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The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth¹

By D. PAULY

Abstract

The present paper is an attempt to interpret some of the data on fish growth available in the literature, emphasis being given to a reassessment of von Bertalanffy's theory of growth as applied to fishes.

In that theory, growth is defined as the net result of two processes with opposite tendencies, one synthesizing native protein (anabolism), the other degrading it (catabolism). Both food and oxygen supply are needed for anabolism, and this investigation presents evidence suggesting that, in fishes, it is primarily oxygen – rather than food supply – which limits anabolism and hence growth. This is due chiefly to the facts that fishes cannot store but small amounts of oxygen, and that the respiratory area of fishes (the gills) cannot grow as fast as body weight. The latter feature has the effect that relative gill area (= gill surface area/body weight) always decreases with increasing body weight, which itself results in a lowered food conversion efficiency with increasing body weight.

It is shown that, as a rule, fishes that are able to reach a very large size (e. g., bluefin tuna) tend to have gills growing in proportion to a power of weight quite close to unity (0.90) while small fishes (e. g., guppy) have gills growing in proportion to a power of weight of $\frac{2}{3}$ or less. The von Bertalanffy Growth Formula (VBGF), the derivation of which is based on the assumption of the universal validity of the ' $\frac{2}{3}$ rule' is therefore considered to be a special case of a generalized formula (the 'generalized VBGF') whose properties and applications are discussed.

Kurzfassung

Über die Beziehungen zwischen der Größe der Kiemenoberfläche und der Wachstumsrate von Fischen: Eine Verallgemeinerung von v. Bertalanffy's Theorie über das Wachstum

Der vorliegende Beitrag ist ein Versuch, veröffentlichte Daten über das Wachstum von Fischen neu zu interpretieren. Dabei wird der Versuch gemacht, von Bertalanffy's Theorie des Wachstums – sofern sie die Fische betrifft – zu erweitern.

Diese Theorie definiert das Wachstum als Nettoergebnis zweier Prozesse mit umgekehrten Vorzeichen; der eine synthetisiert neues Protein (Anabolismus), der andere baut eben dieses Protein ab (Katabolismus). Sowohl Nahrung als auch Sauerstoff werden für den Anabolismus benötigt; in der vorliegenden Untersuchung wird vorgeschlagen, daß

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es in Fischen vornehmlich der Sauerstoff ist, der das Wachstum limitiert, nicht das Futterangebot. Dies liegt vor allem daran, daß Fische Sauerstoff nicht in nennenswerten Mengen speichern können, und daß die relative Kiemenfläche (= Kiemenfläche/Körpergewicht) mit steigendem Gewicht stets abnimmt, wodurch die Umsetzungsrate der aufgenommenen Nahrung ständig herabgesetzt wird.

Es wird gezeigt, daß Fische, die ein hohes Endgewicht erreichen (z. B. der rote Thun), Kiemen haben, die proportional zu einer Potenz des Gewichtes von fast eins wachsen (etwa 0,90), während kleinbleibende Fische (z. B. Guppy) Kiemen haben, die mit einer Potenz des Gewichtes von $2/3$ oder weniger wachsen. Die von Bertalanffy Wachstumsformel (englisch: VBGF), die auf der Grundlage einer Allgemeingültigkeit der „ $2/3$ -Regel“ basiert, wird deshalb als ein Spezialfall einer „verallgemeinerten VBGF“ betrachtet, deren Herleitung und Anwendungen in Details diskutiert werden.

Introduction

The present paper is an attempt to interpret some of the data on fish growth and metabolism available in the literature.

There is a tremendous amount of data on the growth of fish, yet very little success has been achieved in reducing this mass of unrelated facts into a set of general rules which could be used e.g. to predict growth patterns in little-investigated fish stocks, or to accelerate the growth of cultured fish.

Moreover, the few broad generalizations available, such as for example von Bertalanffy's theory of growth (as applied to fishes) have hardly ever been reassessed in the light of recent data, leaving the field open to unrestrained empiricism (e.g. KNIGHT 1968; ROFF 1980) and to ad hoc explanations – one per investigated stock – as to why fish grow the way they do.

The present paper thus aims at assessing the validity of some concepts of fish growth, and represents an attempt to formulate some basic rules which should apply to a vast number of fishes, and may be later incorporated into a comprehensive theory of fish growth.

To formulate these basic rules, it was necessary to make some simplifying assumptions concerning the biology and ecology of fishes. Thus, for example, it was not possible to investigate the effect of reproduction, migrations or seasonal variations of environmental parameters on growth. This may limit the overall applicability of the views presented here.

The general course of any venture of this kind is, however, to start off with simplifying assumptions, formulate whatever general rules seem to apply, and only then to incorporate real-life complexity. The validity of the general rules presented here will thus be determined, among other things, by their suitability to future refinements and incorporation of more complex interrelationships.

2 Historical notes on growth studies in fishes

ARISTOTLE (384–322 B. C.) is reported to be the first scientist to have commented on the growth of fish, reporting in his *Historia Animalium* that the fishermen of ancient Greece knew how to distinguish three size (age) groups of tuna, which were called auxids, pelamyds and “fullgrown tuna”. The fishermen also observed that the scarcity of pelamyds one year created a failure of the fishery in the next, making this the first ever account in fish population dynamics (D'ARCY THOMPSON 1910; BELL 1962).

M. MALPIGHI (1628–1694) presented views on respiration in living organisms which in retrospect would seem to make him the first naturalist to have conceived ideas of what may be called an evolutionary and physiological understanding of fish growth.

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NORDENSKIÖLD (1946 p. 162) writes:

... Upon this MALPIGHI now bases an universal theory of respiration applicable to all living creatures – which, for all its conjectural ideas represent a shrewd guess as to the uniformity of life-phenomena in all organisms. He believes that the more perfect the living beings are, the smaller their respiratory organs are: man and the higher animals do with a pair of lungs of comparatively small size, whereas fishes have numerous closely ramified gills, and the trachea of insects spread throughout the entire body.

and:

With regard to the significance of respiration for living beings, he [MALPIGHI] believes that it consists in promoting the mobility and “fermentation” of the alimantal juices.

Two concepts upon which MALPIGHI speculated will be here of importance in dealing with fish growth:

1. The concept that the size of the respiratory organs is related to the degree of “perfection” of an animal, and
2. The concept that the respiratory organs (here the gills) are essential for the assimilation (“fermentation”) of ingested food.

These two ideas are indeed key concepts for the understanding of fish growth processes.

The pioneers of age reading in fishes were VAN LEEUWENHOEK (1632–1723) who aged carps by means of their scales, and HEDERSTRÖM (1959, original 1759) who was first to report on rings in fish bones (vertebrae).

After a lag phase lasting more than a century, aging techniques were rediscovered by HOFFBAUER (1898) working on scales, by REIBISCH (1899), who initiated the use of otoliths, and by HEINCKE (1905), who worked with various other bones. The method of aging fishes by analyzing length frequencies was pioneered by PETERSEN (1892) and FULTON (1904).

The beginning of the century saw in many European and North American waters the first signs of what was later to be called overfishing and questions pertaining to the growth of fish became one of the primary concerns of the emerging science of fishery biology (see bibliographies by MOHR 1927, 1930, 1934 and GRAHAM 1943).

In the decades which followed, aging techniques became more accurate and refined, while reliable methods for the back-calculation of fish length as well as for the validation of aging techniques were developed (review by SUVOROV 1959). As a result, a vast body of empirical size-at-age data could be accumulated which pertained to most commercially relevant species of the marine and fresh waters of Europe and North America.

Several attempts were made during this period to develop mathematical formulae which (1) describe fish growth, both in terms of length and weight, (2) could easily be incorporated in yield models, (3) allow for inter- and intraspecific comparisons of the growth of different stocks, and (4) be easy to fit to any set of growth data.

All properties listed are significant to the field of fishery science, and most of the growth formulae that were proposed failed to display this whole set of properties. High order polynoms, for example, which describe fish growth well enough for stock assessment purposes, have failed to become established in fishery science, possibly because they neither give insight into growth processes nor allow for inter-stock comparisons. Other growth curves, proposed by GOMPertz (1825), ROBERTSON (1923), PEARL and REED (1923), RICHARDS (1959), or by KRÜGER (1964) have the disadvantage of being quite difficult to handle and to fit a set of size-at-age data, not to mention the fact that all of these curves have been derived on the basis of purely empirical considerations, or of biological reasoning that is clearly erroneous (see BEVERTON and HOLT 1957, pp. 97–99, and von BERTALANFFY 1951, pp. 298–303 for extensive discussions of some of these formulae).

The first, and hitherto only formula which apparently fulfills the criteria listed above was developed by LUDWIG VON BERTALANFFY in a series of papers starting in 1934. The formula was fully discussed in the 2nd Edition (1951) of his book, *Theoretische Biologie*, Vol. 2, which will serve throughout the present paper as the key to his theory.

The major idea involved in this theory is that growth in animals is conceived as the result of two different processes with opposite tendencies, or

$$\frac{dw}{dt} = Hw^d - kw^m \quad \dots 1.$$

where $\frac{dw}{dt}$ is the rate of growth, w is the animal's weight, while H and k are coefficients of anabolism and catabolism, respectively. This differential equation can be integrated in two different manners:

- a. By setting the value of d and m at $2/3$ and 1 , respectively. This leads to what will be called here the special Von Bertalanffy Growth Formula or VBGF (it is called "special" because it represents a special case of the generalized VBGF; see below).
- b. By allowing the value of d and m to take range of values. This leads to what will be here called the generalized VBGF.

BEVERTON and HOLT (1957), by reformulating the special VBGF and incorporating it into their yield model, demonstrated its wide applicability and attempted to interpret some of the VBGF's parameters biologically.

The first version of the generalized VBGF goes back to RICHARDS (1959). He, however, introduced his version of the VBGF as a purely empirical formula, setting no theoretical limits as to the possible values of the exponents relating anabolism and catabolism to weight. A version of the generalized VBGF meant to better express the metabolic considerations underlying the derivation of the special VBGF was proposed by TAYLOR (1962).

3 Working definitions of growth and of "growth data"

Leaving aside malignant growth, growth in fish may be simply defined as the change over time of the body mass of a fish, being the net result of two processes with opposite tendencies, one increasing body mass (anabolism), the other decreasing body mass (catabolism) (see Equation 1). Note that the definition implies that growth may be negative (when anabolism < catabolism).

Growth, as defined here, thus relates weight (actually, mass) and time. Growth data are, therefore, such data which relate, directly or indirectly, weight and time such that the growth process may be reconstructed from them.

Thus, data pertaining to the maximum size reached by the fish of a given stock in a given habitat can be considered to be growth data because this maximum size (L_{max} , W_{max}) can be assumed to represent the size at which the process expressed in Equation (1) comes to an end, with

$$Hw^d - kw^m = 0 \quad \dots 2.$$

This consideration also applies to the largest size ever recorded for a given fish species $L_{(max. ever)}$, $W_{(max. ever)}$.

4 Some basic assumptions, conventions and limitations

The following assumptions are made throughout the present work (except when relaxations are expressly mentioned):

1. Body mass is expressed in terms of body weight. All weights are expressed in grams (g) and always refer to round (ungutted) weight.
2. Weight is assumed to be proportional to the cube of length wherever not otherwise mentioned. CARLANDER (1969) has demonstrated that values of the length exponent widely differing from 3 (e.g. < 2.5 and > 3.5) are generally questionable and/or based

on too limited a size range. The proportionality constant used for length-weight conversion, called condition factor (c.f.) is here

$$\text{c.f.} = \frac{W \cdot 100}{L^3} \quad \dots 3.$$

and is based on total length, cm and g round weight.

3. Time is here always expressed in years. This also applies to all growth or other rates.
4. The considerations exposed here apply to fish which derive the overwhelming part of the oxygen they need through the use of gills. Fishes known to derive most or even a large proportion of their oxygen from cutaneous respiration (e. g., *Anguilla* spp.) or from auxiliary organs suited to breathing air (e.g. the osteoglossid *Arapaima gigas*) are expressly excluded.
5. Except for part 9.6, which deals with some questions pertaining to the growth of fish larvae, only fish past metamorphosis are considered.
6. Seasonal aspects of the growth of fish are not considered explicitly (but see PAULY and GASCHÜTZ 1979, or GASCHÜTZ et al. 1980).

5 A biological model of fish growth and its mathematical formulation

5.1 Von Bertalanffy's concept of fish growth

In order to set the proper basis for the generalization of the VBGF, it would seem appropriate to present von Bertalanffy's concept of growth as applied to fishes. At first, an attempt will be made to break down VON BERTALANFFY's line of arguments into a series of discrete statements the validity of which may be assessed separately. Most statements are based on Chapter 7, Part 4 of VON BERTALANFFY (1951).

- Statement 1. Growth is the net result of two continuous processes with opposite tendencies, one building up body substances (anabolism), the other breaking down body substances (catabolism). (Equation 1).
- Statement 2. Growth ceases when catabolism is equal to anabolism. (Equation 2).
- Statement 3. Catabolism occurs in all living cells of a fish and is therefore directly proportional to the mass of the fish's body, hence, also to its weight.
- Statement 4. In fishes, anabolism is proportional to respiratory rate. (See VON BERTALANFFY 1951, Table 19, p. 280).
- Statement 5. In fishes, respiratory rate is proportional to a surface. (VON BERTALANFFY 1951, Table 19, p. 280).
- Statement 6. Growth is therefore limited by a surface.
- Statement 7. The surface which limits growth increases in proportion to a linear dimension squared (isometric growth).
- Statement 8. The fact that the respiratory rate of the guppy *Lebistes reticulatus* increases with the $2/3$ power of its weight (or in proportion to the square of its length) is a proof of the correctness of the whole line of argument (Statement 1 through 7).
- Statement 9. Deviations from the " $2/3$ rule" of metabolism do occur, but not in fishes (VON BERTALANFFY 1951, Chapter 6, Part 2).
- Statement 10. The constant k in the negative term of Equation 1 may be considered to express the "Abnutzungsquote" (wear and tear quota) of RUBNER (1911), that is the fraction of the body mass which degrades per unit time. The constant k, however, may be identified, in general, with any "growth inhibiting, mass proportional factor" (VON BERTALANFFY 1938).

VON BERTALANFFY's theory of growth, as applied to fishes, is here summarized in the form

of a graphic model (Fig. 1), which is based mainly on Chapters 6 and 7 in VON BERTALANFFY (1951). The model is described in the following paragraphs.

The fish feeds, and its food (here represented by protein) is assimilated, that is, broken down into amino acids, in which form it joins the "Amino-Acid-Pool" (AAP) in the fish body. Part of the amino acids of the Amino-Acid-Pool is "burned" (see Excretion I in Fig. 1) and the chemically bound energy so obtained is used for the synthesis of native protein, the building material being drawn from the AAP. Simultaneously, with this process of synthesis, there is a continuous degradation of the body's native proteins.

On the other hand, the rate of synthesis of body substances (hence, also the replacement of degraded substances) is limited both by the rate of replenishment of the AAP (to which the degradation process itself partly contributes) and by the amount of oxygen available for

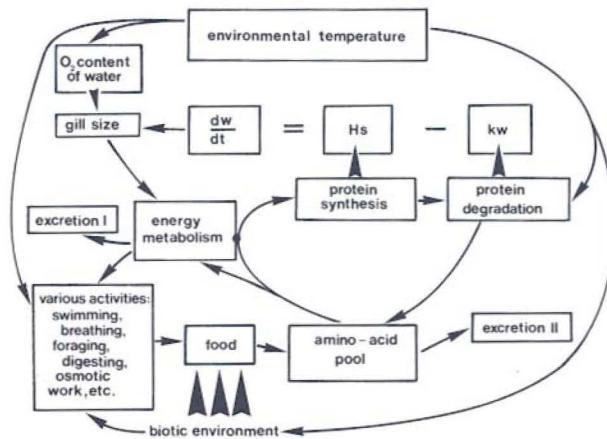


Fig. 1. Simplified model of fish growth, with emphasis on the role and supply of oxygen (see text)

the oxidation of parts of the AAP. A good oxygen supply allows for the synthesis of a maximum amount of body substance from the AAP; a poor oxygen supply allows for only a limited rate of synthesis and a part of the AAP spills over and "is excreted by the gills and kidney as incompletely oxidized nitrogenous compound" (WEBB 1978); see also FORESTER and GOLDSTEIN (1969), SAVITZ (1969, 1971), OLSON and FROMM (1971) and NIIMI and BEAMISH (1974). This excretion is referred to as "Excretion II" in Fig. 1.

The sum of synthesis minus breakdown of body substance when positive, results in body growth which, among other things, also increases gill size and therefore increases the total amount of oxygen that can penetrate into the body per unit time. The body weight, however, tends to increase faster than gill area (see below) and the relative gill area (= gill area/body weight) diminishes with increasing body size.

Thus, the oxygen supply per body weight unit steadily diminishes as weight increases, resulting in a relatively lower energy metabolism, hence, rate of synthesis. The amount of body substance degraded per unit time, on the other hand, increases in direct proportionality to the body weight, and the growing fish gradually reaches a point where the synthesis of body substances is just sufficient to replace degraded substances. Thus, net growth become nil (at asymptotic size).

WEBB (1978) among others, confirms this indirectly by stating that the magnitude of nitrogenous loss (Excretion II) increases with size, being lower in actively growing, small fishes. The same process may be demonstrated by computing growth conversion efficiency (= food intake/growth increment), for fishes of different sizes, such experiments always showing a decreased conversion efficiency with increasing size (JONES 1976; KINNE 1960; GERKING 1971; MENZEL 1960). This point is discussed in more detail in section 8.

This presentation of VON BERTALANFFY'S conception of fish growth could be concluded here if it were not necessary to consider three of the most frequent misunderstandings connected with this theory:

Misunderstanding I. RICKER (1958) writes:

VON BERTALANFFY has tried to provide (the VBGF) with a theoretical physiological basis, and he apparently considers it a generally applicable growth law. However, one of the fundamental assumptions he uses is that anabolic processes in metabolism are proportional to the area of an organism's effective absorptive surfaces. This could seem reasonable if food were always available in excess, so that absorptive surface could actually be a factor limiting growth; and in the guppy experiments which are quoted in support of this relationship, food was actually provided in excess. In nature, fish are usually less fortunate; this is shown by the small average volume of food commonly found in their stomachs and also by the great variability in their observed growth rates, both when we compare individual fish in the same environment and when we compare populations from different (but physically similar) waters. Thus it seems unlikely that available absorptive surface is commonly a factor limiting the growth of wild fish.

This statement by RICKER (1958, p. 196), which is to be found also in the last edition (1975) of his book, makes a strong case against gut surface as the limiting surface for fish growth. VON BERTALANFFY, however, insisted that, in fishes, anabolism is proportional to respiratory rate, and that respiratory rate is proportional to a surface.

The same misunderstanding is to be found in BEVERTON and HOLT (1957, p. 32) who write:

Following general physiological concepts, VON BERTALANFFY suggests that the rate of anabolism could be assumed proportional to be resorption rate of nutritive material and therefore proportional to the magnitude of the resorptive surface. . . .

Misunderstanding II.

VON BERTALANFFY explicitly stated that a surface limits anabolism and that therefore anabolism is proportional to the second power of length. While it will here be suggested that a physical surface does indeed limit anabolism, it will also be shown that this surface grows in proportion of the second power of length in only a few cases. The point here is that VON BERTALANFFY limited the meaning of the word "surface" to its geometric property of increasing in proportion to the 0.667th power of the volume of a body with constant linear proportions, overlooking the fact that a "surface" can very well grow allometrically (e.g. as the surface of the brain cortex in the ontogeny of primates). Thus, the concept of a growth and metabolic type located "between surface and weight proportionality" as used by VON BERTALANFFY himself, is a misnomer, as we may still have, in this growth and metabolic type, a surface proportionality.

Misunderstanding III.

With several authors, particularly URSIN (1967, 1979), a misunderstanding occurs which is probably due to the inconsistent use of the terms "breakdown" and "catabolism" in VON BERTALANFFY'S writings.

The complete breakdown of body substance (here: protein) involves a long series of single steps and a large number of different enzymes. These many steps may, however, be simply grouped into two main phases:

Phase I (Pre-oxidative Phase). The reactions occurring here have two features in common:

1. They are mildly exergonic (production of waste heat);
2. They do not require oxygen.

Thus, proteins may lose their quaternary and tertiary structure and be hydrolyzed down to their component amino-acids without these processes having to be coupled with any energy-providing exergonic reactions, and without any oxygen being used up.

Phase II (Oxidative Phase). The reactions occurring here have the following features:

1. They are strongly exergonic (production of ATP);
2. They require oxygen.

At the end of Phase II, the amino-acids are broken down into H₂O, CO₂, and NH₃, and a

large amount of ATP has been obtained which may be used for synthesis of new proteins as well as to meet the energy demand of various activities.

Obviously, when writing that the "catabolism" of fishes is proportional to their body mass, VON BERTALANFFY meant Phase I only. The "preoxidative" breakdown indeed cannot be anything but proportional to body mass, that is, to the amount of body proteins that may be degraded and hydrolized into their component amino-acids, and which thereby are indeed removed from the body's pool of native proteins. (see section 9.4 for details).

As soon as these proteins are hydrolized, they become part of the AAP (see Fig. 1) together with amino-acids obtained from the resorption of food, and may become part of what VON BERTALANFFY calls "Betriebsstoffwechsel" (energy metabolism). On the other hand, energy metabolism is limited by the supply of oxygen which is proportional to a power of weight markedly smaller than unity. That is, the second phase of catabolism generally cannot be proportional to weight.

The division of catabolism into two distinct phases, only the second of which requires oxygen, is made in most physiology texts (see SCHEER 1969, p. 21; SCHUMACHER 1971, p. 278, or KARLSON 1970, p. 129 ff.). This division, however, was not made explicitly by VON BERTALANFFY for the derivation of his theory of growth. This omission is probably the cause for *Misunderstanding III*.

Thus, URSIN (1967, p. 2359) writes:

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 the other, mainly the gills. With our basic assumption of isometric growth, this means that catabolism is proportional to $w^{2/3}$. As discussed elsewhere, this is also known to be untrue, so that the assumption of isometric growth must be abandoned for the occasion. In fact the gills do not grow isometrically with the body, because new units are being added as the fish grows.

This statement by URSIN (1967) expresses one of the key concepts of his growth model (URSIN 1967, 1979).

The point, however, is that the first phase of the catabolic process, for which no oxygen is needed is sufficient to degrade native protein. It is therefore necessary for the body to resynthesize these lost proteins if it is to maintain a constant pool of native proteins, and to synthesize protein in excess of these losses if growth is to occur. Thus, Equation 1 implies that the rate of anabolism is the rate of synthesis of native proteins, while the rate of catabolism is the rate at which proteins are denaturated and/or hydrolized. Thus, k indeed represents a "growth-inhibiting, mass-proportional factor", as suggested by VON BERTALANFFY (1938).

A discussion of the same characters and properties of the factor k is given in section 9.4.

5.2 The Generalized von Bertalanffy Growth Formula: Integration and Properties

As mentioned previously, there are basically two manners in which Equation 1 may be integrated. One well known and well-documented manner consists of attributing fixed values to the weight exponents. Thus Equation 1 may be rewritten as

$$\frac{dw}{dt} = Hw^{2/3} - kw \quad \dots 4.$$

when d and m are assumed to be equal to $2/3$ and 1, respectively. This, upon integration and assuming that weight is proportional to the third power of length, results in

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad \dots 5.$$

and for length growth,

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where W_t and L_t are the size at age t , W_∞ and L_∞ express the asymptotic size and K and t_0 are constants. (See BEVERTON and HOLT 1957, for the integration and HOHENDORF 1966, for a discussion of some properties of the special VBGF.)

In this paper, it will be demonstrated that the definition $d = 2/3$ applies very rarely in fishes, for which reason d should be allowed to take values other than $2/3$. RICHARDS (1959) and TAYLOR (1962) have relaxed both constraints ($d = 2/3$ and $m = 1$), but considered cases pertaining to growth in length only.

The integration of equation (1) to a generalized version of the VBGF for both length and weight growth were presented in PAULY (1979). Here, only the definitions used in the course of the integration of equation (1) are presented, together with those equations pertaining to important properties of the generalized VBGF.

The substances needed for anabolism have to enter into the fish body across some surface, s , whose increase with fish size may be described by

$$s = p \cdot L^a \quad \dots 7a.$$

where L refers to any linear dimension of the fish (e.g., body length); a is a power whose range of biologically possible values is discussed below, and p is a proportionality constant.

Catabolism¹, on the other hand, may be considered to be directly proportional to weight, while weight itself may be related to any linear dimension of the fish, such as body length, by

$$w = q \cdot L^b \quad \dots 7b.$$

where L is the fish length; q is a proportionality constant; and b is a power generally ranging between values of 2.5 to 3.5 (CARLANDER 1969) and $b > a$.

Other definitions used in the course of the integration are

$$K = \frac{k}{3} \quad \dots 8.$$

and

$$D = b-a \quad 9.$$

The integration, for weight growth results in

$$W_t^D = W_\infty^D (1 - e^{-\frac{3KD}{b}(t-t_0)})^b \quad 10.$$

which can be simplified, when $b = 3$ to

$$W_t = W_\infty (1 - e^{-KD(t-t_0)})^{3/D} \quad 11$$

Similarly, for length, we have

$$L_t^D = L_\infty^D \cdot (1 - e^{-KD(t-t_0)}) \quad 12.$$

or

$$L_t = L_\infty \cdot (1 - e^{-KD(t-t_0)})^{1/D} \quad \dots 13.$$

It will be noted that all of these versions of the generalized VBGF (Equation 10 to 13) reduce to the corresponding forms of the special VBGF (Equation 5 and 6), when both limiting surface and body weight increase isometrically with weight (i.e. $a = 2$, $b = 3$ and $D = 1$).

The slope of the generalized VBGF for weight growth (equation 10 and 11) is, at any weight (W_t)

$$\frac{dw_t}{dt} = 3KW_t \left[\left(\frac{W_\infty}{W_t} \right)^{D/b} - 1 \right] \quad \dots 14.$$

¹ here, and for the rest of this paper, the term "catabolism" refers to "pre-oxidative" catabolism, as defined above.

while the value of the slope of the inflexion point may be obtained from

$$\frac{dw_i}{dt} = 3KW_\infty \cdot \frac{D}{b} \left(1 - \frac{D}{b}\right)^{b/D-1}$$

which reduces, when $D = 1$ and $b = 3$ to

$$\frac{dw_i}{dt} = \frac{4K}{9} \cdot W_\infty \quad \dots 16.$$

The size (W_i) at the point of inflexion of the weight growth curve, finally is given by

$$W_i = \left(1 - \frac{D}{b}\right)^{b/D} \cdot W_\infty \quad \dots 17.$$

from which, when $D = 1$ and $b = 3$, it follows that

$$W_i = 0.2963 \cdot W_\infty \quad \dots 18.$$

as given by BEVERTON and HOLT (1957) and HOHENDORF (1966). An interesting property of Equations 12 and 13 the generalized VBGF for length growth is the occurrence of an inflexion point (when $D < 1$) at age t_i , the value of which can be estimated from

$$t_i = t_0 - \frac{\log_e D}{KD} \quad \dots 19.$$

Thus, t_i moves toward t_0 when D increase toward 1, with no inflexion point left when $D = 1$, as in the special VBGF for length.

5.3 Fitting of the generalized VBGF

The generalized VBGF may be fitted to growth data using any of the methods used for fitting the special VBGF, except for the fact that values of L_t^D have to be used instead of L_t values¹.

Thus, the Ford-Walford plot, for example, when used in conjunction with the generalized VBGF simply consists of a plot of L_{t+1}^D on L_t^D , or

$$L_{t+1}^D = \text{intercept} + \text{slope} \cdot L_t^D \quad \dots 20.$$

where

$$L_\infty = \left(\frac{\text{intercept}}{1-\text{slope}}\right)^{1/D} \quad 21$$

and

$$K = \frac{\log_e \text{slope}}{-D} \quad 22.$$

(see below for the estimation of D)

6 The concept of the physiologically limiting surface

6.1 Preliminary identification of the "physiologically effective surface"

The anabolism of fishes is, according to VON BERTALANFFY, limited by some physiological surface. This section presents indirect evidence which should help in the identification of this surface.

¹ The BASIC computer program presented in GASCHÜTZ et al. 1980 is available from the author; it can be used to fit the generalized VBGF to both weight and length at age data.

The relationships between gill surface area and growth performance in fish

Anabolism, the synthesis of body substance, is in fishes a matter of adequate food (the necessary condition) as well as a matter of oxygen supply (the sufficient condition), as fishes derive the energy for the synthesis of body substances exclusively from the oxidation of energy-rich assimilates. Thus, the physiologically limiting surface may be represented by the gills, by the gut, or by any of the internal surfaces across which assimilates and/or oxygen have to be transported.

TAYLOR (1962) writes that:

Raw material for the building-up processes (anabolism) must enter the organism through a boundary, a surface or series of surfaces beginning with the epithelial cell membranes and perhaps ending with the transport of material across the surface of subcellular bodies such as the microsomes and mitochondria where metabolic processes continue.

TAYLOR (1962) apparently assumed that internal surfaces are the ones that are limiting anabolism and he stated that "these surfaces are, in part, at least undetermined or undetermined".

Few empirical data are available which could be used to assess the likelihood that in fishes it is the gut surface which limits anabolism. PARKER and LARKIN (1959), citing SZARKI et al. (1956), state that the absorptive surface area of the gut of *Abramis brama* grows by means of infolding approximately in proportion to weight.

On the other hand, URSIN (1967, p. 2358) estimates the gut surface of *Solea solea* as $2.12 \cdot W^{0.57}$ (cm², g), with $n = 8$ and 95% confidence intervals for the exponent ranging from 0.33 to 0.80. The figure of 0.57 is close to the values of 0.58 and 0.59 estimated here from data in HARDER (1964) for *Rutilus rutilus* and *Gobio gobio* (Table 1). Thus, there is evidence, at least for these species, that the gut surface of fish may grow in proportion to a

Table 1. Relationship between weight and gut surface in two species of fish

<i>Rutilus rutilus</i>		<i>Gobio gobio</i>	
weight (g)	gut surface (cm ²)	weight (g)	gut surface (cm ²)
32.21	14.0	31.78	13.1
85.65	56.0	26.68	11.0
116.24	75.5	34.48	16.0
98.67	66.0	40.97	19.2
157.42	104.0	47.00	22.0
166.23	105.5	49.45	23.2

R. rutilus $y = 0.794 + 0.580x, r = 0.994^{**}$
G. gobio $y = 0.802 + 0.591x, r = 0.993^{**}$

with $x = \log_{10}$ weight and $y = \log_{10}$ gut surface
 Source of data: HARDER (1964, Table 6)

power of weight $\ll 1$. On the other hand, for the idea of the gut as a limiting surface to have any meaning at all, one must assume that the fishes, through more or less continuous feeding, keep the resorptive area of their gut in permanent contact with ingested food. This, however, is evidently not the case (see quotation above from RICKER 1958).

Another line of evidence arguing against the gut surface as the physiologically limiting surface of anabolism is provided by the fact that relative gut length (= gut length/fish length) – hence, relative absorptive area – is in fishes more closely related to the mode of feeding than to the growth performance. Thus, tuna, which belong to the fastest growing fishes, have extremely short guts, while mullets, which have extremely long, coiled guts, display only moderate growth performance (see Table 4 for growth data, and HARDER 1964 for a review of gut length in different fish species).

In addition to this is the fact that fishes can store energy-rich substances in the form of fat (or liver oil), this form of storage lasting as long as necessity dictates, generally over a significant part of the year (ILES 1974). This storage allows fishes to maintain anabolic activities long after feeding and food resorption have been completed, thus making the

scope of the anabolic processes independent of the gut surface. This is also noted by ILES (1974) who stated that "... the incorporation of food into the metabolic pool on the one hand and the anabolic process on the other are distinct processes."

In contrast, it may be recalled here that fishes cannot store significant amounts of O₂, which is best illustrated by the fact that most fish die within a short period of time when kept in anoxic water.

The following properties of fish gills make them candidates for the physiologically effective surface:

- 1 Oxygen is essential for the synthesis of body substance.
- 2 The total amount of oxygen which can diffuse into a given body per unit time follows Fick's law of diffusion

$$Q = \frac{dP \ U \ A}{WBD} \quad \dots \ 23.$$

where Q is the oxygen uptake (ml/hr), U is Krogh's diffusion constant, that is, the number of ml of oxygen which diffuse through an area of 1 mm² in one minute for a given type of tissue (or material) when the pressure gradient is one atmosphere of oxygen per μ (micron); A is the total respiratory surface of the gills (total area of the secondary lamellae) and dP is the difference between the oxygen pressure on either side of the membrane, in atm. WBD is the Water Blood Distance, that is, the thickness of the tissue between water and blood in μ (DE JAGER and DEKKERS 1975).

Of the four parameters which determine the value of Q, only A may be assumed to vary much as body size increases, thus making gill size the key regulating factor for oxygen uptake in growing fishes.

- 3 Fish gills grow in proportion to a power of weight lower than unity. (See MUIR 1969; HUGHES 1970; and especially DE JAGER and DEKKERS 1975).
- 4 The power of weight in proportion to which the gills of an "average" fish grow is about 0.8, which is the very power linking, in "average" fishes, energy metabolism and weight (WINBERG 1960; DE JAGER and DEKKERS 1975).
- 5 There is very little oxygen dissolved even in the best aerated water – say, as compared with the O₂ content of air. Additionally, water is an extremely dense medium – again, as compared with air and a very large quantity of water must be inspired and expired to extract the oxygen necessary to maintain life functions. In comparison with land animals, fishes – and all other aquatic animals for that matter – must extract the oxygen they need from a medium about 840 times denser and 55 times more viscose than air, containing 30 times less oxygen, and in which the diffusion through membranes takes 300,000 times longer than in air (SCHUMANN and PIPER 1966). It is not surprising, then, that a large proportion of the metabolic energy of fish should go to breathing, itself. SCHUMANN and PIPER (1966) found, for example, that the tench *Tinca tinca* uses about 33 % (range 18–44 %) of its standard energy metabolism only to cover its breathing activities as opposed to a value of about 2 % in the mammal *Homo sapiens*.
- 6 Large gills expose the fish to problems, some of which are discussed here.
 - a Very large gills offer an increased resistance to the flow of water, and a large amount of energy must be diverted to overcome this resistance. In active fishes, this resistance can be overcome only by constant swimming with more or less open mouth (ram-jet ventilation).
 - b The large gills needed by very large fishes require modification of the whole head and anterior part of the body and a specific mode of feeding (filtering plankton) as is the case with *Rhincodon typus* and *Cetorhinus maximus*, the two largest fishes (NORMAN & FRASER 1963). That is, extremely large gills lower the number of niches that can be occupied by a given species.
 - c Large gill area implies very reduced spaces between the secondary gill lamellae

(HUGHES and MORGAN 1973a). There is, therefore, a permanent danger of clogging, for which reason large-gilled fishes cannot frequent waters containing suspended solids in large amounts, such as estuarine areas. This, again, limits the number of potential niches.

d In order to fulfill their various respiratory and excretory functions, the gills of fish must be relatively "open" to the outer medium. This, on the other hand, makes them the first organs to be affected by noxious substances dissolved in the water (HUGHES and MORGAN 1973a). For this reason, the gills also represent the weakest link in a fish's line of defense against osmotic stress.

e "The gill tissue of fishes is an ideal site for parasitic infection [...] as [...] the gills are very well perfused with blood and usually well oxygenated" (HUGHES and MORGAN 1973a).

The potential problems associated with the possession of extremely large gills suggest that in any fish species, a gill size should have evolved which allows for a good supply of oxygen – hence, for the potential for rapid growth – only up to a given size, optimal for the niche occupied.

6.2 The allometric growth of gills

As a rule, the total gill area of a fish of any size can be expressed by the equation

$$G = a \cdot W^{d_g} \quad \dots 24.$$

where G is the gill area, W is the fish weight, d_g is an exponent with values ranging between 0.5 and 0.95, and a is a species specific constant, here called Gill Area Index (GAI). When W is expressed in gram, and G in cm^2 , a (= GAI) is the gill area in cm^2 of a fish weighing 1 g.

It should be noted that Equation (24) has the same form as the following equation which, in fishes, is used to relate O_2 consumption and weight:

$$Q = a' \cdot W^{d_q} \quad \dots 25.$$

where Q is the O_2 consumption, W is the fish weight, d_q is an exponent generally ranging between 0.5 and 0.95, and a' is a species specific constant the value of which, however, is also largely determined by the level of activity of the investigated fish (see WINBERG 1960 for an exhaustive review and discussion).

Few authors have explicitly stated that d_g should, in general, be equal to d_q . DE JAGER and DEKKERS (1975) did so and took the average of their mean value of $d_g = 0.811$ with their mean value of $d_q = 0.826$ to a mean value of $d = 0.82$. This value of $d = 0.82$ was subsequently applied by them to all of the gill size and fish respiration data available and used to obtain gill size and respiratory rate estimates for "standard" fishes of 200 g (DE JAGER and DEKKERS 1975; DE JAGER et al. 1977).

On the other hand, several authors have pointed out the wide variations in the values of d obtained from various groups of fishes, suggesting, for example, values of d up to unity and above.

It appears, however, that many of these extreme values are based upon either erroneous methods in the estimation of gill size (see DE JAGER and DEKKERS 1975, for a list and critique of several papers giving such estimates) or erroneous methods in respiration studies (see WINBERG 1960, for a review of the most common pitfalls). Also, it repeatedly appeared that such extreme estimates were based upon a very limited range of size.

Extreme values which cannot, however, be so dismissed are provided by the tunas, with values of d ranging up to 0.9 (MUIR 1969) and by the cyprinodonts, with values of d as low as 0.5 (VON BERTALANFFY 1951; WINBERG 1960). As these two taxa are almost at the extreme ends of the size range in fishes, an attempt is made here to test whether the value of

d (both d_g and d_q) can be simply expressed as a function of the maximum size reached in various stocks (W_{max}).

A compilation of literature values of d was undertaken for this purpose (Table 2). The data gathered are very heterogenous in quality. Values which seemed suspect have been listed as such (Table 3) and are not used for further calculations. The body size to which the

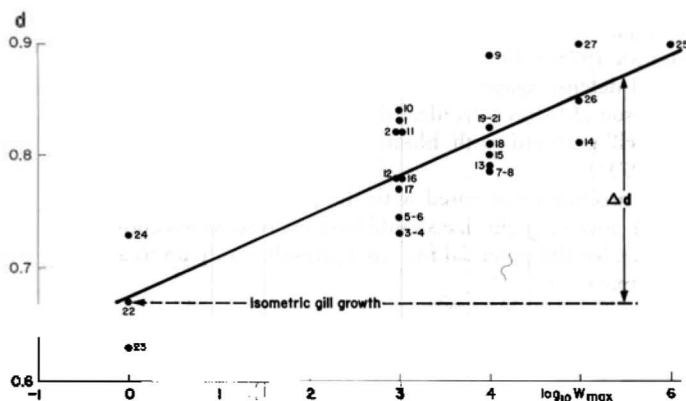


Fig. 2. Relationship between the power of weight in proportion of which anabolism increases (d) and the maximum weight commonly reached in a given species (W_{max}). Based on data of Table 2

values of d are related refer to maximum weight as estimated mainly from data in PAULY (1978a). In order to prevent bias, these estimates were rounded off to the nearest whole power of 10; the base 10 logarithm was then taken (see Table 2 and Fig. 2).

The correlation between the values of d and the logarithm of the maximum weight indices is, with 20 dF, significant ($P = 0.001$, $r = 0.830$) and may be expressed by the regression

$$d = 0.6742 + 0.03574 \log W_{max} \quad \dots 26.$$

A first interpretation of this result is that the gills of most fish grow allometrically with a value of $d > 2/3$, the exceptions being the Cyprinodontidae and probably the other fishes the adult size of which remains near one gram. In other fishes, the gills grow with a positive allometry and the value of d is close to 0.8 for the fish of "average" size because the majority of fish hitherto investigated happen to reach weights ranging between 10^2 and 10^4 gram. Finally, the large, active tuna have gills which grow almost as fast as their body weight ($d \approx 0.9$).

NIKOLSKY (1957) gave for *Rhincodon typus* a maximum size of 20 m, corresponding to a weight of about 60 tons. This maximum weight, when inserted into Equation 26, suggest a value of $d = 0.95$ which may correspond to the highest possible value of d in fishes.

Since, when weight growth is isometric

$$D = 3 \cdot (1-d) \quad \dots 27.$$

(see equation 9), we also have

$$D \approx 3 \cdot [1 - (0.6742 + 0.03574 \cdot \log W_{max})] \quad 28.$$

which can be used to directly estimate D from estimate of W_{max} .

Table 2. Some values of the power of body weight in proportion to which the gill area of fish increase (d). Based on gill surface or respiratory surface areas.

No.	Taxon	Value of d	Gill(G) or Respir. (R)	Author(s)	Original data in	Remarks ¹	Weight ² (g)
1	<i>Tilapia mossambica</i>	0.83	R	JOB 1963	Same	mean of two extreme values of d	10 ³
2	<i>Tilapia zillii</i>	0.82	R	SCHULZE-WIEHENBRAUCK 1977	Same	-	10 ³
3	<i>Tinca tinca</i>	0.79	R	WINBERG 1960	Various authors	p. 87	10 ³
4	<i>Tinca tinca</i>	0.67	G	DE JAGER and DEKKER 1975	Various authors	Table II, p. 283	10 ³
5	<i>Carassius auratus</i>	0.81	R	WINBERG 1960	Various authors	p. 82	10 ³
6	<i>Carassius auratus</i>	0.68	G	Original	SOLEWSKI 1957	from Fig. 8 in CZOŁOWSKA 1965	10 ³
7	<i>Cyprinus carpio</i>	0.72	G	Original	SOLEWSKI 1957	from Fig. 8 in CZOŁOWSKA 1965	10 ⁴
8	<i>Cyprinus carpio</i>	0.85	R	WINBERG 1960	Various authors	p. 83	10 ⁴
9	<i>Abramis brama</i>	0.89	R	WINBERG 1961	KUSNETZOVA 1956	p. 3	10 ⁴
10	<i>Rutilus rutilus</i>	0.84	G	Original	LANDOLT and HILL 1975	d value recalculated from author's data	10 ³
11	Cyprinidae	0.82	R	WINBERG 1960	Various authors	p. 105	10 ³
12	<i>Micropterus dolomieu</i>	0.78	G	MUIR 1969	PRICE 1931	classic study, d value highly reliable	10 ³
13	<i>Trematomus bernachii</i>	0.79	R	WOHLSCHLAG 1960	Same	p. 289	10 ⁴
14	Acipenseridae	0.81	R	WINBERG 1960	Various authors	p. 86, 5 spp.	10 ⁵
15	<i>Scyllium</i> spp.	0.80	R	WINBERG 1960	BUYTENDIJK 1910	-	10 ⁴
16	<i>Opsanus tau</i>	0.78	G	HUGHES and GRAY 1972	Same	d value reported as 0.79 in DEJAGER and DEKKER 1975	10 ³
17	<i>Coregonus</i> spp.	0.77	R	WINBERG 1961	Various authors	-	10 ³
18	Salmonidae	0.81	R	WINBERG 1960	Various authors	11 species	10 ⁴
19	<i>Gadus morhua</i>	0.82	R	EDWARD et. al. 1972	Same	-	10 ⁴
20	<i>Gadus morhua</i>	0.79	R	SAUNDERS 1963	Same	starved fish	10 ⁴
21	<i>Gadus morhua</i>	0.87	R	SAUNDERS 1963	Same	fed fish	10 ⁴
22	<i>Lebistes reticulatus</i>	0.67	R	v. BERTALANFFY 1951	Same	v. BERTALANFFY's confirmation of 2/3 rule	10 ⁰
23	<i>Gambusia affinis</i>	0.63	R	WINBERG 1960	MAKSUDOV 1940	p. 90, d probably not significantly ≠ 0.67	10 ⁰
24	Cyprinodontidae	0.73	R	WINBERG 1961	Various authors	p. 2	10 ⁰
25	<i>Thunnus thynnus</i>	0.90	G	MUIR 1969	MUIR and HUGHES 1969	-	10 ⁶
26	<i>Katsuwonus pelamis</i>	0.85	G	MUIR 1969	MUIR and HUGHES 1969	-	10 ⁵
27	<i>Thunnus albacares</i>	0.90	G	MUIR 1969	MUIR and HUGHES 1969	-	10 ⁵
Generalizations:							
	All freshwater fishes	0.81	R	WINBERG 1961	Various authors	-	
	All marine fishes	0.80	R	WINBERG 1961	Various authors	-	
	Fishes	0.78	R	ZEUTHEN 1953	Various authors	-	
	"GRAY's intermediates" (various marine teleosts)	0.82	G	URSIN 1967	GRAY 1954	See URSIN 1967, p. 2450 for fishes included in plot	
	Fishes	0.82	R&G	DEJAGER and DEKKER 1975	Various authors	most recent literature review on gill size and respiration in fishes	

¹ Page number refers to original publication.

² To eliminate possible bias, the maximum weight estimated for each species from MUUS-DAHLSTRÖM (1973 & 1974) and from PAULY (1978a) was rounded off or up to the closest whole power of 10.

Table 3. Values of d (power relating weight to gill area) thought to be unreliable and therefore not included in Table 2

Taxon	d	Gill (G) or Resp. (R)	Author	Original Data	Remarks
<i>Rhigophila dearboni</i>	0.96	R	WOHLSCHLAG (1963)	Same	WOHLSCHLAG (1963) reports high variability, a small range of weight and himself assumes value of d is too high
<i>Coregonus sardinella</i>	0.89	R	WOHLSCHLAG (1957)	Same	Value widely differs from value of d = 0.77 for <i>Coregonus</i> spp. in Table 5
<i>Zoarces viviparus</i>	0.98	G	URSIN (1967)	WIEDEMAN SMITH	Value of d contradicts URSIN's own estimate of d for "GRAY's intermediate" (see Table 5). Also: value of d is not documented
"all fishes"	2/3	R	v. BERTALANFFY (1951)	Previous studies by same author	Value assumed by VON BERTALANFFY on the basis of metabolic data on <i>Lebistes reticulatus</i> only

7 The relationship between gill area and growth performance

The main question examined in this section is whether there is a relationship, in fishes, between the growth performance of fishes and size of their gills as expressed by the Gill Area Index (GAI, see above for definition).

One problem, however, is that there is no index in the literature which could be used to compare the growth of fishes differing both in their asymptotic size and growth rate. (See PAULY 1979 for a detailed problem statement.)

Deriving a suitable index of growth performance is, however, relatively simple.

As shown previously, the rate of growth at the point of inflexion of the weight growth curve (special VBGF) is

$$\frac{dw_i}{dt} = \frac{4}{9} 10^P \quad 29.$$

when

$$P = \log (K \cdot W_\infty) \quad \dots 30.$$

Here are the properties of P as an index of growth performance and its advantages as compared with other indices previously used in the literature:

- The index P is related to the maximum rate of growth displayed by growing fishes, that is to a well-defined point of their growth curve, and to a point that is highly relevant to applied problems (e. g. fishery and aquaculture yields).
- The index P can be used to compare the growth of fishes widely differing in their growth parameters, size, longevity and body shapes.
- Finally, P can be corrected easily for the effects of different environmental temperatures on the growth of different stocks, and thus allow for the comparison of the growth performance of stocks occurring in widely differing habitats (PAULY 1979).

The GAI data used here are from HUGHES and MORGAN (1973b), pertaining to marine fishes, with the following advantages:

- The compilation covers over a large number of fish species, which allowed for a large number (42) of marine species in which both gill surface and growth data were available.

- b. HUGHES and MORGAN (1973b) checked and standardized the data presented in a large number of original publications.
- c. The use of one single source of data prevented biased data selections by this author.
- d. Using data for marine fishes only tends to reduce the effects of habitat heterogeneity on the gill size/growth relationship.

The data were processed as follows:

1. For each species for which growth data were available, the growth parameters of the special VBGF were estimated using one of the standard methods (PAULY 1978a). When several sets of growth data were available, only the best documented one was used.
2. Using the values of asymptotic weight obtained in step 1 as estimates of maximum weight, values of d were calculated for each species by means of Equation 26.

Table 4. Data for establishing a relationship between gill area and growth performance. See text

No.	Species	W_{∞}	K	d	P	GAI
1	<i>Scylliorhinus caniculus</i>	550	0.530	0.772	2.46	8.54
2	<i>Squalus acanthias</i>	8280	0.074	0.814	2.79	13.37
3	<i>Raja clavata</i>	10644	0.15	0.818	3.20	4.46
4	<i>Latimeria chalumnae</i>	69900	0.209	0.847	(4.16)	(0.773)*
5	<i>Clupea harengus</i>	277	0.290	0.761	1.90	14.9
6	<i>Brevoortia tyrannus</i>	1009	0.343	0.782	2.54	51.58
7	<i>Engraulis encrasicolus</i>	24	1.123	0.723	1.43	55.13
8	<i>Merlangius merlangus</i>	472	0.426	0.770	2.30	10.51
9	<i>Pollachius virens</i>	11331	0.141	0.819	3.20	15.18
10	<i>Hippocampus (hudsonius)</i>	14	2.50	0.715	1.54	1.71
11	<i>Zeus faber</i>	7187	0.298	0.812	3.33	5.17
12	<i>Mugil cephalus</i>	13890	0.110	0.822	3.18	6.47
13	<i>Roccus lineatus</i>	17543	0.186	0.827	3.51	12.11
14	<i>Pomatomus saltatrix</i>	5808	0.197	0.809	3.06	24.55
15	<i>Trachurus trachurus</i>	598	0.270	0.773	2.21	17.00
16	<i>Coryphaena hippurus</i>	22070	0.575	0.829	4.10	18.80
17	<i>Maena smaris</i>	117	0.218	0.748	1.41	4.64
18	<i>Tautoga onitis</i>	2845	0.165	0.798	2.67	15.55
19	<i>Crenilabrus melops</i>	190	0.359	0.756	1.83	9.29
20	<i>Labrus merula</i>	990	0.234	0.781	2.36	4.32
21	<i>Blennius pholis</i>	54	0.90	0.736	1.69	6.29
22	<i>Zoarces viviparus</i>	965	0.203	0.781	2.29	12.54
23	<i>Callionymus lyra</i>	53	0.490	0.736	1.14	5.90
24	<i>Trichiurus lepturus</i>	4663	0.296	0.805	(3.14)*	(0.654)*
25	<i>Scomber scombrus</i>	977	0.262	0.781	2.41	22.14
26	<i>Scomberomorus maculatus</i>	6911	0.20	0.811	3.14	24.68
27	<i>Scorpaena (porcus)</i>	869	0.177	0.779	2.19	2.90
28	<i>Trigla gurnardus</i>	534	0.312	0.772	2.22	4.57
29	<i>Cottus gobio</i>	6	0.550	0.702	0.52	11.90
30	<i>Cottus bubalis</i>	102	0.230	0.746	1.37	9.31
31	<i>Acanthocottus scorpius</i>	377	0.539	0.766	2.31	3.91
32	<i>Thunnus thynnus</i>	987388	0.067	0.888	4.82	28.07
33	<i>Thunnus albacares</i>	198940	0.250	0.864	4.70	32.83
34	<i>Euthynnus alliteratus</i>	44869	0.164	0.840	3.87	84.40
35	<i>Sarda sarda</i>	3434	0.693	0.801	3.38	27.50
36	<i>Katsuwonus pelamis</i>	55200	0.179	0.844	3.99	54.67
37	<i>Pleuronectes platessa</i>	2171	0.170	0.793	2.57	14.45
38	<i>Platichthys flesus</i>	1058	0.229	0.782	2.38	13.02
39	<i>Lophopsetta maculata</i>	806	0.242	0.778	2.29	7.76
40	<i>Pseudopleuronectes americanus</i>	2881	0.113	0.798	2.51	7.58
41	<i>Opsanus tau</i>	568	0.258	0.773	2.17	5.78
42	<i>Lophius piscatorius</i>	53952	0.060	0.843	3.51	6.14

* not used

3. On the basis of the values of d , values of GAI were estimated from the gill surface area and weight data of Table 4 in HUGHES and MORGAN (1973b).

The data so obtained are summarized in Table 4. Of the GAI and P values in Table 4, two appear at first sight quite peculiar, namely 0.773 for *Latimeria chalumnae* (No. 4) and 0.654 for *Trichiurus lepturus* (No. 24). Both values are so low that they do not even fit into the frame of Fig. 3, in which all other values form an easily identifiable cluster. These two values, therefore, I think are either erroneous, or they express specific features of the two fishes in question; both alternatives suggested that No. 4 and No. 24 should be excluded from the data set prior to further analysis.

When the remaining data (40 pairs of GAI and P values) are considered, there is a significant correlation between \log_{10} GAI and the index of growth performance P ($r =$

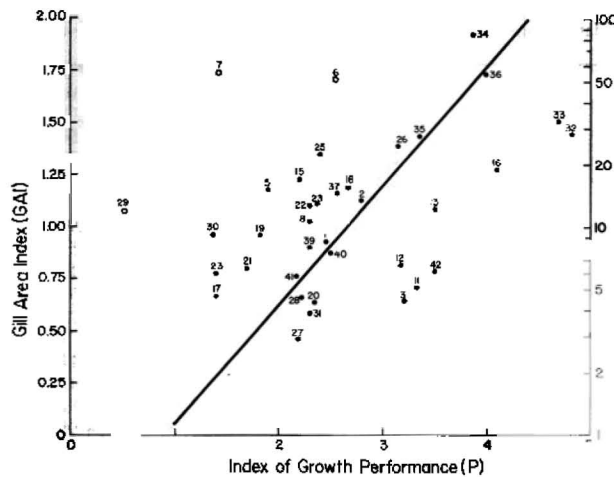


Fig. 3. Functional relationship between \log_{10} GAI (Gill Area Index) and the index of growth performance P in marine fish (see text for definitions of these variables). The three open dots were not used in the computations

0.431, $P = 0.01$). Deletion of 3 apparent outliers (No. 6, 7 and 29 on Table 4), however, greatly improves the correlation which increases to $r = 0.661$ (with 35 dF). The improved relationship is also expressed by the functional regression:

$$\log_{10} \text{GAI} = -0.528 + 0.574 P \quad \dots 31.$$

which is used here, instead of a "normal", predictive regression because both GAI and P are estimated with error (RICKER 1973).

As a whole, the data of Table 4 can be used to reject the null hypothesis of no relationship between gill area and growth performance. Also, it will be noted that it is mainly active, pelagic fishes which are found above the regression line, while less active demersal fishes are found predominantly below the regression line (Fig. 3).

8 The direct relationship between oxygen supply and growth

While the previous section shows a positive correlation between growth performance and gill size in marine fishes, it remains to demonstrate that:

1. Oxygen supply – hence, also gill size – determines growth performance when other potentially limiting factors are experimentally kept constant; and
2. Oxygen supply – hence also gill size – determines food conversion efficiency.

The data of STEWART et al. (1967) on the growth of juvenile *Micropterus salmoides* kept under reduced oxygen concentrations, and the data of THIJL (1977) on the growth of juvenile *Cyprinus carpio* kept under heightened oxygen concentrations were used here to

demonstrate how oxygen supply determines growth performances. Selected data from both studies are summarized in Table 5.

In the case of *M. salmoides*, only those data of STEWART et al. (1967) were used which pertained to O₂ saturation lower than 100 %, since high O₂ saturation (near and above 100 %) induces gas bubble disease. Also, those data were not considered which referred to fishes kept under varying oxygen saturations. The remaining data, pertaining to 23 individual fishes kept at a mean temperature of 26 °C and at oxygen concentrations ranging from 1.6 to 8.1 mg O₂/liter, are presented in Table 5.

Of the data of THIEL (1977), obtained in temperatures ranging from 23 to 36 °C, only those were used which pertained to a temperature of 26 °C. This allows comparison with

Table 5. Data on the growth of juvenile *Micropterus salmoides* and *Cyprinus carpio* kept in different oxygen concentrations and fed ad libitum, at temperatures near 26 °C

<i>Micropterus salmoides</i> : data extracted from Table 1 in STEWART et al. (1967)					<i>Cyprinus carpio</i> : data extracted from Table 1 and page 18-19 in THIEL (1977)				
Exp. No.	°C	mgO ₂ /l	Percent Saturation	W ₀ ¹	Increment ²	Bar over Atm. Press.	mgO ₂ /l	W ₀ ¹	Increment ²
1	25.0	1.6	19.4	2.47	0.067	0	5.42	5.1	0.04
1	25.1	2.3	28.0	2.58	0.103	0	5.42	5.3	0.07
1	25.2	3.0	36.5	2.65	0.167	0	5.42	4.8	0
1	(25.1)	4.2	51.1	2.48	0.223	0	5.42	3.6	0.01
1	25.1	5.8	70.5	2.71	0.250	0	5.42	4.9	0.02
1	25.1	8.1	98.5	2.46	0.249	1	12.39	3.3	0.20
2	25.9	1.7	21.0	6.55	-0.033	1	12.39	4.1	0.23
2	25.9	2.6	32.1	6.13	0.120	1	12.39	5.8	0.25
2	26.0	3.8	47.0	6.90	0.225	1	12.39	3.9	0.24
2	(26.0)	5.4	66.8	6.90	0.305	1	12.39	6.0	0.23
3	26.0	2.1	26.0	3.44	0.117	1.5	16.05	4.6	0.28
3	26.0	3.4	42.1	3.50	0.160	1.5	16.05	3.8	0.15
3	(26.0)	5.9	73.0	3.13	0.263	1.5	16.05	6.2	0.21
4	26.1	2.1	26.0	3.36	0.118	1.5	16.05	4.2	0.25
4	(26.1)	3.4	42.1	3.42	0.232	1.5	16.05	4.1	0.21
4	26.1	5.9	73.1	3.52	0.277	2	18.8	6.2	0.32
5	25.7	1.9	23.4	4.16	0.140	2	18.8	5.8	0.29
5	25.8	3.2	39.5	4.38	0.265	2	18.8	5.6	0.26
5	25.8	5.1	62.9	4.07	0.329	2	18.8	3.8	0.19
5	25.8	8.0	98.6	4.29	0.433	2	18.8	4.6	0.22
6	(26.6)	1.9	23.3	3.39	0.084				
6	25.6	3.8	46.6	3.25	0.192				
6	(25.6)	8.1	99.3	3.19	0.186				

¹ initial weight, in g
² gram/day

the data of STEWART et al. (1967) and reduces a whole series of duplicated experiments to a single, typical example. The data, extracted from Table 1 and pp. 18-19 in THIEL (1977) and summarized in Table 5, were obtained from fishes kept in pressure tanks, such that the oxygen concentration of the water could be increased well above normal levels without unduly increasing the oxygen saturation.

The correlations between the variables O₂ content (x), initial weight (y) and daily growth increment (z) are as follows:

	<i>M. salmoides</i>	<i>C. carpio</i>
r _{xy}	-0.116	0.170
r _{xz}	0.755	0.872
r _{yz}	-0.002	0.253

In both cases, there is a significant correlation ($P = 0.01$) between oxygen concentration and growth increment, and no significant correlation between the other combinations of variables.

The effect of reduced O_2 content seems to have been direct, i. e., by leading to a reduction of the rate of synthesis (see Fig. 1) as well as indirect, i. e., by reducing food intake (STEWART et al. 1967 speak here of reduced "appetite"). It could be argued, therefore, that it is mainly the reduced food intake which reduces the growth of fishes kept at reduced O_2 concentrations, not the low O_2 concentrations itself.

The reduced "appetite" of fishes kept at low oxygen levels seems, however, to be mainly a regulating factor by which means the fishes prevent their AAP from being flooded. Since, under conditions of reduced oxygen availability, the ingested food (amino-acids) can neither be used for synthesis of new body substance (O_2 being needed for synthesis) nor as burning material (O_2 is also needed in this process), the amino-acid would have to be excreted, which costs energy – hence, oxygen. So, under reduced levels of oxygen the best policy is not to ingest food in the first place.

The fact that in fishes, the food conversion efficiency (= weight increase/food intake) generally decreases with increasing fish size suggests similarly that reduced "appetite" cannot be the main cause for the slow growth of large fishes.

The food conversion efficiency (α) of fishes is generally expressed as

$$\alpha = a \cdot W^b \quad \dots 32.$$

where b has a negative sign and an absolute value ($|b|$) which should be close to $(1-d)$.

An example is presented which illustrates the character of the relationship between food conversion efficiency and size, hence, also between food conversion efficiency and relative gill area.

The example is an analysis of data on *Epinephelus guttatus* from MENZEL (1960), summarized in Table 6. Here, the relationship between conversion efficiency (α) and weight is

$$= 0.726 W^{-0.23} \quad 33$$

The value of W_{\max} in Caribbean *Epinephelus guttatus*, as derived from data in THOMPSON and MUNRO (1978), is 2324 g, which, inserted into Equation 26 provides an estimate of $d = 0.79$. Note that $|b| = 0.23 \approx 1.00 - 0.79$. That is, the decrease of relative gill size with increasing body weight explains most of the decrease in conversion efficiency associated with increasing sizes.

Similarly, JONES (1976) estimated the following relationship for gadoids:

$$\alpha_2 = 0.73 \cdot W^{-0.15} \quad \dots 34.$$

where α_2 is the net growth efficiency. Note that $1.00 - 0.15 = 0.85$, which is close to the values of d given for cod in Table 2. On this relationship (34), JONES (1976) writes:

"These results suggest that in gadoids, net growth efficiency decreases with increasing body weight, but that the rate of decline is only detectable at the lower end of the weight scale. GERKING (1966) obtained similar results with bluegill sunfish *Leopomis macrochirus* (Rafinesque)."

Various reasons have been given to explain this decrease of food conversion efficiency. Most of them have been discussed by GERKING (1952), from whose paper the following hypotheses are summarized:

1. The reduction of growth efficiency may be the result of "ageing". GERKING (1952) considers this a pseudo- (or circular) explanation, an opinion with which I fully agree.
2. Stomach and gut surface may increase in proportion to a power of weight lower than unity.
3. The digestive enzymes may not supply the same amount of nutrient material per unit body weight in fishes of different sizes.

4. Possibly the decreased protein utilization is associated with a change in metabolism or with some bodily process which controls metabolism.
5. The thyroid hormones may have a direct influence on the conversion of nutrient protein to body substance.

Later, GERKING (1971) added the hypothesis that –

6. The decrease of protein conversion efficiency may be explained by differential rates of protein synthesis.

Hypothesis 2 above has been discussed in connection with Misunderstanding 1, and the case presented there also argues against hypothesis 3. On the other hand, hypotheses 5 and 6, which imply intricate regulating processes, seem superfluous as hypothesis 4 alone explains why growth efficiency decreases with increasing size: the “change in metabolism” assumed by GERKING (1952) can be quite simply attributed to the reduction of oxygen availability in the tissues of fishes of increasing size, which is itself due to the fact that the gills do not grow in proportion to the weight of the fishes.

9 The generalized VBGF: parameter definitions

9.1 Introductory remarks

Equation 13 contains four parameters, L_{∞} , K , D and t_0 , while Equation 10 contains the additional parameter b , the exponent of the length/weight relationship in Equation 7b, and W_{∞} instead of L_{∞} .

In addition to these explicit parameters, the use of the VBGF implies the existence of another, “hidden” parameter, called here W_x (or L_x). This parameter refers to the point of the VBGF representing the minimum weight (or length) to which the equation applies.

In the following paragraphs, definitions of the VBGF parameters are presented which may help to interpret their numerical values as obtained from various fish stocks.

9.2 Asymptotic size (W_{∞} and L_{∞})

RICKER (1975) defines asymptotic size as the mean size the fish of a given population would reach if they were allowed to live and grow indefinitely. However, a generally good agreement between values of L_{\max} and L_{∞} has been convincingly demonstrated (in small fishes) by various authors (e. g., BEVERTON 1963). This well-documented phenomenon prompted TAYLOR (1962) to the formulation of the rule of thumb:

$$L_{\max}/0.95 \approx L_{\infty} \quad \dots 35.$$

which allows for the estimation of reasonable values of asymptotic length in small fishes. In large fishes, such as tuna or billfishes, this rule of thumb cannot be used to obtain estimates of L_{∞} for use in conjunction with the special VBGF. The reason for this is discussed in the following paragraphs.

Very good length-at-age data have been presented by SELLA (1929) on the growth of the giant bluefin (*Thunnus thynnus*) which when used in conjunction with the special VBGF (that is, with $D = 1 \Leftrightarrow d = 2/3$, implying isometric gill growth), provides estimates of $K = 0.043$ and $L_{\infty} = 505$ cm, a length that is more than 1.5 times the maximum length of about 330 cm recorded for this species (TIEWS 1963) (Fig. 4A).

Using a condition factor of 1.70 calculated from data in MUUS and DAHLSTRÖM (1974), an asymptotic weight of 2190 kg is obtained, which is three times larger than the highest weight reported by TIEWS (1963). The real value of d in *Thunnus thynnus*, however, is not $2/3$ as implied in the special VBGF, but 0.90 as given by MUIR and HUGHES (1969). This

provides an estimate of $D = 0.3$ (see Equation 27) which, when used in conjunction with the generalized VBGF, provides, with the same growth data, an estimate of $K = 0.410$ and $L_\infty = 332$ cm, while the condition factor used above provides an estimate of $W_\infty = 622$ kg. Both values of asymptotic size (332 cm and 622 kg) correspond very well with the values of L_{\max} and W_{\max} reported by TIEWS (1963) for various Atlantic stocks (Fig. 4B).

It will be noticed, also, that the fit of the special VBGF to the data of SELLA (1929) is about as good as the fit of the generalized VBGF to the same data (see Fig. 4), for which

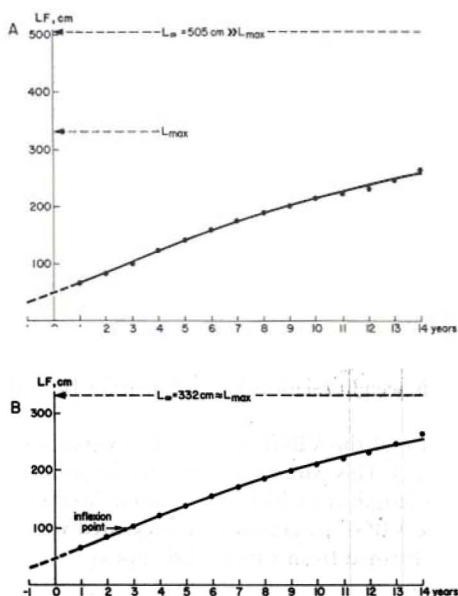


Fig. 4. Growth of *Thunnus thynnus*. Based on data of SELLA (1929). Note that curve A (special VBGF) has a value of L_∞ much larger than L_{\max} , while curve B (generalized VBGF) has a value of L_∞ almost equal to L_{\max} . A Ford-Walford plot was used to estimate the parameters

reason the quality of the fit could not be meaningfully used to estimate (e. g. by iteration) a reasonable value of D .

Another important result emerging from this application of the generalized VBGF is that the inflexion point, the position of which may be estimated from Equation 19, cannot be seen by a mere visual inspection of the size-at-age data (see Fig. 4B).

This exercise, here demonstrated with bluefin tuna, could be extended to a whole series of large fishes with the main result remaining the same: when the special VBGF is used, the value of asymptotic size obtained from a set of size-at-age data differs from the maximal sizes recorded from the same stock by an amount which increases with Δd (see Fig. 2). Or, expressed differently: the more erroneous the assumption that $d = 1/3$ is, the greater the difference between W_{\max} and W_∞ , or L_{\max} and L_∞ .

The generalized VBGF, on the other hand, provides estimates of W_∞ and L_∞ which are generally very close to the values of W_{\max} and L_{\max} when the appropriate value of d (and consequently of D) is used.

The closeness of W_{\max} and L_{\max} and L_∞ respectively, indeed allows for the application of TAYLOR's rule of thumb (Equation 35) to the stocks of any fish species. It may also be suggested that -

$$\sqrt[3]{W_{\max}} / 0.95 \approx \sqrt[3]{W_\infty} \quad \dots 36.$$

But it must be remembered that these rules of thumb apply to the whole range of weights which fish can reach only in conjunction with the generalized VBGF and appropriate values of D . Also, it must be kept in mind that these rules of thumb apply to

L_{max} and W_{max} only, that is, to the greatest sizes recorded from given stocks, not the greatest size on record for a given species of fish ($L_{(max. ever)}$, $W_{(max. ever)}$).

9.3 The surface factor: D

This parameter may be defined as the difference between the power of length in proportion to which weight increases and the power of length in proportion to which gill surface increases.

When weight growth is isometric, or only slightly allometric, D can be obtained directly from equation 28 or from d and equation 27, while d itself may be obtained either from metabolic or gill studies, when available.

9.4 The stress factor: K

This parameter is the most difficult to visualize. As discussed previously, K is proportional to k, hence to the rate of degradation of body protein (see equations 1 and 8). Protein degradation is an intricate process which, in opposition to protein synthesis, has been

Table 6. Conversion efficiency of food in the red hind *Epinephelus guttatus*, as based on data in MENZEL (1960)

Weight (g)	α^2
216	0.247
285	0.219
319	0.160
392	0.153
424	0.179
628	0.161
647	0.177
649	0.187

¹ Mean of initial and end weight. - ² $\alpha = \frac{\text{growth increment}}{\text{food intake}}$

hitherto relatively little investigated. A brief review of some of the preliminary findings in this field may, however, help in defining K more precisely than hitherto done.

Only one paper was found which deals with protein degradation in fishes (SOMERO and DOYLE 1973). For this reason it is necessary to rely on data pertaining mainly to mammals and bacteria (BRANDTS 1967; RECHCIGL 1971; GOLDBERG and DICE 1974; GOLDBERG and ST. JOHN 1976; MCLENDON and RADANY 1978). The consensus among these authors is as follows:

1. Intracellular proteins are in a state of equilibrium in which the proteins are continuously broken down and replenished by synthesis (RECHCIGL 1971, p. 237).
2. There is, however, a great heterogeneity in turnover rates of different proteins (see RECHCIGL 1971, Table 1).
3. At least in the case of enzymes, it has been demonstrated that proteins are synthesized at constant rates, while a constant fraction of native molecules present in the tissues is destroyed per unit time. That is, the rate of synthesis conforms to zero order kinetics, whereas the degradation process conforms to first order kinetics, or

$$\frac{dC}{dt} = k_s - k_d C \quad 37.$$

- where C is the amount of protein present at time t , k_s is the rate constant for synthesis (i. e., the amount synthesized per unit time) and k_R is the first-order rate constant for protein degradation (i.e., the fraction of protein molecules present that are degraded per unit time, RECHCIGL 1971, p. 272) (Note the similarity of Equation 37 with Equation 1.)
4. The applicability of first-order kinetics in point (3) implies that protein molecules "are being destroyed in a random fashion, without regard to their age and that in a given period of time, newly formed [. . .] molecules had the same risk of being destroyed as older ones." (RECHCIGL 1971, p. 275)
 5. It seems that it is the conformational changes (changes in the tertiary and quaternary structure) or proteins which first make the protein molecules susceptible to further degradation by proteolytic enzymes. (RECHCIGL 1971, p. 287; SOMERO and DOYLE 1973; GOLDBERG and DICE 1974).
 6. Therefore, temperature, which has a great influence on the configurational stability of proteins, indirectly determines the rate of protein degradation (BRANDTS 1967).
 7. Points (5 and 6), it should be noted, imply the existence of a direct proportionality between *in vivo* estimates of protein degradation rates and *in vitro* determination of configurational stability. The existence of this proportionality has been recently demonstrated by MCLENDON and RADANY (1978).

As a whole, the most recent reviews of the process of protein degradation (including GOLDBERG and St. JOHN 1976) confirm the "textbook" statements, cited in connection with Misunderstanding III; they define protein catabolism as a process requiring neither metabolic energy nor free oxygen. The situation is evidently different in the case of the breakdown of amino-acids, but K , it must be remembered, refers to native protein.

Protein degradation in the body of a living fish must be continuously compensated for by synthesis of new protein. A correlation between oxygen consumption and the rate of protein degradation – as expressed by K – is therefore to be expected. This is probably the reason why the changes of K over a wide range of temperatures can be well described by a curve derived from respiratory experiments (PAULY 1979).

In addition to expressing protein degradation, K also expresses (indirectly) those abiotic and biotic factors which limit oxygen availability for protein synthesis. Thus, for example, osmotic stress, which uses up metabolic energy that could otherwise be used for protein synthesis, tends to raise the value of K , and to lower the value of asymptotic size (PAULY 1979a). Similarly, sex-specific metabolic rates, e.g. with the females using up less oxygen than the males, result in sex-specific growth rates, with the females displaying a better growth (a higher value of P), a lower value of K and a higher value of asymptotic size than the males (see WOHLISCHLAG 1962). Finally, food, space and sexual competition also result in higher values of K and lower values of P and asymptotic size, the reason again being the diversion of a larger part of the oxygen supply to various activities, away from protein synthesis. It would, therefore, seem appropriate to refer to K as a general "stress factor" rather than as a more specific "coefficient of catabolism." The word "stress" here refers to the sum total of all effects which raise the value of K , that is, extreme temperatures or salinities, population densities that are too high for a given food supply, etc.

9.5 The origin of the growth curve: t_0

This parameter is defined as "the hypothetical age the fish would have had at zero length had they always grown in the manner described by the equation" (RICKER 1975). However, since fishes do not always grow in the manner described by the VBGF, t_0 is not a biological parameter. This parameter cannot, therefore, be used to estimate values of K from values of L_∞ and length at birth (e.g., as done by HOLDEN 1974 in elasmobranchs). This procedure yields, in fact, growth parameters widely differing from those obtained by using normal length-at-age data, as shown in PAULY (1978a, 1978c).

9.6 The starting size: L_x and W_x

Since t_0 is a parameter which cannot be interpreted biologically, the length at age zero may not be interpreted biologically either, e. g., as length at birth or length at hatching. This creates a new problem, namely the identification of the lowest size from which on the VBGF may be assumed to describe the growth of a fish. For a preliminary exploration of this problem, it is necessary to return to questions of fish anatomy.

DE SYLVA (1974) investigated the development of the respiratory system of herring (*Clupea harengus*) and plaice (*Pleuronectes platessa*) larvae, and presented data which may help in identifying the starting size. Figure 5 shows the relationship of gill area to weight in the larvae and young juveniles of these two species.

The data show that the gill surface of larvae grow with a power of weight considerably higher than one. This implies that the gill surface of larvae cannot be limiting for their growth, not even considering the fact that fish larvae, in addition to their gills, use their

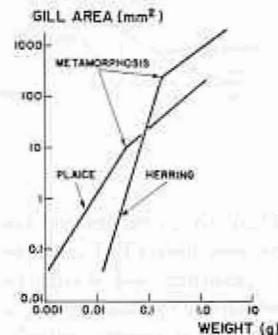


Fig. 5. Development of the gill surface area in larval herring and plaice. Note that slope is much higher than unity prior to metamorphosis, after which the slopes decline to values lower than unity. Redrawn from DE SYLVA (1974)

whole body surface, particularly the primordial fin fold, for respiratory purposes. This is in accord with the results from studies of larval growth, which generally suggest a logarithmic growth in fish larvae (both in length and weight), as well as a strong dependence of larval growth on food supply (see CUSHING 1975, p. 127 ff.).

This is also confirmed by the results of BLAXTER and HEMPEL (1966) who, on the basis of studies of food conversion efficiencies, found that the metabolism of larval herring is proportional to a power of weight very close to unity. The results of HOLLIDAY et al. (1966), reanalyzed by BLAXTER and HEMPEL (1966), on the oxygen consumption of herring larvae also confirm that the metabolism of larvae is directly proportional to weight. This proportionality does not, however, hold for long, and a marked transition occurs at metamorphosis, where the cutaneous contribution to total respiration is markedly reduced by the acquisition of scales and by the loss of the well capillarized primordial fin folds. Also, at metamorphosis, the gills cease to grow in proportion to a power of weight higher than unity and continue their growth in proportion to a power of weight close to that reported from juvenile and adult herring (0.79) and plaice (0.85).

These results correspond remarkably well with the data of Fig. 2 and Table 2 which suggest a value of $d \approx 0.8$ for fishes in the weight range of adult herring and plaice. It would thus appear that the size of metamorphosis should more or less correspond to the starting size (L_x and W_x).

Figure 6 finally, shows the different "origins" of a typical growth curve, along with a suggested code for the identification of the curve's features. The most important function of Fig. 6, however, is to show the difference between the origin of the VBGF (t_0) and the beginning of "prenatal" growth (t_f = time of fertilization) as well as the conceptual difference between L_0 (the length at time zero predicted by the VBGF) and L_b (the length

at birth or at hatching). It is not impossible, however, that L_x , the starting size (of the VBGF) should be equal to L_0 (and L_b) in which case the VBGF would describe the growth of a fish from its birth. This case, which is most likely to occur in elasmobranchs (the young of which very much resemble the adult), would still allow for t_0 to differ from t_f , and hence precludes the use of the gestation period as an estimate of t_0 .

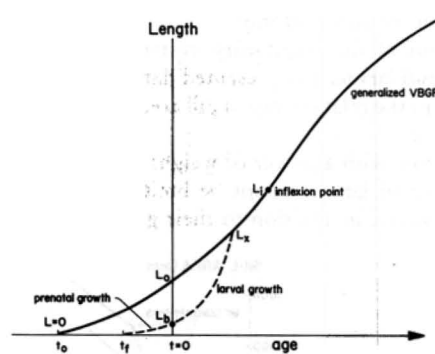


Fig. 6. Origins of a growth curve: some definitions. L_i = length at inflexion point; L_x = length from which on the VBGF describes the fish's growth; L_0 = length at age zero, as predicted by downward extrapolation of VBGF; L_b = real length at age zero (length at birth or hatching); t_0 = theoretical origin of growth curve on time axis; t_f = time of fertilization (e.g. beginning of intrauterine growth)

10 Discussion

Throughout the animal kingdom, the surfaces through which metabolism occurs tend to become diversified as organizational level increases. Thus, the surfaces through which food is absorbed and wastes released become gradually separated from the surface through which the exchange of O_2 and CO_2 occurs, which results, in the long (evolutionary) run, in the case of aquatic animals, in guts distinctly separated from the gills (see REMANE 1967). Increase in size and performance of aquatic animals, hence, increased independence from external factors can be attained only by an increase of metabolic rate, that is, the processing of more food. More food to process, on the other hand, implies greater relative gut and gill surfaces, the latter supplying the O_2 necessary for the various metabolic processes.

The agnathous animals which gave rise to the modern fishes were generally small and, as suggested by their anatomy, quite sluggish animals (see e. g., STENSIÖ 1958). However, with the gradual loss of their heavy armor and the acquisition of fins, the ancestors of the recent fishes became able to colonize the whole water column. The higher level of activity displayed there required more food, and was correlated both with the acquisition of an improved organ for the prehension and the preliminary processing of food (jaws), as well as with an improvement in the performance and the size of the gills. (Fig. 7)

The further evolution of these two organ systems finally led to a gradual reorganization of the whole head region, the extent of which may be appreciated when comparing the small and intricate plumbing system of ancient agnathans with the streamlined gills that almost fill up the head of modern fishes (see Fig. 7).

In one species, the whale shark *Rhincodon typus*, the gills have reached such a size that the shape of the whole body is affected. TINKER and DE LUCAS (1973) write on this: "The whale shark is the world's largest fish. It has a gigantic body which is thickest in the area of the gills and tapers off gradually toward the tail."

The most advanced recent fishes - in both the systematic and physiological sense - are the large scombroids, such as the Thunninae or the Istiophoridae. In these fishes, the highest stage in the development of gills has been reached which allows for metabolic performances unequalled in any other fishes, as expressed by their trans-oceanic migrations and their elevated body temperatures. These fishes seem indeed to have reached a metabolic level that has gradually turned from an asset to a liability, as suggested by KEARNEY (1975)

on the basis of the observation that the tropical tuna are forced, from time to time, to plunge into deeper water because they cannot meet their need for oxygen in the warm surface waters of the tropical zones of the oceans. (See also SHARP 1978)

Another evolutionary line in fishes is the trend toward breathing air, mainly in tropical and subtropical fishes (Anabantidae, Clariidae, Osteoglossidae, etc.). These fishes, the anabolism of which are constrained neither by the size of their gills, nor by the oxygen content of the water bodies in which they occur, tend to have growth curves of a shape markedly differing from the normal VBGF type (see PAULY 1979, Fig. 24 for an example). More data, however, must be compiled and analyzed for a clear pattern to emerge, and more thought must be devoted to the question as to what, if not gill size, is limiting for their growth.

In any case, the fact that the largest freshwater fish – *Arapaima gigas*, with a maximum weight of about 200 kg (FRANK 1973) – should be an obligatory air breather, is in itself of considerable interest, because it suggests that very large fishes must either use ram-

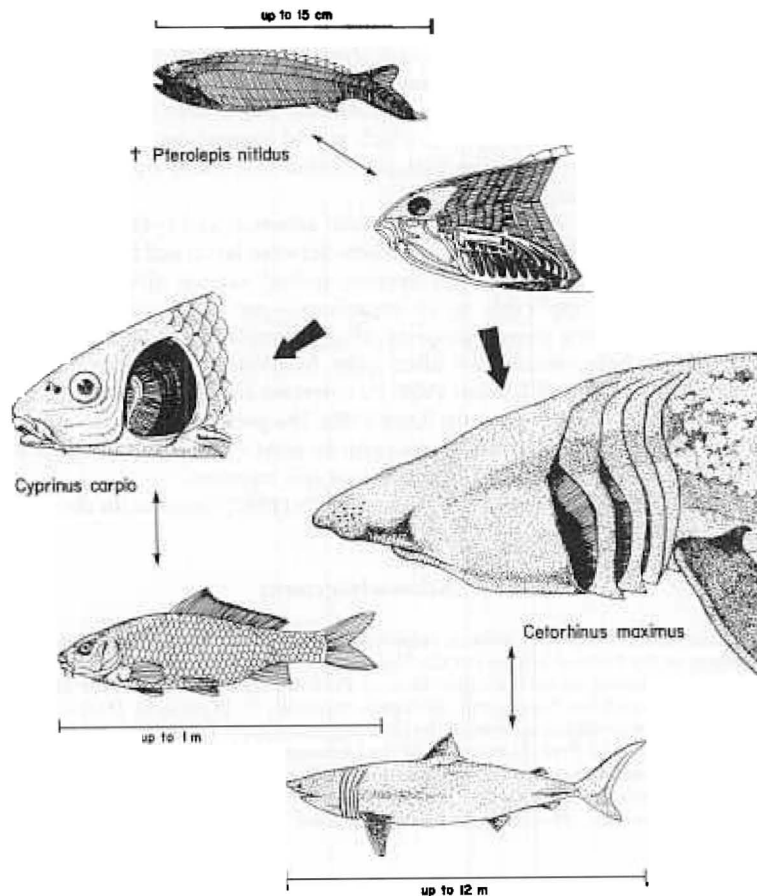


Fig. 7. The evolution of large gills: examples. Note the transition from a segmental respiratory system, occupying a small part of the head's volume to a more compact system occupying the larger part of the head's volume. (Thick arrows suggest evolutionary trends, not phylogenetic relationships.) Redrawn and adapted from STENSIÖ 1958, STORER and USINGER (1957) and MUUS-DAHLSTRÖM (1973, 1974)

ventilation, as in the case of the largest oceanic fishes, or resort to air-breathing, as in the case of many large freshwater fishes of the tropics and subtropics.

I am aware that my suggestion of a limiting role of the gills (and of oxygen supply to the tissue) in the growth of fish is still at the hypothesis stage, and in need of experimental testing.

The hypothesis offers a single, simple explanation to a whole set of growth-related phenomena, such as:

- size-related migration and distribution patterns (SHARP 1978)
- the link between growth and temperature (TAYLOR 1958; PAULY 1979)
- the link between natural mortality, growth parameters and environmental temperature (PAULY 1978b, 1980)
- the remarkably constant ratio between mean size at first maturity and asymptotic size in different groups of fish (BEVERTON 1963; CUSHING 1968; PAULY in prep.).

It should be mentioned, however, that various authors object to the idea of an external respiratory surface being limiting for the growth of animals. HARDING (1977) writes, for example, that "metabolism is universally related to some power of weight near $\frac{3}{4}$, from bacteria to whales, which suggest that it is a property of the cell".

In the case of fishes, we know, however, that the power in question (= d) may be as low as 0.5 (WINBERG 1961, working on cyprinodontids), and as high as unity (BLAXTER and HEMPEL 1966, working on fish larvae), which would suggest that the value of $\frac{3}{4}$ as an average figure completely masks the biological features revealed by the differences in d values between different organisms.

These differences in d values, such as between spherical and cylindrical bacteria (VON BERTALANFFY 1951, p. 282) or that discussed here between larval and fully metamorphosed fish, or between large and small fish species, indeed suggest that there is no single "universal" value of d applicable to all organisms - not even to all fishes - and that therefore $d \approx 0.75$ is not a general property of organisms or of their cells.

The VBGF has been criticized - often quite frivolously - by several authors, e. g. RICHARDS 1959; PARKER and LARKIN 1959; PALOHEIMO and DICKIE 1965; KNIGHT 1968; RICKER 1958; 1975, and most recently ROFF 1980. The present paper is to my knowledge the first - outside of von Bertalanffy's own contributions - in which an attempt is made to validate the logic which led to the formulation of this equation.

This paper may thus be seen as an answer to Roff's (1980) "motion for the retirement of the von Bertalanffy Function".

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