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A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality[1]

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ABSTRACT

A simple metabolic model describing growth as the difference between what enters the body and what leaves it, is elaborated assuming that synthetic processes (the building-up, the anabolism) are consuming energy supplied by processes of decomposition (the break-down, the catabolism). This leads to partitioning total catabolism into two components, one being a function of the rate of synthesis, another keeping the body functioning independently of synthesis. The rate of synthesis is described as a function of food taken, of the efficiencies of digestion and energy conversion, and of the absorbing surface of the intestine. Catabolic processes are supposed to be functions of the oxygen concentration in the water, the absorbing surface of the gills, and the rate of oxygen transport. Both kinds of processes are made functions of temperature in the way enzymatic processes usually are. Assuming that molecular interactions accidentally go wrong makes natural mortality, like growth, a function of the rates of anabolic and catabolic processes and body size.

Application of the model to data of length-at-age, food and oxygen consumption, weight loss, gill area, and natural mortality indicates that at least some of the main hypotheses cannot be rejected on available evidence.

INTRODUCTION

THE METABOLIC growth model was advanced by Pütter (1920), the first to realize the usefulnes of the truism, that what remains in the body is the difference between what comes in and what goes out. The rate of intake of food, he considered, must be surface dependent whereas the rate of break-down, occurring everywhere in the body, must depend on body weight. Thus:

$$dw/dt = \mathrm{H}\, w^{2/3} - k\, w \qquad \ldots\ldots(1)$$

If w is the weight in grams and t the time in seconds, the coefficient of anabolism, H, has the dimension $g^{1/3}$ $\text{sec},^{-1}$ and the coefficient of catabolism is k sec^{-1}. Pütter's paper is a remarkably early attempt at turning natural history into science through a mathematical modelling of biological phenomena.

The work was continued by von Bertalanffy in his original papers (1934, 1938) and in several more recent ones (e.g., 1964). Other developments were made by Beverton and Holt (1957, 1959), Taylor (1958, 1962), and most recently by Paloheimo and Dickie (1965, 1966a, b). Independently, a similar model was developed for unicellular organisms by Rashevsky (1960), operating on the molecular level. The metabolic model has been abundantly

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applied, particularly in fishery biology, but a gap has developed between the students of growth and the physiologists developing empirical models of metabolic phenomena (e.g. Winberg, 1956, 1962; Ivlev, 1961a, b), this, apparently, because the relationship between growth and respiration has remained insufficiently known. The present paper is a faltering attempt towards a better understanding of these interrelations.

The notation is rather extensive. To aid memory, the symbols used are listed and explained in Appendix I.

In the first part of the paper a model is developed on the assumption that the fish lives in an entirely stable environment. In the sections following, the model is elaborated to allow for differences in food supply, temperature, and oxygen contents of the water. An additional hypothesis on metabolic processes as a cause of natural mortality is also developed. Finally, the links to a less elaborate, but in fact very similar model by Winberg are indicated.

Admittedly, the model is hard to perceive because of the large number of parameters successively introduced. On the other hand, I *think* it has one virtue: that of being consistent with itself.

Quite another problem is whether the model has anything to do with the real world. That is investigated in Appendixes II–XIV, where various sorts of data, mostly from literature, are fitted to appropriate parts of the model in order to find out if the various hypotheses advanced can be rejected. It is not attempted to prove the hypotheses. With the approach to scientific method adopted here nothing can be proved, but a hypothesis can be rejected when it is shown with a high degree of probability to be false. When a rejected hypothesis is part of a more extensive model, one must accept the observed limitations of the applicability, or the involved part of the model must be broken down and advanced in another shape. The model below was developed that way. With this approach the same set of data can fail to reject any of two alternative hypotheses, and particularly, when the information is veiled by large measuring errors. The idea is that until we obtain possession of material which can reject the hypothesis, the latter is good enough for our purpose.

It was intended to develop the model by reasoning only, but it soon became apparent that empirical relationships had to be incorporated here and there. Mathematical approximations were used frequently, too, in order to simplify expressions which are difficult to handle. The two methods, the use of empirical relationships and of mathematical approximations, are closely related. In both cases, the first approximation is a single point (say, a mean value) and the second a straight line (a tangent or secant of any curve). Only the third and consecutive approximations provide the choice of various possibilities of which the exponential function (i.e., a per cent change) often seems the simplest.

A third kind of approximations comes in useful after a model has been developed. Scrutiny of the model reveals situations when replacement of certain variables by constants provides simple relationships (linear, parabolic,

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ect.) between two quantities. A good experimental set-up in which the variables in question are kept reasonably constant and where the two quantities can be measured leads to rejection of the hypothesis in a large part of the cases when it is false.

Another important method of testing hypotheses is to estimate the same parameter in different ways and compare the results. This approach has been used extensively in the present paper.

A really up-to-date account should deal with the energy transfer on a molecular level, a subject, however, which I do not master. Instead, I shall deal with changes of mass, and under the following assumptions:

that the specific gravity of the fish is equal to one ($g = cm^3$);

that the proportions of the body are constant (isometric growth: surface $= q' l^2$, weight $= q l^3$, where l is length (exceptions are made for absorbing surfaces);

that the food has the same chemical constitution as the fish;

that the synthetic processes have negative entropy (are not spontaneous); and

that the energy necessary for these processes is supplied by oxidations requiring free oxygen.

These assumptions were made in order to simplify the model.

THE METABOLIC GROWTH MODEL

A. THE BASIC EQUATION

Generalized, Pütter's model (equation 1) becomes

$$dw/dt = \Phi(dR/dt) - \Gamma(w, \Phi(dR/dt)) \qquad .....(A1)$$

where w is weight, dR/dt the food consumed in unit time, and t time. The equation expresses that the quantity absorbed is a function of the quantity eaten, whereas the quantity lost is a function of (1) the size of the fish, because even in a fasting fish every cell must metabolize to remain alive; and (2) of the food absorbed, because digesting and assimilating food require energy.

By writing the left-hand side of equation A1 as an ordinary differential equation instead of a partial one, it is specified that we are assuming that the growth rate is a function of body weight and time and of these only. That means that if ration is a function of anything but weight and time (e.g. of the food concentration in the water) fixed values of other variables must be chosen before integrating. As shown below, ration can, and, indeed, in a marginal situation must be written as a function of body size because there is an upper limit to what a fish of a given size can eat.

In this paper the right-hand terms of equation A1 shall be called "the anabolic term" (the first one) and "the catabolic term" (the second one).

Let it be assumed for the moment that the food consumed is completely digested and that the intestine is always full. This is the marginal situation mentioned above. The quantity absorbed now is proportional with the absorbing surface which, in case of isometric growth, is proportional with $w^{2/3}$. The area of the intestine and, indeed, its inner surface, is tricky to measure because postmortal changes occur. A few pilot experiments were rather discouraging, e.g., from measurement of eight soles (*Solea solea*) the outer surface of the intestine was estimated as

$$2.12\, w^{0.57}\ \mathrm{cm}^2$$

where the superscript, 0.57, has a 95% confidence interval from 0.33 to 0.80. Until more becomes known of this subject we shall cautiously put, in equation A1,

$$\Phi\,(d\mathrm{R}/dt) = d\mathrm{R}/dt = dr/dt = h_1\, w^m \qquad \ldots\ldots(\mathrm{A2})$$

where dr is the quantity absorbed from the intestine. Equation A2 describes total, or gross, anabolism as it is supposed to be when the intestine is full and the food is completely digested. What may happen when the fish is given restricted rations and when digestion is not complete is discussed in a later paragraph (Growth and Food).

The catabolic term of equation A1, $-\Gamma(w,\ \Phi\ (d\mathrm{R}/dt))$, can be assumed to consist of two additive terms representing (1) the catabolism of a fasting fish (we shall call it "the fasting catabolism"); and (2) the extra catabolism necessitated by feeding ("the feeding catabolism"), partly because mechanical work is involved in eating and digestion, and partly because an extra breakdown is necessary to supply free energy for synthesis of tissue. Fasting catabolism plus feeding catabolism make up the total catabolism of a fed fish. We shall assume that fasting catabolism depends on the size of the fish only and that feeding catabolism depends on the quantity of food absorbed only and constitutes a constant fraction, α, of gross anabolism. Of course, more elaborate models can be made, but it is not attempted here. The size of α is determined by the heat loss (the inefficiency of energy transfer) and the loss of energy through the urine. Casey (1962, p. 173 and 178) considers an energy transfer loss of 63% (observed in the human respiratory enzyme system) as a probable upper limit (i.e., $\alpha \geq 0.63$) whereas Winberg (1956) finds that yolk energy is transferred to the fish foetus with a loss of only 35% ($\alpha = 0.35$). The energy loss through urine seems to be insufficiently known at present. Thus, the lowest value of α to be expected is 0.35 whereas values twice as high are more likely to be met with. α is estimated in Appendix VII.

According to the foregoing we can write

$$-\,\Gamma\,(w,\ \Phi\,(d\mathrm{R}/dt)) = -\,\varphi\,(w) - \gamma\,(dr/dt) \qquad \ldots\ldots(\mathrm{A3})$$

where the first of the right-hand terms represents the fasting catabolism and the second term represents the feeding catabolism. By means of equation A2, the latter can be expanded as

$$-\,\gamma\,(dr/dt) = -\,\alpha\, h_1\, w^m \qquad \ldots\ldots(\mathrm{A4}).$$

Note that here, as elsewhere in the paper, expressions for catabolism are given a negative sign. In other words: growth is considered the sum of the effects of anabolism and catabolism, the latter being negative. Thus, the net anabolism can be defined as the sum of gross anabolism (equation A2) and feeding catabolism (equation A4):

$$\Phi\,(dR/dt) - \gamma\,(dr/dt) = h_1\,w^m - \alpha\,h_1\,w^m = (1-\alpha)\,h_1\,w^m = H\,w^m \quad \ldots(A5)$$

still on the assumption that the intestine is always full and the food completely digested. Putting $m = 2/3$ gives the anabolic term, $H\,w^{2/3}$ of Pütter's approximation, equation 1.

The fasting catabolism, $-\varphi(w)$, equals Pütter's catabolic term, $-kw$, and is the rate of weight loss of a fish behaving normally. Putting $\varphi(w) = k\,w$ as Pütter did, is unsatisfactory because there is now sufficient evidence from respiration experiments that fasting catabolism is not usually proportional with weight. Apparently, it was overlooked that although catabolic processes are going on all over the body, the necessary oxygen supply has to be introduced through some surface or other, mainly the gills. With our basic assumption of isometric growth this means that catabolism is proportional with $w^{2/3}$. As discussed in several of the Appendixes, this is also known to be untrue, so that the assumption of isometric growth must be abandoned for the occasion. In fact (App. XIV) the gills do not grow isometrically with the body, because new units are being added as the fish grows. Retaining the assumption of isometric growth of the body as a whole we can describe the surface areas of body and gills by

$$\left.\begin{aligned} S_b &= A_b\,w^{2/3} \\ S_g &= A_g\,w^{n_g} \end{aligned}\right\} \quad \ldots\ldots(A6).$$

The rates of respiration of a fasting fish through skin and gills are

$$\left.\begin{aligned} (dO_2/dt)_b &= -\,B_b\,S_b \\ (dO_2/dt)_g &= -\,B_g\,S_g \end{aligned}\right\} \quad \ldots\ldots(A7)$$

where $-B_b$ and $-B_g$ are the rates of oxygen consumption in unit time and area. Total fasting respiration becomes

$$(dO_2/dt)_{fasting} = -\,(B_b\,A_b\,w^{2/3} + B_g\,A_g\,w^{n_g} = -\,\omega\,k\,w^n \quad \ldots\ldots(A8)$$

where $2/3 < n < n_g$. The reason for factoring the right hand constant into ω and k emerges when ω is defined as the proportionality constant relating the oxygen consumption of a fasting animal to weight loss,

$$\omega = dO_2/dw.$$

Returning to equation A3 we can now put

$$-\varphi(w) = \frac{1}{\omega}(dO_2/dt)_{fasting} = (dw/dt)_{fasting} = -k\,w^n \quad \ldots\ldots(A9).$$

ω and n are dimensionless. k is a proper rate constant (dimension, time^{-1}) only for $n = 1$. Otherwise it has the obscure dimension of weight^{1-n} time^{-1}.

The rate of feeding catabolism, expressed as weight loss, was found to be

$$-\gamma\,(dR/dt) = -\alpha\,h_1\,w^m \quad \ldots\ldots(A4).$$

The corresponding oxygen consumption is

$$(dO_2/dt)_{feeding} = \omega\,(dw/dt)_{feeding} = -\omega\,\alpha\,h_1\,w^m \quad \ldots\ldots(A10).$$

Adding equation A9 to equation A10 gives the oxygen consumption of fed fish as

$$(dO_2/dt)_{fed} = (dO_2/dt)_{feeding} + (dO_2/dt)_{fasting} = -\omega\,\alpha\,h_1\,w^m - \omega\,k\,w^n \ldots\ldots(A11).$$

$\omega\alpha h_1$, ωk, m, and n are estimated from oxygen consumption data in App. IV; ω is estimated in App. V.

There is one difficulty with equation A8 which has been passed over tacitly above, as elsewhere in the paper. It was assumed, in fact, that any change in the oxygen consumption due to activity or temperature changes causes proportional change in gill respiration and skin respiration. This, however, is not to be expected. Increased respiration probably to a large extent is effected by an increased rate of ventilation of the gills. Thus B_g will increase more than B_b and not only k (on the right-hand side) will increase, but so will n. The same reasoning applies to the oxygen consumption of a fed fish: a higher proportion of the oxygen passes through the gills than in a fasting one. This does not cause much trouble, though, because the total oxygen consumption of a fed fish is regulated by the rate of food consumption which is proportional with a low power, m, of w. Other complications, masking the effect of increased gill respiration probably occur. For instance, it is doubtful whether the rate of gill ventilation can in practice be altered proportionally with the oxygen demand in fish of all sizes when temperature or activity increases. If it cannot, n_g is not constant. To elucidate these things would mean to build a detailed model of gill respiration which is not attempted here.

Equation A11 is often sucessfully approximated by a single exponential term,

$$dO_2/dt = -D\,w^d \quad \ldots\ldots(A12)$$

which is valid whether the fish has eaten or not (see App. II and IV). d attains values between m and n. The energy equivalent of equation A12 is the metabolic term, T, of Winberg's (1956, p. 209) growth equation.

Evaluating k from weight loss data for fasting fishes is simplest by integrating equation A9:

$$(dw/dt)_{fasting} = -k\, w_n \qquad \ldots\ldots(A9)$$

$$w_t^{1-n} = w_o^{1-n} - (1-n)\, {}_nk\, t\ (n \neq 1) \qquad \ldots\ldots(A13)$$

$$ln\ w_t = ln\ w_o - {}_1k\, t\ (n = 1) \qquad \ldots\ldots(A14)$$

where w_o is the initial weight. The subscripts, n and 1, of k were introduced to distinguish between estimates based on A13 and A14. Given two points, $(w_o, 0)$ and (w_t, t), through which all curves determined by equations A13 and A14 must go, the computation of ${}_nk$ (i.e., of k for $n \neq 1$) is often facilitated by eliminating t from equations A13 and A14, putting $w_t = C\, w_o$ (C slightly smaller than one) and putting

$$\frac{C^{1-n} - 1}{(1-n)\ ln\ C} = 1.$$

This leads to

$$ln\ {}_nk = ln\ {}_1k + (1-n)\ ln\ w_o \qquad \ldots\ldots(A15)$$

which with equation A14 gives quick solutions for ${}_nk$. They are often very accurate because the curves described by equations A13 and A14 are almost straight lines for weight losses of, say, up to 20%.

In practice, n cannot be estimated from individual fasting experiments. This is another effect of equations A13 and A14 being practically linear. Data for a wide range of weight (several fasting experiments with fish of different size) are necessary for estimating n (see Appendix IX). Parameter estimates from the weight loss of fasting fishes are made in App. VIII and IX.

According to the foregoing we have

$$\begin{aligned} dw/dt &= \Phi\,(dR/dt) - \Gamma\,(w, \Phi\,(dR/dt)) \\ &= \Phi\,(dR/dt) - \gamma\,(dr/dt) - \varphi\,(w) \\ &= h_1\, w_m - \alpha\, h_1\, w^m - k\, w^n \\ &= (1-\alpha)\, h_1\, w^m - k\, w^n \\ &= Hw^m - k\, w^n \qquad \ldots\ldots(A16). \end{aligned}$$

Reducing to the linear dimension gives

$$\frac{dw^{1/3}}{dt} = \frac{H}{3}\, w^{m-2/3} - \frac{k}{3}\, w^{n-2/3} \qquad \ldots\ldots(A17)$$

because

$$\frac{dw^{1/3}}{dt} = \frac{1}{3} w^{-2/3} \frac{dw}{dt}.$$

Putting, in accordance with an assumption made in the introduction, $w = ql^3$, where l is body length, equation A16 becomes

$$\frac{dl}{dt} = \frac{H}{3q^{1-m}}\, l^{3m-2} - \frac{k}{3q^{1-n}}\, l^{3n-2} = El^{3m-2} - Kl^{3n-2} \qquad \ldots\ldots (A18)$$

where E and K are constants.

When the increment, dw/dt or dl/dt, is zero, the fish has reached its asymptotic size. Equations A16 and A18 give

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \ldots\ldots (A19)$$

$$L_\infty = q^{-1/3}\left(\frac{H}{k}\right)^{\frac{1}{3(n-m)}} = \left(\frac{E}{K}\right)^{\frac{1}{3(n-m)}} \qquad \ldots\ldots (A20)$$

where W_∞ is the asymptotic weight and L_∞ the asymptotic length.

Paloheimo and Dickie (1965) found empirically that fish growth is not asymptotic which raises the question whether W_∞ and L_∞ are artefacts, brought into existence by introducing approximations. This is quite possible because the exponential expressions (equations A2 and A9) for anabolism and catabolism are approximative only.

Inflections on the growth curves are found by differentiating equations A16 and A18 and putting the derivatives equal to zero, e.g.,

$$\frac{dl}{dt} = El^{3m-2} - Kl^{3n-2} \qquad \ldots\ldots (A18)$$

$$\frac{d^2l}{dt^2} = \left((3m-2)\ El^{3(m-1)} - (3n-2)\ Kl^{3(n-1)}\right)\frac{dl}{dt} \qquad \ldots\ldots (A19)$$

$$(3m-2)\ EL_I^{3(m-1)} - (3n-2)\ KL_I^{3(n-1)} = 0 \qquad \ldots\ldots (A20)$$

$$L_I = \left(\frac{3m-2}{3n-2}\,\frac{E}{K}\right)^{\frac{1}{3(n-m)}} = L_\infty\left(\frac{3m-2}{3n-2}\right)^{\frac{1}{3(n-m)}} \qquad \ldots\ldots (A21)$$

and similarly

$$W_I = W_\infty\left(\frac{m}{n}\right)^{\frac{1}{(n-m)}} \qquad \ldots\ldots (A22).$$

The weight curve is inflected for all values of m and n while the length curve has an inflection for $m > 2/3$ only. Estimates of m, based on the assumption

$w = ql^3$ so far have given values about or below 2/3 so that appreciable inflection of the length curve can scarcely be expected. Taylor (1962), however, has shown that the generalization $w = ql^C$ leads to inflected length curves for $C \neq 3$ (anisometric growth).

The approximation, $m = 2/3$, $n = 1$, leads to Pütter's growth equation (equation 1) which has several virtues. It lends the simple physical dimensions of speed and rate (length time^{-1} and time^{-1}) to H and k. It is easily integrated (elegantly by Beverton and Holt, 1957) while for most other values of m and n integration must be made numerically. Astoundingly, it also very often provides a fine representation of growth data which has ensured it a wide application in the yield assessments of fishery biologists. Its main limitation is that further reasoning on physiological lines often leads the investigator astray so that his hypotheses are easily rejected by experiment. The assumption of weight proportionality of catabolism, for instance, is seldom acceptable in respiration studies.

With Pütter's approximation we have

$$\frac{dw}{dt} = \mathrm{H}w^{2/3} - kw \qquad \ldots\ldots(1)$$

$$\frac{dl}{dt} = \mathrm{E} - \mathrm{K}l \qquad \ldots\ldots(\mathrm{A}23)$$

$$\mathrm{W}_\infty = \left(\frac{\mathrm{H}}{k}\right)^3 \qquad \ldots\ldots(\mathrm{A}24)$$

$$\mathrm{L}_\infty = \frac{\mathrm{E}}{\mathrm{K}} \qquad \ldots\ldots(\mathrm{A}25)$$

$$\mathrm{W}_\mathrm{I} = \frac{8}{27}\,\mathrm{W}_\infty \qquad \ldots\ldots(\mathrm{A}26)$$

$$l_t = \mathrm{L}_\infty\,(1-e^{-\mathrm{K}(t-t_o)}) \qquad \ldots\ldots(\mathrm{A}27)$$

$$w_t = \mathrm{W}_\infty\,(1-e^{-\mathrm{K}(t-t_o)})^3 \qquad \ldots\ldots(\mathrm{A}28)$$

where $\mathrm{K} = \frac{k}{3}$, and t_o is the time when $l_t = 0$. The estimation of t_o is not dealt with in the present paper. The reader is referred to Beverton and Holt (1957, p. 284.)

B. GROWTH AND FOOD

In the first paragraph it was assumed that the fish had always eaten as much as it possibly could and that all what it ate was absorbed by the intestine.

We shall now look into the situation when the fish has opportunity to eat only a fraction of the highest possible ration and when a fraction of the food is discarded as excrements. To that end two new parameters shall be defined, namely, f, the feeding level, and β, the fraction absorbed of the food eaten.

The feeding level, f, we shall define as the fraction eaten of the quantity which could possibly be eaten. The latter is given by equation A2:

$$dR/dt = h_1 w^m$$

so that

$$f = \frac{dR/dt}{h_1 w^m} \qquad \ldots\ldots(B1)$$

and equation A2 can be re-written as

$$dR/dt = h_1 f w^m \qquad \ldots\ldots(B2).$$

The fraction, β, absorbed of the food eaten can be considered constant as Winberg (1956) does, putting $\beta = 0.8$ in which, however, is included the energy losses with the urine. In the present model these are incorporated in α. Most authors, however, consider β a decreasing function of the feeding level. Brody and Procter (1933) (cited in Brody, 1945, p. 78) and Kostitzin (1937, p. 163) developed empirical models which, however different they may look, are very like each other.

Kostitzin's model was applied by Beverton and Holt (1957, p. 113). In both, the maximum utilization of food is low because the weight loss during energy transfer and other losses are implicit, whereas in the model developed in the preceding paragraph they are given explicitly as the collective term, $-\gamma\ (dr/dt)$, of equation A3. Thus, neither Brody's nor Kostitzin's formulations are directly applicable and must be replaced by a more appropriate formulation. The development of a realistic model of the mechanics and chemistry of digestion is probably premature so that any attack on the problem has to be largely empirical. I have made some simple reasoning which is not, however, proof against a rigorous mathematical criticism. It led to a simple function

$$\beta = 1 - e^{-h_2/f} \qquad \ldots\ldots(B3)$$

which has largely the properties one would require of β. At maximum feeding ($f = 1$) the fraction absorbed is minimum: $\beta = 1 - e^{-h_2}$. For $f \rightarrow 0$, $\beta \rightarrow 1$. Equation B3 is applied to data in App. VII and seems to work satisfactorily. The new parameter, h_2. has no dimension.

In a more general form equation A2 now can be written

$$\Phi\ (dR/dt) = dr/dt = \beta\, dR/dt = h_1 f \beta w^m = h w^m \qquad \ldots\ldots(B4).$$

The present and preceeding paragraphs can be summarized as follows:

$$\textit{Feeding level} = f = \frac{dR/dt}{h_1\ w^m} \qquad \ldots\ldots(B1)$$

$$\textit{Rate of feeding} = \textit{ration eaten} = dR/dt = h_1 f w^m \qquad \ldots\ldots(B2)$$

$$\textit{Fraction absorbed of food eaten} = \beta = 1 - e^{-h_2/f} \qquad \ldots\ldots(B3)$$

$$\textit{Rate of gross anabolism} = \textit{ration absorbed} = \Phi\ (dR/dt) = dr/dt = \beta\ dR/dt = h_1 f\ \beta\ w^m = hw^m \qquad \ldots\ldots(B4)$$

$$\textit{Rate of net anabolism} = \textit{gain} = (1-\alpha)\ dr/dt \qquad \ldots\ldots(B5)$$

$$\textit{Rate of feeding catabolism} = -\alpha\ dr/dt \qquad \ldots\ldots(B6)$$

$$\textit{Rate of fasting catabolism} = -\ kw^n \qquad \ldots\ldots(B7)$$

$$\textit{Rate of growth} = dw/dt = (1-\alpha)\frac{dr}{dt} - kw^n = (1-\alpha)\ h_1 f\ \beta\ w^m - kw^n = \mathrm{H}w^m - kw^n \qquad \ldots\ldots(B8)$$

Equation B8 contains a detailed expression for the

$$\textit{Instantaneous coefficient of net anabolism} = \mathrm{H} = (1-\alpha)\ (1-e^{-h_2/f})h_1 f = (1-\alpha)\ \beta\ h_1 f = v\ h_1 f \qquad \ldots\ldots(B9)$$

In the interpretation of v, see equation B20. In the simple model developed in the preceding paragraph we had $\mathrm{H} = (1-\alpha)h_1$ (equation A16) because $f = 1$ and $\beta = 1$ by definition. Equations A17–A28 remain valid in the more elaborate model of the present paragraph when the expanded expression for H, equation B9, is inserted.

An interesting point is the determination of the maintenance ration, i.e. the ration allowing the fish just to maintain its weight. The problem has two aspects. One is to find the ration to be given in order to keep the body weight constant, another to find how much of a bigger ration will be used for maintenance purposes. In the former case the feeding level, f, is a function of body size because a fish which has grown as big as it can will need full ration ($f = 1$) to keep its weight up. A smaller fish must be given a comparatively smaller ration ($f < 1$; $f \rightarrow 0$ for $w \rightarrow 0$) to prevent it from growing further. In fact, giving maintenance ration to a fish which has not reached its potential full size amounts to putting its present weight equal to W_∞.

In the case where a fish is fed more than maintenance ration, the feeding level is independent of body size (f = constant) and, accordingly β, the fraction absorbed of the food eaten, is constant. In the other case β varies with body size because it is a function of f.

Basically, the maintenance ration must make up for the weight loss, $-kw^n$ (e.g. gram per day), but in order to synthesize a similar amount, kw, of tissue some energy is wasted in the activities of acquiring and synthesizing it. Thus, the rate of dissipation of matter in the body is the sum of the fasting catabolism and the fraction α of the maintenance food absorbed. The maintenance ration to be absorbed therefore is

$$\left(\frac{dr}{dt}\right)_{maint} = \alpha\left(\frac{dr}{dt}\right)_{maint} + kw^n \qquad \ldots\ldots(\mathrm{B10})$$

from which

$$(dr/dt)_{maint} = kw^n/(1-\alpha) \qquad \ldots\ldots(\mathrm{B11}).$$

From this point of the analysis the attention must be divided between the two situations discussed above. First, assume that the fish is fed maintenance ration and not more than that. We can put $w = \mathrm{W}_\infty$ and $\beta = g(f)$ must be specified as $\beta_{maint} = g'(\mathrm{W}_\infty)$ because now $f = f_{maint} = g''(\mathrm{W}_\infty)$. By means of equations B4 and B11 we have

$$\beta_{maint}\left(\frac{d\mathrm{R}}{dt}\right)_{maint} = \left(\frac{dr}{dt}\right)_{maint} = \frac{k\,\mathrm{W}_\infty^n}{1-\alpha} \quad \text{and the}$$

$$\mathit{Maintenance\ ration} = (d\mathrm{R}/dt)_{maint} = \frac{k\mathrm{W}_\infty^n}{(1-\alpha)\beta_{maint}} \qquad \ldots\ldots(\mathrm{B12}).$$

β_{maint} decreases when W_∞ increases. Using a crude approximation we can put

$$\beta_{maint} = \mathrm{C}_1\,\mathrm{W}_\infty^{-\mathrm{C}_2} \ (\mathrm{C}_1 \text{ and } \mathrm{C}_2 \text{ positive})$$

from which

$$(d\mathrm{R}/dt)_{maint} = \frac{k}{\mathrm{C}_1(1-\alpha)}\,\mathrm{W}_\infty^{\,n+\mathrm{C}_2} \qquad \ldots\ldots(\mathrm{B13})$$

indicating, that a plot of log maintenance ration against log body weight has a slope $>n$ if C_2 is significant. A slope $<n$ should not be possible. For an application of equation B13, see App. VII.

Maintenance ration can also be defined by means of equation B2, writing

$$(d\mathrm{R}/dt)_{maint} = h_1\, f_{maint}\, \mathrm{W}_\infty^m \qquad \ldots\ldots(\mathrm{B14})$$

which is permissible because the maintenance ration is the whole ration taken. f_{maint} is a function of w and is found by putting dw/dt equal to zero in equation B8 and solving for f. Thus,

$$\mathit{Maintenance\ feeding\ level} = f_{maint} = \frac{k\,w^n}{(1-\alpha)\,\beta\,h_1\,w^m} = \frac{k}{v\,h_1}\,w^{n-m} \qquad \ldots\ldots(\mathrm{B15}).$$

In the other situation to be considered, in which the actual ration given is above maintenance ration, equation B11 can be written

$$\beta \left(\frac{d\mathrm{R}}{dt}\right)_{mr} = \left(\frac{dr}{dt}\right)_{mr} = \frac{kw^n}{1-\alpha} = \left(\frac{dr}{dt}\right)_{maint}$$

and we have the

$$\textit{Maintenance requirements} = (d\mathrm{R}/dt)_{mr} = \frac{kw^n}{(1-\alpha)\beta} = kw^n/v \quad \ldots\ldots(\mathrm{B}16)$$

where β is independent of body size but remains a function of the feeding level, f. v is defined below (equation B20). The higher f is, the smaller is β and the higher the maintenance requirements for fish of any size. Corresponding to each feeding level there is one value of w (the highest) for which $w = \mathrm{W}_\infty$, $\beta = \beta_{maint}$ and $(d\mathrm{R}/dt)_{mr} = (d\mathrm{R}/dt)_{maint}$. For $w < \mathrm{W}_\infty$, $(d\mathrm{R}/dt)_{mr} > (d\mathrm{R}/dt)_{maint}$. The whole trouble comes from developing β as a function of f (equation B1). When β is assumed a constant fraction of the ration as Winberg (1956) does, putting $\beta = 0.8$, then $(d\mathrm{R}/dt)_{mr} = (d\mathrm{R}/dt)_{maint}$.

A convenient expression for maintenance catabolism is easily derived by allotting a negative sign to the right-hand side of equation B10 and inserting equation B11:

$$-\alpha\left(\frac{dr}{dt}\right)_{maint} - kw^n = -\frac{\alpha kw^n}{1-\alpha} - kw^n = -\frac{kw^n}{1-\alpha}$$

Thus we have:

$$\textit{Maintenance catabolism} = -\frac{kw^n}{1-\alpha} \quad \ldots\ldots(\mathrm{B}17)$$

which is proportional with fasting catabolism and independent of β. In equation B17 it is expressed in terms of dissipation of matter, but it may as well be thought of in terms of oxygen consumption by introducing $\omega = d\mathrm{O}_2/dw$:

$$\left(\frac{d\mathrm{O}_2}{dt}\right)_{maint} = -\frac{\omega}{1-\alpha}kw^n \quad \ldots\ldots(\mathrm{B}18).$$

Note that a plot of maintenance oxygen consumption against body weight gives an estimate of n whereas a plot of maintenance ration against body weight does not (equation B13).

We further have:

$$\textit{Growth food} = \frac{d\mathrm{R}}{dt} - \left(\frac{d\mathrm{R}}{dt}\right)_{mr} = h_1 f w^m - \frac{kw^n}{(1-\alpha)\beta} = \frac{dw/dt}{v} \quad \ldots\ldots(\mathrm{B}19)$$

(v is defined below)

Efficiency of utilization of growth food for growth

$$= v = \frac{dw/dt}{dR/dt - (dR/dt)_{mr}} = (1-\alpha)\beta \qquad \text{.....(B20)}$$

Efficiency of utilization of total food for growth

$$= u = \frac{dw}{dR} = -\frac{k}{h_1 f} w^{n-m} \qquad \text{.....(B21).}$$

u and v are dimensionless. Notice that v is independent of body size. v is always positive; u is negative for $dw/dt < 0$.

The maximum utilization of food with respect to feeding level is found by differentiating equation B21 with respect to f, putting $du/df = 0$ and solving for f:

$$f_{\max} = -\frac{h_2}{ln\,\dfrac{k}{h_1 h_2(1-\alpha)} + (n-m)\; ln\; w} \qquad \text{.....(B22).}$$

In order to find the total amount of food, R_t, eaten by the fish from its birth until the time t we shall, to facilitate integration, revert to Pütter's approximation (equation 1 or, integrated, equation A28):

$$w_t = W_\infty (1-e^{-Kt})^3 \qquad \text{.....(A28)}$$

which means putting $m = 2/3$ and $n = 1$. For simplicity, the fish is assumed to be born at time $t = 0$ which puts the initial weight to zero. We have from equation B2

$$dR/dt = h_1 f w_t^m = h_1 f W_\infty^m (1-e^{-Kt})^{3m} \qquad \text{.....(B23)}$$

which gives, for constant f,

$$R_t = h_1 f W_\infty^m \int_0^t (1-e^{-Kt})^{3m}\, dt \qquad \text{.....(B24).}$$

The integration is simple for $m = 1/3$, $m = 2/3$, and $m = 1$. Results for intermediate values of m can be obtained by interpolation (see discussion below of an analogous situation leading to equation B34).

For $m = 2/3$ equation B24 becomes

$$R_t = \frac{h_1 f W_\infty^{2/3}}{2K} (2K + (1-e^{-2Kt}) - 4(1-e^{-Kt})) \qquad \text{.....(B25).}$$

The integrated efficiency of utilization of total food for growth becomes

$$U = \frac{\int_o^t \frac{dw}{dt}}{\int_o^t \frac{dR}{dt}} = \frac{w_t}{R_t} = \frac{W_\infty^{1-m}}{h_1 f} \frac{(1-e^{-Kt})^3}{\int_o^t (1-e^{-Kt})^{3m} dt} \quad \text{.....(B26)}$$

where the integral can be evaluated as above. Note that Pütter's approximation is used only in the growth curve proper. Other parameters remain as they were.

An equation for maintenance requirements corresponding to equation B23 is similarly derived from equation B16:

$$(dR/dt)_{mr} = \frac{kw^n_t}{v} = \frac{kW^n_\infty}{v} (1-e^{-Kt})^{3n} \quad \text{.....(B27).}$$

This, too, is easily integrated to give $R_{t.\,mr}$. The difference $R_t - R_{t.\,mr}$ is the growth food which, by multiplication by v gives the total production of fish meat. These things are perhaps of limited interest because as fish grow some of them usually die. A more realistic model, therefore, incorporates mortality, as suggested below in an approach closely related to that made by Beverton and Holt (1957, paragraph 9.4.3.) who used, however, the Pütter approximation throughout.

For a population with a constant instantaneous mortality, Z, we have

$$N_t = N_o e^{-Zt}$$

where N_t is the number present at time t, and N_o the initial number. Therefore, multiplying equations B23 and B27 by N_t we get

$$_{pop}(dR/dt) = h_1\, f\, w_t^m\, N_t = h_1\, f\, W_\infty^m\, N_o(1-e^{-Kt})^{3m} e^{-Zt}$$

$$_{pop}(dR/dt)_{mr} = \frac{k\, w_t^n N_t}{v} = \frac{k\, W_\infty{}^n\, N_o}{v} (1-e^{-Kt})^{3n}\, e^{-Zt}$$

where W_∞ and K, and those only, are Pütter parameters.

Integrated, these equations become, for any constant f,

$$_{pop}R_t = h_1 f\, W_\infty{}^m N_o \int_o^t (1-e^{-Kt})^{3m}\, e^{-Zt}\, dt = h_1 f\, W_\infty{}^m\, N_o\, J_I \quad \text{.....(B28)}$$

$$_{pop}R_{t.\,mr} = \frac{k\, W_\infty{}^n N_o}{v} \int_o^t (1-e^{-Kt})^{3n}\, e^{-Zt}\, dt = \frac{k\, W_\infty{}^n N_o}{v} J_{II} \quad \text{.....(B29)}$$

where the integrals J_I and J_{II} are to be evaluated below.

The food utilized for growth up to time t is

$$ {}_{pop}R_{t.g} = {}_{pop}R_t - {}_{pop}R_{t.mr} = N_o \left(h_1 f\, W_\infty^m\, J_I - \frac{k\, W_\infty^n}{v}\, J_{II}\right) \quad \ldots\ldots (B30) $$

which, multiplied by v and divided by N_o gives the annual production per fish originally present and still not over t years old:

$$ A.P./N_o = v\, {}_{pop}R_{t.g}/N_o = H\, W_\infty{}^m\, J_I - k\, W_\infty{}^n\, J_{II} \quad \ldots\ldots (B31). $$

Remember, that W_∞ is a Pütter parameter, whereas H and k are not. $H = v\, h_1\, f$ is substituted from equation B9.

Equation B31 can be derived directly from the growth equation without the detour through consumption (see Beverton and Holt, 1957, eq. (9. 19)):

$$ A.P. = \int_o^t (dw/dt)_t\, N_t\, dt = \int_o^t (H\, w^m{}_t - k\, w^n{}_t)\, N_t\, dt $$

$$ = N_o\, H \int_o^t w^m{}_t\, e^{-Zt}\, dt - N_o\, k \int_o^t w^n{}_t\, e^{-Zt}\, dt $$

$$ = N_o\, H\, W_\infty^m\, J_I - N_o\, k\, W_\infty^n\, J_{II} \quad \ldots\ldots (B31). $$

This way, equation B31 turns out to contain an unnecessary complication: since Pütter's parameters are introduced in the expansion of $w^m{}_t$ and $w^n{}_t$ they might as well be introduced at once. That would be in accordance with our assumption, that the growth curves of most fishes are adequately described by Pütter's approximation. Thus,

$$ A.P. = \int_o^t (dw/dt)_t\, N_t\, dt = \int_o^t (H\, w^{2/3}{}_t - k\, w_t)\, N_t\, dt $$

$$ = N_o\, W_\infty^{2/3}\, H \int_o^t (1-e^{-Kt})^2\, e^{-Zt}\, dt - N_o\, W_\infty\, k \int_o^t (1-e^{-Kt})^3\; e^{-Zt}\; dt $$

and, because $H = k\, W_\infty^{1/3}$ (equation A19),

$$ A.P. = N_o\, {}_1k\; {}_1W_\infty\, (J_{2/3} - J_{3/3}) \quad \ldots\ldots (B32) $$

where suffixes 1 are introduced to indicate that both k and W_∞ are Pütter parameters. Putting

$$ N_o\, {}_1W_\infty^{2/3}\, J_{2/3} = \bar{P}_{w^{2/3}},\; N_o\, {}_1W_\infty\, J_{2/3} = \bar{P}_w \text{ and } {}_1k = 3K \text{ gives} $$

$$ A.P. = 3\, K\, (W_\infty^{1/3}\, \bar{P}_{w^{2/3}} - \bar{P}_w) $$

which is equation (9. 23) of Beverton and Holt (1957) except for the interval over which there was integrated.

The overall efficiency of utilization of total food for growth by the whole population up to time t is

$$ {}_{pop}U_t = A.P./{}_{pop}R_t \qquad \ldots\ldots(B33) $$

and can be estimated using either expression for A.P. (see equations B31 and B32). However, since more parameter estimates are involved in equation B31 than in B32 the two estimates of ${}_{pop}U_t$ are not expected to be identical.

The integrals J_I and J_{II} are easily evaluated for $m = 2/3$ and $n = 1$ which, however, means to extend the use of Pütter's approximation beyond the growth curve proper. The approximation can be avoided by graphical interpolation after evaluating the integral

$$ J_x = \int_o^t (1-e^{-Kt})^{3x}\, e^{-Zt}\, dt $$

for $x = \{ 0, 1/3, 2/3, 1, 4/3 \}$:

$$ J_o = \int_o^t (1-e^{-Kt})^o\, e^{-Zt}\, dt = A; \qquad A = \frac{1-e^{-Zt}}{Z} $$

$$ J_{1/3} = \int_o^t (1-e^{-Kt})\, e^{-Zt}\, dt = A - B; \qquad B = \frac{1-e^{-(Z+K)t}}{Z+K} $$

$$ J_{2/3} = \int_o^t (1-e^{-Kt})^2\, e^{-Zt}\, dt = A - 2B + C; \qquad C = \frac{1-e^{-(Z+2K)t}}{Z+2K} $$

$$ J_{3/3} = \int_o^t (1-e^{-Kt})^3\, e^{-Zt}\, dt = A - 3B + 3C - D; \qquad D = \frac{1-e^{-(Z+3K)t}}{Z+3K} $$

$$ J_{4/3} = \int_o^t (1-e^{-Kt})^4\, e^{-Zt}\, dt = A - 4B + 6C - 4D + E; \qquad E = \frac{1-e^{-(Z+4K)t}}{Z+4K} $$

$$ \ldots\ldots(B34). $$

Beverton and Holt (1957) define annual production (A.P.) as the production of only the exploited phase of the population. The same restriction is not made here: annual production can be estimated for any phase (any age interval). All integrations are made between zero time and time t. Integrations from $t = t_1$ to $t = t_2$ are supposed to be made in two stages, from 0 to t_2 and from 0 to t_1, subtracting afterwards the latter from the former. This simplifies each integration which is advantageous if the computations are to be made by means of programmed desk-top calculators or computers. It probably simplifies programming, shortens the program, and reduces the demands for memory.

The parameters of the present paragraph can be estimated from data on growth rate and ration eaten (App. VII). Several may as well be determined from data on ration eaten and oxygen consumption (App. IV).

C. GROWTH AND TEMPERATURE

Several attempts at describing growth or respiration as a function of temperature have been made. Some attacks are clearly empirical, others less so, speaking in vague terms of, e.g. the effect of interaction of enzymes; a rigorous mathematical model based on kinetic forces (Rashevky, 1960) is strictly applicable on the cellular level only. Pütter's (1920) hydraulic analog leads to sensible results but, unfortunately, I cannot quite follow his argument and therefore must refrain from discussing it. A reasoning along chemical lines, however, leads easily to an applicable although perhaps too flexible model.

Assume that metabolic processes in general proceed as described by the Michaelis–Menten equation, i.e. that enzyme, substrate, and water form a complex which under splitting of the water and substrate molecules forms products and free enzyme.

With additional assumptions specified by Casey (1962, p. 203) whose notation is used below, the velocity of the catalyzed process is

$$v_2 = -\frac{d[\mathrm{S}]}{dt} = \frac{k_2[\mathrm{E}]_o\,[\mathrm{S}]_o}{k_{-1}k_1^{-1} + [\mathrm{S}]_o}$$

where brackets denote concentrations in moles or gram per cm^3. E is enzyme and S substrate; the subscript *o* denotes initial concentrations; k_1 and k_{-1} are the rate constants for forward and backward reactions at the formation of the Michaelis complex, ES; k_2 is the rate at which products are formed; t is time.

Assume also that the velocity of each process involved is a function of activation energy and thus, in solutions, of temperature according to the equation of Arrhenius:

$$k = \mathrm{A}\,e^{p\tau}$$

where τ is the temperature in centigrades and A is the rate constant for $\tau = 0$.

Then
$$v_2 = -\frac{d[\mathrm{S}]}{dt} = \frac{\mathrm{A}_2 e^{p_2\tau}\;[\mathrm{E}]_o\,[\mathrm{S}]_o}{\mathrm{A}_{-1}e^{p_{-1}\tau}\;\mathrm{A}_1^{-1}\;e^{-p_1\tau} + [\mathrm{S}]_o}$$

$$\frac{1}{v_2} = \frac{\mathrm{A}_{-1}}{\mathrm{A}_1\mathrm{A}_2\,[\mathrm{E}]_o\,[\mathrm{S}]_o}\;e^{(p_{-1}-p_1-p_2)\tau} + \frac{1}{\mathrm{A}_2\,[\mathrm{E}]_o}\;e^{-p_2\tau}$$

Putting $\frac{1}{\mathrm{A}_2\,[\mathrm{E}]_o} = b$, $\frac{\mathrm{A}_{-1}}{\mathrm{A}_1\,[\mathrm{S}]_o}\,b = a$ and $p_{-1}-p_1-p_2 = p_0$ gives

$$\frac{1}{v_2} = a e^{p_0\tau} + b e^{-p_2\tau} \qquad \text{.....(C1)}$$

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where a, b, and p_2 are positive, p_o either negative or positive. When concentration is measured in g cm^{-3}, v_2 has the dimension g cm$^{-3}t^{-1}$. Since we are assuming a density of one for the fish body, g and cm^{-3} cancel out and v_2 becomes a rate constant (reciprocal of time). If the growth equation is written in the form

$$\frac{dw}{dt} = \eta w - \kappa w$$

η and κ are, for any fixed value of w, rate constants supposed to behave according to equation C1:

$$\frac{1}{\eta} = {}_\eta a e^{\eta p_0 \tau} + {}_\eta b e^{-\eta p_2 \tau} \qquad .....(C2)$$

$$\frac{1}{\kappa} = {}_\kappa a e^{\kappa p_0 \tau} + {}_\kappa b e^{-\kappa p_2 \tau} \qquad .....(C3).$$

Substituting in equations C2 and C3 H for η and k for κ is formally wrong (except for Pütter's k in equation (1)). Yet they provide good working approximations with the virtue of depending less (or not at all) upon body size than η and κ. Thus,

$$\frac{1}{\mathrm{H}} = {}_\mathrm{H} a e^{\mathrm{H} p_0 \tau} + {}_\mathrm{H} b e^{-\mathrm{H} p_2 \tau} \qquad .....(C4)$$

$$\frac{1}{k} = {}_k a e^{k p_0 \tau} + {}_k b e^{-k p_2 \tau} \qquad .....(C5).$$

For applications see App. III and XIII. The applications show that equation C5 may often be further simplified to a single exponential function,

$$k = k_o l^{p_k \tau} \qquad .....(C6)$$

where p_k is positive.

Differentiating equation C1 with respect to τ, putting the derivative equal to zero and solving for τ gives τ_m, the temperature for which v_2 has maximum.

$$\tau_m = \frac{ln\left(\frac{p_2}{p_0}\frac{b}{a}\right)}{p_0 + p_2} \qquad .....(C7).$$

The maximum exists only for $p_0 > 0$. Taking τ' as an exit instead of 0 C does not vitiate the proportionality with Kelvin degrees and, for $p_0 = p_2 = p$ and $a = b$ reduces equation C1 to

$$\frac{1}{v_2} = \frac{1}{v_2{}'} \cosh p(\tau - \tau') \qquad .....(C8)$$

which is the catenary curve found empirically by Janisch (1927) to describe the temperature dependence of the growth rate of young animals. It was applied to fishes by Ursin (1963a). The introduction of equation C8 is a trick rather than an approximation because when equation C1 represents a symmetrical curve, a and b usually differ by several size orders. It is a demonstration of the general flexibility of compound exponential functions. The experience warns against putting too much faith into the physiological relevance of parameter values estimated from such curves (Riggs, 1963).

The above results incorporated in equation A19 gives the asymptotic weight as a function of temperature. Thus, using equations C4 and C6 and omitting for simplicity the subscript H:

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} = \left[(ae^{p_0\tau} + be^{-p_2\tau})\ k_o e^{p_k\tau} \right]^{-\frac{1}{n-m}} \qquad \ldots\ldots(C9.)$$

Differentiating with respect to τ, putting $dW_\infty / d\tau = 0$ and solving for τ gives the temperature, $\tau_{\infty m}$, at which the asymptotic weight is maximum:

$$\tau_{\infty m} = \frac{ln \left(\frac{p_2 - p_k}{p_0 - p_k} \frac{b}{a} \right)}{p_0 + p_2} \qquad \ldots\ldots(C10).$$

The maximum exists when

(1) $p_0 < -p_k$ and $p_2 < p_k$

(2) $p_0 > -p_k$ and $p_2 > p_k$

The growth rate as a function of temperature is obtained by inserting equations C4 and C5 into equation B8:

$$\frac{dw}{dt} - = (ae^{p_0\tau} + be^{-p_2\tau})^{-1} w^m - k_o\, e^{p_k\tau} w^n \qquad \ldots\ldots(C11).$$

Differentiating $\frac{dw}{dt}$ with respect to τ for constant w and putting the derivative equal to zero leads to the expression

$$k_o p_k e^{p_k \tau_{mg}} w^{n-m} = \frac{p_2 b e^{-p_2 \tau_{mg}} - p_0 a e^{p_0 \tau_{mg}}}{(be^{-p_2 \tau_{mg}} + ae^{p_0 \tau_{mg}})^2} \qquad \ldots\ldots(C12)$$

which can be solved by iteration for τ_{mg}, the temperature at which the growth rate is maximal, for any fixed body size. In one of the limiting cases, $w = 0$, we have $\tau_{mg} = \tau_m$ (equation C7) because, by experience, $n > m$, so that the second right-hand term of equation C11 disappears more rapidly than the first one when $w \rightarrow 0$. At the other limit, $w = W_{\infty m}$ (the value W_∞ attains for $\tau = \tau_{\infty m}$) we have $\tau_{mg} = \tau_{\infty m}$. Application: App. XIII.

D. FASTING CATABOLISM AND OXYGEN SUPPLY

The best clue to the understanding of the relationship between the rate of catabolic processes and the oxygen concentration of the surrounding medium is probably found in Rashevsky's cell model. It has the virtue of being based on phenomena (mainly diffusion and permeability) for which comparatively precise theories are available. In Rashevsky (1960), to which the reader is referred, he has developed a simple model of oxygen supply and oxygen consumption of unicellular organisms, or of individual cells of a multicellular organism.

Let c be the outer oxygen concentration (g cm^{-3}) and Q the rate of oxygen consumption (g cm^{-3} sec^{-1}), with Q* being the asymptotic value of Q, corresponding to $c = \infty$. Then Rashevsky's equation (55) can be written

$$\frac{c}{Q/Q^*} = -\Lambda Q^* + \xi\left(1-\frac{Q}{Q^*}\right)^{-1} \qquad .....(D1)$$

where Q and Q*, being consumptions, are negative. ξ is the concentration of intermediary metabolic products (g cm^{-3}, examplified in the model by lactic acid) and does not particularly interest us here. Λ (sec) is the duration of the oxygen transport through external and internal media and through the cell membrane. Equation D1 is not defined for $Q = Q^*$ in which case, according to Rashevsky's equation (54), Q is independent of Λ. Equation D1 is linear in cQ^*/Q and $(1-Q/Q^*)^{-1}$ so that Λ and ξ can be estimated when Q is known for a range of values of c, some of which are high enough to permit a guess at the asymptote, Q*.

To adapt equation D1 to multicellular organisms is mainly to sum up the oxygen consumptions of individual cells. The organization, however, of such organisms complicates matters because an intermediate medium, the blood, is often introduced between the water and the cell plasma. Λ, therefore, must be redefined to cover the full transport time of oxygen from the water, through the gills, within the blood and through cell membranes and plasma to the exact spot where it is being used. The new Λ has two main components. One is the sum of the Λ,s of individual cells through or into which the oxygen must pass. This first component, Λ_1, is a function of the organizatorial level of the animal and of cell size, but is assumed to be independent of body size. The second component is the transport time for oxygen in the vascular system. The simplest assumption is that it is proportional with length or, because $w = ql^3$, with $w^{1/3}$. Then,

$$\Lambda = \Lambda_1 + \lambda w^{1/3} \qquad .....(D2)$$

where the dimension of λ is sec $g^{-1/3}$. Inserting the foregoing in equation D1 gives

$$\frac{c}{Q/Q^*} = -(\Lambda_1 + \lambda w^{1/3})\,Q^* + \xi\,(1 - \frac{Q}{Q^*})^{-1} \qquad .....(D3).$$

Thus, when data for oxygen concentration, c, and consumption, Q, are available for a range of body size, separate estimates of Λ_1 and λ can be made by application of equation D2. See App. VI.

Confining ourselves to the study of fasting catabolism we have by means of equation A9

$$\left.\begin{aligned} wQ &= \left(\frac{dO_2}{dt}\right)_{fasting} = \omega\left(\frac{dw}{dt}\right)_{fasting} = -\,\omega\, k w^n \\ Q &= -\,\omega\, k w^{n-1};\; k = -\frac{Q}{\omega}\, w^{1-n} \\ Q^* &= -\,\omega\, k^*\, w^{n-1};\; k^* = -\frac{Q^*}{\omega}\, w^{1-n} \end{aligned}\right\} \qquad .....(D4)$$

where k^* is the value k attains when $c = \infty$. Equation D4 shows how equation D3 can be applied to data of weight loss during fasting, namely, by the substitution of the rate of weight loss per cm^3 (i.e., per g) for the corresponding rate of oxygen consumption:

$$Q = \frac{\omega}{w}\left(\frac{dw}{dt}\right)_{fasting}.$$

When k is a simple exponential function of temperature,

$$k = k_o e^{p_k T} \qquad .....(C6)$$

Λ and Λ_1 are likely to have negative temperature coefficients, because having the dimension of time they can be considered reciprocal rate constants. Even λ, also having time in the denominator of the dimensional expression (sec $g^{-1/3}$), is suspected of having a negative temperature coefficient. Tentatively, therefore,

$$\Lambda = \Lambda_0 e^{p_\Lambda T};\; \Lambda_1 = \Lambda_0\, e^{p_{\Lambda 1} T};\; \lambda = \lambda_0 e^{p_\lambda T} \qquad .....(D5)$$

where the p's are negative. Again, see App. VI.

E. METABOLIC RATES AND NATURAL MORTALITY

Natural mortality, as usually defined by fishery biologists, is the sum of all causes of mortality except fishing and tagging mortalities. Thus, natural mortality may have both physiological and environmental components. An example of the latter is the activity of predators. Most predators of fish probably are other fish so that the chance of a fish being eaten depends, among other things, upon the number of fish bigger than itself. The reality of a correlation of natural mortality with growth parameters is beyond doubt after the studies of Taylor (1958) and of Beverton and Holt (1959) although uncertainty remains as to which parameter, or parameters, the correlation concerns. Roughly, the situation is that small species have a higher natural mortality rate than big ones. More shall be said on this subject here whereas another aspect of the problem, that of the possibly shorter life-span of small species due to early onset of senility, is passed over.

Since every time a molecular interaction occurs within a cell there must be a chance that something will go wrong, it is not unreasonable to assume that natural mortality as a physiological phenomenon is proportional with the density of molecular interactions in unit time. It can also be assumed that a constant percentage of the cells of the body can be maladjusted at the same time without causing disaster and that, because cell size is usually constant, units of weight can be dealt with instead of number of cells. For the sake of simplicity it shall further be assumed that the number of molecular interactions, and the proportion of faulty interactions, is the same when 1 g of substance is being built up as when it is broken down.

Putting $h_1 f \beta = h$ and dividing the growth equation for the whole fish,

$$dw/dt = h\,w^m - \alpha\,h\,w^m - k\,w^n \qquad \ldots\ldots(\mathrm{B8})$$

by w gives the growth rate per gram:

$$\frac{dw/dt}{w} = h\,w^{m-1} - \alpha\,h\,w^{m-1} - k\,w^{n-1} \qquad \ldots\ldots(\mathrm{E1}).$$

On the assumptions made above, the density of molecular interactions is proportional with the right-hand side of equation E1 when each term is allotted a positive sign. This density, again, should be proportional with the natural mortality to the extent that mortality is a metabolic event. We therefore can put

$$\mathrm{M} = \mu\left((1+\alpha)\,h\,w^{m-1} + k\,w^{n-1}\right)$$

where M is the instantaneous coefficient of natural mortality and μ a dimensionless proportionality constant. Inserting $\mathrm{H} = (1-\alpha)h$ from equation B8 gives

$$\mathrm{M} = \mu\left(\frac{1+\alpha}{1-\alpha}\,\mathrm{H}\,w^{m-1} + k\,w^{n-1}\right) \qquad \ldots\ldots(\mathrm{E2})$$

as applied in App. XII.

Parameter estimates have shown that the second term of equation E2 is probably negligible. Frank approximations led to the rule of thumb,

$$\mathrm{M} \approx w^{-1/3}$$

for species of a size order of $\mathrm{W}_\infty = 10^3$g.

F. LINKING UP WITH WINBERG'S MODEL

One of the major obstacles encountered when comparing mathematical models is a trivial one: that of notation. Differences in notation often obscure important identities or disagreements of basic concepts and underlying assumptions. In order to evaluate the specific merits of each model and decide which can be used with most advantage in the actual situation it is necessary to realize the limitations of applicability of the individual models and the functional relationships between their parameters. There are two recently published models covering more or less the same ground as the one presented. One was described by Winberg in 1956, the other by Paloheimo and Dickie in three papers (1965, 1966a, b). A key to the notation of Winberg's model in terms of the present one is given below, after a discussion of some interesting points. A similar translation of the Paloheimo–Dickie model was intended but not made because it would have been too complicated for practical purposes.

Winberg's growth equation, "the basic balanced equation," is an energy account. It runs (1956, p. 209)

Energy of weight increase + energy of metabolism
= physiologically useful energy
= 0.8 times the energy of the ration

or, in letters (p. 228)

$$P + T = 0.8 \text{ R}.$$

The physiologically not useful energy of the food, 0.2 R, is that lost in excrements and urine. The estimate was obtained experimentally as an average for several investigations. A possible dependence upon the feeding level (as assumed by Kostitzin, Ivlev, and myself) is not discussed. The estimated useful fraction, 0.8, is closely related to β which is the fraction absorbed of the food eaten (equation B3). The energy loss through urine is not accounted for specifically in the present model, but is included in α. For most purposes we can, I think, put $0.8 \text{ R} = \beta \, d\text{R}/dt = dr/dt$ where the left-hand term is in Winberg's terminology and the others in mine.

Winberg's energy of metabolism, T, is total catabolism in the other model apart from the fact that one computes in calories, the other in units of weight. T is estimated as the energy equivalent of the oxygen consumption of a comparatively quiet fish, and multiplied by 2 to match the metabolism of the more active, feeding fish. To Winberg, the metabolic level is a function of activity. He does not appreciate feeding catabolism as physiologically distinct from active metabolism. The present paper (following Saunders 1963, see App. IV) recognizes feeding catabolism as a mainly physiological event: the fed fish has a higher metabolic rate than the fasting one, even when at rest. The activity necessitated by feeding is here pushed into the background, being made proportional with the ration taken.

Winberg develops T as a function of body size by means of the so-called "basic equation."

$$Q = A \, w^k$$

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where Q is the
tively quiet fish
conversion of o

(the symbol C_1
equation A12 i

which specifies,
Converting equ
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where D, howe
and $C_3 \, \beta \, d\text{R}/d$

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$T =$

where Q is the rate oxygen consumption in millilitres per hour of a comparatively quiet fish, measured at 20 C. Introducing an expression, C_1, for the conversion of oxygen consumed to calories liberated we have

$$T = 2C_1 Q = 2C_1 A w^k$$

(the symbol C_1 is my own invention). The foregoing is virtually the same as equation A12 in the present paper,

$$dO_2/dt = -D w^d$$

which specifies, however, neither feeding level, nor activity, nor temperature. Converting equation A12 from gram per hour to energy equivalents by multiplying by C_2 we have

$$T \approx C_2 D w^d$$

where D, however, is a function of the feeding level. Writing $C_3\, dw/dt$ for P and $C_3\, \beta\, dR/dt$ for 0.8 R Winberg's balanced equation becomes

$$C_3\, dw/dt = C_3\, \beta\, dR/dt - C_2\, D\, w^d$$

or

$$C_3\, dw/dt = C_3\, dr/dt - C_2\, D\, w^d.$$

C_3 is common to the increment and food terms because we are here assuming that the fish and its food have the same chemical composition (see Introduction) Winberg finds $d \approx 0.8$ which is a good working approximation irrespective of the feeding level. Saunders (see App. IV) found $d = 0.79$ for fed cod and $d = 0.84$ for fasting ones.

Winberg did not develop dr/dt as a function of body size which limits the applicability of the model. However, inserting equation B4 does it:

$$C_3\, dw/dt = C_3\, h\, w^m - C_2\, D\, w^d.$$

In this form and evaluated for some fixed feeding level (e.g. that corresponding to twice the "basic" metabolic level, as Winberg finds it useful to do) "the balanced equation" should be more handy for a purpose for which it has been used: the computation of food or oxygen requirements or of the growth rate of fishes in pond farms. In its original form the equation fails to indicate that the growth rate slows down in old (big) fishes.

The coefficients cannot, unfortunately, be estimated from growth data alone because feeding catabolism, $\alpha\, h\, w^m$ in the present model, in Winberg's is added to the positive term as well as to the negative one and cancels out in studies of growth curves. Partitioning total catabolism into feeding and fasting components we have by means of equation A11

$$T = C_2\, D\, w^d \approx C_2\, (\omega\, \alpha\, h\, w^m - \omega\, k\, w^n) = C_3\, (\alpha\, h\, w^m - k\, w^n).$$

Insertion in Winberg's equation gives

$$C_3\, dw/dt = C_3\, h\, w^m - C_3\,(\alpha\, h\, w^m + k\, w^n) = C_3\,(1-\alpha)\, h\, w^m - C_3\, k\, w^n = C_3\, H\, w^m - C_3\, k\, w^n$$

which apart from the conversion to energy equivalents is identical with equation B8.

Except for the small differences in the underlying assumptions of the two models discussed above, the following key to Winberg's notation can be used:

WINBERG'S NOTATION	NOTATION OF THE PRESENT PAPER
p (cal/time)	dw/dt (weight/time)
T (cal/time)	Total catabolism $= -(h\, w^m + k\, w^n)$; (weight/time)
R (cal/time)	dR/dt (weight/time)
0.8 (pure number)	β (pure number)
0.8 R (cal/time)	dr/dt (weight/time)
Q (vol/time)	dO_2/dt (weight/time)
A (vol^{1-k}/time)	D (weight^{1-d} /time)
k (pure number)	d (pure number)
$K_1 = 100p/R$ (pure number)	$100\, u = 100\, dw/dR$(pure number)
$K_2 = K_1/0.8$ (pure number)	$100\, u/\beta$ (pure number)

SUMMARY AND DISCUSSION

The metabolic model have two fundamental parameters, namely the powers m and n in the equation

$$\frac{dw}{dt} = H\, w^m - k\, w^n \qquad \ldots\ldots(B8)$$

upon which further parameter estimation depends. They can be defined as the values making the instantaneous coefficients, H and k, of anabolism and catabolism independent of body weight during the growth of the individual. So many attempts at estimating m and n were made in the Appendixes below that a survey of methods and results is called for. Afterwards, other parameters shall be discussed.

ESTIMATES OF n

There are three entirely independent ways of estimating n: (1) From growth data, inserting simultaneous observations of increment and weight in equation B8 or one of its derivatives (App. X); (2) From the rate of catabolism of fasting fishes. When no food is given the anabolic term of equation B8 is zero. Assuming that the oxygen consumed is used up in catabolic processes we have

$$\frac{dO_2}{dt} = \omega \frac{dw}{dt} = -\,\omega\, k\, w^n$$

where $\omega = dO_2/dw$. Using logarithms, n can be estimated as the slope of a straight line when values of weight and either oxygen consumption or weight loss rates are inserted (App. IV, V, and IX). Fed fishes cannot be used because activities of feeding and assimilation are assumed to increase the metabolic rate proportionately, i.e. with w^m, according to the anabolic term of equation B8. Fish fed maintenance ration are an exception (see equation B17). (3) From observations on respiratory surface and body size, assuming that the oxygen consumption of a fasting fish is proportional with respiratory surface (App. XIV).

The estimates made in App. II–XIV are listed in Table I. The figures in parentheses are 95% confidence intervals. There is no obvious disagreement between the results obtained with different methods, so that the model cannot be rejected on this evidence. The interspecific differences are probably not reliable. As a common estimate, $n = 5/6$ seems to be the best guess.

ESTIMATES OF m

There seems to be two ways of estimating m independently of other parameters. 1. Measuring the absorbing surface of the intestine on the assumption that absorption is proportional with the absorbing surface. There are technical difficulties and no reliable estimate is available. 2. Measuring the rate of food consumption in a medium of constant food concentration. This requires the further assumption that food consumption is proportional with absorption, i.e. that the digestion of the ingested food is as efficient in a small specimen as in a big one. Few and rather contradictory data are available.

There are two other methods of estimating m which can be used only when n and k are known. 3. One method is based on the oxygen consumption of fed fishes on the assumption that the extra respiration of fed fishes, as compared with fasting ones, is proportional with the quantity of food absorbed, i.e. with the absorbing surface of the intestine. Thus

$$\left(\frac{dO_2}{dt}\right)_{feeding} = \left(\frac{dO_2}{dt}\right)_{fed} - \left(\frac{dO_2}{dt}\right)_{fasting} \approx -\left(D_w{}^{d} - \omega k w^n\right) \approx -\omega \alpha\, h\, w^m$$

where the proportionality constants do not interest us in this connection. I know of only one investigation of the sort (Saunders, 1963, on cod). 4. The last method is to compute m from growth rate data. Rearranging the growth equation and taking logarithms gives

$$ln\left(\frac{dw}{dt} + k\, w^n\right) = ln\ \mathrm{H} + m\ ln\ w \qquad \text{.....(B8).}$$

The estimate of m is unbiased only when the theoretical values, instead of estimates, of k and n can be inserted.

The estimates made are listed in Table I. They tend to $m < 2/3$. Owing to the many sources of bias it is not yet warranted, however, to reject definitely

TABLE I. Estimates of n, m, and p_k made in various ways in App. II–XIV.

Method of estimation	App. No.	Estimate of n	Estimate of m	Estimate of p_k
Oxygen consumption, many species	II	≥ 0.75		
" " goldfish	III			0.083
" " cod	IV	0.84	0.69	0.060
" " tench	V	0.71		0.084
" " speckled trout	VI			0.090
Food consumption, plaice	VII		0.34; 0.53; 0.65	
Surface of intestine, sole			0.57 (0.33–0.80)	
Weight loss, tench	V			0.096
" " *Lebistes*	VIII			0.071
" " " acclimated	VIII			0.048
" " several species	IX	0.83 (0.78–0.89)		
Growth rates, many species	X	0.83 (0.77–0.89)	for n = 0.83: 0.59 (0.56–0.61)	
" " *Lebistes*	XIII		for n = 1: 0.50 (0.42–0.58)	0.085
Respiratory surface, *Micropterus*	XIV	<0.78		
" " many species	XIV	<0.83		
" " *Zoarces*, eel	XIV	0.83		

the hypothesis of isometric growth (i.e. $m = 2/3$) involved in Pütter's original model. The low value ($m = 0.50$) for *Lebistes*, a very small fish, raises a suspicion that m may be a function of asymptotic size. An increase of m from 0.50 in the smallest species to 0.67 in the biggest ones would not be at variance with the findings in App. X.

The present knowledge of m is not as precise as that of n although it is good enough for most practical purposes. Even the original model, with $n = 1$ and $m = 2/3$, is still the best approach in many cases, particularly because it is easily integrated and describes nicely the growth curves of most fishes. It should probably not be abandoned except when the line of reasoning makes it necessary to use more accurate estimates of the parameters, particularly in metabolic studies.

It is remarkable how well the Pütter approximation has worked in the extensive model developed by Beverton and Holt (1957). Through over 400 pages of text there is only one situation, as far as I can see, where the approximation would lead to obvious disaster. It is in the case of estimating the maintenance ration as a function of body size (p. 301). According to the model the maintenance ration should be almost proportional with the catabolic rate ($-kw$) with reversed sign and, thus, with body weight. That, however, is a hypothesis which can easily be rejected. Beverton and Holt avoid the trouble by introducing an empirical relationship, ζw^j. By an unfortunate choice of experimental data they are led to the belief that $j = 2/3$, whereas $j = n = 5/6$ would have been more appropriate. With this small amendment the Beverton–Holt model remains unrejected as far as it goes, because separate estimation of catabolic parameters was not attempted elsewhere, except for casual references to a paper by von Bertalanffy in which some misconceptions had crept in.

ESTIMATES OF H AND k

The equation for asymptotic size

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \text{.....(A19)}$$

shows that one or several of the four fundamental parameters of the growth equation are functions of asymptotic size, i.e. of the size of the species. There is plenty of evidence (App. II) that with few exceptions n is practically constant throughout the animal kingdom, and in App. IX it was found that the coefficient of fasting catabolism, k, is independent of asymptotic size in fishes. Thus, either H or m, or both, must depend upon asymptotic size. Assuming m constant it was found in App. X that at about 10 C the mean value of H varies (in units of $g^{0.44}$ $years^{-1}$) from 1 in small species to 40 in big ones. At the same temperature k was found to be about 2.5 $g^{1/6}$ $years^{-1}$ as an average for 81 fish species. The obscure dimensional relations are introduced with the exponential functions H w^m and $k\ w^n$ in the growth model. One of several advantages of Pütter's simple model:

$$\frac{dw}{dt} = \mathrm{H}\ w^{2/3} - k\ w \quad \text{or} \quad \frac{dl}{dt} = \mathrm{E} - \mathrm{K}\ l \qquad \text{.....(A23)}$$

is that the coefficients have the simple physical dimensions of rate and speed.

The variation of k with temperature was investigated for several species (App. III-VI, VIII, and XIII) and that of H for *Lebistes* (App. XIII). k increases almost exponentially with temperature. The temperature coefficient, p_k of equation C6: $k = k_0\ e^{p_k T}$ was estimated in several ways, and the results listed in Table I.

The average of the eight available estimates is $p_k = 0.78$ which means that a temperature increase of 10 C causes k to increase by a factor 2.2 or approximately, what one would expect in a simple chemical process. The two estimates for *Lebistes*, acclimated since birth to the experimental temperature are interesting because Stroganov (1956) found that fish respiration is less dependent on temperature in the vicinity of the temperature to which the fish is accustomed. Accordingly, the estimate from weight loss data ($p_k = 0.048$) is definitely on the low side. That from growth data ($p_k = 0.085$) over the same temperature range, however, is not. Winberg (1956) doubts the validity of Stroganov's conclusions and points out that even if reliable they would not necessarily lead to a reduced temperature coefficient over a wide range of temperature.

The exponential approximation,

$$k = k_0\ e^{p_k T} \qquad \text{.....(C6)}$$

is not sufficiently good when a wide temperature interval is investigated, as for instance in App. III (28 C). In such cases it is necessary to return to the theoretically better founded approximation.

$$\frac{1}{k} = a\ e^{p_0 T} + b\ e^{-p_2 T} \qquad \text{.....(C5)}$$

which describes adequately the respiration of Krogh's famous goldfish as a function of temperature (App. III). Anabolic processes, as indicated by the instantaneous coefficient H, seem to have a definite temperature maximum. This was found in the single case investigated here (App. XIII) and is confirmed by previous work (Ursin 1963a, b). The model describes the variations adequately by means of a sum of two exponentials.

A hypothesis on the influence of the oxygen concentration in the surrounding medium is presented in what is probably the most airy part of the model. The duration of oxygen transport in the body (through tissues and in the vascular system) is involved and is estimated indirectly in

App. VI. The obvious way to reject the hypothesis is to obtain somehow a direct measurement of the duration of oxygen transport and compare with the estimates obtained by indirect methods. These indicated that the average time needed by an oxygen molecule to travel from a situation immediately outside the gill surface to the exact spot where it is being used is of the size order 10^2 sec. The choice of the speckled trout, *Salvelinus fontinalis,* for the computations in App. VI is probably a lucky one although it was made merely because good data were available. The respiration of *Salvelinus* is unimpeded only at oxygen concentrations above the saturation point of water, and the effects of oxygen concentration upon the catabolic processes can be followed over a wide range of concentration. In many other species the respiration seems to be practically maximum at an oxygen concentration slightly over the asphyxiation level, as can be seen from data compiled by Winberg (1956).

The model of the influence of feeding upon growth is closely related to that presented by Beverton and Holt (1957). In the present model, however, the partitioning of total catabolism into fasting catabolism ($-k\,w^n$ in the growth equation) and feeding catabolism ($-\alpha\,h\,w^m$), the latter proportional with anabolism, is more complete. We have

$$\frac{dw}{dt} = h\,w^m - (k\,w^n + \alpha\,h\,w^m) = \mathrm{H}\,w^m - k\,w^n \qquad \ldots..(\mathrm{B8}).$$

This formulation seems to have led to more adequate concepts of efficiency of food conversion as a function of time and size (equations B20, B21, and B26).

The same formulation is used in a model of natural mortality as a metabolic event. It is assumed that each molecular reaction has an equal chance to go wrong, with the risk of killing the fish. Assuming further, that the number of molecular reactions performed is proportional with the sum of the weights of material built up and material broken down, leads to a hypothesis (equation E2) implying that small species have the highest mortalities. This is in accordance with experience, but it is not quite obvious how, if wrong, the basic concepts of the hypothesis (mortality introduced with molecular interactions) can be rejected by direct observation.

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APPENDIXES

The examples below (App. II–XIV) are selected in such a way that, as far as possible, they indicate different ways of estimating the same parameter. Of particular interest is to obtain estimates of the same parameter from both respiration and growth data because the limitations of the applicability of the model can be expected to come out clearly that way. This, however, has not been possible with all parameters.

It was attempted to keep each example independent of the others. This, however, could not be accomplished because it was often necessary to "borrow" a parameter estimate from another example. Particularly, App. X, XI, and XII are closely linked by parameter estimates, and so are App. VIII and XIII.

Under each caption are listed the parameters estimated in that paragraph. An index of the notation adopted is given as App. I. It includes references to parameter estimates in the examples. A discussion of methods and results of parameter estimations is found above.

Many linear regression analyses, by the method of least squares, have been made regardless of the fact that the independent variable varies stochastically. This means that the slopes are more or less underestimated throughout.

APP. I. NOTATION

Most of the symbols used are defined below. Some of those omitted are of restricted use in the paragraphs "Growth and Food" or "Growth and Temperature" and do not appear in the final equations. Others are auxiliary parameters introduced occasionally in the Appendixes. Some letters from the standard notation of mathematical statistics have been used without, I hope, great risk of confusion with the parameter notation.

After each definition is added, in parentheses, the serial number of the equation in which the letter in question is introduced. The parenthesis is followed by the serial numbers of Appendixes in which estimates are made. A following expression, in brackets, indicates the dimension of the quantity in terms of W, weight; L, length; T, time; and C, temperature. Empty brackets indicate a pure number. Thus, e.g. B7 IV, VII [$W^{1/3}T^{-1}$] means that the parameter in question is introduced in equation B7, estimated in App. IV and VII, and expressed in terms of cube root of weight per unit time. The frequent use of empirical approximations lends non-physical dimensions to many quantities, e.g. powers of length other than 1, 2, or 3. Sometimes, the dimension of one parameter depends on the value of another.

Finally, the corresponding letter in the notation of Beverton and Holt (1957) is stated when the identity of the parameters is obvious, except for slight differences in the underlying assumptions.

LATIN LETTERS

A_b	Proportionality constant relating body area to body weight. A6 XIV [$L^2\ W^{-2/3}$]
A_g	Proportionality constant relating gill area to body weight. A6 XIV [$L^2\ W^{-n_g}$]
a b	Constants entering the expression for the velocity of enzymatic processes as a function of temperature. With suffixes indicating the group of processes (e.g. anabolic) concerned. C1–C5 III, XIII [Dimensions as v_2^{-1}]
B_b	Rate of oxygen consumption through the skin, in unit time and area. A7 [$W\ L^{-2}\ T^{-1}$]
B_g	Rate of oxygen consumption through the gills, in unit time and area. A7 [$W\ L^{-2}\ T^{-1}$]
C	Designates various arbitrary constants.
c	Oxygen concentration of the outer medium. D1 [$W\ L^{-3}$]
D	The instantaneous coefficient of oxygen consumption, disregarding the feeding condition of the fish. A12 II, IV [$W^{1-d}\ T^{-1}$]
d	The power of weight with which the rate of oxygen consumption is proportional, disregarding the feeding condition of the fish. A12 II, IV [ ]

E	The instantaneous coefficient of anabolism in the equation of growth in length (E $H/(3q^{1-m})$). A18 XIII $[L^{3(1-m)}\ T^{-1}]$. E
e	The base of natural logarithms. [ ]
f	The feeding level, i.e. the fraction of maximum food consumption practised. B1 VII
f_{maint}	The value of f corresponding to maintenance ration. B14 VII [ ]
f_{max}	The value of f ensuring maximum utilization of food for growth. B22 VII [ ]
H	The instantaneous coefficient of net anabolism. (Suffixes (${}_1H$ and ${}_nH$) indicate differen caused by the choice of values of other parameters.) 1 VII, X, XI, XII $[W^{1-m}\ T^{-1}]$.
h	The instantaneous coefficient of gross anabolism. B4 $[W^{1-m}\ T^{-1}]$
h_1	Another instantaneous coefficient of gross anabolism, made independent of rate of fo consumption and of fraction absorbed. A2 VII $[W^{1-m}\ T^{-1}]$
h_2	An arbitrary constant entering the expression for fraction food absorbed, β. B3 VII
J_x	An integral, further specified by some suffix. B28 VII [ ]. $\overline{P}_w\ x\ /\ R\ W_\infty{}^{2/3}$
K	The instantaneous coefficient of catabolism in the equation of growth in length ($K = k/(3\ q^{1-n})$). A18 XII $[L^{3(1-n)}\ T^{-1}]$. K
k	The instantaneous coefficient of fasting catabolism. (Suffixes (${}_1k$ and ${}_nk$) indicate differences caused by the choice of values of other parameters) 1 III, IV, VII, VIII, I X, XI, XIII $[W^{1-n}\ T^{-1}]$. k
k_0	k at 0 C. C6 III, V, VIII
k^*	The value of k when the outer oxygen concentration is infinite. D4
L_∞	Asymptotic length. A20 XIII [L]. L_∞
L_I	Length at point of inflection of the curve of growth in length. A21 [L]
l	Body length as a variable. [L]. l
l_t	Body length as a function of time. A27 [L]. l_t
M	The instantaneous coefficient of natural mortality. E2 XII $[T^{-1}]$. M
m	The power of weight with which the rate of anabolism is proportional. A2 IV, VII, X XIII [ ]. n
N_t	The number of fish in a population at time t. [ ]. N_t
N_0	The initial number. [ ]
N_r	The number of recruits at time t_r. [ ]. R
n	The power of weight with which the rate of fasting catabolism is proportional. A8 IV V, IX, X, XIV [ ]. m and j
n_g	Power of body weight with which gill area is proportional. A6 XIV [ ]
p p_0 p_2	Temperature coefficients of processes. Suffixes indicate the group of processes (e.g. anabolic) concerned. C1–C6, D5 III, IV, V, VI, VIII, XIII $[C^{-1}]$
pop	As a suffix distinguishes population parameters, accounting for mortality. B28
Q	Rate of oxygen consumption per unit body volume (or, because $w = ql^3$, per unit body weight). D1 $[W\ L^{-3}\ T^{-1}]$ or $[T^{-1}]$
Q*	The value of Q for infinitely high oxygen concentrations in the outer medium. D1
q	Proportionality factor relating body weight to body length. $[W\ L^{-3}]$. q
q'	Proportionality factor relating body surface to body length. [ ]. p
R	Weight of food consumed. A1 [W]. ξ

R_t	Food consumed up to time t. B24 VII [W]. ξ
r	Weight of food absorbed. [W]
S_b	Body surface area excluding gills. A6 XIV [L^2]
S_g	Gill surface area. A6 XIV [L^2]
t	Time. 1 [T]. t
t_0	The time when the length of the fish is zero (the alleged birthday). A27 [T]. t_0
t_r	The age at recruitment counted from the moment when $t = 0$. [T]. t_ρ
t'_r	$= t_0 + t_r$: the age at recruitment counted from the alleged birthday, t_0. VII [T]
U	Effiency of utilization of total food up to time t. B26 VII [ ]
u	Efficiency of utilization of total food for growth, i.e. the fraction of total food actually appearing as growth. B21 VII [ ]
v	Efficiency of utilization of growth food for growth, i.e. the fraction of growth food actually appearing as growth. B20 VII [ ]. ϵ
v_2	Velocity of an enzymatic process. C1 [$W\ L^{-3}\ T^{-1}$] or [$L^{-3}\ T^{-1}$] or [T^{-1}]
W_∞	Asymptotic weight (suffixes (${}_1W_\infty$, ${}_nW_\infty$) indicate differences caused by the choice of other parameters). A19 VII, X, XI, XIII [W]. W_∞
$W_{\infty m}$	The maximum value of asymptotic weight as a function of temperature. See τ_{mg} [W]
W_I	Weight at point of inflection of the curve of growth in weight. A22 [W]
w	Body weight as a variable. [W]. w
w_t	Body weight as a function of time. (w_0, weight at time zero, etc.). A13 [W]. w_t
$\hat{w}$	Approximate mean weight of fish used in the estimation of a growth curve. (9–3) X, XII [W]
Z	The instantaneous coefficient of total mortality. B28 [T^{-1}]

Greek Letters

α	The fraction of gross anabolism spent on feeding catabolism. A3 VII [ ]
β	Fraction absorbed of food eaten. [ ]
β_{maint}	Fraction absorbed of maintenance ration. B12 VII [ ]
η	Proper rate constant of anabolism. C2 [T^{-1}]
κ	Proper rate constant of catabolism. C3 [T^{-1}]. k
Λ	Duration of oxygen transport. D1, D2 VI [T]
Λ_0	Λ at 0 C. D5 VI
Λ_1	Duration of oxygen transport through tissues. D2 VI [T]
Λ_{10}	Λ_1 at 0 C. D5 VI
λ	Coefficient of the duration of oxygen transport in the vascular system. D2 VI [$T\ W^{-1/3}$]
λ_0	λ at 0 C. D5 VI
μ	Proportionality constant relating natural mortality to metabolic rate. E2 XII [ ]
ξ	The concentration in the cell of certain intermediary metabolic products. D1 [$W\ L^{-3}$]
τ	Temperature in degrees centigrade. [C]
τ_m	The temperature at which an enzymatic process has maximum. C7 XIII [C]
$\tau_{\infty m}$	The temperature at which maximum asymptotic weight is attained. C10 XIII [C]
τ_{mg}	The temperature at which the growth rate is maximal. C12 XIII [C]
ω	Weight of oxygen consumed per unit weight lost during fasting. A10 V [ ]

APP. II. OXYGEN CONSUMPTION AS A FUNCTION OF BODY SIZE THROUGHOUT THE ANIMAL KINGDOM

ESTIMATES OF m AND n

Numerous experiments on oxygen consumption (see Hemmingsen, 1960) have shown that the relationship

$$\frac{dO_2}{dt} = Dw^d \qquad \ldots\ldots(A12)$$

where D and d are constants is a good approximation over a wide range of body size with d almost independent of the systematical position of the animal when insects are excepted. Few authors, however, state definitely how long the experimental animals had been fasting before the experiments and whether the fasting, if any, had its full effects on the respiration when the oxygen consumption was measured. Equation A12, therefore, is an approximation intermediary between equations A8 and A11 describing the oxygen consumption of fasting and fed fishes, respectively. Hemmingsen estimated $d = 0.75$ as an average for all animal groups. When homoiotherms, insects, and unicellular organisms are excluded, $d = 0.82$ is obtained (data read from Hemmingsen's (1960) fig. 3, 4, 5, 7, and 8). Individual estimates outside the range $2/3 < d < 1$ are rare. Since we have $d \leq n$, estimates of d are underestimates of n.

Winberg (1956, 1961) made a thorough and critical survey of the literature on fish respiration and found, for various systematical and ecological groups of fishes, mean values of d ranging from 0.78 to 0.81. Again, the utilization of the results is restricted by incomplete knowledge of the feeding condition of the animals during the experiment.

APP. III. OXYGEN CONSUMPTION OF A GOLDFISH

ESTIMATES OF k AND ITS TEMPERATURE COEFFICIENTS

Ege and Krogh (1914) owned a particularly sluggish goldfish (*Carassius auratus*) which they used in a series of respiration experiments. The respirational rate was unaffected by narcotics and the fish seemed able to adapt itself rapidly to any temperature between 0 and 28 C. It was usually allowed only 1 or ½ hr for acclimation to another temperature. Yet the results of 24 consecutive experiments were markedly stable and in accordance with Krogh's further work on other animals.

It is not definitely stated that the fish was fasting during the 22 days the experiments lasted, but the care with which many influences were brought under control infers that it probably was. Anyway, we shall assume so.

The interpretation of the experiments is based on equations A8 and C5:

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\ k\ W^n \qquad \ldots\ldots(A8)$$

$$\frac{1}{k} = {}_k a e^{{}_k p_0 \tau} + {}_k b e^{-{}_k p_2 \tau} \qquad \ldots\ldots(C5).$$

The weight of the fish, W = 9.3 g, is constant. Combining equations A8 and C5 and putting $n = 1$ we have

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = \frac{{}_k a}{\omega W}\ e^{{}_k p_0 \tau} + \frac{{}_k b}{\omega W}\ e^{-{}_k p_2 \tau} \qquad \ldots\ldots(2\text{-}1)$$

which is easily solved if data are available for four equidistant values of τ, particularly when as in the present case the lowest temperature is zero. Let i be the temperature interval and put

$$e^{i\ {}_k p_0} = A,\ e^{-i\ {}_k p_2} = B,$$

$$\frac{{}_k a}{\omega W} = a',\ \frac{{}_k b}{\omega W} = b' \text{ and } \frac{\tau}{i} = T\ (T = 0,\ 1,\ 2,\ 3),$$

then

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = a'\ A^T + b'\ B^T \qquad \ldots\ldots(2\text{-}2).$$

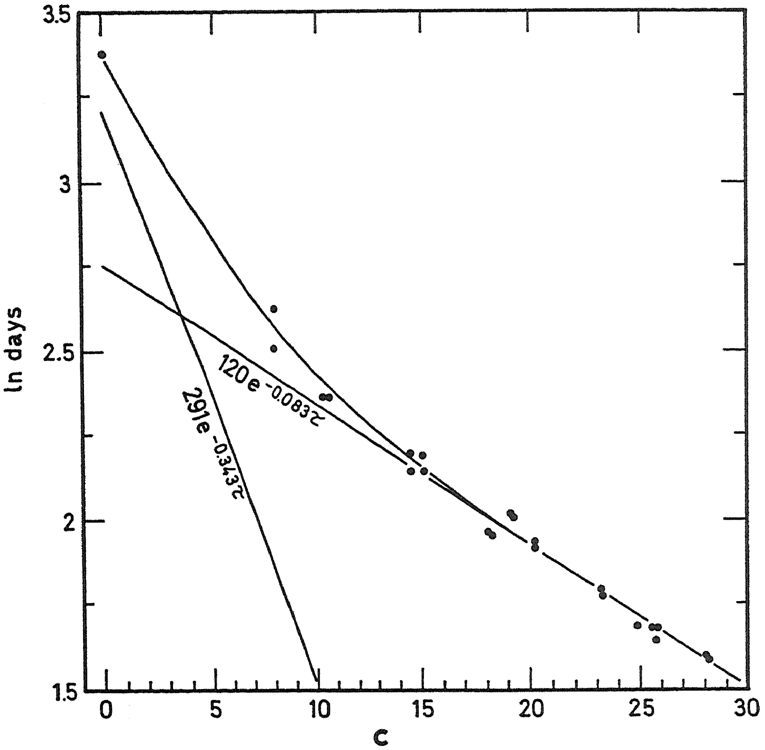
The observations are stated as cm³ of oxygen absorbed per minute and kg of body weight. They can be converted to grams oxygen per day for the whole fish by simple arithmetics, using the approximation $Q_w = Q_v\ (1 - \tau/273)32/22400$, where Q_w is the weight of oxygen in grams and Q_v its volume in cm³. The converted data are plotted against temperature in App. Fig. 1. An eye-fitted curve was read off at the temperatures 0, 8.6, 17.2, and 25.8. C (i.e. i = 8.6 C). The four observations were

T (°C×8.6^{-1})	$-\frac{dt}{dO_2}$ (days g^{-1})
0	41.2
1	74.2
2	29.7
3	14.2

The solution of equation 2-1 by the use of equation 2-2 is

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = 120\ e^{-0.0830\tau} + 291\ e^{-0.343\tau}$$

days per gram oxygen. Because $p_0 < 0$ the two right-hand terms of equation C5 are not distinguishable from each other.

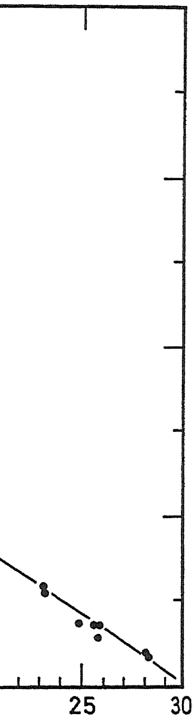


APP. FIG. 1. Oxygen consumption of one particular goldfish at a range of temperatures. The curved line is estimated from the model applied. Straight lines represent the two simple exponentials which, on summing, produced the curve. Units on the ordinate are days per gram oxygen absorbed (log scale). App. III.

$^{-1})$

$91\ e^{-0.343\tau}$

s of equation C5 are not di-



goldfish at a range
the model applied.
which, on summing,
am oxygen absorbed

For ω = 0.30 (see App. IV) and W = 9.3 g we further have

$$\left.\begin{matrix} {}_k a \\ {}_k b \end{matrix}\right\} \quad \left\{\begin{matrix} 336 \\ 813 \end{matrix}\right.$$

from which, with equation C5

$$\frac{1}{{}_1k} = 336\ e^{-0.0830\tau} + 813\ e^{-0.343\tau}\ \text{days.}$$

Notice (App. Fig. 1) that the first term alone is a good approximation at temperatures over 12 C. This simplifies the expression to equation C6:

$${}_1k = k_0\ e^{p_k\tau} \qquad \ldots\ldots(\text{C6})$$

$${}_1k = 1.09\ e^{0.0830\tau}\ \text{years}^{-1}$$

although the approximation makes the expression more or less empirical because it fits the points at any reasonably short range of temperature, also below 12 C. When its use is not warranted the estimates of k_0 and p_k depend upon the temperature interval covered.

Krogh's goldfish has become famous for the clarity and simplicity of the experiments and particularly because later research on many species and on large materials has confirmed the general applicability of the results (Winberg, 1956).

APP. IV. OXYGEN CONSUMPTION OF FED AND FASTING COD

ESTIMATES OF ωk, p_k, $\omega \alpha h$, m, AND n

A paper by Saunders (1963) contains data for estimation of ωk, $\omega \alpha h$, m, and n from equations A8 and A11.

Saunders (1963) investigated the rate of oxygen consumption in fed and fasting Atlantic cod (*Gadus morhua*) of a size range of 0.1–7 kg. He found that respiration decreased during the 1st week of fasting and, therefore, let the fish fast for 1 week before measuring the fasting metabolism. The experimental device left the fish room for natural behaviour, and no attempt was made to reduce the oxygen consumption to a minimum, as is often done in similar work, e.g. through anaesthetizing the fish or by selecting the lowest respirational rates observed. The oxygne consumption was estimated for fed cod at two temperatures and for fasting cod at three. The results were, in terms of the equation

$$-\frac{dO_2}{dt} = Dw^d \qquad \ldots\ldots (A12).$$

τ	Fasting		Fed	
	D = ωk			
(°C)	(g^{1-n} years^{-1})	d = n	D	d
5	1.59	0.791	–	–
10	1.32	0.886	2.88	0.831
15	1.99	0.845	5.71	0.757
Mean	1.63	0.841		

Oxygen consumption was measured in grams per year and the weight of the fish in grams. For fasting cod D and d are identical with k and n because equation A12 turns into equation A8,

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\, k\, w^n \qquad \ldots\ldots (A8).$$

The additional parameters, $\omega\ \alpha\ h$ and m, for feeding cod are found by subtracting the oxygen consumption of fasting cod from that of fed ones,

$$\left(\frac{dO_2}{dt}\right)_{fed} - \left(\frac{dO_2}{dt}\right)_{fasting} = \left(\frac{dO_2}{dt}\right)_{feeding} = -\,\omega\ \alpha\ h\ w^m \ \ldots\ldots (A10).$$

τ (°C)	$\alpha\ \omega\ h$ (g^{1-m} years^{-1})	m
10	2.05	0.716
15	4.04	0.669
Mean	3.04	0.692

Whereas the estimate of n (= 0.84) is in accordance with the results obtained in other examples, the estimate m = 0.69 is fairly high.

Neither the rate of weight loss during fasting, nor the chemical composition of the cod used were recorded. $\omega = dO_2/dw$, therefore, could not be determined from the material. However, another analysis of the composition of young cod is available (see App. V), namely, $\omega = 0.27$. Hence, $k = 6.0\ g^{0.16}$ years^{-1} ($\tau = 10$ C) and $\alpha h = 11.3\ g^{0.31}$ years^{-1} ($\tau = 12.5$ C).

The values of ωk and $\omega \alpha h$ at each temperature can be adjusted to the mean values of m and n by computing the rates of oxygen consumption of fed and fasting cod of about average size (1200 g) by means of the parameter estimates already made. Insertion in equations A8 and A10 with $n = 0.841$ and $m = 0.692$ gives the adjusted estimates:

τ	ωk	$\omega \alpha h$
5	1.12	–
10	1.38	2.51
15	2.04	3.19

The model of the temperature dependence of h and k developed above (equations C4 and C5) are not applicable because four sets of data are required (there are four parameters) whereas only two sets in the case of h and three in the case of k are available. The fact that equation C4 is actually in terms of H is unimportant because according to equations B4 and B8 $H = (1 - \alpha)\ h$. The frank and almost empirical approximation to equation C5 is applicable, though. We find $\omega k_0 = 3.11$ and $kp = 0.060$.

APP. V. OXYGEN CONSUMPTION AND WEIGHT LOSS IN FASTING TENCH

ESTIMATES OF ω, k, p_k, AND n

Lindstedt (1914) investigated the oxygen consumption of starved tench (*Tinca tinca*), stating for each experiment the temperature, τ, and the weight of the fish, w. Because the same specimens were used several times without being fed, the values of w in successive experiments indicate the weight loss. The weight range of the fish used was 8–240 g, and the temperature range was 0–25 C.

Using approximations, we have from equations A8 and C6

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\, k_0\, e^{p_k \tau}\, w^n \text{ g days}^{-1}$$

$$-\left(\frac{dw}{dt}\right)_{fasting} = k_0\, e^{p_k \tau}\, w^n \text{ g days}^{-1}.$$

Taking logarithms and applying linear regression analysis with two independent variables (τ and w) gives

$$ln\left(-\frac{dO_2}{dt}\right) = -6.372 + 0.0841\,\tau - 0.7241\, ln\, w$$

$$ln\left(-\frac{dw}{dt}\right) = -5.520 + 0.0962\,\tau + 0.7032\, ln\, w$$

from which

$$ln\left(-\frac{dO_2}{dt}\right) - ln\left(-\frac{dw}{dt}\right) = ln\,\frac{dO_2}{dw} = ln\,\omega = -0.8528 + 0.0121\,\tau - 0.0209\, ln\, w$$

where the two last terms are assumed not to be significant. Thus, $\omega = 0.426$ g oxygen consumed per g weight loss during fasting.

We also have $\overline{n} = 0.714$, ${}_k\overline{p} = 0.090$, and $k_0 = 0.00401 \text{ g}^{0.287}$ days^{-1} $= 1.46 \text{ g}^{0.287}$ years^{-1} ω can also be computed from the chemical composition of the fish because according to Krogh (1916) the quantities of oxygen used in catabolic processes are for 1 g of protein: 1.42 g; fat: 2.89 g; carbohydrate: 0.53 g. Analyses of tench are not available, but Åhman and Jørgensen (1964) published analyses of protein and fat contents of whole fish of a number of species. Assuming that there has been a glycogen content of 2% (which does not matter much, anyway) the following estimates of ω could be made:

	ω	
	Range	Mean
Clupea harengus	0.31–0.64	0.46
Clupea sprattus	0.34–0.61	0.47
Osmerus eperlanus		0.32
Mallotus villosus	0.36–0.50	0.43
Rutilus rutilus		0.34

(*Continued*)

(Concluded)	ω Range	ω Mean	
Belone bellone	0.31–0.45	0.38	
Gadus morhua		0.27	avg 0.30
Merlangius merlangus		0.27	
Trisopterus minutus		0.32	
Micromesistius poutassou	0.23–0.32	0.28	
Boreogadus esmarkii		0.43	
Pollachius virens		0.25	
Perca fluviatilis		0.31	
Trachurus trachurus		0.48	
Ammodytidae sp.		0.39	
Trachinus draco		0.35	
Scomber scombrus	0.35–0.63	0.48	
Zoarces viviparus		0.29	
Eutrigla gurnardus		0.45	
Acanthocottus scorpius		0.31	
Pleuronectes platessa *Platichthys flesus* *Microstomus kitt*		0.23	

The variation is due mainly to differences in fat contents. Species which are usually thin have values of ω about 0.30 (about 2% fat). Similar values are obtained for thin specimens of species (e.g. herring) which sometimes have high fat contents. For such species the methods outlined in the present paper should be used with particular caution because the basic assumption (see Introduction) on constant chemical composition of the fish is not very likely to hold.

The protein contents of the 21 species varies but little. The range is 12.5–17.0% with a mean value of 15.30%. The 95% confidence interval of single observations is 13.19–17.41%.

APP. VI. OXYGEN CONSUMPTION OF SPECKLED TROUT AT DIFFERENT OXYGEN CONCENTRATIONS

ESTIMATES OF Λ, Λ_1, λ, ωk p_Λ, p_{Λ_1}, p_λ, AND p_k

Job (1955) investigated the oxygen consumption of speckled trout (*Salvelinus fontinalis*) of sizes from 5 to 1000 g at oxygen concentrations from 2×10^{-6} to 20×10^{-6} g cm^{-3}. The fish had been fasting for a couple of days. The experiments were made at temperatures of 5, 10, 15, and 20 C, but for the present purpose the results were pooled into two groups, of 5–10 and 15–20 C. "Guesstimates" of the asymptotic rate of oxygen consumption, Q^*, were obtained by putting the highest observed value of the oxygen consumption, Q, (for each body size and temperature) equal to 0.95 Q^*. The data refer to "active metabolism" which means that the fish have been labouring under an unusual stress. The results, therefore, should not be generalized, but considered an example of computation only.

The treatment of the data is essentially fitting them to equation D3:

$$\frac{c}{Q/Q^*} = -(\Lambda_1 + \lambda w^{1/3})\, Q^* + \xi \left(1 - \frac{Q}{Q^*}\right)^{-1} \qquad \ldots\ldots (D3)$$

in order to estimate the transport time (seconds) for oxygen, $\Lambda = \Lambda_1 + \lambda w^{1/3}$ (equation D2). Equation D3 is linear in cQ^*/Q and $(1-\frac{Q}{Q^*})^{-1}$ for any fixed value of body size. For a fish weighing 5 g the data at temperatures of 5–10 C are given in App. Table I where, in units of 10^{-6} g cm^{-3} sec^{-1}, $Q^*\{5\text{ C}\} = -0.0844$ and $Q^*\{10\text{ C}\} = -0.1028$ with the arithmetic mean $Q^*\{7.5\text{ C}\} = -0.0936$. Equation D3 becomes

APP. TABLE I. Oxygen consumption of speckled trout weighing 5 g (App. VI, from Job, 1955).

Temp (C)	Oxygen concn, c 10^{-6}g cm^{-3}	Oxygen consumption, Q 10^{-6}g cm^{-3} sec^{-1}	Relative consumption rate Q/Q^*	$\frac{c}{Q/Q^*}$	$(1-\frac{Q}{Q^*})^{-1}$
5	1.97	–0.0183	0.217	9.08	1.28
5	3.95	–0.0437	0.518	7.63	2.07
5	5.92	–0.0556	0.659	8.98	2.93
5	7.89	–0.0731	0.866	9.11	7.46
5	11.84	–0.0802	0.950	12.46	20.00
10	3.58	–0.0659	0.641	5.59	2.78
10	5.37	–0.0969	0.943	6.69	17.54
10	7.16	–0.0882	0.858	8.34	7.04
10	10.74	–0.0977	0.950	11.31	20.00

$$\frac{c}{Q/Q^*} = 7.4983 + 0.1320\left(1 - \frac{Q}{Q^*}\right)^{-1}$$

with

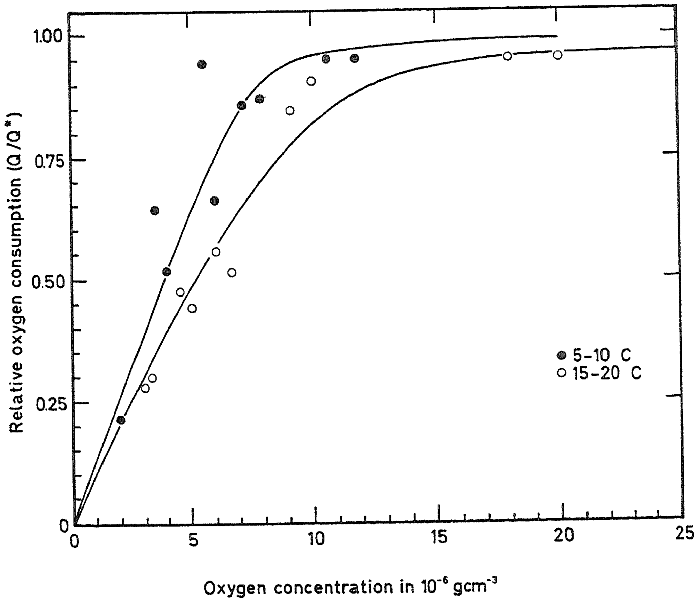
$$-\Lambda Q^* = -(\Lambda_1 + \lambda w^{1/3})\, Q^* = 7.4983 \times 10^{-6}\text{g cm}^{-3}$$

which for $Q^* = -0.0936 \times 10^{-6}$g cm^{-3} gives

$$\Lambda = \Lambda_1 + 1.710\,\lambda = 80.1 \text{ sec.}$$

App. Fig. 2 illustrates the fit of observations to a curve based on the above parameter values, and a similar curve for 17.5 C, again with $w = 5$ g. Separate estimates of Λ_1 and λ require data for other values of w, which were, therefore, estimated in the same way as above:

Weight w, g	Transport time for oxygen (*sec*)		Ratio $\frac{\Lambda\{17.5\text{ C}\}}{\Lambda\{7.5\text{ C}\}}$
	$\tau = 7.5$ C	$\tau = 17.5$ C	
5	80	47	0.59
15	100	64	0.64
45	89	86	0.97
135	124	102	0.82
405	139	128	0.92
1000	176	190	1.08



App. Fig. 2. *Salvelinus fontinalis.* Oxygen consumption as a function of oxygen concentration in the water. The curves are estimated from equation D3. App. VI.

The ratios between the two sets of observations indicate the temperature dependence of Λ.

The equation

$$\Lambda = \Lambda_0 e^{p_\Lambda \tau} \ (p_\Lambda \text{ negative}) \qquad \ldots\ldots(D5)$$

gives
$$\frac{\Lambda\{17.5\ \mathrm{C}\}}{\Lambda\{\ 7.5\ \mathrm{C}\}} = e^{10\,p_\Lambda}.$$

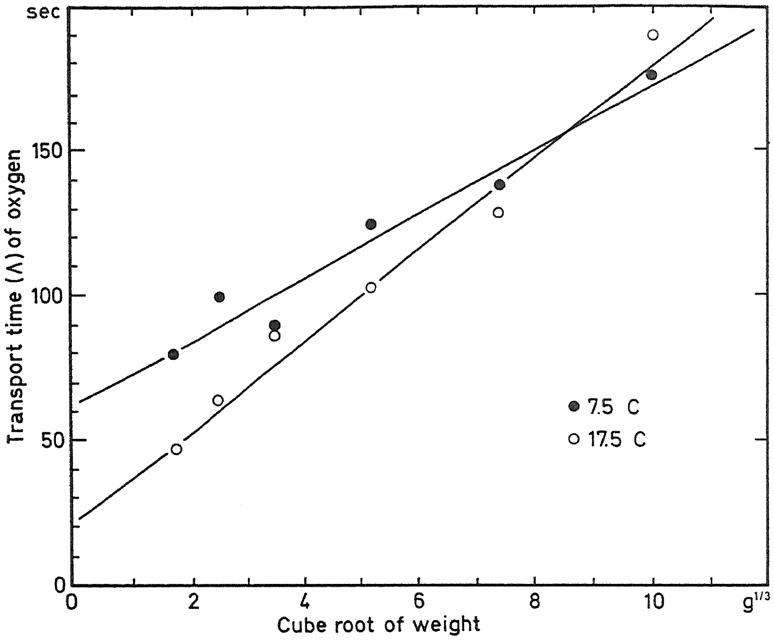
The mean ratio is 0.837 so that $p_\Lambda = -0.018$.

The fit of the above data to

$$\Lambda = \Lambda_1 + \lambda w^{1/3} \qquad .....(\mathrm{D2})$$

is illustrated in App. Fig. 3 where the estimated straight lines have

	7.5 C	17.5 C
Λ_1	62.3	22.2
λ	11.0	16.0.



App. Fig. 3. *Salvelinus fontinalis.* Estimated duration of oxygen transport in the fish body as a function of body size. App. VI.

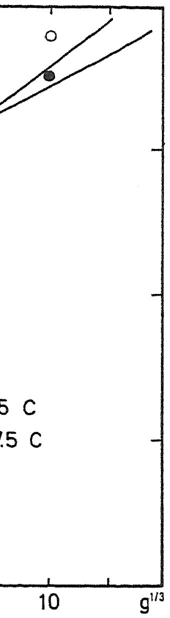
The temperature coefficient of Λ_1 is negative, as expected from equation D5:

$$e^{10\,p_{\Lambda_1}} = \frac{22.2}{62.3} = 0.356;\ p_{\Lambda_1} = -0.103$$

whereas that of λ is, surprisingly, positive:

$$e^{10\,p_\lambda} = \frac{16.0}{11.0} = 1.45;\ p_\lambda = 0.037.$$

.....(D2)



oxygen transport
VI.

tion D5:

3

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The reasoning leading to equation D2 may be too simple. It seems possible to argue, e.g. a proportionality with the second power of length, i.e. $\Lambda = \Lambda_1 + \lambda w^{2/3}$. Therefore, the estimates of Λ were fitted also to a second power polynomial,

$$\Lambda = \Lambda_1 + \lambda_1 w^{1/3} + \lambda_2 w^{2/3}$$

with the results:

τ	7.5 C	17.5 C
Λ_1	69.5	33.7
λ_1	7.70	10.6
λ_2	0.288	0.466
$s^2\{\Lambda \mid w^{1/3}\}$	80.6	72.5
$s^2\{\Lambda \mid w^{2/3}\}$	103	111
$s^2\{\Lambda \mid w^{1/3}, w^{2/3}\}$	100	77.3

The smallest variance is obtained by means of equation D2 which therefore cannot be rejected for the present.

An estimate of $\omega\, k$ and of the temperature coefficient, p_k of k (equation C6) can be based on Job's (1955) Fig. 2 which gives the rate of oxygen consumption for $w = 1$ g as:

Temperature τ, C	Oxygen consumption Active metabolism $\omega\, k$, 10^{-6} g^{1-n} sec^{-1}	 Standard metabolism $\omega\, k$, 10^{-6} g^{1-n} sec^{-1}
5	0.0752	0.0198
10	0.123	0.0396
15	0.166	0.0554
20	0.305	0.0792

These estimates are independent of n because $1^n = 1$. Fitting linearly (i.e. logarithmically) to equation C6 after multiplication by ω, (equation C4):

$$ln\ \omega k = ln\ \omega k_0 + p_k \tau$$

gives, for active metabolism,

$$ln\ \omega k = -3.0426 + 0.09004\tau$$

$$s^2\ \{\omega k \mid \tau\} = 0.007697.$$

Correcting for the bias introduced with the log transformation (Hald, 1952, p. 161) by adding $s^2/2$ to the logarithmic mean, and taking the antilog leads to

$$\omega k = 0.0479 \times 10^{-6}\ e^{0.0900\,\tau}\ g^{1-n}\ sec^{-1} = 1.51\ e^{0.0900\,\tau}\ g^{1-n}\ years^{-1}$$

for active metabolism and similarly to

$$\omega k = 0.0141 \times 10^{-6}\ e^{0.0899\,\tau}\ g^{1-n}\ sec^{-1} = 0.446\ e^{0.0899\,\tau}\ g^{1-n}\ years^{-1}$$

for standard metabolism. Standard metabolism, it should be mentioned, in Job's (1955) definition is as artificial as active metabolism. It is the lowest metabolic rate observed during a 24-hr experimental period.

Chemical analysis of the fish was not made. In the absence of weight loss data, therefore, ω cannot be estimated. Assuming that trouts are fat we can, however, make a guess by means of the list of calculated ω values given in App. V. $\omega = 0.4$ seems a reasonable value. Thus,

$$k_0 = 3.8 \text{ g}^{1-n} \text{ years}^{-1} \quad \text{for active metabolism}$$

$$k_0 = 1.1 \text{ g}^{1-n} \text{ years}^{-1} \quad \text{for standard metabolism}$$

The value for normal behaviour should be found between these extremes.

APP. VII. GROWTH AND FEEDING OF PLAICE

ESTIMATION OF METABOLIC PARAMETERS OF YOUNG PLAICE

ESTIMATES OF m, k, h_1, h_2, H, f, α, AND W_∞

Dawes (1930, 1931) fed young plaice (*Pleuronectes platessa*) varying quantities of mussel meat and found the growth rate. The material is to some extent unsatisfactory; yet it provides data for estimation of several parameters introduced in the paragraph on Growth and Food. For simplicity it shall be assumed that mussel meat is identical with plaice meat. A correction for differences of available free energy per gram would enter the expression for the ration which would have to be multiplied by a conversion factor in order to change the ration actually eaten to the equivalent amount of fish.

Estimates of n, the parameter of the dependence of fasting catabolism upon body size, cannot be made. Results obtained in several other examples indicate that $n = 5/6$ is a fairly good guess, and it shall be used.

m, the corresponding parameter of anabolism, can be estimated by plotting ration against weight on a log scale (equation B2):

$$\frac{dR}{dt} = h_1 f w^m,$$

using data for any given feeding level (i.e., f constant, $f \neq 0$). Bückmann (1952, p. 12) compiled data from Dawes's experiments and from his own, using plaice given surplus food. The results are widely varying:

	m
Dawes	0.65
Bückmann 1950 expt.	0.53
" 1951 expt.	0.34

ranging, in fact, from 1/3 to 2/3. For the present purpose, the estimate from Dawes's experiments shall be used, only rounded off for convenience to 2/3. The corresponding solution for the coefficient of anabolism is $h_1 f = 0.299$ $g^{1/3}$ days^{-1}.

The material is not ideal for estimating the coefficient of fasting catabolism, k, but there are two ways of doing it. One fish (A1, Table I, Dawes, 1930, p. 148) lost weight steadily during 4 months and eventually died. Odds are that for some reason, this fish did not eat at all. Fitting the weight-at-time data to equations A14 and A15 as if a deliberate fasting experiment had been made gives, with $n = 5/6$, $k = 0.00734$ $g^{1/6}$ days^{-1}. For fish given surplus food, growth data can be compiled for 18 incidents of plaice weighing about 36 g and for 15 incidents of plaice weighing about 51 g. Here, as elsewhere in the present example, observations at extreme temperatures were omitted, so that the experiments can be considered made at about 16 C. We find

w (g)	36	51
dw/dt (g days^{-1})	0.30	0.37

which, inserted in $dw/dt = Hw^{2/3} - kw^{5/6}$, gives

$$H = 0.04091 \text{ g}^{1/3} \text{ days}^{-1}$$
$$k = 0.00737 \text{ g}^{1/6} \text{ days}^{-1}.$$

Since the two estimates of k coincide, we can put $k = 0.0074$.

Equations B3 and B8 give

$$\frac{dw}{dt} + k\,w^n = (1-\alpha)\,h_1 f\,(1-e^{-h_2 f^{-1}})\,w^m \qquad \ldots\ldots(6\text{-}1)$$

the left side of which is determined by sets of observations of growth rate and weight when k and n are already known. The right-hand term contains the ration eaten, dR/dt, factored into

$h_1 f w^m$ where m is known. f, however, is unknown, as are also α and h_2. Putting $f = 1$ for Dawes's "maximum feeding" is scarcely warranted because Bückmann (1952) found that the ration eaten depends upon the amount of surplus food given:

Given, g	Eaten, g
546	264
273	206
182	166
137	134

An ogive with higher and lower asymptotes is indicated, but Dawes's data do not allow an estimate of f. Models by Ivlev (1961) and Rashevsky (1959) are perhaps applicable but there are problems, inconvenient to tackle in the present context. Remembering that the present computation is to be considered an example only, we shall put $f = 0.9$ for "maximum feeding." For estimation of parameters of equation 6-1 two sets of data are necessary. Let one be the already used fish weighing about 51 g and fed surplus food ("maximum requirements") and let the other be the mean values for 11 incidents when fish weighing about 31 g were fed maintenance ration, or approximately so. We have

	"Maintenance"	"Maximum"
w (g)	31	51
$\frac{dw}{dt}$ (g days^{-1})	−0.01	0.37
$\frac{dR}{dt}$ (g days^{-1})	0.54	3.69

Thus, for "maximum" ($f = 0.9$):

$$h_1 = \frac{dR/dt}{f\ w^m} = \frac{3.69}{0.9\times 13.8} = 0.297 \qquad \ldots\ldots(6\text{-}2)$$

and, by means of h_1, for "maintenance":

$$f = \frac{dR/dt}{h_1\ w^m} = \frac{0.54}{0.29\times 9.87} = 0.184.$$

Inserting $h_1 = 0.297$ into $h_1 f = 0.299$ which was found above, gives $f = 1$ for "maximum feeding." Putting $f = 1$ in equation 6-2, however, does not make the agreement any better. The difference is ascribed to the variance of the mean values used.

Note, that the value of f for maintenance refers to $w = 31$ g specifically. For increasing weight the maintenance f increases towards 1. It is also important that feeding maintenance ration to a fish of weight w amounts to putting $w = W_\infty = \varphi\ (f)$.

Inserting the two sets of data tabulated above, with the respective values of f, in equation 6-1 gives solutions, first for h_2 by iteration, and then for α:

$$h_2 = 1.026;\ 1-\alpha = 0.223;\ \alpha = 0.777.$$

$(1-\alpha)$ is, to a first approximation, the efficiency of energy transfer (and α, the entropy increase).

The constant parameters now known, the dependence of some quantities upon f can be tabulated, namely the instantaneous coefficient of net anabolism,

$$\mathrm{H} = (1-\alpha)\ h_1 f\ (1-e^{-h_2}f) \qquad \ldots\ldots(\mathrm{B9})$$

the asymptotic weight,

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \ldots\ldots(A19)$$

and the maintenance ration,

$$(dR/dt)_{maint} = h_1 f_{maint} W_\infty^{\ m} \qquad \ldots\ldots(B14).$$

f	H ($g^{1/3}$ $days^{-1}$ × 10^2)	$w = W_\infty$ (g)	$(dR/dt)_{maint}$ (g $days^{-1}$)
0.10	0.663	5.60×10^{-1}	2.02×10^{-2}
0.15	0.993	6.34	1.53×10^{-1}
0.184	1.22	2.12×10	4.19×10^{-1}
0.20	1.32	3.47×10	6.30×10^{-1}
0.25	1.63	1.24×10^2	1.84
0.40	2.45	1.42×10^3	1.50×10
0.47	2.76	2.95×10^3	2.87×10
0.60	3.26	7.81×10^3	7.06×10
0.80	3.83	2.10×10^4	1.81×10^2
0.90	4.06	2.95×10^4	2.55×10^2
1.00	4.25	3.90×10^4	3.42×10^2

The estimate of H for $f = 0.9$ is in agreement with the one obtained above, $H = 4.09 \times 10^{-2}$, when estimating k. The asymptotic weight of North Sea plaice, $W_\infty = 2.9 \times 10^3$ g, as estimated by Beverton and Holt (1957) corresponds to $f \approx 0.47$ which means that North Sea plaice eat half as much as those of Dawes's plaice given mussel meat in surplus. The result seems plausible. The underestimate of the maintenance ration for $f = 0.184$, where 0.42 g was expected and 0.54 g observed, is probably due to inaccuracies of the estimates of k and f.

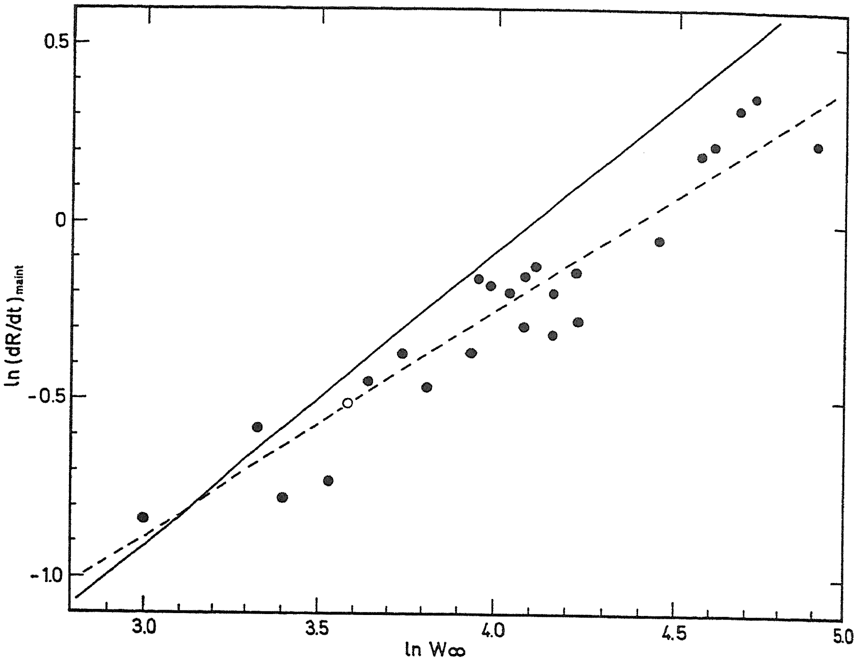
App. Fig. 4 is a plot of $ln\ (dR/dt)_{maint}$ against $ln\ w = ln\ W_\infty$. Individual entries are 26 maintenance experiments by Dawes. The period of observation was over 100 days, the temperature between 13 and 19 C, and the total change in weight less than ±0.5 g. The broken line shows the best fit of these points to a straight line. The slope is 0.63 with 95% confidence intervals of 0.42–0.84. The solid line shows the maintenance ration according to the present model, as computed above. It has a slope of $0.83 = n$ within the range of w considered. For higher values of w the slope increases slowly as required in the model according to which it is $\geq n$ (equation B13 and the text connected with it). Beverton and Holt (1957) accepted the slope estimated from Dawes's data at its face value, putting for simplicity $(dR/dt)_{maint} = C\ w^{2/3}$ and incorporated this expression in a model of growth and feeding. Paloheimo and Dickie (1966a), however, computed the metabolic rates of Dawes's plaice, plotted them against weight, and found suspiciously shallow slopes for the fish fed maintenance rations as well as for those fed in surplus. Thus, Dawes's data may be biased in some way.

The feeding level, f_{max}, ensuring maximum utilization of food is a function of body size and is determined by

$$f_{max} = - \frac{h_2}{ln \dfrac{k}{h_1 h_2 (1-\alpha)} + (n-m)\ ln\ w} \qquad \ldots\ldots(B22)$$

whereas the maximum instantaneous efficiency of utilization of total food for growth is given by equations B21 and B22 as

$$u_{max} = (1-\alpha)\ (1-e^{-h_2/f_{max}}) - \frac{k\ w^{n-m}}{h_1\ f_{max}} \qquad \ldots\ldots(6\text{-}3)$$



App. Fig. 4. Maintenance ration of plaice plotted against weight, both on a log scale. Data from Dawes. The broken line is a least square fit to individual observations. The full line is that expected from the model. The difference is not significant at the 95% level. App. VII.

and the ration to ensure maximum utilization is (from equation B2)

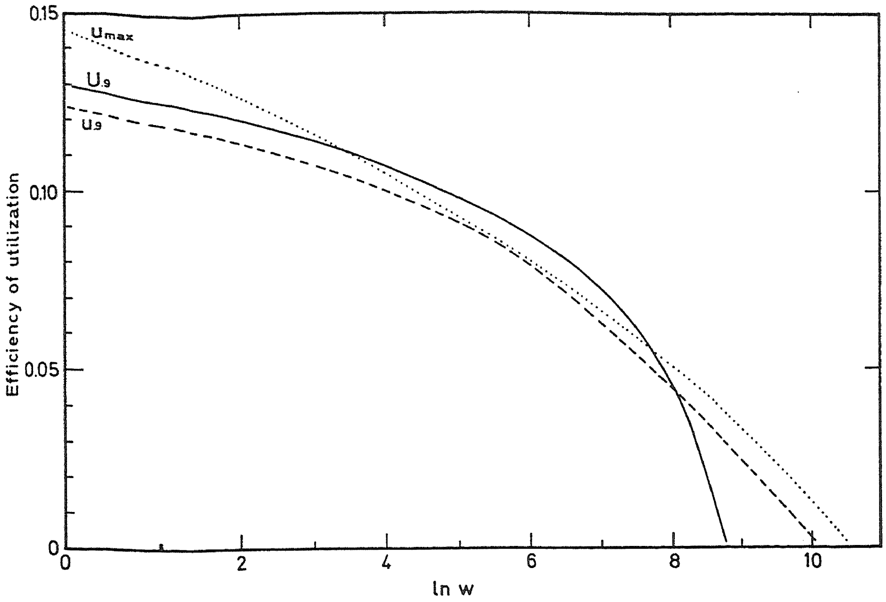
$$\left(\frac{dR}{dt}\right)_{max} = h_1 \, f_{max} \, w^m \qquad \ldots\ldots(6\text{-}4).$$

These quantities are tabulated below. The lowest weight for which full ration is the most efficient is found by putting $f_{max} = 1$ in equation B22 and solving for w. $u_{max} = 0$ is the limiting case for which full ration is maintenance ration (bottom row of the foregoing table). It leads to $W_{\infty max}$ (here 39 kg) and is independent of the rations given to the younger stages (the mysterious "equifinality of growth" of early authors).

We have:

w (g)	f_{max}	u_{max}	$(dR/dt)_{max}$ (g days^{-1})
10^{-2}	0.342	0.179	4.71×10^{-3}
10^{-1}	0.392	0.164	2.50×10^{-3}
1	0.460	0.146	1.37×10^{-1}
10	0.555	0.123	7.66×10^{-1}
10^{2}	0.701	0.0960	4.48
10^{3}	0.951	0.0654	2.83×10
1.39×10^{3}	1.000	0.0610	3.68×10
10^{4}	1.000	0.0291	1.38×10^{2}
3.90×10^{4}	1.000	0.0000	3.42×10^{2}

u_{max} is plotted against weight in App. Fig. 5.



APP. FIG. 5. Estimates of food utilization for growth by plaice based on Dawes' data and plotted against weight on a log scale. u_{max}: maximum efficiency ($f = f_{max}$); $u_{.9}$: efficiency at constant feeding level, $f = 0.9$; $U_{.9}$: efficiency of total food consumed during the life of the fish. In principle an integration of $u_{.9}$, but using different approximations. See also tables in the text and App. VII.

For constant f the total amount of food consumed by any one fish of weight w_t up to time t is given by

$$R_t = \frac{h_1 f W_\infty^{2/3}}{2K} (2Kt + (1-e^{-2Kt}) - 4(1-e^{-Kt})) \quad .....(B25)$$

where W_∞ and $K = k/3$ are estimated from equation 1, i.e. with $m = 2/3$ and $n = 1$. The growth rate data used above to determine k and H for $m = 2/3$ and $n = 5/6$ give, for $m = 2/3$ and $n = 1$:

$$K = 0.0006027 \text{ days}^{-1}$$

$$W_\infty = 6352 \text{ g.}$$

These, inserted in equation B25 with $f = 0.9$ and in equation A28 with $t_0 = 0$, give total food consumed, weight-at-time, and, by division, the efficiency U of utilization of total food for growth (equation B26):

t (days)	R_t (g)	w_t (g)	U	u
100	8.35	1.28	0.130	0.122
200	8.12×10	9.36	0.115	0.111
400	5.98×10^2	6.28×10	0.105	0.098
800	4.04×10^3	3.57×10^2	0.0885	0.080
1600	2.35×10^4	1.51×10^3	0.0642	0.066
3200	1.08×10^5	3.97×10^3	0.0368	0.057
∞	∞	6.35×10^3	0	0.029

The last column shows the instantaneous efficiency, u, computed as before but with $f = 0.9$ throughout. Full agreement between the curves for U and u cannot be obtained because different approximations to the growth function were used (App. Fig. 5).

When maintenance requirements are covered additional food consumed will be utilized for growth independently of body size and with an efficiency given by equation B20, e.g.:

$$v = (1-\alpha)\ (1-e^{-h_2/f}) = 0.152 \quad \text{for } f = 0.9.$$

When considering the results obtained in the present example it should be remembered that there is reason (Bückmann 1952) to believe that the plaice in Dawes's experiments shared the rations with crustaceans entering the well boxes in which the fish were kept. Accordingly, all coefficients of utilization are suspected to be underestimates.

SOME POPULATION PARAMETERS FOR NORTH SEA PLAICE

ESTIMATES OF ${}_{pop}\mathrm{R}$, ${}_{pop}\mathrm{R}_{mr}$, ${}_{pop}\mathrm{R}_g$, A.P., AND ${}_{pop}\mathrm{U}$

The above results can be utilized on the population level if some additional parameters are available as for instance for North Sea plaice, so thoroughly analyzed by Beverton and Holt (1957). Unfortunately these authors were dealing almost exclusively with the stock of adult plaice so that in order to make the computations as an exercise we must assume that the growth and metabolic parameters in young plaice are the same as in adults. We shall compute the whole food consumption of the adult population and partition the consumption into maintenance requirements and growth food (${}_{pop}\mathrm{R}$, ${}_{pop}\mathrm{R}_{mr}$ and ${}_{pop}\mathrm{R}_g$, equations B28–B30). Also the annual production (A.P., equations B31 and B32) and the efficiency of utilization of total food for growth by the population (${}_{pop}\mathrm{U}$, equation B33) shall be computed.

Since the feeding level of North Sea plaice is not known a priori, it is necessary to take the observed growth curve as an exit. The Pütter parameters (equation A28) as estimated by Beverton and Holt are: $W_\infty = 2867$ g, $K = 0.10$ years^{-1} and $t_0 = -0.82$ years. From these authors we shall also take the age at recruitment, t_r, the total mortality coefficient, Z, and the annual number of recruits, N_r (R in the terminology of Beverton and Holt):

$$t_r = 3.72 \text{ years}, \ Z = 0.83 \text{ years}^{-1}, \ N_r = 2.8 \times 10^8.$$

Accepting t_0 as the birthday of the plaice we can put

$$_0t_r = t_r + t_0 = 4.54 \text{ years}$$

and

$$N_r = N_0\, e^{-4.54Z} = 2.8 \times 10^8;\ N_0 = 2.8 \times 10^8 \times e^{3.77} = 1.2 \times 10^{10}$$

where N_0 is fictitious because the pre-recruit mortality is not known. The feeding level, f, was estimated above by means of the W_∞ of Beverton and Holt, and for n a value of 5/6 again has to be assumed. The other parameters are estimated from Dawes's data. Thus,

$$f = 0.47;\ n = 5/6;\ m = 2/3;\ h_1 = 0.297 \text{ g}^{1/3} \text{ days}^{-1}$$

$$h_2 = 1.03;\ \alpha = 0.777;\ k = 0.0074 \text{ g}^{1/6} \text{ days}^{-1}.$$

These estimates were made at a temperature of approximately 16 C, which affects the values of h_1 and k. A reduction to 10 C, the approximate mean temperature of the North Sea, has to be made. In a previous paper (Ursin, 1963a, Fig. 4) was estimated the variation with temperature of a quantity (the growth rate of very young plaice) almost proportional with h_1. The correction factor from 16 to 10 C is 0.79. The temperature correction for k can be based on results obtained for goldfish in App. III, because there is evidence (Winberg, 1956) that the temperature relations of catabolic processes do not differ appreciably from one species to another. The estimates based on a fit of data to equation C5 (the elaborate one with four parameters) show that the correction factor is 0.71. Therefore, changing also the time unit, we have

$$\tau = 10 \text{ C}: h_1 = 0.297 \times 0.79 \times 365 = 85.6 \text{ g}^{1/3} \text{ years}^{-1}$$

$$k = 0.0074 \times 0.71 \times 365 = 1.92 \text{ g}^{1/6} \text{ years}^{-1}$$

further

$$\beta = 1-e^{-h_2/f} = 0.888;\ v = (1-\alpha)\ \beta = 0.198;\ H = v\ h_1 f = 7.97.$$

The next step is to evaluate the integral

$$J_x = \int_0^t (1-e^{-Kt})^{3x}\ e^{-Zt}\ dt \qquad \ldots\ldots(50)$$

for $x = m = 2/3$ and for $x = n = 5/6$, and both for $t = \infty$ and $t = {}_0t_r$.

The method is indicated in equation B34: evaluating J_x for $x = \{0,\ 1/3,\ 2/3,\ 3/3,\ 4/3\}$ and interpolating graphically. The results were

	$t = \infty$	$t = 4.54$	Difference
J_0	1.20482	1.17610	0.02782
$J_{1/3}$	0.12955	0.11750	0.01205
$J_{2/3}$	0.025155	0.019829	0.005326
$J_{3/3}$	0.006678	0.004271	0.002407
$J_{4/3}$	0.002171	0.001056	0.001115
$J_I = J_{2/3}$			0.00533
$J_{II} = J_{5/6}$			0.00358

Of course, the choice of $m = 2/3$ saves one interpolation.

We can now compute, for the adult population (from $t = {}_0t_r$ to $t = \infty$)

$${}_{pop}R = h_1 f\, W_\infty{}^m\, N_0 \int_{{}_0t_r}^{\infty} (1-e^{-Kt})^{3m}\ e^{-Zt}\ dt \qquad \ldots\ldots(B28)$$

$$= 85.6 \times 0.47 \times 2867^{2/3} \times 1.2 \times 10^{10} \times 0.00533 = 5.2 \times 10^{11} g$$

which is the food eaten by one year-class from recruitment to death, or by all year-classes in 1 year. Assuming that the North Sea population of adult plaice is distributed over 10^{11} m^2 puts the annual consumption to 5.2 g of mussel meat per m^2, or probably 10 g of bottom animals, shells etc. included.

For most purposes it is perhaps more convenient to compute food consumption etc. per recruit, using $N_r = N_0\ e^{-(t_r-t_0)Z} = 0.0231\ N_0$. Thus,

$${}_{pop}R/N_r = 1877\ g$$

and similarly, by means of equations B29 – B33:

$${}_{pop}R_{mr}/N_r = 1145\ g;\ {}_{pop}R_g/N_r = 732\ g$$

$$A.P./N_r = \begin{cases} 145\ g & (B31); \\ 103\ g & (B32); \end{cases} \qquad {}_{pop}U = \begin{cases} 0.077\ (B33\ and\ B31) \\ 0.055\ (B33\ and\ B32). \end{cases}$$

On contemplating the overall efficiency of food utilization, which is very low, 5–8%, two things should be considered. The figure is too low if, as mentioned above, some of the food of Dawes's plaice was actually eaten by amphipods. Moreover, ${}_{pop}U$ is not a measure of the efficiency of energy transfer because a fraction, $1-\beta$, of the ration is not utilized by the fish at all. There are also losses through urine which are not specified in the model (included in α).

APP. VIII. WEIGHT LOSS OF FASTING *LEBISTES* MALES

ESTIMATES OF k AND p_k

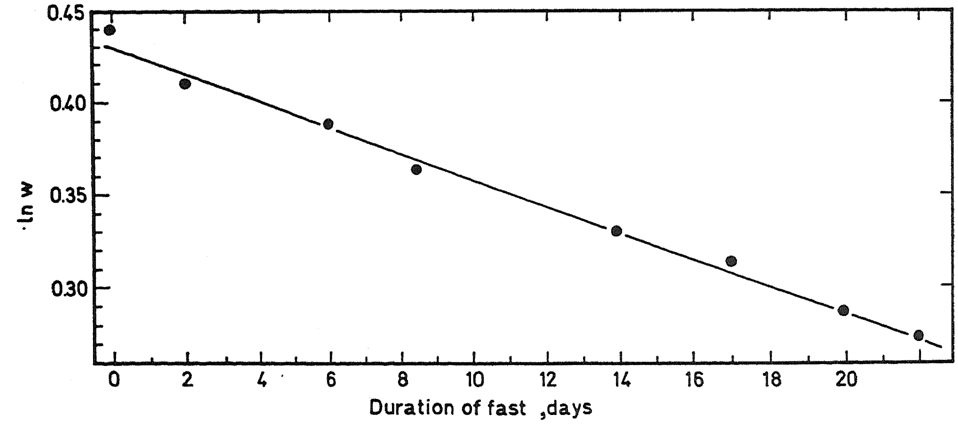
Over 100 male guppies (*Lebistes reticulatus*) were reared in the laboratory by Mr Chr. Frandsen at constant temperatures between 16.5 and 32.0 C. They were progeny of fish obtained from the Botanical Gardens of Copenhagen, where a population had been kept for many years without introduction of fish from elsewhere. When 1–1½ years old, they were starved for about 3 weeks while being weighed with a few days' interval. During fasting they were kept in half-litre jars lowered into the 6-litre jars in which they had been reared and where the females of the same batch were still present. The temperatures were those at which the fish had been reared. The water in the small jars was renewed, and the jars cleaned, every day. There was no aeration and no heating apparatus in the small jars. The chance that the fasting fish should find anything to eat was small. There were 1–11 fish in each jar, 4 on an average. The mortality during the fast was generally small, until the fish had lost about 20% of the initial weight which seems to be what a male guppy can stand loosing without suffering permanent injury. Fish reared below 18 C could not fast successfully; most of them died after a few days, having suffered a weight loss as high as those starved at 30 C. These fish were omitted from the computations.

k was estimated for each fish from

$$\ln w_t = \ln w_0 - {}_1kt \qquad \ldots\ldots \text{(A14)}$$

this being made possible by individual differences of colour pattern and fin shape. There was no obvious deviation from the expected straight-line relationship except that sometimes, towards the end of an experiment, the weight suddenly increased, probably as a result of disturbance of the water balance in the body. In such cases, the last observations were discarded. In App. Fig. 6 and the table below are given the average weights of the largest batch (11 fish) during 22 days of fasting at 22.2 C; all specimens survived.

Days t	Mean weight w (g)	*ln* mean weight $\ln w + 2.3026$
0	0.1424	0.4400
2	0.1382	0.4098
6	0.1353	0.3883
9	0.1319	0.3635
14	0.1278	0.3316
17	0.1254	0.3128
20	0.1221	0.2861
22	0.1205	0.2730



APP. FIG. 6. *Lebistes*: 11 males. Mean weight (log scale) during fasting at 22.2 C. App. VIII.

The total loss was 15% of the initial weight. Equation A14 gives ${}_1k$ = 0.007222 days^{-1} = 2.638 years^{-1}. Using equation A14 means putting $n = 1$. The correction for $n \neq 1$ is given by equation A15 as $(1-n)\ ln\ w_0$. For $n = 5/6$ the corrected value is ${}_{5/6}k$ = 1.93 g$^{1/6}$ years^{-1}. Since the weight of *Lebistes* males deviates from unity (gram) by one size order only, the difference between ${}_1k$ and ${}_nk$ ($n \neq 1$) is smaller than in most other fishes. As the material does not permit an estimate of n, the approximation $n = 1$ has been used throughout.

App. Table II and App. Fig. 7 show $ln\ k$ as a function of temperature. The fitted regression line (equation 14) is

$$ln\ {}_1k = 0.04914 + 0.4765\ \tau$$

$$s^2 = 0.05433 \text{ (average)}$$

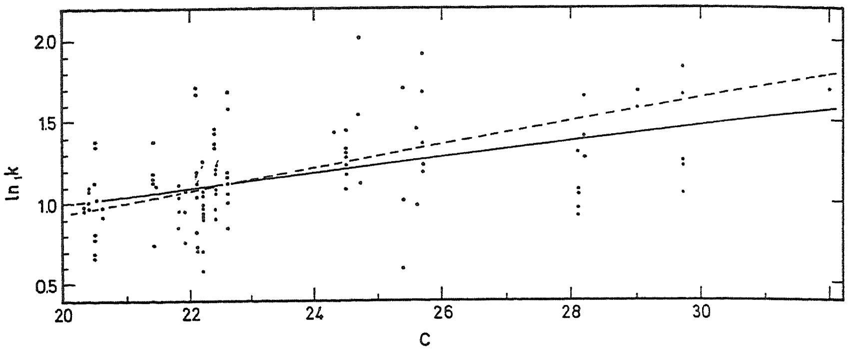
correction for ln transformation $= s^2/2 = 0.02716$, approximately

corrected equation: $ln\ {}_1k = 0.07630 + 0.04765\ \tau$

$$ {}_1k_0 = 1.08 \text{ years}^{-1},\ p_k = 0.0476.$$

App. Table II. Rate of weight loss expressed as $ln\ k$ (where $\frac{-dw}{dt} = k\ w$) in 110 *Lebistes* males kept fasting at the temperatures at which they had been reared. Each row indicates an individual experiment. (See App. Fig. 6, App. VIII.)

Temp (C)	$ln\ k$										
32.0	1.69										
29.7	1.05	1.22	1.24	1.66	1.85						
29.0	1.58	1.68									
28.2	1.27	1.41	1.65								
28.1	0.91	1.06	1.06	1.07	1.30						
25.7	1.17	1.23	1.37	1.67	1.90						
25.6	0.98	1.45									
25.4	0.58	1.01	1.69								
24.7	1.12	1.54	2.01								
24.5	1.30										
24.5	1.07	1.17	1.22	1.23	1.29	1.31	1.44				
24.3	1.43										
22.6	0.84	1.12	1.17	1.58	1.68						
22.6	1.00	1.05	1.17								
22.4	1.07	1.18	1.18	1.24	1.34	1.34	1.42	1.45			
22.4	0.90	0.96	1.07	1.20	1.26	1.45					
22.2	0.58	0.70	0.91	0.91	0.93	0.97	0.98	1.04	1.07	1.21	1.25
22.1	0.73	1.14	1.16								
22.1	0.71	0.82	1.04	1.11	1.16	1.71					
22.1	1.66										
21.9	0.75	0.95	1.08								
21.8	0.85	0.95	1.03	1.10							
21.4	1.11	1.12	1.15	1.37							
21.4	0.73	1.18									
20.6	0.91	0.97									
20.5	0.68	1.12	1.38								
20.5	0.67	0.77	0.80	1.02	1.35						
20.4	0.97	1.00	1.09	1.09							
20.3	0.97	0.97									



APP. FIG. 7. *Lebistes*. Rate of weight loss, expressed by the coefficient, $_1k$, of fasting catabolism (log scale), as a function of temperature. Males fasting at the temperatures at which they were reared. Observations at temperatures of 16.8–17.8 C were discarded together with an aberrant observation at 20.4 C (by $k = 2.38$). The full line is fitted by the method of least squares. The broken line was computed in the same way from 101 observations of males kept at room temperature (about 22 C) until few days before the experiments. See App. Table II. App. VIII.

There is no obvious curvilinear tendency so that the hypothesis of exponential increase (equation C6) cannot be rejected. A rigorous statistical treatment of the material, however, has been refrained from because of irregularities causing the variance about the regression line to vary from one set of data to another. Bartlett's test applied to variances based on four observations at least, gave $\chi^2 = 42.6$ for 18 df ($0.99 < P < 0.995$).

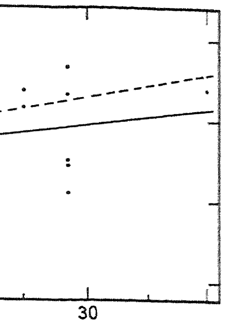
A similar set of data was procured in the following way. A large number of *Lebistes* males were obtained from the Botanical Gardens of Copenhagen and kept for 1 or several months in a large aquarium in the laboratory. They were transferred, in numbers about 10, to 6-litre jars at temperatures from 16 to 32 C. The temperature change was made at a rate of about 1 C per day. Then the fish were starved for about 3 weeks, the water being changed with a few days' interval. The water was aerated and in some jars were heating or cooling devices. In spite of careful cleaning, some growth of bacteria was noticed in the jars. The fish therefore may have got small amounts of food during the experiment. Again fish kept at 16 C died after a few days.

The result, based on 101 specimens starved at temperatures between 19.5 and 31.7 C was

$$ln\ k = -0.4737 + 0.07095\ \tau$$

$$_1k_0 = 0.655 \text{ years}^{-1} \text{ (corrected for log transf.)};\ p_k = 0.0710.$$

The line (broken) is entered in App. Fig. 6. It intercepts with the one derived before at room temperature, 22 C, to which the fish had been acclimated before the fasting experiment. There are many possible explanations of the difference between the two lines (which seems to be significant), because many influences were not under control during these primitive experiments. The simplest explanation is, that the difference is due to acclimation. The fish in the first experiment had been acclimated to the experimental temperature for their whole life, in the second for a few days only. Winberg (1956), however, reviewed critically the literature on temperature acclimation in fishes and doubts the reliability of alleged acclimation effects reported by various authors. In the present case many other influences may have interfered.



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APP. IX. WEIGHT LOSS OF FASTING FISH OF VARIOUS SPECIES

ESTIMATES OF k AND n

App. Table III lists estimates of the coefficient, k, of fasting catabolism from fasting experiments with various species, from literature and my own observations. As in the preceding examples the estimates were made from

$$ln\ w_t = ln\ w_0 - {}_1kt \qquad \text{.....(A14)}$$

which gives the value, $_1k$, which k takes on for $n = 1$. The value $_nk$, of k for $n \neq 1$ is given by

$$ln\ {}_nk \approx ln\ {}_1k + (1-n)\ ln\ w_0 \qquad \text{.....(A15).}$$

App. Table III. The coefficient of fasting catabolism, k, determined from the weight loss of fasting fishes, at experimental temperature and adjusted to 20 C by means of the temperature coefficient, $p_k = 0.05$, found in App. IX.

Species	References	Initial weight w_0, g	Initial weight $ln\ w_0$	Temp (C)	$_1k_{obs}$ years^{-1}	$ln\ {}_1k_{obs}$	$ln\ {}_1k_{20}$
Anguilla ang.	Reuss and Weinland, 1912, p. 290	0.168	−1.78	18.8	4.64	1.53	1.59
		0.168	−1.78	12.5	3.09	1.13	1.50
	Lipschütz, 1911 p. 123	0.212	−1.55	17.4	6.99	1.94	2.07
	Own observations	0.929	−0.07	20.8	4.94	1.60	1.56
		0.432	−0.84	20.8	6.03	1.80	1.76
		1.19	0.17	19.4	4.74	1.56	1.59
		2.16	0.77	20.1	2.70	0.99	0.99
Tinca tinca	Lindstedt, 1914	140	4.94	13.0	1.18	0.16	0.51
Cyprinus carpio	Ivlev, 1961b, Table 75	0.53	−0.63	22	4.54	1.51	1.41
	Lipschütz, 1911, p.64	1.33	0.29	15.0	2.40	0.88	1.13
	Kestner and Plaut, 1924 (from Knauthe)	601	6.40	18.0	1.31	0.30	0.40
Abramis brama	Ivlev, 1961b, Table 75	0.32	−1.14	22	4.32	1.46	1.36
Rutilus r. caspicus		0.53	−0.63	22	4.66	1.54	1.44
Silurus glanis		0.86	−0.15	22	3.84	1.35	1.25
Lebistes reticulatus	App. VIII	0.13	−2.04	23.6	3.22	1.17	0.99
Carassius auratus	Own observations	2.81	1.03	20	3.11	1.13	1.13
		28.4	3.35	20	1.78	0.58	0.58
Perca fluviatilis		2.46	0.90	18	5.28	1.66	1.76
		6.22	1.83	20.6	5.24	1.66	1.63
		4.31	1.46	21	4.78	1.56	1.51
Gobius sp.		0.500	−0.69	11.5	1.87	0.63	1.06
		0.412	−0.89	15.0	3.58	1.28	1.53
		0.274	−1.29	20.5	5.44	1.69	1.66
Solea solea		2.38	0.87	21.6	3.75	1.32	1.24
Platichthys flesus		4.73	1.55	17.1	3.31	1.22	1.36
		4.98	1.60	17.1	1.99	0.69	0.84
Pleuronectes platessa		4.26	1.45	17.1	1.43	0.35	0.50
	Dawes, 1930 (fish A1)	44.0	3.78	14.8	1.43	0.35	0.61

The fasting experiments were made at different temperatures, most of them not far from room temperature. Adjustment to 20 C was made by means of the temperature coefficient, p_k = 0.05, estimated in App. VIII for male *Lebistes* kept fasting at the temperature at which they had been reared. Thus,

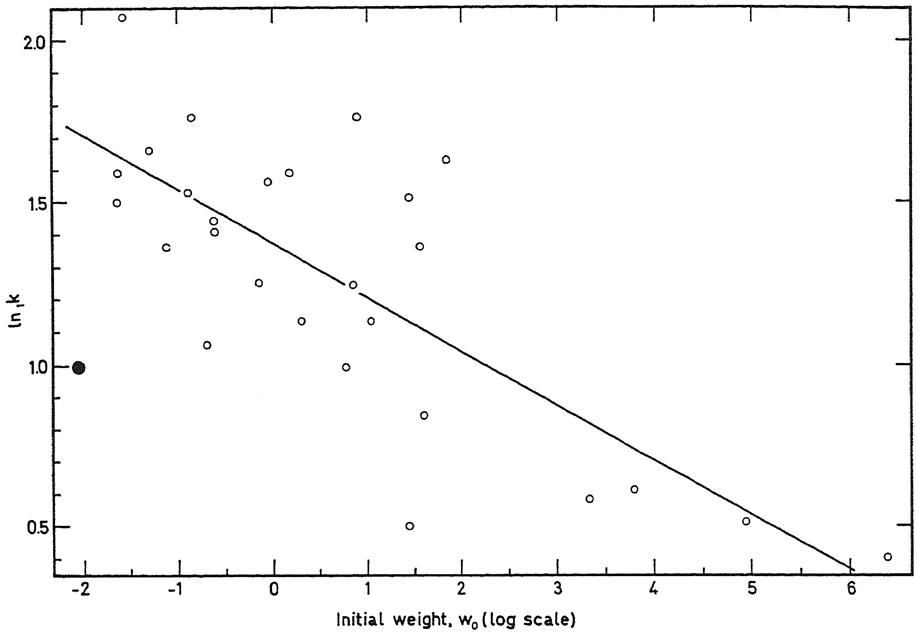
$$k_{20} = k_{obs}\, e^{-0.05\,(T-20)}$$

which holds for any n.

Equation A15, rearranged,

$$\ln\, {}_1k_{20} \approx \overline{\ln\, {}_nk_{20}} - (1-n)\ \ln\, w_0$$

provides a means of estimating n and a mean value of ${}_nk$ from a straight line if n is constant. The notation $\overline{\ln\, {}_nk_{20}}$ indicates that the intercept is the mean of the logarithmic values. The independent variable is $\ln w_0$. The data in App. Table III are plotted in App. Fig. 8. The value for *Lebistes* males (from App. VIII) is very low. *Lebistes* is, however, the only tropical fish in the assembly and is, therefore, excluded from the computations. Disregarding interspecific differences, the remaining data give



App. Fig. 8. The regression upon body size of the coefficient, ${}_1k$, of fasting catabolism at 20 C. From weight loss during fasting. Various species, *Lebistes* given special signature. See App. Table III. App. IX.

$$\ln\, {}_1k_{20} = 1.3753 - 0.1670\ \ln\, w_0$$

where

$$\overline{ln\ {}_nk_{20}} = 1.3753$$

$$s^2\left\{ ln\ {}_1k_{20} \mid ln\ w_0 \right\} = 0.08427 \quad (25\ \mathrm{df})$$

$$ln\ \overline{{}_nk_{20}} = \overline{ln\ {}_nk_{20}} + s^2/2 = 1.4175;\ \overline{{}_nk_{20}} = 4.13\ \mathrm{g}^{1-n}\ \mathrm{years}^{-1}$$

$$_nk_{10} = {}_nk_{20}\ \mathrm{e}^{-10\ pk} = 2.50\ \mathrm{g}^{1-n}\ \mathrm{years}^{-1}$$

$$s^2\left\{\overline{{}_nk_{20}}\right\} = s^2\left\{ln\ {}_1k_{20} \mid ln\ w_0\right\}\left(\frac{1}{\mathrm{N}} + \frac{(\overline{ln\ w_0})^2}{\mathrm{SSD}\left\{ ln\ w_0 \right\}}\right) = 0.004357$$

(Hald, 1952, equation (18.4.3)).

95% confidence interval:

$$1.28 < ln\ \overline{{}_nk_{20}} < 1.55;\ 3.6 < \overline{{}_nk_{20}} < 4.7$$

$$1-n = 0.1670;\ n = 0.833 = 5/6$$

$$s^2\left\{ 1-n \right\} = s^2\left\{ n \right\} = 0.0007806$$

95% confidence interval of n: 0.78–0.89

Ivlev (1961b, Table 79) investigated the weight loss at complete fasting of 12 species of fish living in the southern part of the Soviet Union. The initial weight was not stated, but all the fish were 25–30 days old at the beginning of the fast. Thus, they must have been of approximately the same size and the k values, therefore, directly comparable. What makes these experiments particularly interesting is the wide range of asymptotic size of the species in question. There are among them three small species and two very big ones. Any dependence of k upon asymptotic size (i.e. "the size of the species") as opposed to the actual size of the experimental animal should come out clearly in these circumstances. The asymptotic sizes of the experimental animals are not known, of course, but I have (App. Table IV) entered a tentative value for each species. It is quite obvious that k and W_∞ are not correlated to any appreciable extent.

APP. TABLE IV. The coefficient of fasting catabolism, k, at 20 C determined from the weight loss during fasting. All fish were 25–30 days old. W is a very rough guess of the asymptotic size of the species. (App. IX from Ivlev, 1961, Table 79.)

Species	W (g)	$_1k_{20}$ years^{-1}
Acipenser stellatus	10^5	1.21
Silurus glanis	10^5	1.15
Esox lucius	10^4	1.11
Cyprinus carpio	10^4	1.32
Caspialosa volgensis	10^3	1.01
Tinca tinca	10^3	1.28
Abramis brama	10^3	1.24
Perca fluviatilis	10^3	1.18
Rutilus rutilus caspicus	10^2	1.35
Alburnus alburnus	10	1.36
Neogobius melanostomus	10	1.07
Cobitis taenia	10	1.28

APP. X. GROWTH PARAMETERS ESTIMATED FROM LENGTH-AT-AGE DATA FOR 81 FISH SPECIES

ESTIMATES OF m, n, H, k, W_∞

The present example deals essentially with the application of the generalized growth equation,

$$\frac{dw}{dt} = Hw^m - kw^n \qquad \ldots\ldots(B8)$$

to alleged growth data from field studies. Particularly, it deals with the problem of estimating m and n so that H and k are constant throughout the growth curve. The data were compiled from the easiest available literature. Salmonids were omitted because their growth parameters seemed to fall into two groups, one with very high, another with very small values. Thus, their inclusion would increase unduly the variance. Given the choice of several sets of data for any one species of other families one set was selected which covered a high number of age-groups was based on a large material and was not obviously biased by unsatisfactory methods of sampling. Species and authors are listed in App. Table V.

The first step was to estimate H and k from equation A18, putting $m = 2/3$ and $n = 1$ (Pütter's approximation):

$$\frac{dl}{dt} = \frac{H}{3q^{1/3}} - \frac{k}{3}\,l \qquad \ldots(9\text{-}1)$$

by fitting annual increments linearly to corresponding body lengths (total lengths; standard and fork lengths were converted). When a weight–length key was given, $q = w/l^3$ was estimated from it. When q could not be estimated a value for a fish of similar shape was inserted. W_∞ was computed from equation A24 as $(H/k)^3$. The estimates are listed in App. Table V.

For further reasoning we shall speak in terms of weight so that

$$\frac{dw}{dt} = Hw^{2/3} - kw \qquad \ldots\ldots(1)$$

is Pütter's approximation to the generalized growth equation

$$\frac{dw}{dt} = Hw^m - kw^n \qquad \ldots\ldots(B8).$$

There are two aspects of the dependence of H and k on body size. These parameters may depend either on the actual size, w, of the animal, or they may depend on the size of the species, i.e. on W_∞. More relevantly, perhaps, the latter possibility could be put: W_∞ may depend on either H or k, or both. Anyway, if H or k, or both, are functions of w because erroneous values of m and n have been used, a false relationship of H and k with W_∞ is introduced when the parameters are estimated from growth curves. Such estimates require a large part of the growth curve and therefore must be based on bigger specimens of a large species than of a small one. In order to avoid this difficulty we shall refer to App. IX where, based on Ivlev's observations, it was found that k is independent of W_∞. When that is so, H must be functionally related to W_∞ because

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \ldots\ldots(A19)$$

rearranged and in logarithmic form gives

$$ln\,H = ln\,k + (n-m)\,ln\,W_\infty \qquad \ldots\ldots(9\text{-}2)$$

which is linear in ln H and ln W_∞.

APP. TABLE V. Growth parameters estimated from length-at-age data for 81 species of fish (App. X).

Reference	Species	$\hat{w}$ 10^2g	$n=1;\ m=2/3$ ${}_1k$ y^{-1}	${}_1H$ cm y^{-1}	${}_1W_\infty$ 10^3 g	$n=0.8321;\ m=0.5611$ B	${}_nk$ $g^{1-n}y^{-1}$	${}_nH$ $g^{1-m}y^{-1}$	${}_nW_\infty$ 10^3 g	m (second estimate)
Hodgson, 1925	*Clupea harengus*	0.41	1.64	8.92	0.164	1.0031	3.49	13.2	0.225	0.55
Motoda, 1963	*Clupea pallasii*	4.3	0.644	5.00	0.469	1.0048	1.79	9.49	0.475	0.62
Iles and Johnson, 1962	*Clupea sprattus*	0.068	1.75	5.47	0.0306	1.0030	2.41	6.70	0.0435	0.57
Phillips, 1948	*Sardinops coerulea*	2.2	0.789	5.01	0.257	1.0047	1.95	8.85	0.263	0.60
Nawratil, 1961	*Sardinops ocellata*	1.1	1.05	7.52	0.369	1.0033	2.32	12.4	0.487	0.60
Bougis, 1952 (after Storrow)	*Sardina pilchardus*	0.93	2.10	9.93	0.108	1.0048	4.48	16.1	0.112	0.42
FAO, 1960 (Nair)	*Sardinella longiceps*	0.41	0.937	5.10	0.160	1.0031	1.73	7.56	0.229	0.63
FAO, 1960 (Ben-Tuvia)	*Sardinella maderensis*	0.49	0.296	2.58	0.672	1.0021	0.57	3.90	1.24	0.74
Bougis, 1952 (after de Navarro)	*Sardinella aurita*	1.2	0.903	6.30	0.337	1.0035	2.01	10.4	0.433	0.61
Bougis, 1952 (after d'Ancona)	*Alosa fallax*	2.7	0.652	7.36	1.47	1.0028	1.66	13.3	2.16	0.65
Frost and Kipling, 1959	*Esox lucius*, males	25	1.26	16.5	2.23	1.0051	4.66	37.6	2.20	0.45
Muir, 1960	*Esox masquinongy*	18	0.210	6.11	24.6	1.0021	0.741	13.5	44.6	0.72
Da Franca, 1953	*Gambusia holbrookii*, females	0.014	2.51	3.34	0.00239	1.0042	2.66	3.47	0.00266	0.65
Hewson, 1955	*Lota lota*	25	0.218	4.78	10.3	1.0031	0.811	10.9	14.5	0.72
Bougis, 1952 (after Letaconnoux)	*Gadiculus thori*	0.18	2.00	6.67	0.0377	1.0039	3.25	9.08	0.0440	0.48
Bougis, 1952 (after Chevey)	*Gadus luscus*	0.93	0.947	5.78	0.221	1.0037	2.03	9.29	0.272	0.59
Kohler, 1964	*Gadus morhua*	16	0.376	9.28	15.2	1.0024	1.30	20.3	25.4	0.67
Ketchen, 1961	*Gadus macrocephalus*	22	1.59	27.2	5.01	1.0038	5.76	61.1	6.11	0.36
Messtorff, 1959	*Merlangius merlangus*, males	1.6	0.813	5.71	0.347	1.0038	1.90	9.74	0.418	0.61
Steele, 1963	*Pollachius virens*	26	0.441	9.11	8.87	1.0033	1.65	20.9	11.8	0.68
Ursin, 1963b	*Boreogadus esmarkii*	0.34	2.13	7.94	0.0509	1.0043	3.86	11.5	0.0563	0.52
Beverton and Holt, 1957	*Melanogrammus aeglefinus*	3.0	0.744	7.87	1.19	1.0031	1.94	14.3	1.62	0.61
(after Raitt)	*Merluccius merluccius*	16	0.672	17.4	17.7	1.0022	2.32	38.0	30.6	0.62
Bagenal, 1954	*Platichthys stellatus*, females	18	0.823	14.5	5.32	1.0034	2.92	31.9	6.80	0.58
Orcutt, 1950	*Platishthys flesus*	1.4	1.02	7.15	0.358	1.0037	2.32	12.1	0.444	0.57
Zemskaja, 1959	*Microstomus pacificus*, males	2.0	1.47	10.9	0.403	1.0039	3.60	19.1	0.473	0.52
Hagerman, 1952										

(*Continued*)

APP. TABLE V. Growth parameters estimated from length-at-age data for 81 species of fish (App. X). — (*Concluded*)

Reference	Species	$\hat{w}$ 10^2g	$n=1$; $m=2/3$ $_1k$ y^{-1}	$_1H$ cm y^{-1}	$_1W_\infty$ 10^3 g	B	$n=0.8321$; $m=0.5611$ $_nk$ $g^{1-n}y^{-1}$	$_nH$ $g^{1-m}y^{-1}$	$_nW_\infty$ 10^3 g	m (second estimate)
Rae, 1951	*Microstomus kitt*	2.7	0.822	6.87	0.596	1.0038	2.10	12.5	0.722	0.60
Kändler, 1949	*Rhombus maximus*, females	1.1	0.255	5.06	7.86	1.0012	0.560	8.31	21.0	0.74
Bowers, 1959	*Glyptocephalus cynoglossus*, males	1.8	0.931	7.44	0.513	1.0035	2.23	12.9	0.658	0.60
Kändler and Thurow, 1959	*Limanda limanda*, females	2.2	0.577	6.71	1.56	1.0026	1.43	11.8	2.40	0.67
Tåning, 1948	*Pleuronectes platessa*	3.3	0.663	6.44	1.05	1.0035	1.66	11.8	1.39	0.61
Southward, 1962	*Hippoglossus stenolepis*	72	0.274	8.53	29.4	1.0031	1.22	21.7	41.0	0.69
Sigurdsson, 1956	*Hippoglossus hippoglossus*	123	0.132	8.91	315	1.0017	0.638	24.2	667	0.71
Bagenal, 1955	*Hippoglossoides platessoides*, males	0.27	1.57	5.07	0.0334	1.0046	2.72	7.16	0.0356	0.55
Pruter and Alverson, 1962	*Hippoglossoides robustus*, females	0.34	0.310	2.15	0.337	1.0023	0.560	3.13	0.576	0.74
Beverton and Holt, 1957 (after Bückmann)	*Solea solea*	2.4	1.18	9.75	0.578	1.0037	2.94	17.4	0.710	0.55
Bougis, 1952 (after Furnestin)	*Lepidorhombus whiff-jagonis*	2.0	0.139	4.47	33.2	1.0009	0.304	7.84	161	0.73
Matsuura, 1961	*Pseudorhombus cinnamomeus*	2.8	0.973	8.18	0.596	1.0039	2.51	14.8	0.699	0.55
Miller, 1961	*Gobius paganellus*, females	0.022	1.45	2.64	0.00662	1.0035	1.60	2.87	0.00859	0.50
Bougis, 1952 (after Zei)	*Maena smaris*	0.17	1.50	5.09	0.0389	1.0038	2.44	6.89	0.0463	0.55
Chang, 1951	*Callionymus lyra*, males	0.27	0.789	5.78	0.391	1.0020	1.36	8.15	0.733	0.66
Jones and Hynes, 1950	*Gasterosteus aculeatus*	0.0068	1.50	2.11	0.00277	1.0031	1.42	2.03	0.00377	0.75
Jones and Hynes, 1950	*Pygosteus pungitius*	0.0055	3.65	3.36	0.000787	1.0039	3.29	3.15	0.000854	0.44
Jones, 1953	*Perca fluviatilis*	0.34	0.413	2.53	0.228	1.0026	0.748	3.68	0.356	0.74
Scofield, 1931	*Roccus lineatus*, males	12	0.746	12.8	5.01	1.0031	2.46	27.1	6.97	0.59
Young, 1963	*Paralabrax clathratus*	2.6	0.254	3.94	3.94	1.0020	0.631	7.08	7.49	0.70
Gravier, 1961	*Morone punctata*	6.2	0.225	4.65	8.87	1.0020	0.664	9.19	16.3	0.72
Whitney, 1961a	*Bairdiella isistius*	0.31	2.24	8.13	0.0477	1.0043	3.99	11.7	0.0526	0.41
Joseph, 1962	*Roncador stearnsi*	11	0.838	11.5	2.57	1.0037	2.71	24.0	3.13	0.57

Jones and Hynes, 1950	*Gasterosteus aculeatus*	0.0068	1.50	2.11	0.00277	1.0031	1.42	2.03	0.00377	0.75
Jones and Hynes, 1950	*Pygosteus pungitius*	0.0055	3.65	3.36	0.000787	1.0039	3.29	3.15	0.000854	0.44
Jones, 1953	*Perca fluviatilis*	0.34	0.413	2.53	0.228	1.0026	0.748	3.68	0.356	0.74
Scofield, 1931	*Roccus lineatus*, males	12	0.746	12.8	5.01	1.0031	2.46	27.1	6.97	0.59
Young, 1963	*Paralabrax clathratus*	2.6	0.254	3.94	3.94	1.0020	0.631	7.08	7.49	0.70
Gravier, 1961	*Morone punctata*	6.2	0.225	4.65	8.87	1.0020	0.664	9.19	16.3	0.72
Whitney, 1961a	*Bairdiella isistius*	0.31	2.24	8.13	0.0477	1.0043	3.99	11.7	0.0526	0.41
Joseph, 1962	*Roncador stearnsi*	11	0.838	11.5	2.57	1.0037	2.71	24.0	3.13	0.57

Joseph, 1962	*Menticirrhus undulatus*	6.7	1.10	12.8	1.55	1.0037	3.28	25.3	1.89	0.54
Whitney, 1961b	*Cynoscion xanthulus*	14	2.34	38.9	4.58	1.0033	7.90	83.6	6.02	0.37
Baxter et al., 1960	*Seriola dorsalis*	85	0.385	13.3	41.0	1.0029	1.76	34.5	58.9	0.62
Tsukahara, 1962	*Trichiurus lepturus*	2.9	0.617	8.61	2.71	1.0024	1.60	15.6	4.54	0.67
Bougis, 1952 (after Desbrosses)	*Mullus surmuletus*	1.1	1.48	10.5	0.350	1.0033	3.27	17.2	0.457	0.51
Bougis, 1952	*Mullus barbatus*	0.41	2.18	9.54	0.0839	1.0039	4.07	14.1	0.0990	0.41
Bougis, 1952 (after Heldt)	*Chrysophrys aurata*	6.4	2.00	21.2	1.19	1.0040	5.92	42.0	1.38	0.33
Bougis, 1952 (after Letaconnoux)	*Trachurus trachurus*	0.93	0.574	5.86	1.06	1.0022	1.23	9.46	1.86	0.67
Carlisle et al., 1960	*Amphisticus argenteus*, males	1.4	0.666	6.84	1.09	1.0025	1.53	11.5	1.74	0.64
Bougis, 1952 (after Serbetis)	*Mugil auratus*	2.2	1.01	11.7	1.55	1.0026	2.50	20.6	2.42	0.59
Bougis, 1952 (after Serbetis)	*Mugil capito*	3.6	0.966	12.0	1.94	1.0028	2.60	22.4	2.85	0.58
Bougis, 1952 (after Heldt)	*Mugil cephalus*	10	1.88	25.1	2.39	1.0037	5.99	52.0	2.92	0.34
Clark, 1925	*Leuresthes tenuis*, females	0.27	2.20	7.57	0.0408	1.0043	3.83	10.7	0.0448	0.43
Walford, 1932	*Sphyraena argentea*	8.6	1.09	14.8	2.53	1.0035	3.39	30.3	3.24	0.56
Yunokawa, 1951	*Chelidonichthys kumu*	3.5	0.763	8.96	1.62	1.0030	2.04	16.6	2.31	0.62
Mio, 1961	*Evynnis japonica*	2.5	0.903	11.9	2.26	1.0024	2.28	21.2	3.75	0.59
Pruter, 1954	*Anopoploma fimbria*, males	18	0.705	10.7	3.50	1.0040	2.48	23.6	4.08	0.56
Chatwin, 1958	*Ophiodon elongatus*	50	0.640	13.9	10.3	1.0039	2.67	34.3	12.2	0.56
O'Connell, 1953	*Scorpaenichthys marmoratus*, females	13	1.55	23.5	3.46	1.0036	5.17	50.0	4.33	0.30
Nédélec, 1958	*Scomber scombrus*	3.0	1.20	9.60	0.516	1.0041	3.12	17.5	0.585	0.51
Fitch, 1951	*Pneumatophorus diego*	0.35	0.859	3.26	0.0548	1.0043	1.56	4.75	0.0608	0.63
FAO, 1963 (Yoshida and Otsu)	*Thunnus germo*	57	0.516	15.9	29.4	1.0029	2.20	39.7	43.0	0.61
Tiews, 1957	*Thunnus thynnus*	318	0.402	26.4	284	1.0024	2.29	78.9	467	0.64
FAO, 1963 (Yamanaka)	*Thunnus orientalis*	466	0.523	37.3	364	1.0023	3.18	116	585	0.57
FAO, 1963 (Demir)	*Sarda sarda*	21	0.539	11.4	9.40	1.0027	1.95	25.5	9.45	0.60
FAO, 1963 (Mimura)	*Parathunnus mebachi*	30	0.111	10.5	852	1.0008	0.425	24.5	3125	0.72
FAO, 1963 (Mimura)	*Neothunnus macropterus*	148	0.970	43.6	90.8	1.0027	4.87	120	138	0.48
Shiokawa, 1962	*Sebastes pachycephalus*	0.41	0.552	4.03	0.389	1.0023	1.03	5.96	0.654	0.69
Mio, 1960b	*Sebastes inermis*	0.69	1.10	8.08	0.398	1.0028	2.24	13.6	0.596	0.56
Mio, 1960a	*Sebastiscus marmoratus*	0.41	0.746	6.86	0.778	1.0019	1.39	10.2	1.53	0.65
von Betalanffy, 1951 (after Darjavin)	*Acipenser stellatus*	97	0.162	7.19	87.3	1.0024	0.757	19.0	145	0.72
Bougis, 1952 (after Classen)	*Acipenser sturio*	195	0.288	13.3	98.6	1.0029	1.51	37.7	143	0.66

If the approximations $m = 2/3$ and $n = 1$ made above do not stabilize H and k, the estimates obtained probably correspond to some sort of mean value of the body sizes covered by the material. Let this mean weight be denoted $\hat{w}$. Then, because Pütter's approximation is known to describe satisfactorily the rate of growth of most fishes, we may put

$$\frac{dw}{dt} = {}_1\mathrm{H}\hat{w}^{2/3} - {}_1k\hat{w} = {}_n\mathrm{H}\hat{w}^{m} - {}_n\mathrm{H}\hat{w}^{n} \qquad .....(9\text{-}3)$$

where m and n stand for the values which make H and k independent of w. The suffixes are introduced to avoid confusion of the two sets of parameters. On the further assumption that each term, i.e. each product of a coefficient and a power of weight, is numerically correct, the expressions for H and k in equation 9-3 can be separated:

$${}_1\mathrm{H}\hat{w}^{2/3} = {}_n\mathrm{H}\hat{w}^{m};\ ln\ {}_1\mathrm{H} = ln\ {}_n\mathrm{H} - (2/3-m)\ ln\ \hat{w} \qquad .....(9\text{-}4)$$

$${}_1k\hat{w} = {}_nk\hat{w}^{n};\ ln\ {}_1k = ln\ {}_nk - (1-n)\ ln\ \hat{w} \qquad .....(9\text{-}5).$$

Notice the similarity of equation 9-5 with equation A15. n and ${}_nk$ are easily determined from equation 9-5 by plotting $ln\ {}_1k$ against $ln\ \hat{w}$ for the individual species listed in App. Table V. Equation 9-4 cannot be utilized in the same way because $ln\ {}_n\mathrm{H}$ is a function of W_∞ (equation 9-2). One problem is the determination of $\hat{w}$ because it is not clear how the mean shall be weighted. The weight of a fish whose length is the arithmetic mean of the mean lengths of individual age-groups has been used: $\hat{w} = q\,\bar{l}^{3}$. App. Fig. 9A is a plot of $ln\ {}_1k$ against $ln\ \hat{w}$ as defined above. Denoting by $\overline{ln\ {}_nk}$ the mean of log values the estimated straight line has the properties:

$$ln\ {}_1k = \overline{ln\ {}_nk} - (1-n)\ ln\ \hat{w} \qquad .....(9\text{-}5)$$

$$ln\ {}_1k = 0.6884 - 0.1679\ ln\ \hat{w}$$

$$s^2\left\{ ln\ {}_1k \mid ln\ \hat{w} \right\} = 0.4256 = s^2\ (79\ \mathrm{df})$$

$$ln\ \overline{{}_nk} = \overline{ln\ {}_nk} + s^2/2 = 0.9012;\ {}_nk = 2.46\ \mathrm{g}^{1-n}\ \mathrm{years}^{-1}$$

$$s^2\left\{ ln\ \overline{{}_nk} \right\} = s^2\left(\frac{1}{\mathrm{N}} + \frac{(\overline{ln\ \hat{w}})^2}{\mathrm{SSD}\left\{ ln\ \hat{w} \right\}}\right) = 0.008349$$

$$95\%\ \text{confidence interval} : 0.72 < ln\ \overline{{}_nk} < 1.08;\ 2.1 < \overline{{}_nk} < 3.0$$

$$n = 0.8321$$

$$s^2\left\{ 1-n \right\} = s^2\left\{ n \right\} = 0.0009790$$

$$95\%\ \text{confidence interval} : 0.77 < n < 0.89.$$

Most of the species used are from temperate waters, a few are arctic, and some tropical. Therefore, a mean temperature of 10 C seems a good guess. The agreement between the results obtained here and the estimates based on weight loss of fasting animals (App. IX) is striking: $n = 0.83$; ${}_nk_{10} = 2.5$.

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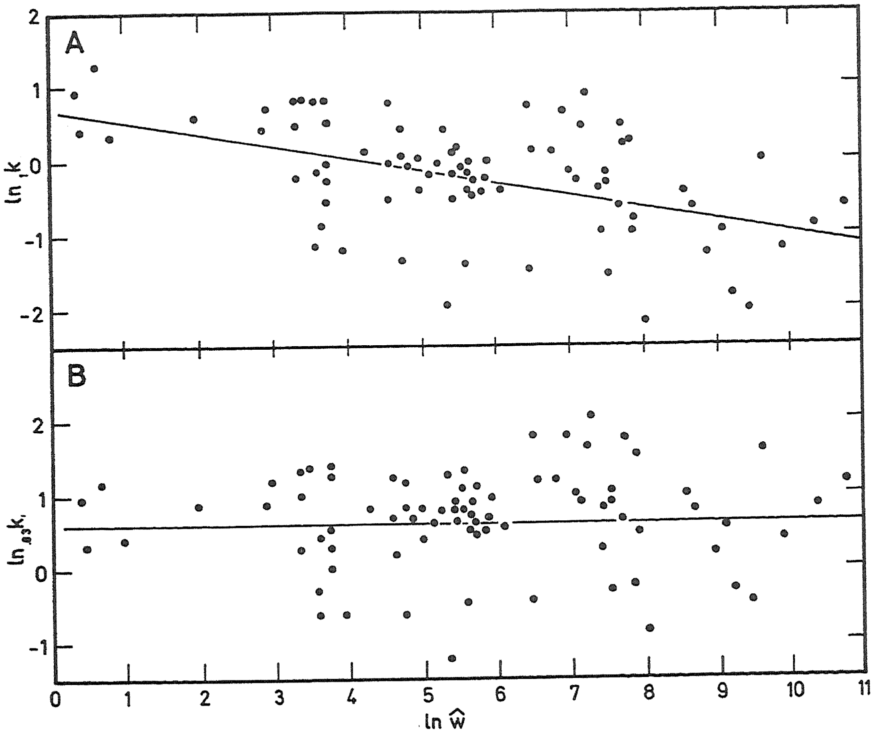


App. Fig. 9. A, the coefficient, k, of fasting catabolism, determined from the catabolic term, $-k\,w$, of the simple growth equation, dw/dt $Hw^{2/3} - k\,w$, and plotted against the mean weight, $\hat{w}$, of the fish from which it was determined. B, the same computed from the equation $dw/dt = H\,w^{0.56} - {}_nk\,w^{0.83}$; no significant regression upon body size. From length-at-age data for 81 fish species. App. X.

For the estimation of m an approximation method can be used. Consider equations 9-3, 9-4, and 9-5. An underlying assumption is that the anabolic and catabolic parameters, H and k, of the approximation $dw/dt = Hw^{2/3} - kw$ are correct for one value, $\hat{w}$, of w. This involves that at weight $\hat{w}$ each of the right-hand terms is separately correct. Another assumption is that even the approximation describes a growth curve satisfactorily. Of that there is plenty of evidence in literature. These assumptions have worked well. For body weights different from $\hat{w}$, however, the first assumption (the reliability of each term separately) can scarcely be retained whereas as to the second assumption, there is plenty of evidence in fishery biological literature that it is safe enough. Therefore, we can put

$$\frac{dw}{dt} = {}_1\mathrm{H}\hat{w}^{2/3} - {}_1k\hat{w} = {}_n\mathrm{H}\hat{w}^{m} - {}_nk\hat{w}^{n} \qquad \ldots\ldots(9\text{-}3)$$

$$\frac{dw}{dt} = {}_1\mathrm{H}w_1{}^{2/3} - {}_1kw_1 = {}_n\mathrm{H}w_1{}^{m} - {}_nkw_1{}^{n} \qquad \ldots\ldots(9\text{-}6)$$

where w_1 differs slightly, but distinctly, from $\hat{w}$. Putting $\hat{w} = Cw_1$, C differing enough from one to make rounding off errors from tables inconspicuous, and inserting equations 9-4 and 9-5 gives, after some rearrangement,

$$m = 2/3 - \frac{ln\ \mathrm{B}}{ln\ \mathrm{C}} \qquad \ldots\ldots(9\text{-}7)$$

where

$$B = (1 + \frac{{}_1k}{{}_1H} \hat{w}^{1/3} (C^{2/3-n} - C^{-1/3})).$$

B was computed for each of the 81 species in App. Table V for $ln\ C = 0.03$, i.e. $\hat{w} = 1.03\ w_1$. The mean and the 95% confidence interval of the mean are 1.00317 ± 0.00062 from which $m = 0.561$ with a 95% confidence interval of 0.540–0.582. This is an underestimate of the real variance because $n = 0.832$ (estimated above) was considered constant instead of being a stochastic variable. As expected, the estimate of m changes slowly with C. Putting $ln\ C = 0.6$ (i.e. $\hat{w} = 1.8\ w_1$) seems to reduce m from 0.56 to 0.54, although the computation was carried through for a few species only.

The estimate $m = 0.56$ was used in subsequent computations. At a late stage of the investigation, however, it was found advisable to check the approximation method by means of the more direct, but also more tedious, procedure of inserting the estimates of $\overline{{}_nk_{10}} = 2.5$ and $n = 5/6$ from fasting experiments (App. IX) in the growth equation

$$\left(\frac{dl}{dt} + K\, l^{3n-2}\right) = E\, l^{3m-2} \qquad \ldots\ldots (A18)$$

$$K = \frac{k}{3\, q^{1-n}}$$

in order to obtain, by means of a log scale plot, an estimate of $3m-2$ as the slope of a straight line. This was done for each of the 81 species (App. Table V, right-hand column). Interspecific differences of k were neglected, but species-specific values of q were used in the computation of K. The mean of 81 estimates of m was 0.588 (95% confidence limits: ±0.023), which is slightly higher than the figure, 0.561, found by means of the approximation method. The difference was considered too small to warrant an extensive re-computation of subsequent estimates. The new estimates of m had no significant regression upon body size, expressed as $ln\ \hat{w}$. The 95% confidence limits of the slope were 0.12 and –0.0085. Thus the possibility of m varying appreciably with body size or asymptotic size still has to be borne in mind.

Inserting the mean values of m (the first estimate) and n into equations 9-4 and 9-5 for each species provides individual estimates of ${}_nH$ and ${}_nk$ and, by means of equation A19, of ${}_nW_\infty$ (App. Table V). The new values of k are independent of body size. (App. Fig. 9B. The line, $\overline{ln\ {}_nk} = 0.688$ estimated from equation 9-5, is inserted).

The relationship between the estimates of asymptotic weight obtained by means of the two sets of parameters, Pütter's approximation ($m = 2/3$, $n = 1$) and the more correct one ($m = 0.56$, $n = 0.83$) can be expressed by means of equations A19, 9-4, and 9-5 as

$$ln\ {}_nW_\infty = \frac{1}{n-m} \left(\frac{ln\ {}_1W_\infty}{3} - (m + 1/3 - n)\ ln\ \hat{w}\right) \qquad \ldots\ldots (9\text{-}8).$$

With the present estimates, $m = 0.56$ and $n = 0.83$ the foregoing becomes

$$ln\ {}_nW_\infty = 1.23\ ln\ {}_1W_\infty - 0.23\ ln\ \hat{w}.$$

App. Table V gives ${}_nW_\infty = 1.42\ {}_1W_\infty$ as an average for all species.

The variation of ${}_nH$ with ${}_nW_\infty$ is given by equation 9-2 in the form

$$ln\ \overline{{}_nH} = ln\ \overline{{}_nk} + (n-m)\ ln\ {}_nW_\infty$$

which with the above parameter values becomes

$$\ln \overline{{}_nH} = 0.90 + 0.27 \ln {}_nW_\infty.$$

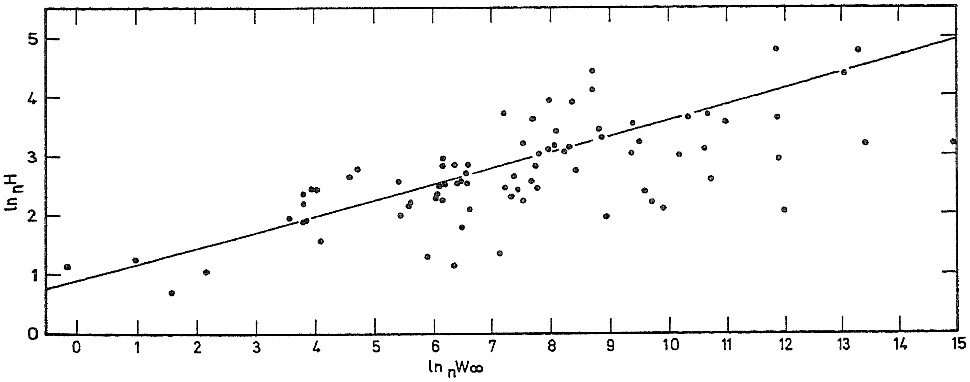
Values of ${}_nH$ for individual species (from App. Table V) are plotted against asymptotic size (log scale) in App. Fig. 10. The line just estimated is inserted. For the approximate size range of fish species,

$$10^{-1}\ \mathrm{g} < W_\infty < 10^5\ \mathrm{g}$$

the range of ${}_nH$ is

$$1.3 < \overline{{}_nH} < 40$$

in terms of $g^{0.44}$ years^{-1}.



APP. FIG. 10. The coefficient, H, of net anabolism, computed from the equation $dw/dt = H\, w^{0.56} - k\, w^{0.83}$ and plotted against asymptotic weight (log scale) 81 fish species. App. X.

The situation of individual points in App. Fig. 10 reflects that on App. Fig. 9 (k against body size). This is due to the correlation of k with H introduced with the techinque of calculation. Each pair of values was computed from the slope and intercept of one and the same straight line.

APP. XI. SEXUAL DIFFERENCES IN GROWTH PARAMETERS

ESTIMATES OF H, *k*, AND W_∞

The difference between male and female growth curves can be expressed empirically in terms of the growth parameters H (net anabolism), *k* (fasting catabolism) and W_∞ (asymptotic weight). We have from equation A19, arranged as equation 9-2,

$$ln\, H_{\text{♀}} = ln\, k_{\text{♀}} + (n-m)\, ln\, W_{\infty\text{♀}} \qquad \ldots\ldots(10\text{-}1)$$

$$ln\, H_{\text{♂}} = ln\, k_{\text{♂}} + (n-m)\, ln\, W_{\infty\text{♂}} \qquad \ldots\ldots(10\text{-}2).$$

Assuming a linear relationship between the log scale sexual differences of *k* and W_∞ we have

$$ln\, k_{\text{♀}} - ln\, k_{\text{♂}} = A + B\,(ln\, W_{\infty\text{♀}} - ln\, W_{\infty\text{♂}}) \qquad \ldots\ldots(10\text{-}3).$$

Subtracting equation 10-2 from equation 10-1, solving for $(ln\, k_{\text{♀}} - ln\, k_{\text{♂}})$ and inserting in equation (10-3) gives

$$ln\, H_{\text{♀}} - ln\, H_{\text{♂}} = A + (n-m+B)\,(ln\, W_{\infty\text{♀}} - ln\, W_{\infty\text{♂}}) \qquad \ldots\ldots(10\text{-}4).$$

For $A = B = 0$ the differences between male and female parameters are due to differences of H exclusively. For $A = 0$, $B = m-n$, the whole difference is placed upon *k*.

App. Table VI lists male and female parameters for 19 species of fish, one set for each species. The computations were made in the same way as in App. X, putting $n = 0.832$ and $m = 0.561$, as estimated in that example. Fitting to equation 10-3 gives

$$A = -0.02816;\ B = -0.3164$$

$$s^2\left\{\underline{ln\, k_{\text{♀}} - ln\, k_{\text{♂}}}\ \middle|\ \underline{ln\, W_{\infty\text{♀}} - ln\, W_{\infty\text{♂}}}\right\} = s^2 = 0.04463$$

$$s^2\{A\} = 0.002839;\quad A/s\{A\} = -0.53.$$

Thus, A is not significantly different from zero and can be neglected. We then have, as the best estimate of a straight line through the origin (Hald 1952),

$$B = -0.3277;\ s^2\{B\} = 0.003677$$

95% confidence interval: $\quad -0.456 < B < -0.200.$

The estimate of $m-n = -0.271$ is within this range. For the present, therefore, the hypothesis $B = m-n$ cannot be rejected and we may put

$$ln\, H_{\text{♀}} - ln\, H_{\text{♂}} = 0;\ H_{\text{♀}} = H_{\text{♂}} \qquad \ldots\ldots(10\text{-}5)$$

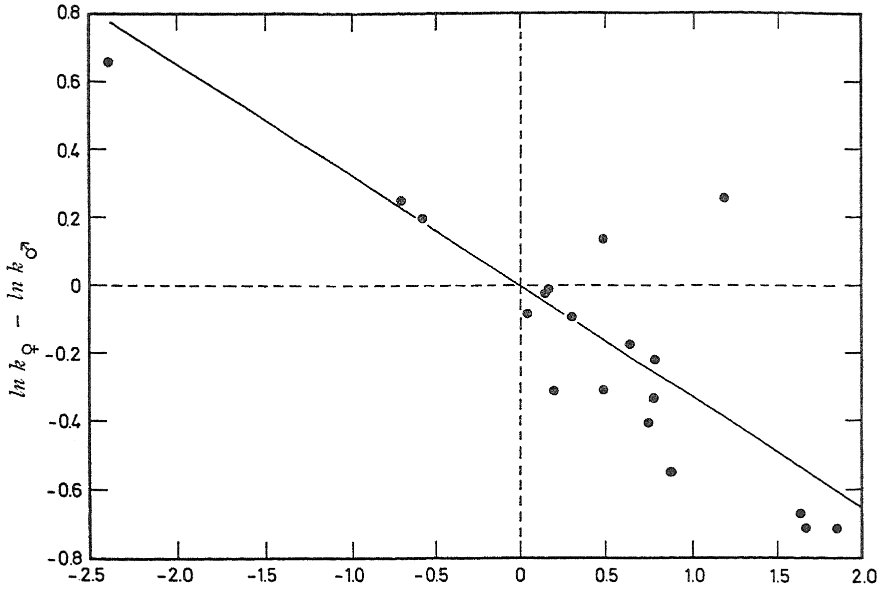
$$ln\, k_{\text{♀}} - ln\, k_{\text{♂}} = (n-m)\,(ln\, W_{\infty\text{♀}} - ln\, W_{\infty\text{♂}})$$

$$W_{\infty\text{♀}} = W_{\infty\text{♂}}\left(\frac{k_{\text{♀}}}{k_{\text{♂}}}\right)^{\frac{1}{n-m}} \qquad \ldots\ldots(10\text{-}6)$$

for most species, apparently, $k_{\text{♀}} < k_{\text{♂}}$, as can be seen in App. Fig. 11.

APP. TABLE VI. Growth parameters of males and females of the same species (App XI).

Species	Reference	Males						Females								
		$n=1;\ m=2/3$			$n=0.8321;\ m=0.5611$			$n=1;\ m=2/3$			$n=0.8321;\ m=0.5611$					
		$\ln \hat{w}$	$\ln {}_1k$	$\ln {}_1H$	$\ln {}_nk$	$\ln {}_nH$	$\ln_n W_\infty$	$\ln \hat{w}$	$\ln {}_1k$	$\ln {}_1H$	$\ln {}_nk$	$\ln {}_nH$	$\ln_n W_\infty$	$\ln_n W_\infty ♀ - \ln_n W_\infty ♂$	$\ln_n k ♀ - \ln_n k ♂$	$\ln_n H ♀ - \ln_n H ♂$
Mallotus villosus	Pitt, 1958	3.18	1.00	2.40	1.53	2.73	4.43	2.94	1.28	2.48	1.78	2.79	3.72	−0.71	0.25	0.60
Esox lucius	Frost and Kipling, 1959	7.34	0.23	2.80	1.46	3.58	7.80	7.91	−0.42	2.42	0.91	3.26	8.67	0.87	−0.55	−0.32
Gadus morhua	Saemundsson, 1923	7.55	−1.12	2.36	0.15	3.16	11.1	7.62	−1.16	2.37	0.12	3.17	11.2	0.14	−0.03	0.01
Merlangius merlangus	Messtorff, 1959	4.84	−0.207	1.74	0.61	2.25	6.05	4.97	−0.538	1.47	0.30	1.99	6.24	0.19	−0.31	−0.26
Platichthys stellatus	Orcutt, 1950	6.40	0.481	2.97	1.56	3.65	7.71	7.06	−0.295	2.67	0.89	3.42	9.34	1.63	−0.67	−0.23
Platichthys flesus	Kändler and Thurow, 1959	6.18	−1.11	1.55	−0.07	2.20	8.38	6.51	−1.02	1.78	0.07	2.47	8.86	0.48	0.14	0.27
Limanda limanda	Kändler and Thurow, 1959	5.17	0.215	2.23	1.08	2.78	6.27	5.48	−0.550	1.94	0.37	2.52	7.93	1.66	−0.71	−0.26
Microstomus pacificus	Hagerman, 1952	5.20	0.386	2.39	1.26	2.94	6.20	5.92	−0.0769	2.18	0.92	2.81	6.97	0.77	−0.34	−0.13
Microstomus kitt	Rae, 1948	5.64	−0.112	1.91	0.83	2.51	6.20	6.04	−0.591	1.66	0.42	2.30	6.94	0.74	−0.41	−0.21
Glyptocephalus cynoglossus	Bowers, 1959	5.18	−0.0715	2.01	0.80	2.56	6.49	4.99	0.152	2.06	0.99	2.59	5.90	−0.59	0.19	0.03
Pleuronectes platessa	Petersen, 1922	4.38	−0.128	1.51	0.61	1.97	5.02	4.70	−0.333	1.49	0.46	1.99	5.65	0.63	−0.15	0.02
Hippoglossoides platessoides	Bagenal, 1955	2.86	0.451	1.62	0.93	1.92	3.65	4.14	0.486	2.05	1.18	2.49	4.83	1.18	0.25	0.57
Gobius paganellus	Miller, 1961	1.82	0.418	1.04	0.72	1.23	1.88	1.79	0.343	0.970	0.64	1.16	1.92	0.04	−0.08	−0.07
Callionymus lyra	Chang, 1951	3.30	−0.237	1.75	0.32	2.10	6.57	3.04	0.470	1.79	0.98	2.11	4.17	−2.40	0.66	0.01
Roccus lineatus	Scofield, 1931	6.83	−0.293	2.55	0.85	3.27	8.93	7.61	−1.15	2.25	0.13	3.05	10.8	1.84	−0.72	−0.22
Amphisticus argenteus	Carlisle, 1960	5.46	−0.407	1.92	0.51	2.50	7.34	5.91	−0.699	1.87	0.29	2.49	8.12	0.78	−0.22	−0.01
Leuresthes tenuis	Clark, 1925	2.94	0.940	2.07	1.43	2.38	3.51	3.22	0.788	2.02	1.33	2.36	3.80	0.29	−0.10	−0.02
Anoplopoma fimbria	Pruter, 1954	7.40	−0.288	2.37	0.95	3.15	8.12	7.67	−0.647	2.16	0.64	2.97	8.60	0.48	−0.31	−0.18
Scorpaenichthys marmoratus	O'Connell, 1953	7.40	0.506	3.17	1.75	3.95	8.12	7.72	0.440	3.16	1.74	3.98	8.27	0.15	−0.01	0.03



App. Fig. 11. The ratio between the catabolic rates of males and females of the same species, plotted against the corresponding ratios of asymptotic size. Log scale. App. XI.

Notice, that in the analysis of interspecific differences (App. X) it was found that asymptotic size of a species is determined by H exclusively, whereas in the comparison of males and females of the same species the present analysis indicates dependence of asymptotic size upon *k* only.

APP. XII. NATURAL MORTALITY AND ASYMPTOTIC SIZE IN VARIOUS FISHES

ESTIMATES OF M AND μ

Equation E2 gives the dependence of natural mortality, M, upon body size and the parameters of anabolism and catabolism as

$$M = \mu \left(\frac{1+\alpha}{1-\alpha} H w^{m-1} + k w^{n-1}\right) \qquad \ldots\ldots (E2).$$

Data on growth and natural mortality in a number of fish species were published by Beverton and Holt (1959, Table I). They listed L_∞ cm, $k/3$ years^{-1} and M years^{-1} (App. Table VII of

APP. TABLE VII. Parameters of growth and natural mortality in various fishes. Adapted from Beverton and Holt (1959, Table I).

Species	$ln\ {}_1W_\infty$	$ln\ {}_1k$	M years^{-1}	$ln\ {}_nW_\infty$
Clupea harengus	5.49	0.13	0.25	5.86
Clupea harengus	4.41	0.67	0.78	4.75
Clupea pallasii	4.71	−0.14	0.56	5.06
Sardinops coerulea	5.07	0.16	0.15	5.43
Gadus callarias	9.93	−0.51	0.2	10.44
Gadus minutus, males	4.29	0.23	1.1	4.63
Gadus minutus, females	4.83	0.18	0.9	5.18
Gadus virens	9.30	−0.56	0.15	9.79
Merluccius merluccius, males	6.63	−0.94	0.6	7.04
Merluccius merluccius, females	7.56	−1.20	0.5	8.00
Pleuronectes platessa, males	6.72	−0.80	0.22	7.13
Pleuronectes platessa, females	8.04	−1.43	0.12	8.49
Pseudopleuronectes americanus	6.63	0.18	0.3	7.04
Solea vulgaris	6.27	0.18	0.25	6.67
Acipenser fulvescens	10.83	−1.90	0.01	11.36
Acipenser medirostris *Acipenser transmontanus*	12.39	−1.71	0.03	12.97
Blennius pholis	3.78	−0.11	0.9	4.10
Callionymus lyra, males	4.95	0.25	0.96	5.31
Callionymus lyra, females	3.87	0.50	0.86	4.20
Cottus gobio, males	1.20	0.74	1.1	1.45
Cottus gobio, females	1.26	0.18	0.9	1.51
Cottus gobio, males	0.90	0.99	0.9	1.14
Cottus gobio, females	0.90	0.41	0.8	1.14
Phoxinus phoxinus	1.89	0.50	1.1	2.16
Gasterosteus aculeatus	0.99	0.65	0.9	1.23
Gasterosteus pungitius	−0.33	1.76	1.1	−0.13
Cynoscion macdonaldi	9.84	−0.11	0.3	10.35
Perca fluviatilis	5.49	−0.51	0.29	5.86
Perca fluviatilis	5.88	−0.94	0.16	6.27
Stizostedion canadensis	6.36	−0.87	0.44	6.76
Dasyatis akajei, females	10.32	−1.20	0.4	10.84
Pneumatophorus diego	6.36	0.18	0.9	6.76
Neothunnus macropterus	11.04	0.41	0.8	11.58

the present paper). M was estimated independently of the growth parameters, which were computed by means of equation A23, thus putting $n = 1$ and $m = 2/3$. In order to adapt the estimates to the present model L_∞ was turned into W_∞ by assuming $W_\infty = q\,L_\infty^3$, $q = 0.009$. The mean size, $\hat{w}$, of the fish from which the parameter estimates were made was assumed to be determined by

$$ln\ \hat{w} = 0.92\ ln\ {}_1W_\infty - 0.92 \qquad \ldots\ldots(11\text{-}1)$$

which is the empirical relationship estimated from App. Table V. As in the preceding examples, ${}_1W_\infty$ designates the estimate of W_∞ obtained for $m = 2/3$ and $n = 1$. The relationship between ${}_nW_\infty$ and ${}_1W_\infty$ is given by equation 9-8. The estimates, $m = 0.56$ and $n = 0.83$, made in App. X give

$$ln\ {}_1W_\infty = 1.23\ ln\ {}_nW_\infty - 0.23\ ln\ \hat{w} \qquad \ldots\ldots(11\text{-}2).$$

Inserting 11-1 into 11-2 and rearranging leads to

$$ln\ {}_nW_\infty = 0.97\ ln\ {}_1W_\infty - 0.20 \qquad \ldots\ldots(11\text{-}3).$$

The values of $ln\ {}_nW_\infty$ of App. Table VII were computed by means of 11-3.

Equation 11-3 into 11-1 and rearranging gives

$$ln\ \hat{w} = 0.89\ ln\ {}_nW_\infty - 1.10 \quad \text{or} \quad \hat{w} = {}_nW_\infty{}^{0.89}/3.00 \qquad \ldots\ldots(11\text{-}4).$$

By means of equation A19, written in the form

$${}_nH = {}_nk\ {}_nW_\infty^{n-m}$$

and substituting $\hat{w}$ for w, equation E2 can be expressed as

$$M/\mu = \frac{1+\alpha}{1-\alpha}\ {}_nk\ {}_nW_\infty^{n-m}\ \hat{w}^{m-1} + {}_nk\ \hat{w}^{n-1} \qquad \ldots\ldots(11\text{-}5).$$

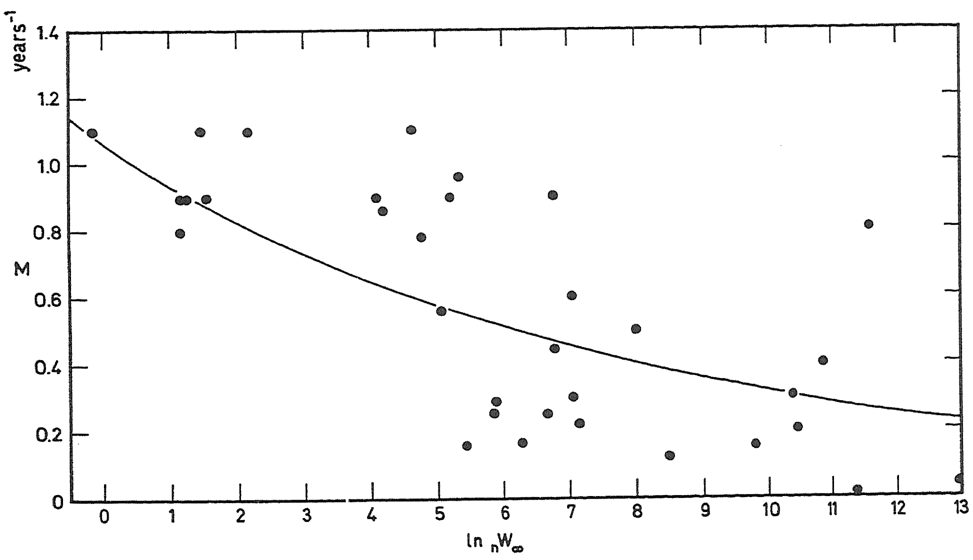
Inserting the following values of the parameters:
$\alpha = 0.8$ (as estimated for plaice in App. VII)
$ln\ \overline{{}_nk} = ln\ {}_nk = 0.9$; ${}_nk = 2.5$ (average for 81 species, App. X)
$n = 0.83$; $m = 0.56$ (also from App. X)
gives, after insertion of 11-4

$$M/\mu = 36.5\ {}_nW_\infty^{-0.122} + 3.02\ {}_nW_\infty^{-0.151} \qquad \ldots\ldots(11\text{-}6).$$

Inserting a range of values of asymptotic size provides a set of figures proportional with natural mortality (disregard the third column for the moment):

$ln\ {}_nW_\infty$	M/μ years^{-1}	M years^{-1}
0	39.53	1.07
2	30.85	0.83
4	24.10	0.65
6	18.82	0.51
8	14.70	0.40
10	11.47	0.31
12	8.96	0.24
14	7.00	0.19

So far, the data in App. Table VII have not been used at all. As there is no independent means of estimating the proportionality factor, μ, the analysis cannot be carried through without the use of fresh data. After a few trials it was found that the value $\mu = 0.027$ distributes the 33 individual observations of App. Table VII with about equal numbers on either side of the curve (16 above, 17 below). It was therefore adopted and used in computing the estimates of M in the third column above. The observations are plotted and the curve drawn in App. Fig. 12. The



APP. FIG. 12. The instantaneous coefficient, M, of natural mortality as a function of asymptotic size in fishes. Each entry represents one species (data from App. Table VII). The regression line is computed by means of the model by inserting parameter estimates made in previous examples into equation E2. App. XII.

agreement is fair enough so that the evidence of available material does not reject the hypothesis on the relationship between metabolic rates and natural mortality laid down in equation E2. The model implies that the smaller of the two sexes (usually the male) has the higher mortality, as is often observed (e.g. Beverton and Holt, 1959).

Mortality due to predation probably operates in almost the same way as mortality due to metabolic activities and is perhaps quite considerable. The value of μ used above is therefore likely to be an overestimate. It should preferably be determined in studies of carefully protected populations with predation nil or constant.

The present knowledge of actual parameter values indicates that equation E2,

$$M/\mu = \frac{1+\alpha}{1-\alpha} H\, w^{m-1} + k\, w^{n-1}$$

can be simplified without introducing serious bias. Parameter estimates made in various examples indicate that likely values are:

$$k \approx 1;\ 1 < H < 10^2;\ \frac{1+\alpha}{1-\alpha} \approx 10$$

$$m \approx 2/3;\ n \approx 5/6$$

where H is an increasing function of asymptotic size, as indicated by equation A19. Consider two fish species of extreme asymptotic sizes, 10^{-1} g and 10^{6} g. Let them be hatched weighing 10^{-4} g and 10^{-3} g, respectively. The H value for the small species will be about 1 and for the big one it is not over 10^{2}. We then have

The small species				The big species			
$M/\mu = 10\,w^{-1/3} + w^{-1/6}$				$M/\mu = 1000\,w^{-1/3} + w^{-1/6}$			
w (g)	$10\,w^{-1/3}$	$w^{-1/6}$	M/μ years^{-1}	w (g)	$1000\,w^{-1/3}$	$w^{-1/6}$	M/μ years^{-1}
10^{-4}	220	5	225	10^{-3}	10,000	3	10,003
10^{-3}	100	3	103	1	1,000	1	1,001
10^{-2}	50	2	52	10^{3}	100	0.3	100.3
10^{-1}	20	2	22	10^{6}	10	0.1	10.1

Thus, neglecting the second term of equation E2 is of no consequence for big species and leads to an overestimate of 10% for fully grown specimens of very small species. We can put

$$M = \mu \frac{1+\alpha}{1-\alpha} H \; w^{m-1}$$

which can be further simplified to

$$M = \mu' \; w^{m-1}.$$

Here, however, the proportionality constant, μ', is a function of W_∞. Putting $m = 2/3$ gives that natural mortality is roughly inversely proportional with the cube root of weight:

$$M = \mu'/w^{1/3}.$$

Take North Sea plaice as an example. The natural mortality was estimated by Beverton (Beverton and Holt, 1959, p. 151) as 0.22 years^{-1} for males and 0.12 years^{-1} for females. Averaging and assuming that the mean weight of the fish investigated was about 500 g, we have $M = 0.17$, $w^{-1/3} = 0.125$. The following table can be set up:

w (g)	$w^{-1/3}$	M years^{-1}	Mortality (%)	
10^{-3}	10.0	13.5	3.6 per day	
10^{-2}	4.64	6.26	1.6 per day	
10^{-1}	2.15	2.90	22 per month	
1	1.00	1.35	11 per month	
10	0.464	0.626	5.1 per month	
10^{2}	0.215	0.290	25 per year	
10^{3}	0.100	0.135	13 per year	
10^{4}	0.0464	0.0626	6.1 per year	
500	0.126	0.17	16 per year	$\mu' = 1.35$

If it does at all make sense to assume that the anabolic parameters are constant through the whole life of the fish, we find that larval mortality amounts to a few per cent per day, and that the recently settled bottom stages have a mortality of 20–30% per month. Both of these figures seem reasonable enough. The table also discloses a useful rule of thumb: for species of the size order $W_\infty = 10^3$ g we have

$$M = w^{-1/3}$$

and also, that when the weight is multiplied by 10 the natural mortality is halved.

APP. XIII. GROWTH OF *LEBISTES RETICULATUS*

Most growth data for fishes refer to medium-sized species, so that it was thought valuable to investigate an extreme case in some detail. The smallest easily kept species available was the guppy, *Lebistes reticulatus*, a stock of which was obtained from the Botanical Gardens of Copenhagen by the courtesy of the chief gardener, Mr Nilaus Jensen. They were primitive and uniform guppies which had not been mixed with other populations for many years. Mr Christian Frandsen conducted the growth experiments with great care and pet shop equipment.

When choosing *Lebistes* I was not aware that objections to the use of a cyprinodont fish for the purpose can be made. Various attempts to determine the power n of the catabolic term, $k\,w^n$, in cyprinodonts have given low values, $n = 2/3$, which seem to be unique in the animal kingdom (see Winberg, 1956, 1961; Paloheimo and Dickie, 1966a). Whether this is due to some unknown physiological difference between cyprinodonts and other fishes or is the effect of some bias or other, it is likely to show up somewhere in the present work.

The experiments fall into two groups, one in which the fish were reared separately at room temperature and another in which they were reared in groups at a range of temperatures. When the growth experiments had come to an end the surviving males were used for fasting experiments (see App. VIII). Some results of the fasting are utilized directly in the present example.

SINGLE SPECIMENS AT ROOM TEMPERATURE

ESTIMATES OF k AND m

In each of two experiments 12 new-born *Lebistes* were placed in 1.5-liter glass jars, one in each jar, at room temperature. Once every day, except on Sundays, they were fed commercial dry fish food in surplus, the surplus being removed by snails. The water was changed every 3 months. The temperature was read daily, except on Sundays. The fish were measured once a week in the first months and at longer intervals later on. Measurements were made from the tip of the nose to the tip of the tail, in units of 0.02 cm. After 406 days in the first experiment, and after 365 days in the second one, the surviving fish were kept fasting for about 3 weeks. In this period the water was renewed and the jar cleaned every 2nd day. At the same time the fish were weighed with an accuracy of 0.0001 g, the fourth decimal apparently being useless because of differences in the amount of water adhering to the skin. In the first experiment the fish were fed again afterwards and the fasting repeated, so that duplicate determinations became available.

The temperature oscillated irregularly between 19 and 23 C and was usually about 21 C. Most of the time the fish were exposed to natural daylight and dark, but towards the end of the experiment they were moved to a darkened room with artificial light 14 hr per day. Linear regression analyses were made with the growth rate as the dependent variable and with body length, temperature, and hours of daylight as independent variables. The inclusion of temperature or daylight, or both, often reduced the variance, but never significantly, not even when several sets of data were pooled. Therefore no further attention was paid to these variables, the mean temperature being about 20.5 C and the mean day length about 12 hr.

In the second experiment the fish for no apparent reason grew very little in the first months. In both experiments the females were virgin.

Since growth curves for single fish are scarce in literature, the length measurements of the 12 *Lebistes* from the first and more successful experiment are given in App. Table VIII. First, we shall test Pütter's approximation:

$$\frac{dw}{dt} = {}_1\mathrm{H}w^{2/3} - {}_1kw \quad \text{or} \quad \frac{dl}{dt} = {}_1\mathrm{E} - \frac{{}_1k}{3}l \quad \ldots\ldots(1), \text{(A23)}$$

using, as before, the suffix 1 to distinguish the Pütter parameters. Fitting length increments versus length (adults only) to a straight line produced 11 estimates of $ln\ {}_1k$ from the first experiment (App. Table VIII, omitting one fish in which sex reversal was observed). Fasting experiments

APP. TABLE VIII. Growth in length of 12 *Lebistes* reared separately in 1.5 liter jars. The measurement is given in italics the first time the sex could be determined. When 30 weeks old, fish No. 3 apparently changed from female to male. Measurements were to nearest unit below (f, female; m, male). Length in units of 0.02 cm.

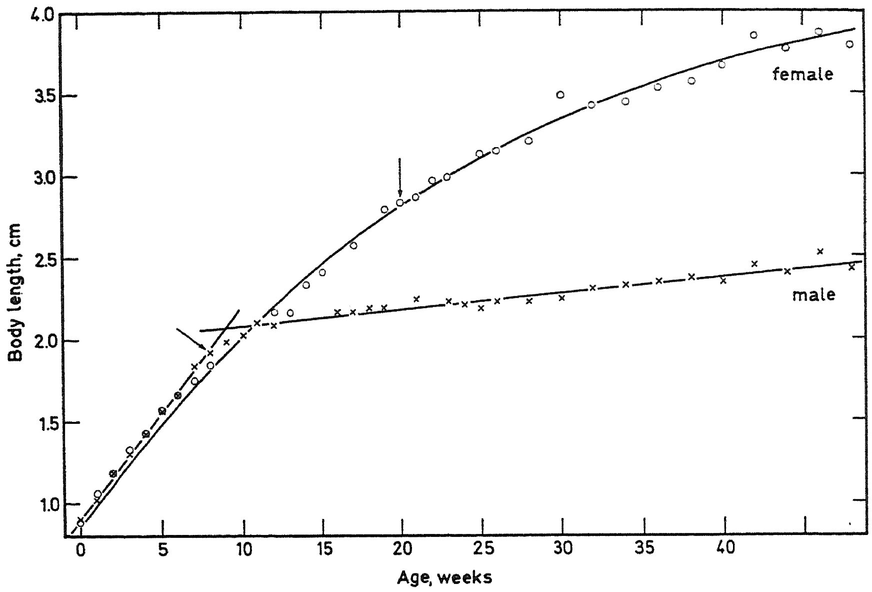
Age (weeks)	Length											
	1 f	2 m	3 fm	4 f	5 m	6 f	7 f	8 m	9 f	10 f	11 m	12 f
0	46	45	46	47	46	43	44	46	43	43	40	43
1	53	51	52	55	53	50	53	49	51	48	49	50
2	60	59	60	66	60	58	59	58		56	54	58
3	64	65	62	73	64	63	66	65	62	66	61	69
4	72	71	69	81	71	66	71	73	67	70	67	74
5	79	78	77	87	79		78	83	76	74	71	79
6	85	83	83	94	84		83	89	84	81	73	83
7	*91*	92	*89*	*106*	*90*		87	101	89			
8	101	*96*	98	110	93	81	92	*105*	*95*			
9	107	99	105	120	97	84						
10	113	101	111	124	100	90				103	84	97
11	116	105	116	128	103	96				107	89	99
12	121	104	121	133	104		108	111	112	112	93	*106*
13							108	113	116	117	95	110
14						112	116	115	120	118	97	
15						118	120	117	123	121	99	119
16	132	108	133	150	108	121						123
17	134	108	133	151	107	*126*	128	120	135	*130*	*101*	133
18	137	109	136	152	107	128			143	132	104	136
19	139	109	136	158	108		139	118	146	133	101	140
20							*141*	118	149	138	102	140
21	142	112	142	161	109	137	143	118	149	139	108	144
22						141	148	119	150			
23	151	111	141	170	113	143	149	118		148	106	151
24	155	110	141	171	116					152	105	157
25	159	109	140	173	112	151	156	121	154	148	106	157
26	162	111	140	175	112		157	121	157	151	107	159
28	167	111	139	176	111		160	121	164	158	106	165
30	176	112	*140*	192	112	163	174	121	171	161	106	169
32	179	115	143	197	112	168	171	121	170	167	106	171
34	181	116	142	204	114	176	172	123	177	173	109	174
36	192	117	143	209	114	187	176	128	179	174	110	174
38	192	118	145	216	114	188	178	128	181	180	113	176
40	192	117	144	216	115	191	183	126	186	197	113	181
42	198	122	149	218	116	196	192	131	199	196	110	177
44	203	120	148	223	116		188	131	201	198	113	179
46	212	126	153	227	123		193	136	206	201	116	181
48	213	121	149	221	118		189	135	210			
50	215	123	150	223	118							
52	216	124	152	221	123					205	117	
54								134	215			
58	218	124	155		121							

(see App. VIII) produced estimates of $ln\ _1k$ for 14 fish from both experiments. In neither case the difference between males and females was significant. The data are:

	df	$\overline{ln\ _1k}$	$s^2\{y\|x\}$	$ln\ \overline{_1k} = \overline{ln\ _1k} + (s^2\{y\|x\}/2)$	$\overline{_1k}$
Growth	11	1.73	0.396	1.93	6.89
Fasting	13	1.04	0.0625	1.08	2.93

where df is the number of degrees of freedom and where y stands for increment and x for length. Means and variances differ significantly so that the physiological interpretation of equation 1 must be rejected if the data are reliable. The inclusion of growth data from the second experiment does not change the picture, but since the juvenile growth in that experiment was abnormal it was considered safer to use these fish for the final fasting experiment only.

Empirically, the rejected equation gives a nice enough fit to data, for females at least, as examplified in App. Fig. 13 in which is shown a growth curve of a female (App. Table VIII, No. 7) fitted to equation 1 by the aid of equation A27; it is based on both juvenile and adult growth. The growth of juvenile males does not differ significantly from that of juvenile females, but with the onset of maturity the male curves change abruptly (see App. Fig. 13). The entire male curve gives a poor fit to equation 1 and is better described by two straight lines, one for juveniles and another for adults. Fits of equation 1 to each of the two parts of the male growth curve separately is technically quite possible but leaves the parameter values more or less accidental.



APP. FIG. 13. *Lebistes*. Growth curves of one male and one female (from App. Table VIII, fish No. 2 and 7). Arrows indicate when the sex was first recognized. Female data are fitted to equation A27. App. XIII.

The parameters m and n of the generalized growth equation,

$$\frac{dw}{dt} = \mathrm{H}\, w^m - k\, w^n \quad \text{or} \quad \frac{dl}{dt} = \mathrm{E}\, l^{3m-2} - \mathrm{K}\, l^{3n-2} \ldots\ldots (\mathrm{B18}), \quad (\mathrm{A18})$$

were in App. X estimated as $m = 0.56$, $n = 0.83$. These values based on a large number of species were found to stabilize k on the level indicated by fasting experiments (App. IX) on several species. If the above values of m and n are applicable to *Lebistes* a plot of $(dl/dt)\ l^{2-3m}$ against $l^{3(n-m)}$ should give a value of k (i.e. of $_{.83}k$) which is not significantly different from a similar estimate from weight loss data for fasting animals. In the same way as above we get

	df	$ln\ _{.83}k$	$s^2\{y\|x\}$	$\overline{ln\ _{.83}k}$	$\overline{_{.83}k}$
Growth	11	1.47	0.347	1.64	5.17
Fasting	13	0.803	0.221	1.02	2.79

The difference between the two estimates of k is smaller than for $m = 2/3$, $n = 1$. Yet, the difference is significant and the hypothesis $m = 0.56$, $n = 0.83$, must be rejected, too.

There is no means of estimating independently both m and n from the *Lebistes* data. This, I think, could be done only by means of respiration data for animals of different size, i.e. from experiments like those Saunders (1963) made on cod (see App. IV). *Lebistes*, however, would present extreme difficulties because of the short size range covered by the species: birth, 10^{-2} g; first maturity, 10^{-1} g; asymptotic size, males 10^{-1} g, females 1 g. The short size range, however, with the small deviation from unit weight gives the advantage that an error in the estimate of n influences only slightly the estimates of other parameters. Notice the reasonably small differences of the estimates of $_1k$ and $_{.83}k$ above. Thus, sticking to Pütter's n (= 1) is likely to lead to useful although somewhat biased estimates of other parameters.

Another problem is that the reason why the hypotheses regarding m and n must be rejected is unknown. It may be that the two sets of values tested just don't apply to *Lebistes*. However, it is also possible that the assumptions underlying the estimation of k from fasting experiments do not hold. For instance, the chemical composition of the body may have changed during the fasting experiments, or the behaviour of fasting *Lebistes* may have differed significantly from that of fed ones (although no such difference was observed). Accepting the fasting estimate of k presents the more interesting possibilities for further analysis, and this, admittedly, is the reason why it has been done below.

Having thus defined $n = 1$, and k equal to the value of k obtained from fasting experiments we are landed with the following variety of equation A18:

$$ln\left(\frac{dl}{dt} + \frac{k}{3}\, l\right) = ln\ \mathrm{E} + (3m-2)\ ln\ l \qquad \ldots\ldots (12\text{-}1)$$

which is linear with slope 3m–2. Eleven estimates of m from growth data for males and females from the first experiment have a mean value of 0.500 with a 95% confidence interval of ± 0.078. The mean is not significantly different from the estimate, $m = 0.561$, based on growth data for 81 species (App. X). Inserting $m = 1/2$ in equation 12-1 leads to the growth equation

$$\frac{dl}{dt} = \mathrm{E}\, l^{-1/2} - \mathrm{K}\, l$$

$$\mathrm{E} = \frac{\mathrm{H}}{3q^{1/2}}\,;\ \mathrm{K} = \frac{k}{3} \qquad \ldots\ldots (12\text{-}2)$$

which shall be further investigated in the next paragraph.

GROWTH RATES AT DIFFERENT TEMPERATURES

ESTIMATES OF k, p_k, H, $_{H}a$, $_{H}b$, $_{H}p_0$, $_{H}p_2$, τ_m, W_∞, $\tau_{\infty m}$, $W_{\infty m}$ AND τ_{mg}

New-born *Lebistes*, most of them born at room temperature, were placed in 39 6-liter glass jars, about 15 in each jar. The jars were aerated and many of them heated electrically. The treatment of the fish was the same as in the experiments with single specimens (see above). The mortality was generally low. Quite often, some few died in the 1st week, but afterwards, the mortality was low and sometimes nil until some accident (e.g. break-down of the temperature regulation) occurred. Whenever mortality had occurred, the corresponding observation of increment was discarded. Still, the whole curve is biased if the fish which died had other growth parameters than the survivors. Most series were carried through the 1st year of life and some up to 500 days. In the end, the males were kept fasting for about 3 weeks (see App. VIII). Females could not be used in fasting experiments because of interfering cyclic weight changes.

Most jars were kept in a room with no daylight but artificially illuminated 14 hr of the day. The temperature oscillated 1 C, occasionally 2 C, on either side of the mean. Within experiments, however, there was no significant dependence of growth rate upon temperature, or upon day length in the few series which were not artificially illuminated.

ESTIMATING THE COEFFICIENT OF FASTING CATABOLISM, k

An appropriate although to some extent arbitrary growth equation for *Lebistes* was derived above (equation 12-2) which on rearrangement becomes

$$\frac{dl}{dt}\, l^{1/2} = \mathrm{E} - \mathrm{K}\, l^{3/2} \qquad \ldots\ldots(12\text{-}2)$$

from which K can be determined as the slope of a straight line. The corresponding estimate of E is of little interest because K and E are heavily correlated when estimated from the same straight line. The fish in three of the original 39 jars died so early that they cannot be used for estimation of adult fish parameters. Thus 36 estimates of K are available for each sex. The variance of K varies significantly from one series to another, major influences apparently being the number of observations, the general smoothness of the growth curve, and the size range between the first and the last observation, this latter being quite a problem with males which sometimes grew less than 1 mm from the sex became distinguishable until the end of the experiment. Five estimates of K for males and another five for females were discarded because the variances were conspicuously higher than in the remaining 31 experiments. The 95% confidence interval of K in many cases included zero, particularly for males. The estimates of k (= 3K) and their variances are listed in App. Table IX. k (in terms of years^{-1}) is plotted against temperature in App. Fig. 14. Log scales were not used because there are a few negative values for males. Direct comparison with App. Fig. 7 (App. VIII), which gives the corresponding relationship for fasting experiments with males, is not possible, but the regression line from App. Fig. 7 has been entered in App. Fig. 14. It is obvious that we cannot reject the hypothesis that the quantities k, as estimated from fasting experiments and from growth experiments, are the same. The experiments, however, are not satisfactory because as already explained it resulted that females, except virgin ones, are unsuitable for fasting experiments and males are unsuitable for growth experiments. Some very high entries for males (App. Fig. 14) leap into the eye. They are probably biased by including observations of juvenile growth. After all, the definition of a juvenile *Lebistes* as one in which the sex cannot be determined by inspection is rather arbitrary. Even for females the variance about the regression line is very high. Application of equation C6 to female data gives an estimate of the 95% confidence interval of the temperature coefficient,

$$p_k = 0.0848 \pm 0.0971$$

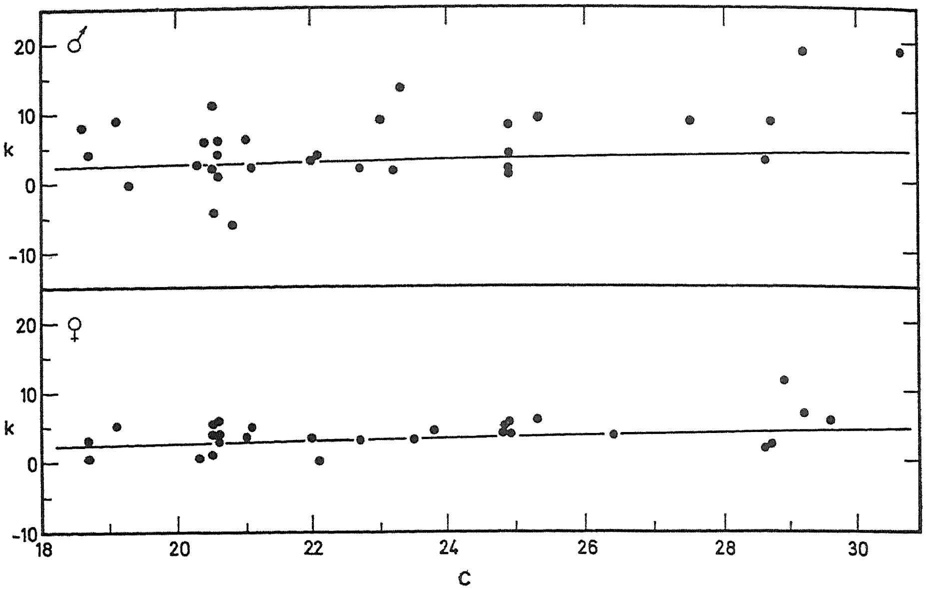
so that the hypothesis $p_k = 0$ cannot be rejected.

APP. TABLE IX. *Lebistes reticulatus.* Values of k and their variance estimated from growth data by means of equation 12-2. Estimates discarded owing to a conspicuously high variance are in italics. Adults only (App. XIII, cf. App. Fig. 14).

Temp τ (C)	Males		Females	
	k = 3K (years^{-1})	s_k^2	k = 3K (years^{-1})	s_k^2
18.6	8.15	24.6	3.20	3.02
18.7	4.49	22.5	0.547	4.54
19.1	9.01	14.3	5.62	6.11
19.3	-0.485	10.0	*7.71*	52.5
20.3	2.68	9.45	0.391	0.728
20.4	5.78	16.3	6.23	2.75
20.5	11.2	11.1	5.39	0.471
20.5	-4.59	34.2	0.885	7.52
20.5	*3.75*	136	4.18	0.891
20.5	2.35	2.40	4.41	0.773
20.6	5.93	33.7	3.66	1.60
20.6	3.97	1.93	2.90	0.238
20.6	0.919	6.11	3.90	2.02
20.8	-6.08	21.1	3.71	1.30
21.0	6.20	17.0	3.45	2.71
21.1	2.13	4.93	5.19	0.816
22.0	3.02	9.32	3.43	1.01
22.1	3.59	33.1	0.142	3.76
22.3	*12.4*	96.8	*-3.35*	19.1
22.7	2.02	20.2	3.25	5.61
23.5	9.07	9.58	2.98	0.979
23.7	1.38	33.0	*6.63*	31.0
23.8	13.7	13.4	4.79	0.588
24.9	1.22	4.53	4.11	0.816
24.9	1.83	4.97	4.80	5.69
24.9	4.29	6.05	4.23	2.78
24.9	2.22	15.0	5.34	7.36
25.3	9.55	10.6	6.15	1.64
26.4	*-9.88*	121	4.45	8.03
27.5	8.72	10.5	*11.0*	33.8
28.6	3.00	3.82	1.90	3.42
28.7	9.75	4.12	2.64	1.49
28.9	*4.57*	119	11.6	7.20
29.2	18.5	25.8	7.25	2.90
29.6	*21.2*	93.6	5.71	1.01
30.7	18.1	31.1	*8.00*	118

ESTIMATING THE COEFFICIENT OF NET ANABOLISM, H

Since there is no evidence to the contrary, it can be assumed for the present that k is the same in male and female *Lebistes*. k of juveniles is not known at all, but we shall make the simple as-



APP. FIG. 14. *Lebistes.* Values of ${}_1k$ estimated from growth data. The regression lines are reproduced from App. Fig. 7 which gives similar data (log scale, however) for fasting experiments. App. XIII.

sumption that it is the same as in adults. Thus, the entire variation of the growth curve with sex and developmental stage is placed upon E of equation 12-2 so that E can be estimated from

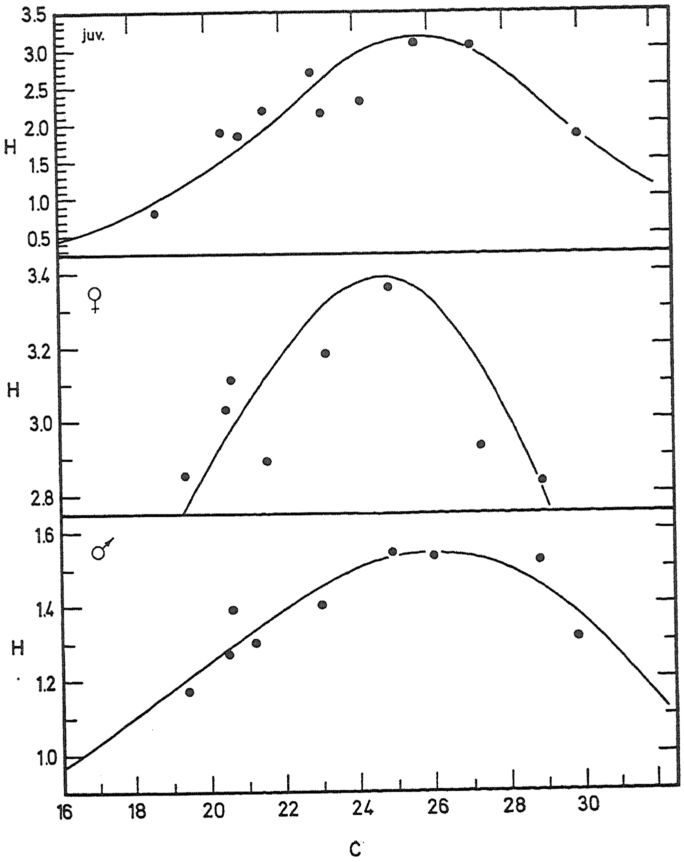
$$E = \frac{dl}{dt}\, l^{1/2} + K\, l^{3/2}.$$

To avoid artificial correlation of E and K, the estimate of k made in App. VII:

$$K = k/3 = 3.24\, e^{0.0476\, \tau}$$

must be inserted. The computation of $H = 3\, E\, q^{1/2}$ requires estimates of $q = w/l^3$. Plausible values of q were found to be 0.010 for females, 0.009 for juveniles, and 0.008 for males. Insertion of the appropriate value of k gives for each experiment a number of estimates of E, one for each observation of growth rate, dl/dt, and length, l. The means of these estimates for each experiment were arranged according to temperature and pooled within short temperature ranges to make the presentation clearer. Thus the following results were obtained (see App. Fig. 15):

Females				Males			
τ (C)	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)	τ (C)	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)
19.4	9.50	2.85	0.351	19.4	3.59	1.17	0.855
20.5	10.1	3.03	0.330	20.5	3.89	1.27	0.787
20.6	10.4	3.11	0.322	20.6	4.24	1.39	0.719
21.6	9.62	2.89	0.346	21.2	3.99	1.30	0.769
23.2	10.6	3.18	0.314	23.0	4.29	1.40	0.714
24.9	11.2	3.36	0.298	24.9	4.72	1.54	0.649
27.3	9.75	2.93	0.341	26.0	4.69	1.53	0.654
29.6	9.45	2.83	0.353	28.7	4.66	1.52	0.658
				29.8	4.00	1.31	0.763



App. Fig. 15. *Lebistes*. The coefficient, H, of net anabolism plotted against temperature and fitted to the reciprocal of equation C4. H is determined from growth data, using the approximation $dw/dt = \mathrm{H}\, w^{1/2} - k\, w$. App. XIII.

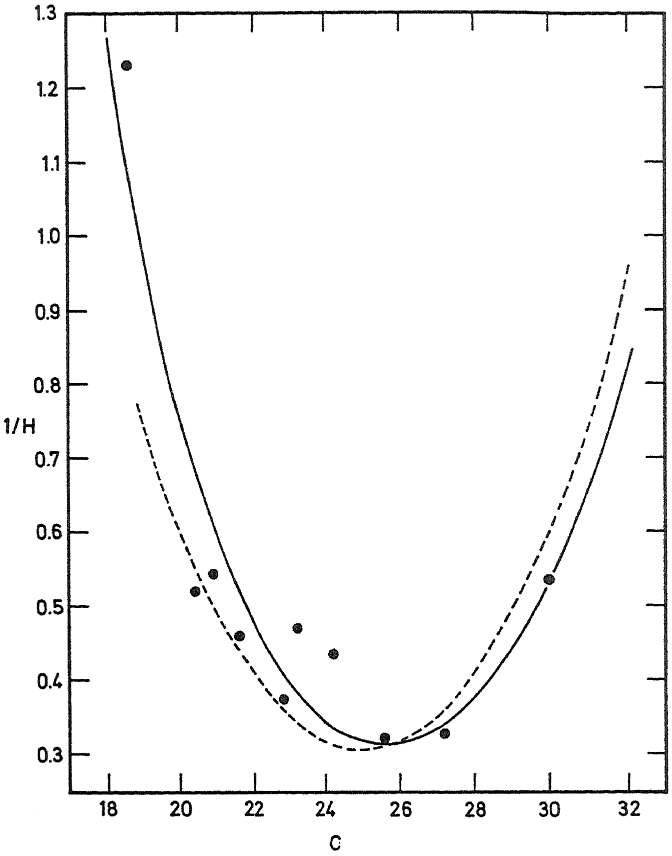
For juveniles, corresponding data were obtained in a slightly different way to avoid irregularities during the first time after birth and when sexual maturity is approaching. From plots of length against age was read the time to grow from a length of 1.2 cm to 1.4 cm (dt/dl, measured in days per 0.2 cm). The mean temperature in the period concerned was computed and the data arranged according to temperature. dt/dl was converted to dl/dt expressed in cm per year, and mean values of temperature and dl/dt computed for groups of four observations, each group covering a short temperature range. E and, hence, H then could be estimated as above (see App. Fig. 15 and 16)

τ (C)	$\frac{dl}{dt}$ (cm years^{-1})	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{\mathrm{H}}$ (years g$^{-1/2}$)
18.6	2.73	4.40	0.812	1.23
20.4	4.69	6.75	1.92	0.521
20.9	4.41	6.46	1.84	0.543
21.6	5.40	7.64	2.18	0.459

(*Continued*)

(*Concluded*)

τ (C)	$\frac{dl}{dt}$ (cm years^{-1})	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)
22.8	6.88	9.41	2.68	0.373
23.2	5.18	7.49	2.13	0.469
24.2	5.61	8.07	2.30	0.435
25.6	7.98	10.90	3.11	0.322
27.2	7.75	10.76	3.07	0.326
30.0	3.83	6.56	1.87	0.535



APP. FIG. 16. *Lebistes*. 1/H (see App. Fig. 15) for juveniles, plotted against temperature and fitted to equation C4. The dotted line was made by fitting data given by Gibson and Hirst to a catenary curve. App. XIII.

The relevant parameters are given by

$$\frac{1}{H} = a\ e^{p_0\tau} + b\ e^{p_2\tau} \qquad .....(C4).$$

$\frac{1}{H}$
(years g$^{-1/2}$

0.373
0.469
0.435
0.322
0.326
0.535

iveniles,
e dotted
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.....(C4

Rough estimates of the four parameters, a, b, p_0 and p_2, can be made as in App. III by reading off four values from eye-fitted curves through the observations. For instance, putting $T = \tau/3.75$, $A = e^{3.75\,p_0}$ and $B = e^{3.75\,p_2}$, and reading off such a curve for males at $T = 5, 6, 7, 8$ gave

τ	T	H	$\frac{1}{H}$
18.75	5	1.16	$0.862 = u = a\,A^5 + b\,B^5$
22.50	6	1.42	$0.704 = v = a\,A^6 + b\,B^6$
26.25	7	1.54	$0.649 = x = a\,A^7 + b\,B^7$
30.00	8	1.36	$0.735 = y = a\,A^8 + b\,B^8$

and, by simple arithmetics,

$$\left.\begin{matrix} A \\ \\ B \end{matrix}\right\} = \frac{(u\,y - v\,x) \pm \sqrt{(u\,y - v\,x)^2 - 4\,(u\,x - v^2)\,(v\,y - x^2)}}{2\,(u\,x - v^2)} = \left\{\begin{matrix} 2.0228 \\ \\ 0.7455 \end{matrix}\right.$$

$$A = e^{3.75\,p_0} = 2.0228 \qquad\qquad B = e =^{-3.75\,p_2} 0.7455$$

$$p_0 = 0.1879 \qquad\qquad p_2 = 0.07835$$

Simultaneous solution of two of the original four equations gives $a = 0.001419$ and $b = 3.5347$ so that

$$\frac{1}{H} = 0.00142\ e^{0.188\,\tau} + 3.53\ e^{-0.0784\,\tau}$$

for males.

Similarly, for females,

$$\frac{1}{H} = 0.000340\ e^{0.222\,\tau} + 1.77\ e^{-0.0856\,\tau}$$

and for juveniles,

$$\frac{1}{H} = 0.0000292\ e^{0.247\,\tau} + 185\ e^{-0.278\,\tau}.$$

Curves computed by means of the foregoing estimates are shown in App. Fig. 15 and 16. They fit the original points well enough; App. Fig. 15 shows plots of H against temperature; App. Fig. 16 is a plot of 1/H against temperature for juveniles and includes an independent estimate (from Ursin, 1963a, Fig. 8) based on the early growth of *Lebistes* reared by Gibson and Hirst. This second estimate is a fit to a catenary curve (equation C8) and is in reasonable accordance with the new result.

The maxima of the three curves of App. Fig. 15 are given by

$$\tau_m = \frac{ln\left(\frac{p_2}{p_0}\ \frac{b}{a}\right)}{p_0 + p_2} \qquad \ldots\ldots(C7)$$

as: juveniles 25.7 C, females 24.7 C, and males 26.1 C. It is not known whether the differences are significant or not.

ESTIMATING THE ASYMPTOTIC SIZE, W_∞ OR L_∞

The asymptotic weight as a function of temperature is given by equation C9 which for $m = 1/2$ and $n = 1$ becomes

$$W_\infty = [(a e^{p_0 \tau} + b\ e^{-p_2 \tau})\ k_0\ e^{p_k \tau}]^{-2} \qquad \ldots\ldots(12\text{-}3)$$

with maximum at temperature

$$\tau_{\infty m} = \frac{ln\left(\dfrac{p_2 - p_k}{p_0 + p_k} \dfrac{b}{a}\right)}{p_0 + p_2} \qquad \ldots\ldots(\text{C10}).$$

The letters p_2, p_0, b, and a refer to equation C4, i.e. they are anabolic parameters.

Converting weight to length by means of $w = q\ l^3$ and inserting the previously estimated parameter values in equations 12-3 and C10 provides points on the curves of App. Fig. 17 which shows L_∞ as a function of temperature for juveniles, females, and males. Maximum asymptotic size, $W_{\infty m}$, is reached at the following temperatures (equation C10) and with the values indicated (equation 12-3):

	$\tau_{\infty m}$ (C)	$W_{\infty m}$ (g)
Juveniles	25.0	0.768
Females	21.4	1.07
Males	21.7	0.204

Direct observation of L_∞ is impossible, but the length at the end of the growth experiment should be an underestimate of L_∞ for adults. Omitting series which did not survive 300 days we are left with 33 mean lengths of males and 32 of females. Pooling, as usual, over short ranges of temperatures provides the observations set out in App. Fig. 17. The hypotheses indicated by the curves obviously cannot be rejected by means of these observations. They are all situated below the curves, as they should be, and have roughly the right trend.

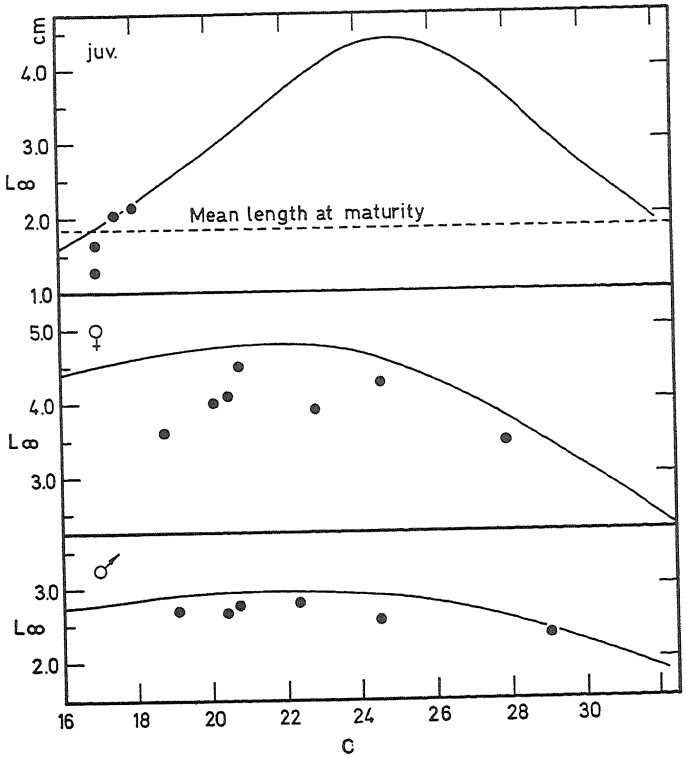
Juvenile L_∞ is usually purely hypothetical because the part of the curve effectuated before the onset of maturity is almost linear. Inspection of App. Fig. 17, however, shows that at low temperatures the juvenile L_∞ is considerably smaller than that of adults. If the estimates are correct it may even be smaller than the mean size at maturity which is 1.86 cm with a 95% confidence interval of 0.04 cm and no significant regression upon temperature. Thus, sexual maturity should not be reached at all below 17 C (see App. Fig. 17, juveniles) about which temperature the juvenile growth curve must be almost completed before the onset of maturity.

In fact, the fish in the four coldest jars developed growth curves as described. One is shown in App. Fig. 18. Arrows indicate when the first and the last fish could be identified to sex. At an age of about 175 days the juveniles seem to approach an asymptotic size of about 1.65 cm, but soon afterwards start growing rapidly, obviously with the parameters of the adults. These fish lived at temperatures about 18.8 C in the first 77 days and after the 287th day. When 78–286 days old (the interval concerning us here) they were kept at about 17 C. The "guesstimate" of $L_\infty = 1.65$ cm at 17 C is indicated on App. Fig. 17 and so are three other low-temperature observations. They are in good accordance with the expected values.

MAXIMUM GROWTH RATE AS A FUNCTION OF TEMPERATURE AND BODY SIZE

The growth equation with temperature incorporated can be expressed as

$$\frac{dw}{dt} = (a\ e^{p_0 \tau} + b\ e^{-p_2 \tau})^{-1}\ w^m - k_0\ e^{p_K \tau}\ w^n \qquad \ldots\ldots(\text{C11}).$$



APP. FIG. 17. *Lebistes*. Estimated variation of asymptotic length, L_∞, with temperature. The observed lengths of males and females at the end of the growth experiment are indicated. On juveniles approaching L_∞ before becoming mature, see text. App. XIII.

Inserting the parameter values already found in the present Appendix with various values of τ and w produces curves like those in App. Fig. 19 which show the variation of male growth rate. The bigger the fish, the narrower the temperature interval within which it can grow. The negative growth rates indicate that a fish grown large at temperatures near $\tau_{\infty m}$ = 21.7 C must loose weight when placed at extreme temperatures, even when fed their usual rations.

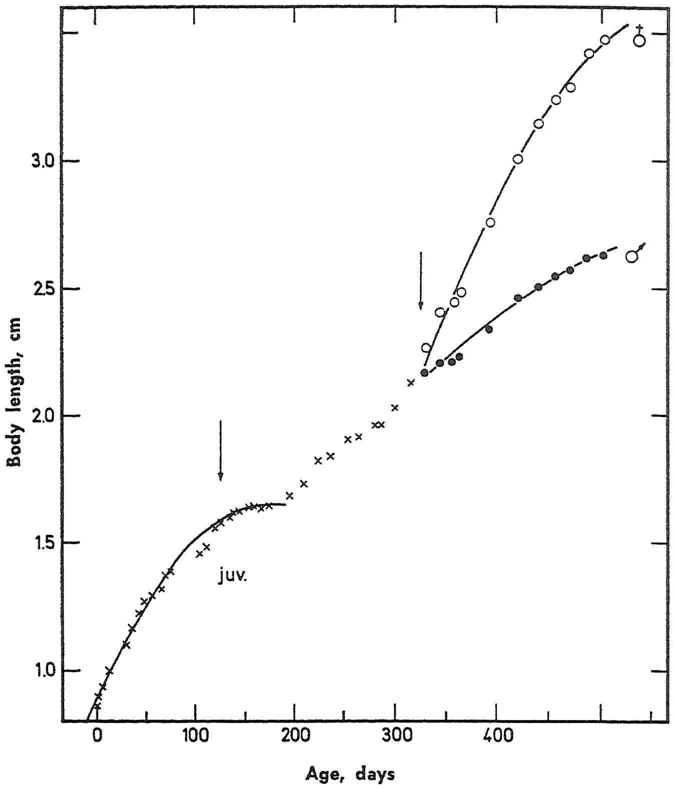
The temperature at which the growth rate is maximal, τ_{mg}, is given implicitly by

$$k_0 p_k \, e^{p_k \tau_{mg}} \, w^{n-m} = \frac{p_2 \, b \, e^{-p_2 \tau_{mg}} - p_0 \, a \, e^{p_0 \tau_{mg}}}{(b \, e^{-p_2 \tau_{mg}} + a \, e^{p_0 \tau_{mg}})^2} \qquad \ldots\ldots (C12)$$

which must be solved by iteration. The broken line in App. Fig. 19 indicates such solutions for males. Plotting τ_{mg} against weight for juveniles, females, and males describes the temperature trends ensuring maximum growth rate during the whole life of the fish (App. Fig. 20). The end point of each curve is $W_{\infty m}$, by definition. The apparent discrepancy between males and females is due to the choice of independent variable. If it is assumed that the two sexes grow towards $W_{\infty m}$ at the same relative rate of speed, i.e. if temperature is plotted against

$$\frac{w - W_{mat}}{W_{\infty m} - W_{mat}}$$

where W_{mat} is the weight at maturity, the two curves almost cover each other.



APP. FIG. 18. *Lebistes.* Length plotted against age for a batch of fish kept at low temperatures (17–19 C), with eye-fitted growth curves. Arrows indicate the times when the first and the last specimen could be identified to sex. The juveniles seem to approach an asymptotic size of their own before becoming mature. App. XIII.

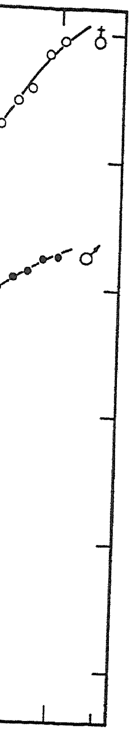
It should be interesting to know if the fish "prefer" the temperature at which they grow fastest. If they do, the two sexes stick together whereas the new-born young ones move away from them towards a higher temperature, thus escaping predation by adults.

EXAMPLE 13. GILL AND BODY SURFACE AREAS AND METABOLIC RATE

ESTIMATES OF n, n_g, A_b AND A_g

The parameters of respiratory surface and of oxygen consumption in relation to surface are given by

$$\left.\begin{aligned} S_b &= A_b\, w^{2/3} \\ S_g &= A_g\, w^{n_g} \end{aligned}\right\} \quad \ldots.(A6)$$



or a batch
ted growth
e last spec-
o approach
App. XIII.

ature at which they grow
n young ones move away
adults.

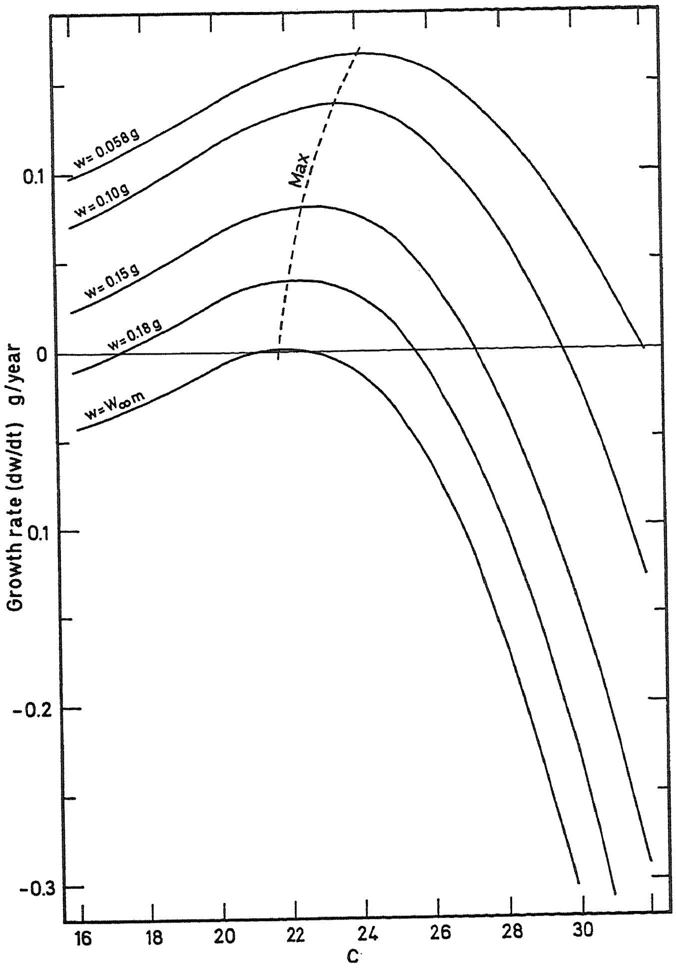
METABOLIC RATE

on in relation to surface

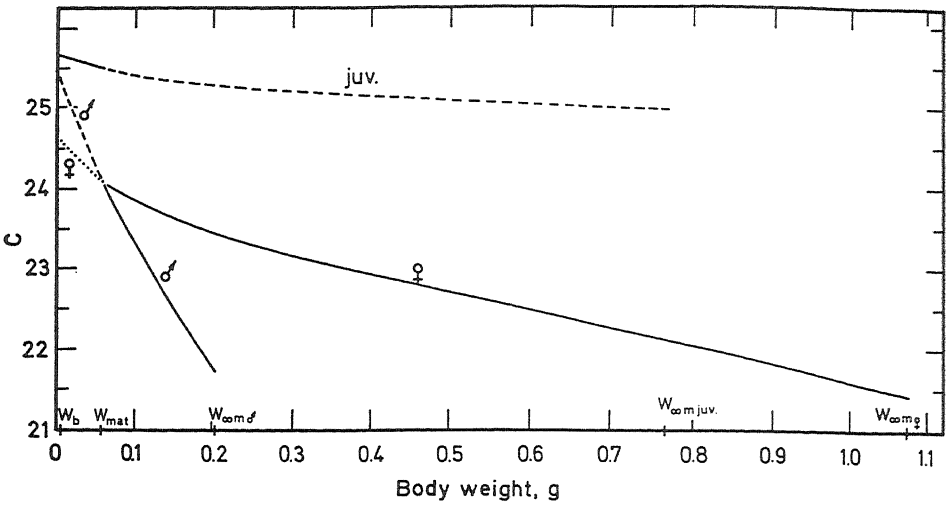
....(A6

$$\left.\begin{aligned}\left(\frac{dO_2}{dt}\right)_b &= -\ B_b\ S_b\\ \left(\frac{dO_2}{dt}\right)_g &= -\ B_g\ S_g\end{aligned}\right\}\qquad .....(A7)$$

where the subscripts *b* and *g* stand for body and gills respectively.



App. Fig. 19. *Lebistes*. Growth rates of males of various sizes over a range of temperatures. The broken line connects the maxima. App. XIII.



App. Fig. 20. *Lebistes*. The temperatures producing maximum growth, plotted as a function of body weight. W_b: weight at birth; W_{mat}: weight at maturity; $W_{\infty m}$: highest asymptotic weights (the maxima in App. Fig. 17). Parts of the curves which cannot be made the object of observation (immature fish of adult size; mature fish of juvenile size) are dotted. App. XIII.

The parameters are generally difficult to estimate and the relevant literature correspondingly scarce and not too reliable. Price (1931, cited by Fry 1957) measured the gill area of the small-mouthed black bass (*Micropterus dolomieu*) and found

$$n_g = 0.785; \; A_g = 8.65 \text{ cm}^2\text{g}^{-0.785}$$

so that

$$0.667 < n < 0.785$$

Gray (1954) studied the gill area of 31 species of marine fishes. Disregarding interspecific differences equation A6, rearranged as

$$\frac{S_g}{w} = A_g \, w^{(n_g-1)}$$

provides an estimate of n_g. App. Fig. 21 is a log scale plot of gill area per unit body weight against body weight (from Gray's Table I). There is one entry for each species. Six species are described by Gray as active and rapidly swimming (circles in App. Fig. 21). Four others are called sluggish. In the latter group (squares in App. Fig. 21) I have included the eels. Obviously, the more active the species (i.e. the higher its maintenance catabolism) the larger its gill area. The regressions are not significant in the small groups of active or sluggish fishes, but for the remaining 19 species of more ordinary behaviour we get

$$S_g/w = 13.92w^{-0.181} \text{ cm}^2\text{g}^{-1}$$

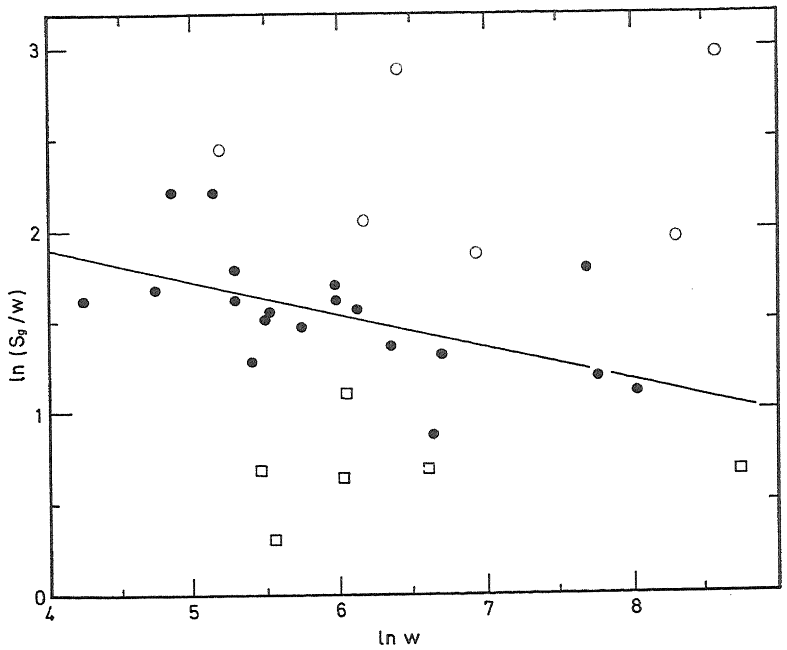
$$n_g = -0.181 + 1 = 0.819$$

95% confidence interval:

$$0.805 < n_g < 0.833$$

from which

$$0.667 < n < 0.833.$$



App. Fig. 21. Relative gill surface area, S_g/w, as a function of body weight, w. Thirty-one species of marine fishes (from Gray). Circles indicate particularly active species, squares particularly sluggish ones. The regression line is a least squares fit to the observations, omitting circles and squares. App. XIV.

It is doubtful, however, whether the assumption holds, that n_g is the same in all species. The body surface area of fishes varies appreciably as a result of differences in shape (Gray, 1953) and as a result of different development of fins and other protuberances. If skin respiration is at all significant, its importance varies with the ratio between gill and body areas. For constant n_g, n varies, and vice versa. To determine n_g in a fish with a small gill area and a large body area Mr S. Wiedemann Smith has made some pilot observations on *Zoarces viviparus*, a slender and sluggish fish likely to fulfil the requirements. On the second left gill bar the number of filaments was counted, and so was the number of lamellae on one of the longer filaments. The breadth and height of a lamella was measured. Assuming the lamellae to be infinitely thin rectangular plates an index of gill area is: breadth of lamella × height of lamella × number of lamellae on filament × number of filaments.

With isometric growth the two measurements should be proportional with body length whereas the numbers should be independent of body size. This would make gill surface proportional with l^2, as required. The observations are listed in App. Table X. A log scale linear regression of each quantity against 1 provided the following estimates of the powers of length with which they are proportional:

	Power, with 95% confidence interval	Isometric value of power
Breadth of lamella	0.948 ± 0.122	1
Height of lamella	0.931 ± 0.165	1
Number of lamellae	0.902 ± 0.131	0
Number of filaments	0.156 ± 0.061	0
Sum of powers	2.937	2

APP. TABLE X. *Zoarces viviparus*. Counts and measurements for estimate of gill surface index (App. XIV).

Length of fish (cm)	Breadth of lamella (10^{-3} cm)	Height of lamella (10^{-3} cm)	No. of lamellae on filament	No. of filaments on gill bar
7.5	25	9	35	45
7.5	28	8	40	47
10.0	38	11	47	46
11.0	41		40	46
11.5	44	15	54	45
12.0	41	14	54	51
12.5	38	12	55	48
13.0	50	12	60	46
14.0	44	11	70	48
15.0	50	15	65	48
15.5	50	16	66	
17.0	59	16	73	51
19.5	72	21	87	54
19.5	75	19	76	50
22.5	62	24	93	53
23.0	84	25	97	52
23.5	81	24	115	57

The isometric values for lamellar growth are within the confidence intervals of the estimates. The numbers, however, increase disproportionately, particularly the number of lamellae per filament which increases almost proportionately with body length. The effect is that, in *Zoarces viviparus*, gill area is proportional with body weight, or almost so. This was to be expected if n, rather than n_g, is a constant for fishes. However, there is no theoretical background for expecting n constant, but empirically, there is a good deal of evidence (see the foregoing Appendixes) that putting $n = 5/6$ is not far off the mark.

When fishes of the same size are compared, it is found (Gray, 1954) that the ratio gill area/body area is 5 or 10 times higher in active fishes than in sluggish ones. For medium-sized fishes it is of size order 10 in active species and 1 in sluggish ones. Skin respiration, therefore, is probably of little importance in active fishes, except in the youngest stages, whereas in sluggish fishes it may or may not be important, depending on the actual rate of oxygen consumption of fish skin. Facts on this subject are scarce. I have found one paper only (Krogh, 1904) dealing with the partitioning of total respiration between gill and skin respiration.

Krogh (1904), using European eels, *Anguilla anguilla*, in spite of obvious technical difficulties, managed to obtain data which are at least suggestive. The method was to carry out two sets of experiments using the same eels in both. In one set, the animals were left free and undisturbed, in another the mouth and gill slits were closed by sutures. Clearly, only a fish with a low metabolic rate would stand a treatment like that and in fact the eels were often moribund at the end of the second experiment. The mean values from sets VI, VII, and VIII are: $w = 118$ g, $\tau = 16$ C, total oxygen consumption = 33.90 cm^3 kg^{-1} hours^{-1}, oxygen consumption through the skin = 21.36 cm^3 kg^{-1} hours^{-1}, ratio skin respiration/total = 0.63. To evaluate these data the body and gill areas must be known. Krogh measured the surface (including fins but omitting the buccal cavity) of an eel 70.0 cm long and weighing 680 g. He found $S_b = 916$ cm^2. Hence, $A^b = S_b/w^{2/3} = 11.8$ cm^2 g$^{-2/3}$. The gill area was not measured, but from Gray (1954) can be borrowed data on the American relative of the European eel, *Anguilla rostrata*. Gray found, for

$w = 428$ g, $S_g = 1293$ cm^2. Putting $n_g = 1$, as found above for *Zoarces*, another slender and sluggish fish, gives $A_g = S_g/w = 3.02$ cm^2 g^{-1}. For an eel of 118 g the above parameter estimates give

$$S_g = 356 \text{ cm}^2;\ S_b = 285 \text{ cm}^2;\ S_b/(S_g + S_b) = 0.44.$$

According to this, the body area is less than half the total area and the skin respiration is more than half the total respiration, i.e. $B_b > B_g$. This is scarcely feasible. Remembering the difficulties encountered when measuring surfaces and oxygen consumption, a reasonably conservative judgment is that, in the eel, body and gills contribute each to about half the total surface and to half the total oxygen consumption. The value of n, accordingly, will be about midway between 2/3 and 1 ($= n_g$) i.e. $n = 5/6$.