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## **Gill size and temperature as governing factors in fish growth: A generalization of von Bertalanffy's growth formula (2<sup>nd</sup> edition)**

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**Institute for the Oceans and Fisheries,  
The University of British Columbia, Canada**

# **Gill size and temperature as governing factors in fish growth: A generalization of von Bertalanffy's growth formula (2<sup>nd</sup> edition)**

Daniel Pauly

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## Foreword I

I am deeply honored to write the foreword for the re-publication of Daniel Pauly's PhD thesis, "*Gill size and temperature as governing factors in fish growth: A generalization of von Bertalanffy's growth formula.*" Sixteen years ago, as I embarked on my postdoctoral fellowship with Daniel at the University of British Columbia, I had the opportunity to read the original type-written version of this report. It was an inspiring experience, as I found myself amazed by the depth and breadth of new ideas and perspectives packed into this thesis. I can trace the foundation of many of Daniel's seminal works, including estimating natural mortality rates for fishes, studying the growth of tropical fishes, and developing FishBase.

The innovative concepts presented in Daniel's thesis have significantly influenced my own research, particularly in studying the effects of climate change on fish and fisheries. One of the most notable collaborations that emerged from this inspiration is our study on the impact of climate change on fish body size<sup>1</sup> (Cheung et al. 2013). This study makes quantitative projections of the reduction of maximum body size of marine fish under climate change, a conclusion that Daniel postulated in his thesis more than four decades ago. Our study has stimulated extensive discussions and debates about the factors and mechanisms determining fish body size and growth in relation to the Gill-Oxygen Limitation Theory (GOLT) proposed by Daniel in his thesis.

Re-publishing Daniel dissertation as a *Fisheries Centre Research Report* is both timely and crucial. As I re-read it, I am again struck by its relevance and the innovative ideas it contains. The concepts and methodologies presented remain highly pertinent to current research in fish biology and fisheries science. Daniel foresaw and identified key research questions related to the discussion and debate about GOLT four decades ago. Much of his current work addresses these questions with the data and models now available to him. Making this work more accessible will undoubtedly benefit a new generation of researchers and practitioners.

I am confident that this re-publication will continue to inspire and inform the field, just as it did for me sixteen years ago. Daniel's pioneering work remains a cornerstone of our understanding of fish growth and the broader impacts of environmental changes on marine life.

William Cheung  
Professor and Director, Institute for the Oceans and Fisheries  
University of British Columbia,  
Vancouver, May 17, 2024

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<sup>1</sup> Cheung, W.W.L., J.L. Sarmiento, J. Dunne, T.L. Frölicher, V.W.Y. Lam, M.L.D. Palomares, R. Watson and D. Pauly. 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3: 254-258. doi 10.1038/NCLIMATE1691.

## Foreword II

Biological organisms are limited beings. This is not only true for bacteria and fish, but also for scientists<sup>2</sup>. Understanding these diverse types of organisms requires an understanding of their specific limitations, which include constraints on their ability to absorb and metabolize energy from their environment, grow and reproduce, maintain their organic functions up to a certain age, and incessantly process information about their surroundings. Limitations are not maladaptations, but essential characteristics of living beings in a world that presents an indefinite variety of opportunities, constraints, and threats. Every possible ecological niche requires physiological adaptations that will be less beneficial in other situations; at the same time, ‘perfect’ adaptations into specific niches increase the risk of extinction in the case of sudden environmental change. Conversely, even generalists cannot do everything – and not everything at the same time: their energy budgets are limited and they have to divide their resources and time between different functions and activities.

The theoretical approach developed in the 1979 dissertation of Daniel Pauly takes these limitations seriously and treats them as the fundamental factors that shape and underlie all forms of biological organization. This doctoral research both foreshadowed and already contained much of what would later become the Gill-Oxygen Limitation Theory or GOLT<sup>3</sup>. This theory, which allows for generalized explanations of central life-history traits of fishes and other water-breathing animals – especially their growth, maturation, and reproduction – has become increasingly important in the context of the climatic transition through which our planet is going. The explanatory potential of the theoretical model presented in this dissertation was not yet fully foreseeable in the late 1970s and early 1980s, a period when the consequences of global climate change were neither urgently felt nor prominently featured in scientific and public discourse. Four decades later, the landscape has drastically changed, and so far, all predictions of the GOLT have been validated. As predicted, fish grow faster but to lower maximum sizes at higher temperatures, their sizes are reduced at lower oxygen levels, and their first maturation and reproduction are predictable and impacted by temperature and oxygen availability, to name only the central tenets of the theory.

Daniel Pauly’s dissertation – and of the GOLT – are built on earlier theoretical work, mainly on the growth model developed by August Pütter (1879-1929) and Ludwig von Bertalanffy (1901-1972). Pütter and von Bertalanffy were pioneers in the mathematization of physiological processes and developed new approaches to conceptualizing and modelling biological processes and organisms<sup>4</sup>. In his later life, von Bertalanffy would become famous as the founder of the General System Theory, a framework that proposed to understand complex phenomena as systems of mutually interacting components. While his systems-theoretical work only took form after his pioneering contributions to theoretical biology, it was clearly influenced by his work on biological organisms. In this theory, organisms could be understood as systems that are thermodynamically open but functionally closed. This means that organisms can exchange energy and resources with their environment but at the same time they are self-organizing systems that can regulate their internal states and the mutual interactions of their various components and organs.

Understanding organisms as systems with permeable boundaries between themselves and their environment

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<sup>2</sup> Wimsatt, W. C. 2007. *Re-engineering philosophy for limited beings: Piecewise approximations to reality*. Harvard University Press, Cambridge, Mass.

<sup>3</sup> Pauly, D. 2019. *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals – 2nd Edition*. International Ecology Institute, Oldendorf/Luhe, Germany, 279 p. and Pauly, D. 2021. The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances*, 7(2), eabc6050.

<sup>4</sup> Pütter, A. (1920). Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere*, 180: 298–340 and Bertalanffy, L. von (1934). Untersuchungen über die Gesetzlichkeit des Wachstums: I. Teil: Allgemeine Grundlagen der Theorie; Mathematische und physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, 131: 613-652.

already implies that all processes of exchange are limited because resources can only enter the system through a surface. The system is thus both time- and surface-limited. While both Pütter and von Bertalanffy modeled the relationship between an organism and its volume analogue to square-cube laws and thus with scaling exponents of 2/3, Daniel Pauly's work showed that gill surface area and metabolic rate scaled identically and with exponents of 0.6-0.9. It is one of the central tenets of the GOLT – and of the present work – that biological organisms, which exist in a three-dimensional world and are thus submitted to the dimensional tension between surfaces and volumes, do not blindly obey surface volume laws. Instead, the GOLT rephrases the underlying physical principles in Darwinian terms and explains deviations from the 2/3-rule as an adaptive optimization for which correlates in growth rate, activity level, or juvenile mortality rates in the respective species can be found. In this respect, Pauly's work presents a Darwinian approach to von Bertalanffy's systems-oriented framework.

In recent years, the GOLT has become a topic of debate among respiratory physiologists working on fish. The main objection to the GOLT seems to be its point of departure, i.e., that organisms are intrinsically limited in their physiological capacity to take up and metabolize resources. The current debate does not revolve around the data or their correctness and the main contention is the fundamental assumption of such underlying constraints. The belief of the critics of the GOLT that biology always produces adaptations that overcome basic limitations is interesting in itself and it may reveal a deeper pattern that underlies many current scientific frameworks.

Ignoring the limitations that constrain biological processes makes it difficult to explain why organisms do not grow and reproduce infinitely, and why they are not immortal<sup>5</sup>. The only alternative to constraint-based explanations would be the assumption that organisms would at some point 'decide' that further growth, reproduction or cell renewal would be unnecessary or that 'enough is enough.' There is no plausible biological mechanism that could warrant this assumption. The only life forms for which self-determined constraints are an option are humans. However, as our current half-hearted attempts to live more 'sustainably' show that self-constraint is more an ideal than a reality even in our species.

All organisms are limited beings, but modern humans have created cultures and economies that brought about a historically unique situation. We have learned to exploit energetic resources that place us outside natural carbon cycles by using energy that has been stored underground for millions of years. Ca. 80% of our primary energy consumption comes from fossil fuels, and using energy that belongs to the carbon cycles of a distant past seems to blur our awareness that life on our planet is energy-limited.

This diagnosis may seem far-fetched but the inability to understand organisms as the limited beings that they are may be a result of a specific historical lifestyle that knows no limits and which, therefore, is not attuned to the limitations that constrain biology. Any theory that aims to explain physiological processes on the level of whole organisms, and to understand organisms as parts of ecosystems, however, must take limitations seriously. The GOLT – and the dissertation that inspired it – is therefore of greater relevance than just for research on fish respiration: it brings us back to the rich tradition of biological thinking that connects thinkers as diverse as Lamarck, Goethe, Darwin, Pütter, Thompson, and von Bertalanffy, all of whom understood physiological processes as structured by economic principles.

Understanding the limitations that regulate the exchange of energy and resources between organisms and their environments is not only crucial to understand life itself but it also allows for insights into the historical state in which we find ourselves: a situation that has placed us outside the planetary boundaries of global carbon cycles. A reflection on this unique historical situation and its *unlimited* lifestyles may benefit from a better

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<sup>5</sup> Maynard Smith, J. 1978. Optimization theory in evolution. *Annual Review of Ecology and Systematics*, 9: 31-56.

understanding of the physiological and ecological limitations that underlie biological life. Daniel Pauly's extraordinary contributions to fisheries science – and science in general – have shaped entire fields and disciplines and I am convinced that his early work on the growth and respiration of fishes will have the same impact<sup>6</sup>. The present dissertation is a technical scientific text but it foreshadows a way of looking at the biological world in a way that allows for deeper insights into what organisms are, under which constraint they operate and how they inhabit their world.

Johannes Müller  
Leiden University  
May 14, 2024

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<sup>6</sup> See Grémillet, D. 2021. *The Ocean's Whistleblower: The Remarkable Life and Work of Daniel Pauly*. Greystone Books, Vancouver.



## **Preface to the 2<sup>nd</sup> edition**

It is not often that one sees the second edition of a doctoral thesis, let alone one that is 45 years old. However, there are good reasons why this work, originally conceived as providing a methodology for inferring the growth parameters of fish exploited by tropical fisheries, is being re-issued when our main environmental problem is global warming.

The work presented here was performed from January 1977 to December 1978, following my return from nearly two years of fisheries work in Indonesia. There, I was confronted with a near absence of information on the growth of local fish even though the 'Indonesian-German Fisheries Development Project' I worked for was tasked to perform 'stock assessments.'

Thus, when I returned to Kiel University and its Institute of Marine Sciences, I decided to find out how fish grew; the idea was that if general patterns emerged, they could be applied to the many species we had no hope of studying one at a time.

I probably succeeded in showing that local conditions can influence the growth patterns of fish but that their intrinsic growth performance is not at the mercy of local conditions. I think I succeeded in showing that these patterns are determined by a major anatomical feature – the surface area of their gills.

This strong dependence of the growth of fish on their gill surface area also impacts other aspects of their biology, such as their food conversion efficiency and their response to the oxygen content and the temperature of the water they are in.

However, this work received only a modest number of citations. Rather, its most successful follow-up was indirect, as the growth parameters and related information gathered to make its various points formed, about ten years later, the basis of the non-taxonomic part of FishBase ([www.fishbase.org](http://www.fishbase.org)), the immensely successful online encyclopedia of fishes.

Yet, the ideas in this work, because of its emphasis on oxygen supply and demand in relation to temperature, gradually began to be considered in earnest by colleagues as the effects of global warming became increasingly manifest. Thus, William Cheung, other colleagues, and I used its logic for a paper published in 2013, which predicted how increasing ocean water temperatures would reduce the sizes that fish could reach<sup>7</sup>.

For some reason, this paper provoked the ire of a coterie of respiratory physiologists who began attacking the theoretical considerations behind what, in the process, gradually morphed into what some colleagues and I now call the Gill-Oxygen Limitation Theory (GOLT).

The GOLT, however, does not consist only of the ideas in this document. Instead, while it builds thereon it, it also incorporates elements that I gradually developed since 1979, notably work on the timing of first reproduction in fish (1984), on food conversion efficiency (1986), and later on invertebrates such as squids (1998), all of which emphasized the crucial role of oxygen supply<sup>8</sup>.

While drafting the original version of this document, and for decades thereafter, I was very conscious that the hypotheses I proposed remained just that, hypotheses, and that some colleagues may one day publish a

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<sup>7</sup> Cheung et al. 2013. Signature of ocean warming in global fisheries catch. *Nature* 497: 365-368.

<sup>8</sup> These three papers are Pauly (1984, 1986, and 1998).

reasonable argument that would refute them, e.g., based on one or several features of fish physiology that I had overlooked. What my critics wrote, however, was so weird that I gained the confidence I previously lacked. I gradually realized that if there was something fundamentally wrong with the GOLT, my critics would have found it. They would not need to resort to the absurdities I have been confronted with in the last years, and which I was given the opportunity to address in 2021<sup>9</sup>.

This version of the ‘founding document,’ as it were, should help those interested in the GOLT because the original was created with a typewriter (remember?) and was a bit messy.

This version presents the text of ‘Pauly (1979)’ with only typographical errors tacitly corrected. The tables contain the exact same information as in the first version, but some have been reorganized to require less space, and are presented jointly after the bibliography, as they impeded the reading of the text. Similarly, the figures present the same information as before, but most are smaller, while their axis labels have been made more explicit. As for the scientific names of fish, several have changed due to improvement in fish taxonomy, but their older version will still lead to the currently valid names in FishBase, and thus to the growth and other data on the species in question.

The key differences between this and the original version are:

- The addition at the end of the front matters of a table defining the variables and acronyms used in the text and its exhibits;
- The addition of an appendix with a more concise integration of the generalized von Bertalanffy growth function (VBGF); and
- The addition of multiple footnotes updating the text, i.e., presenting how an issue it mentioned had been dealt with since it was initially raised. These footnotes mainly refer to publications by me or others, and their full references are included in a final appendix.

I thank William Cheung and Johannes Müller for kindly contributing Forewords I and II, respectively, for making me aware of some issues that required explanatory footnotes. Also, I take this opportunity for thanking Cui ‘Elsa’ Liang and Ivar Ekeland for their help with the equations presenting the derivations of the generalized von Bertalanffy growth function. Finally, I hope this second edition will be of some assistance to colleagues interested in the GOLT.

Daniel Pauly  
Vancouver, B.C.  
May 2024

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<sup>9</sup> See ‘the Gill-Oxygen Limitation Theory and its Critics’ (Pauly 2021).

## **Preface to the 1<sup>st</sup> edition**

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 a 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.

Kiel, Germany

January 1979

## 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<sup>10</sup>, 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 inter-relationships 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.

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<sup>10</sup> By "close to unity," I meant around 0.9; important is that is *below* 1.

## Extended summary<sup>11</sup>

The work before you is an attempt to identify the factors which govern the growth of fishes. In this process, rules are sought which would help in the estimation of growth parameters in little-studied, especially tropical fish populations. The data used for this study originate mainly from an earlier publication by this author, which gathered the growth parameters from over 500 fish species in over 1500 populations, including newly computed parameters in about 100 cases.

Von Bertalanffy's theory of growth postulates that the growth of organisms can be understood as the net result of two processes with opposite effects, one that build up body substances (anabolism), the other breaking down these substances (catabolism)<sup>12</sup>. It is here demonstrated that recent biochemical studies fully confirm this part of the theory.

On the other hand, it is shown here that the assumption of a general applicability of the '2/3 rule' of metabolism cannot be maintained, at least as fish are concerned. This rule, which states that the oxygen (O<sub>2</sub>) consumption of fish is proportional to their weight raised to a power of 2/3 appears to apply only to very small fishes (e.g., guppies). The power of weight to which respiration is proportional increases to 0.80 in fishes of average size, and to 0.90 in tuna and other large fishes. For this reason, it is appropriate to consider the von Bertalanffy growth equation, which is based on the '2/3 rule' as a special case of a 'generalized von Bertalanffy equation,' whose integration and properties are discussed in detail.

One problem with comparative growth studies is the comparability of growth curves in length or weight of the fish in different populations, or of different species. It is shown here that the slope at the inflection point (i.e., maximum weight gain per time) of a weight growth curve provides an intuitive and expressive index of the growth performance of fishes. Indeed, this index, *P*, takes a characteristic range of values for each species, genus, and/or ecological group; thus, when an estimate of the asymptotic weight is available, the von Bertalanffy parameter *K* can be obtained. This procedure, which appears to be particularly useful to estimate the growth parameters of tropical fish populations, can be facilitated by a 'auximetric 'grid,' here presented as a new graphic approach for comparing the growth performance of fishes.

The dependence of fish growth on their oxygen supply is discussed. Thus, it is shown that gill surface area, which determines oxygen supply, is correlated in marine fishes with a growth performance index, *P*, presented in the main text. A possibly limiting role of gill area of fish – and thus of their O<sub>2</sub> supply - is also noted in conjunction with the individual growth of fish. Thus, the decline of food conversion efficiency, which tends to occur with increasing size, is explained as the result of a declining O<sub>2</sub> supply, caused by the decline of gill surface area/body weight.

The relationship between the mean environmental temperature and the growth parameters of fish was studied. Using data covering 300 populations, it is shown that the *K* parameter of the von Bertalanffy growth function, which is proportional to catabolism (as mentioned above), increases with temperature in the same manner as Krogh's 'standard curve' of metabolism.

A biological interpretation of these findings may be seen in the denaturation of body proteins (i.e., catabolism, see above), which is temperature dependent, and which imposes a requirement for the re-synthesis of these denatured proteins, which requires O<sub>2</sub>. Recent biochemical publications support this interpretation.

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<sup>11</sup> This was originally in German, as required for theses in Germany that are written in English.

<sup>12</sup> I should have mentioned August Pütter's work, which I now understand formed the basis of the VBGF.

The close relationship between the parameter  $K$  and oxygen consumption also occurs at very low temperatures, at which 'cold adaptation' manifests itself in both an increase O<sub>2</sub> consumption and in  $K$  values. This is, also based on biochemical publications, attributed to the 'cold denaturation' of proteins, i.e., to the fact that very cold temperature (< 3-4 °C) increase the rate of protein denaturation as do increasing temperature.

The relationship between  $K$  and asymptotic length ( $L_{\infty}$ ) in about 1000 populations in 130 species was studied quantitatively. It appeared that  $L_{\infty}$  (and, similarly  $W_{\infty}$ , the asymptotic weight) changes in a characteristic manner when  $K$  varies. What appeared was that

$$\log(K) = a - (2/3) \cdot \log(L_{\infty}^3)$$

In this form, however, this equation applies only to the special VBGF. (Note that  $L_{\infty}^3$  may here, as well, be replaced by  $W_{\infty}$ )<sup>13</sup>.

This relationship can be used, jointly with the relationships between  $K$  and temperature, to describe quantitatively the relationship between the mean environmental temperature and the asymptotic length (or the asymptotic weight) of various populations. This is aligned with the widely accepted perception that fish exposed to warm water remain smaller than their conspecific in colder water, except at temperature lower than 3–4 °C, where a temperature decrease leads to smaller asymptotic sizes.

Other aspects of fish growth are dealt with cursorily, i.e., the growth of fish larvae and of air-breathing fish, as well as the role of gills in fish evolution.

Some methodological aspects of this work are dealt with in the Discussion. This covered the issues connected with the use of secondary data, their required standardization, and the possible sources of associated errors. These issues are, however, more than compensated for by the advantages provided by the use of secondary data. Notably, their use allows the perception and the documentation of connections and relationships that a single scientist, working only with his own data, would have difficulties identifying and documenting.

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<sup>13</sup> The letter 'a,' in this equation was later replaced by  $\emptyset$ ' (see, e.g., Pauly 1998).

## Definitions of acronyms and parameters used

Definitions of the parameters, symbols and acronyms that occur on more than one page	
Item (unit)	Definition
$\Leftrightarrow$	Corresponding to...
$\Delta$	A difference in time, length, or other.
$ x $	Absolute value of x
$a$	Intercept in linear regressions; also: multiplicative term of an LWR or in a relationship linking food conversion efficiency ( $E$ ) and weight and a term in the equation $\log(K) = a - (2/3) \cdot \log(L_\infty^3)$ , now replaced by $\varnothing'$ , as in $\varnothing' = \log(K) - 2 \cdot \log(L_\infty)$ .
$b$	Exponent of a length-weight relationship, i.e., $W = a \cdot L^b$ ; usually, $b = 3$ or $b \approx 3$ ; also exponent of a relationship linking $E$ with body weight (now $\beta_1$ or $\beta_2$ )
$C$	An integration parameter; see Equations (79-80)
$^{\circ}\text{C}$	Degree Celsius; previously 'Centigrade'
c.f.	Condition factor, defined by $c.f. = W \cdot 100/L^3$ ; here c.f. is always based on TL, cm and round weight in g.
$d$	Exponent in a relationship linking respiratory surface and weight, i.e., $S = \alpha \cdot W^d$
$D$	A convenience parameter equal to $3(1-d)$ or $b(1-d)$ , where $b$ is from an LWR
$dW/dt$	Growth rate, in weight (or mass)
$E$	Food conversion efficiency, i.e., growth increment/food ingested in a given time span
g	Gram
$GSI$	The gill surface area in $\text{cm}^2$ of a fish weighting 1 g.
$H$	Coefficient of anabolism, i.e., of protein synthesis
$k$ ( $\text{year}^{-1}$ )	Coefficient of catabolism; here: of protein denaturation; note that $k = 3K$
$K$ ( $\text{year}^{-1}$ )	In the VBGF, the rate at which asymptotic size is approached
$L$ (cm)	Any measure of body length, with $L_t$ the length at age $t$
$L_\infty$ (cm)	Asymptotic length in the VBGF, reached after an infinitely long time
$L_{max}$	The largest fish in a species or population, depending on context
$L_{ever}$	Length of the largest specimen recorded for a given species (concept defined but not used)
LWR	Length-weight relationship, of the form $W = a \cdot L^b$
$n$	Weight exponent of anabolism in Equation (1); now replaced by $d$ ; also used for 'number of cases'
$m$	Weight exponent of catabolism in Equation (1), later ignored because $m = 1$ ;
$P$	Index of growth performance defined by $P = \log(K \cdot W_\infty)$
$S$ ( $\text{cm}^2$ )	A surface; here respiratory surface, i.e., gill surface area, as in $S = \alpha \cdot W^d$
$Q_{10}$	Coefficient expressing the increase in some activity due to a temperature increase of $10^{\circ}\text{C}$ .
$t$ (year)	Absolute age; relative age = $t - t_0$
$t_0$ (year)	The usually negative 'age' at $L = 0$ predicted by the VBGF
TL	Total length (note also FL, i.e., fork length, used for scombroids such as tuna)
VBGF	Von Bertalanffy Growth Function; here: Equation (2)
$W$ (g)	Weight (or mass); $W_t$ is weight at age $t$ ; here: live or wet weight
$W_\infty$ (g)	Asymptotic weight in the VBGF, as reached after an infinitely long time
$W_{ever}$	Weight of the heaviest specimen recorded for a given species (concept defined but not used)
$W_{max}$	The heaviest fish in a species or population, depending on context
WBD	Water-Blood Distance; thickness of the epithelia of gill lamellae

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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 and 1934 for the earlier works)<sup>14</sup>.

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 '*Preliminary 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.<sup>15</sup> 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 'full-grown 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

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<sup>14</sup> Erna W. Mohr also published in 1921 a key early paper on the growth of tropical fishes (see Mohr 1994).

<sup>15</sup> These effects are now dealt with in Pauly (2019) and Pauly et al. (2023).

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. Nordenskjöld (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 tracheae 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 (1631-1723) 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 polynomials, 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 curve, proposed by Gompertz (1825), Robertson (1923), Pearl and 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 and Holt 1957, p. 97-99, and von Bertalanffy 1951, p. 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 2<sup>nd</sup> edition (1951) of his book, *Theoretische Biologie* (Vol. 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

$$dW/dt = HW^n - kW^m \quad \dots 1)$$

where  $dW/dt$  is the rate of growth,  $W$  is the animal's weight, while  $H$  and  $k$  are coefficients of anabolism and catabolism respectively.<sup>16</sup> 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 values of  $n$  and  $m$  to take a wide range of values. This leads to what will be here called the generalized VBGF.

Beverton and Holt (1957), by reformulating the special VBGF and incorporating it into their yield model, demonstrated its wide applicability and attempted to interpret some of the VBGF's parameters biologically. 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<sup>17</sup>. 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.

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<sup>16</sup> This equation is based on the work of Pütter (1920), whose contribution is recognized in Pauly (2019).

## 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 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

$$HW^n - kW^m = 0 \quad \dots 2)$$

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 (TL) except in tuna and other large scombroids where fork length (FL) 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 condition factor (c.f.) is here

$$c.f. = W \cdot 100/L^3 \quad \dots 3)$$

and is always based on TL, cm and round weight<sup>18</sup>.

- 3) Time is here always expressed in years. This also applies to all growth or other rates.
- 4) The considerations exposed here apply to fish which derive the overwhelming part of the oxygen they need through the use of gills. Fishes known to derive most or even a large proportion of their oxygen from cutaneous respiration (e.g., *Anguilla* spp.) or from auxiliary organs suited to breathing air (e.g., *Clarias* spp.) are expressly excluded from the general considerations presented here. (Questions pertaining to air-breathing fishes are briefly mentioned in Chapter 10).
- 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 ( $p < 0.05$ ) two asterisks: highly significant ( $p < 0.01$ ).

### 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 and 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)<sup>19</sup>.

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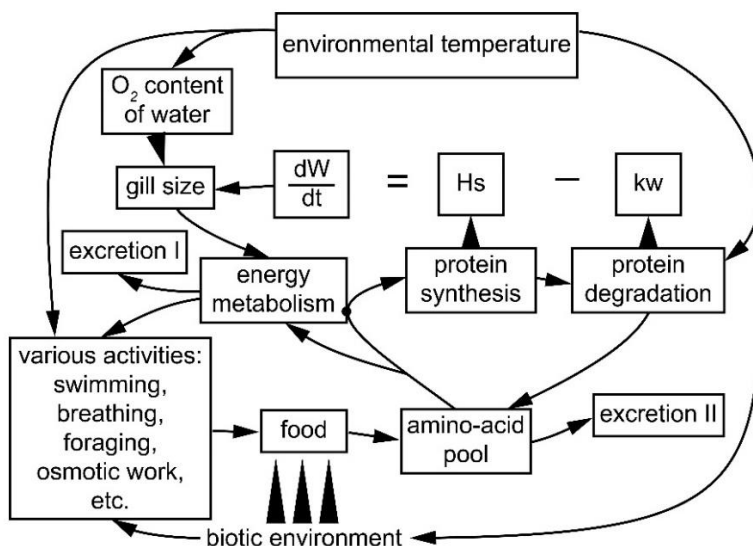
<sup>18</sup> An assumed c.f. is here represented by 'c.f.  $\doteq$  0.6.'

<sup>19</sup> This is was an error in von Bertalanffy's theory. The '2/3 rule' was consistent with the results of his experiments with guppies (von Bertalanffy 1951), but he would have found other value if he had worked with fishes that can reach larger sizes (see Figure 2 and Equation 70).

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 (Figure 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 Figure 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).



**Figure 1.** Simplified model of fish growth, based mainly on von Bertalanffy (1951)<sup>20</sup>.

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 and Goldstein 1969; Savitz 1969 and 1971; Olson and Fromm 1971, and Niimi and Beamish 1974) (Excretion II in Figure 1).

A part of the available oxygen and protein is used for the formation of gonadal products which from a certain size

<sup>20</sup> In this conceptualization, the metabolic cost of various activities such as, e.g., breathing, moving around, digesting food, etc., are implicitly incorporated in the anabolic term because they demand oxygen, just as the synthesis of new proteins (i.e., growth) requires. The ‘catabolic term’ (i.e., ‘ $kw$ ’ in Figure 1) is limited to the first phase of protein denaturation, which does not consume oxygen. This is still a point of contention by some respiratory physiologists, who equate this term with the standard metabolic rate and thus claim that the GOLT is not supported empirically because standard metabolism scales with weight with an exponent  $<1$ . Here, however, this term is assumed to scale with weight (i.e., with an exponent of 1), as all proteins in a fish’s body are subject to denaturation (albeit at different rates).

on leave the body periodically<sup>21</sup>. 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 (= gill size/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 (growth increment/food intake), 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, p. 224) 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 and 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

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<sup>21</sup> The main reason why the impact of reproduction on the growth of iteroparous fish is not necessarily a noticeable component of their growth is presented in Pauly et al. (2023).

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 0.667<sup>th</sup> 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-oxidative phase). The reactions occurring here have two features in common:

- 1) They are mildly exergonic (production of waste heat);
- 2) They do not require oxygen<sup>22</sup>.

Thus, proteins may lose their tertiary and quaternary structure and be hydrolyzed 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 (Oxidative 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<sub>2</sub>O, CO<sub>2</sub> and NH<sub>3</sub>, 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 'pre-oxidative' breakdown indeed cannot be anything but proportional to body mass, that is, to the amount of body proteins that may be degraded and hydrolyzed 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 hydrolyzed, they become part of the 'amino-acid pool' (see Figure 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 oxidized 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. 129 ff). This division, however, was not made explicitly by von Bertalanffy for the derivation of his theory of growth. This omission is probably the cause for Misunderstanding III.

Ursin (1967, p. 2359) writes:

*"Apparently, it was overlooked that although catabolic processes are going on all over the body, the necessary[!] oxygen supply has to be introduced through some surface or the other, mainly the gills. With our basic assumption of isometric growth, this means that catabolism is proportional to  $W^{2/3}$ . As discussed elsewhere, this is also known to be untrue, so that the assumption of isometric growth must be abandoned for the occasion. In fact, [...] the gills do not grow isometrically with the body, because new units are being added as the fish grows."*

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

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<sup>22</sup> More precisely, they do not *consume* oxygen; see Pauly and Lam (2023).

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 denatured and/or hydrolyzed. 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)

$$dW/dt = HW^n - kW^m \quad \dots 1)$$

may be rewritten

$$dW/dt = HW^{2/3} - kW^m \quad \dots 4)$$

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

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

and for length growth,

$$L_t = L_\infty (1 - e^{-KD(t-t_0)}) \quad \dots 6)$$

where  $W_t$  and  $L_t$  are the size at age  $t$ ,  $W_\infty$  and  $L_\infty$  express asymptotic size, while  $K$  and  $t_0$  are constants whose properties will be discussed in Chapter 9 (see Beverton and 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  $n = 2/3$  applies very rarely in fishes, for which reason  $n$  should be allowed to take values of  $n \neq 2/3$ . Richards (1959) and Taylor (1962) have relaxed both definitions ( $n \neq 2/3$  and  $m \neq 1$ ), 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. Dirk Reimers, Kiel University, Department of Experimental Physics<sup>23</sup>.

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

$$S = p \cdot L^a \quad \dots 8a)$$

where  $L$  refers to any linear dimension of the fish (e.g., body length);  $a$  is a power whose range of possible values

<sup>23</sup> Equations (8) to (66) were rewritten in compact form by Dr. Cui 'Elsa' Liang, whom I thank for her help in this.

is discussed elsewhere and  $p$  is a 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

$$W = q \cdot L^b \quad \dots 8b)$$

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 term of weight. Given these definitions, length can be expressed in form of weight though

$$L = (W/q)^{1/b} \quad \dots 9)$$

From which it follows that

$$S = p(W/q)^{a/b} = [p/(q^{a/b})]W^{a/b} \quad \dots 10)$$

The new expression for  $S$  is substituted into Equation (7) which results in

$$dW/dt = [Hp/(q^{a/b})]W^{a/b} - kW \quad \dots 11)$$

Defining

$$E = Hp/(q^{a/b}) \quad \dots 12a)$$

and

$$K = k/3 \quad \dots 12b)$$

and inserting into Equation (11) results in

$$dW/dt = EW^{a/b} - 3Kw \quad \dots 13)$$

Rearranging gives

$$dW/dt + 3Kw - EW^{a/b} = 0 \quad \dots 14)$$

Defining

$$u = W^{[1-(a/b)]} = W^{D/b} \quad \dots 15)$$

and substituting into Equation (14) gives

$$du/dt + (D/b)3Ku - (D/b)E = 0 \quad \dots 16)$$

or

$$du/dt = (D/b)E - (D/b)3Ku \quad \dots 17)$$

That is

$$dt = (b/D) [du/(E - 3Ku)] \quad \dots 18)$$

which, integrated, gives

$$\int_{t_0}^t dt = (b/D) \int_{u_0}^{u_t} [1/(E - 3Ku)] du = t - t_0 \quad \dots 19)$$

or, estimated

$$(b/D)(1/-3K) \ln(E - 3Ku) \Big|_{u_0}^{u_i} + c = t - t_0 \quad \dots 20)$$

hence,

$$\ln(E - 3Ku) \Big|_{u_0}^{u_t} - (3DK/b)c = -(3DK/b)(t - t_0) \quad \dots 21)$$

When

$$t \rightarrow 0 \leftrightarrow u_t \rightarrow u_0 \quad \dots 22)$$

we have

$$-(3DK/b)c = + (3DK/b)t_0 \quad \dots 23)$$

which gives

$$c = -t_0 \quad \dots 24)$$

Substituting for c in Equation (21), we obtain

$$\ln[(E - 3KW_t^{D/b})/(E - 3KW_0^{D/b})] + (3DK/b)t_0 = -(3DK/b)(t - t_0) \quad \dots 25)$$

or

$$\ln[(E - 3KW_t^{D/b})/(E - 3KW_0^{D/b})] = -3DKt/b \quad \dots 26)$$

which gives

$$3KW_t^{D/b} = (-E + 3KW_0^{D/b})e^{-3DKt/b} + E \quad \dots 27)$$

and

$$W_t^{D/b} = (E/3K) - [(E/3K) - W_0^{D/b}]e^{-3DKt/b} \quad \dots 28)$$

Now, when  $t \rightarrow \infty$ , we have

$$W_t^{D/b} \rightarrow W_\infty^{D/b} = E/3K \quad \dots 29)$$

and by substitution into Equation (28),

$$W_t^{D/b} = W_\infty^{D/b} - (W_\infty^{D/b} - W_0^{D/b})e^{-3DKt/b} \quad \dots 30)$$

Defining

$$t = t_0 \leftrightarrow W_t = 0 \quad \dots 31)$$

and inserting into Equation (30) gives

$$W_\infty^{D/b} - (W_\infty^{D/b} - W_0^{D/b})e^{-3DKt_0/b} = 0 \quad \dots 32)$$

and

$$W_0^{D/b} = W_\infty^{D/b}(1 - e^{3DKt_0/b}) \quad \dots 33)$$

which, combined with Equation (30) gives

$$W_t^{D/b} = W_\infty^{D/b} - [W_\infty^{D/b} - W_\infty^{D/b}(1 - e^{3DKt_0/b})]e^{-3DKt/b} \quad \dots 34)$$

and

$$W_t^{D/b} = W_\infty^{D/b} - W_\infty^{D/b} e^{-3DK(t-t_0)/b} \quad \dots 35)$$

This, rearranged, gives

$$W_t^{D/b} = W_\infty^{D/b}(1 - e^{-3DK(t-t_0)/b}) \quad \dots 36)$$

or, in a form easier to handle

$$W_t = W_\infty (1 - e^{-3DK(t-t_0)/b})^{b/D} \quad \dots 37)$$

Equation (37) is the generalized VBGF for weight growth.

The definition of  $D$  in Equation (15) implies that

$$D = b - a \quad \dots 38)$$

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

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

when  $a = 2$  and  $b = 3$ .

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

$$dW/dt = W_\infty^{b/D} (1 - e^{-3DK(t-t_0)/b})^{(b/D)-1} (3D/b)K e^{-3DK(t-t_0)/b} \quad \dots 39)$$

or

$$dW/dt = W_\infty 3K (1 - e^{-3DK(t-t_0)/b})^{(b/D)-1} e^{-3DK(t-t_0)/b} \quad \dots 40)$$

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

$$1 - e^{-3DK(t-t_0)/b} = (W_t/W_\infty)^{D/b} \quad \dots 41a)$$

and

$$e^{-3DK(t-t_0)/b} = (W_\infty^{D/b} - W_t^{D/b})/W_\infty^{D/b} \quad \dots 41b)$$

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

$$dW/dt = 3KW_\infty (W_t/W_\infty)^{(D/b)[(b/D)-1]} [(W_\infty^{(D/b)} - W_t^{(D/b)})/W_\infty^{D/b}] \quad \dots 42)$$

$$dW/dt = 3KW_\infty (W_t/W_\infty)^{[1-(D/b)]} [(W_\infty^{(D/b)} - W_t^{(D/b)})/W_\infty^{D/b}] \quad \dots 43)$$

$$dW/dt = 3KW_t^{[1-(D/b)]} (W_\infty^{D/b} - W_t^{D/b}) \quad \dots 44)$$

$$dW/dt = 3KW_t [(W_\infty/W_t)^{D/b} - 1] \quad \dots 45)$$

which reduces to

$$dW/dt = 3KW_t [(W_\infty/W_t)^{1/3} - 1] \quad \dots 46)$$

when  $a = 2$  and  $b = 3$ .

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

$$d^2W/dt^2 = 3K[(W_\infty/W_t)^{D/b} - 1] + 3KW_t [-(D/b)(1/W_t)(W_\infty/W_t)^{D/b}] \quad \dots 47)$$

$$d^2W/dt^2 = 3K[(W_\infty/W_t)^{D/b} - 1 - (D/b)(W_\infty/W_t)^{D/b}] \quad \dots 48)$$

$$d^2W/dt^2 = 3K\{[1 - (D/b)](W_\infty/W_t)^{D/b} - 1\} \quad \dots 49)$$

Setting Equation (48) to zero, and  $W_t = W_i$ , it follows that

$$(W_\infty/W_i)^{D/b} = b/(b - D) \quad \dots 50)$$

or

$$W_\infty/W_i = [b/(b - D)]^{b/D} \quad \dots 51)$$

Thus, it follows that

$$W_i = [b/(b - D)]^{-b/D} W_\infty = [(b - D)/b]^{b/D} W_\infty \quad \dots 52)$$

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

$$dW_i/dt = 3K(W_\infty^{D/b} W_i^{1-(D/b)} - W_i) \quad \dots 53)$$

Substituting Equation (52) into Equation (53) gives

$$dW_i/dt = 3K\left\{W_\infty^{D/b} \left[\frac{(b - D)}{b}\right]^{b/D} W_\infty^{1-(D/b)} - \left[\frac{(b - D)}{b}\right]^{b/D} W_\infty\right\} \quad \dots 54)$$

$$dW_i/dt = 3K\left\{\left[\frac{(b - D)}{D}\right]^{b/D[1-(D/b)]} W_\infty - \left[\frac{(b - D)}{b}\right]^{b/D} W_\infty\right\} \quad \dots 55)$$

$$dW_i/dt = 3KW_\infty\left\{\left[\frac{(b - D)}{b}\right]^{(b/D)-1} - \left[\frac{(b - D)}{b}\right]^{b/D}\right\} \quad \dots 56)$$

and finally

$$dW_i/dt = 3KW_\infty(D/b)[1 - (D/b)]^{(b/D)-1} \quad \dots 57)$$

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

$$dW_i/dt = 3KW_\infty(1/3)[1 - (1/3)]^2 = KW_\infty(4/9) \quad \dots 58)$$

when  $a = 2$  and  $b = 3$ .

Equation (51) may be rearranged to

$$W_i/W_\infty = [1 - (D/b)]^{b/D} \quad \dots 59)$$

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

$$W_i = 0.2963 W_\infty \quad \dots 60)$$

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

The generalized VBGF for length has the form

$$L_t^D = L_\infty^D(1 - e^{-KD(t-t_0)}) \quad \dots 61)$$

or

$$L_t = L_\infty(1 - e^{-KD(t-t_0)})^{1/D} \quad \dots 62)$$

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

$$t_i = t_0 - (\ln D / KD) \quad \dots 63)$$

Thus,  $t_i$  moves toward  $t_0$  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 except for the fact that values of  $L_t^D$  have to be used instead of  $L_t$  values. Similarly, values of  $3\sqrt{W_t^D}$  may be used instead of  $3\sqrt{W_t}$  then 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

$$L_{t+1}^D = a + b \cdot L_t^D \quad \dots 64)$$

where  $L_\infty = (a / (1 - b))^{1/D} \quad \dots 65)$

and

$$K = -\ln(b) / D \quad \dots 66)$$

(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 *Salvelinus 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 and Moore 1974), and which then begins to undertake annual seaward migrations, spending each summer in sea water and overwintering in fresh water (Moore and 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 and 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 “[r]aw 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 indeterminate.”

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

On the other hand, Ursin (1967, p. 2358) estimates the gut surface of *Solea solea* to be  $2.12 \cdot W^{0.57}$  (cm<sup>2</sup>, 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 absorptive area of their gut in permanent contact with ingested food. This, however, is evidently not the case (See Ricker 1958).

Another line of evidence arguing against the gut surface as the physiologically limiting surface of anabolism is provided by the fact that relative gut length (= gut length/fish length) - hence relative absorptive area - is in fishes 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<sub>2</sub>, 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

$$Q = dP \cdot U \cdot A / WBD \quad \dots 67)$$

where  $Q$  is the oxygen uptake (ml/hour),  $U$  is Krogh's diffusion constant, that is, the number of ml of oxygen which diffuse through an area of 1 mm<sup>2</sup> in one minute for a given type of tissue (or material) when the pressure gradient is one atmosphere of oxygen per  $\mu$  (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  $\mu$  (De Jager and 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 and 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' fish links energy metabolism and weight (Winberg 1960; De Jager and Dekkers 1975);
- 5) There is very little oxygen dissolved even in the best-aerated water - say, as compared with the O<sub>2</sub> 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 and Piiper (1966), shows the enormous difference between breathing air and breathing water. In comparison with land animals, fishes - and other aquatic animals for that matter - must extract the oxygen they need from a medium 840 times denser and 55 times more viscous 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 and 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<sup>24</sup>.

- 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 favor a specific mode of feeding (filtering plankton), as is the case with *Rhincodon typus* and *Cetorhinus maximus*, the two largest fishes (Norman and Fraser 1963). That is, extremely large gills lower the number of niches that can be occupied by a given species;

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<sup>24</sup> Oops! This should have been 'in humans.'

- c. Large gill area implies very reduced spaces between the secondary gill lamellae (Hughes and Morgan 1973a). There is therefore a permanent danger of clogging, for which reason large-gilled fishes cannot frequent waters containing suspended solids in large amounts, such as close inshore 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 and Morgan 1973a). For this reason, the gills also represent the weakest link in a fish's line of defense against osmotic stress;
- e. *"The gill tissue of fishes is an ideal site for parasitic infection...as...the gills are well per-fused with blood and usually well oxygenated, and hence the environment is very favorable from this point of view"* (Hughes and Morgan 1973a).

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

#### 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

$$G = a \cdot W^{d_G} \quad \dots(68)$$

where  $G$  is the gill area,  $W$  is the fish weigh,  $d_G$  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<sup>2</sup>,  $a$  (the  $GSI$ ) is the gill area in cm<sup>2</sup> of a fish weighting 1 g.

It should be noted that Equation (68) has the same form as the following equation which, in fishes, relates O<sub>2</sub> consumption and weight:

$$Q = a \cdot W^{d_Q} \quad \dots(69)$$

where  $Q$  is the O<sub>2</sub> 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).

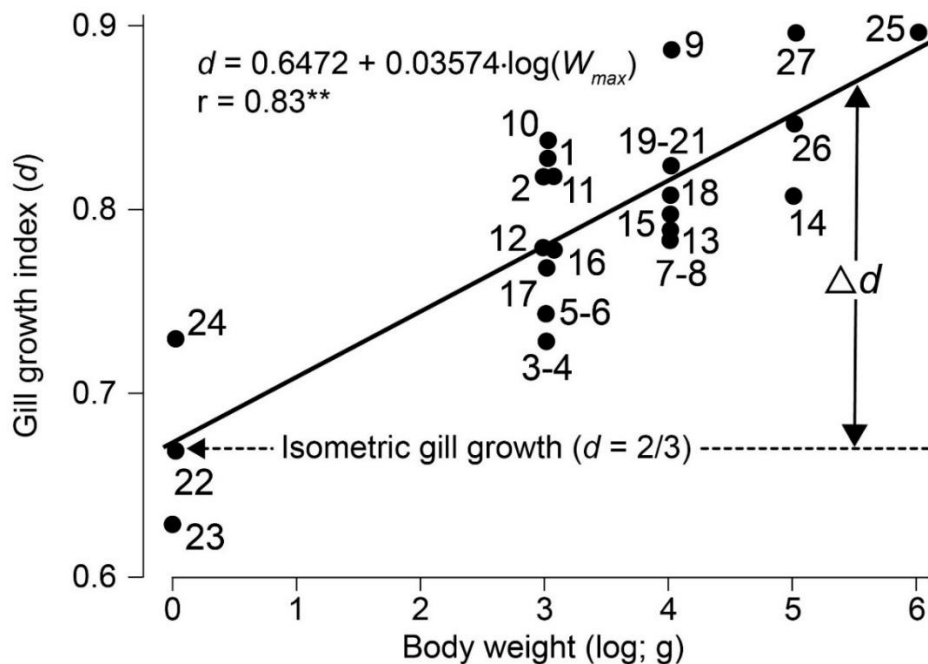
Few authors have explicitly stated that  $d_G$  should, in general, be equal to  $d_Q$ . De Jager and Dekkers (1975) did so and took the average of their mean value of  $d_G = 0.811$  with their mean value of  $d_Q = 0.826$  to a mean value of  $d = 0.82$ . This value of  $d = 0.82$  was subsequently applied by them to all of the gill size and fish respiration data available and used to obtain gill size and respiratory rate estimates for "standard" fishes of 200 g ( $A_{200}$  and  $M_{200}$  of De Jager and 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 and Dekkers 1975, for a list and critique of several papers giving such estimates) or erroneous methods in respiration studies (see Winberg 1960, for a review of the most common pitfalls). Also, it repeatedly appeared that such extreme estimates were based upon a very limited range of sizes.

Extreme values which cannot, however, be discussed away are provided by the tuna, with values of  $d_G$  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<sup>25</sup>.

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  $10^6$  grams (See Table V and Figure 2).



**Figure 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).

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

$$d = 0.6742 + 0.03574 \cdot \log(W_{\infty}) \quad \dots 70)$$

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

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 Cyprinodontidae and probably all other tiny fishes measuring only a few centimeters and weighing less than or little above one gram.

<sup>25</sup> Shortly after this was written, I came across the article by Te Winkel (1935), pertaining to an extremely small fish ( $W_{max} = 0.03$  g), whose gill surface area in relation to their weight produced an estimate of  $d = 0.60$  (Pauly 1982), fitting closely on Figure 1 and matching the predicted value of  $d$  from Equation 70.

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  $10^4$  grams. Finally, the large, active tuna have gills which grow almost as fast as their body weight ( $d = 0.9$ ). Nikolsky (1957) gave for *Rhincodon typus* a maximum size of 20 m, which corresponds to a weight of about 60 t when using the condition factor of 0.77 suggested by length/weight measurements on this fish (Angel, undated). The weight of 60 t, when inserted into Equation (70), suggest a value of  $d = 0.95$  which may correspond to the highest possible  $d$  value in fishes<sup>26</sup>.

## 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 ( $dW/dt$ ) 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 and Holt 1959; Hohendorf 1966; Mitani 1970; Banerjii and Krishnan 1973, and especially Mio 1965) have attempted to compare the growth performance of various fishes by comparing their value of  $L_\infty$  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  $L_\infty$  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<sup>27</sup>;

<sup>26</sup> The maximum length of 20 m for *Rhincodon typus* appears to have been confirmed by Chen et al. (1997), but it still strains credulity. However, the corresponding weight was 34 t, which is lower than my estimate, and which would lead to a maximum  $d$  value of 0.92.

<sup>27</sup> Actually, one *can* compare the growth of fish and other animals using length, but for this to make sense, they must have similar shapes. Thus, a length-based growth performance index (such, e.g., as  $\theta' = \log(K) + 2\log(L_\infty)$ ) can be used to compare the growth of different population of the same species, or of species differing in their coloration; however, for comparisons involving species of different shapes, an

- 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 ( $dW/dt$ ), or slope of the weight growth curve, has in all fishes a maximum, ( $dW/dt_{max}$ ) whether  $dW/dt$  is plotted against age or against size. Weight growth curves have one, and only maximum 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  $dW/dt_{max}$  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

$$dW/dt_{max} = 4/9 \cdot K \cdot W_{\infty} \quad \dots 71)$$

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

$$dW/dt_{max} = 4/9 \cdot 10^P \quad \dots 72)$$

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  $dW/dt_{max}$ , 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  $dW/dt_{max}$  irrespective of their values of  $W_{\infty}$  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)<sup>28</sup>. The abscissa scale of an auximetric grid consists of values of  $\log(W_{\infty})$  (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 ( $W_{\infty}, K$ ) to the baseline represents  $P$  and is therefore a direct indication of growth performance (see Figure 3 for a first example).

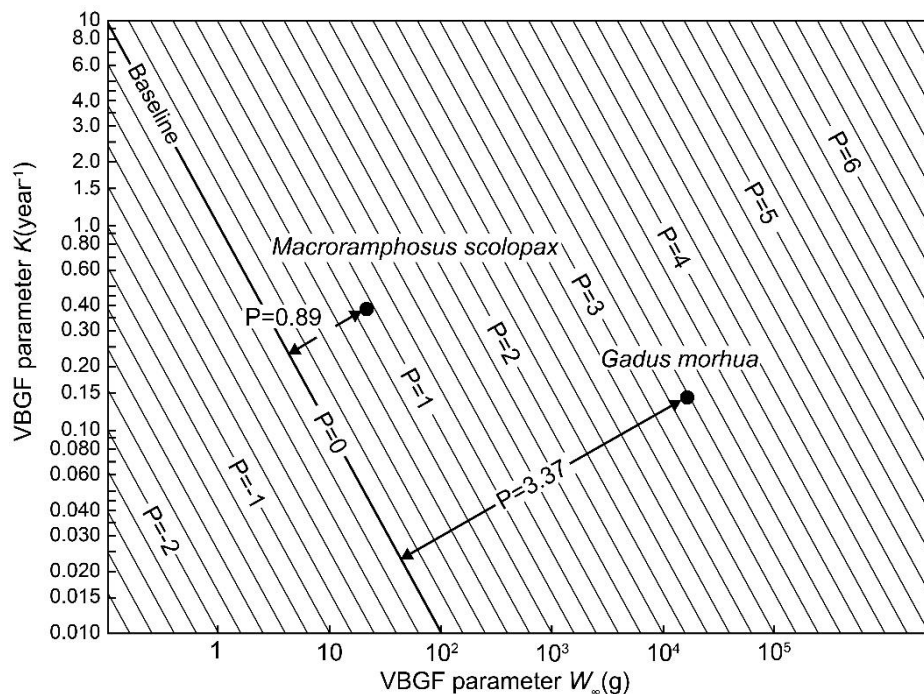
The auximetric grid also allows for the separation and definition of taxa by means of their growth parameters. Examples are given in Figure 6, where values of  $K$  and  $W_{\infty}$  for seventeen (17) species of Scombridae (Scombrinae

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index based on weight is required, such as  $\log(K) + 2\log(W_{\infty})$ .

<sup>28</sup> The 'metric' part of auximetric is also from the Greek, i.e., from 'metreo,' to measure. Also note that 'auximetric plot' or 'graph' would have been better than 'grid.' This, fortunately, has not prevented the concept from being used, as can be ascertained by entering the term 'auximetric' in Google Scholar.

and Thunninae) are plotted together with values of  $K$  and  $W_\infty$  for, three (3) species of Cyprinidontidae (♂♂ and ♀♀), and in Figure 7 where the growth parameters for thirteen (13) species were plotted.



**Figure 3.** Auximetric grid: demonstrating the concept of  $P$  (see text).

Values of  $K$ ,  $W_\infty$  and  $P$  for fresh water fishes are given in Table VII which, when plotted into an auximetric grid (Figure 4), allow for a preliminary estimate of that area of the grid occupied by freshwater fishes. The same procedure, when applied to data on marine fishes (Table VIII and Figure 5) reveals that, as a whole, the area covered by the marine fishes is much larger than that covered by the fresh water fishes, and the range of  $P$  values is much wider (-0.70 to 5.79 for marine fishes as compared to -0.30 to 3.98 for freshwater fishes). Also remarkable is the feature that marine fishes may have much higher values of  $K$  than freshwater fishes for the same value of  $W_\infty$ , but that the lowest values of  $K$  for a given  $W_\infty$  are about the same in marine and fresh water fishes.

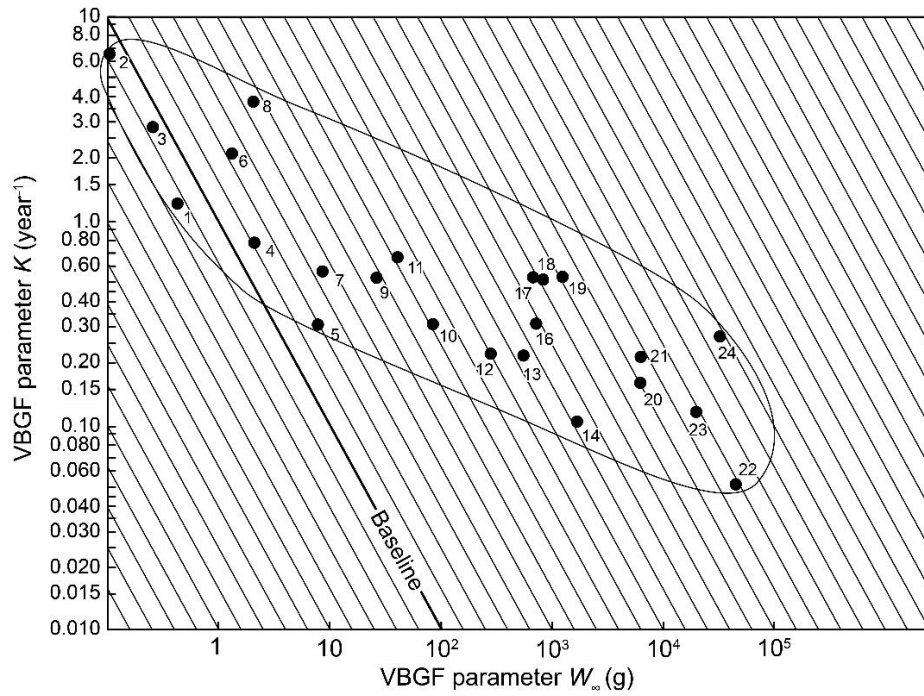


Figure 4. Auximetric grid: selected freshwater fishes (see also Table VII; number 15 is deleted).

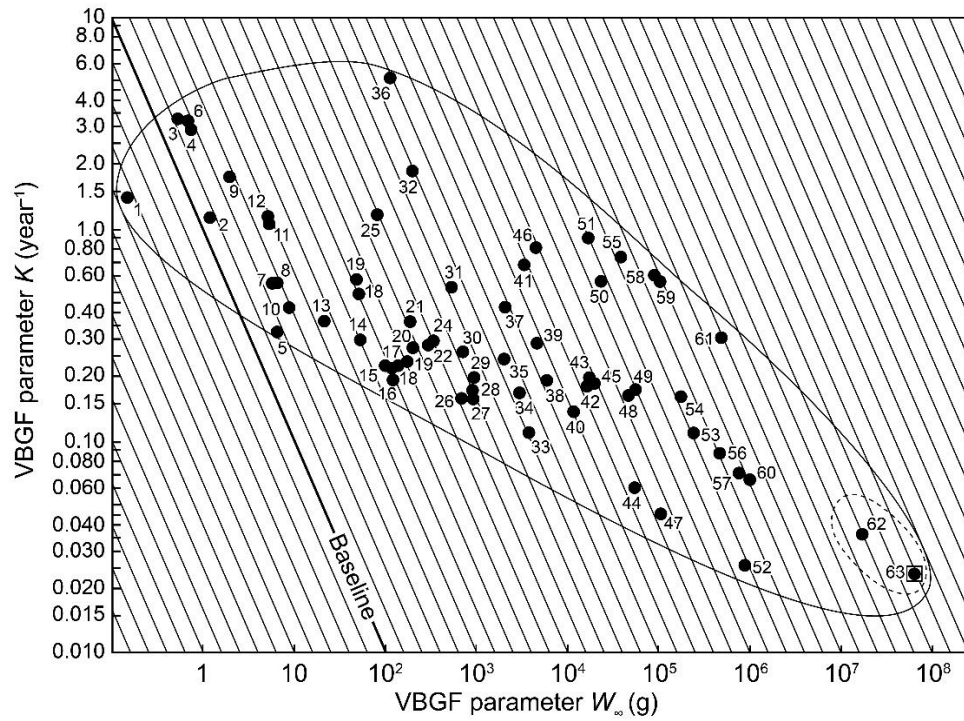


Figure 5. Auximetric grid: selected marine and brackish water fishes (see also Table VII).



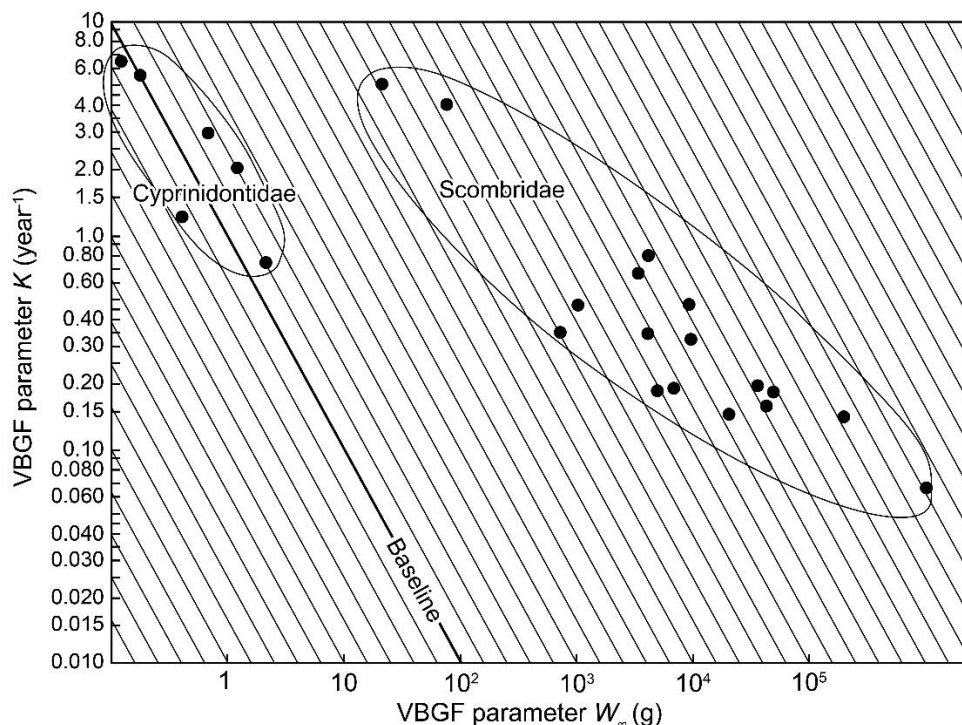


Figure 6. Auximetric grid: Scombridae and Cyprinodontidae.

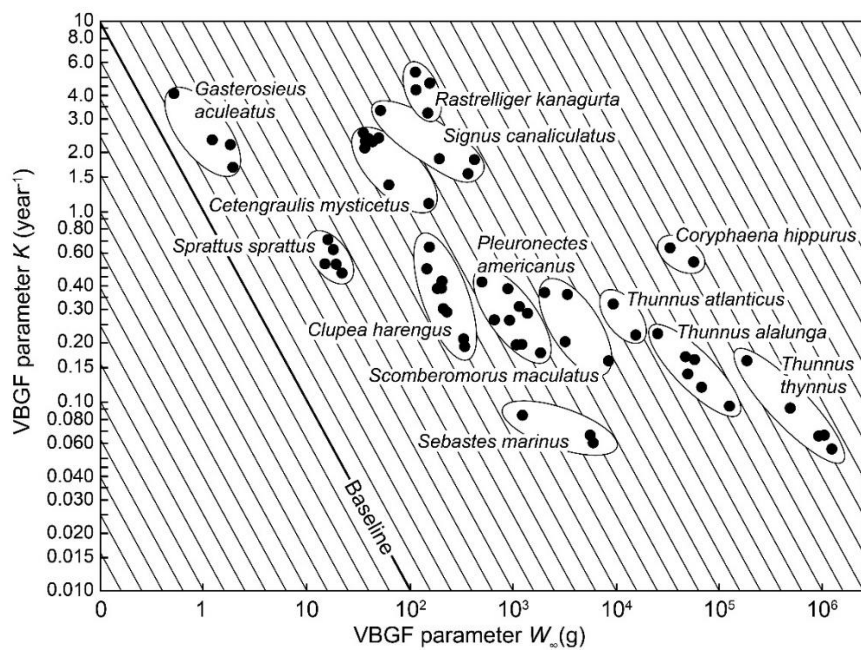


Figure 7. Auximetric grid: plot of different stocks in 13 different fish species.

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  $W_{\infty} = 60$  t 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 Figure 5, no. 62 and 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 Figures 8 and Figure 9 for preliminary examples);

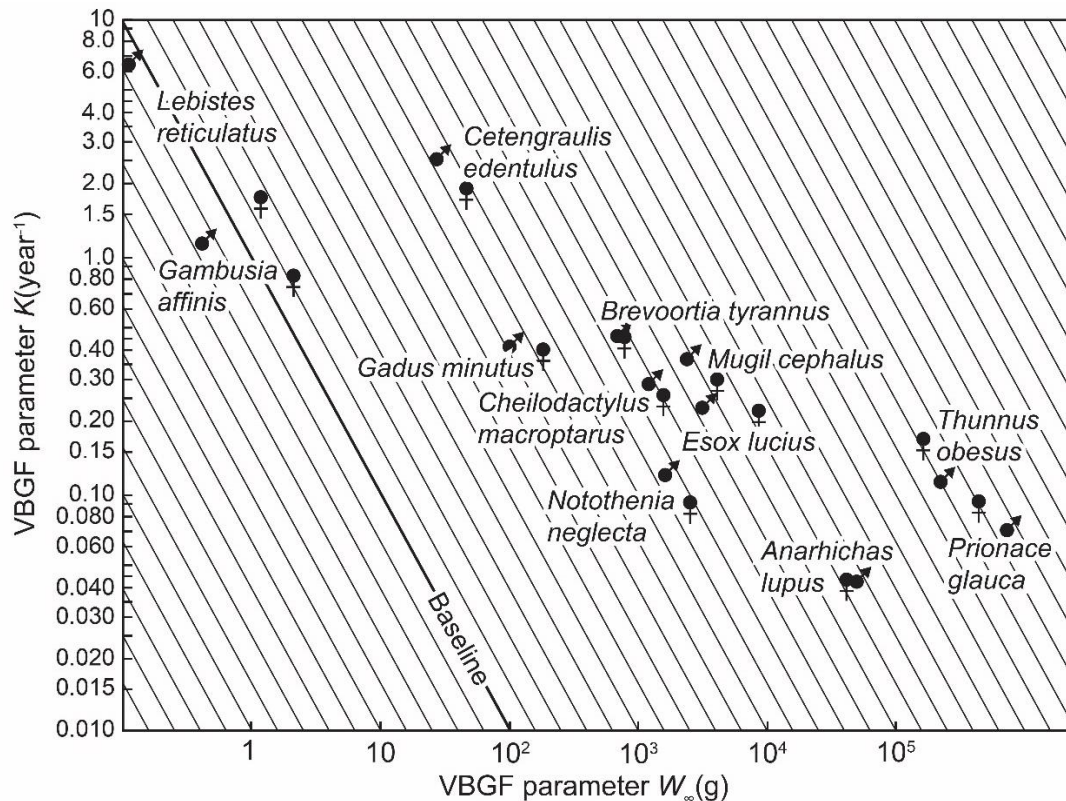
- Identification of erroneous literature values of  $K$  for given values of  $W_\infty$  (or vice-versa) through comparisons with other  $K/W_\infty$  pairs pertaining to the same species.

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.

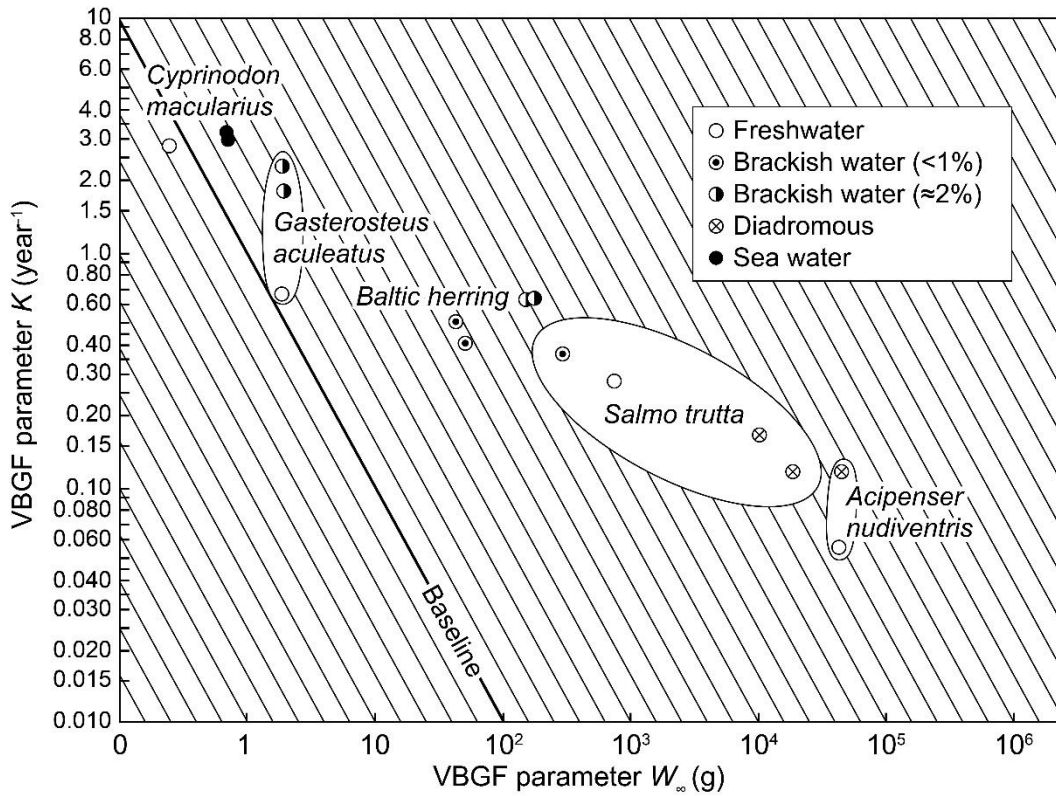
#### 5.4. Intraspecific growth comparisons

The concept of  $P$  and of the auximetric grid need further development to allow for intraspecific comparisons. Various authors have reported that in different stocks of a given species, the values of  $W_\infty$  and  $L_\infty$  tend to decrease when  $K$  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  $\log(L_\infty^3)$  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.



**Figure 8.** Auximetric grid: sex-specific growth parameters in 12 selected fish species.



**Figure 9.** Auximetric grid: the effect of salinity on 5 selected fish species.

Because  $L_{\infty}^3$ , as a whole, is proportional to  $W_{\infty}$ , 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  $\log(W_{\infty})$ . 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  $L_{\infty}^3$  values (see Table IX and Pauly 1978a, for data on the 7 species in question).

When the positive values of  $b$  are excluded, a mean value of  $b = -0.632 \pm 0.386$  is obtained (Table X). Similarly, a mean value of  $b = -0.714 \pm 0.279$  is obtained when plotting  $\log(K)$  against  $\log(W_{\infty})$  in various fish stocks whose growth parameters were compiled for the investigation on the inter-relationships 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). It seems, therefore, legitimate to take an unweighted mean of these two independently obtained mean values of  $b$ , such that

$$b = (-0.632 - 0.714)/2 = -0.673 \quad \dots 73)$$

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

$$\log(K) = a - (2/3) \cdot \log(W_{\infty}) \quad \dots 74)$$

The value of the slope ( $\approx -2/3$ ) 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  $W_{\infty}$ , 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  $W_\infty$ , or  $\log(K)$  should be inversely proportional to the log of the gill surface at  $W_\infty$ , or to  $W_\infty^{2/3}$  when the special VBGF is used, as was here the case.

It appears, therefore, that the empirical data which lead to the mean estimates of  $b \approx -2/3$  (- 0.632 and 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  $\log(W_\infty)$  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 (p. 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  $L_\infty$  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<sub>2</sub> 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<sup>29</sup>;
- $q$  is a correction factor for converting respiratory rates to 20 °C (taken from Winberg 1960 and 1971);

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<sup>29</sup> 'Centigrade' is now outdated, and 'Celsius' should be used instead.

- % is the respiratory rate, in% of the respiratory rate at 20 °C (= 100%);
- $\log(\%) = y$  is the common logarithm of the percentage value, and
- $\hat{y}$  is the estimated value of  $y$  based on the 4th degree polynomial:

$$\hat{y} = d_0 + d_1 + d_2T^2 + d_3T^3 + d_4T^4 \quad \dots(74)$$

where

$$\begin{aligned} d_0 &= +0.920810504 \\ d_1 &= +0.080976405 \\ d_2 &= -0.001930460 \\ d_3 &= +0.000032193 \\ d_4 &= -0.000000159 \end{aligned}$$

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

$$\hat{y}' = d_0 + d_1 + d_2T^2 + d_3T^3 \quad \dots(75)$$

where

$$\begin{aligned} d_0 &= +0.080976405 \\ d_1 &= -0.003860920 \\ d_2 &= +0.000096578 \\ d_3 &= -0.000000635 \end{aligned}$$

$\ln(\hat{y}')$  is the natural logarithm of the  $\hat{y}'$  values;

$Q_{10}$  is the temperature coefficient (increase of respiration rate caused 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  $L_\infty$  (or  $W_\infty$ ) 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  $L_\infty$  (or  $W_\infty$ ) 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  $L_\infty$  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 and Lieth (1967).

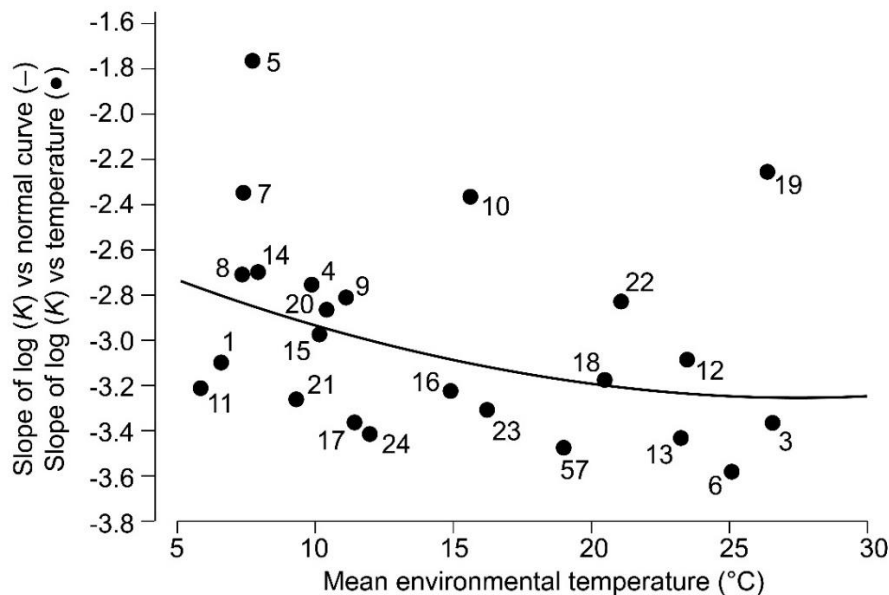
The sets of growth parameters for fishes from water bodies which could not be located or were too imprecise were omitted along with most of the data relating to fresh water fishes in areas where the mean *annual air temperature is*  $< 0^\circ\text{C}$ . *Table XIII summarizes the growth and temperature 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;
- $\ln(b)$  is the natural logarithm of the slope of the regression line;
- $T$  is the mean value temperature for a given species;
- $\ln(b)_n$  is the natural logarithm of the slope of Krogh's normal curve at  $T$ , as based on Equation 75;
- $\Delta \ln(b)$  is the difference between the empirical value of  $\Delta \ln(b)$  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 ( $\ln(b) = 0.015$ , see Table XIV) which suggests that the real  $\ln(b)$  values are well described by the values derived from Krogh's normal curve, and that the latter curve, therefore, may be used to describe the relationship between  $K$  and temperature in the 5 to 30° C range (Figure 10).



**Figure 10.** Showing the similarity of the slope of plots of  $\log(K)$  on temperature and the slope of Krogh's normal curve (see also Table XIV and text).

### 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  $\log(W_\infty)$  and/or  $L_\infty^3$  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 XIIIa-h.

Of 18 species for which  $\log(W_\infty)$  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  $W_{\infty}$  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  $L_{\infty}$  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.*"<sup>30</sup>

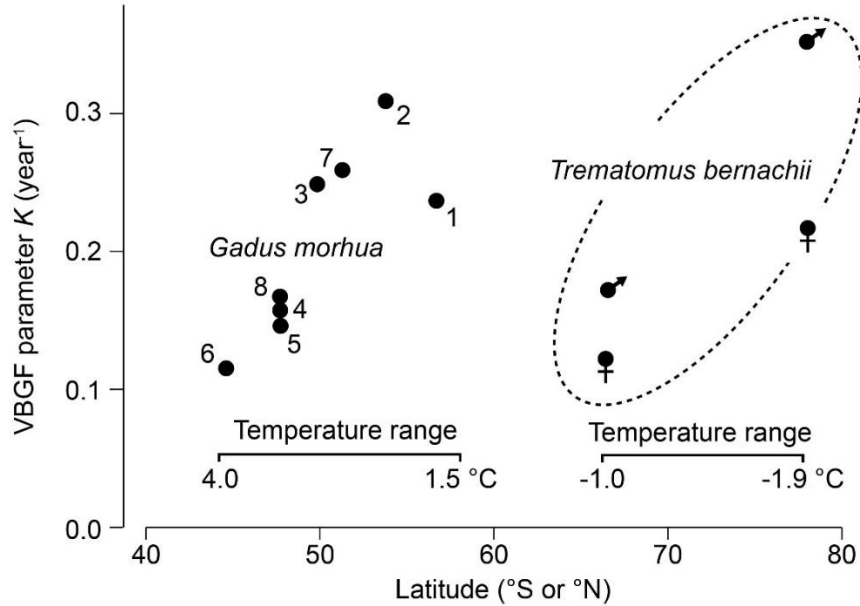
The results of May et al. (1965) or the rule of Suvorov (1959) have apparently never been incorporated into any generalized theory of fish growth, possibly because they seem to contradict the well-known 'Bergmann rule' which states that animals tend to reach a larger adult size, the lower the mean temperature 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<sub>2</sub> 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 (Figure 11) and an attempt has therefore to be made to convert the latitude values into estimates of environmental temperature.

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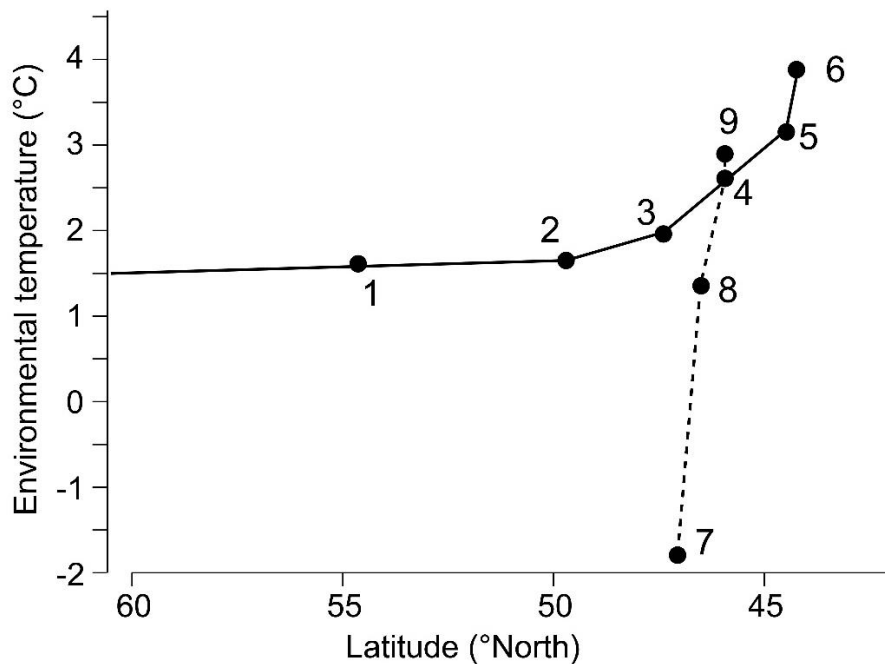
<sup>30</sup> There is recent evidence that cold-adapted cod have higher mitochondrial activity and maintenance metabolic rate (Lannig et al. 2023).



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

The average temperature profile profiles over the continental shelf off Labrador and Newfoundland presented by May et al. (1965; Figures 4A to F, and Figure 5A to C) may be used to estimate the mean temperature for the various cod stocks 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 XV, Figure 12). From Figure 12, a temperature estimate can be obtained for each of the stocks whose growth parameters and mean latitude were given (Table XV).



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



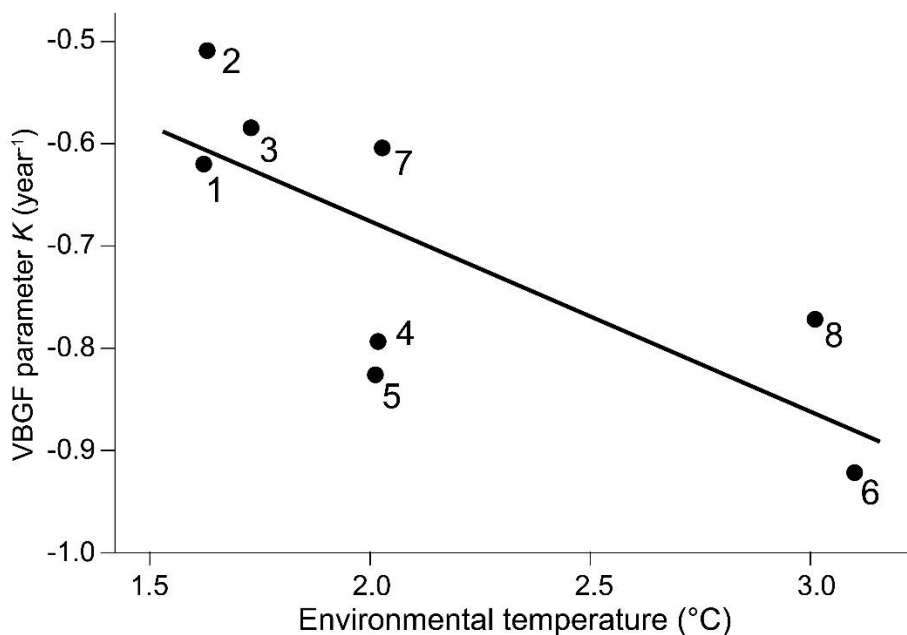
As assumed by May et al. (1965), there is a close negative relationship between latitude and temperature (Figure 12). Consequently, there is a close negative relationship between  $\log(K)$  and environmental temperature (Figure 13) which may be expressed by the equation:

$$\log(K) = -0.318 - 0.181 \cdot T; r = -0.755^* \quad \dots 76)$$

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

$$\log(K) = -1.564 + 0.094 \cdot T \quad \dots 77)$$

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  $T = 4\text{-}5^\circ\text{C}$ , at which  $K$  should be lowest. Other data which could be used to quantify the relationship between  $K$  and temperature in very cold environments ( $-2$  to  $+4^\circ\text{C}$ ) are very scanty.

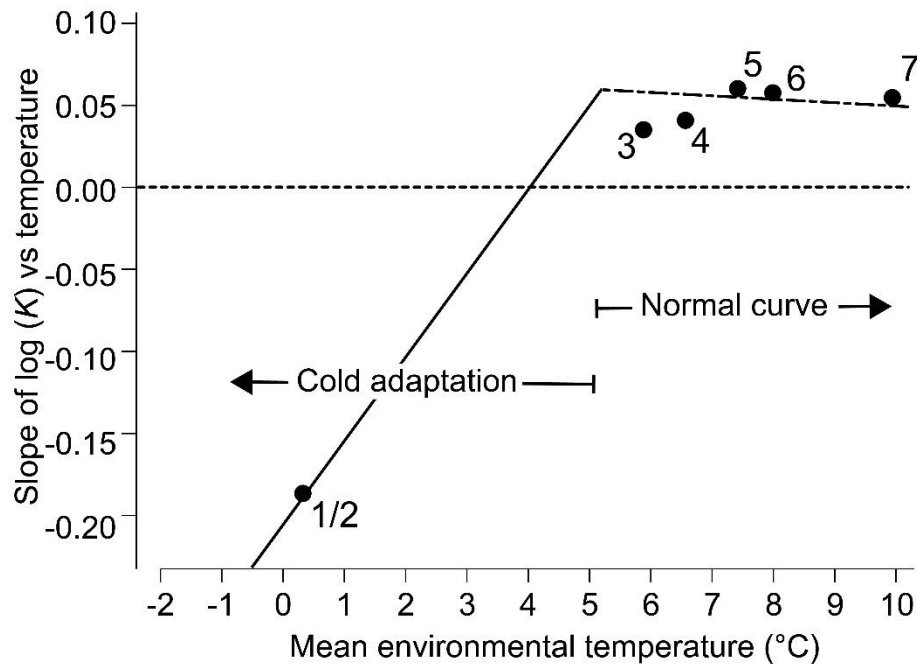


**Figure 13.** Plot of  $\log(K)$  on temperature [for] cold-adapted cod (Labrador – Newfoundland).

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 Figure 11). In this species, the slope relating  $\log(K)$  to environmental temperature is  $-0.193$ , a value close to that obtained from cod data ( $-0.181$ ). These two values of  $b$  were used for the plot in Figure 14 where, for lack of a better alternative, a straight line was drawn which links the value of  $b$  at  $5^\circ\text{C}$  (the end of Krogh's normal curve) to the mean of the coordinates for the two cold-adapted fishes ( $b =$



-0.187;  $T = +0.3^{\circ}\text{C}$ ). This procedure appears justified, as the data on cod suggest a higher slope value at lower temperatures than at higher temperatures (see Figure 13).



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

Thus,  $b$  may be estimated for the range  $-2^{\circ}\text{C}$  to  $5^{\circ}\text{C}$  from

$$b = -0.2044 + 0.0537 \cdot T \quad \dots 78)$$

(see Figure 14). When integrating Equation (78) to

$$\log(K) = -0.2044 \cdot T + 0.0537 \cdot T^2 + C \quad \dots 79)$$

the value of  $C$  may be defined such as to adjust the value of  $\log(K)$  to its value at  $5^{\circ}\text{C}$  ( $= 1.2848$ ), or

$$C = 1.2848 - (-0.2044 \times 5 + (0.0537/2) \times 5^2) = 1.6356 \quad \dots 80)$$

Thus, Equation (79) becomes

$$\log(K) = 1.6356 - 0.2044 \cdot T + 0.02685 \cdot T^2 \quad \dots 81)$$

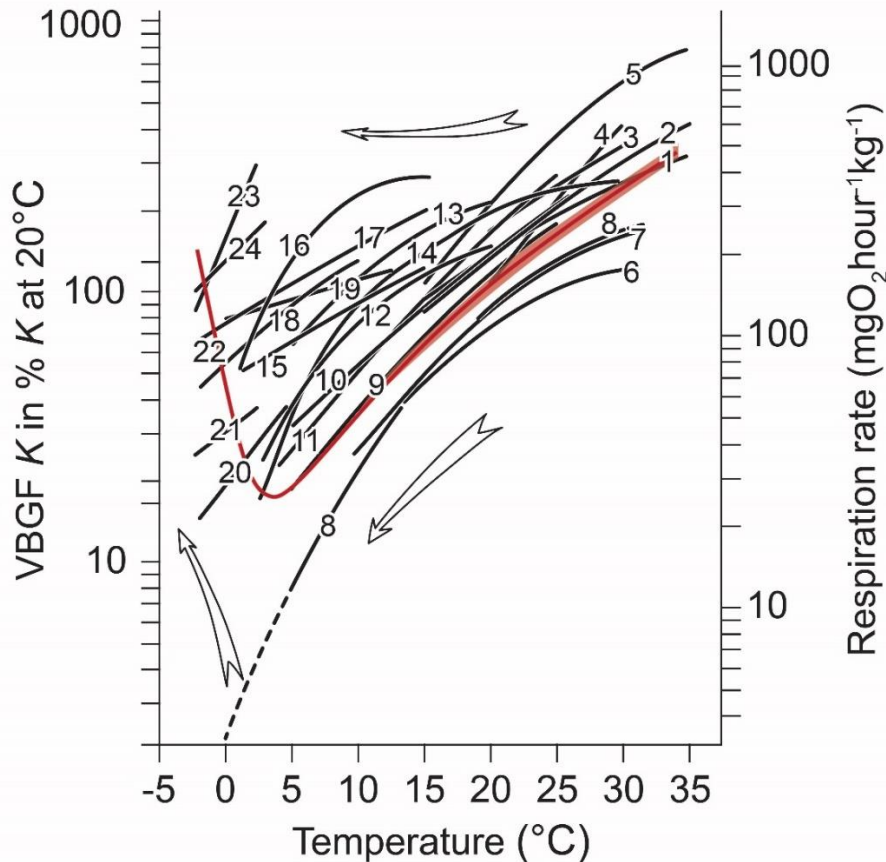
From the values provided by Equation (81), multiplicative factors can be derived which correspond to the conversion factors given by Winberg (1960, 1971) for use in connection with Krogh's normal curve (see Table XII).

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

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).”

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).<sup>31</sup>



**Figure 15.** Showing that  $K$  is proportional to respiratory rate over the whole range of temperatures at which fishes occur, including polar temperatures where ‘cold’ adaptation’ tends to increase metabolic rates.<sup>32</sup> Based on Figure 7 in Wohlschlag (1964b; “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, Antarctic.”), with superposition of  $K$  values derived from Table XII.

### 6.5. The concept of $P_{20}$

Table XVII allows for the conversion of any set of  $K$  and  $W_{\infty}$  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

<sup>31</sup> Despite their tentative nature, the ideas presented here, which I did not further pursue in the 3 decades that followed, turned out to be confirmed, notably by Privalov (1990); see Pauly and Lam (2023).

<sup>32</sup> The red line was grey in the original.

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 and 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  $W_{\infty}$  were estimated, and values of  $P_{20}$  calculated;
- 4) Values of  $d$  were calculated for each value of  $W_{\infty}$  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 and 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 pair.

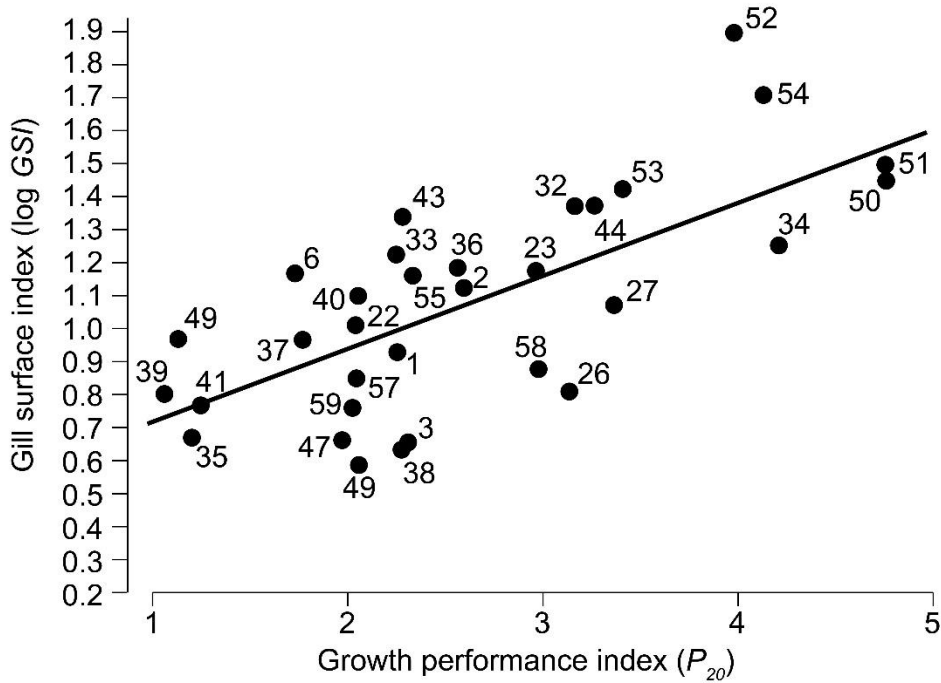
The data so obtained are summarized in Table XVIII. For further interpretation, it appears appropriate to divide the data in Table XVIII into marine fishes (42 spp.), and fresh water fishes (18 spp.).

The plot of  $\log(GSI)$  against  $P_{20}$  in marine fishes (Figure 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

$$\log(GSI) = 0.488 + 0.233 \cdot P_{20} \quad \dots 82)$$

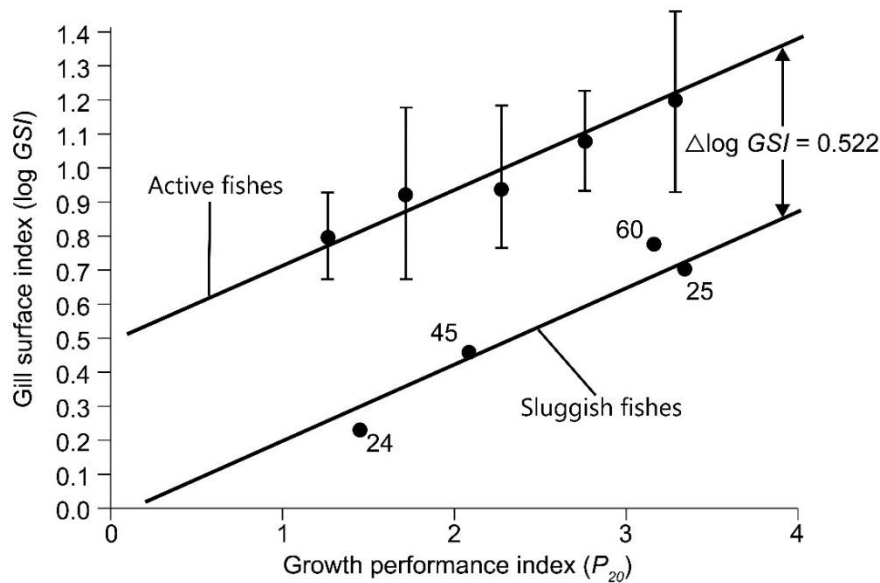
from which values of  $GSI$  may be obtained from values of  $P_{20}$ .

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 Figure 16 and Table XVIII).



**Figure 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 Figure 16 do not, however, include all marine fishes. Four values (not the outliers mentioned above) were not plotted into Figure 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 Figure 17 and fitted with a line with the same slope as Equation (82) passing through their mean value of  $\log(GSI)$  and  $P_{20}$ .



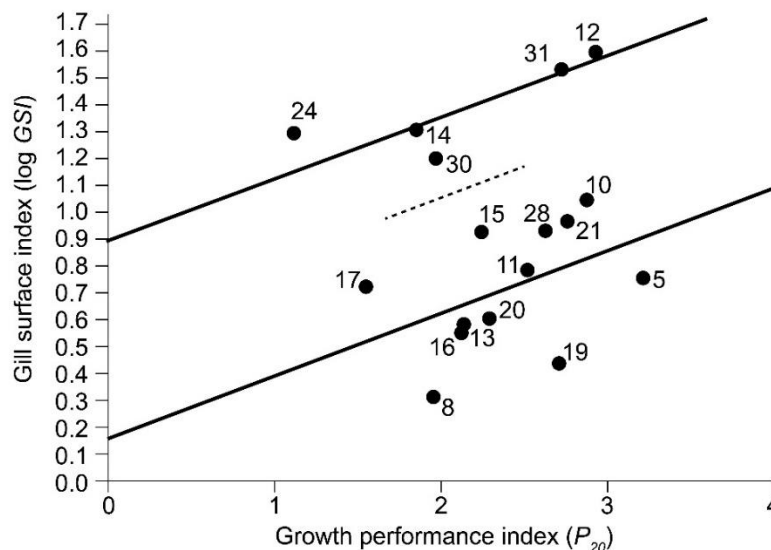
**Figure 17.** Showing that sluggish fishes have for the same growth performance ( $P_{20}$ ) smaller gill surfaces (*GSI*) that active fishes (see also Table XVIII).

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 Figure 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 had 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 Figure 17 also express different metabolic levels, as these sluggish fish may be assumed to require less O<sub>2</sub> 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 Figure 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 Figure 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 Figure 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.



**Figure 18.** A possible interpretation for the relationship between gill size ( $GSI$ ) and growth performance ( $P_{20}$ ) in freshwater 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 and Dekker (1975), as well as those provided by Hughes and 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

$$\log(WBD) = 1.3268 - 1.0755 \cdot \log(GSI) + 0.3567 \cdot \log(P_{20}) \quad \dots 83)$$

which is highly significant ( $R = 0.869^{**}$ ).

The main point is, however, that the coefficient which links  $\log(GSI)$  to  $\log(WBD)$  is here  $-1.076$  ( $\approx -1$ ). 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 and Dekker (1975) obtain a value of only  $-0.744$  for the slope of their plot of  $\log(WBD)$  against  $\log(\text{oxygen uptake})$ .

## 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  $26^\circ C$  and at oxygen concentrations ranging from 1.6 to 8.1 mg  $O_2$ /liter, are presented in Table XX.

Of the data of Thiel (1977), obtained in temperatures ranging from  $23$  to  $36^\circ C$ , only those were used which pertained to  $26^\circ C$ . 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 p. 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<sub>2</sub> content (x), initial weight (y) and daily growth increment (z) are as follows:

Coefficient	<i>M. salmoides</i>	<i>C. carpio</i>
$r_{xy}$	-0.116	0.170
$r_{xx}$	0.755**	0.875**
$r_{yz}$	-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*

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

while in *C. carpio*, the relationship is

$$z = -0.0915 + 0.165 \cdot x + 0.0116 \cdot y, \quad R = 0.878^{**} \quad \dots 85)$$

Note that in both cases it is x (O<sub>2</sub> content) which removes almost all of the variance.

The effect of reduced O<sub>2</sub> 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. 1967 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<sub>2</sub> concentrations, not the low O<sub>2</sub> 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<sub>2</sub> being needed for synthesis), nor as burning material (O<sub>2</sub> is also needed in this process). The amino acids 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 (E= growth increment/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 (= gill area/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 (E) of fishes is generally expressed as

$$E = a \cdot W^b \quad \dots 86)$$

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).<sup>33</sup> The values of  $|b|$  will be close to (1 - *d*) in all cases where the food intake

<sup>33</sup> A much better equation for expressing the relationship between *E* and *W* is  $E = (1 - W/W_{\infty})^{\beta}$ , proposed in Pauly (1986; see also Silvert and Pauly 1987); it helped reinforce the case made further below.

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 and 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 ( $E$ ) and weight is

$$E = 0.726 \cdot W^{-0.23} \quad \dots 87)$$

The value of  $W_\infty$  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  $|b| = 0.23$  ( $1.00 - 0.79$ ). 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 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:

$$E_2 = 0.73 \cdot W^{-0.15} \quad \dots 88)$$

where  $E_2$  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.)

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 Paloheimo and 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, 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

$$L_t^D = L_\infty^D (1 - e^{-KD(t-t_0)}) \quad \dots 61$$

and for weight

$$W_t = W_\infty (1 - e^{-3DK(t-t_0)/b})^{b/D} \quad \dots 37$$

Equation (61) contains four parameters,  $L_\infty$ ,  $K$ ,  $D$  and  $t_0$ , while Equation (37) contains the additional parameter  $b$ , the exponent of the length/weight relationship in Equation (5b).

When weight growth is isometric,  $b$  is equal to 3, and Equation (37) reduces to

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

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.

## 9.2. Asymptotic size ( $W_\infty$ or $L_\infty$ )

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<sup>34</sup> or by some mass mortality. If this closeness of the largest size to asymptotic size cannot be demonstrated, then it may indeed be considered that  $W_\infty$  and  $L_\infty$  are artefacts, resulting from 'forcing' the VBGF upon size-at-age data.

However, a generally good agreement between values of  $L_{max}$  and  $L_\infty$  has been convincingly demonstrated (in small fishes) 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

$$L_{max} = 0.95 \cdot L_\infty \quad \dots 92)$$

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  $L_\infty$  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) (Figure 19).

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  $D = 0.3 \Leftrightarrow 3 \cdot (1 - 0.9)$ , which, when used in conjunction with the special VBGF, provides, with the same data of Table II, an

<sup>34</sup> The words 'by man' reflects the way I thought (or failed to think) 5 decades ago.

estimate of  $K = 0.410$  and  $L_{\infty} = 332$  cm, while the condition factor used above provides an estimate of  $W_{\infty} = 622$  kg. Both values of asymptotic size (332 cm and 622 kg) correspond very well with the values of  $W_{max}$  and  $L_{max}$  reported by Tiews (1963) for various Mediterranean and North Atlantic stocks (Figure 20).

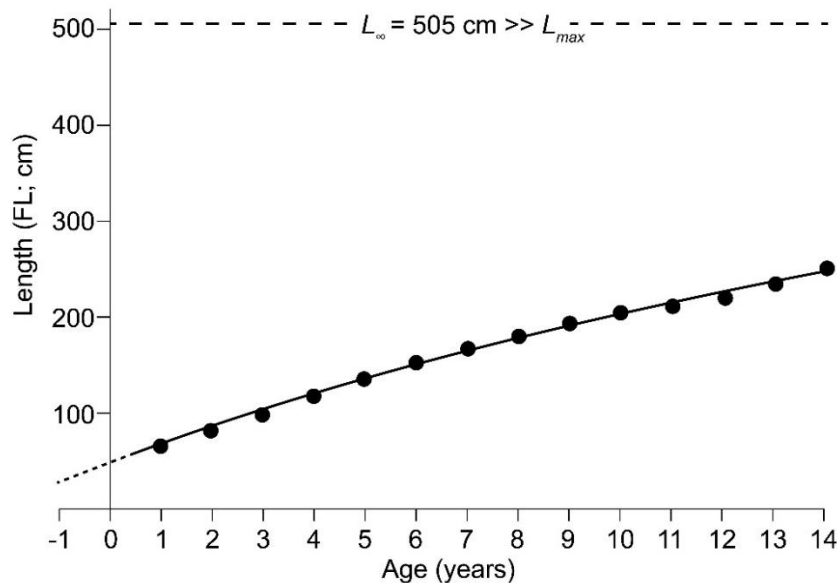
It will be noticed, however, that the fit of the special VBGF to the data of Sella (1929) is almost as good as the fit of the generalized VBGF to the same data (See Figure 19 and 20), for which reason the quality of the fit could not be meaningfully used to estimate by iteration a meaningful value of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

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 Figure 20).

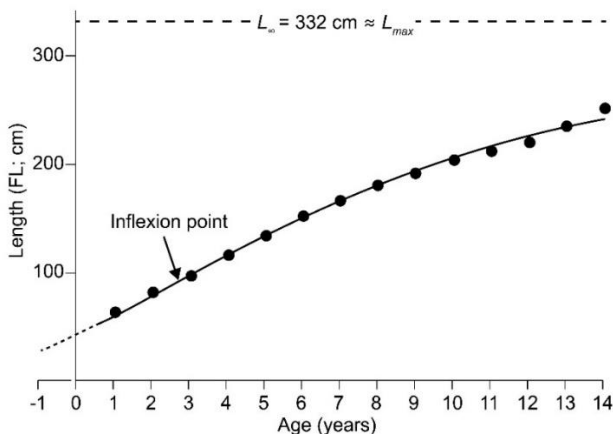
This exercise, here demonstrated with bluefin tuna, could be extended to a whole series of large fishes with the main result remaining the same: when the special VBGF is used, the value of asymptotic size obtained from a set of size-at-age data differs from the maximal sizes recorded from the same stock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

The generalized VBGF, on the other hand, provides estimates of  $W_{\infty}$  and  $L_{\infty}$  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 van Bertalanffy based his theory, as well as the validity of the generalization and interpretation of the VBGF presented by this author.



**Figure 19.** Length growth curve of *Thunnus thynnus*, special VBGF ( $D = 1$ ). Note that  $L_{\infty}$  is much higher than  $L_{max}$  ( $\approx 330$  cm).



**Figure 20.** Length growth curve of *Thunnus thynnus*, generalized VBGF ( $D = 0.3$ ). Note that  $L_{\infty}$  is very close to  $L_{max}$  ( $332 \approx 330$  cm)

The closeness of  $W_{max}$  and  $W_{\infty}$  and of  $L_{max}$  and  $L_{\infty}$ , 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

$$\sqrt[3]{W_{max}} \approx \sqrt[3]{W_{\infty}} \quad \dots 93)$$

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 (Thurrow 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  $W_{\infty}$  and  $L_{\infty}$ .

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  $W_{\infty}$  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 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.”*<sup>35</sup>

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.”*

<sup>35</sup> Note that the latter argument, suggesting that an “apparent asymptote” can be caused by food conversion efficiency dropping to zero would actually be a *real* asymptote.

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 Cyprinodontidae, 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

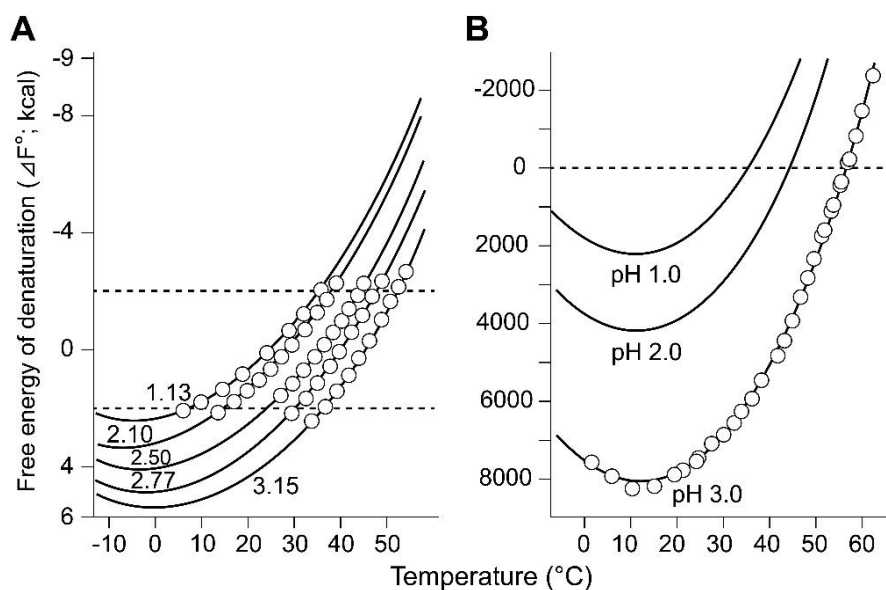
$$dC/dt = ks - k_D C \quad \dots 94)$$

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 [Figure 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 (Figure 7 and 8 in Brandts 1967) are shown in Fig. 21.



**Figure 21.** Thermodynamical stability of two proteins in relation to temperature. Right: Ribonuclease; left: Chromotrypsinogen (from Brandts 1967; note inverted 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 Figure 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 cofactors. 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 (p. 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 lowers the value of asymptotic size (see examples of Figure 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: $t_0$**

This parameter is defined as the hypothetical age the fish would have had at zero length had they always grown in the manner described by the equation (Ricker 1975). However, fishes do not always grow in the manner described by the equation, and  $t_0$  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

$$L_b/L_\infty = 1 - e^{-K(-t_0)} \quad \dots 95)$$

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  $t_0$ .

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  $t_0$  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  $t_0$  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  $t_0$  from an estimate of  $K$  and  $L_\infty$ .

This equation is

$$\log(-t_0) = -0.3922 - 0.2752 \cdot \log(L_\infty) - 1.038 \cdot \log(K) \quad \dots 96)$$

and is based on 153 triplets of values of  $t$ ,  $L_\infty$  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 o (see Pauly 1978a)<sup>36</sup>. 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  $x = \log(K) = y$ ):

$\Sigma x = 242.61959$	$\Sigma x^2 = 18.64374$	$\Sigma xy = -141.46073$
$\Sigma y = -71.39158$	$\Sigma y^2 = 67.73370$	$\Sigma xz = -63.53239$
$\Sigma z = -52.67110$	$\Sigma z^2 = 68.29293$	$\Sigma yz = -3.37471$

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  $L_\infty = 130$  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, p. 62 - 63).

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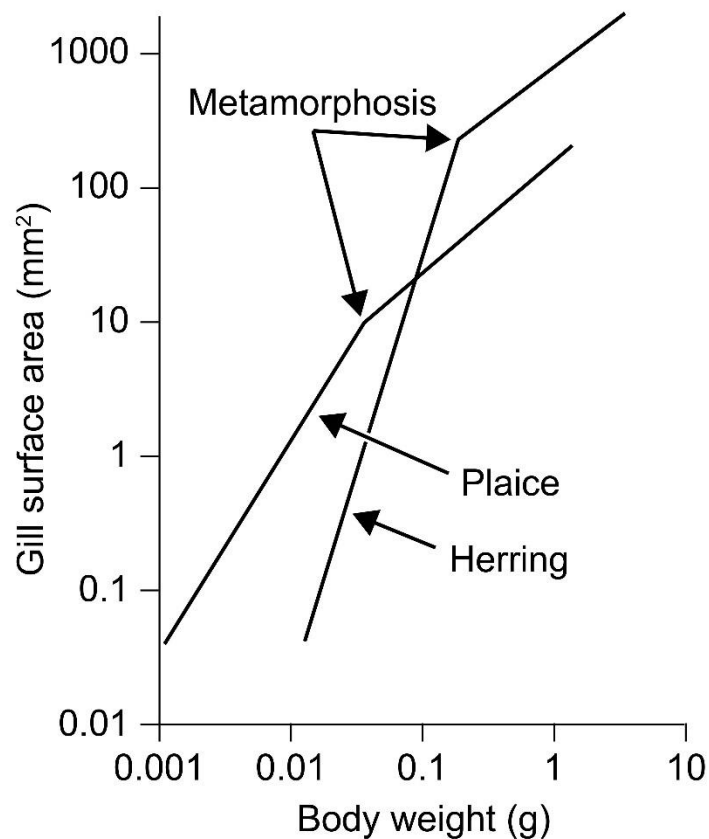
<sup>36</sup> 'Code o' meant that the growth parameters  $L_\infty$ ,  $K$  and  $t_0$  originated from one of the references cited in this compilation, rather than being computed by me, based on data in such references.



### 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.



**Figure 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<sup>37</sup>. This is in accord with the results from studies of larval growth which generally suggest a logarithmic<sup>38</sup> 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

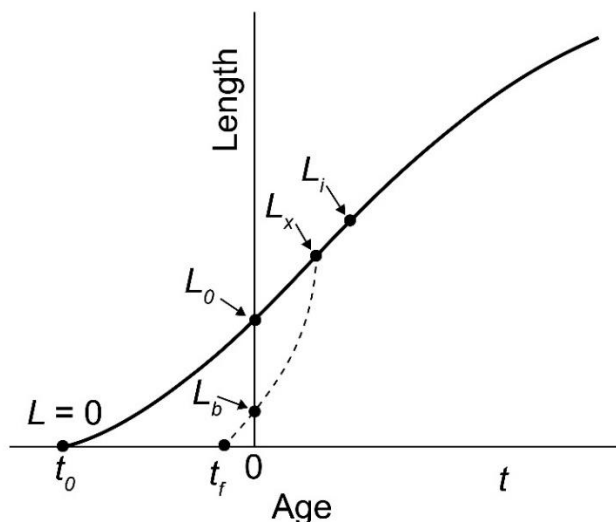
<sup>37</sup> See Teletchea and Pauly (2024) for some implications.

<sup>38</sup> What was meant was 'exponential' growth.

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<sup>39</sup> 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 Figure 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 ( $L_b$ ), 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 ( $L_x$ ).



**Figure 23.** Graphical representation of the biological and mathematical origins of the VBGF (scales: arbitrary units).

These considerations suggest that positive values of  $t_0$  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  $t_0$  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  $t_0$  which are biologically impossible. This criterion obviously does not allow for the identification of those erroneous values of  $t_0$  which happen to be negative.<sup>40</sup>

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.

<sup>39</sup>This, again, was not the *'mot juste'*; I meant that the primordial fin fold is 'well supplied with capillaries.'

<sup>40</sup> While it was correct to consider that the growth of larvae is not described by the VBGF, and that this contributes to its failure to describe growth curves near their origins, it was wrong to suggest – by default – that this was the main issue with the VBGF when applied to young stages (as implied by Figure 23). In fact, the VBGF also fails to describe the growth of early juveniles, for the same reason that it doesn't apply to larvae: they are not (yet) oxygen limited (see Post and Lee 1996). Therefore, their growth *in length* is often linear, as a result of the interaction between food abundance (or scarcity) and natural mortality (see, e.g., Le Pape and Bonhommeau 2015).

## 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 assimilated and wastes excreted becomes gradually separated from the surface through which the exchange of O<sub>2</sub> and CO<sub>2</sub> 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<sub>2</sub> 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.

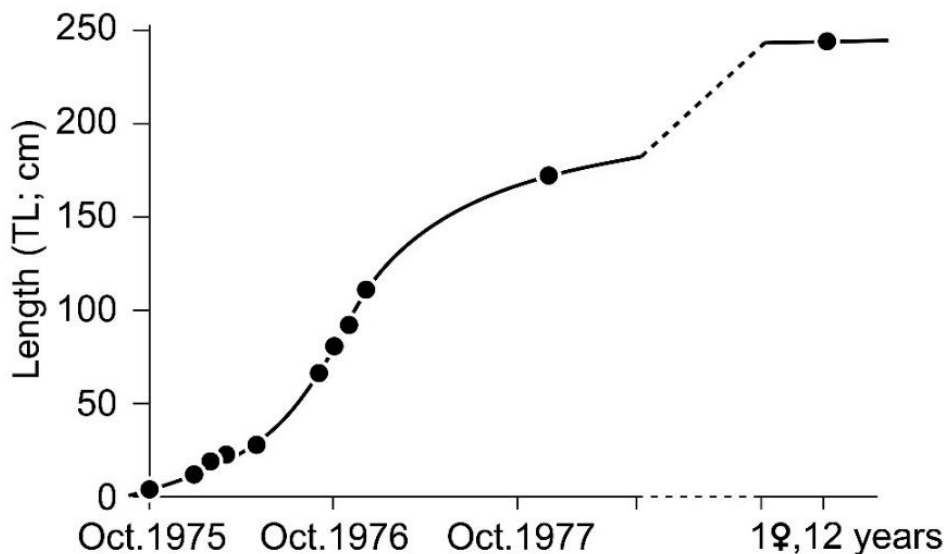
The further evolution of these two organ systems led finally to a gradual reorganization of the whole head region, the extent of which may be appreciated when comparing recent agnatha with gnathostomous fishes (see Lehman 1959). The most advanced recent fishes - in both the systematic and physiological 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<sub>2</sub> in the warm surface water of the tropical zones of the oceans<sup>41</sup>.

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<sub>2</sub> 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 Figure 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.

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<sup>41</sup> Now, it appears that the converse applies: because of increasing hypoxia in deeper water, yellowfin and bluefin tuna cannot remain in deeper water as long as they did previously, which render them more vulnerable to fishing gear operating near the sea surface, e.g., purse seines. Humphries et al. (2024).



**Figure 24.** Length-growth curve of *Arapaima gigas* in a Peruvian lake, based on data provided by Claudia Wosnitza (pers. comm.)<sup>42</sup>.

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 their reproductive strategies. Such a uniform pattern has already been suggested by Beverton (1963), who found that the ratio  $L_m/L_\infty$  ( $L_m$  = length at first maturity) is fairly constant in the Clupeidae and Engraulidae, even over a relatively wide range of values of  $L_\infty$ .

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<sup>43</sup>. The uniformity of these growth patterns may be used to estimate growth parameters in various relatively little investigated stocks.

Also, 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 ecotype 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  $t_o$  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)<sup>44</sup>.

<sup>42</sup> This growth curve was subsequently published by Wosnitza (1984; see also Pauly 2019, p. 84-86).

<sup>43</sup> The findings of Pauly (1984), confirmed by Meyer and Schill (2021), Chen et al. (2021), Chu and Pauly 2024) and others demonstrate that  $L_m$  and  $L_\infty$  (and/or  $L_{max}$ ) are indeed closely (but not linearly) related, via an oxygen-dependent mechanism.

<sup>44</sup> The article by Pauly (1978b), based on 122 estimates of natural mortality ( $M$ ) was rendered obsolete by Pauly (1980) which analyzed, in greater detail, 175 estimates of  $M$ .

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 is 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<sup>45</sup>.

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<sup>45</sup> The issues of both using other people's data and making one's data available for use by colleagues were developed further in Pauly (1987 and 1994) and were addressed in practice, for ichthyology and fisheries research, by the creation of FishBase ([www.fishbase.org](http://www.fishbase.org)), whose first non-taxonomic information consisted mainly of the growth parameters in Pauly (1978a), also extensively used here.

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<sup>46</sup> The captions of table I to XIX are here shortened to fit on one line per item. The original captions are still available for each item.

**Table I.** Tagging-recapture data on *Istiophorus platypterus* as an example of growth data. Selected and adapted from Mather *et al.* (1974, tables 1-4)<sup>a)</sup>.

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  $L_{\infty} = 238$  cm and  $K = 1.20$  year<sup>-1</sup>.

**Table II.** Size-at-age of *Thunnus thynnus*, based on data of Sella (1929).

Age (year)	Length (cm)	Age (year)	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

**Table III.** Relationship between weight and gut surface in two species of fish (source of data: Harder 1964, Table 6).

<i>Rutilus Rutilus</i>		<i>Gobio gobio</i>	
Weight (W; g)	Gut surface (S; cm <sup>2</sup> )	Weight (W; g)	Gut surface (S; cm <sup>2</sup> )
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	25.2
166.23	105.5	49.45	23.2
log(W) = 0.794+0.580·log(S); r = 0.994**		log(W) = 0.802+0.591·log(S); r = 0.99**	

**Table IV.** Comparison of water and air as breathing media<sup>a)</sup>

Property	Water	Air	Water/Air
<b>O<sub>2</sub> content</b>	6,2 ml O <sub>2</sub> /liter	188 O <sub>2</sub> /liter	q/30
<b>Viscosity</b>	1.000 Centipoise	0.018 Centipoise	55/1
<b>Density</b>	1.000 g/cm <sup>3</sup>	0,00119 g/cm <sup>3</sup>	850/1
<b>Diffusion constant<sup>b)</sup></b>	3.4·10 <sup>-5</sup>	11	1/300,000

a) Table taken from Schuman and Piiper (1966); b) the diffusion constant corresponds to the constant U of Equation (67), but it has here the dimension (ml/min)/(cm<sup>2</sup>·atm/cm).

**TABLE V.** Values of the power of weight in proportion to which the gill surface area of fish increases; gill surface (G) or respiratory studies (R)

No.	Taxon	d-value	G/R	Authors(s)	Original data in:	Remarks*	W (g)
1	<i>Tilapia mossambica</i>	0.83	R	Job (1963)	Same	Mean of extreme values of d	10 <sup>3</sup>
2	<i>Tilapia zillii</i>	0.82	R	Schulze-Wiehenbrauck (1977)	Same	--	10 <sup>3</sup>
3	<i>Tinca tinca</i>	0.79	R	Winberg (1960)	Various authors	Page 87	10 <sup>3</sup>
4	<i>Tinca tinca</i>	0.67	G	De Jager and Dekker (1975)	Various authors	Table II, p. 283	10 <sup>3</sup>
5	<i>Carassius auratus</i>	0.81	R	Winberg (1960)	Various authors	Page 82	10 <sup>3</sup>
6	<i>Carassius auratus</i>	0.69	G	Solewki (1957)	Same	From Figure 8 in Czolaska (1965)	10 <sup>3</sup>
7	<i>Cyprinus carpio</i>	0.72	G	Solewki (1957)	Same	From Figure 8 in Czolaska (1965)	10 <sup>4</sup>
8	<i>Cyprinus carpio</i>	0.85	R	Winberg (1960)	Various authors	Page 83	10 <sup>4</sup>
9	<i>Abramis brama</i>	0.89	R	Winberg (1961)	Kusnetzova (1956)	Page 3	10 <sup>4</sup>
10	<i>Rutilus rutilus</i>	0.84	G	Landolt and Hill (1975)	Same	d recalculated from authors' data	10 <sup>3</sup>
11	Cyprinidae	0.82	R	Winberg (1960)	Various authors	Page 105	10 <sup>3</sup>
12	<i>Micropterus dolomieu</i>	0.78	G	Muir (1969)	Price (1931)	Classic study, d value highly reliable	10 <sup>3</sup>
13	<i>Trematomus bernachii</i>	0.79	R	Wohlschag (1960)	Same	Page 289	10 <sup>4</sup>
14	Acipenseridae	0.81	R	Winberg (1960)	Various authors	Page 86, 5 species	10 <sup>5</sup>
15	<i>Scyllium</i> spp.	0.80	R	Winberg (1960)	Buytendijk (1910)	--	10 <sup>4</sup>
16	<i>Opsanus tau</i>	0.78	G	Hughes and Gray (1972)	Same	0.79 in De Jager and Dekker (1975)	10 <sup>3</sup>
17	<i>Coregonus</i> spp.	0.77	R	Winberg (1961)	Various authors	--	10 <sup>3</sup>
18	Salmonidae	0.81	R	Winberg (1960)	Various authors	11 species	10 <sup>4</sup>
19	<i>Gadus morhua</i>	0.82	R	Edward et al. (1972)	Same	--	10 <sup>4</sup>
20	<i>Gadus morhua</i>	0.79	R	Saunders (1963)	Same	Starved fish	10 <sup>4</sup>
21	<i>Gadus morhua</i>	0.87	R	Saunders (1963)	Same	Fed fish	10 <sup>4</sup>
22	<i>Lebistes reticulatus</i>	0.67	R	von Bertalanffy (1951)	Same	v. Bertalanffy's 'confirmed' 2/3 rule	10 <sup>0</sup>
23	<i>Gambusia affinis</i>	0.63	R	Winberg (1960)	Maksudov (1940)	Page 90, d prob. not signif. ≠ 0.67.	10 <sup>0</sup>
24	Cyprinodontidae	0.73	R	Winberg (1961)	Various authors	Page 2	10 <sup>0</sup>
25	<i>Thunnus thynnus</i>	0.90	G	Muir (1969)	Muir and Hughes (1969)	--	10 <sup>6</sup>
26	<i>Katsuwonus pelamis</i>	0.85	G	Muir (1969)	Muir and Hughes (1969)	--	10 <sup>5</sup>
27	<i>Thunnus albacares</i>	0.90	G	Muir (1969)	Muir and Hughes (1969)	--	10 <sup>5</sup>
<b>Generalizations:</b>							
	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 (1958)	Various authors		
	'Grey's intermediates'	0.82	G	Ursin (1967)	Gray (1954) on various teleost. fishes; see Ursin (2450) for spp.		
	Fishes	0.82	R, G	De Jager and Dekker (1974)	Various authors; Most recent review on gill size and resp. in fish		

\*Page numbers refer to original publication; \*\* to eliminate possible bias, the maximum weight estimated for each species from Muus-Dahlström (1973 and 1974) was rounded off or up to the closest whole power of 10.



**Table VI.** Values of  $d$  (power relating weight to gill surface) thought to be unreliable and therefore not included in Table V (R = respiration; G = gills).

Taxon	$d$	R or G	Author	Original data	Remarks
<i>Rhagophila dearboni</i>	0.96	R	Wohlschlag (1963)	Same	Wohlschlag (1963) reports high variability, a small range of weights and himself assumes value of $d$ is too high
<i>Coregonus sardinella</i>	0.89	R	Wohlschlag (1957)	Same	Value differs widely from value of $d = 0.77$ for <i>Coregonus</i> spp. in Table V.
<i>Zoarces viviparus</i>	0.96	G	Ursin (1967, p. 2451- 2452)	S. Wiedeman-Smith (unpublished)	Value of $d$ contradicts Ursin's own estimate of $d$ for 'Gray's intermediates' (see Table V) <sup>47</sup>
'All fishes'	2/3	R	v. Bertalanffy (1951)	Previous studies by the same author	Value assumed by von Bertalanffy on the basis of metabolic data on <i>Lebistes reticulatus</i> only.

**Table VII.** Growth parameters of selected freshwater fishes showing their range of  $P$  values (see also Figure 4)

No.	Family	Species	$W_{\infty}$	K	P	Based on data of:
1	Cyprinodontidae	<i>Gambusia affinis</i> ♂	0.42	1.2	-0.20	Beverton and Holt (1959); A: c.f. $\div 0.9$
2	Cyprinodontidae	<i>Lebistes reticulatus</i> ♂	0.101	6.868	-0.16	Ursin (1967, p. 2437), no. 5
3	Cyprinodontidae	<i>Cypinodon macularius</i>	0.251	2.843	-0.15	Kinne (1960); 30 °C
4	Cyprinodontidae	<i>Gambusia affinis</i> ♀	2.14	0.8	0.23	Beverton and Holt (1959); A: c.f. $\div 0.9$
5	Cottidae	<i>Cottus beldingii</i>	7.24	0.316	0.36	Ebert and Summerfelt (1969)
6	Cyprinodontidae	<i>Lebistes reticulatus</i> ♀	1.3	2.121	0.44	Ursin (1967, p. 2437), no. 4
7	Cyprinidae	<i>Phoxinus phoxinus</i>	8.24	0.58	0.68	Frost (1943)
8	Cyprinidae	<i>Brachydanio rerio</i>	1.93	3.963	0.88	Eaton and Farley (1974)
9	Salmonidae	<i>Leucichthys alpenae</i>	25.5	0.518	1.12	Carlander (1950); S. Lake Michigan
10	Percidae	<i>Acerina cernua</i>	76.7	0.314	1.38	Bauch (1966)
11	Cyprinidae	<i>Blicca bjorkna</i>	39.3	0.684	1.43	Berg et al. (1949)
12	Centropomidae	<i>Ambloplites rupestris</i>	257	0.22	1.75	Hile (1941)
13	Cyprinidae	<i>Chondrostoma nasus</i>	484	0.217	2.02	Berg et al. (1949)
14	Catastomidae	<i>Catastomus commersoni</i>	1653	0.104	2.24	Carlander (1950)
15	-	-	Deleted <sup>48</sup>			-
16	Cichlidae	<i>Tilapia esculenta</i>	734	0.32	2.37	Garrod (1959)
17	Cichlidae	<i>Tilapia galilea</i>	676	0.52	2.55	Ben-Tuvia (1956)
18	Characinidae	<i>Hydrocyon forskalii</i>	793	0.519	2.61	Rafail et al. (1973)
19	Centropomidae	<i>Micropterus dolomieu</i>	1174	0.534	2.80	Carlander (1950), N.-Cent. Hiwasse L.
20	Percidae	<i>Lucioperca lucioperca</i>	6106	0.168	3.01	Nikolsky (1957)
21	Esocidae	<i>Esox Lucius</i>	6049	0.23	3.14	Johnson (1966)
22	Acipenseridae	<i>Acipenser nudiiventris</i>	44290	0.053	3.35	Nikolsky (1957); Aral Lake <sup>49</sup>
23	Cyprinidae	<i>Cirrhinus mrigala</i>	18804	0.122	3.36	Hanumentharo (1974)
24	Cyprinidae	<i>Catla catla</i>	33992	0.280	3.98	Natarajan and Jhingran (1963)

<sup>47</sup> Actually, the value of  $d = 0.96$  originates from my misreading of Ursin's confusing text, which states that "in *Zoarces viviparus*, gill area is proportional with body weight, or almost so" (p. 2452), but later, states that "putting  $n = 5/6$  is not far off the mark." Given that his  $n$  corresponds to  $d$ , this would imply that  $d = 0.83$ , which would have allowed this estimate to be included in Table V.

<sup>48</sup> I don't remember why.

<sup>49</sup> The Aral 'Lake', or rather 'Aral Sea,' had no outlet. Its water, therefore, had a high salt content, which increased when the freshwater that rivers brought was diverted to irrigate cotton fields. The Aral Sea, which began to shrink in the 1960s has now largely disappeared.

**Table VIIIa.** Growth parameters of selected marine and brackish water fishes showing their range of *P* values (see also Figure 5)

No.	Family	Species	$W_{\infty}$	<i>K</i>	<i>P</i>	Based on data of:
1	Myctophidae	<i>Notolychnus valdiviae</i>	0.14	1.411	-0.70	Legand (1967)
2	Gasterosteidae	<i>Apeltes quadratus</i>	1.23	1.174	0.16	Schwarz (1965); c.f. $\div$ 0.6
3	Cyprinodontidae	<i>Cyprinodon macularius</i>	0.538	3.391	0.26	Kinne (1960); S = 3.5%, 25 °C
4	Cyprinodontidae	<i>Cyprinodon macularius</i>	0.703	2.995	0.32	Kinne (1960); S = 3.5%, 30 °C
5	Myctophidae	<i>Myctophum punctatum</i>	6.56	0.323	0.33	Wörner (1975); c.f. $\div$ 0.9
6	Cyprinodontidae	<i>Cyprinodon macularius</i>	0.710	3.223	0.36	Kinne (1960); S = 3.5%, 30 °C
7	Myctophidae	<i>Benthoosema glaciale</i>	5.72	0.45	0.41	Gjøsaeter (1973); c.f. $\div$ 0.9
8	Syngnathidae	<i>Siphonostoma typhle</i>	6.2	0.558	0.54	Worthmann (1975)
9	Gasterosteidae	<i>Gasterosteus aculeatus</i>	1.97	1.778	0.55	Worthmann (1975)
10	Myctophidae	<i>Myctophum affine</i>	9.0	0.42	0.58	Odate (1966); c.f. $\div$ 0.9
11	Syngnathidae	<i>Nerophis ophidion</i>	5.46	1.052	0.76	Worthmann (1975)
12	Myctophidae	<i>Scopelopsis multipunctatus</i>	5.4	1.118	0.78	Legand (1967)
13	Macrorhamphosidae	<i>Macrorhamphosus scolopax</i>	21.7	0.36	0.89	Brèthes (1975)
14	Blenniidae	<i>Blennius pholis</i>	54	0.30	1.21	Qasim (1957)
15	Cottidae	<i>Taurulus bubalis</i>	102	0.230	1.37	Lamp (1965)
16	Cottidae	<i>Cottus kessleri</i>	118	0.197	1.37	Berg et al. (1949)
17	Maenidae	<i>Maena smaris</i>	117	0.218	1.41	Zeis (1951)
18	Callyonimidae	<i>Callyonimus lyra</i>	52.5	0.49	1.41	Chang (1951); c.f. $\div$ 0.5
19	Gadidae	<i>Trisopterus esmarkii</i>	47.7	0.59	1.45	Raitt (1968)
20	Pomadasyidae	<i>Rhonciscus striatus</i>	142	0.229	1.51	Latif and Shenouda (1972)
21	Cynoglossidae	<i>Cynoglossus macrolepidotus</i>	170	0.239	1.61	Kutty and Qasim (1969)
22	Engraulidae	<i>Engraulis anchoita</i>	212	0.230	1.69	Fuster de Plaza (1964)
23	Labridae	<i>Symphodus melops</i>	190	0.359	1.83	Guinard (1966)
24	Notothenidae	<i>Trematomus bernachii</i>	309	0.29	1.95	Wohlschlag (1962)
25	Carangidae	<i>Selaroides leptolepis</i>	85	1.155	1.99	Morsuwan (1970)
26	Polynemidae	<i>Polynemus heptadactylus</i>	718	0.157	2.05	Kagwade (1970)
27	Sparidae	<i>Dentex macrophthalmus</i>	941	0.162	2.18	Nguyen and Wojciechowski (1972) <sup>50</sup>
28	Scorpaenidae	<i>Scorpaena porcus</i>	869	0.177	2.19	Berg et al. (1949)
29	Zoarcidae	<i>Zoarces viviparus</i>	965	0.203	2.29	Wheeler (1969)
30	Sciaenidae	<i>Pseudotolithus elongatus</i>	715	0.274	2.29	Le Guen (1971)
31	Scyliorhinidae	<i>Scyliorhinus canicular</i>	550	0.53	2.46	Zupanovic (1961)

<sup>50</sup> This reference replaces “In Pauly (1978a),” which erroneously cited Yasuda (1950) as the source of this species’ growth parameters.

**Table VIIIb.** Growth parameters of selected marine and brackish water fishes showing their range of *P* values (see also Figure 5)

No.	Family	Species	$W_{\infty}$	$K$	$P$	Based on data of:
32	Leiognathidae	<i>Leiognathus equulus</i>	197	1.884	2.57	Chabanne and Plante (1966)
33	Labridae	<i>Labrus bregylta</i>	3830	0.107	2.61	Guinard (1966)
34	Labridae	<i>Tautoga onitis</i>	2845	0.165	2.67	Cooper (1967)
35	Scombridae	<i>Rastrelliger kanagurta</i>	117	5.16	2.67	George and Banerji (1964)
36	Serranidae	<i>Epinephelus guttatus</i>	2089	0.243	2.71	Thompson and Munro (1977)
37	Mugilidae	<i>Mugil cephalus</i>	2078	0.435	2.96	Berg et al. (1947)
38	Pomatomidae	<i>Pomatomus saltatrix</i>	5808	0.197	3.06	Van der Elst (1976)
39	Trichiuridae	<i>Trichiurus lepturus</i>	4663	0.296	3.14	Wojciechowski (1976)
40	Gadidae	<i>Pollachius virens</i>	11331	0.141	3.20	Nikolsky (1957)
41	Thunnidae	<i>Sarda sarda</i>	3434	0.693	3.38	Dardignac (1962)
42	Gadidae	<i>Gadus morhua</i>	16350	0.181	3.47	Jones (1966)
43	Acipenseridae	<i>Acipenser stellatus</i>	15675	0.192	3.48	Berg et al. (1947)
44	Lophiidae	<i>Lophius piscatorius</i>	53952	0.060	3.51	Connolly (1920)
45	Serranidae	<i>Roccus lineatus</i>	17543	0.186	3.51	Scofield (1931)
46	Thunnidae	<i>Auxis thazard</i>	4394	0.829	3.56	Sivasubramaniam (1973)
47	Acipenseridae	<i>Acipenser gueldenstaedtii</i>	97200	0.045	3.64	Nikolsky (1957)
48	Thunnidae	<i>Euthynnus alliteratus</i>	44869	0.164	3.87	Postel (1956)
49	Thunnidae	<i>Katsuwonus pelamis</i>	55200	0.179	3.99	Marcille and Stequert (1976)
50	Acipenseridae	<i>Huso huso</i>	149100	0.097	4.16	Nikolsky (1957)
51	Thunnidae	<i>Katsuwonus pelamis</i>	16000	0.940	4.18	Brock (1954)
52	Istiophoridae	<i>Tetrapterus albidus</i>	861500	0.026	4.35	In: Pauly (1978a)
53	Thunnidae	<i>Thunnus obesus</i> ♂	234961	0.114	4.43	Shomura and Keala (1963)
54	Thunnidae	<i>Thunnus obesus</i> ♀	165108	0.167	4.44	Shomura and Keala (1963)
55	Istiophoridae	<i>Istiophorus platypterus</i>	36740	0.764	4.44	De Sylva (1957)
56	Carcharhinidae	<i>Prionace glauca</i>	447750	0.091	4.61	Stevens (1975)
57	Carcharhinidae	<i>Prionace glauca</i>	738000	0.072	4.73	Stevens (1975)
58	Carcharhinidae	<i>Eulemia milberti</i>	89190	0.610	4.74	Springer (1960)
59	Carcharhinidae	<i>Eulemia milberti</i>	99740	0.580	4.76	Springer (1960)
60	Thunnidae	<i>Thunnus thynnus</i>	978388	0.067	4.82	Sella (1929)
61	Thunnidae	<i>Thunnus thynnus</i>	504835	0.308	5.19	Westmann and Neville (1942)
62	Lamnidae	<i>Cetorhinus maximus</i>	13820	0.045	5.79	Pauly (1978c)

**Table IXa.** Plots of  $\log(K)$  against  $\log(L_{\infty}^3)$ ; 'Page' refers to Pauly (1978a); % values refer to significance level.

Page	Species	n	b	r	95%	99%
28	<i>Ammodytes marinus</i>	5	-0.456	0.535	--	--
28	<i>Ammodytes tobianus</i>	6	-0.322	0.746	--	--
28	<i>Anarhichas lupus</i>	3	-0.754	0.992	--	--
28	<i>Anarhichas minor</i>	3	-0.912	0.998	X	--
29	<i>Argentineus silus</i>	8	-0.396	0.835	X	x
30	<i>Scophthalmus maximus</i>	5	-0.755	0.979	X	x
31	<i>Lepidorhombus megastoma</i>	4	-0.395	0.999	X	x
32	<i>Branchiostegus japonicus</i>	6	-0.367	0.759	--	--
32	<i>Branchiostegus auratus</i>	4	-1.394	0.930	--	--
33	<i>Trachurus japonicus</i>	3	-1.071	0.934	--	--
33	<i>Trachurus trachurus</i>	4	-0.312	0.972	X	--
36	<i>Tilapia esculenta</i> <sup>a)</sup>	4	-2.050	0.688	--	--
37	<i>Tilapia mossambica</i>	9	-0.822	0.844	X	x
37	<i>Tilapia nilotica</i>	3	-0.777	0.999	X	--
38-39	<i>Clupea harengus</i>	38	-0.260	0.386	--	--
40	<i>Sardina pichardus</i>	18	-0.521	0.663	X	x
41	<i>Sardinella albella</i>	4	-0.387	0.858	--	--
41	<i>Sardinella eba</i>	3	-0.822	0.922	--	--
41	<i>Sardinella longiceps</i>	5	-0.347	0.832	--	--
42	<i>Sardinella aurita</i>	13	-0.644	0.732	X	x
42	<i>Sardinops melanostica</i>	3	-1.983	0.834	--	--
42	<i>Sardinops ocellata</i>	3	0.023	0.063	--	--
43	<i>Sardinops caerulea</i>	19	-0.437	0.542	X	--
44-46	<i>Brevoortia tyrannus</i>	43	-0.252	0.361	X	--
46	<i>Sprattus sprattus</i>	10	-0.523	0.358	--	--
46	<i>Clupea pallasii</i>	3	1.276	0.861	--	--
46	<i>Clupeonella delicatula</i>	3	-0.673	0.502	--	--
47	<i>Hilsa ilisha</i>	3	-1.138	0.639	--	--
47	<i>Sardinops neopilchardus</i>	3	6.267	0.624	--	--
48	<i>Myoxocephalus Scorpius</i>	3	-0.488	0.982	--	--
49-50	<i>Abramis brama</i>	26	-0.580	0.694	X	X
50	<i>Rutilus Rutilus</i>	4	-0.369	0.789	--	--

a) Excluding the data of Cridland (1960).

**Table IXb.** Plots of  $\log(K)$  against  $\log(L_{\infty}^3)$ ; 'Page' refers to Pauly (1978a); % values refer to significance level.

Page	Species	n	b	r	95%	99%
51	<i>Barbus brachycephalus</i>	4	-0.410	0.975	X	--
51	<i>Varicorhinus capoeta</i>	3	-0.568	0.985	--	--
51	<i>Cyprinus carpio</i>	4	-0.099	0.274	--	--
52	<i>Lebistes reticulatus</i>	16	-0.545	0.893	X	X
54	<i>Engraulis japonicus</i>	15	-0.639	0.846	X	X
54	<i>Engraulis ringens</i>	3	-0.054	0.089	--	--
55	<i>Engraulis encrasicholus</i>	16	-0.713	0.660	X	X
55	<i>Cetengraulis edentulous</i>	4	-0.744	0.990	X	X
55	<i>Cetengraulis mysticetus</i>	11	-1.111	0.616	X	--
57-58	<i>Engraulis mordax</i>	26	-1.095	0.897	X	X
59	<i>Esox Lucius</i>	8	-0.473	0.783	X	--
60-62	<i>Gadus morhua</i>	49	-0.395	0.652	X	X
63	<i>Melanogrammus aeglefinus</i>	13	-0.344	0.776	X	X
62	<i>Trisopterus esmarkii</i>	3	-0.312	0.777	--	--
64	<i>Theraga chalcogramma</i>	4	-0.251	0.881	--	--
64	<i>Micromesistius poutassou</i>	6	-1.137	0.919	X	X
64	<i>Pollachius virens</i>	5	-0.396	0.830	--	--
65	<i>Lota lota</i>	4	0.071	0.077	--	--
65-69	<i>Merlangius merlangus</i>	93	-0.719	0.872	X	X
70	<i>Gasterosteus aculeatus</i>	4	-0.628	0.968	X	X
70	<i>Gerres punctatus</i>	3	-1.015	0.975	--	--
72	<i>Istiophorus platypterus</i>	3	-0.768	0.956	--	--
72	<i>Tetrapterus audax</i>	4	-1.741	0.918	--	--
73	<i>Crenilabus rupestris</i>	3	0.428	0.997	(x)	--
73	<i>Labrus berggylta</i>	3	-0.462	0.998	X	--
74	<i>Symphodus rostratus</i>	3	-0.886	0.847	--	--
74	<i>Tautogalabrus adspersus</i>	4	-0.350	0.926	--	--
76	<i>Leiognathus bindus</i>	6	-0.283	0.775	--	--
76	<i>Leiognathus lineolatus</i>	3	-0.730	0.993	--	--
76	<i>Leiognathus splendens</i>	5	-0.141	0.207	--	--
79	<i>Merluccius merluccius</i>	17	-0.181	0.500	X	--
80	<i>Merluccius gayi</i>	7	-0.649	0.971	X	x

**Table IXc.** Plots of  $\log(K)$  against  $\log(L_{\infty}^3)$ ; ‘Page’ refers to Pauly (1978a); % values refer to significance level.

Page	Species	n	b	r	95%	99%
81	<i>Mugil cephalus</i>	9	-0.366	0.846	X	X
81	<i>Mugil saliens</i>	3	-0.246	0.362	--	--
82	<i>Mugil aurata</i>	4	-0.365	0.780	--	--
83	<i>Nemipterus virgatus</i>	6	0.160	0.297	--	--
84	<i>Nemipterus japonicus</i>	6	-0.896	0.931	X	X
85	<i>Notothenia neglecta</i>	4	-0.595	0.642	--	--
85	<i>Notothenia rossii</i>	3	-0.407	0.998	X	--
85	<i>Trematomus bernachii</i>	6	-0.568	0.682	--	--
86	<i>Osmerus eperlanus</i>	12	-0.378	0.832	X	X
86	<i>Mallotus villosus</i>	4	-0.563	0.992	X	--
87	<i>Neoplatycephalus macrodon</i>	6	-0.614	0.928	X	X
88	<i>Perca fluviatilis</i>	7	-0.813	0.909	X	X
88	<i>Lucioperca lucioperca</i>	5	-0.286	0.881	X	--
89	<i>Pleuronectes platessa</i>	3	-0.461	0.976	X	X
90	<i>Pleuronectes americanus</i>	10	-0.712	0.771	X	X
90	<i>Platichthys stellatus</i>	4	-0.818	0.835	--	--
90	<i>Platichthys flesus</i>	3	-0.691	0.875	--	--
91	<i>Hippoglossus platessoides</i>	10	-0.330	0.382	X	--
91	<i>Hippoglossus hippoglossus</i>	6	-0.700	0.864	--	--
93	<i>Brachydeuterus auratus</i>	4	-0.123	0.266	--	--
94	<i>Raja hollandi</i>	4	-1.358	0.947	--	--
95	<i>Salmo trutta</i>	15	-0.065	0.187	--	--
95	<i>Salmo salar</i>	3	-0.838	0.740	X	X
96	<i>Coregonus clupeaformis</i>	6	-0.217	0.626	--	--
96	<i>Coregonus laveretus</i>	7	-1.083	0.967	X	X
97	<i>Thymallus arcticus</i>	3	-0.287	0.285	--	--
97	<i>Thymallus thymallus</i>	3	-0.771	0.799	--	--
97	<i>Oncorhynchus keta</i>	4	-0.728	0.669	--	--
97	<i>Leucichthys artedi</i>	5	-0.194	0.335	--	--
98	<i>Pseudotolithus senegalensis</i>	5	-0.507	0.925	X	--
98	<i>Pseudotolithus typus</i>	6	-0.256	0.807	--	--
98	<i>Nibea nibe</i>	9	-0.718	0.885	X	X

**Table IXd.** Plots of  $\log(K)$  against  $\log(L_{\infty}^3)$ ; ‘Page’ refers to Pauly (1978a); % values refer to significance level.

Page	Species	n	b	r	95%	99%
99	<i>Leiostomus xanthurus</i>	3	-0.601	0.967	--	--
100	<i>Cynoscion nebulosus</i>	9	-0.628	0.894	X	X
101	<i>Cololabis saira</i>	3	-0.777	0.978	--	--
102	<i>Rastrelliger kanagurta</i>	8	-1.588	0.971	X	X
102	<i>Rastrelliger neglectus</i>	5	-1.176	0.856	--	--
102	<i>Scomberomorus maculatus</i>	4	-0.533	0.839	--	--
103	<i>Scomber scombrus</i>	12	-1.074	0.895	X	X
103	<i>Pneumatophorus japonicus</i>	7	-0.200	0.879	X	x
104	<i>Sebastes marinus</i>	5	-0.264	0.758	--	--
104	<i>Sebastes mentella</i>	3	-0.554	0.899	--	--
104	<i>Sebastes alutus</i>	3	-1.299	0.913	--	--
105	<i>Lateolabrax japonicus</i>	3	-0.304	0.987	--	--
105	<i>Dicentrarchus labrax</i>	3	-0.598	0.759	--	--
107	<i>Siganus canaliculatus</i>	4	-0.317	0.916	--	--
108	<i>Taius tumifrons</i>	4	-0.558	0.992	X	x
109	<i>Chrysophris aurata</i>	4	-0.390	0.823	--	--
109	<i>Chrysophris major</i>	4	-0.445	0.778	--	--
109	<i>Pagellus centrodontus</i>	3	-0.789	0.999	X	--
110	<i>Squalus acanthias</i>	9	-0.768	0.813	X	x
111	<i>Saurida undosquamis</i>	3	0.570	0.978	--	--
112	<i>Thunnus albacares</i>	18	-0.846	0.501	X	--
113	<i>Thunnus alalunga</i>	12	-0.657	0.933	X	x
113	<i>Sarda sarda</i>	6	-1.156	0.958	X	x
114	<i>Thunnus maccoyi</i>	3	-1.129	0.424	--	--
114	<i>Katsuwonus pelamis</i>	6	-0.269	0.277	--	--
115	<i>Thunnus thynnus</i>	6	-0.525	0.997	X	x
115	<i>Thunnus obesus</i>	7	-1.441	0.764	X	--
116	<i>Trichiurus lepturus</i>	6	-0.076	0.485	--	--
116	<i>Chelidonichthys kumu</i>	3	-0.180	0.760	--	--
117	<i>Zeus faber</i>	3	-1.116	0.971	--	--

**Table X.** Summary of  $\log(K)$  against  $\log(\text{asymptotic size})$ : summary of data

a) Plots of $\log(K)$ against $\log(L_{\infty}^3)$ :					
No of units	No. of regressions	No of units	No. of regressions	No of units	No. of regressions
3	39	10	3	18	2
4	25	11	1	18	1
5	11	12	3	26	2
6	15	13	2	38	1
7	5	15	2	43	1
8	3	16	2	49	1
9	5	17	1	93	1

Number of regressions = 126; w/ positive b-values = 7; w/ negative values = 119. Mean  $b$  (excl. negative values) = - 0.632 (s.d. = 386)

b) Plots of  $\log(K)$  against  $\log(W_{\infty})$ :

Number of regressions = 29; positive values of  $b = 0$ ; mean value of  $b = -0.714$  and s.d. = 0.279 excluding *Engraulis mordax* (see Table XI)

**Table XI.** Plots of  $\log(K)$  against  $\log(W_{\infty})$ : summary of data\*

No.	Species	n	r	A	b	Tab. XIII
1	<i>Abramis brama</i>	17	0.721	1.077	-0.528	c
2	<i>Brevoortia tyrannus</i>	19	0.829	1.075	-0.550	d
3	<i>Centengraulis mysticetus</i>	9	0.489	1.675	-0.815	e
4	<i>Clupea harengus</i>	10	0.079	-0.041	-0.176	f
5	<i>Coregonus lavaretus</i>	6	0.971	2.784	-1.056	e
6	<i>Gadus morhua</i>	11	0.910	2.095	-0.679	h
7	<i>Gasterosteus aculeatus</i>	4	0.969	0.494	-0.626	a
8	<i>Engraulis mordax</i> *	20	0.926	2.064	-1.457	a
9	<i>Esox lucius</i>	7	0.833	1.368	-0.541	d
10	<i>Lepibema chrysops</i>	12	0.771	2.826	-1.089	d
11	<i>Lepomis macrochirus</i>	14	0.914	1.151	-0.646	d
12	<i>Merluccius merluccius</i>	16	0.495	-0.085	-0.179	c
13	<i>Micromesistius poutassou</i>	6	0.800	2.083	-1.001	b
14	<i>Mugil cephalus</i>	8	0.862	0.676	-0.377	c
15	<i>Nemipterus japonicus</i>	6	0.931	1.649	-0.894	a
16	<i>Pomoxis nigromaculatus</i>	15	0.848	2.105	-0.872	f
17	<i>Pleuronectes americanus</i>	10	0.823	1.437	-0.668	b
18	<i>Sardinella aurita</i>	9	0.691	2.175	-1.084	b
19	<i>Sardinops caerulea</i>	9	0.854	1.624	-0.874	c
20	<i>Scomber scombrus</i>	8	0.870	2.082	-0.907	b

\* Mean  $b = -0.751$ , s.d. = 0.319; mean excluding *Engraulis mordax* (the only species more than 2 s.d. from the mean) = 0.714, s.d. = 0.279.

**Table XII.** Krogh's Normal Curve: basic data, polynomial approximation and derived data (see text)

°C	q <sub>r</sub>	% of 20 °C	log(%)	log(%) = y	ŷ'	ln(ŷ')	Q <sub>10</sub>
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	0.4493	-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	-3.377	2.2
25	0.659	151.7	2.181	2.180	0.0349	-3.049	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	-3.3626	2.2
29	0.481	207.9	2.318	2.318	0.0347	-3.3597	2.2
30	0.444	225.2	2.353	2.352	0.0349	-3.3546	2.2

**Table XIIIa** (Part 1 of 2). Relationship of *K* to mean environmental temperature: *Engraulis mordax*; from Pauly (1978a, p. 57-58), but excluding 'Southern California' stock [locality not specific enough]. All localities: California Coast; temperatures from Bayliff (1967);  $\log(W_\infty) = 2.496 - 0.048 \cdot T$ ,  $r = -0.371$ .

Locality	<i>T</i> (°C)	<i>L</i> <sub>∞</sub>	<i>W</i> <sub>∞</sub>	<i>K</i>
San Francisco	12.8	20.1	57	0.32
Monterey 1946-1951	13.1	23.1	86	0.20
Monterey 1952-1953	13.1	23.1	86	0.20
Monterey 1953-1954	13.1	27.0	138	0.10
Monterey 1954-1955	13.1	19.8	54	0.20
Monterey 1955-1956	13.1	21.9	74	0.19
Santa Barbara 1953-1954	15.1	20.0	56	0.26
Santa Barbara 1954-1955	15.1	18.6	45	0.44
Santa Barbara 1956-1957	15.1	20.5	60	0.33
Malibu 1956-1957	16.1	18.7	46	0.58
Santa Monica 1956-1957	16.1	18.9	47	0.47
Los Angeles 1952-1953	16.7	18.4	44	0.45
Los Angeles 1953-1954	16.7	21.1	66	0.21
Los Angeles 1954-1955	16.7	18.3	43	0.48
Los Angeles 1955-1956	16.7	18.7	46	0.41
Los Angeles 1956-1957	16.7	17.2	36	0.83
San Pedro 1955-1956	16.7	16.4	31	0.95
San Pedro 1956-1957	16.7	19.0	48	0.56
Newport 1955-1956	15.9	16.5	31	0.61
Newport 1956-1957	16.5	19.3	50	0.34
San Clemente 1956-1957	15.9	19.1	49	0.40
Oceanside 1955-1956	16.8	31.0	209	0.09
Oceanside 1956-1957	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



**Table XIIIa** (Part 2 of 2). Relationship of  $K$  to mean environmental temperature: *Nemipterus japonicus* and *Gasterosteus aculeatus* from Pauly (1978a, p. 70 and 84); sea surface temperature from Anon. (1944).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Gasterosteus aculeatus</i></b>				
Roscoff (France); brackish waters ♂	12.5	4.6	0.63	4.20
Roscoff (France); brackish waters ♀	12.5	6.0	0.63	2.40
Eelgrass beds, Kiel Bay (Germany)	8.2 <sup>a)</sup>	6.9	2.14	1.79
Ooster Schelde, The Netherlands	10.8	6.7	1.95	2.32
Log( $W_{\infty}$ ) = 1.088 - 0.086·T; r = - 0.724; a) from Wortmann (1975).				
<b><i>Nemipterus japonicus</i></b>				
Andra-Orissa Coast	27.5	30.5	284	0.314
Andra-Orissa Coast	27.5	20.9	91	0.648
Andra-Orissa Coast	27.5	30.7	289	0.294
Off Borneo (Malaysia)	28.4	28.9	241	0.470
Hong Kong ♂	23.3	38.0	549	0.130
Hong Kong ♀	23.3	34.0	393	0.190
Log( $W_{\infty}$ ) = 4.419 - 0.076·T; r = - 0.663				

**Table XIIIb** (Part 1 of 2). Relationship of  $K$  to mean environmental temperature: *Pleuronectes americanus* and *Micromesistius poutassou* from Pauly (1978a, p. 90 and 64).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Pleuronectes americanus</i>, with data from Poole (1969)<sup>a)</sup> and Diaz (pers. comm.)<sup>b)</sup></b>				
Great South Bay, N.Y.	9.7	35.7	666	0.285
Northumberland 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
Charleston Pond, R.I. ♀	10.5	39.8	946	0.384
Narraganset Bay, R.I. ♂	10.5	43.6	1243	0.199
Narraganset Bay, R.I. ♀	10.5	45.5	1413	0.283
Passamaquoddy Bay (US/Canada)	6.7	41.6	1080	0.195
Annapolis Bay	15.5 <sup>b)</sup>	43.6	1243	0.323
Peronic and Gardiners Bays	6.1	50.6	1943	0.175
Log( $W_{\infty}$ ) = 3.279 - 0.024·T; r = - 0.330; b) from [?] Diaz (pers. comm.).				
<b><i>Micromesistius poutassou</i>; bottom or near-bottom temperatures combined from Schroeder (1963) and Anon (1944).</b>				
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, Mediterranean	16	31.8	322	0.365
Log( $W_{\infty}$ ) = 2.843 - 0.026·T; r = - 0.802				

**Table XIIIb** (Part 2 of 2). Relationship of  $K$  to mean environmental temperature: *Scomber scombrus* and *Sardinella aurita* from Pauly (1978a, p. 103 and 42); the temperatures are from Anon (1944).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Scomber scombrus</i></b> : excluding North Sea, Central North Sea and Newfoundland stocks				
English Channel and Irish Sea	10.7	41.8	659	0.430
Western Mediterranean	18.7	35.0	375	0.500
New England	10.0	46.1	900	0.234
New England	10.0	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	10.0	47.3	977	0.262
Southern North Sea	11.2	42.0	669	0.238
$\text{Log}(W_{\infty}) = 3.278 - 0.041 \cdot T; r = -0.774^*$				
<b><i>Sardinella aurita</i></b> : excluding 4 stocks with extreme values of $L_{\infty}$				
Pointe Noire, Congo	25.0	26.0	158	1.023
Pointe Noire, Congo	25.0	26.0	158	1.028
Balearic Islands, Spain	18.7	27.7	191	0.447
Balearic Islands, Spain	18.7	30.0	243	0.350
Balearic Islands, Spain	18.7	35.0	386	0.250
Agean Sea	19.1	29.0	220	0.500
Castiglione Bight, Algeria	18.7	25.0	141	0.534
Cost of Israel	22.2	31.1	271	0.250
Rio de Janeiro, Brazil	23.2	24.5	132	0.423
$\text{Log}(W_{\infty}) = 2.831 - 0.025 \cdot T; r = -0.466$				

**Table XIIIc** (Part 1 of 2). Relationship of  $K$  to mean environmental temperature: *Sardinops caerulea* and *Mugil cephalus* from Pauly (1978a, p. 43 and 81); temperature from Anon (1944).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Sardinops caerulea</i></b> : excluding 'California' and 'British Columbia.'				
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
San Pedro	16.7	26.1	142	0.520
San Pedro	16.7	27.6	168	0.530
San Pedro	16.7	26.9	156	0.560
San Pedro	16.7	25.7	136	0.550
San Pedro	16.7	26.8	154	0.590
Monterey	13.1	30.0	216	0.350
$\text{Log}(W_{\infty}) = 2.775 - 0.036 \cdot T; r = -0.903^*$				
<b><i>Mugil cephalus</i></b>				
Marmara Sea, Turkey	16.1	71.5	4386	0.254
Bosphorus, Turkey	16.1	105	13890	0.110
Tunisian Coast ♂	18.7	48.6	1377	0.290
Tunisian Coast ♀	18.7	54.6	1953	0.200
Texas Coast ♂	26.4	40.0	768	0.367
Texas Coast ♀	26.4	42.2	902	0.327
Taiwan Coast, China ♂	22.4	49.8	1482	0.393
Taiwan Coast, China ♀	22.4	58.3	2502	0.301
$\text{Log}(W_{\infty}) = 5.246 - 0.094 \cdot T; r = -0.806^*$				

**Table XIIIc** (Part 2 of 2). Relationship of  $K$  to mean environmental temperature: *Merluccius merluccius* from Pauly (1978a, p. 79); excluding 'Mediterranean;' bottom and near-bottom temperatures combined from Schroeder (1963) and Anon. (1944).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Merluccius merluccius</i></b>				
Biscaya, N. Spain	11	105	8100	0.184
Off Morocco	14	85.0	4400	0.210
Off Morocco	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 Coast of North Africa	16	38.4	396	0.220
Marmara Sea, Turkey	15	44.0	596	0.130
Marmara Sea, Turkey	15	60.0	1512	0.100
Central Adriatic Sea	16	62.0	1668	0.344
Off Tunisia	16	40	448	0.200
Costa Brava, Spain	16	28.9	169	0.634
Costa Brava, Spain	16	59.6	1482	0.390
Costa Brava, Spain	16	60.8	1573	0.255
Costa Brava, Spain	16	19.7	54	0.446
Costa Brava, Spain	16	43.3	568	0.142

$$\text{Log}(W_{\infty}) = 7.551 - 0.302 \cdot T; r = -0.721^{**}$$

**Table XIIId** (Part 1 of 2). Relationship of  $K$  to mean environmental temperature: *Esox lucius* and *Lepomis macrochirus*; data from Carlander (1950, p. 121); air temperature from Walter and Lieth (1967).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Esox Lucius</i></b>				
Minnesota, Lake of the Woods,	2.3	172	30531	0.064
Minnesota	5.2 <sup>a)</sup>	128	12583	0.131
Minnesota	5.2	208	53993	0.069
Minnesota	5.2	126	12002	0.124
Minnesota	5.2	125	11719	0.133
Wisconsin	5.8 <sup>a)</sup>	133	14116	0.167
Ohio	11.8 <sup>a)</sup>	142	17180	0.162

$$\text{Log}(W_{\infty}) = 4.385 - 0.021 \cdot T; r = -0.221; a) \text{ central location in each state.}$$

<b><i>Lepomis macrochirus</i></b>				
Iowa, East Lake	11.4	24.1	367	0.318
Indiana, Foots Pond	11.4	19.5	194	0.518
Indiana, Re Haw Hill Lake	11.1	31.4	811	0.231
Indiana, average	11.4	29.8	693	0.196
Indiana, Foot Pond	11.4	19.8	203	0.479
Indiana, Muskellunge Lake	9.7	23.2	327	0.338
Ohio, Kiser Lake	11.1	19.2	185	0.340
Ohio, 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

$$\text{Log}(W_{\infty}) = 3.046 - 0.048 \cdot T; r = -0.353$$

**Table XIIIId** (Part 2 of 2). Relationship of *K* to mean environmental temperature: *Lepibema chrysops* and *Brevoortia tyrannus*.

Locality	<i>T</i> (°C)	<i>L</i> <sub>∞</sub>	<i>W</i> <sub>∞</sub>	<i>K</i>
<b><i>Lepibema chrysops</i></b> : data: Carlander (1950, p. 121); air temperatures: Walter and Lieth (1967).				
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
Iowa, Spirit Lake ♀	8.3	39.6	776	0.508
Iowa, Clear Lake	7.9	36.9	628	0.585
Iowa, Storm Lake	8.6	39.2	753	0.729
Minnesota	5.2	48.0	1382	0.228
Minnesota	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
Iowa, Spirit Lake ♀	8.3	42.9	987	0.503
Iowa, Clear Lake	7.9	40.4	824	0.591
Log( <i>W</i> <sub>∞</sub> ) = 3.398 - 0.061· <i>T</i> ; r = - 0.881;				
<b><i>Brevoortia tyrannus</i></b> ; from Pauly (1978a, p. 45), based on Henry (1971); temperatures from Anon. (1944)				
'South Atlantic' (n =6)	--	--	--	--
'Middle Atlantic' (n =6)	--	--	--	--
'North Atlantic' (n = 7)	--	--	--	--
The data of Henry (1967) consist of weight-at-age pairs from which <i>W</i> <sub>∞</sub> and <i>K</i> were directly estimated. The values of <i>L</i> <sub>∞</sub> in Pauly (1978a) were obtained with a condition factor c.f. = 1.61, which may be used for conversions back to weight.				

**Table XIIIe** (Part 1 of 2). Relationship of *K* to mean environmental temperature: *Abramis brama*; data from Pauly (1978a, p. 49)<sup>a)</sup>; air temperatures from Walter and Lieth (1967).

Locality	<i>T</i> (°C)	<i>L</i> <sub>∞</sub>	<i>W</i> <sub>∞</sub>	<i>K</i>
Aral Lake	6.6	51.9	2097	0.153
Aral Lake	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
Depr 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	0.81
Vistula, near Warsaw	7.6	125	29300	0.045
Lake Constance	8.6	84.2	8954	0.110
Müggelsee, 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
Log( <i>W</i> <sub>∞</sub> ) = 4.108 - 0.041· <i>T</i> ; r = - 0.271; a) some values had to be omitted because the sampling area could not be located.				

**Table XIIIe** (Part 2 of 2). Relationship of  $K$  to mean environmental temperature for *Coregonus lavaretus* and *Cetengraulis mysticetus*; based on Pauly (1978a, p. 96 and 56).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
<b><i>Coregonus lavaretus</i></b> ; excl. Peene-Achterwasser stock; air temperature Walter and Lieth (1967).				
Lower Lena River	(2) <sup>a)</sup>	96.8	10844	0.032
Haweswater and Hullswater	9.5	41.0	827	0.741
Attersee, Germany	7.9	43.8	1008	0.447
Lake Constance	8.5	44.0	1022	0.298
Lake Constance	8.5	39.8	757	0.417
Lake Constance	8.5	52.8	1766	0.267
Log( $W_{\infty}$ ) = 4.325 - 0.153· $T$ ; $r$ = - 0.954 <sup>**</sup> ; a) assumed water temperature				
<b><i>Cetengraulis mysticetus</i></b> ; excl. 2 <sup>nd</sup> Gulf of Fonseca stock; sea surface temperature: Bayliff (1967)				
Almejas Bay	28.4	19.9	63	1.23
Guyamas 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
Gulf of Panama	27.3	20.4	68	1.31
Colombia	26.8	17.2	41	2.09
Gulf of Guyaquil	24.9	17.4	42	1.34
Log( $W_{\infty}$ ) = 1.249 - 0.017· $T$ ; $r$ = 0.355;				

**Table XIIIf** (Part 1 of 2). Relationship of  $K$  to mean environmental temperature: *Pomoxis nigromaculatus*; based on data in Carlander (1950, p. 206); air temperatures from Walter and Lieth (1967).

Locality	$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$
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	39.1	1143	0.182
Minnesota	5.2	40.3	1178	0.191
Minnesota	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 - 0.048· $T$ ; $r$ = - 0.769 <sup>**</sup>				

**Table XIIIg** (Part 2 of 2). Relationship of  $K$  to mean environmental temperature: *Clupea harengus* (Buchan stock); data from Pauly (1978a, p. 38), but excluding the 1956 year class.

Year class (A = abundance index) <sup>a)</sup>	$T$ (°C) <sup>b)</sup>	$L_{\infty}$	$W_{\infty}$	$K$
1952 (A = 5.8)	9.1	31.1	226	0.28
1953 (A = 4.5)	10.0	30.6	215	0.42
1954 (A = 4.6)	9.5	30.7	217	0.30
1955 (A = 2.4)	9.6	32.1	248	0.31
1957 (A = 3.0)	9.7	32.9	267	0.28
1958 (A = 4.3)	9.6	33.3	277	0.29
1959 (A = 1.2)	10.1	32.9	267	0.32
1960 (A = 10.5)	10.1	32.7	262	0.42
1961 (A = 4.7)	9.8	32.7	262	0.48
1962 (A = 4.0)	9.1	31.5	234	0.43
Log( $K$ ) = - 1.138 + 0.070· $T$ ; $r$ = 0.281. Also: log( $K$ ) = - 1.112 + 0.062· $T$ - 0.012·A; $r$ = 0.442; a) index of stock abundance based on Figure 138 in Burd (1978); b) mean annual temperature at the year of birth of a given year class, as given by the Service Océanographique, Intern. Counc. Explor. Mer (various years) and Dietrich (1962).				

**Table XIIIg.** Relationship of  $K$  to mean environmental temperature: *Lebistes reticulatus*; by sex; data from Ursin (1967, p. 2441)<sup>a</sup>.

$T$ (°C)	$K_{\text{♂}}$	$K_{\text{♀}}$	$T$ (°C)	$K_{\text{♂}}$	$K_{\text{♀}}$
18.6	2.72	1.07	22.7	0.67	1.08
18.7	1.50	0.18	23.3	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	25.5	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	1.75	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

a) Negative values of  $K$  and values in italics were omitted, the latter being considered erroneously by Ursin (1967).

**Table XIIIh.** Relationship of  $K$  to mean environmental temperature: *Gadus morhua*; mean surface temperatures and  $L_{\infty}$  data from Taylor (1958, Table 1).

$T$ (°C)	$L_{\infty}$	$W_{\infty}$	$K$	$P$	$W_{\infty 20}$	$K_{20}$	$P_{20}$
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	146.4	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	--	--	Mean 3.20

a)  $W_{\infty}$  was computed assuming c.f. = 1.0;  $P = \log(K) + \log(W_{\infty})$ ;  $W_{\infty 20}$  was derived using multipliers (qw) in Table XVII;  $P_{20} = \log(K_{20}) + \log(W_{\infty 20})$  and  $\log(W_{\infty}) = 5.186 - 0.111 \cdot T$ ;  $r = -0.735^{**}$

**Table XIV.** Plots of  $\log(K)$  against temperature (5 to 30 °C): summary of data (see also Figure 10)

No	Species	n	r	a	b	°C	ln(b)	ln(bn)	$\Delta\ln(b)$
1	<i>Abramis brama</i>	17	0.416	-1.243	0.045	6.4	-3.102	-2.812	-0.290
2	<i>Brevoortia tyrannus</i>	19	0.526	-0.974	0.028	18.9	-3.376	-3.264	-0.310
3	<i>Centegraulis mysticetus</i>	9	0.397	-0.0526	0.031	26.5	-3.474	-3.362	-0.112
4	<i>Clupea harengus</i> <sup>a)</sup>	10	--	--	0.062	9.7	-2.781	-2.963	0.174
5	<i>Coregonus lavaretus</i> <sup>a)</sup>	6	0.964	-1.833	0.168	7.5	-1.784	-2.861	1.077
6	<i>Cyprinodon macularius</i> <sup>b)</sup>	5	--	--	0.025	25.0	-3.689	-3.335	-0.334
7	<i>Gadus morhua</i> <sup>c)</sup>	11	0.840	-1.564	0.094	7.2	-2.364	-2.848	-0.486
8	<i>Gadus morhua</i> <sup>d)</sup>	12	--	--	0.065	(7.2)	-2.733	-2.848	0.115
9	<i>Gasterosteus aculeatus</i>	4	0.762	-0.238	0.058	11.0	-2.847	-3.009	0.162
10	<i>Engraulis mordax</i>	25	0.501	-1.832	0.088	15.5	-2.430	-3.171	0.741
11	<i>Esox lucius</i>	7	0.638	-1.165	0.040	5.7	-3.219	-2.781	-0.438
12	<i>Lebistes reticulatus</i> <sup>e)</sup> ♀	32	0.372	-0.937	0.041	23.4	-3.194	-3.342	0.148
13	<i>Lebistes reticulatus</i> <sup>e)</sup> ♂	28	0.278	-0.503	0.029	23.2	-3.540	-0.3540	-0.201
14	<i>Lepibema chrypsos</i>	12	0.752	-0.870	0.066	7.8	-2.718	-2.875	0.157
15	<i>Lepomis microchirus</i>	14	0.506	-1.013	0.049	11.1	-3.016	-3.013	-0.003
16	<i>Merluccius merluccius</i>	16	0.242	-1.178	0.037	14.8	-3.297	-3.148	-0.149
17	<i>Micomesistius poutassou</i>	6	0.729	-0.854	0.033	11.3	-3.411	-3.021	-0.390
18	<i>Mugil cephalus</i>	8	0.752	-1.363	0.038	20.4	-3.270	-3.296	0.026
19	<i>Nemipterus japonicus</i>	6	0.856	-2.990	0.094	26.3	-2.364	-3.361	0.997
20	<i>Pomoxis nigromaculatus</i>	15	0.856	-1.123	0.055	10.3	-2.900	-2.981	0.081
21	<i>Pleuronectes americanus</i>	10	0.639	-0.950	0.037	9.2	-3.297	-2.933	-0.362
22	<i>Sardinella aurita</i>	9	0.627	-1.438	0.053	21.0	-2.937	-3.308	0.370
23	<i>Sardinops caerulea</i>	9	0.834	-0.843	0.034	16.1	-3.381	-3.189	-0.192
24	<i>Scomber scombrus</i>	8	0.560	-0.818	0.031	11.8	-3.474	-3.040	-0.433

a) See multiple regression, Table XIII f; b) in Taylor (1962) from Kinne (1960); c) Table XIII and Taylor (1958); d) in Jones (1976), based on Taylor (1958); e) data from Ursin (1967, p. 2441; see Table XIII g). Also, Ursin (1967) gives estimates of the slope of  $\ln(K)$  against temperature as estimated from fasting *L. reticulatus* ♂. These plots provide an equally good fit to the normal curve (see Ursin 1967, 2414 ff).

**Table XV.** Data on cold-adapted cod (based on May et al. 1965). [The numbers 1-9 refer to the lines in Figure 12; those from 1-8 refer to the dots in Figure 13]

Location	Line or dot	$L_{\infty}$ (cm)	K (year <sup>-1</sup> )	Mean (N) latitude	Mean temp. (°C)
Seal Island	1	--	--	54.2	1.6
Bonavista	2	--	--	49.3	1.7
St John – Flemish Cap	3	--	--	47.0	2.0
St John – Southeast Edge	4	--	--	45.6	2.7
Grand Bank	5	--	--	44.2	3.5
Southwest Edge	6	--	--	44.0	4.0
Avalon Channel	7	--	--	46.5	-1.8
St Pierre Bank (N)	8	--	--	46.1	1.4
St Pierre Bank (S)	9	--	--	45.6	2.9
ICNAF 2H	1	64	0.24	55.5	1.6
ICNAF 2I	2	65	0.31	53.5	1.6
ICNAF 3K	3	77	0.26	51.0	1.7
ICNAF 3L	4	102	0.16	47.0	2.0
ICNAF 3M	5	98	0.15	47.0	2.0
ICNAF 3N-O	6	130	0.12	44.5	3.1
ICNAF 3P <sub>N</sub>	7	78	0.25	49.5	≈ 2
ICNAF 3P <sub>S</sub>	8	101	0.17	47.0	≈ 3

**Table XVI.** Growth parameter and environmental temperature of some *Trematomus bernachii* stocks (Family Notothenidae).

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

**Table XVII.** Multipliers<sup>a)</sup> for the conversion of values of  $K$ ,  $W_\infty$  and  $L_\infty$  to 20 °C.

°C	$q_K$	$q_{W_\infty}$	$q_{L_\infty}$	°C	$q_K$	$q_{W_\infty}$	$q_{L_\infty}$
-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	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	1.54	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	1.54	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

a) These multipliers apply only in conjunction with parameters of the special VBGF

**Table XVIIIa.** Relationship between gill size and growth performance (basic data).

No.	Fam.	Species	$W_\infty$	$K$	$D$	$T, ^\circ\text{C}$	$P_{20}$	$GSI$	Remarks
1	98	<i>Scylliorhinus caniculus</i>	550	0.530	0.772	10	2.25	8.54	Marine
2	102	<i>Squalus acanthias</i>	8280	0.074	0.814	10	2.57	13.37	M
3	108	<i>Raja clavata</i>	10644	0.150	0.818	10	2.29	4.46	M
4	152	<i>Latimeria chalumnae</i>	69900	0.209	0.847	20	4.17	0.773	M; not used
5	179	<i>Acipenser stellatus</i>	15675	0.192	0.824	8	3.21	5.79	Freshwater
6	206	<i>Clupea harengus</i>	277	0.290	0.761	10	1.69	14.9	M
7	206	<i>Brevoortia tyrannus</i>	1009	0.343	0.782	18	2.50	51.58	M; not used
8	206	<i>Alosa kessleri</i>	603	0.349	0.774	10	1.94	2.03	F
9	207	<i>Engraulis encrasicolus</i>	24	1.123	0.723	12	1.36	55.13	M; not used
10	219	<i>Salmo trutta</i>	6520	0.185	0.811	10	2.87	11.10	F
11	219	<i>Salmo gairdneri</i>	952	0.563	0.781	10	2.52	6.09	F
12	234	<i>Esox lucius</i>	6049	0.230	0.809	10	2.93	40.27	F
13	285	<i>Catosomus commersoni</i>	1653	0.104	0.789	15	2.14	3.84	F
14	286	<i>Chondrostoma nasus</i>	484	0.217	0.770	12	1.85	20.45	F
15	286	<i>Tinca tinca</i>	493	0.710	0.770	12	2.24	8.47	F
16	286	<i>Carassius auratus</i>	508	0.334	0.771	15	2.13	3.55	F
17	286	<i>Rutilus rutilus</i>	321	0.163	0.764	12	1.55	5.28	F
18	286	<i>Blicca bjoerkna</i>	2025	0.101	0.764	12	1.19	40.54	F; not used
19	286	<i>Cyprinus carpio</i>	4866	0.157	0.805	12	2.72	4.44	F
20	299	<i>Ictalurus nebulosus</i>	1150	0.216	0.784	15	2.30	4.00	F
21	356	<i>Lota lota</i>	4535	0.237	0.805	8	2.76	9.23	F
22	356	<i>Merlangius merlangus</i>	472	0.426	0.770	8	2.03	10.51	M
23	356	<i>Pollachius virens</i>	11331	0.141	0.819	8	2.93	15.18	M
24	368	<i>Hippocampus (hudsonius)</i>	14	2.50	0.715	15	1.45	1.71	M
25	403	<i>Zeus faber</i>	7187	0.298	0.812	20	3.33	5.17	M
26	407	<i>Mugil cephalus</i>	13890	0.110	0.822	16	3.11	6.47	M
27	415	<i>Roccus lineatus</i>	17543	0.186	0.827	12	3.35	12.11	M
28	423	<i>Micropterus dolomieu</i>	1174	0.534	0.784	12	2.63	8.64	F
29	427	<i>Acerina cernua</i>	77	0.314	0.742	8	1.11	19.78	F
30	427	<i>Perca fluviatilis</i>	1184	0.123	0.784	8	1.97	16.33	F



**Table XVIIIb.** Relationship between gill size and growth performance (basic data).

No.	Fam.	Species	$W_{\infty}$	$K$	$D$	$T, ^{\circ}\text{C}$	$P_{20}$	$GSI$	Remarks
31	427	<i>Lucioperca lucioperca</i>	6106	0.168	0.810	8	2.74	34.17	F
32	433	<i>Pomatomus saltatrix</i>	5808	0.197	0.809	24	3.13	24.55	M
33	33	<i>Trachurus trachurus</i>	598	0.270	0.773	20	2.21	17.00	M
34	441	<i>Coryphaena hippurus</i>	22070	0.575	0.829	25	4.19	18.80	M
35	453	<i>Maena smarís</i>	117	0.218	0.748	10	1.19	4.64	M
36	476	<i>Tautoga onitis</i>	2845	0.165	0.798	10	2.55	15.55	M
37	476	<i>Crenilabrus melops</i>	190	0.559	0.756	15	1.74	9.29	M
38	476	<i>Labrus merula</i>	990	0.234	0.781	15	2.27	4.32	M
39	508	<i>Blennius pholis</i>	54	0.900	0.736	12	1.04	6.29	M
40	522	<i>Zoarces viviparus</i>	965	0.203	0.781	8	2.02	12.54	M
41	532	<i>Callionymus lyra</i>	53	0.490	0.736	12	1.25	5.90	M
42	538	<i>Trichiurus lepturus</i>	4663	0.296	0.805	20	3.57	0.654	M; not used
43	539	<i>Scomber scombrus</i>	977	0.262	0.781	10	2.24	22.14	M
44	540	<i>Scomberomorus maculatus</i>	6911	0.200	0.811	25	3.23	24.68	M
45	558	<i>Scorpaena (porcus)</i>	869	0.117	0.779	15	2.09	2.90	M
46	559	<i>Trigla gurnardus</i>	534	0.312	0.772	8	1.95	4.57	M
47	570	<i>Cottus gobio</i>	6	0.550	0.702	8	0.25	11.9	M; not used
48	570	<i>Cottus bubalis</i>	102	0.250	0.746	8	1.10	9.31	M
49	570	<i>Acanthocottus scorpius</i>	377	0.539	0.776	8	2.04	3.91	M
50	579	<i>Thunnus thynnus</i>	987 kg	0.067	0.888	16	4.74	28.07	M
51	579	<i>Thunnus albacares</i>	199 kg	0.250	0.864	24	4.77	32.83	M
52	579	<i>Euthynnus alliteratus</i>	44869	0.164	0.840	24	3.94	84.40	M
53	579	<i>Sarda sarda</i>	3434	0.693	0.801	20	3.38	27.50	M
54	579	<i>Katsuwonus pelamis</i>	55200	0.179	0.844	25	4.99	54.67	M
55	585	<i>Pleuronectes platessa</i>	2171	0.170	0.793	8	2.30	14.45	M
56	585	<i>Platichthys flesus</i>	1058	0.229	0.782	8	2.11	13.92	M
57	585	<i>Lophopsetta maculata</i>	606	0.242	0.778	8	2.02	7.76	M
58	585	<i>Pleuronectes americanus</i>	2881	0.113	0.798	8	2.96	7.58	M
59	601	<i>Opsanus tau</i>	568	0.258	0.773	12	2.00	5.78	M
60	602	<i>Lophius piscatorius</i>	53952	0.060	0.843	5	3.16	6.14	M

**Table XIX.** Water-Blood Distance ( $WBD =$  thickness of the gill membrane, in  $\mu$  related to the Gill Size Index ( $GSI$ )<sup>a</sup>) and the growth performance index ( $P_{20}$ ).  $WBD$  data: Hughes and Morgan (1973b) and De Jager and Deller (1975).

No.	Species	$W_{\infty}$	$K$	$^{\circ}\text{C}$	$P_{20}$	$GSI$	$WBD$	$WBD$	% dev.
Elasmobranchs									
1	<i>Scylliorinus caniculus</i>	550	0.530	10	2.25	8.54	11.27	--	--
2	<i>Squalus acanthias</i>	8280	0.074	10	2.57	13.37	10.14	--	--
3	<i>Raja clavata</i>	10644	0.150	10	2.29	4.46	5.99	--	--
4	<i>Raja montagui</i>	2750	0.185	10	2.49	(4.5) <sup>a</sup>	4.85		
Marine teleosts									
5	<i>Clupea harengus</i>	277	0.290	10	1.69	14.9	0.90	1.40	36
6	<i>Pollachius pollachius</i>	5000	0.186	5	2.61	(12.5) <sup>a</sup>	1.50	1.98	24
7	<i>Trachurus trachurus</i>	598	0.270	20	2.21	17.00	2.22	1.34	-66
8	<i>Scomber scombrus</i>	977	0.262	10	2.24	22.14	1.22	1.01	-21
9	<i>Oligocottus maculosus</i>	13	0.208	10	0.22	(3.5) <sup>a</sup>	3.60	3.21	-12
10	<i>Thunnus albacares</i>	199 kg	0.250	24	4.77	32.85	0.53	0.87	39
11	<i>Katsuwonus pelamis</i>	55200	0.179	25	4.09	54.67	0.60	0.47	-27
12	<i>Pleuronectes platessa</i>	2171	0.170	8	2.30	14.45	2.62	1.62	-62
13	<i>Plathychthys flesus</i>	1058	0.229	8	2.11	13.02	2.00	1.75	-14
14	<i>Solea solea</i>	482 <sup>b</sup>	0.42 <sup>b</sup>	7	2.01	(5) <sup>a</sup>	2.80	4.82	42
15	<i>Opsanus tau</i>	568	0.258	12	2.00	5.78	5.00	4.12	-21
Freshwater teleosts									
16	<i>Salmo gairdneri</i>	962	0.563	10	2.52	6.09	6.19	4.23	-46
17	<i>Tinca tinca</i>	493	0.710	10	2.24	8.47	3.50	2.84	-23
18	<i>Rutilus rutilus</i>	321	0.163	10	1.55	5.28	2.00	4.14	52
19	<i>Ictalurus nebulosus</i>	1150	0.216	15	2.30	4.00	10.00	6.43	-56
20	<i>Perca fluviatilis</i>	1184	0.123	10	1.97	16.33	0.9 <sup>c</sup>	1.34	33

a) Values of  $GSI$  in brackets are estimated from closely related fishes and/or from Equation (105); b) growth parameters and temperature estimates from Pauly (1978b); c) original value given s ' $<1$ .'

**Table XX.** Data on the growth of the juveniles of *Micropterus dolomieu* and *Cyprinus carpio* kept at different oxygen concentration and fed *ad libitum*, at temperature near 26 °C.

<i>Micropterus dolomieu</i> : data extracted from Table I in Steward <i>et al.</i> (1967)					<i>Cyprinus carpio</i> : data extracted from Table I and p. 18-19 in Thiel (1977)			
Exp.	Diss. O <sub>2</sub> (mgO <sub>2</sub> /l)	Saturation (% O <sub>2</sub> )	Initial W (W <sub>0</sub> )	Increment (g/day)	Bar. (+ 1 atm.)	Saturation (% O <sub>2</sub> )	Initial W (W <sub>0</sub> )	Increment (g/day)
1	1.6	19.4	2.47	0.067	0	5.42	5.1	0.04
1	2.3	28.0	2.58	0.103	0	5.42	5.3	0.07
1	3.0	36.5	2.65	0.167	0	5.42	4.8	0
1	4.2	51.1	2.48	0.225	0	5.42	3.6	0.01
1	5.8	70.5	2.71	0.250	0	5.42	4.9	0.02
1	8.1	98.5	2.46	0.249	1	12.39	3.3	0.20
2	1.7	21.0	6.55	-0.033	1	12.39	4.1	0.23
2	2.6	32.1	6.13	0.120	1	12.39	5.8	0.25
2	3.8	47.0	6.90	0.225	1	12.39	3.9	0.24
2	5.4	66.8	6.90	0.305	1	12.39	6.0	0.23
3	2.1	26.0	3.44	0.117	1.5	16.05	4.6	0.28
3	3.4	42.1	3.50	0.160	1.5	16.05	3.8	0.15
3	5.9	73.0	3.13	0.263	1.5	16.05	6.2	0.21
4	2.1	26.0	3.36	0.118	1.5	16.05	4.2	0.25
4	3.4	42.1	3.42	0.232	1.5	16.05	4.1	0.21
4	5.9	73.1	3.52	0.277	2	18.8	6.2	0.32
5	1.9	23.4	4.16	0.140	2	18.8	5.8	0.29
5	3.2	39.5	4.38	0.265	2	18.8	5.6	0.26
5	5.1	62.9	4.07	0.329	2	18.8	3.8	0.19
5	8.0	98.6	4.29	0.433	2	18.8	4.6	0.22
6	1.9	23.3	3.39	0.084	--	--	--	--
6	3.8	46.6	3.25	0.192	--	--	--	--
6	8.1	99.3	3.19	0.186	--	--	--	--

**Table XXI.** Conversion efficiency of food ( $E = \text{growth increment/food intake}$ ) vs. weight ( $W$ , g) in the red hind *Epinephelus guttatus* (based on data in Menzel 1960)<sup>a)</sup>

Weight	$E$	T (°C)	Weight	$E$	T (°C)
216	0.247	28	424	0.179	19
285	0.219	19	628	0.161	19
319	0.160	23	647	0.177	28
392	0.153	28	649	0.187	23

a)  $\log(E) = -0.191 - 0.2286W; E = 0.726 \cdot W^{-0.23}$

**Table XXII.** Growth and food conversion efficiency (*E*) in *Cyprinodon macularius* (based on data in Kinne 1960)

Age <sup>a)</sup>	Experiment A			Experiment B			Experiment C			Experiment D			Experiment E		
	<i>L</i>	<i>W</i>	<i>E</i>	<i>L</i>	<i>W</i>	<i>E</i>	<i>L</i>	<i>W</i>	<i>E</i>	<i>L</i>	<i>W</i>	<i>E</i>	<i>L</i>	<i>W</i>	<i>E</i>
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)	0.0420	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	--	2.090	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	(2.170)	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	2.060	0.1255	--	--	--	--	2.79	0.3534	--	2.87	0.3892	--	2.25	0.1696	--

a) Values in brackets are interpolated.

**Table XXIII.** Summary of data on *Cyprinodon macularius* (based on data in Table XXII)<sup>a)</sup>

Exp. <sup>c)</sup>	°C	S (%)	Table <sup>d)</sup>	<i>K</i>	<i>W</i> <sub>∞</sub>	<i>d</i>	<i>P</i> <sub>20</sub>	<i>R</i>	<i>a</i>	<i>b</i>
A	30	0	8	2.843	0.251	0.653	0.30	-0.911	0.029	-0.364
B	25	3.5	6	3.391	0.538	0.665	0.44	-0.865	0.058	-0.469
C	30	3.5	8	2.885	0.703	0.669	0.50	-0.927	0.036	-0.526
D	30	3.5	6	3.223	0.710	0.669	0.54	-0.0941	0.052	-0.404
E	35	3.5	6	5.467	0.209	0.650	0.32	-0.738	0.016	-0.714

a) The columns *r*, *a* and *b* refer to  $E^b = a \cdot W^b$ , as obtained from plots of  $\log(E)$  vs.  $\log(W)$ ; b) *E* = growth increment/food intake; c) Experiment in Kinne (1960); d) Table number in Kinne (1960).

**Table XXIV.** Partial correlation coefficients relating food conversion efficiency (*E*), weight (*W*) and food ration (*R*) in Paloheimo and Dickie (1966)<sup>a)</sup>.

<i>Pleuronectes platessa</i>		<i>Cyprinodon macularius</i>		<i>Salmo trutta</i>		<i>Limanda yokohamae</i>		<i>Lepomis</i> sp.	
<i>r</i> <sub>KW-R</sub>	<i>r</i> <sub>ER-W</sub>	<i>r</i> <sub>EW-R</sub>	<i>r</i> <sub>ER-W</sub>	<i>r</i> <sub>EW-R</sub>	<i>r</i> <sub>ER-W</sub>	<i>r</i> <sub>EW-R</sub>	<i>r</i> <sub>ER-W</sub>	<i>r</i> <sub>EW-R</sub>	<i>r</i> <sub>ER-W</sub>
-0.12	-0.18*	0.17	-0.81**	-0.30	0.09	-0.84**	0.41	-0.65	-0.36
-0.12	-0.09	0.02	-0.57**	-0.14	-0.10	-0.91**	0.43		
0.30	0.13	-0.05	0.14	-0.70	0.63	Mean = -0.875 vs. 0.420			
0.10	-0.35**	0.22	-0.57**	0.19	-0.30				
0.13	0.21**	0.03	-0.70**	0.43	-0.45				
0.22**	-0.10	0.55	-0.68**	Mean = -0.065 vs. -0.068					
0.02	0.13	0.61**	0.75**						
0.11	0.20*	Mean = 0.221 vs -0.608							

Mean = 0.135 vs. -0.006

a) Mean of 5 spp.:  $r_{EW-R}$  better than  $r_{ER-W}$

## Appendices

### Appendix 1: Compact integration and some properties of the generalized VBGF

A retired Professor of Mathematics Dr. Ivar Ekeland (see [https://en.wikipedia.org/wiki/Ivar\\_Ekeland](https://en.wikipedia.org/wiki/Ivar_Ekeland)), kindly provided a more compact integration of the generalized von Bertalanffy Growth Function (VBGF) to this author. This is presented and commented below, along with some of its properties.

The integration starts with a slightly modified version of Pütter's equation of 1920, i.e.,

$$dW/dt = H' \cdot S - k \cdot W \quad \dots 1)$$

where  $dW/dt$  expresses the rate of growth,  $H' \cdot S$  expresses the rate of synthesis of body substances (mainly proteins) or 'anabolism', and  $k \cdot W$  express the rate of breakdown of body substance or 'catabolism,' here understood as consisting mainly of the spontaneous denaturation of proteins, and more precisely the loss of their quaternary structure (see Chapter 3).

The oxygen required for synthesis have to enter into the body of a water-breathing ectotherm (WBE, e.g., a fish, crustacean, mollusk or other) through gills or another respiratory surface ( $S$ ) whose increase with the length ( $L$ ) of the WBE's body (or another of its linear dimensions) can be described by

$$S = p \cdot L^a \quad \dots 2)$$

Catabolism, or more specifically, spontaneous protein denaturation, can be assumed to occur through a WBE's body; thus, it will be proportional to its volume or weight ( $W$ ). Weight, on the other hand, can be related to any linear dimension of a WBE by a length-weight relationship (LWR) of the form

$$W = a \cdot L^b \quad \dots 3)$$

The values of  $b$  are generally limited between 2.5 and 3.5 in fishes (Froese 2006) and between 2 and 4 in crustaceans (Pauly et al. 2022) and other WBE (see [www.sealifebase.org](http://www.sealifebase.org)). Also note the restriction that  $a < b$ , or  $a/b < 1$ . The parameter  $d (= a/b)$ , i.e., the weight exponent in the relationship  $S \propto W^d$ , takes, in water-breathing ectotherms (WBE), values ranging from 0.6 to 0.9, with large  $d$ -values occurring in larger and/or more active WBE (see Chapter 7).

Thus, in the following,  $d = a/b$  and  $D = b - a$ , or  $D = b(1 - d)$ , which simplifies numerous equations. (Note, however, that the parameter  $d$  is different from the letter  $d$  in differential expressions such as  $dW/dt$  or  $dU/dt$ ).

Thus, Equation (1) becomes

$$dW/dt = HW^d - kW \quad \dots 4)$$

If we divide both sides by  $W^d$ , we get

$$\frac{1}{W^d} \cdot \frac{dW}{dt} = H - kW^{1-d} \quad \dots 5)$$

Defining  $U = W^{1-d}$ , the equation becomes

$$\frac{1}{1-d} \cdot \frac{dU}{dt} = H - kU \quad \dots 6)$$

Which can be rewritten

$$\frac{dU}{H-kU} = (1-d)dt \quad \dots 7)$$

Integrating both sides from an arbitrary time  $t_0$ , with  $U(t_0) = u_0$ , we get

$$\frac{1}{k} \cdot \ln\left(\frac{H-kU}{H-kU_0}\right) = (1-d)(t - t_0) \quad \dots 8)$$

Taking exponentials, this becomes:

$$H - kU(t) = (H - ku_0) \cdot e^{-(k(1-d)(t-t_0)} \quad \dots 9)$$

Letting  $t \rightarrow \infty$  and  $U(t) \rightarrow u_\infty = H/k$ , the above equation is rewritten as

$$ku_\infty - kU(t) = ku_\infty - ku_0) \cdot e^{-(k(1-d)(t-t_0)} \quad \dots 10)$$

$$U(t) = u_\infty - (u_\infty - u_0) \cdot e^{-k(1-d)(t-t_0)} \quad \dots 11)$$

Setting  $u_0 = 0$ , this becomes:

$$U(t) = u_\infty \cdot (1 - e^{-k(1-d)(t-t_0)}) \quad \dots 12)$$

And with  $U = W^{1-d}$ , this becomes:

$$W_t = W_\infty (1 - e^{-k(1-d)(t-t_0)})^{1/(1-d)} \quad \dots 13)$$

where  $W_\infty$  is the asymptotic weight, i.e., the mean weight the individuals of the population in question would reach after an infinitely long time.

In the particular case of  $a = 2$  and  $b = 3$  (i.e.,  $d = 2/3$ ), this becomes

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad \dots 14)$$

With  $D = b - a$ , then  $1 - a/b = D/b$  and Equation (13) becomes

$$W_t = W_\infty (1 - e^{-\frac{kD}{b}(t-t_0)}) \quad \dots 15)$$

And with  $K = 3k$ , this becomes

$$W_t = W_\infty (1 - e^{-\frac{3KD}{b}(t-t_0)})^{(b/D)} \quad \dots 16)$$

or somewhat simplified

$$W_t = W_\infty (1 - e^{-KD(t-t_0)})^{(b/D)} \quad \dots 17)$$

where  $K$  is the rate (of dimension time<sup>-1</sup>) at which  $W_\infty$  is approached. Note that  $K$  is *not* a growth rate. As for  $t_0$ , it is the (usually negative) 'age' the individuals would have at  $W = 0$  if they had always grown in the manner described by the VBGF - which they can't have, because the VBGF cannot describe growth *in utero* (e.g., for sharks), not the growth of larvae, very young fish and other WBE not yet limited by their oxygen supply.

The weight at which  $dW/dt$  is maximum ( $W_i$ ) is obtained by setting the derivative of Equation (17) equal to zero:

$$\frac{a}{b} \cdot HW_i^{d-1} - k = 0 \quad \dots 18)$$

Thus,  $W_i$  is given by

$$W_i = \left(\frac{kb}{aH}\right)^{(a-b/b)} = \left(\frac{kb}{aH}\right)^{-D/b} \quad \dots 19)$$

Using  $H/k = u_\infty = W_\infty^{D/b}$ , this becomes

$$W_i = \left(\frac{1}{W_\infty^{D/b}} \cdot \frac{b}{a}\right)^{b/D} = W_\infty \left(1 - \frac{D}{b}\right)^{b/D} \quad \dots 20)$$

Also note

$$W_i/W_\infty = \left(1 - (D/b)\right)^{b/D} \quad \dots 21)$$

i.e.,

$$W_i = W_\infty(1 - (D/b))^{b/D} \quad \dots 22)$$

Thus, when  $a = 2$  and  $b = 3$  (i.e.,  $d = 2/3$  and  $D = 1$ )

$$W_i = W_\infty \cdot \left(\frac{2}{3}\right)^3 = (8/27) \cdot W_\infty \cong 0.3 \cdot W_\infty \quad \dots 23)$$

The age ( $t_i$ ) corresponding to  $W_i$  is given by

$$t_i = t_0 - (\ln(D/b)/(KD)) \quad \dots 24)$$

For length, the generalized VBGF is

$$L_t = L_\infty(1 - e^{-KD(t-t_0)})^{1/D} \quad \dots 25a)$$

or

$$L_t^D = L_\infty^D(1 - e^{-KD(t-t_0)}) \quad \dots 25b)$$

where  $L_\infty$  is the asymptotic length, corresponding to  $W_\infty$  and where all other parameters are defined as for Equation (17).

Equation (25), when  $D \neq 1$ , has an inflection point ( $L_i$ ) at

$$L_i = L_\infty(1 - e^{-\ln(D)})^{1/D} \quad \dots 26)$$

with the age ( $t_i$ ) corresponding to  $L_i$  given by

$$t_i = t_0 - (\ln(D)/(KD)) \quad \dots 27)$$

An interesting property of the standard VBGF (i.e., Equation 26, with  $D = 1$ ) is that its first derivative is

$$dL/dt = \alpha - K \cdot L \quad \dots 28)$$

i.e., the growth rate in length ( $dL/dt$ ) is a linear function of length whose slope is  $-K$ .

Thus, preliminary estimates of the parameters of the growth curve of the individuals in a population of WBE can be obtained, given a minimum of two lengths ( $L_1, L_2$ ) separated by a relatively short time (or age interval ( $t_2 - t_1$ )) and an estimate of asymptotic obtained from  $L_\infty \approx L_{max}$ , i.e., the length of the largest individual in that population and the expression:

$$K \approx ((L_2 - L_1)/(t_2 - t_1))/L_{max} \quad \dots 29)$$

Finally, another important feature of the standard VBGF is the age at which 95% of the asymptotic length is reached, which is often assumed to correspond to be their longevity ( $T_{max}$ ) is given by  $T_{max} = t_0 + 2.996/K$  (Taylor 1958), which can be simplified to:

$$T_{max} \approx 3/K \quad \dots 30)$$

A rough estimate of the uncertainty inherent in Equation (30) is provided by assuming that the longest-lived individual reaches at least 90% and at most 99% of their asymptotic length, which provides limits for  $T_{max}$  of  $2.3/K$  and  $4.6/K$  (see Pauly et al. 2022).

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