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GILL SIZE AND TEMPERATURE AS GOVERNING FACTORS IN FISH GROWTH: A GENERALIZATION OF VON BERTALANFFY'S GROWTH FORMULA

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Preface

The present report, based on a dissertation presented at Kiel University in January, 1979, has been written

a) in order to allow for the presentation, under one cover, of the large amount of tabular data used to derive certain relationships pertaining to fish growth,

b) in order to allow for colleagues to comment on some new concepts in fish growth prior to their regular publication in much shortened version.

Critique and comment would therefore be appreciated. This refers especially to data which could be used as a test case for the validity of the concepts presented here.

D.P.

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Abstract

In von Bertalanffy's theory, growth is defined as the net result of two processes with opposite tendencies, one synthesizing native protein (anabolism), the other degrading the protein (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 growth performance. This is due chiefly to the fact that the respiratory area of fishes (the gills) do not grow, with increasing size, as fast as body weight, and to the fact that fish can store only very small amounts of oxygen.

It is demonstrated that, as a rule, fishes able to reach a large size (e.g. tuna) tend to have gills growing in proportion to a power of weight close to unity, while small fishes (e.g. guppy) have gills growing in proportion to a power of weight close to 2/3. The von Bertalanffy growth formula (VBGF), whose derivation rests on the assumption of the universal validity of the "2/3 rule", is therefore considered to be a special case of a generalized formula ("generalized VBGF") which is derived here, and whose properties and applications are discussed.

Various properties of the VBGF's parameters are discussed in detail, particularly the relationship between the values of K and estimates of mean environmental temperature, where a clear, regular pattern could be demonstrated, which is closely allied to Krogh's normal curve (of metabolism against temperature). Also, a close relationship between K and the asymptotic size of a large number of stocks is demonstrated, which further emphasizes the uniformity of growth patterns in fishes and which can be used to estimate growth parameters in certain stocks and assess the interrelationships between various species, particularly through the use of a newly developed "auximetric grid".

Potential applications for these theoretical considerations are discussed, particularly as the demonstrated uniformity of fish growth patterns and the established relationships allow for the estimation, in the field, of the growth parameters of tropical and other little-investigated fish stocks.

Kurzfassung

Vorliegende Arbeit ist ein Versuch, die Faktoren zu identifizieren, die das Wachstum von Fischen bestimmen. Dabei wird nach Regeln gesucht, mit deren Hilfe die Wachstumsparameter von wenig untersuchten, vornehmlich tropischen Beständen bestimmt werden können.

Die Daten, die für diese Untersuchung verwendet wurden stammen im Wesentlichen aus einer früheren Veröffentlichung dieses Autors, in der die Wachstumsparameter von über 500 Fischarten und über 1 500 Einzelbeständen zusammengestellt wurden. Dabei wurden Parameterwerte in etwa 1 000 Fällen neu berechnet.

Von Bertalanffy's Wachstumstheorie postuliert u.a., daß organisches Wachstum als das Nettoergebnis zweier entgegengesetzter Prozesse begriffen werden kann, wobei der eine aufbauender Art (Anabolismus) und der andere abbauender Art ist (Katabolismus). Es wird gezeigt, daß neuere biochemische Untersuchungen diesen Teil der Theorie voll bestätigen.

Andererseits wird gezeigt, daß die Annahme einer Allgemeingültigkeit der "2/3 Regel" des Metabolismus, zumindest was die Fische betrifft, nicht aufrechterhalten werden kann. Diese Regel, die besagt, daß der O_2 Verbrauch von Fischen proportional zur 2/3 Potenz ihres Gewichtes steigt, wenn die Fische wachsen, scheint nur bei sehr kleinen Fischen

(e.g. bei den Guppys) zuzutreffen. Erwähnte Potenz steigt andererseits auf etwa 0.80 bei den Fischen mittlerer Größe, und auf 0.90 und mehr bei den Thunen und anderen großen Fischen.

Daher scheint es angebracht, die "von Bertalanffy Wachstumsformel", die auf der "2/3 Regel" basiert, als einen Spezialfall einer "allgemeinen von Bertalanffy Wachstumsformel" zu betrachten, deren Intergration und Eigenschaften detailliert behandelt werden.

Ein Problem vieler vergleichender Wachstumsuntersuchungen ist die Frage nach der Vergleichbarkeit der Längen- oder Gewichtswachstumskurven von Fischen verschiedener Arten und Bestände.

Es wird gezeigt, daß die Steigung am Wendepunkt (der maximale Gewichtzuwachs pro Zeit) einer Gewichtswachstumskurve mittelbar einen anschaulichen und aussagekräftigen Index für die Wachstumsleistung von Fischen liefert. Dieser Index, P genannt, hat nämlich für jede Art, Gattung und/ oder Ökologische Gruppe einen charakteristischen Wertebereich, der, unter Vorgabe eines Schätzwertes für das Endgewicht, dazu benutzt werden kann, den Wachstumsparameter K zu schätzen.

Dieses Verfahren, das besonders für die Schätzung der Wachstumsparameter tropischer Bestände geeignet erscheint, wird besonders durch die Verwendung eines sogenannten "Auximetrischen Netzes" erleichtert, das als neues grafisches Verfahren für die vergleichende Untersuchung der Wachstumsleistung von Fischen vorgestellt wird.

Die Abhängigkeit des Fischwachstums von der Sauerstoffversorgung wird diskutiert. Dabei erweist es sich, daß die Kiemenoberfläche - die ja die Höhe des O_2-Angebots bestimmt - in marinen Fischen eng mit dem Wachstumsindex P (s. oben) korreliert.

Eine mögliche limitierende Rolle der Kiemenoberflächen - d.h. der O_2 Versorgung - wird auch in Zusammenhang mit dem Individualwachstum von Fischen diskutiert. Dabei erweist es sich, daß die mit diesem Wachstum einhergehende Abnahme der Nahrungkonversion auf eine schlechter werdende O_2-Versorgung zurückgeführt werden kann, die ihre Ursache in einer wachstumsbedingten Abnahme der relativen Kiemenoberfläche $(\frac{\text{Kiemenoberfläche}}{\text{Körpergewicht}})$ hat.

Die Beziehung zwischen der mittleren Umwelttemperatur und den Wachstumsparametern von Fischen wurden untersucht. Anhand eines Datenmaterials, das 300 Einzelbestände umfaßt wird gezeigt, daß der Parameter K der von Bertalanffy Wachstumsformel, der obenerwähntem Katabolismus proportional ist, sich im Temperaturbereich 5° bis 30° C so ändert wie von der Krogh'schen Standardkurve (des Metabolismus) beschrieben.

Eine biochemische Deutung für diesen Befund kann darin gesehen werden, daß die Degradation von körpereigenem Eiweiß (Katabolismus, s. oben) in Abhängigkeit von der Temperatur erfolgt, und daß dieses Eiweiß, unter entsprechendem O_2-Verbrauch, laufend neusynthetisiert werden muß. Biochemische Arbeiten, die diese Deutung stützen, werden diskutiert.

Die enge Beziehung zwischen dem Parameter K und dem Sauerstoffverbrauch wurde auch bei den extrem niedrigen Temperaturen nachgewiesen, bei denen die sogenannte "cold adaptation" den Effekt hat, sowohl den O_2-Verbrauch als auch K zu erhöhen. Dies wird, ebenfalls gestützt auf biochemische Arbeiten, als die Wirkung einer "cold denaturation" von Körpereiweiß angesehen, d.h. auf die Tatsache zurückgeführt, daß sehr niedrige Temperaturen ($<3 - 4^\circ$ C) ebenso wie erhöhte Temperaturen zu einer Erhöhung der Rate führen, mit der Körpereiweiß abgebaut wird.

Die Beziehung zwischen K und der asymptotischen Länge (L_∞) in etwa 1 000 Beständen und etwa 130 Arten wurde quantitativ untersucht. Dabei erweist es sich, daß L_∞ (und entsprechend auch W_∞, das asymptotische Gewicht) sich in bestimmter Weise ändert, wenn sich K ändert. Dabei gilt:

$$\log K = a - 2/3 \log L_\infty^3 .$$

Diese Gleichung gilt allerdings in dieser Form nur bei Verwendung der speziellen VBGF (L_∞^3 kann hier auch durch W_∞ ersetzt werden).

Diese Beziehung kann - zusammen mit der zwischen K und der Temperatur fesgestellten Beziehung - dazu benützt werden, die Beziehung zwischen der mittleren Umwelttemperatur und der asymptotischen Länge (bzw. dem asymptotischen Gewicht) von Beständen quantitativ zu fassen. Dabei wird die allgemeine Erfahrung bestätigt, daß Warmwasserfische kleiner bleiben als ihre Artgenossen aus kälteren Gewässern, wobei wieder die Ausnahme gilt, daß unterhalb von $3 - 4^\circ$ C, kältere Temperaturen eine Erniedrigung der Endgröße zur Folge haben.

Andere Aspekte des Fischwachstums werden nur kurz gestreift, so das Wachstum von Larven und von luftatmenden Fischen, sowie die Rolle der Kiemen bei der Evolution der Fische.

Einige methodische Aspekte der vorliegenden Arbeit werden in der Diskussion behandelt. Dabei wird die Problematik der Verwendung von Fremddaten, und insbesondere die möglichen Fehlerquellen und die Notwendigkeit der Standardisierung dieser Daten diskutiert. Dabei wird die Ansicht vertreten, daß die Nachteile einer Verwendung von Fremddaten bei weitem durch die Vorteile dieser Arbeitsmethode wettgemacht werden.

Der Hauptvorteil der Methode, Fremddaten zu verwenden, wird vor allem darin gesehen, daß durch sie Zusammenhänge erkannt und belegt werden können, die ein einzelner Forscher, der nur mit eigenen Daten arbeiten würde, nur sehr schwer erkennen und belegen könnte.

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1. INTRODUCTION

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

Since the very onset of fishery biology as a science of its own - near the end of the nineteenth century - growth has ranked among the most investigated aspects of the biology of fishes, and a vast body of empirical data has been gathered (See bibliographies by Mohr, 1927, 1930 & 1934 for the earlier works).

Most of the data, however, pertain to fishes of temperate waters. Tropical fishes have received relatively little attention, one of the results being that our understanding of many aspects of the population dynamics of tropical fish stocks is, in many cases, too limited to allow for rational stock management (Pauly, 1978d). An attempt has been made, therefore, to give special emphasis to tropical fishes wherever the data appeared sufficient, and to concentrate on those aspects of growth which tropical and temperate fishes commonly share, such as to be able to apply to tropical fishes those general rules obtained from data pertaining to temperate fishes.

The main source of data for the present work is the "Compilation of Fish Length Growth Parameters" (Pauly, 1978a) which was completed for the purposes mentioned above. This compilation gives values for the parameters of the von Bertalanffy Growth Formula (VBGF) pertaining to more than 1500 different fish stocks, distributed in more than 500 different species, 300 genera and 100 families. About 2/3 of the growth parameter estimates included are original values that were estimated from "raw" growth data available in the literature, using various methods outlined in an introductory section of this compilation.

The data included pertain mainly to marine temperate fishes, although growth parameters for about 120 tropical species have been included. The data included in this compilation were used mainly to answer the question: How do fish grow? In the course of this compilatory work, however, a second question gradually emerged, which may be simply put as: Why do fish grow as they do? This question clearly could not be answered by piling up more and more growth parameters, but rather by shifting over to an investigation of some theoretical aspects of fish growth.

The present dissertation may be thus viewed as an attempt to check the validity of some theories of fish growth by means of the empirical data available, and 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.

In order to formulate these basic rules, it became necessary, however, to make some simplifying assumptions concerning the biology and ecology of fishes. Thus, for example, it was not possible to investigate here the effect of reproduction, migrations or seasonal variations of environmental temperature 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, *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. SETTING THE STAGE

2.1. 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. (Account taken from Bell, 1962, but see also D'Arcy Thompson, 1910).

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.

Nordenskiöld (1946, p. 162) writes:

> ... Upon this [...] Malpighi now bases a 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 trachaeae 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 alimental 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, it will be shown in the course of this work, are indeed key concepts for the understanding of fish growth processes.

The pioneers of age reading in fishes were 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 Graham, 1943).

In the decade which followed, aging techniques became more accurate and refined, and methods for the back-calculation of fish length as well as for the validation of aging techniques were developed (See review by Suvorov, 1959). As a result, a vast body of reliable 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 would describe fish growth, both in terms of length and weight, could be incorporated in yield models, and which would allow for inter- and intraspecific comparisons of the growth of different stocks, as well as 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 & Reed (1923), Richards (1959), or recently by Krüger (1964) have the disadvantage of being quite difficult to handle and to fit to 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 apparently erroneous (See Beverton & 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 fulfills all 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*, Band II, which will serve throughout the present work as the key to the theory developed by von Bertalanffy.

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

$$\frac{dw}{dt} = Hw^{n} - kw^{m} \qquad \ldots.1)$$

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 n and m at 2/3 and 1 respectively. This leads to what will be called here the *special* VBGF (it is called "special" because it represents a special case of the generalized VBGF; see below).

b) By allowing the value of n and m to take a wide range of values. This leads to what will be here called the *generalized* VBGF.

Beverton & 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. Ford (1933) and Walford (1946), working independently, proposed a method of estimating the parameters of the special VBGF ("Ford-Walford Plot"; see Ricker, 1958), superior to the one proposed by von Bertalanffy himself (von Bertalanffy, 1934) which required an independent estimate of asymptotic size.

Since these achievements, the special VBGF has completely dominated the field, and the estimation of its parameters has become a routine procedure applied to fish stocks all over the world (See Pauly, 1978a).

The first version of the generalized VBGF apparently goes back to Richards (1959). He, however, introduced his generalized 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).

The present study may be considered an attempt to demonstrate that the generalized VBGF does all the things which von Bertalanffy expected from the special version of his formula. In the course of this exercise, however, some ideas pertaining to fish growth will be presented which go well beyond a mere generalization of the VBGF. Indeed, the goal here is to demonstrate that the generalized VBGF best describes fish growth because it is an expression of the very biological interactions which make fish grow as they do.

2.2. A Working Definition 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). Negative growth will always be mentioned here as such, the tacit implication being that growth has a positive sign.

Growth, as defined here, relates *weight* (actually, mass) and *time*. *Growth data* are, therefore, such data which relate, directly or indirectly, to weight and time such that the growth process may be reconstructed from them. The results of tagging studies in Table I may serve as a first example of growth data in "differential form". Growth data are also weight-at-age data, or more generally, size-at-age data, expressing the size of a given fish or the mean size of the fishes of a given stock at a certain age ("integral form"). Table II gives an example of such data. It should be noted that, according to the definition, data on length-at-age are not growth data in the strict sense, as growth is a process involving body mass. On the other hand, wherever a linear

TABLE I

Tagging-Recapture Data on *Istiophorus platypterus* as an Example of Growth Data. Selected and adapted from Mather *et al*. [1974, Table 1-4].

Length at Tagging (cm)	Length at Recapture (cm)	Time at Large (months)	cm/Month
200	230	11.4	2.6
150	188	5.5	7.3
210	214	1.6	2.5
200	218	4.4	4.1
200	206	2.0	3.0
222	224	2.3	1.0
214	234	13.9	1.4
220	224	3.2	1.2
180	218	11.5	3.3
210	220	4.8	2.1
200	214	4.0	3.5
222	228	4.0	1.5

Note: The method of Gulland and Holt [1959] gives for these data: $L_\infty = 238$ and $K = 1.20$.

TABLE II

Size-at-Age of *Thunnus thynnus*, Based on Data of Sella [1929]

Age (y)	Length (cm)	Age (y)	Length (cm)
1	64	8	182
2	82	9	195
3	98	10	206
4	118	11	216
5	136	12	227
6	153	13	239
7	169	14	254

dimension remains in a reasonably constant relationship with body mass, it is quite obvious that length-at-age data, or in general, data involving change in length may also be used, the limitation being kept in mind, however, that growth in length is only an indirect expression of the underlying increase in body mass. In the present work, the word "size" will be used wherever weight or length may be used interchangeably to express the basic growth process.

On the other hand, problems of allometric "growth," where changes in body proportions are related to changes in overall size, are of concern here only insofar as the allometric "growth" of certain organs (e.g., of the gills) affects growth as defined above.

Finally, data pertaining to the maximum size reached by fishes in a given environment are considered as 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

$$Hw^n - kw^m = 0 \ , \qquad \ldots.2)$$

this consideration also applying to the largest size *ever* recorded for a given fish species, from any environment, any time (L_{ever}, W_{ever}).

2.3. 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, and a constant density equal to unity is assumed throughout.

All weights are expressed in gram (g) and always refer to round (ungutted) weight.

2) Length is expressed in centimeters (cm) and always as total length (LT) except in tuna and other large Scombroids where fork length (LF) is used. Further, weight is assumed to be proportional to the cube of length wherever not otherwise mentioned. Carlander (1968) has demonstrated that values of the length exponent widely differing from 3 (say, < 2.5 and > 3.5) are generally erroneous, and/or based on too limited a size range. The proportionality constant used for length weight conversion, called <u>c</u>ondition <u>f</u>actor (c.f.) is here

$$\text{c.f.} = \frac{w \cdot 100}{l^3} \qquad \ldots .3)$$

and is always based on LT, 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 auxilliary organs suited to breathing air (e.g., *Clarias* spp.) are expressly excluded from the general considerations presented here. (Questions pertaining to air-breathing fishes are briefly mentioned in Chapter 10, p. 129-130).

5) Except for Chapter 9, which concerns itself with some questions pertaining to the growth of fish larvae, only fish after metamorphosis are here considered.

6) Except for Chapter 6, in which questions pertaining to the phenomena of "cold adaptation" are discussed, the temperature range implied in all discussion on temperature refers to the range 5° to 30° C.

7) The following code is used for correlation coefficients (r,R):
   no asterisk: not significant
   one asterisk: significant ($\alpha = 0.05$)
   two asterisks: highly significant ($\alpha = 0.01$)

3. A BIOLOGICAL MODEL OF FISH GROWTH AND ITS MATHEMATICAL FORMULATION

3.1. 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 argument into a series of discrete, basic statements whose validity may then 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). (See Equation 1).

Statement 2. Growth ceases when catabolism is equal to anabolism. (See 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).

The logical consequence of statements 4 & 5 is that in fishes, anabolism is proportional to a surface. This statement, however, was apparently never formulated in any of von Bertalanffy's papers.

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 (Statements 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 "Abnützungsquote" (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" in the fish body. Part of the amino acids of the Amino-acid-Pool are "burned" (see Excretion I of Fig. 1) and the chemically bound energy so obtained is used for the synthesis of native protein, the building material being drawn from the Amino-acid-Pool. Simultaneously, with this process of synthesis there is a continuous degradation of the body's native proteins. (See discussion of K, p.115 ff).

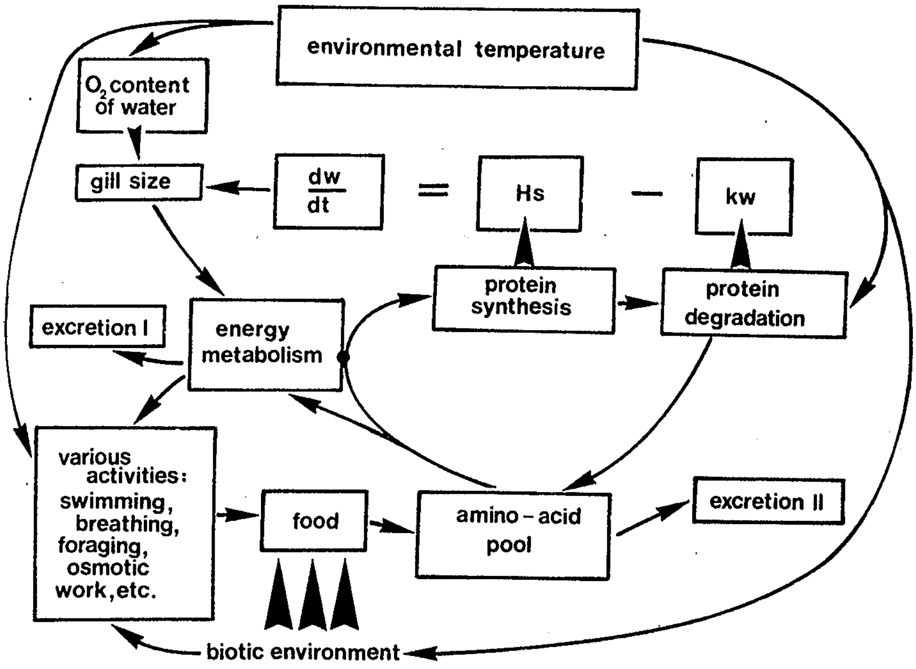


Fig. 1 Simplified model of fish growth, based mainly on V. Bertalanffy (1951).

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 Amino-acid-Pool (to which the degradation process itself partly contributes) and by the amount of oxygen available for the oxidation of the substances from the Amino-acid-Pool. A good oxygen supply will allow for the synthesis of a maximum amount of body substance from the Amino-acid-Pool; a bad oxygen supply will allow for only a limited rate of synthesis and a part of the Amino-acid-Pool spills over and "*is excreted by the gills and kidney as incompletely oxidized nitrogenous compound*" (latter point quoted from Webb, 1978, who cites the works of Forester & Goldstein, 1969, Savitz, 1969 and 1971, Olson & Fromm, 1971, and Niimi & Beamish, 1974) (Excretion II in Fig. 1).

A part of the available oxygen and protein is used for the formation of gonadal products which from a certain size on leave the body periodically.

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 size and the relative gill size $(= \frac{\text{gill size}}{\text{body weight}})$ 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, however, 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, growth becomes nil (at asymptotic size).

Webb (1978) indirectly confirms this point by stating that the magnitude of nitrogenous loss increases with *size*, being lower in actively growing, small fishes. The same concept may be expressed by computing growth conversion efficiency for fishes of different sizes ($\frac{\text{food intake}}{\text{growth increment}}$), such experiments always showing a decreased conversion efficiency with increasing size (Jones, 1976, Kinne, 1960, Gerking, 1971, Menzel, 1960). This point will be discussed in greater detail in Chapter 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 of von Bertalanffy's theory which, up to now, prevented a rational critique of von Bertalanffy's 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 of 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 even 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, wrote 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 & Holt (1957, p. 32) who write:

> Following general physiological concepts, von Bertalanffy suggests that the rate of anabolism could be assumed proportional to the 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 demonstrated that a physical surface does indeed limit anabolism, it will also be demonstrated that this surface is proportional to the second power of length in only a few cases. The point here is that von Bertalanffy limited the meaning of the word "surface" (German: Oberfläche) 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., the surface of the brain cortex in primates, or the gill surface of most fishes). Thus, the concept of a growth and metabolic type located "between surface and weight proportionality" is a misnomer, as we may still have, in this growth and metabolic type, a surface proportionality.

Misunderstanding III. This is 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-oxydative 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 tertiary and quarternary structure and be hydrolized down to their component amino-acids without having to be coupled with any energy-providing exergonic reaction, and without any oxygen being used in the process.

Phase II (Oxydative phase). The reactions occurring here have the following features in common:

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 H_2O, CO_2 and NH_3, and a large amount of ATP has been obtained which may then 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 "preoxydative" 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.

As soon as these proteins are hydrolized, they become part of the "amino-acid pool" (See Fig. 1) together with amino-acids obtained from the resorption of food, and may become part of what von Bertalanffy calls "Betriebstoffwechsel" (energy metabolism). On the other hand, energy metabolism is limited both by the supply of amino-acid to be oxydized as well as by the oxygen supply, the latter being proportional to a power of weight markedly smaller than unity. That is, the second phase of catabolism cannot be weight proportional.

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. 129ff). 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.

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, 1978, Andersen and Ursin, 1977, Sperber *et al.*, 1977).

What is actually overlooked by Ursin (1967) is that the first phase of the catabolic process, where no oxygen is needed (e.g., in the case of protein denaturation), 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. This is exactly what von Bertalanffy meant when restating Pütter's basic equation. Thus, Equation 1 (p. 7) 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 represents a "growth-inhibiting, mass-proportional factor" as formulated by von Bertalanffy (1938).

A detailed discussion of the character and properties of the growth inhibiting factor k is given in Chapter 9.

3.2. The Generalized von Bertalanffy Growth Formula: Integration and Properties

As mentioned in Chapter 2, 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

$$\frac{dw}{dt} = Hw^{n} - kw^{m} \qquad \ldots .1)$$

may be rewritten

$$\frac{dw}{dt} = Hw^{2/3} - kw \qquad \ldots .4)$$

when n 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

$$W_t = W_\infty (1 - e^{-K(t-t_o)})^3 \qquad \ldots.5)$$

and for length growth,

$$L_t = L_\infty (1 - e^{-K(t-t_o)}) \qquad \ldots.6)$$

where W_t and L_t are the size at age t, W_∞ and L_∞ express the asymptotic size, while K and t_o are constants whose properties will be discussed in Chapter 9. (See Beverton & Holt, 1957, for the integration and Hohendorf, 1966, for a discussion of some properties of the special VBGF.)

In the course of the present investigation, however, it will be demonstrated that the definition $n \doteq 2/3$ applies very rarely in fishes, for which reason n should be allowed to take values $\neq 2/3$. Richards (1959) and Taylor (1962) have relaxed both definitions ($n \doteq 2/3$ *and* $m \doteq 1$), but considered cases pertaining to growth in length only.

A generalized version of the VBGF pertaining to growth in weight is presented here. The integration of the basic equation (1) and some further points in the discussion of the properties of the generalized VBGF have been kindly formulated for this author by Cand. rer. nat. D. Reimers, Kiel University, Department of Experimental Physics.

The rate of growth of a fish is described by

$$\frac{dw}{dt} = Hs - kw \qquad \ldots.7)$$

where H•s expresses the rate of build-up of body substance (anabolism) and k•w the rate of breakdown of body substance (catabolism).

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

$$s = p \cdot l^{a} \qquad \text{....8a)}$$

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

Catabolism, 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

$$w = q \cdot l^{b} \qquad \text{....8b)}$$

where l is the fish length; q is a proportionality constant; and b is a power whose range of possible values is discussed elsewhere, the sole restriction here being that $b > a$.

From Equation 8b, length may be expressed in terms of weight by

$$l = \left(\frac{w}{q}\right)^{\frac{1}{b}} \qquad \text{....9)}$$

from which it follows that

$$s = p \cdot \left(\frac{w}{q}\right)^{\frac{a}{b}} = \frac{p}{q^{\frac{a}{b}}} \cdot w^{\frac{a}{b}} \qquad \text{....10)}$$

The new expression for s is substituted into Equation 7 which results in:

$$\frac{dw}{dt} = \frac{Hp}{q^{\frac{a}{b}}} \cdot W^{\frac{a}{b}} - kw \qquad \text{....11)}$$

Defining

$$E \doteq \frac{Hp}{q^{\frac{a}{b}}} \qquad \text{....12a)}$$

and

$$K \doteq \frac{k}{3} \qquad \text{....12b)}$$

and inserting into Equation 11, results in:

$$\frac{dw}{dt} = E\cdot w^{\frac{a}{b}} - 3Kw \qquad \ldots.13)$$

Rearranging gives,

$$\frac{dw}{dt} + 3Kw - Ew^{\frac{a}{b}} = 0 \qquad \ldots.14)$$

Defining

$$u \doteq w^{1-\frac{a}{b}} \doteq w^{\frac{D}{b}} \qquad \ldots.15)$$

and substituting into Equation 14 gives

$$\frac{du}{dt} + \frac{D}{b}3Ku - \frac{D}{b}E = 0 \qquad \ldots.16)$$

or

$$\frac{du}{dt} = \frac{D}{b}E - \frac{D}{b}\cdot 3Ku \qquad \ldots.17)$$

that is,

$$dt = \frac{b}{D}\cdot\frac{du}{E-3Ku} \qquad \ldots.18)$$

which integrated gives,

$$\int_{t_o}^{t} dt = \frac{b}{D}\int_{u_o}^{u_t}\frac{1}{E-Ku}\,du = t - t_o \qquad \ldots.19)$$

or, estimated

$$\frac{b}{D}\left(\frac{1}{-3K}\right)\cdot\ln(E-3Ku)\Big|_{u_o}^{u_t} + c = t - t_o \qquad \ldots.20)$$

hence,

$$\ln(E-3Ku)\Big|_{u_o}^{u_t} - \frac{3DK}{b}\cdot c = -\frac{3DK}{b}(t - t_o) \qquad \ldots.21)$$

when

$$t \to o \Leftrightarrow u_t \to u_o \qquad \ldots.22)$$

we have $-\frac{3D\cdot K}{b}\cdot c = +\frac{3D\cdot K}{b}\cdot t_o$ $\qquad \ldots.23)$

which gives $c = -t_o$ $\qquad \ldots.24)$

Substituting for c in Equation 21, we obtain

$$\ln\left(\frac{E - 3K\cdot W_t^{\frac{D}{b}}}{E - 3K\cdot W_o^{\frac{D}{b}}}\right) + \frac{3DK}{b}\, t_o = -\frac{3DK}{b}(t - t_o) \qquad ....25)$$

or

$$\ln\left(\frac{E - 3K\cdot W_t^{\frac{D}{b}}}{E - 3K\cdot W_o^{\frac{D}{b}}}\right) = \frac{-3DK}{b}\, t \qquad ....26)$$

which gives

$$3K\cdot W_t^{\frac{D}{b}} = (-E + 3K\cdot W_o^{\frac{D}{b}})\cdot e^{-\frac{3DK}{b}t} + E \qquad ....27)$$

and

$$W_t^{\frac{D}{b}} = \frac{E}{3K} - (\frac{E}{3K} - W_o^{\frac{D}{b}})\cdot e^{\frac{-3D}{b}Kt} \qquad ....28)$$

Now, when t → ∞, we have

$$W_t^{\frac{D}{b}} \rightarrow W_\infty^{\frac{D}{b}} = \frac{E}{3K} \qquad ....29)$$

and by substitution into Equation 28,

$$W_t^{\frac{D}{b}} = W_\infty^{\frac{D}{b}} - (W_\infty^{\frac{D}{b}} - W_o^{\frac{D}{b}})\cdot e^{\frac{-3DK}{b}t} \qquad ....30)$$

Defining

$$t = t_o \Leftrightarrow W_t = 0 \qquad ....31)$$

and inserting into Equation 30 gives

$$W_\infty^{\frac{D}{b}} - (W_\infty^{\frac{D}{b}} - W_o^{\frac{D}{b}})\cdot e^{\frac{-3DK}{b}t_o} = 0 \qquad ....32)$$

and

$$W_o^{\frac{D}{b}} = W_\infty^{\frac{D}{b}}(1 - e^{\frac{+3DK}{b}t_o}) \qquad ....33)$$

which combined with Equation 30 gives

$$W_t^{\frac{D}{b}} = W_\infty^{\frac{D}{b}} - [W_\infty^{\frac{D}{b}} - W_\infty^{\frac{D}{b}}(1 - e^{\frac{+3DK}{b}t_o})]\cdot e^{\frac{-3DK}{b}t} \qquad ....34)$$

and

$$W_t^{\frac{D}{b}} = W_\infty^{\frac{D}{b}} - W_\infty^{\frac{D}{b}} \cdot e^{-\frac{3DK}{b}(t-t_o)} \qquad ....35)$$

This, rearranged, gives

$$W_t^{\frac{D}{b}} = W_\infty^{\frac{D}{b}}(1 - e^{-\frac{3D}{b}\cdot K(t-t_o)}) \qquad ....36)$$

or, in a form easier to handle

$$W_t = W_\infty(1 - e^{-\frac{3D}{b}\cdot K(t-t_o)})^{\frac{b}{D}} \qquad ....37)$$

Equation 37 is the generalized VBGF for weight growth.

The definition of D in Equation 15 implies that

$$D \doteqdot b - a \qquad ....38)$$

from which it becomes immediately obvious that the generalized VBGF reduces to the special VBGF when both limiting surface and body weight increase isometrically as length increases.

That is,

$$W_t = W_\infty(1 - e^{-K(t - t_o)})^3 \qquad ....5)$$

when a = 2 and b = 3.

The first derivative of the generalized VBGF (Equation 37) is

$$\frac{dw}{dt} = W_\infty^{\frac{b}{D}}(1 - e^{-\frac{3D}{b}K(t- t_o)})^{\frac{b}{D}-1} \cdot \frac{3D}{b}K \cdot e^{-\frac{3D}{b}K(t - t_o)} \qquad ....39)$$

or

$$\frac{dw}{dt} = W_\infty 3K(1 - e^{-\frac{3D}{b}K(t- t_o)})^{\frac{b}{D}-1} \cdot e^{-\frac{3D}{b}K(t- t_o)} \qquad ....40)$$

We have, on the other hand, the identities (from Equation 36)

$$1 - e^{-\frac{3D}{b}K(t- t_o)} = (\frac{W_t}{W_\infty})^{\frac{D}{b}} \qquad ....41a)$$

and

$$e^{-\frac{3D}{b}K(t- t_o)} = \frac{W_\infty^{\frac{D}{b}} - W_t^{\frac{D}{b}}}{W_\infty^{\frac{D}{b}}} \qquad ....41b)$$

Equations 41a and 41b may be substituted into Equation 40 such that

$$\frac{dw}{dt} = 3KW_\infty \left(\frac{W_t}{W_\infty}\right)^{\frac{D}{b}\left(\frac{b}{D} - 1\right)} \cdot \frac{W_\infty^{\frac{D}{b}} - W_t^{\frac{D}{b}}}{W_\infty^{\frac{D}{b}}} \qquad \text{....42)}$$

$$\frac{dw}{dt} = 3KW_\infty \left(\frac{W_t}{W_\infty}\right)^{1 - \frac{D}{b}} \cdot \frac{W_\infty^{\frac{D}{b}} - W_t^{\frac{D}{b}}}{W_\infty^{\frac{D}{b}}} \qquad \text{....43)}$$

$$\frac{dw}{dt} = 3KW_t^{1 - \frac{D}{b}} \cdot \left(W_\infty^{\frac{D}{b}} - W_t^{\frac{D}{b}}\right) \qquad \text{....44)}$$

$$\frac{dw}{dt} = 3KW_t\left[\left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}} - 1\right] \qquad \text{....45)}$$

which reduces to

$$\frac{dw}{dt} = 3KW_t\left[\left(\frac{W_\infty}{W_t}\right)^{\frac{1}{3}} - 1\right] \qquad \text{....46)}$$

when a = 2 and b = 3.

To obtain the coordinates of the point of inflexion $(w_i ; t_i)$, the second derivative of the generalized VBGF is needed:

$$\frac{d^2w}{dt^2} = 3K\left[\left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}} - 1\right] + 3KW_t\left[-\frac{D}{b} \cdot \frac{1}{w_t} \left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}}\right] \qquad \text{....47)}$$

$$\frac{d^2w}{dt^2} = 3K\left[\left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}} - 1 - \frac{D}{b} \cdot \left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}}\right] \qquad \text{....48)}$$

$$\frac{d^2w}{dt^2} = 3K\left[\left(1 - \frac{D}{b}\right)\left(\frac{W_\infty}{W_t}\right)^{\frac{D}{b}} - 1\right] \qquad \text{....49)}$$

Setting Equation 48 to zero, and $w_t = w_i$, it follows that

$$\left(\frac{W_\infty}{W_i}\right)^{\frac{D}{b}} = \frac{b}{b-D} \qquad \ldots.50)$$

or

$$\frac{W_\infty}{W_i} = \left(\frac{b}{b-D}\right)^{\frac{b}{D}} \qquad \ldots.51)$$

Thus, it follows that

$$W_i = \left(\frac{b}{b-D}\right)^{-\frac{b}{D}} \cdot W_\infty = \left(\frac{b-D}{b}\right)^{\frac{b}{D}} \cdot W_\infty \qquad \ldots.52)$$

Rearranged, Equation 45 gives, for $W_t = W_i$

$$\frac{dW_i}{dt} = 3K[W_\infty^{\frac{D}{b}} \cdot W_i^{1-\frac{D}{b}} - W_i] \qquad \ldots.53)$$

Substituting Equation 52 into Equation 53 gives

$$\frac{dW_i}{dt} = 3K[W_\infty^{\frac{D}{b}} \cdot \left(\left(\frac{b-D}{b}\right)^{\frac{b}{D}} W_\infty\right)^{1-\frac{D}{b}} - \left(\frac{b-D}{b}\right)^{\frac{b}{D}} W_\infty] \qquad \ldots.54)$$

$$\frac{dW_i}{dt} = 3K[\left(\frac{b-D}{D}\right)^{\frac{b}{D}(1-\frac{D}{b})} \cdot W_\infty - \left(\frac{b-D}{b}\right)^{\frac{b}{D}} \cdot W_\infty] \qquad \ldots.55)$$

$$\frac{dW_i}{dt} = 3KW_\infty[\left(\frac{b-D}{b}\right)^{\frac{b}{D}-1} - \left(\frac{b-D}{b}\right)^{\frac{b}{D}}] \qquad \ldots.56)$$

and finally,

$$\frac{dW_i}{dt} = 3KW_\infty \cdot \frac{D}{b}\left(1-\frac{D}{b}\right)^{\frac{b}{D}-1} \qquad \ldots.57)$$

which gives the slope of the growth curve at the point of inflexion. It will be noted that Equation 57 reduces to

$$\frac{dW_i}{dt} = 3KW_\infty \frac{1}{3}\left(1-\frac{1}{3}\right)^2 = KW_\infty \cdot \frac{4}{9} \qquad \ldots.58)$$

when a = 2 and b = 3.

Equation 51 may be rearranged to

$$\frac{W_i}{W_\infty} = (1 - \frac{D}{b})^{\frac{b}{D}} \qquad ....59)$$

from which, when a=2 and b=3, it follows that

$$W_i = 0.2963 \cdot W_\infty \qquad ....60)$$

The integration of the generalized VBGF as related to length is essentially the same as for growth weight (See Taylor, 1962).

The generalized VBGF for length has the form

$$L_t^D = L_\infty^D(1 - e^{-KD(t - t_o)}) \qquad ....61)$$

or

$$L_t = L_\infty(1 - e^{-KD(t - t_o)})^{\frac{1}{D}} \qquad ....62)$$

all symbols being the same as in Equation 6 and with $D = (b - a)$.

An interesting property of Equation 62 is the presence of an inflexion point (i) when $D < 1$, where

$$t_i = t_o - \frac{\ln \cdot D}{KD} \qquad ....63)$$

Thus, t_i moves toward t_o when D increases toward 1.

3.3. Fitting and Applications 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 values. (Similarly, values of $\sqrt[3]{W_t}^D$ may be used instead of $\sqrt[3]{W_t}$ when fitting the generalized VBGF to weight-at-age data.)

As demonstrated by Taylor (1962), 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

$$L_{(t+1)}^{D} = a + b\,L_{t}^{D} \qquad \ldots.64)$$

where

$$L_{\infty} = \left(\frac{a}{1-b}\right)^{\frac{1}{D}} \qquad \ldots.65)$$

and

$$K = \frac{-\ln b}{D} \qquad \ldots.66)$$

(A simple method is given later for the estimation of D).

The paper of Taylor (1962), however, contains several inconsistencies which were either left, or subsequently introduced into his posthumously edited manuscript. Thus, in his examples of fitting the generalized VBGF to length-at-age data in *Salmo gairdneri*, *Acipenser fulvescens* and *Salvelinus alpinus*, the value of K was estimated without taking D into account, which in all three cases resulted in erroneous values of K(as well as in erroneous estimates of t_i and $A_{0.95}$, see Taylor, 1962).

Taylor (1962) used data on the length growth of *Salvenilus alpinus*, published by Grainger (1953) to demonstrate the existence of an inflexion point in the length growth curve of fishes. These data, however, pertain to an anadromous fish which spends the first five to seven years of its life in rivers where its growth is very slow (Grainger, 1953, Moore & Moore, 1974), and which then begins to undertake annual seaward migrations, spending each summer in sea water and overwintering in fresh water (Moore & Moore, 1974). That is, from the age of about six years on, *S. alpinus* spends each growing season in sea water. The inflexion point in the length growth curves published by Grainger (1953) and Moore & Moore (1974) quite clearly reflects the transition of 5 to 7 years old *S. alpinus* into a medium which, in salmonids, tends to promote growth (see Klein, 1974), rather than the inflexion point caused by a value of $D < 1$.

In general, the VBGF, both in its special and generalized versions cannot be fitted to those diadromous fishes which alter their whole physiological set-up as they pass from one medium to another, or to those fishes whose food and feeding habits change markedly in the course of their life.

4. THE CONCEPT OF THE PHYSIOLOGICALLY LIMITING SURFACE

4.1. Preliminary Identification of the "Physiologically Effective Surface"

As pointed out in Chapter 3, the anabolism of fishes is, according to von Bertalanffy, limited by some physiological surface. The present chapter presents indirect evidence which should help in the identification of this surface.

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. Evidence is not available to this author which could help determine if an internal surface is or is not limiting for anabolism.

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.

He apparently assumed that such internal surfaces are the ones that are limiting anabolism and therefore stated that "these surfaces are, in part, at least undetermined or undeterminate."

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 & 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* to be $2.12 \cdot W^{0.57}$ (cm^2, 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* (See Table III). Thus, there is evidence, at least for these species, that the gut surface of fish may grow in proportion to a power of weight << 1. On the other hand, for the concept of 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 Ricker,1958).

TABLE III

Relationship Between Weight and Gut Surface in Two Species of Fish

Rutilus rutilus		*Gobio gobio*	
weight (g)	gut surface (cm^2)	weight	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 weight and y = log gut surface

Source of data: Harder [1964, Table 6]

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 ($= \frac{\text{gut length}}{\text{fish length}}$)

- hence relative absorptive area - is in fishes apparently 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 moderate growth performance (See Table XVIII 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 (See 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, after a thorough review of the pertinent literature, states 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 O_2, which is best illustrated by the fact that all fish die within a short period of time when kept in anoxic water.

The fact that fishes breathe continuously makes it indeed very likely that it is the gill surface which limits anabolism in fishes. 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

$$Q = \frac{dP \cdot U \cdot A}{WBD} \qquad ....67)$$

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 mm^2 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 & Dekkers, 1975).

Of the four parameters which determine the value of Q, only A may be assumed to vary greatly 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 & Dekkers, 1975).

4) The power of weight in proportion to which the gills of an "average" fish grow is about 0.8, that is, the very power which in "average" fishes links energy metabolism and weight. (Winberg, 1960, De Jager & Dekkers, 1975).

5) There is very little oxygen dissolved even in the best aerated water - say, as compared with the O_2 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.

Table IV, taken from Schumann & Piiper (1966), shows the enormous difference between breathing air and breathing water.

TABLE IV

Comparison of Water and Air as Breathing Media¹⁾

Property	Water	Air	Water/Air
O_2-Content	6.2 ml O_2/liter	188 ml O_2/liter	1/30
Viscosity	1.000 Centipoise	0.018 Centipoise	55/1
Density	1.000 $\frac{g}{cm^3}$	0.00119 $\frac{g}{cm^3}$	850/1
Diffusion constant 2)	$3.4 \cdot 10^{-5}$	11	≈1/300000

1) Table taken from Schumann & Piiper (1966)
2) The diffusion constant corresponds to the constant U of Equation 67, but has here the dimension $\frac{ml/min}{cm^2 \cdot atm/cm}$.

In comparison with land animals, fishes - and all other aquatic animals for that matter - must extract the oxygen they need from a medium 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! It is not surprising, then, that a large proportion of the metabolic energy of fish should go to breathing, itself.

Schumann & Piiper (1966) found, for example, that the tench *Tinca tinca* uses about one-third of its standard energy metabolism to cover its breathing activities (range: 18-44%) as compared with a value of about 2% in man.

6) Having large gills exposes the fish to a series of problems, the most important of which are briefly 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 large, active fishes, this resistance can be overcome only by constant swimming with more or less open mouth (ram-jet ventilation).

   b) Very large gills require modification of the whole head and anterior part of the body and favour a 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 & 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 close in-shore and 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 "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 & 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 well perfused with blood and usually well oxygenated, and hence the environment is very favorable from this point of view." (Hughes & 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.

4.2. The Allometric Growth of Gills

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

$$G = a \cdot w^{d_G} \qquad \ldots .68)$$

where G is the gill area, w is the fish weight, d_G is an exponent with values ranging between 2/3 and 0.95, and a is a species specific constant, here called Gill Size Index (GSI). When w is expressed in g, and G in cm^2, a (the GSI) is the gill area in cm^2 of a fish weighing 1 g.

It should be noted that Equation 68 has the same form as the following equation which, in fishes, relates O_2 consumption and weight:

$$Q = a \cdot w^{d_Q} \qquad \ldots.69)$$

where Q is the O_2 consumption, w is the fish weight, d_Q is an exponent generally ranging between 2/3 and 0.95, and a is a species specific constant whose value, 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 & 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 [A_{200} and M_{200} of De Jager & Dekkers, 1975]. (See also 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, even suggesting values of d substantially lower than 2/3 and higher than 0.95, up to unity and above.

It appears, however, that most of these extreme values are based upon either erroneous methods in the estimation of gill size (See De Jager & Dekkers, 1975, for a list and critique of several papers giving such estimates) or erroneous methods in respiration studies (See Winberg, 1960, for a

TABLE V Some Values of the Power of Body Weight in Proportion to which the Gill Surface of Fish Increases (d). Based on Gill Surface or Respiratory Studies.

No.	Taxon	Value of d	Gill(G) or Respir.(R)	Author(s)	Original Data in	Remarks*	Weight**(g)
1	Tilapia mossambica	0.83	R	Job, 1963	Same	mean of two extreme values of d	10^3
2	Tilapia zillii	0.82	R	Schulze-Wiehenbrauck, 1977	Same	----	10^3
3	Tinca tinca	0.79	R	Winberg, 1960	Various authors	p. 87	10^3
4	" "	0.67	G	DeJager & Dekker, 1975	Various authors	Table II, p. 283	10^3
5	Carassius auratus	0.81	R	Winberg, 1960	Various authors	p. 82	10^3
6	" "	0.68	G	Original	Solewski, 1957	from Fig. 8 in Czolaska, 1965	10^3
7	Cyprinus carpio	0.72	G	Original	Solewski, 1957	" " " " " "	10^4
8	" "	0.85	R	Winberg, 1960	Various authors	p. 83	10^4
9	Abramis brama	0.89	R	Winberg, 1961	Kusnetzova, 1956	p. 3	10^4
10	Rutilus rutilus	0.84	G	Original	Landolt & Hill, 1975	d value recalculated from authors' data	10^3
11	Cyprinidae	0.82	R	Winberg, 1960	Various authors	p. 105	10^3
12	Micropterus dolomieu	0.78	G	Muir, 1969	Price, 1931	classic study, d value highly reliable	10^3
13	Trematomus bernachii	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	Scyllium spp.	0.80	R	Winberg, 1960	Buytendijk, 1910	----	10^4
16	Opsanus tau	0.78	G	Hughes & Gray, 1972	Same	d value *reported as 0.79 in DeJager & Dekker, 1975*	10^3
17	Coregonus spp.	0.77	R	Winberg, 1961	Various authors	----	10^3
18	Salmonidae	0.81	R	Winberg, 1960	Various authors	11 species	10^4
19	Gadus morhua	0.82	R	Edward et al., 1972	Same	----	10^4
20	" "	0.79	R	Saunders, 1963	Same	starved fish	10^4
21	" "	0.87	R	Saunders, 1963	Same	fed fish	10^4
22	Lebistes reticulatus	0.67	R	v. Bertalanffy, 1951	Same	v. Bertalanffy's confirmation of 2/3 rule	10^0
23	Gambusia affinis	0.63	R	Winberg, 1960	Maksudov, 1940	p. 90, d *probably not significantly* $\neq$ 0.67	10^0
24	Cyprinodontidae	0.73	R	Winberg, 1961	Various authors	p. 2	10^0
25	Thunnus thynnus	0.90	G	Muir, 1969	Muir & Hughes, 1969	----	10^6
26	Katsuwonus pelamis	0.85	G	Muir, 1969	Muir & Hughes, 1969	----	10^5
27	Thunnus albacares	0.90	G	Muir, 1969	Muir & 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* teleosteans)	0.82	G	Ursin, 1967	Gray, 1954	See Ursin 1967, p. 2450 for fishes included in plot	
	Fishes	0.82	R&G	DeJager & Dekker, 1975	Various authors	most recent literature review on gill size and respiration in fishes	

* Page number refers to original publication.

** 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.

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 discussed away are provided by the tuna, with values of d_Q ranging up to 0.90 (Muir, 1969) and by the Cyprinodonts, with values of d_Q equal to 2/3 (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 in fishes can be simply expressed as a function of size. A compilation of literature values of d was undertaken for this purpose (Table V). The data gathered are very heterogeneous in quality. Values which seemed suspect have been listed as such (Table VI) and are not used for further calculations. The size to which the values of d are related refer to asymptotic weight as estimated from data in Pauly (1978a). In order to prevent bias, these preliminary estimates of asymptotic weight were rounded off to the nearest whole power of 10; the logarithm was then taken. Thus, the fish are assumed to have weights of 10^0, 10^1, 10^2, 10^3, 10^4, 10^5 or 10^6 gram (See Table V and Fig. 2).

The correlation between the values of d and the logarithm of the weight indices is, with 20 dF, highly significant ($r = 0.830^{**}$) and may be expressed by the regression

$$d = 0.6742 + 0.03574 \log W_\infty \qquad \ldots.70)$$

which may be used to estimate d from estimates of asymptotic size.

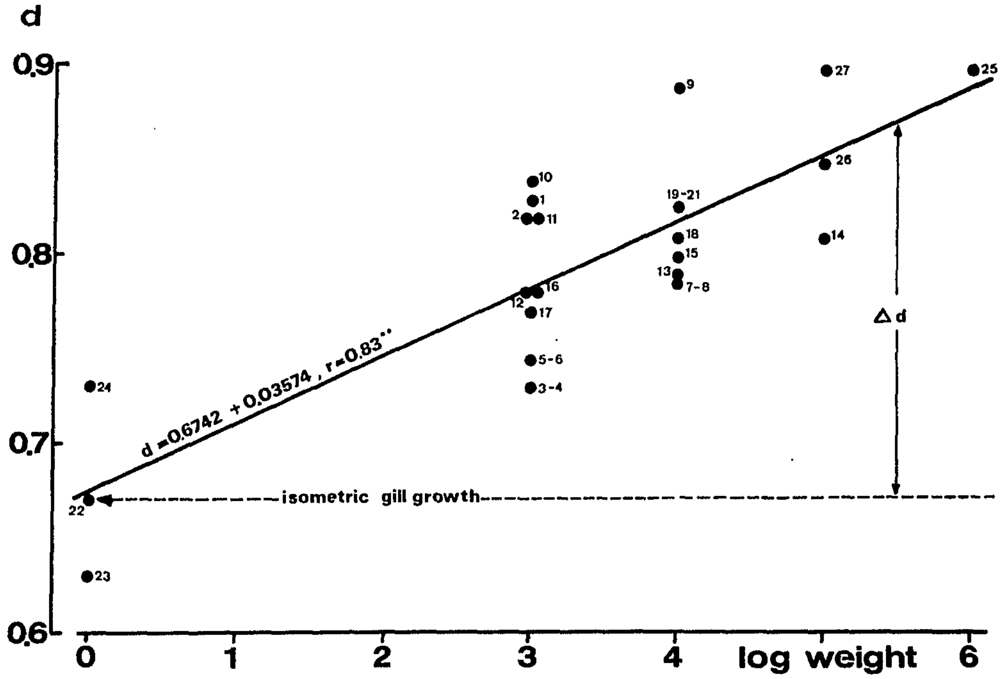


Fig. 2 Plot of the power of weight in proportion to which fish gills grow (d) on the logarithm of the maximum weight (in g) reached by each species. See also Table V.

A first interpretation from this result is that the gills of most fish grow allometrically with a value of d > 2/3, the exceptions being the Cyprinidontidae and probably all other tiny fishes measuring only a few centimeters and weighing less than or little above one gram.

The gills of all other fishes 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 hitherto investigated fish happen to have an asymptotic weight 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, which corresponds to a weight of about 60 tons when using the condition factor of 0.77 suggested by length/weight

TABLE VI

Values of d (Power relating Weight to Gill Surface) thought to be Unreliable and therefore not included in Table V.

Taxon Taxon	d	Gill(G) or Resp.(R)	Author	Original Data	Remarks
Rhagophila dearboni	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.
Coregonus sardinella	0.89	R	Wohlschlag (1957)	Same	Value widely differs from value of d = 0.77 for *Coregonus* Spp in Table V.
Zoarces viviparus	0.98	G	Ursin (1967)	Wiedeman Smith	Value of d contradicts Ursin's own estimate of d for "Gray's intermediate" (see Table V). 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 *Lebistes reticulatus* only.

measurements on this fish (Angel, undated). The weight of 60 tons, when inserted into Equation 70, suggest a value of d = 0.95 which may correspond to the highest possible d value in fishes.

5. COMPARING FISH GROWTH PERFORMANCE

5.1. Comparing the Growth Performance of Different Fishes: The Problem

Since the first systematic studies on the growth of fishes, attempts have been made for both inter- and intra-specific comparison of the growth performance. The compilation by D'Ancona (1937) of length-at-age data on the growth of Mediterranean fishes represents an early attempt to compare the growth of different fishes within the Mediterranean, and to compare Mediterranean fishes with North Atlantic fishes. This compilation was later expanded by Bougis (1952), who used the same method of comparing sets of length-at-age data.

Berg *et al.* (1949) and Nikolsky (1957) similarly compiled size-at-age data of fishes from Soviet waters, while Carlander (1950, 1953 and 1968) compiled a vast body of size-at-age data of fresh-water fishes of the North American continent.

The aforementioned compilations fail, however, to explain why certain fish, in a given environment, grow as they do. The main reason for this failure is most likely that an objective standard for measuring growth performance was lacking. It should be obvious, for example, that simply comparing size-at-age data (or the growth curves derived from them) cannot help in determining which of the tuna or the guppy grows fastest. Tuna may have higher growth rate ($\frac{dw}{dt}$) than guppy, still it is the latter which completes its life cycle first and which therefore may be considered to have grown "fastest." This problem persists when fishes of the same species kept grown under different conditions are compared for their growth performances. Thus, for example, Kinne (1960) writes:

> The results indicate that the differences in growth rate established in young fish do not persist throughout life. Initially slow-growing fishes may surpass initially fast-growing fishes, and finally reach a greater length-at-age.

This quote may indicate the extent of the problem discussed here.

Various authors (Beverton & Holt, 1959, Hohendorf, 1966, Mitani, 1970, Banerjii & Krishnan, 1973, and especially Mio, 1965) have attempted to compare the growth performance of various fishes by comparing their value of L_∞ and K, or the values of the slope and intercept of the corresponding Ford-Walford plots. However, no good index of overall growth performance has emerged because comparing L_∞ and K, or the parameter values of Ford-Walford plots amounts in principle to the same as comparing the growth curves themselves, and the same problems arise as discussed above.

From the statement of problems which have been discussed, the following set of basic requirements may be formulated which should be met by any good index of overall growth performance:

1) It should relate to weight growth, not to length growth;

2) It should consist of a single value;

3) It should be easy to compute;

4) It should be applicable to any fish; and

5) It should be biologically interpretable.

5.2. The Index of Growth Performance, P

The growth rate in weight $(\frac{dw}{dt})$, or slope of the weight growth curve, has in all fishes a maximum, $[(\frac{dw}{dt})_{max}]$, whether $\frac{dw}{dt}$ is plotted against age or against size. Weight growth curves have one, and only one, maximum value of growth rate.

It is therefore proposed that the growth rate at the point of inflexion of a weight growth curve be used as the standard for the comparison of the growth performance of different fishes, because it fulfills all the requirements listed above.

When using $(\frac{dw}{dt})_{max}$ as an index of growth performance, the problems discussed earlier are circumvented, as the growth performance at an objectively defined point of the weight growth curve is used as reference.

In a weight growth curve, the slope at the inflexion point is given by

$$(\frac{dw}{dt})_{max} = \frac{4}{9} \cdot K \cdot W_\infty \qquad \ldots.71)$$

when the weight growth curve is adequately described by the special VBGF (See Hohendorf, 1966, and Chapter 2 for derivations).

The slope at the inflexion point may also be expressed by

$$(\frac{dw}{dt})_{max} = \frac{4}{9} \cdot 10^{P} \qquad \ldots.72)$$

where $P = \log(K \cdot W_\infty) = \log K + \log W_\infty$. As discussed earlier, the growth curves of different fishes cannot be directly compared because the curves themselves are produced by growth rates which change constantly with time and size. The value of P, however, is directly related to $(\frac{dw}{dt})_{max}$, which can be used as an objective standard for comparing different growth performances. Different fishes with the same value of P will thus have the same value of $(\frac{dw}{dt})_{max}$ irrespective of their values of W_∞ or K. The value of P can therefore be used to compare the growth performance of fishes with different values of asymptotic size.

5.3. The Auximetric Grid

The character of the new index P may be best demonstrated by transposition into a special graph, here called *auximetric grid* (from the Greek auxein - to grow). The absissa scale of an auximetric grid consists of values of log W_∞ (in g), while the ordinate scale consists of values of log K (1/year), with the range covered by both scales chosen such that average sized commercial fishes appear near the center of the grid. Also, lines connecting some P values are drawn at regular intervals of P, and a base line selected (at $P = 0$). On such a grid, the distance from a point representing a pair of growth parameters (W_∞, K) to the baseline represents P and is therefore a direct indication of growth performance (See Fig. 3 for a first example). Values of K, W_∞ and P for fresh water fishes are given in Table VII which, when plotted into an auximetric grid (Fig. 4), allow for a preliminary estimate of that area of the grid occupied by fresh water fishes. The same procedure, when applied to data on marine fishes (Table

area covered by the marine

covered by the fresh water fishes, and the

is much wider (-0.70 to 5.79 for marine fishes as compa

to -0.30 to 3.98 for fresh water fishes). Also remarkable is the feature that marine fishes may have much higher values of K than fresh water fishes for the same value of W_∞, but that the lowest values of K for a given W_∞ are about the same in marine and fresh water fishes.

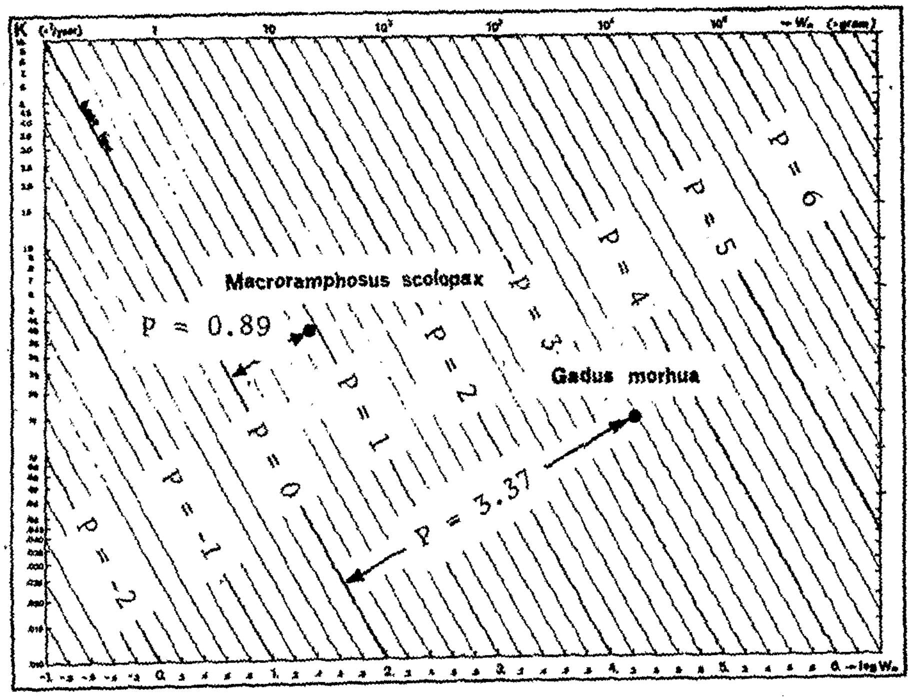


Fig. 3 Auximetric grid: demonstrating the concept of P. (See text).

The auximetric grid also allows for the separation and definition of taxa by means of their growth parameters. Examples are given in Fig. 6, where values of K and W_∞ for seventeen (17) species of Scombridae (Scombrinae and Thunninae) are plotted together with values of K and W_∞ for three (3) species of Cyprinidontidae (♂♂ and ♀♀), and in Fig. 7 where the growth parameters for thirteen (13) species were plotted.

TABLE VII

Growth Parameters of Selected Fresh-Water Fishes,
Showing Their Range of P Values (See also Fig. 4)

No.	Family	Species	W_∞	K	P	Based on data of
1.	Cyprinidontidae	Gambusia affinis ♂	0.42	1.2	-0.30	Beverton & Holt (1959) c.f. ÷ 0.9
2.	"	Lebistes reticulatus ♂	0.101	6.868	-0.16	Ursin (1967, p. 2437) No. 5
3.	"	Cyprinodon macularius	0.251	2.843	-0.15	Kinne (1960) fresh-water 30° C.
4.	"	Gambusia affinis ♀	2.14	0.8	0.23	Beverton & Holt (1959) c.f. ÷ 0.9
5.	Cottidae	Cottus beldingii	7.24	0.316	0.36	Ebert & Summerfelt (1969)
6.	Cyprinidontidae	Lebistes reticulatus ♀	1.5	2.121	0.44	Ursin (1967, p. 2437) No. 4
7.	Cyprinidae	Phoxinus phoxinus	8.24	0.58	0.68	Frost (1943)
8.	"	Brachydanio rerio	1.93	3.968	0.88	Eaton & Farley (1974)
9.	Salmonidae	Leucichthys alpense	25.5	0.518	1.12	Carlander (1950) (South L. Michigan)
10.	Percidae	Acerina cernua	76.7	0.314	1.38	Bauch (1966)
11.	Cyprinidae	Blicca bjorkna	39.3	0.684	1.43	Berg et al. (1949)
12.	Centropomidae	Ambloplites rupestris	257.	0.22	1.75	Hile (1941)
13.	Cyprinidae	Chondrostoma nasus	484.	0.217	2.02	Berg et al. (1949)
14.	Catostomidae	Catastomus commersoni	1653.	0.104	2.24	Carlander (1950)
15.	——— Deleted ———					
16.	Cichlidae	Tilapia esculenta	734.	0.32	2.37	Garrod (1959)
17.	"	Tilapia galilaea	676.	0.52	2.55	Ben-Tuvia (1956)
18.	Characinidae	Hydrocyon forskalii	793.	0.519	2.61	Rafail et al. (1973)
19.	Centropomidae	Micropterus dolomieu	1174.	0.534	2.80	Carlander (1950) N.C. Hiwasse Lake
20.	Percidae	Lucioperca lucioperca	6106.	0.168	3.01	Nikolsky (1957)
21.	Esocidae	Esox lucius	6049.	0.23	3.14	Johnson (1966)
22.	Acipenseridae	Acipenser nudiventris	42290.	0.053	3.35	Nikolsky (1957) Aral Lake
23.	Cyprinidae	Cirrhinus mrigla	18804.	0.122	3.36	Hanumentharo (1974)
24.	"	Catla catla	33992.	0.280	3.98	Natarajan & Jhingran (1963)

TABLE VIIIa

Growth Parameters of Selected Marine and Brackish Water Fishes, Showing Their Range of P Values (See also Fig. 5)

.	Family	Species	W_∞	K	P	Based on data of
.	Myctophidae	Notolychnus valdiviae	0.14	1.411	-0.70	Legand (1967)
..	Gasterosteidae	Apeltes quadracus	1.23	1.174	0.16	Schwarz (1965), c.f. ÷ 0.6
3.	Cyprinodontidae	Cyprinodon macularius	0.538	3.391	0.26	Kinne (1960, 35% & 25° C.)
1.	"	" "	0.703	2.995	0.32	Kinne (1960, 35% & 30° C.)
5.	Myctophidae	Myctophum punctatum	6.56	0.323	0.33	Wörner (1975), c.f. ÷ 0.9
5.	Cyprinodontidae	Cyprinodon macularius	0.710	3.223	0.36	Kinne (1960, 35% & 30° C.)
7.	Myctophidae	Benthosema glaciale	5.72	0.45	0.41	Gjösaeter (1973) c.f. ÷ 0.9
3.	Syngnathidae	Siphonosomatyphle	6.2	0.558	0.54	Worthmann (1975)
9.	Gasterosteidae	Gasterosteus aculeatus	1.97	1.788	0.55	Worthmann (1975)
0.	Myctophidae	Myctophium affine	9.0	0.42	0.58	Odate (1966) c.f. ÷ 0.9
1.	Syngnathidae	Nerophis ophidion	5.46	1.052	0.76	Worthmann (1975)
2.	Myctophidae	Scopelopsis multipunctatus	5.4	1.118	0.78	Legand (1967)
3.	Macrorhamphosid.	Macrorhamphosus scolopax	21.7	0.36	0.89	Brêthes (1975)
4.	Blennidae	Blennius pholis	54.	0.30	1.21	Quasim (1957)
5.	Cottidae	Taurulus bubalis	102.	0.230	1.37	Lamp (1965)
6.	"	Cottus kessleri	118.	0.197	1.37	Berg *et al.* (1949)
7.	Maenidae	Maena smaris	117.	0.218	1.41	Zei (1951)
8.	Callyonimidae	Callyonymus lyra	52.5	0.49	1.41	Chang, Hsaio-Wei (1951) c.f. ÷ 0.5
9.	Gadidae	Trisopterus esmarkii	47.7	0.59	1.45	Raitt (1968)
0.	Pomadasydae	Rhonciscus striatus	142.	0.229	1.51	Latif & Shenouda (1972)
21.	Cynoglossidae	Cynoglossus macrolepidus	170.	0.239	1.61	Krishnan Kutty & Quasim (1969)
22.	Engraulidae	Engraulis anchoita	212.	0.230	1.69	Fuster de Plaza (1964)
23.	Labridae	Symphodus melops	190.	0.359	1.83	Guinard (1966)
24.	Notothenidae	Trematomus bernachii	309.	0.29	1.95	Wohlschlag (1962)
25.	Carangidae	Selaroides leptolepis	85.	1.155	1.99	Morsuwan (1970)
26.	Polynemidae	Polynemus heptadactylus	718.	0.157	2.05	Kagwade (1970)
27.	Sparidae	Dentex macrophtalmus	941.	0.162	2.18	in: Pauly (1978a)
28.	Scorpaenidae	Scorpaena porcus	869.	0.177	2.19	Berg *et al.* (1949)
29.	Zoarcidae	Zoarces viviparus	965.	0.203	2.29	Wheeler (1969)
30.	Sciaenidae	Pseudotolithus elongatus	715.	0.274	2.29	Le Guen (1971)
31.	Scyliorhinidae	Scyliorhinus canicula	550.	0.53	2.46	Zupanovic (1961)

TABLE VIIIb

Growth Parameters of Selected Marine and Brackish Water Fishes, Showing Their Range of P Values (See also Fig. 5)

Nr.	Family	Species	W_∞	K	P	Based on data of
32.	Leiognathidae	Leiognathus equulus	197	1.884	2.57	Chabanne & Plante (196
33.	Labridae	Labrus bergylta	3830	0.107	2.61	Guinard (1966)
34.	"	Tautoga onitis	2845	0.165	2.67	Cooper (1967)
35.	Scombridae	Rastrelliger kanagurta	117	5.16	2.78	George & Banerji (1964
36.	Serranidae	Epinephelus guttatus	2089	0.243	2.71	Thompson & Munro (1977
37.	Mugilidae	Mugil cephalus	2078	0.435	2.96	Berg *et al.* (1949)
38.	Pomatomidae	Pomatomus saltatrix	5808	0.197	3.06	Van der Elst (1976)
39.	Trichiuridae	Trichiurus lepturus	4663	0.296	3.14	Wojciechowski (1971)
40.	Gadidae	Pollachius virens	11331	0.141	3.20	Nikolsky (1957)
41.	Thunnidae	Sarda sarda	3434	0.693	3.38	Dardignac (1962)
42.	Gadidae	Gadus morhua	16350	0.181	3.47	Jones (1966)
43.	Acipenseridae	Acipenser stellatus	15675	0.192	3.48	Berg *et al.* (1949)
44.	Lophiidae	Lophius piscatorius	53952	0.060	3.51	Connolly (1920)
45.	Serranidae	Roccus lineatus	17543	0.186	3.51	Scofield (1931)
46.	Thunnidae	Auxis thazard	4394	0.829	3.56	Sivasubramanian (1973)
47.	Acipenseridae	Acipenser guldenstädti	97200	0.045	3.64	Nikolsky (1957)
48.	Thunnidae	Euthynnus alliteratus	44869	0.164	3.87	Postel (1956)
49.	"	Katsuwonus pelamis	55200	0.179	3.99	in:Marcille & Stequert
50.	Acipenseridae	Huso huso	149100	0.097	4.16	Nikolsky (1957)
51.	Thunnidae	Katsuwonus pelamis	16000	0.949	4.18	Brock (1954)
52.	Istiophoridae	Tetrapterus albidus	861500	0.026	4.35	in: Pauly (1978a)
53.	Thunnidae	Thunnus obesus	234961	0.114	4.43	Shomura & Keala (1963)
54.	"	" "	165108	0.167	4.44	Shomura & Keala (1963)
55.	Istiophoridae	Istiophorus platypterus	36740	0.754	4.44	De Sylva (1957)
56.	Carcharhinidae	Prionace glauca	447750	0.091	4.61	Stevens (1975)
57.	"	" "	738000	0.072	4.73	Stevens (1975)
58.	"	Eulemia milberti	89190	0.610	4.74	Springer (1960)
59.	"	" "	99740	0.580	4.76	Springer (1960)
60.	Thunnidae	Thunnus thynnus	987388	0.067	4.82	Sella (1929)
61.	"	" "	504835	0.308	5.19	Westmann & Neville (19
62.	Lamnidae	Cetorhinus maximus	13820000	0.045	5.79	Pauly (1978c)

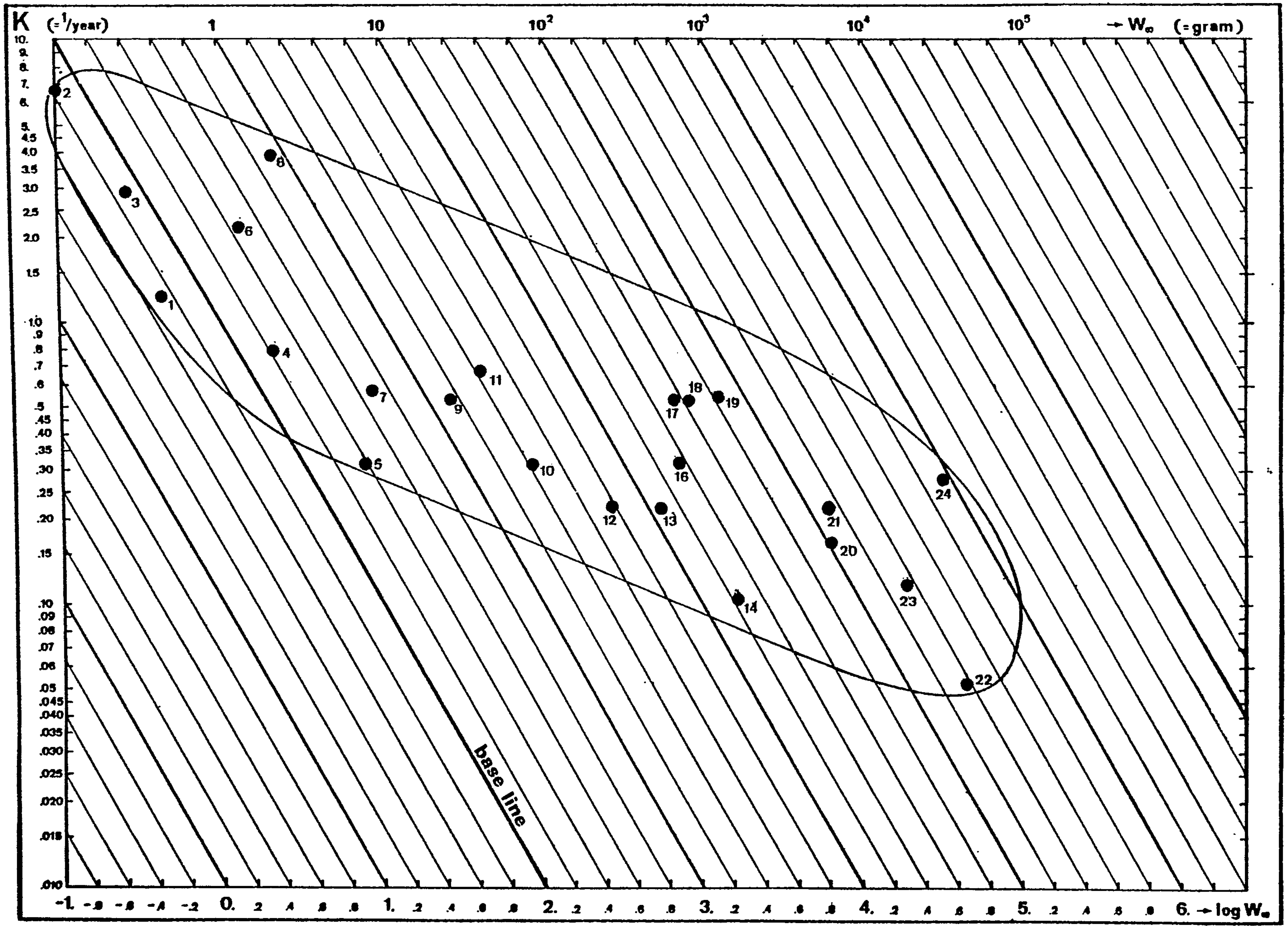


Fig. 4 Auximetric grid: selected fresh water fishes (Nr 15 deleted). See also Table VII.

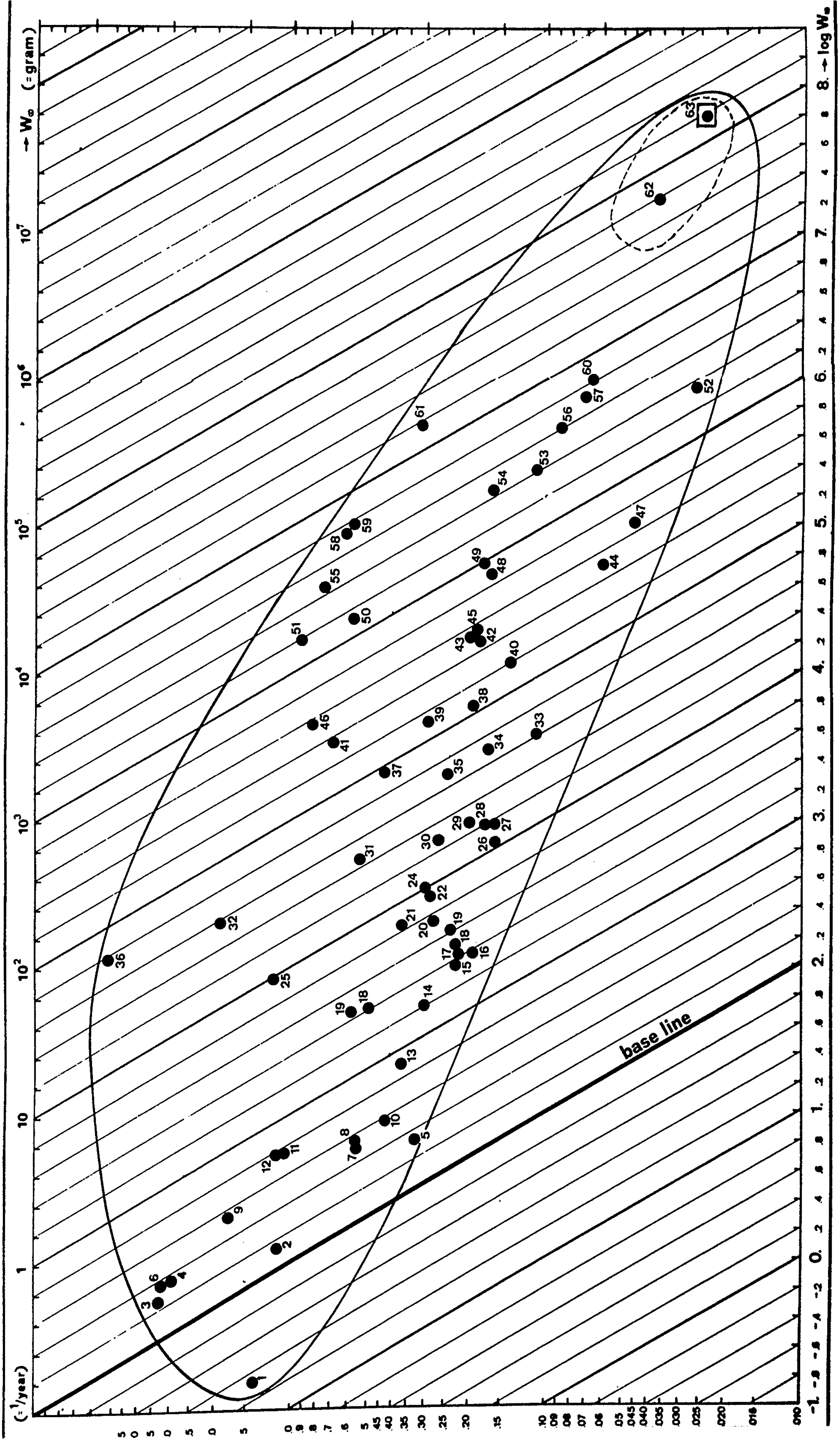


Fig. 5 Auximetric grid: selected marine and brackish water fishes. See also Table VIII.

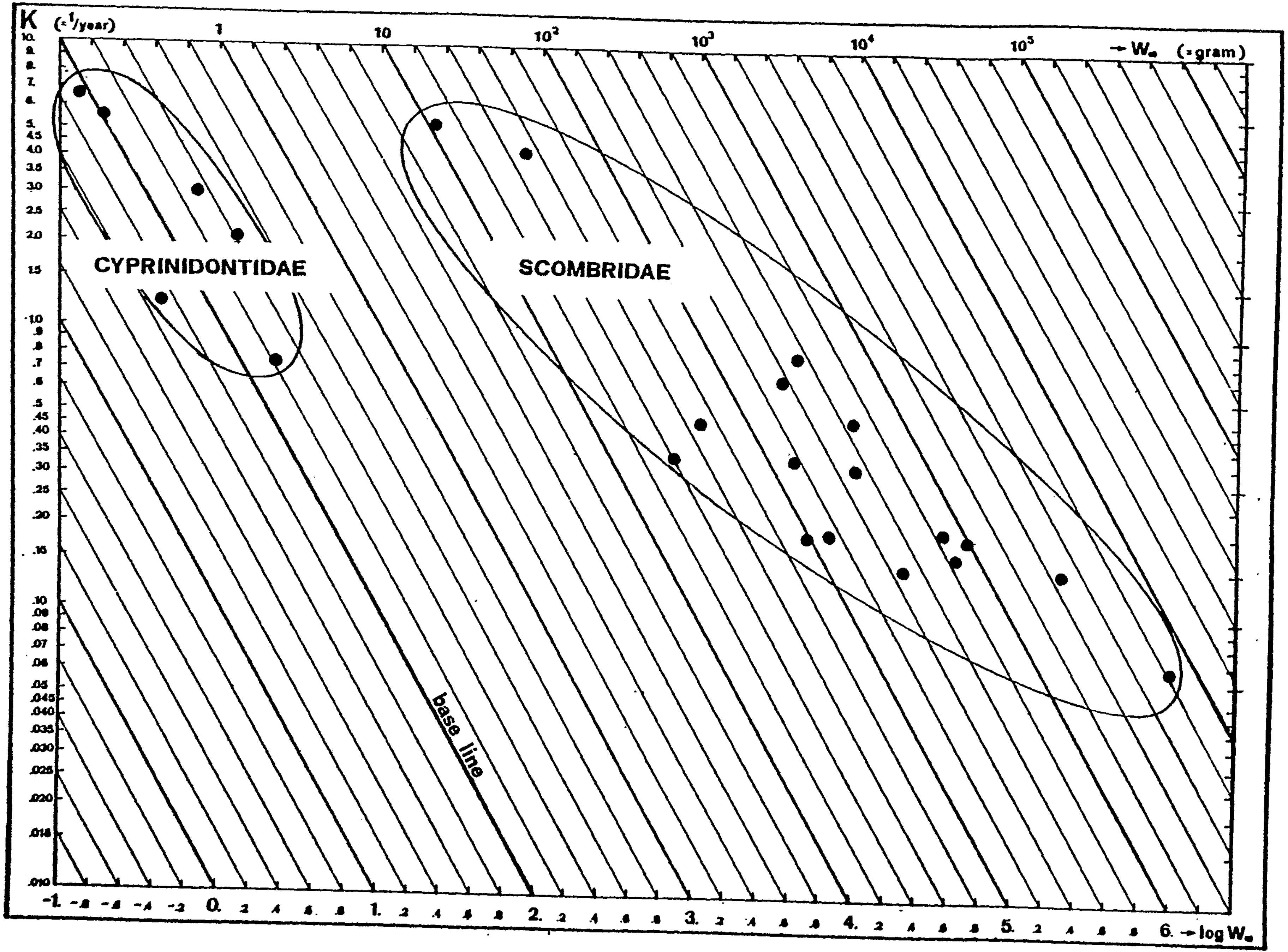


Fig. 6 Auximetric grid: Scombridae and Cyprinidontidae.

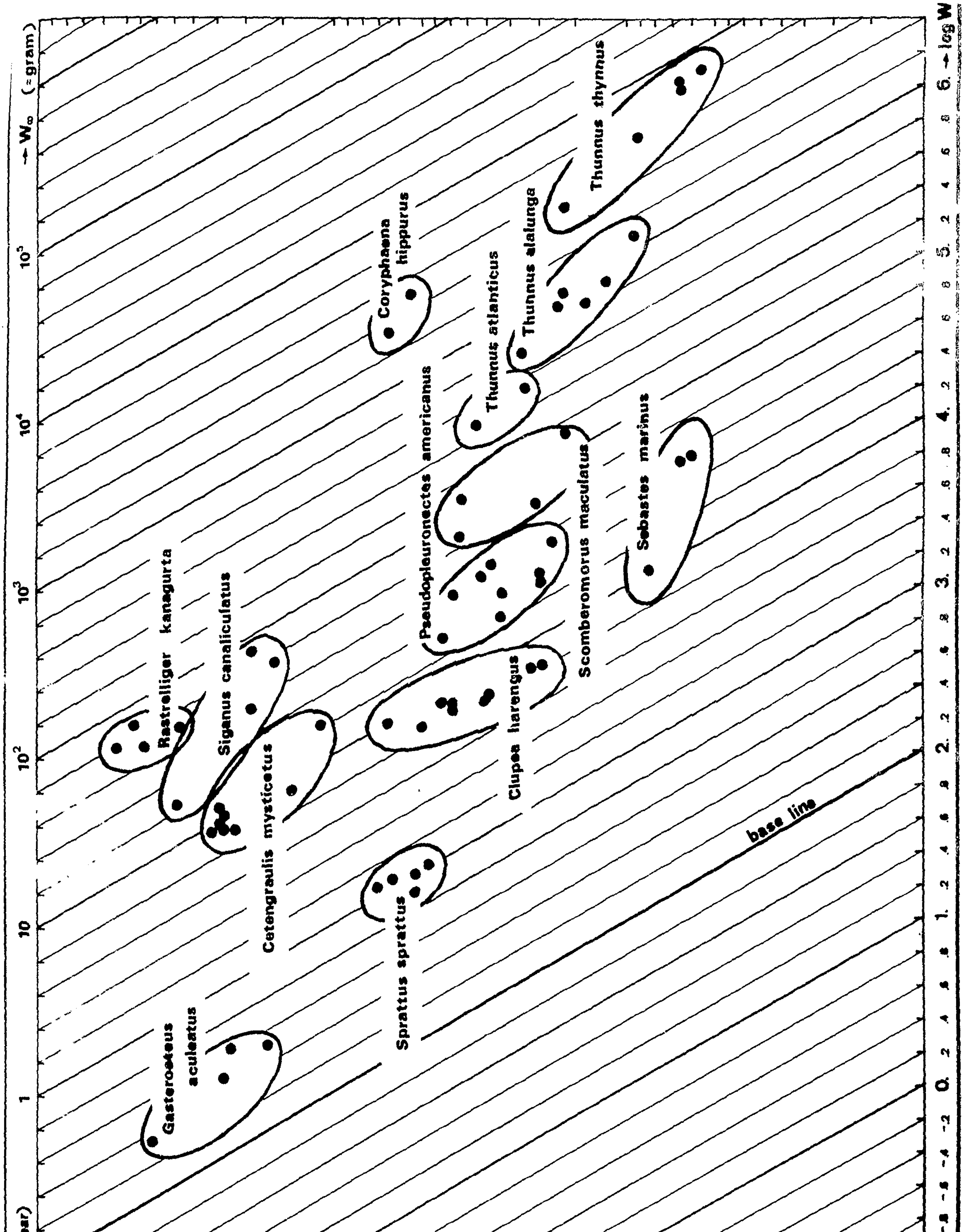


Fig. 7 Auximetric grid: plots of different stocks

Other potential uses of the auximetric grid, which will be discussed in future papers, are:

- Estimation of the value of K in fishes which cannot be aged. For example, the value of $W_\infty \simeq 60$ tons for *Rhincodon typus* (See p. 43) allows for an estimation of K = 0.02 - 0.03 through extrapolation from the value pertaining to *Cetorhinus maximus* (See Fig. 5, No. 62 & 63, and Table VIII).
- Quantification and comparison of the effects of endogenous growth determinants (e.g., sex) as well as environmental factors (e.g., salinity) on the growth of fishes. (See Fig. 8 and Fig. 9 for preliminary examples.)
- Identification of erroneous literature values of K for given values of W_∞ (or vice-versa) through comparisons with other K/W_∞ pairs pertaining to the same species.

The auximetric grid, however, has been presented here primarily to demonstrate that the growth pattern of fishes widely differing in their ecology and taxonomic relationship are essentially uniform and predictable.

5.4. Intraspecific Growth Comparisons

The concept of P and of the auximetric grid need further development to allow for infraspecific comparisons. Various authors have reported that in different stocks of a given species, the value of W_∞ and L_∞ tends to decrease when K

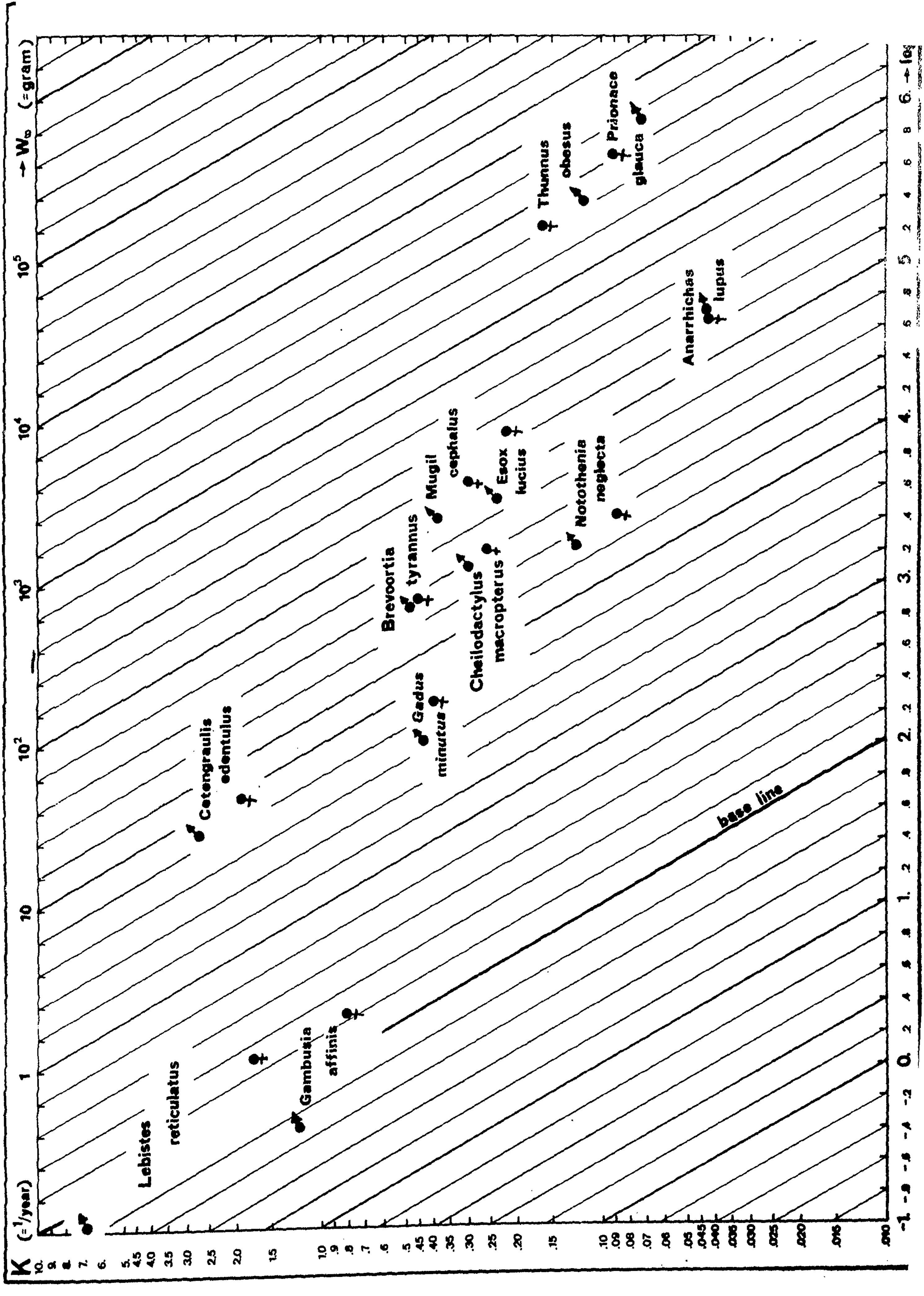


Fig. 8 Auximetric grid: sex-specific growth parameters

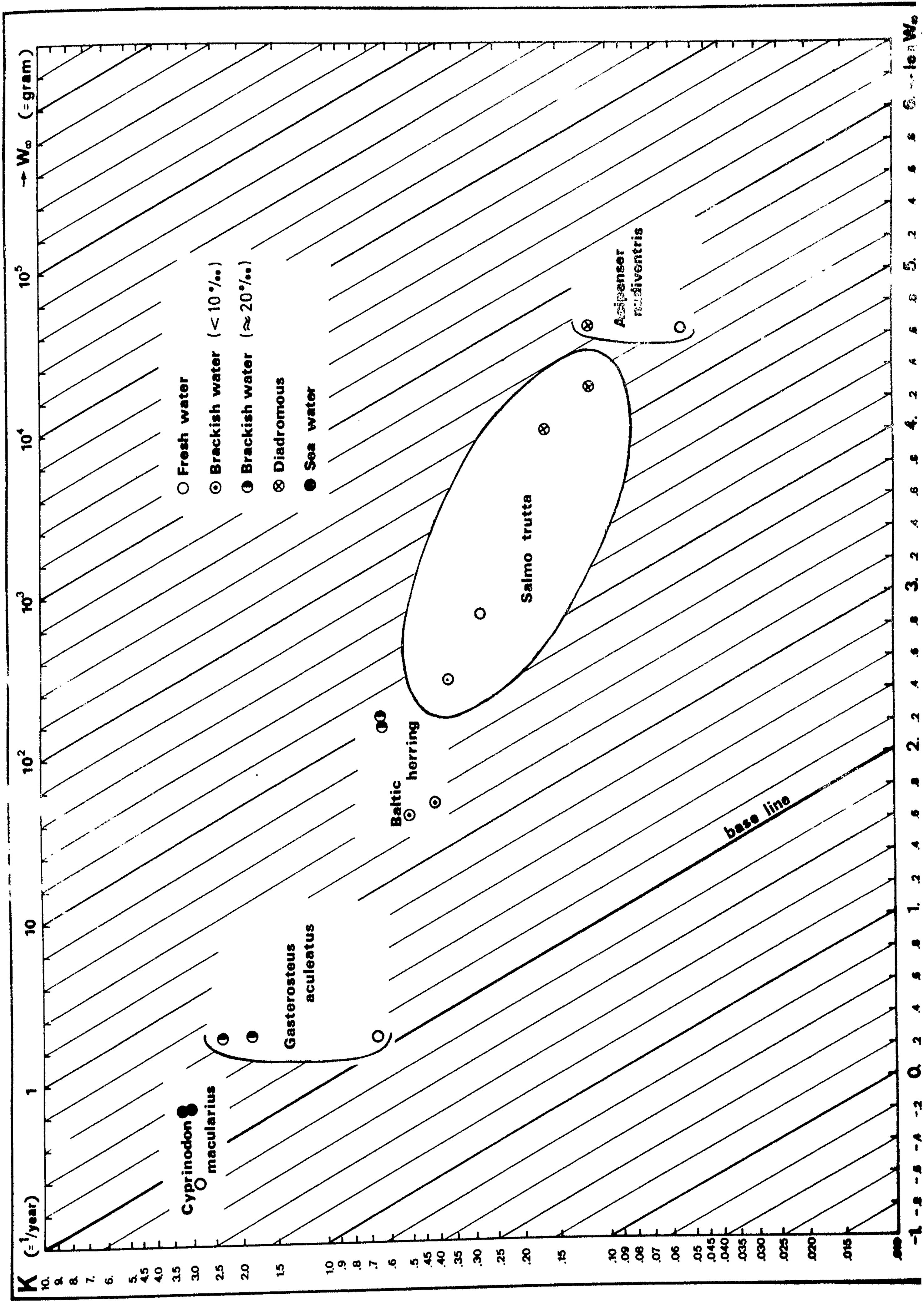


Fig. 9 Auximetric grid: the effect of salinity

increases (See Taylor, 1958, for an example). To this author's knowledge, no attempt has ever been made, however, to investigate the character of these interrelationships in quantitative terms.

Such an attempt may be undertaken here on the basis of the growth parameters calculated and/or compiled by this author (Pauly, 1978a). In this compilation, which gives the growth parameters of 515 different fish species, three (3) or more sets of growth parameters are given for each of 126 species, with a total number of 978 different stocks (Table IXa-d).

A regression of log K on log L_∞^3 was calculated for each of these 126 species. The slopes (b) and the absolute value of the correlation coefficient ($|r|$) for these regressions is given in Table IXa-d.

Because L_∞^3, as a whole, is proportional to W_∞, the values of b and $|r|$ so obtained should, as a rule, be close to the values of b and $|r|$ which would have been obtained from plots of log K against log W .

In 119 cases, the values of b are negative; in only 7 cases are they positive. A simple "sign test" (See Sachs, 1974, p. 247 ff.) reveals that the positive values of b most probably do not originate from the same collective as the negative values. In fact, examination of the original data reveals that positive values of b occur only when a few stocks are plotted which also cover a very limited span of K and L_∞^3 values. (See Table IX and Pauly, 1978a, for data on the 7 spp. in question).

TABLE IXa

Plots of Log K Against Log L_∞^3

Page*	Species	n	b	|r|	Significance level 95%	99%
28	Ammodytes marinus	5	-0.456	0.535		
28	" tobianus	6	-0.322	0.746		
28	Anarhichas lupus	3	-0.754	0.992		
28	" minor	3	-0.912	0.998	x	
29	Argentina silus	8	-0.396	0.835	x	x
30	Scophtalmus maximus	5	-0.753	0.979	x	x
31	Lepidorhombus megastoma	4	-0.395	0.999	x	x
32	Branchiostegus japonicus	6	-0.367	0.759		
32	" auratus	4	-1.394	0.930		
33	Trachurus japonicus	3	-1.071	0.934		
33	" trachurus	4	-0.312	0.972	x	
36	Tilapia esculenta**	4	-2.050	0.688		
37	" morsambica	9	-0.822	0.844	x	x
37	" nilotica	3	-0.777	0.999	x	
38-39	Clupea harengus	38	-0.260	0.386		
40	Sardina pilchardus	18	-0.521	0.663	x	x
41	Sardinella albella	4	-0.387	0.858		
41	" eba	3	-0.822	0.922		
41	" longiceps	5	-0.347	0.832		
42	" aurita	13	-0.644	0.732	x	x
42	Sardinops melanostica	3	-1.983	0.834		
42	" ocelata	3	+0.023	0.063		
43	" caerula	19	-0.437	0.542	x	
44-46	Brevoortia tyrannus	43	-0.252	0.361	x	
46	Sprattus sprattus	10	-0.523	0.358		
46	Clupea pallassii	3	+1.276	0.861		
46	Clupeonella delicatula	3	-0.673	0.502		
47	Hilsa ilisha	3	-1.138	0.639		
47	Sardinops neopilchardus	3	+6.267	0.624		
48	Myoxocephalus scorpius	3	-0.488	0.982		
49-50	Abramis brama	26	-0.580	0.694	x	x
50	Rutilus rutilus	4	-0.369	0.789		

*in Pauly (1978a)
**excluding Cridland's data

TABLE IXb

Plots of Log K Against Log L_∞^3

Page*	Species	n	b	|r|	Significance level 95%	99%
51	Barbus brachycephalus	4	-0.410	0.975	x	
51	Varicorhinus capoeta	3	-0.568	0.985		
51	Cyprinus carpio	4	-0.099	0.274		
52	Lebistes reticulatus	16	-0.545	0.893	x	x
54	Engraulis japonicus	15	-0.639	0.846	x	x
54	" ringens	3	-0.054	0.089		
55	" encrasicholus	16	-0.715	0.660	x	x
55	Cetengraulis edentulus	4	-0.744	0.990	x	x
56	" mysticetus	11	-1.111	0.616	x	
57-58	Engraulis mordax	26	-1.095	0.897	x	x
59	Esox lucius	8	-0.473	0.783	x	
60-62	Gadus morhua	49	-0.395	0.652	x	x
63	Melanogrammus aeglefinus	13	-0.344	0.776	x	x
63	Trisopterus esmarkii	3	-0.312	0.777		
64	Theragra chalcogramma	4	-0.251	0.881		
64	Micromesistius poutassou	6	-1.137	0.919	x	x
64	Pollachius virens	5	-0.396	0.830		
65	Lota lota	4	+0.071	0.077		
65-69	Merlangius merlangus	93	-0.719	0.872	x	x
70	Gasterosteus aculeatus	4	-0.628	0.968		
70	Gerres punctatus	3	-1.015	0.975		
72	Istiophorus platypterus	3	-0.768	0.956		
72	Tetrapterus audax	4	-1.741	0.918		
73	Crenilabrus rupestris	3	+0.428	0.997	x	
73	Labrus berggylta	3	-0.462	0.998	x	
74	Symphodus rostratus	3	-0.886	0.847		
74	Tautogalabrus adspersus	4	-0.350	0.926		
76	Leiognathus bindus	6	-0.283	0.775		
76	" lineolatus	3	-0.730	0.993		
76	" splendens	5	-0.141	0.207		
79	Merluccius merluccius	17	-0.181	0.500	x	
80	" gayi	7	-0.649	0.971	x	x

*in Pauly (1978a)

TABLE IXc

Plots of Log K Against Log L_∞^3

Page*	Species	n	b	|r|	Significance level 95%	99%
81	Mugil cephalus	9	-0.366	0.846	x	x
81	" saliens	3	-0.246	0.362		
82	" aurata	4	-0.365	0.780		
83	Nemipterus virgatus	6	+0.160	0.297		
84	" japonicus	6	-0.896	0.931	x	x
85	Notothenia neglecta	4	-0.595	0.642		
85	" rossii	3	-0.407	0.998	x	
85	Trematomus bernachii	6	-0.568	0.682		
86	Osmerus eperlanus	12	-0.378	0.832	x	x
86	Mallotus villosus	4	-0.563	0.992	x	
87	Neoplatycephalus macrodon	6	-0.614	0.928	x	x
88	Perca fluviatilis	7	-0.813	0.909	x	x
88	Lucioperca lucioperca	5	-0.286	0.881	x	
89	Pleuronectes platessa	3	-0.461	0.976		
90	Pseudopleuronectes americanus	10	-0.712	0.771	x	x
90	Platichthys stellatus	3	-0.818	0.835		
90	" flesus	3	-0.691	0.875		
91	Hippoglossus platessoides	10	-0.330	0.382	x	
91	" hippoglossus	6	-0.700	0.854		
93	Brachydeuterus auritus	4	-0.123	0.266		
94	Raja hollandi	4	-1.358	0.947		
95	Salmo trutta	15	-0.065	0.187		
95	" salar	3	-0.838	0.740		
96	Coregorus clupeaformis	6	-0.217	0.626		
96	" lavaretus	7	-1.083	0.967	x	x
97	Thymallus arcticus	3	-0.287	0.285		
97	" thymallus	3	-0.771	0.799		
97	Oncorhynchus keta	4	-0.728	0.669		
97	Leucichthys artedi	5	-0.194	0.335		
98	Pseudotolithus senegalensis	5	-0.507	0.925	x	
98	" typus	6	-0.256	0.807		
98	Nibea nibe	9	-0.718	0.883	x	x

*in Pauly (1978a)

TABLE IXd

Plots of Log K Against Log L_∞^3

Page*	Species	n	b	|r|	Significance level 95%	99%
99	Leiostomus xanthurus	3	-0.601	0.967		
100	Cynoscion nebulosus	9	-0.628	0.894	x	x
101	Cololabis saira	3	-0.777	0.978		
102	Rastrelliger kanagurta	8	-1.588	0.971	x	x
102	" neglectus	5	-1.176	0.856		
102	Scomberomorus maculatus	4	-0.533	0.839		
103	Scomber scombrus	12	-1.074	0.895	x	x
103	Pneumatophorus japonicus	7	-0.200	0.879	x	x
104	Sebastes marinus	5	-0.264	0.758		
104	" mentella	3	-0.554	0.899		
104	Sebastodes alutus	3	-1.299	0.913		
105	Labeolabrax japonicus	3	-0.304	0.987		
105	Dicentrarchus labrax	5	-0.598	0.769		
107	Siganus canaliculatus	4	-0.317	0.916		
108	Taius tumifrons	4	-0.558	0.992	x	x
109	Chrysophris aurata	4	-0.390	0.823		
109	" major	4	-0.445	0.778		
109	Pagellus centrodontus	3	-0.789	0.999	x	
110	Squalus acanthias	9	-0.768	0.813	x	x
111	Saurida undosquamis	3	+0.570	0.978		
112	Thunnus albacares	18	-0.846	0.501	x	
113	Thunnus alalunga	12	-0.657	0.933	x	x
113	Sarda sarda	6	-1.156	0.958	x	x
114	Thunnus maccoyi	3	-1.129	0.424		
114	Katsuwonus pelamis	6	-0.269	0.277		
115	Thynnus thynnus	6	-0.525	0.997	x	x
115	Thynnus obesus	7	-1.441	0.764	x	
116	Trichiurus lepturus	6	-0.076	0.485		
116	Chelidonichthys kumu	3	-0.180	0.760		
117	Zeus faber	3	-1.116	0.971		

*in Pauly (1978a)

When the positive values of b are excluded, a mean value of b = -0.632 ± 0.386 is obtained (Table X). Similarly, a mean value of b = -0.714 ± 0.279 is obtained when plotting log K against log W_∞ in various fish stocks whose growth parameters were compiled for the investigation on the interrelationships between environmental temperature and growth. (See Table XI for summary, and Table XIII for raw data). The latter mean value of b, although based upon fewer fish species than the first value, is particularly well founded, as the growth parameters used were checked for consistency (See Chapter 6, p. 28 f.). It seems, therefore, legitimate to take an unweighted mean of these two independently obtained mean values of b, such that

$$b = \frac{-0.632 - 0.714}{2} = -0.673 \qquad \ldots.73)$$

or, for simplicity's sake, $b \simeq -2/3$. Thus, as a rule we have

$$\log K = a - 2/3 \log W_\infty \qquad \ldots.74)$$

The value of the slope ($\simeq -2/3$) in Equation 74 can be readily explained. It may be recalled that the VBGF assumes that K is proportional to the rate at which body substances are degraded, and that, at W_∞, the amount degraded per unit time is equal to the amount that is synthesized. As the rate of synthesis is considered proportional to the oxygen supply, hence to gill surface, any change in the value of K should result in a proportional change, with sign changed, of the gill surface at W_∞, or log K should be inversely proportional to the log of the gill surface at W_∞, or to $W_\infty^{2/3}$ when the special VBGF is used, as was here the case.

TABLE X

Plots of Log K Against Log Asymptotic Size. Summary of Data

a) Plots of Log K against Log L_∞^3.

		Number of units	Number of regressions	Number of units	Number of regressions
Total number of regressions	126				
Positive values of b	7	3	39	15	2
Negative values of b	119	4	25	16	2
Mean value of b 0.632*		5	11	17	1
S.d. 0.386*		6	15	18	2
		7	5	19	1
		8	3	26	2
		9	5	38	1
		10	3	43	1
		11	1	49	1
		12	3	93	1
		13	2	Total	126
		Overall number of units (fish stocks):			978

*based on negative values of b only.

b) Plots of Log K against Log W_∞

Number of regressions	20
Positive values of b	none
Negative values of b	20
Mean value of b*	-0.714
n=19 s.d.	0.279*

*excluding E. mordax, see Table XI

TABLE XI

Plots of Log K Against Log W_∞ Summary of Data

No.	Species	n	$\lvert r \rvert$	a	b	Data in Table
1	Abramis brama	17	0.721	1.077	-0.528	XIIIc
2	Brevoortia tyrannus	19	0.829	1.075	-0.550	XIIId
3	Cetengraulis mysticctus	9	0.489	1.675	-0.815	XIIIe
4	Clupea harengus	10	0.079	-0.041	-0.176	XIIIf
5	Coregonus lavaretus	6	0.971	2.784	-1.056	XIIIe
6	Gadus morhua	11	0.910	2.095	-0.679	XIIIh
7	Gasteosteus aculeatus	4	0.969	0.494	-0.626	XIIIa
8	Engraulis mordax	20	0.926	2.064	-1.457	XIIIa*
9	Esox lucius	7	0.833	1.368	-0.541	XIIId
10	Lepibema chrysops	12	0.771	2.826	-1.089	XIIId
11	Lepomis macrochirus	14	0.914	1.151	-0.646	XIIId
12	Merluccius merluccius	16	0.495	-0.085	-0.179	XIIIc
13	Micromesistius poutassou	6	0.800	2.083	-1.001	XIIIb
14	Mugil cephalus	8	0.862	0.676	-0.377	XIIIc
15	Nemipterus japonicus	6	0.931	1.649	-0.894	XIIIa
16	Pomoxis nigromaculatus	15	0.848	2.105	-0.872	XIIIf
17	Pseudopleuronectes americanus	10	0.823	1.437	-0.668	XIIIb
18	Sardinella aurita	9	0.691	2.175	-1.084	XIIIb
19	Sardinops caerula	9	0.854	1.624	-0.874	XIIIc
20	Scomber scombrus	8	0.870	2.082	-0.907	XIIIb
				mean	0.751	
				s.d.	0.319	
				mean, excluding E. mordax	0.714	
				s.d.	0.279	

*Note that only E. mordax lies more than 2 s.d. from the first mean.

It appears, therefore, that the empirical data which lead to the mean estimates of $b \approx -2/3$ (-0.632, -0.714 and -0.673) "confirm" the 2/3 rule implied in the special VBGF. On the other hand, it may be safely assumed that the mean slope value linking log K to log L_∞^3 or to log W_∞ would have been closer to -1, had the generalized VBGF and a value of $d > 2/3$ been used instead of the special VBGF.

6. FISH GROWTH AND MEAN ENVIRONMENTAL TEMPERATURES

6.1. Introductory Review

The literature on the dependence of fish growth on temperature is so vast that no attempt will be made here to do more than mention a few review papers.

D'Ancona (1937) and later, Bougis (1952) demonstrated that Mediterranean fishes tend to stay smaller, and to grow faster than their North Atlantic counterparts. Similarly, von Bertalanffy (1951) derived from his theory of growth that fishes of warm waters should, as a rule, stay smaller than fishes of colder waters, and gave empirical data (pp. 356-357) to support this deduction.

Holt (1960), on mackerels, and especially Taylor (1958), on cod, confirmed that the value of K tends to increase, and the value of L_∞ to decrease with mean environmental temperature.

Bayliff (1967), working on various engraulid species, failed to establish significant relationships between log K and mean surface temperature in any of the four species investigated, while data presented by May *et al.* (1965) suggested that K, in the cod stocks they investigated, is *negatively* correlated with mean environmental temperature.

6.2. The Relationship Between K and Temperature

Von Bertalanffy (1951, p. 355), suggested that catabolism, as expressed by K, should have a high temperature coefficient, because hydrolytic processes are involved (See Misunderstanding III, p. 20, and definition of K, p. 115 ff.) On the other hand, it is well known that there is, for the Q_{10} of most biological reactions, a strong tendency to decrease from about 4-5 at 5° C to about 2 at 30° C (von Bertalanffy, 1951, p. 24, Krüger, 1964, Rose, 1967, Winberg, 1960, Laudien, 1971). This implies that in order to describe the changes of K over this whole range of temperatures, a curve should be used whose Q_{10} varies from 4-5 at 5° C to about 2 at 30° C.

A curve with these properties and which has been used extensively by fishery biologists is available in the form of Krogh's normal curve, which describes the effect of temperature on the standard metabolism (O_2 consumption) of fishes (See Winberg, 1960 for an exhaustive discussion). In this chapter, no attempt will be made to relate K to respiratory rate in biological terms (such an attempt is undertaken in Chapter 9). Rather, Krogh's normal curve will be used here as a purely empirical and well documented curve.

Table XII gives the data on the normal curve that are needed for further computations. In this table:

°C	is the temperature, in °Centigrade
q	is a correction factor for converting respiratory rates to 20° C (taken from Winberg, 1960 & 1971)
%	is the respiratory rate, in % of the respiratory rate at 20° C (= 100%)
log % = y	is the common logarithm of the percentage value
$\hat{y}$	is the estimated value of y based on the 4th degree polynom:

TABLE XII

Krogh's Normal Curve: Basic Data, Polynomial Approximation and Derived Data. See Text.

°C	q_T	% of 20°C	Log %	Log %=y	$\hat{y}'$	Pn $\hat{y}'$	Q_{10}
5	5.19	19.27	1.285	1.281	0.0640	-2.7488	4.4
6	4.55	21.98	1.342	1.344	0.0612	-2.7944	4.1
7	3.98	25.13	1.400	1.404	0.0585	-2.8393	3.8
8	3.48	28.74	1.458	1.461	0.0559	-2.8834	3.6
9	3.05	32.79	1.516	1.516	0.0536	-2.9264	3.4
10	2.67	37.45	1.573	1.568	0.0514	-2.9683	3.3
11	2.40	41.67	1.620	1.678	0.0493	-3.0089	3.1
12	2.16	46.30	1.666	1.667	0.0475	-3.0480	3.0
13	1.94	51.55	1.712	1.713	0.0457	-3.0854	2.9
14	1.74	57.47	1.759	1.758	0.0441	-3.1211	2.8
15	1.57	63.69	1.804	1.802	0.0426	-3.1547	2.7
16	1.43	69.93	1.845	1.844	0.0413	-3.1863	2.6
17	1.31	76.34	1.883	1.884	0.0401	-3.2156	2.5
18	1.20	83.33	1.921	1.924	0.0391	-3.2425	2.5
19	1.09	91.74	1.963	1.963	0.0381	-3.2668	2.4
20	1.00	100.0	2.000	2.000	0.0373	-3.2885	2.4
21	0.920	108.7	2.036	2.037	0.0366	-3.3075	2.3
22	0.847	118.6	2.074	2.074	0.0360	-3.3237	2.3
23	0.779	128.4	2.109	2.109	0.0355	-3.3371	2.3
24	0.717	139.5	2.145	2.145	0.0352	-3.3477	2.2
25	0.659	151.7	2.181	2.180	0.0349	-3.3555	2.2
26	0.609	164.2	2.215	2.214	0.0347	-3.3605	2.2
27	0.563	177.6	2.249	2.249	0.0346	-3.3628	2.2
28	0.520	192.3	2.284	2.284	0.0346	-3.3625	2.2
29	0.481	207.9	2.318	2.318	0.0347	-3.3597	2.2
30	0.444	225.2	2.353	2.353	0.0349	-3.3546	2.2

$$\hat{y} = d_o + d_1T + d_2T^2 + d_3T^3 + d_4T^4 \qquad ....74)$$

where $d_o = +0.920810504$

$d_1 = +0.080976405$

$d_2 = -0.001930460$

$d_3 = +0.000032193$

$d_4 = -0.000000159$

$\hat{y}'$ is values of the first derivative (slope) of Equation 74, based on the 3rd degree polynom:

$$\hat{y}' = d_o + d_1T + d_2T^2 + d_3T^3 \qquad ....75)$$

where $d_o = +0.080976405$

$d_1 = -0.003860920$

$d_2 = +0.000096578$

$d_3 = -0.000000635$

$\ln y'$ is the natural logarithm of the y' values

Q_{10} is the temperature coefficient (increase of respiratory rate produced by a temperature increase of 10° C)

Here we leave the normal curve for a while and return to fish growth data.

In order to assess the character of the relationship between K and mean environmental temperature, the important feature must be considered that K is generally estimated together with L_∞ (or W_∞) and that widely differing sets of K and asymptotic size may all give a reasonable fit to a given set of age-at-length data, especially if these data cover a limited range of sizes-at-age. Here, however, only values of K can be used which are associated with values of L_∞ (or W_∞) reasonably close to the empirical L_{max} (or W_{max}) values of the various stocks. [This selection was not made by Bayliff (1967), who included in his calculations values of K associated with values of L_∞ as high as 55 cm for some engraulid species.]

The growth parameters selected for this investigation are given in Tables XIIIa to h. The data are based upon growth parameters compiled in Pauly (1978a) and on size-at-age data in Carlander (1950) to which Ford-Walford plots were applied.

The sources for the various estimates of mean environmental temperature are given under the species headings. In most cases. these estimates are mean annual surface temperatures, based on the World Atlas of Sea Surface Temperatures (Anon., 1944). In the case of fresh water species, the temperatures are annual mean air temperatures at the closest weather station(s) given in Walter & Lieth (1967). The sets of growth parameters for fishes from water bodies which could not be located or were too imprecise were omitted along with most of the data relating to fresh water fishes in areas where the mean annual air temperature is < 0° C. Table XIII summarizes the growth and temperature data used.

For each species, the parameters of the regression of log K on temperature were estimated. The values obtained for each species are summarized in Table XIV, where

n refers to the number of K and T pairs,

r is the correlation coefficient between log K and T, a is the intercept of the regression line,

b is the slope of the regression line,

lnb is the natural logarithm of the slope of the regression line,

$\overline{T}$ is the mean value of T for a given species,

$\ln b_n$ is the natural logarithm of the slope of Krogh's normal curve at $\overline{T}$, as based on Equation 75 , and

$\Delta\ln b$ is the difference between the empirical value of lnb and the expected value ($\ln b_n$).

As a whole, the fit of the data points to the values derived from Krogh's normal curve is rather good, with the empirical data points evenly distributed above and below the expected values. This results in a mean deviation very close to zero ($\Delta\ln b$ = 0.015, see Table IVX) which suggests that the real lnb values are well described by the values derived from Krogh's normal curve, and that latter curve, therefore, may be used to describe the relationship between K and temperature in the 5 to 30° C range (Fig. 10).

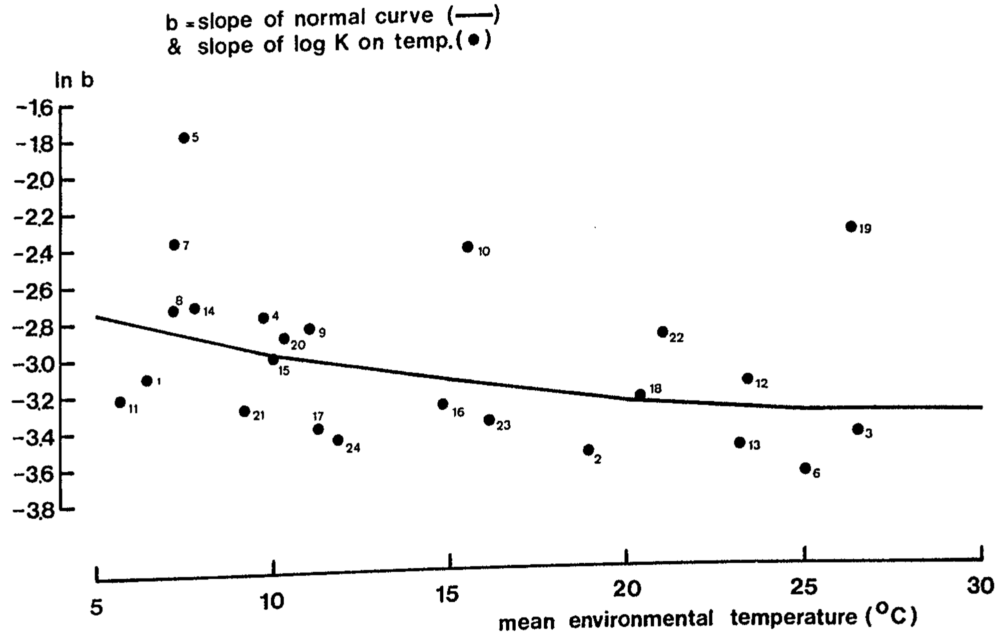


Fig. 10 Showing the similarity of the slopes of plots of log K on temperature and the slope of Krogh's normal curve. See also Table XIV and text.

TABLE XIIIa

Relationship of K to Mean Environmental Temperature

Engraulis mordax

Pauly (1978a, p. 57-58), excluding "Southern California" stock.
All localities: California Coast. Temperature: Bayliff (1967)

Locality	°C	L_∞	W_∞	K
San Francisco	12.8	20.1	57	0.32
Monterey 46-51	13.1	23.1	86	0.20
" 52-53	13.1	23.1	86	0.20
" 53-54	13.1	27.0	138	0.10
" 54-55	13.1	19.8	54	0.20
" 55-56	13.1	21.9	74	0.19
Santa Barbara 53-54	15.1	20.0	56	0.26
" " 54-55	15.1	18.6	45	0.44
" " 56-57	15.1	20.5	60	0.33
Malibu 56-57	16.1	18.7	46	0.58
Santa Monica 56-57	16.1	18.9	47	0.47
Los Angeles 52-53	16.7	18.4	44	0.45
" " 53-54	16.7	21.1	66	0.21
" " 54-55	16.7	18.3	43	0.48
" " 55-56	16.7	18.7	46	0.41
" : 56-57	16.7	17.2	36	0.83
San Pedro 55-56	16.7	16.4	31	0.95
" : 56-57	16.7	19.0	48	0.56
Newport 55-56	15.9	16.5	31	0.61
" 56-57	16.5	19.3	50	0.34
San Clemente 56-57	15.9	19.1	49	0.40
Oceanside 55-56	16.8	31.0	209	0.09
" 56-57	16.8	24.1	98	0.17
San Diego	16.8	16.6	32	0.69
San Diego	16.8	18.2	42	0.48

$\log W_\infty = 2.496 - 0.048T$; $r = -0.371$

Nemipterus japonicus

Pauly (1978a, p. 84), Surface temperature: Anon (1944)

Locality	°C	L_∞	W_∞	K
Andra-Orissa Coast	27.5	30.5	284	0.314
" " "	27.5	20.9	91	0.648
" " "	27.5	30.7	289	0.294
Off Bruneo	28.4	28.9	241	0.470
Hong Kong ♂	23.3	38.0	549	0.13
" " ♀	23.3	34.0	393	0.19

$\log W_\infty = 4.419 - 0.076T$; $r = -0.663$

Gasterosteus aculeatus

Pauly (1978a, p. 70), Surface temperature: Anon (1944)

Locality	°C	L_∞	W_∞	K
Brackish Waters, Roscoff ♂	12.5	4.6	0.63	4.20
" " " ♀	12.5	6.0	1.40	2.40
Eelgrass Beds, Kiel Bay	8.2*	6.9	2.14	1.79
Ooster Schelde, Holland	10.8	6.7	1.95	2.32

*from Worthmann (1975) $\log W_\infty = 1.088 - 0.086T$; $r = -0.724$

TABLE XIIIb

Relationship of K to Mean Environmental Temperature

Pseudopleuronectes americanus

Pauly (1978a, p. 90), with data of Poole (1969)**
Bottom temperature: Colton & Stoddard (1973)

Locality	°C	L_∞	W_∞	K
Great South Bay (N.Y.)**	9.7	35.7	666	0.285
Northcumberland Strait	6.3	39.0	926	0.259
Pubnico Bay	6.1	57.7	2881	0.113
Charleston Pond (R.I.)	10.5	32.6	520	0.428
" " "	10.5	39.8	946	0.384
Narraganset Bay (R.I.)	10.5	43.6	1243	0.199
" " "	10.5	45.5	1413	0.283
Passamaquoddy Bay (USA/Can.)	6.7	41.6	1080	0.195
Anapolis Bay	≈15.5*	43.6	1243	0.323
Peronic & Gardiners Bay	6.1	50.6	1943	0.175

*Diaz, 1977, pers. comm.

$\log W_\infty = 3.279 - 0.024T$; $r = -0.330$

Micromesistius poutassou

Pauly (1978a, p. 64) Bottom or near-bottom temperature combined from Schroeder (1963) and Anon. (1944)

Locality	°C	L_∞	W_∞	K
Faroe Islands	6	33.4	373	0.230
Costa Brava, Spain	16	29.7	262	0.600
Tuscan Archipelago, Italy	15	28.7	222	0.480
Iceland	7	37.4	523	0.360
Scotland, 57°N 11°W	8	39.9	635	0.150
Eastern Spanish Coast, Medit.	16	31.8	322	0.365

$\log W_\infty = 2.843 - 0.26T$; $r = -0.802$

Scomber scombrus

Pauly (1978a, p. 103) and excluding North Sea, Central North Sea, and Newfoundland stocks. Surface temperature: Anon. (1944)

Locality	°C	L_∞	W_∞	k
English Channel & Irish Sea	10.7	41.8	659	0.430
Western Mediterranean	18.7	35.	375	0.500
New England	10.	46.1	900	0.234
New England	10.	44.5	803	0.269
Celtic Sea	11.9	37.4	463	0.470
English Channel	11.7	37.0	447	0.560
New England	10.	47.3	977	0.262
Southern North Sea	11.2	42.0	669	0.238

$\log W_\infty = 3.278 - 0.041T$; $r = -0.774$*

Sardinella aurita

Pauly (1978a, p. 42), excluding four stocks with extreme values of L_∞. Surface temperature: Anon (1944)

Locality	°C	L_∞	W_∞	K
Pointe Noire, Congo	25.0	26.0	158	1.023
" " "	25.0	26.0	158	1.208
Balearic Islands	18.7	27.7	191	0.447
" "	18.7	30.0	243	0.350
" "	18.7	35.0	386	0.250
Agean	19.1	29.0	220	0.500
Castiglione Bight, Algeria	18.7	25.0	141	0.534
Israel Coast	22.2	31.1	271	0.250
Rio de Janeiro, Brazil	23.2	24.5	132	0.423

$\log W_\infty = 2.831 - 0.025T$; $r = -0.466$

TABLE XIIIc

Relationship of K to Mean Environmental Temperature

Merluccius merluccius

Pauly (1978a, p. 79), excluding "Mediterranean" stock. Bottom and near-bottom temperature: combined from Schroeder (1963) and Anon. (1941, 1944)

Locality	°C	L_∞	W_∞	K
Biscaya	11	105.	8100	0.184
off Morocco	14	85.0	4400	0.210
off Morocco, 30-40°N	14	100.	7000	0.158
off Ireland	12	83.9	4134	0.296
off Morocco, Agadir Bight	14	112.	9834	0.121
off Fano, Italy	15	42.1	522	0.405
Mediterranean, North Africa	16	38.4	396	0.220
Marmara Sea	15	44.0	596	0.130
" "	15	60.0	1512	0.100
Central Adriatic	15	62.0	1668	0.344
off Tunesia	16	40.0	448	0.200
Costa Brava, Spain	16	28.9	169	0.634
" " "	16	59.6	1482	0.390
" " "	16	60.8	1573	0.255
" " "	16	19.7	54	0.446
" " "	16	43.3	568	0.142

$\log W_\infty = 7.551 - 0.302T; \quad r = -0.721^{**}$

Sardinops caerula

Pauly (1978a, p. 43), excluding "California" and "British Columbia" stocks. Surface temperature: Anon. (1944)

Locality	°C	L_∞	W_∞	K
San Francisco	12.8	29.5	205	0.398
Baja California	18.5	26.0	141	0.500
San Pedro	16.7	26.0	141	0.540
" "	16.7	26.1	142	0.520
" "	16.7	27.6	168	0.530
" "	16.7	26.9	156	0.560
" "	16.7	25.7	136	0.550
" "	16.7	26.8	154	0.590
Monterey	13.1	30.0	216	0.350

$\log W_\infty = 2.775 - 0.036T; \quad r = -0.903^{**}$

Mugil cephalus

Pauly (1978a, p. 81). Surface temperature: Anon. (1944)

Locality	°C	L_∞	W_∞	K
Marmara Sea	16.1	71.5	4386	0.254
Bosporus	16.1	105.	13890	0.110
Tunisian Coast ♂	18.7	48.6	1377	0.290
" " ♀	18.7	54.6	1953	0.200
Texas Coast ♂	24.6	40.0	768	0.367
" " ♀	24.6	42.2	902	0.327
Taiwan Coast ♂	22.4	49.8	1482	0.393
" " ♀	22.4	59.3	2502	0.301

$\log W_\infty = 5.246 - 0.094T; \quad r = -0.806^{*}$

TABLE XIIId

Relationship of K to Mean Environmental Temperature

Lepibema chrysops

Based on data in Carlander (1950, p. 210). Air temperature: Walter & Leith (1967)

Locality	°C	L_∞	W_∞	K
"Minnesota"	5.2	46.2	1233	0.238
Lake Erie	10.4	35.7	569	0.454
Iowa, Spirit Lake ♂	8.3	37.6	664	0.550
" " " ♀	8.3	39.6	776	0.508
Iowa, Clear Lake	7.9	36.9	628	0.585
" Storm Lake	8.6	39.2	753	0.729
"Minnesota"	5.2	48.0	1382	0.228
"	5.2	45.1	1147	0.235
Lake Erie	10.4	37.5	659	0.456
Iowa, Spirit Lake ♂	8.3	40.6	837	0.552
" " " ♀	8.3	42.9	987	0.503
" Clear Lake	7.9	40.4	824	0.591

$\log W_\infty = 3.398 - 0.061T$; $r = -0.881$**

Brevoortia tyrannus

See Pauly (1978a, p. 45) data of Henry (1971). Surface temperature: Anon. (1944)

Locality	°C	n
South Atlantic	23.3	6
Middle Atlantic	21.1	6
North Atlantic	13.3	7

See precise localities in Henry (1971)

The data of Henry (1971) consist of weight-at-age data from which W_∞ and K have been directly estimated. The values of L_∞ given in Pauly (1978a) were obtained by means of a condition factor of 1.61 which may be used for conversions back to weight.

Esox lucius

Based on data in Carlander (1950, p. 121).

Locality	°C	L_∞	W_∞	K
Minnesota Lake of the Woods	2.3	172	30531	0.067
"Minnesota"	5.2*	128	12583	0.131
"	5.2	208	53993	0.069
"	5.2	126	12002	0.124
"	5.2	125	11719	0.133
"Wisconsin"	5.8*	133	14116	0.167
"Ohio"	11.1*	142	17180	0.162

*Central locations in each state

$\log W_\infty = 4.385 - 0.021T$; $r = -0.221$

Lepomis macrochirus

Based on data in Carlander (1950, p. 184); air temperature: Walter & Lieth (1967).

Locality	°C	L_∞	W_∞	K
Iowa, East Lake	11.4	24.1	367	0.318
Indiana, Foots Pond	11.4	19.5	194	0.518
" Red Haw Hill Lake	11.1	31.4	811	0.231
" average	11.4	29.8	693	0.196
" Foots Pond	11.4	19.8	203	0.479
" Muskellunge Lake	9.7	23.2	327	0.338
Ohio, Kiser Lake	11.1	19.2	185	0.340
" Lake Meander	11.1	27.7	557	0.199
Illinois, 5 Lakes	12.3	23.6	344	0.318
Minnesota	5.2	28.7	619	0.191
Ohio, average	11.1	24.7	395	0.264
Illinois, Homewood Lake	12.3	15.1	90	0.786
Indiana, Foots Pond	11.4	20.1	213	0.500
Illinois, Onized Lake	14.0	23.3	331	0.475

$\log W_\infty = 3.046 - 0.048T$; $r = -0.353$

TABLE XIIIc

Relationship of K to Mean Environmental Temperature

Coregonus lavaretus

(Pauly, 1978a, p. 96), excluding Peene-Achterwasser stock.
Air temperature: Walter & Lieth (1967).

Locality	°C	L_∞	W_∞	K
Lower Lena River	(2)*	96.8	10884	0.032
Haweswater & Hullswater	9.5	41.0	827	0.741
Attersee, FRG	7.9	43.8	1008	0.447
Lake Constance	8.5	44.0	1022	0.298
" "	8.5	39.8	757	0.417
" "	8.5	52.8	1766	0.267

*Assumed water temperature

$\log W_\infty = 4.325 - 0.153T$; $r = -0.954$**

Cetengraulis mysticetus

Pauly (1978a, p. 56) excluding 2nd Gulf of Fonseca stock.
Surface temperature: Bayliff (1967)

Locality	°C	L_∞	W_∞	K
Almejas Bay	24.8	19.9	63	1.23
Guaymas Bay	24.8	17.0	39	2.58
Ahome Point	24.4	17.5	43	2.42
Gulf of Fonseca	29.4	18.5	51	2.92
Montijo Bay	28.7	19.1	56	2.42
Gulf of Panama	27.3	17.9	46	2.36
" " "	27.3	20.4	68	1.31
Columbia	26.8	17.2	41	2.09
Gulf of Guayaquil	24.9	17.4	42	1.34

$\log W_\infty = 1.249 + 0.017T$; $r = +0.355$

Abramis brama

Pauly (1978a, p. 49*), air temperature: Walter & Lieth (1967)

Locality	°C	L_∞	W_∞	K
Aral Lake	6.6	51.9	2097	0.153
" "	6.6	54.1	2000	0.241
Rybinsk Reservoir	2.9	86.1	9574	0.068
Volgograd Reservoir	5.4	111.	20514	0.077
Lake Ladoga	3.3	90.0	10935	0.076
Njemen River	6.5	109.	19425	0.096
Danube Delta	10.8	74.7	6252	0.165
Dnepr, Middle Course	7.0	65.5	4215	0.191
Dnepr Delta	9.8	73.0	5835	0.191
Ilmen Lake	3.3	86.4	9675	0.093
Volga, near Kuybyshev	3.7	93.1	12104	0.081
Vistula, near Warshaw	7.6	125.	29300	0.045
Lake Constance	8.6	84.2	8954	0.110
Muggelsee (near Berlin)	8.3	61.8	3540	0.065
Hjalmaren Lake (Sweden)	5.4	77.2	6900	0.058
Ural River Delta	7.8	52.4	2158	0.429
Pskov Reservoir	4.7	72.9	5811	0.119

*Some values had to be omitted because the sampling area could not be located.

$\log W_\infty = 4.108 - 0.041T$; $r = -0.275$

TABLE XIIIf

Relationship of K to Mean Environmental Temperature

Clupea harengus (Buchan stock)

(Pauly, 1978a, p. 38), excluding year class 1956.

Year Class	°C[1)]	L_∞	W_∞	K	A
1952	9.1	31.1	226	0.28	5.8
1953	10.0	30.6	215	0.42	4.5
1954	9.5	30.7	217	0.30	4.6
1955	9.6	32.1	248	0.31	2.4
1957	9.7	32.9	267	0.28	3.0
1958	9.6	33.3	277	0.29	4.1
1959	10.1	32.9	267	0.32	1.1
1960	10.1	32.7	262	0.42	10.5
1961	9.8	32.7	262	0.48	4.7
1962	9.1	31.5	234	0.43	4.0

$\log K = -1.138 + \underline{0.070T}$, $r = 0.281$

$\log K = -1.112 + \underline{0.062T} - 0.012\,A$, $r\ 0.442$

A = an index of stock abundance, based on Fig. 138 in Burd (1978)

T = temperature, in °C

1) mean annual surface temperature in the year of birth of a given year class, as given by the Service Oceanographique, Intern. Council Explor. Mer. (various years) and Dietrich (1962).

Pomoxis nigromaculatus

Based on data in Carlander (1950, p. 206). Air temperature: Walter & Lieth (1967)

Locality	°C	L_∞	W_∞	K
Minnesota, Lake Vermillion	4.1	44.0	1533	0.184
Minnesota	5.2	46.8	1845	0.174
Indiana, Foots Pond	11.4	38.1	996	0.243
Iowa, Red Haw Hill Lake	11.1	30.4	506	0.555
North Carolina, Hiwassee Lake	15.6	33.4	671	0.593
Tennessee, Norris Lake	15.2	35.6	812	0.447
Indiana, Foots Pond	11.4	37.3	934	0.249
Minnesota	5.2	60.1	3907	0.111
Ohio, average	11.1	39.9	1143	0.182
Minnesota	5.2	40.3	1178	0.191
"	5.2	61.6	4207	0.110
Indiana, Foots Pond	11.4	34.9	765	0.297
Ohio	11.1	36.7	890	0.256
North Carolina, Hiwassee Lake	15.6	33.7	689	0.591
Tennessee, Norris Lake	15.2	35.2	785	0.857

$\log W_\infty = 3.547 - 0.048T$; $r = -0.769^{**}$

TABLE XIIIg

Relationship of K to Environmental Temperature: Ursin's (1967) Data on *Lebistes reticulatus*

All data from Ursin (1967, p. 2441). Negative and italic[1)] value of K omitted.

°C	K ♂	K ♀	°C	K ♂	K ♀
18.6	2.72	1.07	22.7	0.67	1.08
18.7	1.50	0.18	23.5	3.02	0.99
19.1	3.00	1.87	23.7	0.46	--
20.3	0.89	0.13	23.8	4.57	1.60
20.4	1.93	2.08	24.9	0.41	1.37
20.5	3.73	1.80	24.9	0.61	1.60
20.5	--	0.30	24.9	1.43	1.41
20.5	--	1.39	24.9	0.74	1.78
20.5	0.78	1.47	25.3	3.18	2.05
20.6	1.98	1.22	26.4	--	1.48
20.6	1.32	0.44	27.5	2.91	--
20.6	0.31	1.30	28.6	1.00	0.63
20.8	--	1.24	28.7	3.25	0.88
21.0	2.07	1.15	28.9	--	3.87
21.1	0.71	1.73	29.2	6.17	2.42
22.0	1.01	1.14	29.6	--	1.90
22.1	1.20	0.05	30.7	6.03	2.67

1) Values considered to be erroneous by Ursin (1967)

TABLE XIIIh

Relationship of K to Environmental Temperature. Taylor (1958) Data on *Gadus morhua*, with derivation of values of P_{20}

Mean surface temperature, °C 1)	L_∞ 1)	W_∞ 2)	K 1)	P 3)	$W_{\infty 20}$ 4)	K_{20} 4)	P_{20} 5)
11.5	98.8	9644	0.281	3.43	2816	0.641	3.26
7.5	123.5	18837	0.118	3.35	2637	0.440	3.06
4.6	200.3	80361	0.064	3.71	6252	0.316	3.30
5.4	146.6	31507	0.096	3.48	3018	0.474	3.16
8.0	109.6	13165	0.219	3.46	2027	0.762	3.19
6.7	127.6	20776	0.147	3.48	2474	0.610	3.19
5.6	188.5	66978	0.080	3.73	6416	0.384	3.38
9.6	143.5	29550	0.167	3.69	6282	0.408	3.41
8.4	95.9	8820	0.284	3.40	1478	0.939	3.14
6.3	154.0	36523	0.069	3.40	4014	0.302	3.08
5.7	134.0	24061	0.109	3.42	2348	0.517	3.08
mean 7.2	--	--	mean	3.50	--	--	3.20

1) from Taylor (1958, Table 1)

2) assuming a condition factor of 1.00

3) $P = \log K + \log W_\infty$

4) converted with multipliers (qw) in Table XVII

5) $P_{20} = \log K_{20} + \log W_{\infty 20}$

$\log W_\infty = 5.186 - 0.111T$; $r = -0.735^{**}$

TABLE XIV

Plots of Log K Against Temperature (5 to 30°). Summary of Data (See also Fig. 10)

No.	Species	n	r	a	b	°C	ln b	ln bn	Δ ln b	Remarks
1	Abramis brama	17	0.416	-1.243	0.045	6.4	-3.102	-2.812	-0.290	
2	Brevoortia tyrannus	19	0.526	-0.974	0.028	18.9	-3.576	-3.264	-0.310	
3	Centengraulis mysticetus	9	0.397	-0.526	0.031	26.5	-3.474	-3.362	-0.112	
4	Clupea harengus	10	--	--	0.062	9.7	-2.781	-2.956	+0.175	See multiple regression, Table XIIIf
5	Coregonus lavaretus	6	0.964	-1.833	0.168	7.5	-1.784	-2.861	+1.077	
6	Cyprinodon macularius	5	--	--	0.025	25.	-3.689	-3.355	-0.334	{in Taylor (1962) from Kinne (1960)
7	Gadus morhua	11	0.840	-1.564	0.094	7.2	-2.364	-2.848	-0.486	Table XIIIh & Taylor (1958)
8	" "	12	--	--	0.065	(7.2)	-2.733	-2.848	+0.115	{In Jones (1976), based on Taylor (1958)
9	Gasterosteus aculeatus	4	0.762	-0.238	0.058	11.0	-2.847	-3.009	+0.162	
10	Engraulis mordax	25	0.501	-1.832	0.088	15.5	-2.430	-3.171	+0.741	
11	Esox lucius	7	0.638	-1.165	0.040	5.7	-3.219	-2.781	-0.438	
12	Lebistes reticulatus ♀	32	0.372	-0.937	0.041	23.4	-3.194	-3.342	+0.148	} see note
13	" " ♂	28	0.278	-0.503	0.029	23.2	-3.540	-3.339	-0.201	
14	Lepibema chrysops	12	0.732	-0.870	0.066	7.8	-2.718	-2.875	+0.157	
15	Lepomis macrochirus	14	0.506	-1.013	0.049	11.1	-3.016	-3.013	-0.003	
16	Merluccius merluccius	16	0.242	-1.178	0.037	14.8	-3.297	-3.148	-0.149	
17	Micromestitius poutassou	6	0.729	-0.854	0.033	11.3	-3.411	-3.021	-0.390	
18	Mugil cephalus	8	0.752	-1.363	0.038	20.4	-3.270	-3.296	+0.026	
19	Nemipterus japonicus	6	0.856	-2.990	0.094	26.3	-2.364	-3.361	+0.997	
20	Pomoxis nigromaculatus	15	0.856	-1.123	0.055	10.3	-2.900	-2.981	+0.081	
21	Pseudopleuronectes americanus	10	0.639	-0.950	0.037	9.2	-3.297	-2.935	-0.362	
22	Sardinella aurita	9	0.627	-1.438	0.053	21.0	-2.937	-3.308	+0.370	
23	Sardinops caerula	9	0.834	-0.843	0.034	16.1	-3.381	-3.189	-0.192	
24	Scomber scombrus	8	0.560	-0.818	0.031	11.8	-3.474	-3.040	-0.433	

mean = +0.015; s.d. = 0.430

Note: The data for Lebistes reticulatus were obtained from Ursin (1967, p. 2441) (see Table XIIIg). In addition to these data, Ursin (1967) gives estimates of the slope of ln K against temperature as estimated from fasting males L. reticulatus. These plots provide an equally good fit to the normal curve (see data in Ursin, 1967, p. 2414 ff).

6.3. The Relationship Between Asymptotic Size and Temperature

On the basis of a vast body of data, it was demonstrated in Chapter 5.4. that the asymptotic size of fishes decreases with increasing values of K, and an average slope (-2/3) for plots of log K on log W_∞ and/or L_∞^3 was proposed. In the previous section of this chapter, it was demonstrated that the value of K tends to increase with temperature - at least within the range of 5 to 30° C - and that this increase could be described by Krogh's normal curve.

These two relationships suggest that asymptotic size should be negatively correlated with environmental temperature. This inference is confirmed by the empirical data on temperature and asymptotic size compiled in Table XIII (a-h).

Of 18 species for which log W_∞ was plotted against estimates of mean environmental temperature, 17 have a slope with a negative sign. (The only positive slope value is not significantly $\neq 0$). Of the 18 slope values, 8 are significantly lower than zero - 6 at 99% and 2 at 95% level (See Table XIIIa-h).

The data of Table XIII thus confirm that asymptotic size, in fishes, and within the range 5 to 30° C, tends to decrease with increasing temperature. These data, on the other hand, are not sufficient in scope to investigate the relationship between temperature and asymptotic size in quantitative terms. The quantitative relationship between asymptotic size and temperature, however, can be obtained indirectly, by relating asymptotic weight to K by means of Equation 74 , then by relating K to temperature by means of Krogh's normal curve. Table XVII gives factors, obtained in this manner for the conversion of values of W_∞ to their value at 20° C.

6.4. The Phenomenon of "Cold Adaptation" and Fish Growth

The number of authors having noticed and discussed the fact that polar fishes are generally smaller than their (cold) temperate counterparts is very limited, although the fact itself seems to be well established.

Suvorov (1959, p. 348) writes (freely translated):

> The subarctic species are larger than the boreal ones. Maximal sizes are reached in those areas where temperate and arctic water meet.

May *et al.* (1965), who investigated the growth of cod off Labrador-Newfoundland, summarize their findings as follows:

> The highest value of K and lowest values of L_∞ are found in the cooler waters of higher latitudes, while the reverse is true in warmer waters to the South. This does not conform to most of the findings in fisheries literature.

The results of May *et al.* (1965) or the rule of Suvorov (1959) have apparently never been incorporated into any generalized theory of fish growth, possibly because they seem to contradict the well-known "Bergmann rule" which states that animals tend to reach a larger adult size, the lower the mean temperature of their environment is. (See von Bertalanffy, 1951, p. 351 ff.).

Working on the energy metabolism of tropical, temperate and polar fishes, Scholander *et al.* (1953) found that polar fishes display a rate of O_2 consumption much higher than would be expected from an extrapolation - down to subzero temperature - of Krogh's normal curve. These findings were subsequently confirmed by Wohlschlag in a series of papers (1960, 1961, 1962 and 1964).

Considering that catabolism - hence also growth - is closely related to respiratory rate, it would seem that the relatively high respiratory rate of polar fishes could be used to explain the effects reported by Suvorov (1959) and May *et al.* (1965). Suvorov (1959), however, does not present data which could be used to quantify the reported effect. The growth data of May *et al.* (1965), on the other hand, are related to value of latitude (Fig. 11) and an attempt has therefore to be made to convert the latitude values into estimates of environmental temperature.

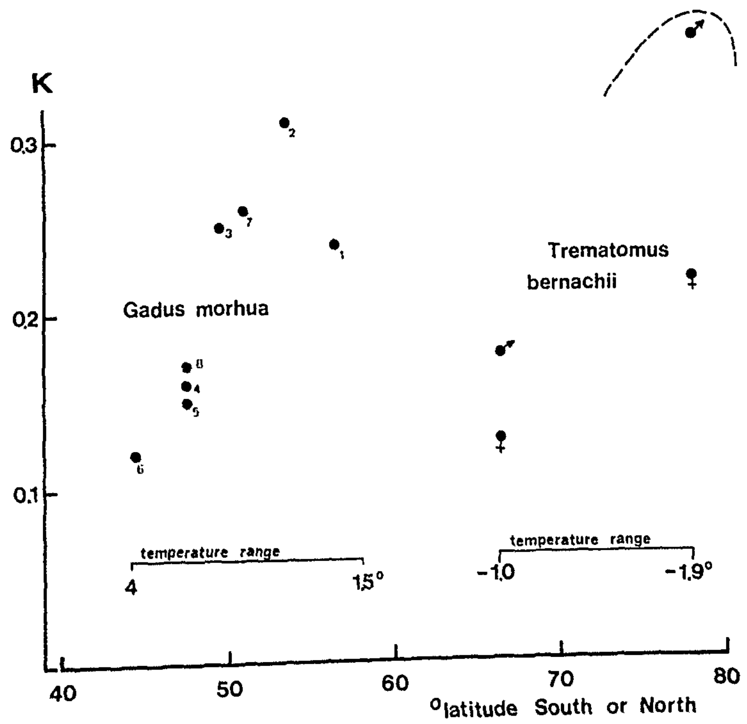


Fig. 11 Plot of K on latitude (North or South in *Gadus morhua* and *Trematomus bernachii*.

The average temperature profiles over the continental shelf off Labrador and Newfoundland presented by May *et al.* (1965, Fig. 4A to F and Fig. 5A to C) may be used to estimate the mean environmental temperature for the various cod stocks that were investigated.

The mean temperature in the depth range 100 to 200 m (sampling depth) was obtained for various latitudes through planimetry of the nine temperature profiles given, and the mean temperatures so obtained plotted against the mean latitude of each profile (Table XVa, Fig. 12). From Fig. 12, a temperature estimate can be obtained for each of the stocks whose growth parameters and mean latitude were given (Table XVb).

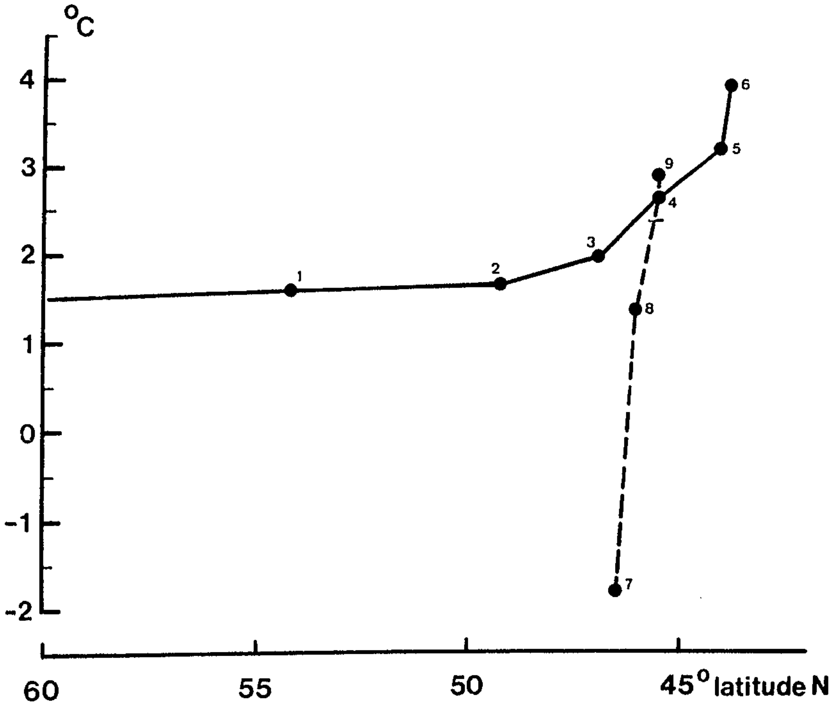


Fig. 12 Conversion of latitude to water temperature, data of May *et al.* (1965).

As assumed by May *et al.* (1965), there is a close negative relationship between latitude and temperature (Fig. 12). Consequently, there is a close negative relationship between log K and environmental temperature (Fig. 13) which may be expressed by the equation:

$$\log K = -0.318 - 0.181 \cdot T; \quad r = -0.755^{*} \qquad \ldots 76)$$

from Equation 76 and the relationship established by Taylor (1958) where

$$\log K = -1.564 + 0.094 \cdot T \qquad \ldots 77)$$

TABLE XV

Data on Cold-Adapted Cod, Based on May *et al.* (1965)

a)

Figure	Location	Line No.	Mean Latitude	Mean Temp.
4A	Seal Islands	1	54.2	+1.6
4B	Bonavista	2	49.3	+1.7
4C	St John - Flemish Cap	3	47.0	+2.0
4D	St John - Southeast Edge	4	45.6	+2.7
4E	Grand Bank	5	44.2	+3.5
4F	Southwest Edge	6	44.0	+4.0
5A	Avalon Channel	7	46.5	-1.8
5B	St Pierre Bank (N)	8	46.1	+1.4
5C	St Pierre Bank (S)	9	45.6	+2.9

b)

No.	ICNAF Area	Mean Latitude	Temperature	K	L_∞
1	2 H	55.5	1.6	0.24	64
2	2 I	53.5	1.6	0.31	65
3	3 K	51	1.7	0.26	77
4	3 L	47	2.0	0.16	102
5	3 M	47	2.0	0.15	98
6	3 N-O	44.5	3.1	0.12	130
7	3 P_N	49.5	≃2.	0.25	78
8	3 P_S	47	≃3.	0.17	101

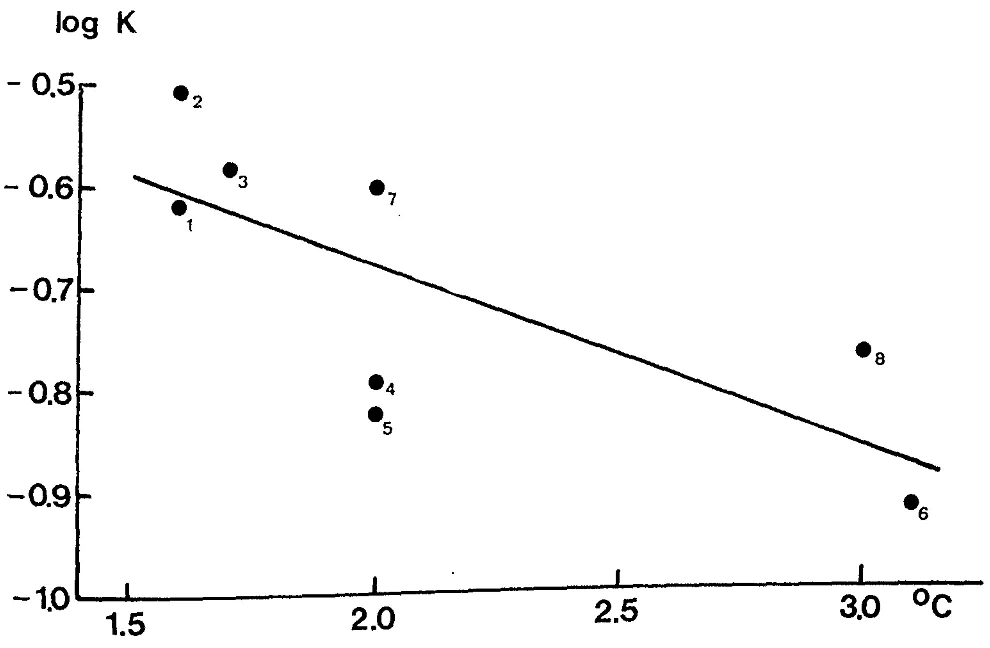


Fig. 13 Plot of log K on temperature, cold-adapted cod (Labrador-Newfoundland).

the temperature which produces the lowest values of K may be estimated as the intersection of the regression lines (Equations 76 and 77). The intersection occurs at T = 4-5°C, at which temperature K should be lowest. Other data which could be used to quantify the relationship between K and temperature in very cold environments (-2 to+4° C) are very scanty.

The growth of stocks of the family Nototheniidae has been investigated by numerous authors (See Pauly, 1978a, or Everson, 1977 for compilations of growth parameters of Nototheniidae and other Antarctic fishes). While covering a considerable number of species, these compilations present only limited data which could be used for comparative studies within single species. Also, the Nototheniids possess a biological feature which makes the use of the VBGF for the description of their growth particularly inappropriate: most Nototheniids apparently change their mode of life quite radically in the course of their life history (transition to feeding on krill?) which might make the use of any *single* set of growth parameters as illusory as in the case of the diadromous *Salvenilus alpinus* (See p. 31 ff.). Thus, in most cases, the growth parameters for Nototheniids appear to be very much more dependent upon the range of size-at-age data used for their determination than, say, in the case of cod.

As a result, the growth parameters of only four well documented stocks, all belonging to the Nototheniid species *Trematomus bernachii*, could be used here for the analysis of the relationship between log K and temperature in Antarctic fishes (Table XVI and Fig. 11). In this species, the slope relating log K to environmental temperature is -0.193, a value close to that obtained from cod data (-0.181).

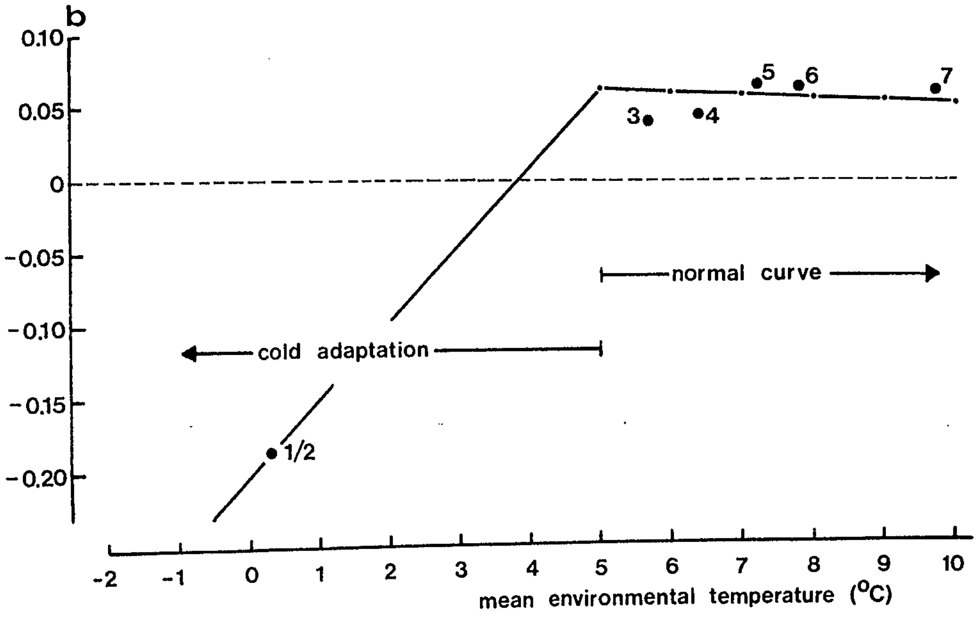


Fig. 14 Slope of plots of log K against temperature for the temperature range -2 to 10°C. 1/2: mean of *G. morhua* and *T. bernachii* slopes (see Tables XV & XVI); 3: *Esox lucius*; 4: *Abramis brama*; 5: *Gadus morhua* (Jones, 1976); 6; *Lepibema chrysops*; 7: *Clupea harengus*. See Table XIV.

These two values of b were used for the plot in Fig. 14 where, for lack of a better alternative, a straight line was drawn which links the value of b at 5° C (the end of Krogh's normal curve) to the mean of the coordinates for the two cold-adapted fishes ($\overline{b}$ = -0.187, $\overline{T}$ = +0.3 °C). This procedure appears justified, as the data on cod suggest a higher slope value at lower temperatures than at higher temperatures (See Fig. 13).

Thus, b may be estimated for the range -2° C to 5° C from

$$b = -0.2044 + 0.0537 \cdot T \qquad \text{.... 78)}$$

(See Fig. 14). When integrating Equation 78 to

$$\log K = -0.2044T + \frac{0.0537}{2} T^2 + C \qquad \text{.... 79)}$$

the value of C may be defined such as to adjust the value of log K to its value at 5° C (= 1.2848), or

$$C = 1.2848 - (-0.2044 \cdot 5 + \frac{0.0537}{2} . \cdot 5^2 = 1.6356 \qquad \text{.... 80)}$$

Thus, Equation 79 becomes

$$\log K = 1.6356 - 0.2044 \cdot T + 0.02685\, T^2 \qquad \text{.... 81)}$$

From the values provided by Equation 81 , multiplicative factors can be derived which correspond to the conversion factors given by Winberg (1960, 1971) for use in connection with Krogh's normal curve (See Table XII).

Table XVII gives values of q_K (conversion factor for K to 20°C) which define the normal curve over the expanded temperature range of -2 to 40°C (the extension in the range 30 to 40°C is based on extrapolation of the normal curve). Note that the q_K value of 0.705 for -2°C is close to the q_K value of 0.717, applying to temperatures of 24°C. That is, cold-adapted fishes growing at a temperature of about -2°C have growth parameters that correspond to those of ecologically similar fishes growing at temperatures of about 24°C.

This confirms Wohlschlag (1962) who writes:

> Thus, not only are these Antarctic fishes cold-adapted with respect to total metabolism, which at low temperature is of the same order as for more temperate species at higher temperatures; they are also "cold-adapted" with respect to growth (anabolism) and maintenance (catabolism).

TABLE XVI

Growth Parameters and Environmental Temperature of Some *Trematomus bernachii* Stocks

(Fam. Nototheniidae)

Locality	°C	L_∞	K	Sex	Author
Terre Adélie	-1.0	28.6	0.185	♂	Hureau (1970)
" "	-1.0	31.4	0.192	♀	Hureau (1970)
McMurdo Sound	-1.9	23.0	0.36	♂	Wohlschlag (1962)
" "	-1.9	30.7	0.22	♀	Wohlschlag (1962)

Plot of log K against temperature: $\log K = -0.918 - 0.193T$

$r = -0.754$

TABLE XVII

Multipliers* for the Conversion of Values of K, W_∞ and L_∞ to 20°C

°C	q_K	q_W*	q_L*	°C	q_K	q_W*	q_L*
-2.0	0.705	1.69	1.19	15	1.57	0.508	0.798
-1.5	0.994	1.01	1.00	16	1.43	0.585	0.836
-1.0	1.36	0.631	0.858	17	1.31	0.667	0.874
-0.5	1.80	0.414	0.745	18	1.20	0.761	0.913
0	2.31	0.285	0.658	19	1.09	0.879	0.958
0.5	2.88	0.205	0.590	20	1.00	1.00	1.00
1	3.48	0.154	0.536	21	0.920	1.13	1.04
2	4.63	0.100	0.464	22	0.847	1.28	1.09
3	5.44	0.079	0.429	23	0.779	1.45	1.13
4	5.65	0.074	0.420	24	0.717	1.65	1.18
5	5.19	0.085	0.440	25	0.659	1.87	1.23
6	4.55	0.103	0.469	26	0.609	2.10	1.28
7	3.98	0.126	0.501	27	0.563	2.37	1.33
8	3.48	0.154	0.536	28	0.520	2.67	1.39
9	3.05	0.188	0.573	29	0.481	3.00	1.44
10	2.67	0.229	0.612	30	0.444	3.38	1.50
11	2.40	0.269	0.646	32.5	0.365	4.54	1.66
12	2.16	0.315	0.680	35	0.299	6.12	1.83
13	1.94	0.370	0.718	37.5	0.246	8.20	2.02
14	1.74	0.436	0.758	40	0.202	11.0	2.22

*q_W & q_L apply only to asymptotic sizes used in conjunction with the special VBGF.

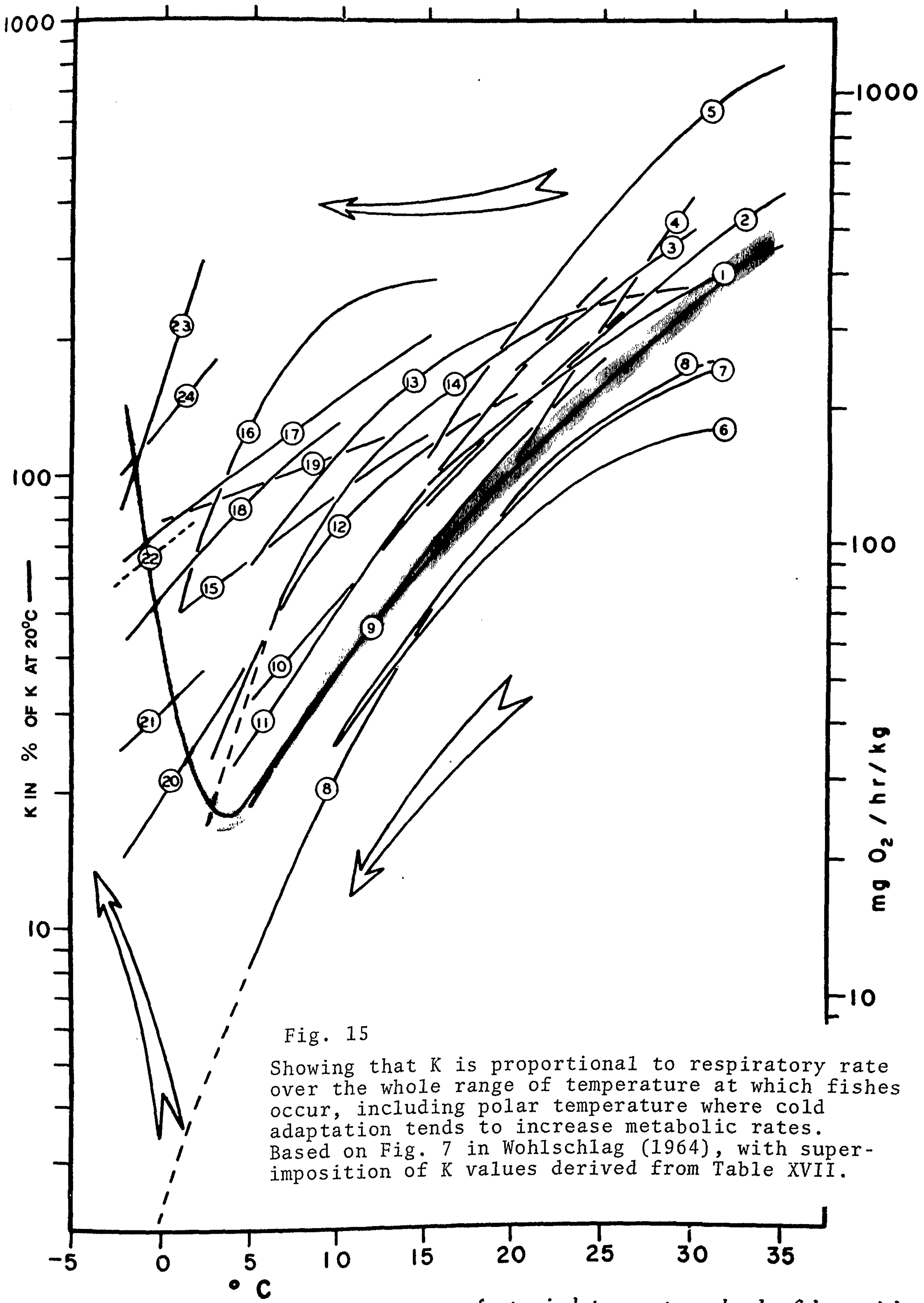


Fig. 15

Showing that K is proportional to respiratory rate over the whole range of temperature at which fishes occur, including polar temperature where cold adaptation tends to increase metabolic rates. Based on Fig. 7 in Wohlschlag (1964), with superimposition of K values derived from Table XVII.

Relationships of metabolism to temperature for tropical, temperate, and polar fishes weighing about 5 grams. Lines 1–5, tropical; lines 6–14, temperate; lines 15–19, arctic; lines 20–24, The close correlation between the growth parameter K and respiratory rate, previously discussed in terms of the normal curve, thus appears to sustain itself at very low temperatures. Indeed, the extension of the normal curve presented in Table XVII can be used to estimate the respiratory rates of fishes at near and subzero temperatures, as suggested by the superimposition of the extended normal curve onto the respiratory curves compiled by Wohlschlag (1964). (See Figure 15.)

A possible interpretation for the physiological cause for the cold adaptation effect will be given in connection with the definition of the growth parameter K (Chapter 9).

6.5. The Concept of P_{20}

Table XVII allows for the conversion of any set of K and W_∞ values to the values they would have had, had the fish grown at 20°C. The new values, K_{20} and $W_{\infty 20}$, allow for the estimation of the value of P at 20°C, or P_{20}, which is here suggested as an indicator of overall growth performance that is both independent of size and of temperature. The concepts of K_{20} and $W_{\infty 20}$ are essentially similar to the convention used by respiratory physiologists to standardize their results by converting them to a standard temperature, generally 20°C (See Winberg, 1960).

7. THE RELATIONSHIP BETWEEN GILL SIZE AND GROWTH PERFORMANCE

The main question examined in this chapter is whether there is a relationship, in fishes, between the growth performance, as expressed in units of P_{20}, and gill size, as expressed by the Gill Size Index (GSI, see p. 39f for definition).

The main advantage of these two indices, it may be recalled, is that they allow for the comparison of gill size and growth performance after removal of the effects of size and temperature on gill size and growth performance.

The GSI data used here are based exclusively on data compiled by Hughes & Morgan (1973b), which has the following advantages:

a) The compilation covers over 100 different fish species, which allowed for a large number (60) of species in which both gill surface and growth data were available.

b) These authors 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.

The data were processed as follows:

1) For each species for which growth data were available, growth parameters were estimated using one of the standard methods. Where several sets of growth data were available, only the best documented was used.

2) A mean temperature was attributed to each set of growth parameters, using the same sources for the temperature data as referenced in Chapter 6.

3) By means of the multipliers in Table XVII, the values of K_{20} and $W_{\infty 20}$ were estimated, and values of P_{20} calculated.

4) Values of d were calculated for each value of W_∞ by means of Equation 70 .

5) On the basis of these values of d, values of GSI were estimated from the gill size-weight data of Table 4 in Hughes & Morgan (1973b). Where several gill size-weight data pairs were given for one single species, the GSI represents the mean of these pairs, with the exception of a few cases where the mean was calculated after the exclusion of never more than one aberrant gill size-weight pairs.

The data so obtained are summarized in Table XVIII. For further interpretation, it appears appropriate to divide the data in Table XVIII into marine fishes (42 spp.), and fresh water fishes (18 spp.).

The plot of log GSI against P_{20} in marine fishes (Fig. 16) suggests a very close relationship between gill size and growth performance.

When four obvious outliers are excluded, a highly significant correlation is obtained (r = 0.730**). The regression line is

$$\log GSI = 0.488 + 0.233\, P_{20} \qquad \ldots. 82)$$

from which values of GSI may be obtained from values of P_{20}.

TABLE XVIII Relationship between Gill Size and Growth Performance, Basic Data

No.	Fam.	Species	W_∞	K	d	T°C	P_{20}	GSI	Remarks
1	98	Scylliorhinus caniculus	550	0.530	0.772	10	2.25	8.54	Marine
2	102	Squalus acanthias	8280	0.074	0.814	10	2.57	13.37	M
3	108	Raja clavata	10644	0.15	0.818	10	2.29	4.46	M
4	152	Latimeria chalumnae	69900	0.209	0.847	20	4.17	0.773	not used
5	179	Acipenser stellatus	15675	0.192	0.824	8	3.21	5.79	Fresh-water
6	206	Clupea harengus	277	0.290	0.761	10	1.69	14.9	M
7	"	Brevoortia tyrannus	1009	0.343	0.782	18	2.50	51.58	not used
8	"	Alosa (Caspialosa) kessleri	603	0.349	0.774	10	1.94	2.03	F
9	207	Engraulis encrasicholus	24	1.123	0.723	12	1.36	55.13	not used
10	219	Salmo trutta	6520	0.185	0.811	10	2.87	11.10	F
11	"	Salmo gairdneri	962	0.563	0.781	10	2.52	6.09	F
12	234	Esox lucius	6049	0.230	0.809	10	2.93	40.27	F
13	285	Catastomus commersoni	1653	0.104	0.789	15	2.14	3.84	F
14	286	Chondrostoma nasus	484	0.217	0.770	12	1.85	20.45	F
15	"	Tinca tinca	493	0.710	0.770	12	2.24	8.47	F
16	"	Carassius auratus	508	0.334	0.771	15	2.13	3.55	F
17	"	Rutilus rutilus	321	0.163	0.764	12	1.55	5.28	F
18	"	Blicca bjoerkna	2025	0.101	0.764	12	1.19	40.54	not used
19	"	Cyprinus carpio	4866	0.157	0.805	12	2.72	4.44	F
20	299	Ictalurus (Ameiurus) nebulosus	1150	0.216	0.784	15	2.30	4.00	F
21	356	Lota lota	4535	0.237	0.805	8	2.76	9.23	F
22	"	Merlangius merlangus	472	0.426	0.770	8	2.03	10.51	M
23	"	Pollachius virens	11331	0.141	0.819	8	2.93	15.18	M
24	368	Hippocampus (hudsonius)	14	2.50	0.715	15	1.45	1.71	M
25	403	Zeus faber	7187	0.298	0.812	20	3.33	5.17	M
26	407	Mugil cephalus	13890	0.110	0.822	16	3.11	6.47	M
27	415	Roccus lineatus	17543	0.186	0.827	12	3.35	12.11	M
28	423	Micropterus dolomieu	1174	0.534	0.784	12	2.63	8.64	F
29	427	Acerina cernua	77	0.314	0.742	8	1.11	19.78	F
30	"	Perca fluviatilis	1184	0.123	0.784	8	1.97	16.33	F
31	"	Lucioperca lucioperca	6106	0.168	0.810	8	2.74	34.17	F
32	433	Pomatomus saltatrix	5808	0.197	0.809	24	3.13	24.55	M
33	436	Trachurus trachurus	598	0.270	0.773	20	2.21	17.00	M
34	441	Coryphaena hippurus	22070	0.575	0.829	25	4.19	18.80	M
35	453	Maena smaris	117	0.218	0.748	10	1.19	4.64	M
36	476	Tautoga onitis	2845	0.165	0.798	10	2.53	15.55	M
37	"	Crenilabrus melops	190	0.359	0.756	15	1.74	9.29	M
38	"	Labrus merula	990	0.234	0.781	15	2.27	4.32	M
39	508	Blennius pholis	54	0.90	0.736	12	1.04	6.29	M
40	522	Zoarces viviparus	965	0.203	0.781	8	2.02	12.54	M
41	532	Callionymus lyra	53	0.490	0.736	12	1.25	5.90	M
42	538	Trichiurus lepturus	4663	0.296	0.805	20	3.57	0.654	not used
43	539	Scomber scombrus	977	0.262	0.781	10	2.24	22.14	M
44	540	Scomberomorus maculatus	6911	0.20	0.811	25	3.23	24.68	M
45	558	Scorpaena (porcus)	869	0.177	0.779	15	2.09	2.90	M
46	559	Trigla gurnardus	534	0.312	0.772	8	1.95	4.57	M
47	570	Cottus gobio	6	0.550	0.702	8	0.25	11.90	not used
48	"	Cottus bubalis	102	0.230	0.746	8	1.10	9.31	M
49	"	Acanthocottus scorpius	377	0.539	0.766	8	2.04	3.91	M
50	579	Thunnus thynnus	987388	0.067	0.888	16	4.74	28.07	M
51	"	Thunnus albacares	198940	0.250	0.864	24	4.77	32.83	M
52	"	Euthynnus alliteratus	44869	0.164	0.840	24	3.94	84.40	M
53	"	Sarda sarda	3434	0.693	0.801	20	3.38	27.50	M
54	"	Katsuwonus pelamis	53200	0.179	0.844	25	4.09	54.67	M
55	583	Pleuronectes platessa	2171	0.170	0.793	8	2.30	14.45	M
56	"	Platichthys flesus	1058	0.229	0.782	8	2.11	13.02	M
57	"	Lophopsetta maculata	806	0.242	0.778	8	2.02	7.76	M
58	"	Pseudopleuronectes americanus	2881	0.113	0.798	8	2.96	7.58	M
59	601	Opsanus tau	568	0.258	0.773	12	2.00	5.78	M
60	602	Lophius piscatorius	53952	0.060	0.843	5	3.16	6.14	M

Note that as would be expected, it is mainly active, pelagic fishes which are found above the regression line, while less active, demersal fishes are found mainly below the regression line (See Fig. 16 and Table XVIII).

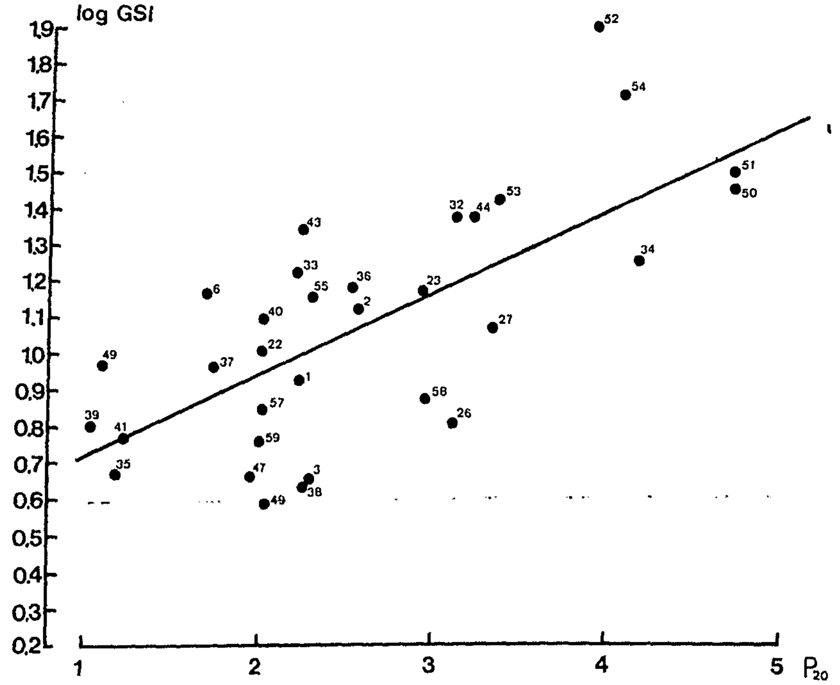


Fig. 16 Relationship between gill surface (GSI) and growth performance (P_{20}) in marine fishes. See also Table XVIII.

This relationship gives support to the hypothesis that it is gill size which determines the growth performance of fish, and that the growth performance of fishes in nature is mainly determined by oxygen availability - rather than food availability. The data of Fig. 16 do not, however, include all marine fishes. Four values (not the outliers mentioned above) were not plotted into Fig. 16 because they pertain to fishes that seem particularly sluggish. Therefore, the GSI/P_{20} values of *Hippocampus* sp, *Scorpaena* sp, *Zeus faber* and *Lophius piscatorius* have been plotted separately in Fig. 17 and fitted with a line with the same slope as Equation 82 passing through their mean value of log GSI and P_{20}.

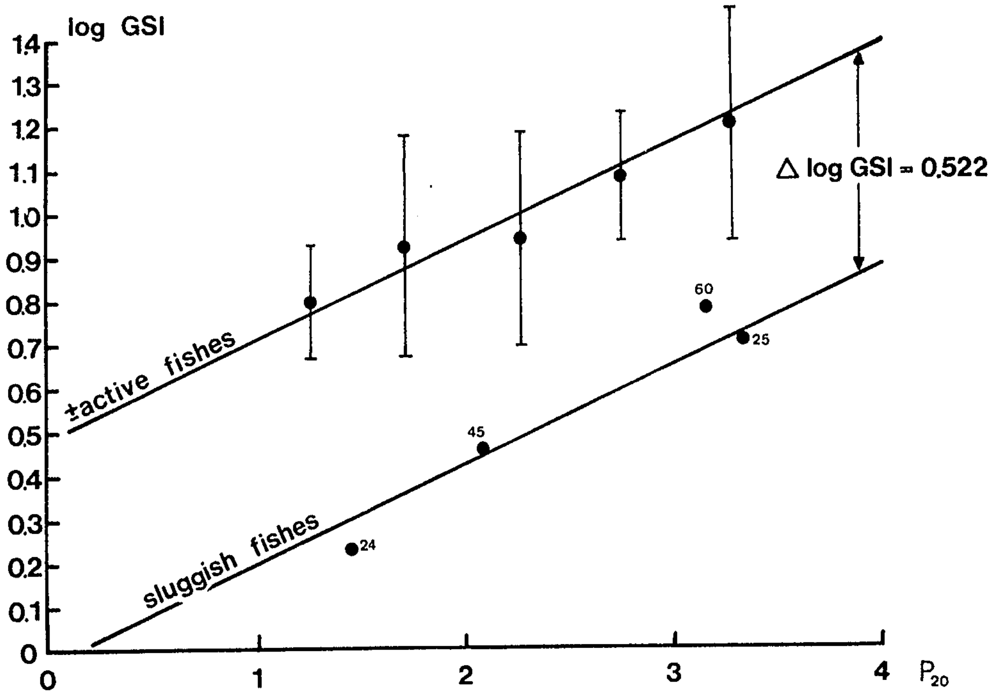


Fig. 17 Showing that sluggish fishes have for the same growth performance (P_{20}) smaller gill surface (GSI) than active fishes. See also Table XVIII.

For comparison, the regression line expressed by Equation 82 has been replotted together with the standard deviations of the empirical points from the regression line. The four fishes named above apparently do not belong to the same collective as the fishes in Fig. 16. These four fishes indeed have one common characteristic: they have a distinct mode of feeding which does not involve actively foraging or chasing their prey. Rather, they wait for the prey to swim near them, and literally suck them in by a sudden opening of the mouth, which is in all four cases structurally modified for that purpose. Additionally, in each of the four cases we have bad to very bad swimmers, including even one mildly aberrant form (*Lophius*) and one very aberrant form (*Hippocampus*).

It is therefore very thinkable that the different levels of log GSI expressed by the two lines in Fig. 17 also express different metabolic levels, as these sluggish fish may be assumed to require less O_2 than their more or less actively foraging counterparts. It appears on the other hand that the ratio of the gill size of the more or less active fishes to that of the sluggish fishes in Fig. 17 is for any value of P_{20} equal to 3.3:1. This value is quite close to the 3:1 ratio proposed for the relationship of the metabolism of free-living fish to their standard (≈ sluggish) metabolism (see Webb, 1978).

The data for fresh water fishes do not allow for any generalizations to be made. In fact, these data do not suggest any clear cut relationship between log GSI and P_{20}. If the same slope is assumed which was estimated in Fig. 16, then two groups of fresh water fishes may be roughly separated: one includes mainly piscivorous fishes, (*Esox*, *Lucioperca* and *Perca*) but also two odd fishes, (*Chondrostoma nasus* and *Acerina cernua*); the other includes mainly omnivorous fishes, such as most Cyprinids (See Table XVIII). These two groups *may* correspond to distinct ecotypes, with distinct gill surface-growth relationships, but it must also be noted that these groups would not have suggested themselves had the marine fishes not provided a slope to force upon the scatter diagram of Fig. 18. As a whole, it is not surprising that the fresh water fishes give such an unclear picture. Limnic ecosystems tend to be more variable than marine ecosystems, and there are manifold other adaptations and hidden factors which can obscure any GSI/P_{20} relationship.

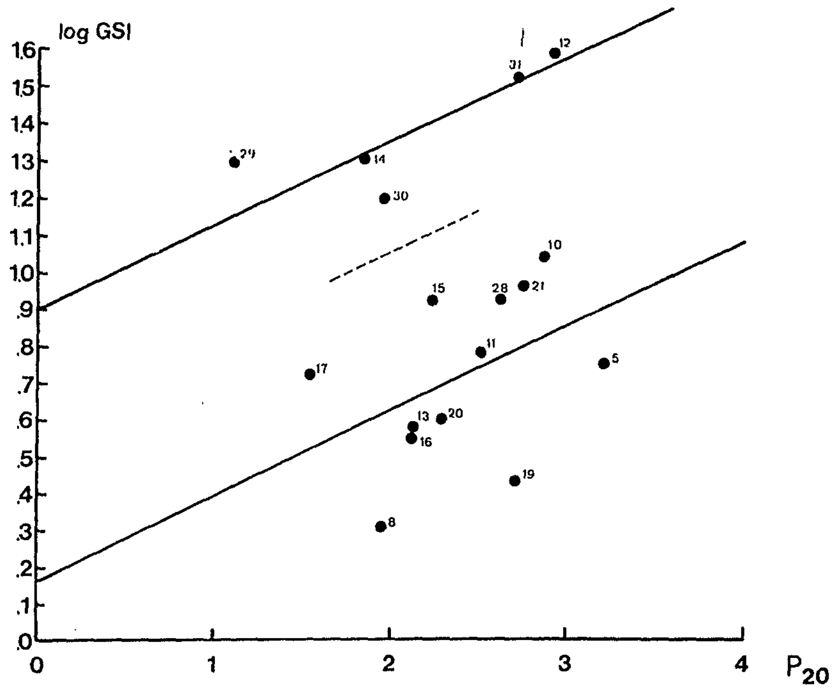


Fig. 18 A possible interpretation for the relationship between gill size (GSI) and growth performance (P_{20}) in fresh water fishes. See also Table XVIII and text.

Therefore, the fresh water fishes cannot, as a whole, be used to either confirm or reject the postulated GSI/P_{20} relationship. Marine fishes, however, do the job quite well, and this is sufficient for the argument presented here.

The concepts of GSI and P_{20} also allow for the examination of a problem previously investigated by De Jager and Dekker (1975) who found that the thickness of the gill membrane was, contrary to expectation, not inversely proportional to oxygen uptake (or gill surface). The data on Water Blood Distance used by De Jager & Dekker (1975), as well as those provided by Hughes & Morgan (1973b), are presented in Table XIX together with the corresponding values of GSI and P_{20} (computation as above). The multiple regression of log WBD on log GSI *and* log P_{20} gives, when elasmobranchs are excluded,

$$\log \text{WBD} = 1.3268 - 1.0755 \log \text{GSI} + 0.3567 \log P_{20}, \; R = 0.869 \quad \ldots . 83)$$

TABLE XIX

Water-Blood Distance (WBD = thickness of gill membranes, in μ) as related to Gill Size Index (GSI) and growth performance (P_{20}) WSD data: Hughes & Morgan (1973b) and DeJager & Dekker (1975)

	No.	Species	W_∞	K	°C	P_{20}	GSI	WBD	$\hat{\text{WBD}}$	% Deviation
elasmobranchus	1	Scylliorhinus caniculus	550	0.530	10	2.25	8.54	11.27	--	--
	2	Squalus acanthias	8280	0.074	10	2.57	13.37	10.14	--	--
	3	Raja clavata	10644	0.150	10	2.29	4.46	5.99	--	--
	4	Raja montagui	2750	0.185	10	2.49	(4.5)[1]	4.85	--	--
marine teleosts	5	Clupea harengus	277	0.290	10	1.69	14.9	0.9	1.40	+36
	6	Pollachius pollachius	5000	0.186	5	2.61	(12.5)[1]	1.50	1.98	+24
	7	Trachurus trachurus	598	0.270	20	2.21	17.00	2.22	1.34	-66
	8	Scomber scombrus	977	0.262	10	2.24	22.14	1.22	1.01	-21
	9	Oligocottus maculosus	13	0.208	10	0.22	(3.5)[1]	3.60	3.21	-12
	10	Thunnus albacares	198940	0.250	24	4.77	32.83	0.53	0.87	+39
	11	Katsuwonus pelamis	55200	0.179	25	4.09	54.67	0.60	0.47	-27
	12	Pleuronectes platessa	2171	0.170	8	2.30	14.45	2.62	1.62	-62
	13	Plathychthys flesus	1058	0.229	8	2.11	13.02	2.00	1.75	-14
fresh-water teleosts	14	Solea solea	482[2]	0.42[2]	7	2.01	(5.)[1]	2.80	4.82	+42
	15	Opsanus tau	568	0.258	12	2.00	5.78	5.00	4.12	-21
	16	Salmo gairdneri	962	0.563	10	2.52	6.09	6.19	4.23	-46
	17	Tinca tinca	493	0.710	10	2.24	8.47	3.50	2.84	-23
	18	Rutilus rutilus	321	0.163	10	1.55	5.28	2.00	4.14	+52
	19	Ictalurus nebulosus	1150	0.216	15	2.30	4.00	10.00	6.43	-56
	20	Perca fluviatilis	1184	0.123	10	1.97	16.33	0.9[3]	1.34	+33

Notes:

1) Values of GSI in brackets are estimated from closely related fishes and/or from Equation 105.

2) Growth parameters and temperature estimates from Pauly (1978b)

3) Original value given as "<1".

which is highly significant (R = 0.869**). The main point is, however, that the coefficient which links log GSI to log WBD is here -1.076 (≈ -1). That is, there is an inverse proportionality between gill size and gill membrane thickness, hence also between oxygen uptake and membrane thickness. This inverse proportionality can only be demonstrated, however, after the effects of differential growth patterns, hence of differential oxygen utilization, are removed. This explains why De Jager & Dekker (1975) obtain a value of only -0.744 for the slope of their plot of log WBD against log Oxygen uptake.

8. THE RELATIONSHIP BETWEEN OXYGEN SUPPLY AND GROWTH

While the previous chapter demonstrated the existence of a positive correlation between gill size and growth performance in marine fishes, it remains to demonstrate that:

1) Oxygen supply - hence also gill size - determines growth performance when other potentially limiting factors are kept (experimentally) 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 Thiel (1977) on the growth of juvenile *Cyprinus carpio* kept under improved oxygen concentrations may be used here to demonstrate how oxygen supply determines growth performance. The data of both studies are summarized in Table XX.

In the case of *M. salmoides*, only those data were used which pertained to O_2 tensions lower than 100%. The reason for this is that high O_2 *tensions* (near and above 100%) tend to depress fish growth. (See Stewart *et al.*, 1967)

Also, those data of Stewart *et al.* (1967) were not considered which referred to fishes kept under varying oxygen concentrations. The remaining data, pertaining to 23 fishes kept at a mean temperature of 26°C and at oxygen concentrations ranging from 1.6 to 8.1 mgO_2/liter, are presented in Table XX.

TABLE XX *Data on the growth of the juveniles of Micropterus salmoides and Cyprinus carpio kept in different oxygen concentrations and fed ad libitum, at temperatures near 26°C*

Micropterus salmoides: data extracted from Table I in Stewart *et al.* (1967)						*Cyprinus carpio*: data extracted from Table I 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

Of the data of Thiel (1977), obtained in temperatures ranging from 23 to 36°C, only those were used which pertained to 26°C. This allows for comparison with 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 I and pp. 18-19 in Thiel (1977) and summarized in Table XX, 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 tension.

The correlations between the variables O_2 content (x), initial weight (y) and daily growth increment (z) are as follows:

	M. salmoides	*C. carpio*
r_{xy}	-0.116	0.170
r_{xz}	0.755**	0.872**
r_{yz}	-0.002	0.253

In both cases there is a highly significant correlation between oxygen concentration and growth increment, and no significant correlation between the other combination of variables. Multiple regression analysis reveals that in *M. salmoides*

$$z = 0.0217 + 0.0366x + 0.0062y, \quad R = 0.760^{**} \qquad \ldots.84)$$

while in *C. carpio*, the relationship is

$$z = -0.0915 + 0.0165x + 0.0116y, \quad R = 0.878^{**} \qquad \ldots.85)$$

Note that in both cases it is x (O_2 content) which removes almost all of the variance.

The effect of reduced O_2 content seems to be direct, i.e., by a reduction of the rate of synthesis (See Figure 1) as well as indirect, i.e., by reducing food intake (Stewart *et al.* speak here of reduced "appetite"). It may be argued that it is, in fact, 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 nothing but a regulating factor by which means the fishes prevent their amino-acid pool from being "flooded." 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 thus 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 growth efficiency α $(= \frac{\text{growth increment}}{\text{food intake}})$ decreases with increasing fish size demonstrates that reduced appetite is not the main cause for reduced growth. On the other hand, increasing fish sizes necessarily imply decreasing relative gill area $(= \frac{\text{gill area}}{\text{body weight}})$ because the gills grow with a power of weight < 1. That is, with increasing fish size, the oxygen supply per unit body weight decreases, which expresses itself in a decreasing food conversion efficiency.

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

$$\alpha = a \cdot w^{b} \qquad ....86)$$

where b has a negative sign and an absolute value ($|b|$) which should be close to (1 - d) (d = the power of weight in proportion to which gills grow). The values of $|b|$ will be close to (1 - d) in all cases where the food intake remains more or less proportional to fish weight, that is, when "appetite" remains constant over a wide range of weight. Where this is not the case, the value of $|b|$ will reflect both the effects of the d value and of the reduced appetite.

No attempt can be made here to separate these two effects. The few data presented here are only to illustrate the character of the relationship between food conversion efficiency and size, hence also between food conversion efficiency and relative gill area.

The examples should show that the values of $|b|$ in Equations 86 & 87 are demonstrably close to 1 - d, as may be expected on theoretical grounds, and in spite of the disturbing effect of different appetites in fishes of different size.

The first set of material discussed in this context is an analysis of data on *Epinephelus guttatus* extracted from Menzel (1960), which is summarized in Table XXI. Here, the relationship between conversion efficiency (α) and weight is

$$\alpha = 0.726\ W^{-0.23} \qquad ....87)$$

TABLE XXI

Conversion Efficiency of Food in the Red Hind *Epinephelus guttatus*, as based on data in Menzel (1960)

Weight (g)[1]	α[2]	°C
216	0.247	28
285	0.219	19
319	0.160	23
392	0.153	28
424	0.179	19
628	0.161	19
647	0.177	28
649	0.187	23

1) Mean of initial and end weight. $\log \alpha = -0.1591 - 0.2286 \log W$

2) $\alpha = \frac{\text{growth increment}}{\text{food intake}}$ $\alpha = 0.726 \cdot W^{-0.23}$

The value of W_∞ for the Caribbean *Epinephelus guttatus*, as given in Pauly (1978b), is 2080 g, which, inserted into Equation 70 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.

For comparison, data presented by Kinne (1960) on the growth and conversion efficiency of *Cyprinodon macularius*, (See Table XXII) have been reanalyzed. The results, summarized in Table XXIII, are basically as expected from the low values of d known from Cyprinodonts (See Figure 2 and Winberg, 1961). The values of $|b|$ are, however, very high, and in only one case is the value of $|b|$ close to $(1 - d)$ (See Table XXIII, experiment A). In the other cases, there seems to have been either other factors which contributed to the high values of b or - and this is more likely - the values of d provided by Equation 70 are too high in the

TABLE XXII Growth and Food Conversion Efficiency in Cyprinodon macularius.
Based on data of Kinne (1960)

Age (weeks)	A			B			C			D			E		
	cm	g	α	cm	g	α	cm	g	α	cm	g	α	cm	g	α
2	0.70	0.0031	--	0.86	0.0064	--	0.84	0.0059	--	0.85	0.0061	--	0.90	0.0074	--
4	0.91	0.0077	--	1.17	0.0182	--	1.17	0.0182	--	1.18	0.0187	--	1.17	0.0182	--
6	1.10	0.0147	--	1.44	0.0370	--	1.40	0.0336	--	1.46	0.0387	--	1.41	0.0344	--
(7)	(1.17)	0.0180	0.132	(1.50)	0.042	0.234	(1.535)	0.046	0.170	(1.575)	0.0500	0.161	(1.51)	0.0430	0.134
8	1.24	0.0220	--	1.66	0.0600		1.67	0.0613	--	1.69	0.0638	--	1.61	0.0541	--
(9)	(1.305)	0.0260	0.112	(1.755)	0.0730	0.235	(1.775)	0.075	0.159	(1.795)	0.0780	0.158	(1.70)	0.0650	0.111
10	1.37	0.0312	--	1.85	0.0869	--	1.88	0.0918	--	1.90	0.0952	--	1.79	0.0777	--
(11)	(1.44)	0.0370	0.089	(1.925)	0.1000	0.163	(1.97)	0.108	0.107	(1.995)	0.1120	0.128	(1.86)	0.0890	0.099
12	1.51	0.0435	--	2.00	0.1134	--	2.06	0.1255	--	2.09	0.1318	--	1.93	0.1004	--
(13)	(1.555)	0.0480	0.072	(2.065)	0.1270	0.138	(2.145)	0.144	0.101	(2.17)	0.1500	0.103	(1.975)	0.1090	0.083
14	1.60	0.0530	--	2.13	0.1406	--	2.23	0.1645	--	2.25	0.1696	--	2.02	0.1173	--
(15)	(1.65)	0.0590	0.077	(2.195)	0.1560	0.115	(2.345)	0.195	0.087	(2.325)	0.1900	0.105	(2.065)	0.1270	0.101
16	1.70	0.0651	--	2.26	0.1722	--	2.36	0.1996	--	2.40	0.2114	--	2.11	0.1362	--
(17)	(1.75)	0.0720	0.086	(2.315)	0.1870	0.148	(2.42)	0.217	0.081	(2.47)	0.2330	0.109	(2.14)	0.1430	0.085
18	1.80	0.0792	--	2.37	0.2025	--	2.48	0.2364	--	2.54	0.2565	--	2.17	0.1499	--
(19)	(1.84)	0.0850	0.070	(2.43)	0.2210	--	(2.525)	0.251	0.057	(2.595)	0.2760	0.086	(2.19)	0.1550	0.063
20	1.88	0.0918	--	2.49	0.2397	--	2.57	0.2670	--	2.65	0.2965	--	2.21	0.1595	--
(21)	(1.91)	0.0970	0.069	(2.53)	0.2530	--	(2.62)	0.285	0.083	(2.695)	0.3140	0.073	(2.22)	0.1620	0.031
22	1.94	0.1022	--	2.57	0.2670	--	2.67	0.3042	--	2.74	0.3323	--	2.23	0.1645	--
24	2.00	0.1134	--	--	--	--	2.73	0.3281	--	2.82	0.3666	--	2.25	0.1696	--
26	2.06	0.1255	--	--	--	--	2.79	0.3534	--	2.87	0.3892	--	2.25	0.1696	--

(values in brackets are interpolated)

TABLE XXIII

Summary of Data on Cyprinodon macularius, based on data in Table XXII

Experiment	Temperature	S%	Table[1]	K	W_∞	d	P_{20}	r	a	b
A	30	0	8	2.843	0.251	0.653	0.03	-0.911	0.029	-0.364
B	25	35	6	3.391	0.538	0.665	0.44	-0.865	0.058	-0.459
C	30	35	8	2.995	0.703	0.669	0.50	-0.927	0.036	-0.526
D	30	35	6	3.223	0.710	0.669	0.54	-0.941	0.052	-0.404
E	35	35	6	5.467	0.209	0.650	0.32	-0.738	0.016	-0.714

Coefficients r, a & b refer to $\alpha^{2)} = a \cdot W^b$, as obtained from plots of log α against log W.

1) Table No. in Kinne (1960)

2) $\alpha = \frac{\text{growth increment}}{\text{food intake}}$

case of the very smallest Cyprinodonts, for which values of d as low as 0.52 have been reported (e.g., by Winberg, 1961). Jones (1976) estimated the following relationship for gadoids:

$$\alpha_2 = 0.73 \cdot W^{-0.15} \qquad \ldots.88)$$

where α_2 is the net growth efficiency. Note that (1.00 - 0.15) = 0.85 is close to the values of d given for cod in Table V. On this relationship, 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 *Lepomis macrochirus* (Rafinesque).

Various reasons have been given to explain this decrease of food conversion efficiency. Most of them have been discussed or mentioned by Gerking (1952), from whose paper the following is adapted:

1) The reduction of growth efficiency may be the result of "ageing". Gerking considers this a pseudo-explanation, an opinion with which this author fully agrees.
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) also added the following hypothesis:

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

Pandian (1967), noting that larger fishes tend to eat less than smaller fishes per unit body weight and that food conversion efficiency is generally negatively correlated with ration (amount of food ingested per unit time), suggested that:

7) Growth efficiency decreases with increasing body weight because ration decreases with increasing body weight.

Finally, Paloheimo and Dickie (1966) denied the very existence of a relationship between conversion efficiency and body weight. They attempted instead to demonstrate that conversion efficiency is more closely related to ration. In order to demonstrate this, they presented a series of partial correlation coefficients supposedly demonstrating that conversion efficiency is more closely related to ration than to size. Table XXIV recalls all partial correlation coefficients presented by Paloheimo and Dickie (1966).

The very data presented by these authors contradict their conclusion: of the five species of fishes they investigated, only one (*Cyprinodon macularius*) displays partial correlation showing a closer relationship between conversion efficiency and ration than between conversion efficiency and size. (Note that these correlation coefficients should have a negative sign.)

TABLE XXIV

Partial Correlation Coefficients Relating Food Conversion Efficiency (K), Weight (W) and Food Ration (R) in Paloheimo & Dickie (1966)

Pleuronectes platessa

	$r_{KW\cdot R}$	$r_{KR\cdot W}$
	-0.17	-0.18*
	-0.12	-0.09
	0.30**	+0.13
	0.10	-0.35**
	0.13	+0.21**
	0.22**	-0.10
	+0.02	+0.13
	-0.11	+0.20*
mean	-0.135	-0.006

Salmo trutta

	$r_{KW\cdot R}$	$r_{KR\cdot W}$
	-0.30	+0.09
	-0.14	-0.10
	-0.70	+0.63
	+0.19	-0.30
	+0.13	-0.28
	+0.43	-0.45
mean	-0.065	-0.068

Cyprinodon macularius

	$r_{KW\cdot R}$	$r_{KR\cdot W}$
	+0.17	-0.81**
	+0.02	-0.57**
	-0.05	-0.14
	+0.22	-0.57**
	+0.03	-0.70**
	+0.55	-0.68**
	+0.61**	-0.75**
mean	+0.221	-0.603

Lepomis sp.

$r_{KW\cdot R}$	$r_{KR\cdot W}$
-0.65	0.36

Limanda yokohamae

	$r_{KW\cdot R}$	$r_{KR\cdot W}$
	-0.84**	+0.41
	-0.91**	+0.43
mean	-0.875	+0.420

Mean of 5 species:

$r_{KW\cdot R} \gg r_{KR\cdot W}$

$-0.300 \gg -0.123$

3 spp. with $r_{KW\cdot R} \gg r_{KR\cdot W}$

1 sp. with $r_{KW\cdot R} \approx r_{KR\cdot W}$

1 sp. with $r_{KW\cdot R} \ll r_{KR\cdot W}$

* significant at 95% confidence level

** significant at 99% confidence level

In another case (*Salmo trutta*), the coefficients are about equal, while the relationship is reversed in the three remaining species. The average for the five (5) species reveals that, as a whole, it is the partial correlation between conversion efficiency and size which is closest (See Table XXIV).

This critique of Paloheimo and Dickie (1966) is confirmed by Gerking (1971), who writes:

> My results favor the second alternative [the relationship linking conversion efficiency and size], in contrast to Palehoimo & Dickie (1966) who suggested that growth efficiency is determined by ration level only and not by the body weight.

That is, there *is* a relationship between growth efficiency and weight and its cause must be explained.

Hypothesis 2 above has been discussed in connection with Misunderstanding 1, p. 18 , and the case presented there also argues against Hypothesis 3. On the other hand, Hypotheses 5 and 6, which imply quite an intricate regulating process, seem superfluous as Hypothesis 4 alone explains why growth efficiency decreases with increasing size: the change in metabolism, assumed by Gerking (1952) and which is well documented, is due quite simply to the reduction of oxygen availability in the tissues of fishes of increasing size, which is itself due to the fact that the gills of fishes do not grow in proportion to their weight.

9. DEFINITION AND DISCUSSION OF THE PARAMETERS OF THE GENERALIZED VBGF

9.1. Introduction

The generalized VBGF for length is

$$L_t = L_\infty(1 - e^{-KD(t - t_0)})^{\frac{1}{D}} \qquad \ldots. 61)$$

and for weight

$$W_t = W_\infty(1 - e^{-\frac{3}{b}KD(t - t_0)})^{\frac{b}{D}} \qquad \ldots. 37)$$

Equation 61 contains four parameters, L_∞, K, D and t_0, while Equation 37 contains the additional parameter b, the exponent of the length/weight relationship in Equation 8b. When weight growth is isometric, b is equal to 3, and Equation 37 reduces to

$$W_t = W_\infty(1 - e^{-KD(t - t_0)})^{\frac{3}{D}} \qquad \ldots. 91)$$

Only this case will be investigated here, as the question of allometric weight growth would lead the present investigation astray.

In addition to the explicit parameters of Equations 61 and 91, the use of the VBGF implies the use of yet another "hidden" parameter, called here W_x (or L_x). This parameter refers to the point of the VBGF representing the lowest weight (or length) from which the VBGF begins to describe the growth of a given fish (stock).

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

5.2. Asymptotic Size (W_∞ & 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.

In a previous paper (Pauly, 1978a), this author insisted that the asymptotic size in a given stock should be equal or close to the mean size of the oldest fish occurring in this stock, granted, obviously, that these fishes have not been decimated by man or by some mass mortality . If this closeness of largest size to asymptotic size cannot be demonstrated, then it may indeed be considered that W_∞ and L_∞ are artefacts, resulting from "forcing" the VBGF upon size-at-age data.

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, Taylor, 1962). This well documented phenomenon has prompted Taylor (1962) to the formulation of the rule of thumb

$$L_{max} \simeq 0.95\ L_\infty \qquad \ldots.\ 92)$$

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 (See Pauly, 1978b for a first implication). The reason for this is discussed briefly here.

Very good length-at-age data have been presented by Sella (1929) on the growth of the giant bluefin *Thunnus thynnus* (Table II). The data, when used in conjunction with the special VBGF (that is, with $D = 1 \Leftrightarrow d = 2/3$, (which implies isometric gill growth), provides estimates of $K = 0.043$ and $L_\infty = 505$ cm, a length that is about 1.5 times the maximum length recorded for this species - that is, about 330 cm, according to Tiews (1963) (Fig. 19).

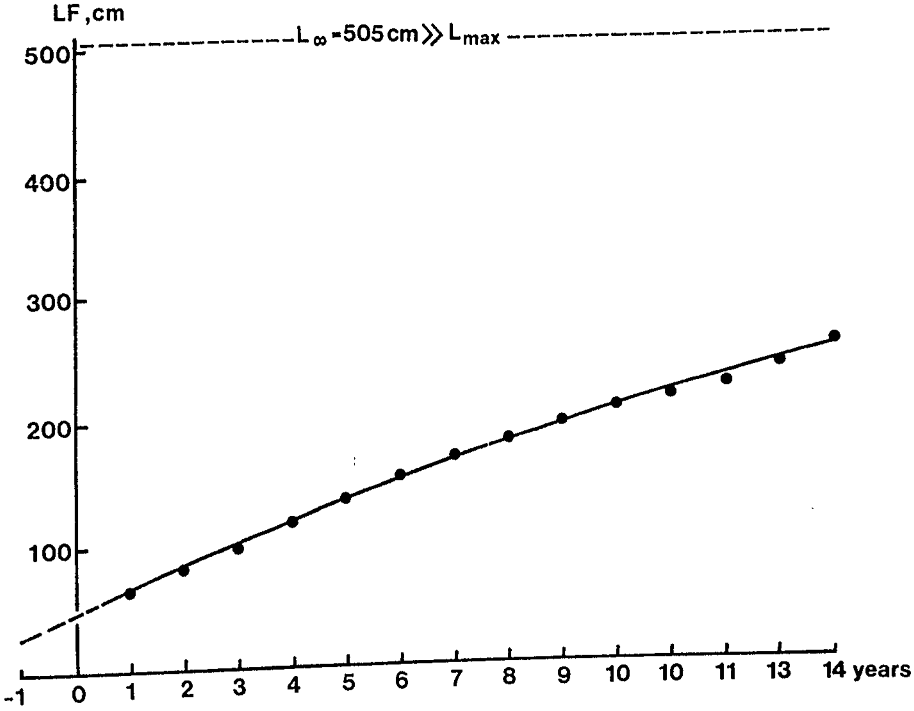


Fig. 19 Length growth curve of *Thunnus thynnus*, special VBGF ($D \doteqdot 1$). Note that L_∞ is much higher than L_{max} (≃ 330 cm)

Using a condition factor of 1.70, an asymptotic weight of 2190 kg is obtained, which is three times heavier than the highest weight reported by Tiews (1963). The real value of d in *Thunnus thynnus* is not, however, 2/3 as implied in the special VBGF, but 0.90 as given by Muir (1969). This provides an estimate of $D = 0.3 \Leftrightarrow 3 \cdot (1 - d)$, which, when used in conjunction with the special VBGF, provides, with the same data of Table II, an estimate of $K = 0.410$ and $L_\infty = 332$ cm, while the condition factor used above provides an estimate of W_∞ = 622 kg. Both values of asymptotic size (332 cm and 622 kg) correspond very well with the values of W_{max} and L_{max} reported by Tiews (1963) for various Mediterranean and North Atlantic stocks (Fig. 20).

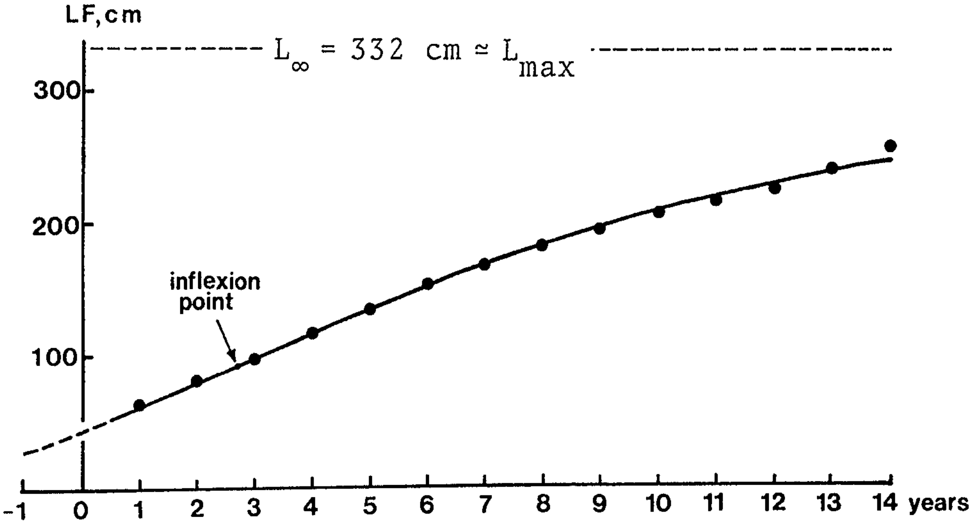


Fig. 20 Length growth curve of *Thunnus thynnus*, generalized VBGF (D = 0.3). Note that L_∞ is very close to L_{max} (332 ≃ 330).

It will be noticed, however, that the fit of the special VBGF to the data of Sella (1929) is almost as good as the fit of the generalized VBGF to the same data (See Fig. 19 and 20), for which reason the quality of the fit could not be meaningfully used to estimate by iteration a meaningful value of D.

Another important result emerging from this application of the generalized VBGF is that the inflexion point, whose position may be estimated from Equation 63 and from the growth parameter values given above, cannot be seen by a mere visual inspection of the size-at-age data (See Fig. 20).

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 d ≑ 2/3 is, the higher 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 very close to the values of W_{max} and L_{max} when the appropriate value of d (and consequently of D) is used.

This seems to confirm the theoretical considerations upon which von Bertalanffy based his theory, as well as the validity of the generalization and interpretation of the VBGF presented by this author.

The closeness of W_{max} and W_∞ and of L_{max} and L_∞ respectively, allows for the application of Taylor's rule of thumb (Equation 92) to the stocks of any fish species. It may also be suggested that

$$\sqrt[3]{W_{max}} \simeq 0.95 \cdot \sqrt[3]{W_\infty} \qquad \ldots.93)$$

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 an appropriate value of D. (See below for the estimation 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 a *given* stock, *not* to L_{ever} and W_{ever} (the greatest size on record for a given species of fish).

Thus, for example, a value of 45 kg may be reached by cod (World Record Marine Fishes, 1978, p. 168), which may correspond to W_{ever} in *Gadus morhua*. Obviously, this value cannot be used as an estimate of asymptotic weight, say in Baltic cod, which reaches a length of about 100 cm and a weight of about 10 kg (Thurow, 1971). In order to distinguish estimates of asymptotic size based upon values of W_{max} or L_{max} from independent estimates of asymptotic size, the convention is proposed to report such estimates as $W_{(\infty)}$ or $L_{(\infty)}$, in opposition to the conventional values of W_∞ and L_∞.

Various authors have contested the validity of the asymptotic size concept. Thus, for example, Paloheimo and Dickie (1965) write:

> In many cases the von Bertalanffy growth curve is fitted to data consisting mainly of young fish well below the projected final size. Hence the value of W_∞ apparently reflects the early growth [....]. The cases where asymptotic growth is confirmed by the data are rather rare due to possibly inadequate sampling [...] An apparent asymptote could be constructed as a manifestation of the older fishes having gotten where the growth efficiency is close to 0 as a consequence of their having failed to evolve a new ecological niche.

Similarly, Parker and Larkin (1959) write in a much quoted article that

> The apparent fit of a von Bertalanffy equation or [Ford-] Walford line may in some cases be forced, as a result of the method of sampling or combining the data.

A similar case is argued by Knight (1968) who considers the concept of asymptotic size to be nothing but "nonsense disguised as mathematics."

The well demonstrated relationship, in fishes, between maximum and asymptotic size seems, however, to refute these authors. Also, Parker and Larkin (1959) give no example of cases where the VBGF has been forced upon size-at-age data, nor explain how (biased?) sampling or data combining can cause an apparent fit to the VBGF. Paloheimo and Dickie (1965) similarly do not present evidence for their contention that authors having used the VBGF have "in many cases" made use mainly of young fish.

9.3. The Surface Factor: D

This parameter is 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 can be assumed to be isometric, D can be obtained directly from $D = 3 \cdot (1 - d)$, while d itself may be obtained either from metabolic or gill studies, when available, or from Equation 70. The value of d that may be obtained from Equation 70 will generally be in good agreement with the real "metabolic value" of d, except perhaps in the case of very small fishes such as the Cyprinidontidae, where the lowest values that d can take seem to go as low as 0.5 (See data of Table V and Winberg, 1961).

9.4. The Stress Factor: K

This parameter is the most difficult to visualize. As discussed previously, K refers to the rate of degradation of body substance, especially body protein. It appears, however, that protein degradation is quite an intricate process which, in opposition to protein synthesis, is relatively little investigated. A brief review of some of the preliminary findings of this growing 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 will be 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 seems 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 for example Table I in Rechcigl, 1971, who gives *in vivo* turnover rate estimates for various enzyme proteins in rat liver).
3) At least in the case of enzyme proteins, it has been demonstrated that proteins are synthesized at constant *rates*, while a *constant fraction* of active molecules present in the tissues are 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

$$\frac{dC}{dt} = ks - k_D C \qquad \ldots .94)$$

where C is the amount of protein present at time t, ks is the rate constant for synthesis (i.e., the amount synthesized per unit time) and k_D 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)

4) The 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) of proteins which first makes 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). Brandts demonstrated that the stability of proteins may be reduced both by temperatures that are too high (heat denaturation) or by temperatures that are too low (cold denaturation). Thus, in the case of the protein ribonuclease, Brandts (1967) found

> ...a continuous decrease in the temperature coefficient, until [...] the free-energy curve goes through a positive maximum corresponding to maximum stability. At this

> temperature, (T max), the native protein has maximum stability, so that denaturation can, in principle, be accomplished by either raising or lowering the temperature from T max [...] the essential features of the ribonuclease thermal transition are undoubtedly typical of most denaturation reactions. The curve in [Fig. 21 here] shows similar free energy profiles for the reversible transition of chromotrypsinogen, which were obtained in analogous [...] manner as those for ribonuclease.

Free energy curves for the proteins ribonuclease and chromotrypsinogen (Fig. 7 and 8 in Brandts, 1967) are shown in Fig. 21.

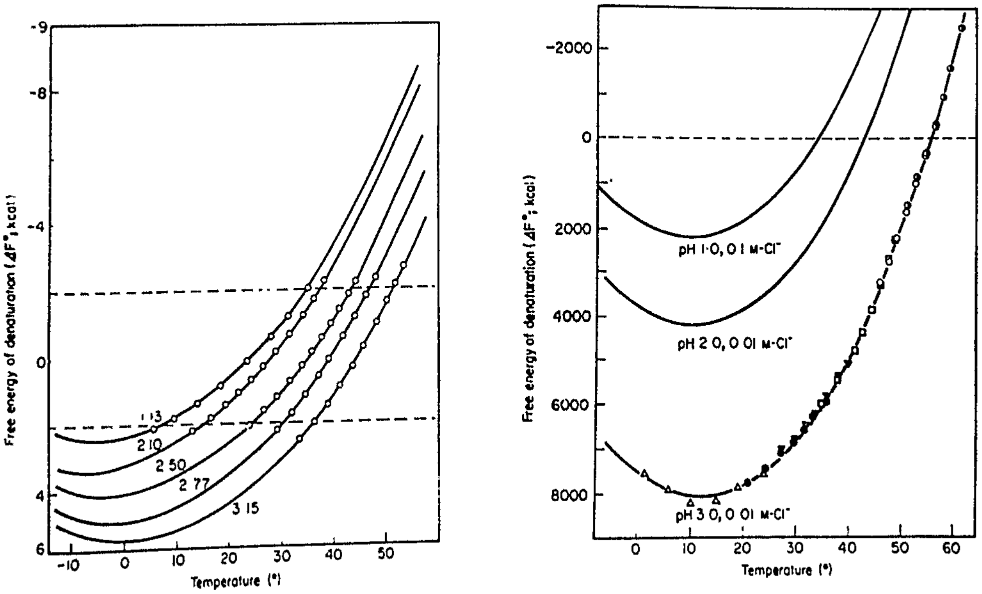


Fig. 21 Thermodynamical stability of two proteins in relation to temperature. Right: Ribonuclease, Left: Chromotrypsinogen. From: Brandts (1967). Note inversed ordinate scale and presence of stability maxima.

The model proposed by Brandts (1967) agrees with the suggestion that K, which expresses overall protein degradation, should have a minimum at a low temperature (See Fig. 15).

7) Point (6), it should be noted, implies 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).

8) Living organisms, however, may be able to regulate - within a limited range - the amount of configurational changes occurring in their constituent proteins, that is, to control the amount of protein that "should" be degraded in order to meet certain metabolic needs (e.g., for some specific amino-acids), and metabolic energy may be used up in the process. Goldberg and St. John (1976) write:

> An important, but still unexplained feature of intracellular protein degradation is its apparent requirement for metabolic energy. In a wide variety of cells, protein degradation can be reduced or blocked completely with inhibitors of energy metabolism. [...] These findings are intriguing because they are unexpected on thermo-dynamic grounds. The hydrolysis of peptide bonds is an exergonic reaction, and none of the known proteolytic enzyme of mammalian or bacterial origin requires energy-rich co-factors. Since these studies have utilized intact cells, they certainly do not prove that metabolic energy is involved directly in the proteolytic reactions.

In the further course of their considerations, Goldberg and St. John (1976) present a vast amount of evidence arguing *against* the direct involvement of ATP (or other energy-supplying compounds) in proteolysis. These points are too numerous and complex to be summarized here, and should be consulted in the original (pp. 789-791).

It thus appears that the most recent reviews of the process of protein degradation confirms the "textbook" statements pertaining to Misunderstanding III and defines *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-acid, but K, it must be remembered, refers only 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 the 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 with temperature can be relatively well described by a curve derived from respiratory experiments.

In addition to expressing protein degradation, K therefore also expresses 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 (See examples of Fig. 9). Similarly, sex-specific metabolic rates, with the males using up more O_2 than the females, 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 (See Wohlschlag, 1962 for a well documented case of sex-specific growth and metabolism). 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 O_2 supply to various activities, away from protein synthesis. It seems therefore appropriate to refer to K as a "stress factor" rather than as a "coefficient of catabolism." The word "stress" here refers to the sum total of all effects which raise the value of K, that is, temperatures that are too high or too low, salinities that are too high or too low, population densities that are too high for a given food supply, etc.

From this definition of K and of stress, it may be derived, among other things, that fish never live stress-free, but that their growth performance (P) and their asymptotic size are highest when K and the associated stress are lowest (e.g., in cod, at a mean environmental temperature of about 4 to 5° C). This is in agreement with the findings of Rumohr (1975), who insisted that there are no growth-enhancing factors, only factors which depress growth and which may be kept to a minimum (e.g., by aquaculturists).

9.5. The Origin of the Growth Curve: t_o

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, fishes do *not* always grow in the manner described by the equation, and t_o is therefore not a biological parameter. This parameter cannot therefore be used to estimate values of K from values of $L_{(\infty)}$ and values of length at birth (e.g., L_b in elasmobranchs, as done by Holden, 1974). Starting from the special VBGF, Holden (1974) derived the equation

$$\frac{L_b}{L_{(\infty)}} = 1 - e^{-K(-t_o)} \qquad \ldots.95)$$

where L_b is the length at birth when $t = 0$, and which he used to estimate values of K from the known length of the gestation period of certain elasmobranchs, assuming that the gestation period is equal to the absolute value of t_o. Some values of "K" obtained in this manner were included in the compilation of growth parameters of this author (Pauly, 1978a, p. 118). It will be noticed, however, that these estimates of "K" differ widely from those obtained using standard methods.

Thus, for example in the case of the basking shark *Cetorhinus maximus*, Holden (1974) gives a value of "K" = 0.118 - 0.143 (with $L_{(\infty)}$ = 1372 cm), whereas Pauly (1978c), using standard methods for the analysis of size-at-age data, obtained a value of K = 0.036, for a slightly lower value of asymptotic length.

The approach of considering the gestation period to provide estimates of t_o thus provides, in the case of *Cetorhinus maximus*, an estimate of K that is more than 350% too high. Other similar examples could be demonstrated on the basis of Holden's (1974) data, but this seems here superfluous, as most authors generally agree that t_o is not a biological parameter.

Some methods (e.g., Gulland and Holt, 1959) provide estimates of K and asymptotic size from tagging and similar data which do not allow for an exact age to be attributed to a certain length, although the growth curve itself can be drawn. For such cases, an empirical expression is proposed here which allows for a preliminary estimate of t_o from an estimate of K and L_∞. This equation is

$$\log(-t_0) = -0.3922 - 0.2752 \log L_\infty - 1.038 \log K \qquad \ldots.96)$$

and is based on 153 triplets of values of t_0, L_∞ and K selected from Pauly (1978a) such as to cover a wide diversity of fish taxa and sizes. Positive values of t_0 were not included and emphasis was given to literature data with the Code 0 (See Pauly, 1978a). The multiple correlation coefficient is 0.685, which, with 150 degrees of freedom, is highly significant (critical value = 0.244).

The sums are (for $\log(-t_0) = z$, $\log L_\infty = x$ and $\log K = y$):

Σx	242.61959	Σx^2	418.64374	Σxy	- 141.46073
Σy	-71.39158	Σy^2	67.73370	Σxz	- 63.53239
Σx	-52.67110	Σz^2	68.29293	Σyz	- 3.37471

These sums may be used for the estimation of confidence intervals, standard deviation, etc.

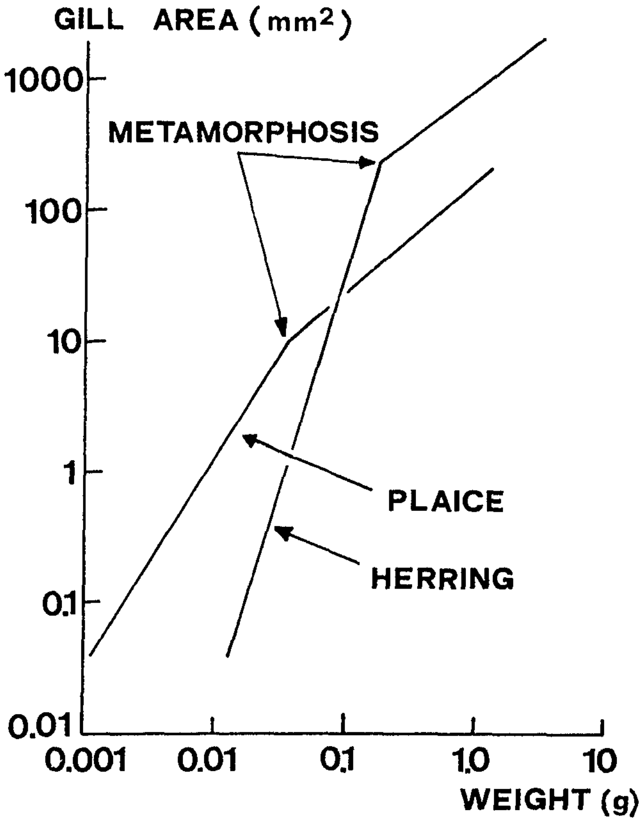
An example may be given for the use of Equation 96 : Draganik and Netzel (1966) estimated from tagging data a value of L_∞ = 130 cm and K = 0.13 in Baltic cod. From Equation 96 a value of t_0 = -0.90 is derived which may be used for the estimation of absolute ages and which compares well with the values of t_0 obtained from length-at-age data in various cod stocks (See Pauly, 1978a, pp. 62-63).

9.6. The Starting Size: L_X and W_X

As shown above, t_0 is a parameter which cannot be interpreted biologically. For this reason, the length at age zero, or L_0, may not be interpreted biologically, for example, as length at birth or length at hatching. This creates a new problem, namely the identification of the lowest size at which 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 22 shows the relationship of log gill area to log weight in the larvae and young juveniles of these two species.

Fig. 22 Development of gill surface in larval herring and plaice (from De Sylva, 1974).



The data indicate quite clearly 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 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, as well as a strong dependence of larval growth on food supply (See Cushing, 1975, p. 127 ff.).

Thus, fish larvae conform to von Bertalanffy's (1951, p. 280) growth and metabolic Type II. This inference is 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 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 these larvae is proportional to weight. Growth and metabolic Type II does not, however, hold for long, and a marked transition occurs at metamorphosis. At this stage, 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 one and continue their growth in proportion to a power of weight close to that reported from juvenile and adult herring and plaice (0.79 in herring and 0.85 in plaice).

These results correspond remarkably well with the data of Fig. 2 and Table V which suggests a value of about 0.8 for fishes of the weight range of adult herring and plaice. It would thus appear that the size at metamorphosis corresponds to the starting size (L_x and W_x). Figure 23, representing the beginning of an arbitrary growth curve, shows (not to scale) the age at fertilization (t_f) of the egg, the length at birth or hatching (L_b) and the logarithmic growth of the larvae up to metamorphosis (L_x), where the fish undergo their transition from growth and metabolic Type II to the growth pattern described by the VBGF with $d \approx 0.8$. Note also that the position of the inflexion point (L_i) is not related to the starting size (L_x).

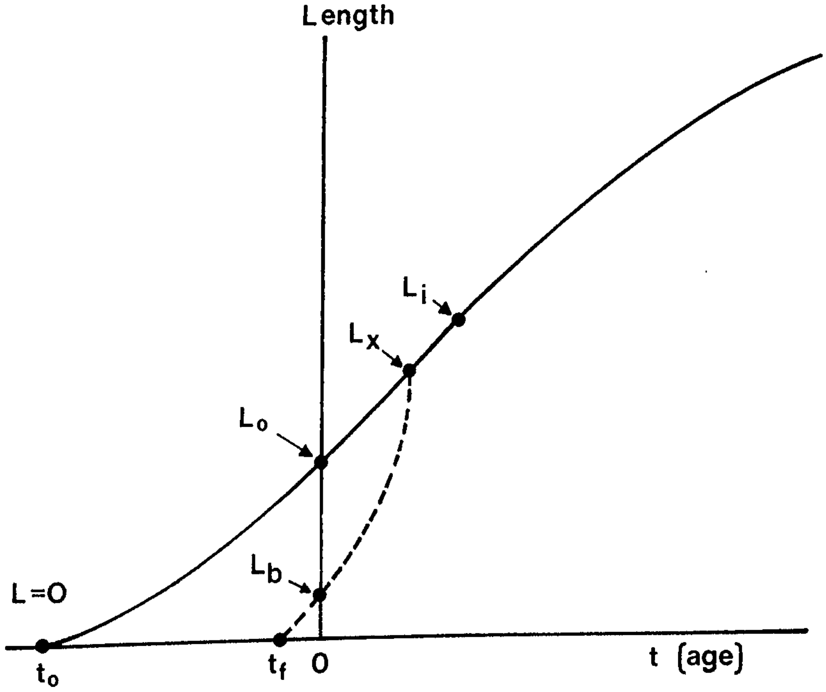


Fig. 23 A graphical representation of the biological and mathematical origin of the VBGF (scales: arbitrary units).

These considerations suggest that positive values of t_o are generally erroneous because they imply negative values of L_b. This provides a criterion for estimating the quality of some estimates of K and t_o based upon size-at-age data: when the value of K is too high, due to biased data, this will result in positive values of t_o which are biologically impossible. This criterion obviously does not allow for the identification of those erroneous values of t_o which happen to be negative.

A further discussion of the starting size (L_x or W_x) is not warranted as the problem of seasonal growth oscillations, which greatly affects the shape of a growth curve, cannot be discussed here.

10. DISCUSSION

Throughout the animal kingdom, the surface through which metabolism occurs tends to become diversified as organizational level increases. Thus, the surface through which food is absorbed and wastes excreted becomes gradually separated from the surface through which the exchange of O_2 and CO_2 occurs. In aquatic animals, this results in specialized gut ± independent of specialized gills (See Remane, 1967). Increase in size and performance of aquatic animals, hence increased independence from external factors, can be reached 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 surface, 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 Lehman, 1959). With the gradual loss of their heavy armors and the acquisition of fins, the ancestors of the recent fishes were able to colonize the whole water column, and to display a higher level of activity. This higher level of activity, requiring more food, was correlated with the acquisition of an improved organ for the prehension and the preliminary processing of food, that is, true jaws as well as an improvement in the performance and the size of the gills.

The further evolution of these two organ systems led finally to a gradual reorganization of the whole head region, the extent of which may be appreciated when comparing recent agnatha with gnathostomous fishes (See Lehman, 1959). The most advanced recent fishes - in both the systematic and physiological sense - seem to be large scombroids such as the Thunninae or the Istiophoridae. In these fishes, the highest stage in the development of gills seems to have been reached, which allows for metabolic performances unequalled in any other fishes, as expressed by their trans-oceanic migrations and their heightened body temperatures. These fishes seem indeed to have reached a metabolic level that has gradually turned from being an asset to being a liability, as suggested by Kearney (1975) on the basis of the observation that the oceanic tuna are forced, from time to time, to plunge into deeper water because they cannot meet their need for O_2 in the warm surface water of the tropical zones of the oceans.

Another evolutionary line of fishes is the trend toward breathing air. This tendency occurs mainly in tropical and subtropical fishes (Anabantidae, Clariidae, Osteoglossidae, etc.). In fact, these fishes, whose anabolism is constrained neither by the size of their gills, nor by the O_2 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 Fig. 24). 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 the growth of these fishes.

In any case, the fact that the largest existing 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-ventilation, as in the case of the largest oceanic fishes, or resort to air-breathing, as in the case of many large limnic forms of the tropics and subtropics.

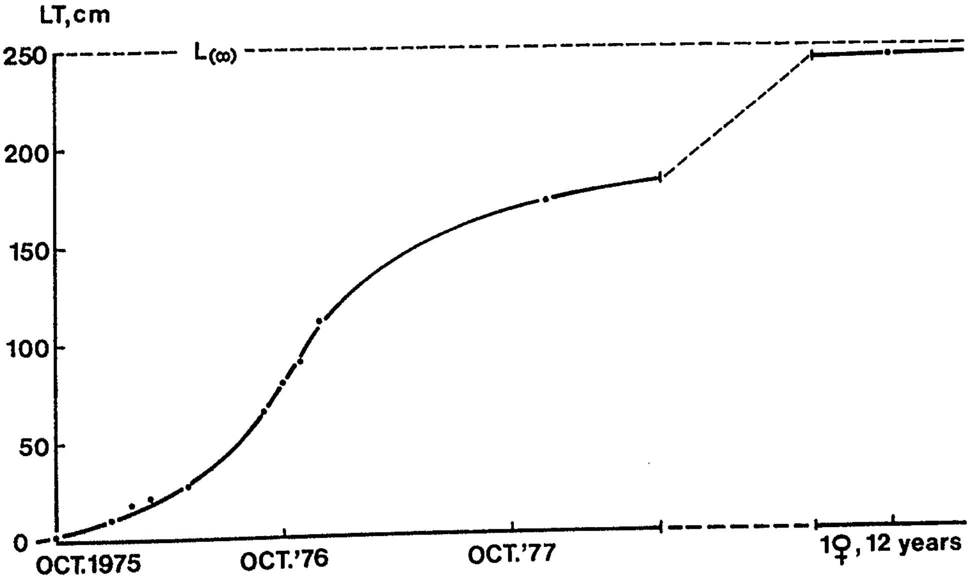


Fig. 24 Length-growth curve of *Arapaima gigas* in a Peruvian lake, based on data provided by C. Wosnitza (pers. comm.).

A significant result of the present study is the demonstration of the relative uniformity of the growth patterns of fishes. As the comparison of values of P in different fishes revealed, there are in fishes of a certain ecotype (or species) only a limited number of values which P can take, and which can be used to characterize this ecotype (or species). This uniformity of growth pattern, demonstrated for all groups so far investigated, may have been acquired throughout the evolutionary history of all fishes through the selective predation of those fishes not having the "right" growth rate for the type of environment and niche occupied.

The uniformity of growth and mortality patterns, which basically involves all fishes, also suggests uniform patterns in the reproductive strategies. Such a uniform pattern has already been suggested by Beverton (1963), who found that the ratio L_m/L_∞ (L_m = length at first maturity) is fairly constant in the Clupeidae and Engraulidae, even over a relatively wide range of values of L_∞. The review of the literature made for the compilation of growth parameters presented earlier (Pauly, 1978a) and the review by Rumohr (1975) suggest that this rule by Beverton (1963) applies, in fact, to basically all fishes. The uniformity of these growth patterns may be used to estimate growth parameters in various relatively little investigated stocks.

Thus, in general, the largest fish of a given stock should help in estimating asymptotic size in that stock, especially when the generalized VBGF is used, while the range of values of P can take in a certain taxon or eco-type may be assessed with the help of an auximetric grid. With P and a value of $W_{(\infty)}$, K can be estimated, while reasonable values of t_0 may be estimated - when necessary - from Equation 96.

Finally, from reasonable values of K and asymptotic size, estimates of M, the exponential coefficient of natural mortality, can be obtained, as demonstrated in a previous paper (Pauly, 1978b).

The possibility to now quickly obtain growth and mortality estimates for most commercially exploited species should, among other things, help to make yield-per-recruit assessment a routine matter, even for tropical fishes (Pauly, 1978d).

The present investigation was greatly influenced by the work of Winberg (1960), particularly as regards the methodical approach. As in the case of Winberg's presentation of metabolic data, an attempt has been made to process the data of a great number of different authors, covering a great variety of fishes, and to formulate from the *data themselves* whatever rules seemed to emerge, independently of the treatment and interpretation of the data by the authors who presented them. This treatment amounts basically to reducing the results obtained by other authors to literature "raw data," to be interpreted with the help of methods similar to those applied to raw data obtained from the field, while - at least in the first run - completely disconsidering the "discussion" part of the various papers used. The disadvantages and advantages of the method may be briefly discussed:

The main disadvantage is that it is sometimes difficult to assess the quality of set of data used. This, however, can be partly offset by the use of a large body of data, which will generally make highly erroneous data sets relatively easy to identify.

A second drawback of the method is that *a posteriori* causal analysis is *per se* extremely difficult when not outright impossible. Thus, in the case of the relationship between gill size and growth performance a highly significant correlation has been here demonstrated which does not *prove*, however, that large gills are the *cause* for good growth performances. Unless the data are seriously biased, however, this relationship indicates something that is more than a mere coincidence. In fact, a relationship of this type can be demonstrated to be meaningless *only* if it can be demonstrated to be a *spurious* relationship. Thus in this case, this would request a demonstration that gill size is correlated to a third "causal" variable which itself correlates with growth performance. (More intermediate variables may be added. See: Partial Correlation and Causal Interpretation in: Blalock, 1972). When such additional variable(s) cannot be identified, then the assumption of a causal relationship may be maintained, if only because effects must have causes.

A third drawback of the method used here may be seen in the danger of selecting those authors whose data fit into some preconceived notion of how things "ought to be." An illustration of this kind of danger is given by the distinction between "likely" and "unlikely" values of d in Tables V and VI. This danger can, in general, be reduced by the inclusion of as many data as possible, but is very real when a limited amount of data are used, as in the present case.

The fourth drawback of this method, finally, is the need to make all kinds of assumptions in making the data sets of different authors somehow comparable. Thus, for example, it is obvious that the growth performance of fishes of different shapes cannot be compared in terms of length growth. Conversion to weight is here imperative. Very often authors who give length-at-age data do not, however, publish conversion factors and factors have to be used which originate from more or less related fish (stocks), the result being that variance is added to the data. In the present investigation, the need to estimate the mean environmental temperature of many fresh water fish stocks represents a similar problem, and its solution - using annual mean air temperatures at the closest weather station - may appear quite outlandish.

The correlations between growth parameters and air temperature that were obtained are, however, in most cases significant, or at least suggestive, even if they are all spurious relationship - as it is, the *real water* temperature (itself correlated with the air temperature) which affects the growth of these fishes.

The only real advantage of the method described above is its potential to generate widely applying *rules* applying to a wide variety of cases.

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