein synthesized. Carbohydrate, available as liver glycogen, blood glucose, and muscle glycogen, is readily available for quick energy (unpublished observations of E.C.Black). As maturity is approached these fish cease feeding and enter freshwater. Energy for ascending streams and for the spawning act is available only through use of stored fat and catabolism of non-essential protein (Green, 1926; Hoar, 1957; Black, 1958a). This material is not available for rapid consumption and thus the rate of supply can restrict the action of the fish in its response to stimuli. If feeding fish are starved for periods prior to exercise, the above mentioned sources of fat and protein must be drawn upon for energy. Thus, coho salmon did not struggle as violently in freshwater, not because of any basic difference in stimulus-response reaction, but because of limited stores or readily available evergy. Jensen's experiment is consistent with this hypothesis. His fish were not fed for six days prior to the test. In addition they may have been considerably adapted to handling. From these argu-
ments, the lack of mortality following hyperactivity of fish in freshwater may be explained as well as giving a mechanism for death following hyperactivity of feeding salmon in sea water.

It would appear that cessation of feeding by Pacific salmon, coincident with approaching maturity and entrance into freshwater, may have contributed significantly to the ability of the fish to migrate extensive distances upstream. If large amounts of muscle glycogen were available there would be no check on the rate of energy expenditure and at rapids or other obstructions salmon might become disoriented from sustaineđ severe activity. The slower mobilization of stored fats and non-essential proteins may act as an effective "meer", preventing disorientation following fatigue, a condition which might lead to passive displacement downstream, thus net loss and needless expenditure of energy. Lack of feeding is thus viewed as a protective mechanism of survival value for Pacific salmon.

## CONCLUSIONS

1. Chinook and coho salmon caught by trolling undergo hyperactivity.
2. This often leads to a distressed condition which is delayed and the severity of which cannot be predicted for any individual at the time of capture.
3. The distressed condition may advance beyond the ability to respond to stimuli or to recover orientation, and
terminate in death.
4. Death resulting from capture by troll has been observed to be of significant magnitude. For coho, mortality lies between 34 percent and 52 percent; for chinook, between 40 and 86 percent.
5. Mortality rate and blood lactate levels are closely correlated in relation to post-exercise time.
6. For fish which died, blood lactate rose until death. Survival occurred either when blood lactate did not reach critical levels (above $125 \mathrm{mg} \%$ ) or reached a critical level and then subsided.
7. No remedy is suggested for delayed mortality from fatigue of troll caught salmon. It is important that it be assessed in tagging programs.
8. Holding salmon for tagging past the period of mortality did not improve tag recovery. It is suggested that the manner of releasing is responsible for additional indiscriminant stress acting in both a lethal and impairing manner.
9. This observation suggests that the largest number of returns can be gained by tagging all fish available and releasing immediately. Subsequent mortality can be assessed by holding lots on board.
10. Adult coho salmon did not appear susceptible to fatigue to a lethal degree in freshwater. This has been postu-
lated as due to cessation of feeding and to have adaptive significance for survival.

## E. THE VALIDITY OF SIZE RESTRICTIONS FOR A STOCK OF CHINOOK

It has been shown that significant mortality ascribable fo hyperactivity results from catching and releasing chinook salmon. Additional mortality from direct injury has been recorded (Parker and Kirkness, 1956 and subsequent observations) amounting to approximately 20 percent. Milne and Ball (1956) report total mortality from coho salmon hooked in the gills, and 50 percent from fish hooked in the eye (through the roof of the mouth). They further report 12 of 67 or 18 percent of the fish caught were either drowned or so severely hooked that they were nearly dead and unfit for tagging.

These observations may be combined with delayed mortality observations into a single instantaneous rate. The instantaneous rate from physical injury is estimated by: $0.2=1-e^{-0.223}$. The delayed mortality rate from hooking and releasing lies between the limits:

$$
0.40=1-e^{-0.512} \text { and } 0.86=1-e^{-1.966} \text { while the empiri- }
$$

cally observed estimate is: $0.71=1-e^{-1.236}$. The total instantaneous rate of mortality ascribable to catching and releasing lies within the limits 0.735 and 2.189. When in-
stantaneous natural mortality is added ( $0.36-0.51$ ) the most optimistic expectation of mortality for the first year after release is an instantaneous rate in excess of 1.0 and the rate may be as high as 2.5. This zone of total instantaneous mortality in relation to size specific growth rate curves from Figure 15 is graphically presented in Figure 17. Ignoring any production lost from the $0 / 2$ group of fish, a size limit of not more than 22.5 inches and probably much less (approximately 15.0 inches for a mean value) could be justified as a restriction to increase the yield in pounds from the stock.

Other advantages may perhaps accrue from a size restriction such as increased spawning escapement, production of a larger size (hence a more valuable product ${ }^{6}$ ) and the avoidance of undersized stocks by the fishermen. The relationship between escapement and return for chinook is not known at present and possible advantages from increased spawning cannot therefore be evaluated. It is certain, however, that the size limit ( 25.0 inches) applied to mature segments of the stock results in increased escapement of the male fraction only (Anon. et al. 1951). The increase in value with increase in size has not been analyzed, but is simply listed as a possible benefit. The avoidance of ac-

[^5]

Figure 17. Length-specific average annual instantaneous growth (weight) rates of life history groups of chinook salmon compared with zone of "size limit mortality".
cumulations of undersized fish by the fishermen has not been generally investigated. The degree to which a size limit will influence such avoidance would depend upon the numbers of legal fish contained in the stock. This fraction would be dynamic and hardly susceptible to a generalized statement.

There remains the possibility that natural mortality rate may increase as the mature segment of the stock becomes increasingly concentrated along migration routes, in channels, and in estuaries. Again, no data appear to be published on this question, hence no evaluation of this effect on the critical size problem can be made. If an increase in natural mortality rate were true, a critical size might be reached at an immature stage, thus indicating the need of a fishery on the immature stock. These remain problems for future research.

With the information now available, the following general conclusions may be put foreward as means of increasing the yield in pounds from the stock of chinook, anticipating no net increase in fishing intensity:
(1) Fishing should be restricted to the maturing stock. This may be accomplished by restricting the area and time of fishing.
(2) Under conditions of (I) above, size limits should be abolished and the use of non-selective gear encouraged.
(3) If fishing is to be permitted on the immature stocks, an increase in yield cannot be expected from a size
limit restriction. A type of gear might be found which is selective for larger fish; however, this would sacrifice the yield possible from the shorter life history types.

## F. GENERAL SUNMARY

The peculiar life history of chinook salmon necessitates consideration of a critical size for each life history type if maximum yield in pounds is held as a desirable objective of management. The essential elements of critical size are growth and natural mortality rates. A concept of growth is proposed in which growth rate is taken to be a product of both physiological and environmental opportunity and analogous to other physiological rates which may be described as proportional to the weight raised to some power. The mathematical result of this concept depicts instantaneous relative growth rate in weight as a declining function of increasing length. Natural mortality rate was assumed to be constant and the general magnitude was computed from tagging and recovery data. The combination of these two rates clearly establishes that, for each life history sub-group of any particular year class, growth in pounds of stock continues until the ultimate year (maturity). Biologically, fishing should be prohibited on the immature accumulations and nonselective fishing for all size groups of the mature elements should be encouraged.

The present practice of fishing on immature stocks, but limiting the retention of fish to those over 25.0 inches, might have justification if no mortality resulted from catching and releasing fish below the legal limit. Observations have shown that approximately 20 percent of small fish taken by troll are so injured as to produce complete mortality. Further observations, on apparently uninjured fish, have demonstrated a delayed mortality of between 40 percent and 86 percent and correlated with the degree of fatigue as measured by blood lactate. This delayed fatigue mortality was studied further with coho salmon and it was found to be serious only in sub-adult feeding fish. Mature fish, after cessation of feeding and entrance into freshwater, were not susceptible to fatigue to the same degree and no deaths ensued from the experimental treatment. This is not to say that other unevaluated effects did not result from the treatment; these were beyond the scope of the present study.

Three general recommendations are proposed:

1. Fishing be restricted to the mature segments of the stock. 2. The capture of all size elements should be encouraged, i.e. fishing made non-selective to size.
2. If fishing is allowed on immature accumulations, size limits will decrease the yield in pounds and should, therefore, be abandonèd.

Further need for research is indicated in each phase
of the problem studied. The major fields which appear profitable are as follows:

1. The relationship between growth rate and metabolic rate in respect to size. It may be possible to establish certain parameters of the growth equation by independent determination of size specific $\mathrm{O}_{2}$ uptake under standard conditions.
2. Further study of the fatigue mortality problem with a view to establishing remedial action. This would do much to aid the study of population structure by taggin and releasing members of the population.
3. The study of population structures with a view to establishing the relative abundance of life history types of each year class in the immature population. From this knowledge a model could be constructed to give details in gains or losses accruing from management restrictions.
4. Implied in (3) above, further experiments to determine the magnitude and stability of natural mortality should be implimented.

## REFERENCES

ADOLPH, E.F. 1949. Quantitative relations in the physiological constitutions of mammals. Science, 109: 579-585.

AL HUSSAINI, A.H. 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits. Anatomy and histology. quart. J. Microscop. Sci., 90: 109-139.

ATM, Gunner. 1949. Influence of heredity and environment on various forms of trout. Inst. Freshwater Res., Drottningholm, Report No. 29: 29-34.

ALLEN, K. Radway. 1953. A method for computing the optimum size-limit for a fishery. Nature, No. 4370, p.210.

ALIEN, K. Radway. 1954. Factors affecting the efficiency of restrictive regulations. I. Size limits. New Zealand J. Sci. and Mech. Sect. B. 35(6): 498-529.

ANON. 1951. Annual report of the Alaska Department of Fisheries. Rept. No. 3. Biological Investigations, pp. 20-42.

ANON. 1953. Annual report of the Alaska. Department of Fisheries. Report No. 5, Taku River Investigation, pp. 22-41.

ANON. 1958. Report of the International North Pacific Fisheries Commission for the year 1957. III. The research program. pp.-23-86.

BATES, Daniel W. and Russell VINSONHALER. 1957. Use of louvers for guiding fish. Trans. Am. Fish. Soc., 86: 38-57.

BAINBRIDGE, F.A. 1931. The physiology of muscular exercise. Third Edition, rewritten by A.V.BOCK and D.B.DILL. Longmans, Green and Co. Ltd., London. 272pp.
von BERTALANFFY, Ludwig. 1938. A quantitative theory of organic growth. (inquires on growth laws, II) Human Biology, $10(2): 181-213$.
von BERTALANFFY, Ludwig. 1949. Problems of organic growth, Nature, 163: 156-58.
von BERTALANFFY, Ludwig. 1950. An outline of General System Theory. Britt. J. Philo. Sci.; 1(2): 134-165.
von BERTALANFFY, Ludwig. 1951. General System Theory: A new approach to unity of science. I. Problems of general system theory: Human Biol., 23: :302-312.
von BERTALANFFY, Iudwig. 1957. Quantitative laws in metabolism and growth. Quart. Rev. Biol., 32(3): 217-231.
von BERTALANFFY, Ludwig, and R.R.ESTWICK. 1953. Tissue respiration of musculature in relation to body size. Am. J. Physiol., 173(1): 50-60.
von BERTALANFFY, Ludwig and R.R.ESTWICK. 1954. Tissue respiration in experimental and congenital pituitary deficiency. Ibid., 177(1): 16-18.

Von BERTALANFFY, Ludwig and W.J.PIROZYNSKI. 1953. Tissue respiration, growth and basal metabolism. Biol. Bull. 105(2): 240-256.

BEVERTON, R.J.H. and S.J.HOLT. 1957. On the dynamics of exploited fish populations. Min. Agr. Fish. and Food, G.B., Fisheries Investigations. Ser. II. 29:- $1-533$.

BliACK, Edgar.C. 1955. Blood levels of hemoglobin and 'lactic acid in some freshwater fishes following exercise. J. Fish. Res. Bd. Canada. 12(6): 917-929.

BLACK, Edgar C. 1957a. Alterations in the blood level of lactic acid in certain Salmonid fishes following muscular activity. I! Kamloops trout, Salmo gairdneri. Ibid., $14(2): 117-134$.

BLACK, Edgar C. 1957b. Alterations in the blood level of lactic acid in certain Salmonid fishes following muscular activity. II. Lake trout, Salvelinus namaycush. Ibid., 14(4): 645-649.

BLACK, Edgar C. 1957c. Alterations in the blood level of lactic acid in certain Salmonid fishes following muscular activity. III. Sockeye salmon, Oncorhynchus nerka. Ibid., 14(6): 807-814.

BIACK, Edgar C. 1958a. Energy stores and metabolism in relation to muscular activity of fishes. - In The Investigation of Fish-Power Problems (Ed. by P.A.IAREIN), pp. 5I-67. University of British Columbia, Canada.

BLACK, Edgar C. 1958b. Hyperactivity as a lethal factor in fish. J. Fish. Res. Bd. Canada, 15(4): 573-586.

BLACK, Virginia Safford. 1957. Excretion and osmoregulation. In The Physiology of Fishes. (Ed. by Margaret E. BROWN). Academic Press, N.Y., pp. 163-205.

BRETT, J.R. 1958. Implications and assessments of environmental stress. In The Investigation of Fish-Power Problems (Ed. by P.A.IARKIN), pp. 69-83. University of British Columbia, Canada.

BRETT, J.R., M.HOLMES and D.F.ALDERDICE. 1958. The effect of temperature "on the cruising speed of young sockeye and coho salmon. J.Fish. Res. Bd. Canada, 15(4): 587-605.

BRODY, Samuel. 1927. Growth and development with special reference to domestic animals. III. Growth rates, their evaluation and significance. Missouri Agr. Exp. Sta. Res. Bull., No. 97, 70 pp.

BRODY, Samuel. 1937. Relativity of physiologic time and physiologic weight. Growth, 1(3): 60-67.

BRODY, Samuel. 1945. Bioenergetics and growth with special reference to the efficiency complex in domestic animals. Reinhold, N.Y. 1023 pp.

BROWN, Margaret E. 1946. The growth of brown trout (Salmo trutta). I. Factors influencing the growth of trout fry. J. EXP. Biol., 22: 118-129.
von BUDDENBROCK, W. 1938. Beobachtungen ueber das Sterbengefangener Seefische und ueber den Milchsaueregehalt des Fischblutes. Rapp. et Proc.-Verb., Cons. Inter. Explor. Mer., $101(I V / 2): 3-7$

CALHOUN, A.J., D.H.FRY, Jr. and E.P.HUGHES. 1951. Plastic deterioration and metal corrosion in Petersen disk fish tags. California Fish and Game, 37(3): 301-314.

COHN, E.A. and H.A.MURRAY. 1927. Physiological ontogeny. 1. The present status of the problem. Quart. Rev. Biol., 2: 469-493.

CROXTON, Frederick E. and Dudley J.COWDEN. 1946. Applied general statistics. (13th printing). Prentice Hall, N. Y. 944 pp .

DEMING, W.E. 1943. Statistical adjustment of data. John Wiley and Son. 261 pp.

ELSON, P.F. 195?. The importance of size in the change from parr to smolt in Atlantic salmon. Canadian Fish Cult., No. 21: 1-6.

FRASER, C. McLean. 1917. On the scales of the spring sâlmon. Cont. to Canadian Biol. 1915-16: 21-28.

FRY, D.H. 1958. Official correspondence, Cal. Dept. Fish and Game, Oct. 14, 1958.

FRY, D.H. and Eldon P.HUGHES. 1951. The California salmon troll fishery. Pac. Mar. Fish. Comm. Bull., 2: 7-42.

FRY, F.E.J. 1957. The aquatic repiration of fish. In The Physiology of Fishes. (Ed. by Margaret E.BROWN), Academic Press, N.Y., Vol. I, Chapter I: 1-63.

GERKING, Shelby D. 1957. Evidence of aging in natural populations. Gerontologia, 1: 287-305.

GRAY, J. ${ }^{\text {J }}$ 1929. 248 The kinetics of growth. J. Exp. Biol.,
GREEN, Chas. W. 1926. The physiology of the spawning migration. Physiol. Rev., 6(2): 201-241.

HAWK, Philip B., L.OSSER and William H.SUNMERSON. 1949. Practical physiological chemistry, 12th Ed. The Blakiston Company, Philadelphia, 1323 pp.

HIATP, Robert W. 1947., Food chains and the feeding cycle in Hawaiian fish ponds. Part I. The food and feeding habits of mullet (Mugil cephalus), milk fish (Chanos chanos) and the tenpounder (Elops machnata). Trans. Am. Fish. Soc., 74: 250-61.

HOAR, W.S. 1939. The thyroid gland of the Atlantic salmon. J. Morph., 65(2): 267-290.

HOAR, W.S. 1957. Endocrine organs. In The Physiology of Fishes. (Ed. Margaret 'E.BROWN), Academic Press, N.Y., Vol. I, Chapt. VI: 245-285.

HOAR, William S. 1957. The gonads and reproduction. In The Physiology of Fishes. Ibid., Vol. I, Chapter VII: 287-321.

HOAR, W.S. and G.M.BELL. 1950. The thyroid gland in relation to the seaward migration of Pacific salmon. Canadian J. Res. D., 28: 126-136.

HUNTSMAN, A.G. 1938. Overexertion as a cause of death of captured fish. Science, 87(2269): 577-578.

JENSEN, Hans M. 1958. Preliminary report on hooking mortality study conducted at Bowman's Bay from March 10-April 9, 1958. Wash. Dept. Fisheries, Seattle. Mimeo. 3 pp.

JOB, S.V. 1954. Oxygen consumption of the speckled trout (Salvelinus fontinalis). Ph.D. Thesis, University of Toronto Library. M.S. (Not consulted, summary given by FRY, F.E.J. 1957).

JOB, S.V. 1955. The oxygen consumption of Salvelinus fontinalis. Univ. Toronto Studies, Biol. Ser.; No. 61. Pub. Ontario Fish. Res. Lab, 73: 1-39.
KALLEBERG, Harry. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar I. and S. trutta I.). Inst. Freshw. Res., Drottingholm. . Report No. 39: 55-98.

KAUFFMAN, Donald E. 1951. Research report on the Washingtion State offshore troll fishery. Pac. Mar. Fish. Comm. Bull. 2, pp. 77-91.
KLUST, Gerhard. 1939. Uber Entwicklung, Bau und Funktion des Darmes beim Karpfen (Cyprinus carpio I.). Int. Rev. d. gesam. Hydrobiol. u. Hydrograph. 39: 498-536.
KLUST, Gerhard. 1940. Uber Entwicklung, Bau und Funktion des Darmes beim Karpfen (Cyprinus carpio). Ibid. 40: 88-173.

LARKIN, P.A., J.G.TERPENNING and R.R.PARKER. 1957. Size as a determinant of growth rate in rainbow trout Salmo gairdneri. Trans. Am. Fish. Soc., 86: 84-96.

LEE, Rosa M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Min. Agr. and Fish., Loñon. Ser. II, 4(2): (microfilm).

MAHER, F.P. and P.A.LARKIN. 1955. Life history of the steelhead trout of the Chilliwack River, British Columbia. Trans. Am. Fish. Soc., 84: 27-38.

MARTIN, W.R. 1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Stud., Biol. Ser. No. 58. Pub. Ontario Fish. Res. Lab., 70: 1-72.

MILNE, D.J. 1957. Recent British Columbia spring and coho salmon tagging experiments, and a comparison with those conducted from 1925 to 1930. Fish. Res. Bd. Canada Bull. No. $113,56 \mathrm{pp}$.

MILNE, D.J. and E.A.R.BALL. 1956. The mortality of small salmon when caught by trolling and tagged or released untagged. Fish. Res. Bd. Canada. Pacific Progress Rept. No. 106: 10-13.

MILNE, D.J. and E.A.R.BALI. 1958. The tagging of spring and coho salmon in the Strait of Georgia in 1956. Ibid. No. 111: 14-18.

MINOT, Charles Sedgewick. 1891. Senescence and Rejuvenation. J. Physiol. 12: 96-153.

MILSEN, Hans. 1941. Der Phasenwechsel des Rheinlachses (Salmo salar L.) unter besonderer Berucksichtigung des \#rndhrungsapparates: Rev. Suisse de Zool. Geneve. 48: supp. p.181.

MOTTLEY, C. MCC. 1942. The use of the scales of the rainbow trout (Salmo gairdneri) to make direct comparisons of growth. Trans. Am. Fish. Soc. 71, pp. 74-79.

NAKATANI, Roy E. 1957. Changes in the inorganic phosphate and lactate levels in blood plasma and muscle tissue of adult steelhead trout after strenuous exercise. $\quad$ Univ. of Washington, School of Fisheries, Tech. Rept., No. 30, 14pp.

NEAVE, Ferris. 1951. Observations on troll-caught salmon of the west coast of Vancouver Island, 1949. Pac. Mar. Fish. Comm. Bull. 2: 94-101.

NEWMAN, Murray A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29(1): 64-81.

PARKER, Robert R. and Walter KIRKNESS. 1956. King salmon and the ocean troll fishery of Southeastern Alaska. Alaska Dept. Fish. Res. Rept., No. 1, 64 pp.

PARKER, Robert R. and Edgar C.BLACK. 1959. Muscular fatigue and mortality in troll caught chinook salmon (oncorhynchus tshawytscha). J. Fish. Res. Bd. Canada; 16(1): 95-106.

PARRY, Gwyneth. 1958. Size and osmoregulation in salmonid fishes. Nature, 181(4617): 1218-1219.

PAULIK, Gerald J. and Allan C.DeLACY. 1958. Changes in the swimming ability of Columbia River sockeye salmon during upstream migration. Univ. of Washington College of Fisheries, Tech. Rept., No. 46, 67 pp .

PAULIK, Gerald J., Allan C. DeLACY and Edwin F. STACY. 1957. The effect of rest on the swimming performance of fatigued adult silver salmon. Univ. of Washington School of Fisheries, Tech. Rept. No. $31,24 \mathrm{pp}$.

PIROZYNSKI, W.J. and Ludwig von BERTALANFFY. 1951. Is the rate of basal metabolism determined by tissue respiration? Proc. Canadian Physiol. Soc. 15th Ann. Meet. pp. 37-38.

PRICE, John W. 1931. Growth and gill development in the small-mouthed black bass, Micropterus dolomieu, Lacepede. Ohio State Univ., Franz Theodore Stone Laboratory, Cont. No. 4,46 pp.

PROSSER, C. Ladd (Editor). 1952. Comparative animal physiologザ. W.B.Saunders, Philadelphia, 888 'pp.
PÜTTER, August. 1920. Studien Hber physiologische Ähnlichkeit. VI. Wachtumsthnlichkeiten. Pflugers Arch. f.d. ges. Physiol., 180: 298-340.

RICH, Willis H. 1925. Growth and degree of maturity of chinook salmon in the ocean. U.S. Bur. Fish., Doc. No. 974, ${ }^{\prime 2}$ pp. 15-90.

RICKER, William E. 1948. Methods of estimating vital statistics of fish populations. Indiana University Publications, Science Series No. 15, 101 pp.

RICKER, W.E. 1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia. 1945(2): 84-94.

RICKER, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada No. 119, 300 pp.

ROBERTSON, O.H. 1957. Survival of precociously mature king salmon male parr (Oncorhynchus tshawytscha juv.) after spawning. Cal. Fish. and Game, 43(2): 119-130.

SECONDAT, Marcel and Diego DIAZ. 1942. Recherches sur la lactacidemie ches le poisson d'eau douce:, Compt. Rend. Acad. Sci. 215: 71-73.

SILLIMAN, Ralph P. 1948. Estimation of the troll catch of Columbia River chinook salmon, Oncorhynchus tshawytscha. U.S. Fish and Wildife, Special Sci. Report, No. 50. 15pp.

SIIUIMAN, Ralph P. 1950. Fluctuations in abundance of Columbia River chinook salmon. U.S. Fish and Wildlife Service, Fishery Bull. 51: 365-383.

SMITH, S.B. 1955. The relation between scale diameter and body length of Kamloops trout, Salmo gairdneri kamloops. J. Fish. Res. Bd. Canada, 12: 742-753.

SNEDECOR, George W. 1950. Statistical Methods. 4th Edition. Iowa State College Press. 485 pp.

STRINGER, G.E. and W.S.HOAR. 1955. Aggressive behavior of underyearling Kamloops trout. Canadian J. Zool., 33: 148-160.

SVERDRUP, H.V., Martin W.JOHNSON and Richard H.FLEMING. 1942. The oceams, their physics, chemistry, and general biology. Prentice Hall, New Jersey. 1087 pp.

SZARSKI, H., E.DELEWSKA, S.LEJA, S.OLECHNOWICZAWA, Z.PREDYGIER, and L.SLANKOWA. 1956. UkYad trawienny lexzxza (Abramis brama L.). (The digestive system of the bream). In Polish with English summary. Studia Soc. Sci. Torunesis, Sect. E: 3(7): 113-146.

WALFORD, Lionel A. 1946. A new graphic method of describing the growth of animals. Biol. Bull., 90(2): 141-147.

WELCH, Paul S. 1955. Limnology. McGraw-Hill, New York, 471 pp.

WEYMOUTH, F.W., J.FIELD II and M.KLEIBER. 1942. Relationship between body size and metabolism. Proc. Soc. Exp. Biol. Med., 49: 367-370.

WIIIMOVSKY, Norman J. and Warren O.FREIHOFER. 1957. Guide to the literature on systematic biology of Pacific salmon. U.S. Fish and Wildlife Ser., Spec. Sci. Rept., Fisheries, No. 209, 266 pp .

ZEUTHEN, Erik. 1953. Oxygen uptake as related to body size in organisms. Quart. Rev. Biol., 28(1): 1-12.

ZEUTHEN, Erik. 1955. Comparative physiology (respiration). Ann: Rev. Physiol., 17: 459-482.

## APPENDIX

## A METHOD OF COMPUTING THE VARIANCE OF COMBINED PROBABILITY ESTIMATES

Mortality of fish is studied and a series of consecutive observations is. obtained. Each estimate of mortality may or may not be based on samples of identical individuals, i.e. each sample may be drawn independently from the population. It is desired to estimate the probability $Q$ that a fish will die prior to or during a time period $t$ and to set up confidence intervals for these probabilities. This procedure would not, of course, be needed if a constant instantaneous mortality obtained throughout the time period. The assumption of random selection must be valid.

The following notation is used.
$\hat{p}_{t}^{t}$ estimates the probability $p_{t}$ that a fish living at time t survives until t+l.
$\hat{q}_{t}$ estimates $q_{t}$, the probability that a fish living at time period $t$ dies before time period $t+1 ; q_{t}=1-p_{t}$.
$x_{t}=$ number of fish alive at time $t$ that survive until time $t+1$.
$\Psi_{t}=$ number of fish alive at time $t$ that die before time $t+1$. $n_{t}=$ number of fish alive and in the experiment at time $t$ $n_{t}=x_{t}+y_{t} ; \quad \hat{p}_{t}=x_{t} / n_{t}$.
$\hat{P}_{t}$ estimates the probability $P_{t}$ that a fish lives until time $t+1$.
$\hat{Q}_{t}$ estimates the probability $Q_{t}$ that a fish dies prior to time $t+1$.

Note: it may also die prior to time $t, t-1$, etc.
The qualification has been given that $n_{t}$ may or may not equal $x_{t-1}$ -

Now $\mathrm{P}_{\mathrm{t}}=\mathrm{p}_{\mathrm{O}} \mathrm{p}_{1} \cdot \cdot \mathrm{p}_{\mathrm{t}-1} \mathrm{p}_{\mathrm{t}} \quad$ or

$$
\begin{equation*}
P_{t=k}=I I_{t=0}^{k} p_{t} \cdot \cdots \cdot \cdots \cdot \cdots \cdot \cdots \cdot \cdots \cdot \cdots \cdot \cdots \cdot \cdots \cdot \tag{1}
\end{equation*}
$$

and $Q_{t} \neq q_{0} q_{1}$. . $q_{t-1} q_{t}$ because a joint probability of death cannot occur, but

$$
\begin{equation*}
Q_{t}=1-P_{t} \tag{2}
\end{equation*}
$$

and can be estimated from this relationship or by use of the log form

$$
\begin{aligned}
Q_{t} & =1-e^{-\left(\operatorname{coln} p_{0}+\operatorname{coln} p_{1}+\cdots+\operatorname{coln} p_{t-1}+\operatorname{coln} p_{t}\right)} \\
\text { or } Q_{t} & \left.=1-e^{-\left(i_{1}\right.}+i_{2}+\cdots+i_{t-2}+i_{t-1}+i_{t}\right)
\end{aligned}
$$

where $i_{t}=\operatorname{coln} p_{t}=$ instantaneous mortality rate (Picker, 1945).

In any case $Q_{t}$ is always estimated from $\hat{P}_{t}$ or its components.
Variance of $\mathrm{p}_{\mathrm{t}}$ is estimated by:

$$
\mathrm{S}_{\hat{p}_{t}^{2}}^{2}=\frac{\hat{\mathrm{p}}_{\mathrm{t}} \hat{\mathrm{q}}_{t}}{n_{\mathrm{t}}} \quad \text { (Snedecor, 1950) }
$$

The variance of $\hat{P}_{t}$ cannot be sums or products of variances of $\hat{p}_{t}$ 's for resulting variances would rapidly diverge and lose meaning. The variance of $\ln \hat{p}_{t}\left(\right.$ or $\left.\operatorname{coln} \hat{p}_{t}\right)$
may be approximated by $S_{\ln }^{2} \hat{p}_{t} \approx \frac{S_{\hat{p}_{t}}^{2}}{\hat{p}_{t}^{2}} \quad$ (Deming, 1943, p.45). These variances are additive and thus:

$$
\begin{equation*}
S_{\ln }^{2} \hat{P}_{t=k}=\varepsilon_{t=0}^{\mathrm{k}} S_{\ln }^{2} \hat{P}_{t} \tag{3}
\end{equation*}
$$

Confidence intervals of $Q_{t}$ can now be set by the relationship:
 The resulting confidence limits are advantageous as they tend to the unequal limits of the Poisson distribution as values of $P \longrightarrow 0$ or l. A schedule of calculations is presented in Table A. Mortality observations were grouped in time periods of one hour and calculations are carried out in Table B.

Table A. Schedule for calculation of standard deviation of $\log _{e}$ survival probability.


Table B. Schedule of calculation of mortality, ocean coho ${ }^{\text {a }}$.

| t | x | \# | n | $\hat{p}$ | $\hat{\mathrm{P}}$ | $S_{\ln \hat{p}}^{2}$ | $S_{\ln } \hat{P}$ | 9 | $\hat{Q}$ | $\bar{Q}$ | i |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 110 | 5 | 115 | 0.9565 | 0.9565 | . 000395 | . 01987 | 0.006 | 0.044 | 0.080 | 0.044 |
| 1 | 89 | 21 | 110 | 0.8091 | 0.7739 | . 002145 | . 05040 | 0.146 | 0.226 | 0.299 | 0.212 |
| 2 | 75 | 14 | 89 | 0.8427 | 0.6522 | . 002097 | .06810 | 0.255 | 0.348 | 0.429 | 0.171 |
| 3 | 72 | 1 | 73 | 0.9863 | 0.6433 | . 000190 | . 06948 | 0.263 | 0.357 | 0.438 | 0.038 |
| 4 | 69 | 3 | 72 | 0.9583 | 0.6165 | . 000604 | . 07370 | 0.288 | 0.384 | 0.474 | 0.043 |
| 5 | 59 | 4 | 63 | 0.9365 | 0.5774 | .001076 | . 08067 | 0.330 | 0.423 | 0.507 | 0.066 |
| 6 | 52 | 0 | 52 | 1.0000 | do | ------ | do | do | do | do | 0 |
| 7 | 47 | 0 | 47 | do | do | ------ | do | do | do | do | 0 |
| 8 | 40 | 1 | 41 | 0.9756 | 0.5633 | . 000610 | . 08436 | 0.336 | 0.437 | 0.522 | 0.025 |

Esee text and Table A. for notation.

LARKIN, P.A., J.G.TERPENNING and R.R.PARKER. 1957. Size as a determinant of growth rate in rainbow trout, Salmo gairdneri. Trans. Am. Fish. Soc., 86: 84-96.

PARKER, Robert R. 1955. Two proposed methods of estimating animal populations. Proc. 7th Alaska Science Conference.

PARKER, Robert R. and Walter KIRKNESS. 1951. Biological investigations. Alaska Dept. Fish., Ann. Rept. No. 2, 1950: 25-42.

PARKER, Robert R. and Walter KIRKNESS. 1954. Estimates of population of spawning king salmon in the Taku River, Alaska, for the year 1951. Proc. 3rd Alaska Sci. Confer., pp. 179-191.

PARKER, Robert R. and Walter KIRKNESS. 1956. King salmon and the ocean troll fishery of Southeastern Alaska. Alaska Dept. Fish., Res. Rept. No. 1, 64 pp.

PARKER, Robert R. and Robert E. VINCENT. 1956. Progress report on research studies at the Kitoi Bay Research Station. Alaska Dept. Fish., Ann. Rept. No. 7, 1955. pp. 25-67.

PARKER, Robert R. and Edgar C. BLACK. 1959. Muscular fatigue and mortality in troll-caught chinook salmon (Oncorhynchus tshawytscha). J. Fish. Res. Bd. Canada. 16(1): 95-106.

PARKER, Robert R., Edgar C.BLACK and Peter A.LARKIN. 1959. Fatigue and mortality of Pacific salmon (Oncorhynchus). J. Fish. Res. Bd. Canada. In press.

PARKER, Robert R. and P.A.IARKIN. 1959. A concept of growth of fishes. Submitted to J. Fish. Res. Bd. Canada.


[^0]:    ${ }^{2}$ a tributary of the Fraser River 60 miles above salt water, in British Columbia.
    $3_{\text {Of mixed origin caught by commercial troll off the cgast }}$ 580 Southeastern Alaska between Sitka and Cross Sound, $57^{\circ}$ to $58^{\circ} \mathrm{N}$ Lat.

[^1]:    ${ }^{4}$ Exponential growth (Brody,1927, 1945) is a limiting case of (A.3) where $d w / d t=k w^{x=1}$
    and the axes are transformed by logarithms.

[^2]:    $8_{\text {The word }}$ stress is used in this paper meaning any trauma and does not imply change in anterior pituitary-interrenal activity, although this may be involved.

[^3]:    A Eleven fish included in the first time period were killed and sampled when landed. The remainder are fish which died in the live boxes. '

[^4]:    afinal blood sample not available.

[^5]:    $6_{\text {The }} 1958$ price structure was such that chinook over 10.0 pounds (approximately 28.0 inches fork length) brought $11 / 2$ times the price per pound paid for fish under that size.

