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EDITED BY
Marty Riche,
Florida Atlantic University, United States

REVIEWED BY
Carlos Alfonso Alvarez-González,
Universidad Juárez Autónoma de Tabasco, Mexico

*CORRESPONDENCE
Eduardo Almansa
eduardo.almansa@ieo.csic.es

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Relationships between the specific growth rate and the thermal-unit growth coefficient applied to cultured juvenile fish

Lorenzo Márquez[1,2], Eduardo Almansa[3]*, Nancy E. Ruiz Díaz[4,5], Manuel Díaz[6] and Francisco J. Moyano[6]

[1]Centro de Investigación, Innovación y Creación UCT, Facultad de Recursos Naturales, Universidad Católica de Temuco, Temuco, Chile, [2]Núcleo de Investigación en Producción Alimentaria, Facultad de Recursos Naturales, Universidad Católica de Temuco, Temuco, Chile, [3]Centro Oceanográfico de Canarias, Instituto Español de Oceanografía, (IEO-CSIC), Santa Cruz de Tenerife, Spain, [4]Programa de Doctorado en Ciencias Agropecuarias, Facultad de Recursos Naturales, Universidad Católica de Temuco, Temuco, Chile, [5]Escuela de Medicina Veterinaria, Facultad de Recursos Naturales y Medicina Veterinaria, Universidad Santo Tomás sede Temuco, Temuco, Chile, [6]Departamento de Biología y Geología, Facultad de Ciencias Experimentales, Universidad de Almería, Almería, Spain

The growth of cultured juvenile fish is usually quantified by two indexes, the specific growth rate or SGR, and the thermal-unit growth coefficient or TGC. The SGR is a relative growth index based on logarithms of body weights, and it decreases with body weight. The classical TGC is based on one-third powers of body weights and the summation of temperature over time. It can also depend on body weight, but it is possible to release this dependency by empirically adjusting the power function in its mathematical definition. These two indexes are usually presented in the same article to compare the growth attained by different groups of fish subjected to different experimental treatments. However, no formal framework linking both indexes is available for researchers up to the moment, the meanings of SGR and TGC remaining unrelated. The present work shows that the TGC of a group of fish growing at a given temperature can be expressed as a function of the SGR. In addition, the relationship between SGR and TGC here reported provides the basis to re-defined the TGC as a size-independent index with application to fish culture.

KEYWORDS

growth indexes, growth models, specific growth rate, thermal-unit growth coefficient, juvenile fish

1 Introduction

The factors affecting fish growth are under intense research. Together with technical equipment, the measurement of growth requires concepts and models of growth (Kaufmann, 1981). Models provide researchers with a temporal function suitably close to a series of fish weights already measured, that can be used to forecast future weights. In contrast, growth indexes are single quantities intended to be a meaningful summary of the growth attained in the past. Two of the most widely used growth indexes in the literature dealing with fish culture are the specific growth rate, SGR, and the thermal-unit growth coefficient, TGC. Indeed, both indexes are frequently used in the same article to compare growth performances among experimental treatments. In this way, a sample of recently published articles (reporting growth trials conducted with several cultured species) indicates that SGR usually ranges between 0.9 and 5.0% day^{-1}, and TGC varies from 0.1 to 3.2 g$^{1/3}$ (°C-day)$^{-1}$, when mean body wet weights are between 3.5 and 270 g (see Supplementary Table 1). In spite of this combined use, to our knowledge, there is no current expectations about what changes in one of these indexes imply for the other one, i.e., their meanings are unconnected.

It is generally accepted that the rate of growth of juvenile fish drops with age or weight, which is just the behavior empirically observed for the specific growth rate. Thus, it is widely known that SGR depends on body weight, and its decreasing pattern was early reported to follow a negative potential function (Jobling, 1983). It also depends on temperature, since fish are ectothermic animals, and the mathematical expression of SGR does not contain any reference to temperature. On the other hand, the classical TGC (based on the 1/3 power of body weight) was introduced as an index not as dependent on weight or temperature as the SGR (Cho, 1992). More recently, Jobling (2003) warned about the dependence of TGC on temperature in some species, and Dumas et al. (2007) demonstrated that the expression of TGC in the rainbow trout can be redefined in relation to body weight to produce an approximately constant index within a given growth stanza. This constant index produces an accurate forecasting of future body weights, and can be used to accurately set food rations according to the record of past weights in commercial cultures of the species.

At this point, we have introduced the connection between a given growth index and a particular growth model. When a growth index is assumed to be constant over time, a certain growth model is generated. For example, an exponential growth pattern arises when the SGR is taken as a constant parameter, whereas a power weight model is associated with a constant TGC. The power model is known to be more appropriate for weight trajectories of juvenile fish (Iwama and Tautz, 1981). Nevertheless, the bulk of works reporting data on fish weight over time are not aimed at disclosing the underlying growth model, but simply at comparing the effects of one or another experimental factor (usually related to the nutrition or environment) on the growth performance *a posteriori*. Indeed, in this type of research, growth trajectories cannot be even roughly delineated, because body weight is measured a few times during the experiment. Under this experimental design, both SGR and TGC, or even simpler indexes, can be used just as indexes to quantify growth and making the comparison among treatments possible. In the works specifically designed to study growth models, the SGR can be useful because it is a meaningful parameter which varies in precise ways with body weight and temperature (Björnsson and Steinarsson, 2002; Björnsson et al., 2007), those dependencies being the core of the model. Nevertheless, the potential interconnection between both indexes remains unclear, precluding a detailed understanding of the shape of growth trajectories. For this reason, this work is intended to clarify the interconnection between SGR and TGC from a theoretical point of view, and to apply it to fish growth.

2 Formal relationship between instantaneous growth indexes

When the specific growth rate is calculated for a given interval, and for one individual, its mathematical expression is (Equation 1),

$$SGR = \frac{\ln W_2 - \ln W_1}{\Delta t} \tag{1}$$

where W_1, W_2 and Δt are body weight at the initial time, body weight at the final time, and the period of time, respectively. The differential expression of the SGR, let us called it the instantaneous growth rate (IGR), is,

$$IGR = \frac{d(\ln W)}{dt} = \frac{dW}{W\ dt} \tag{2}$$

From Equation 2, it is clear that IGR and SGR are the instantaneous and finite versions, respectively, of the same index based on the concept of relative growth, which is a familiar concept frequently found, for example, in financial mathematics. For each individual, the IGR can be defined as the relative increment in weight per unit of time at a given instant, and the SGR is the mean value of the IGR for a given interval. This simple definition of the SGR has the inconvenience of making it dependent on temperature, diet, and body weight. As explained by Kaufmann (1981), the temporal pattern of the IGR is not constant during fish ontogeny.

Cho (1992) proposed the thermal-unit growth coefficient, TGC, (Equation 3), as a derivation of the parabolic growth model (Iwama and Tautz, 1981):

$$TGC = \frac{{W_2}^{1/3} - {W_1}^{1/3}}{\sum_{t1}^{t2} T} \tag{3}$$

where ΣT is the summation of daily temperatures over the period of growth. For the most frequent experimental setup with constant temperature, the expression of TGC can be easily simplified to,

$$TGC = \frac{{W_2}^{1/3} - {W_1}^{1/3}}{T\ \Delta t} \tag{4}$$

Now, following the same reasoning as in the case of SGR, we can define TGC for a given instant, let us call it the instantaneous TGC (ITGC),

$$ITGC = \frac{d(W^{1/3})}{T\ dt} = \frac{1}{3\ T}\ \frac{dW}{W^{2/3}\ dt} \tag{5}$$

As in the case of IGR, the integration of ITGC between t_1 and t_2 gives rise to the TGC. If temperature is a complex function of time, the integration will also produce a complex form of TGC, but temperature is constant or nearly constant in many experiments dealing with fish growth. The second factor in the above expression for ITGC is interesting because it is close to the mathematical expression of IGR. Whereas the equation for IGR implies the speed of change in weight with respect to weight itself, the equation of ITGC implies the speed of change in weight in relation to the 2/3 power of weight. This isomorphism points out to the possibility of establishing a mathematical relationship between the two instantaneous indexes. Another interesting characteristic of the above differential equation is the 2/3 power of weight since, in a number of fish species, the ontogenetic variation of body surface area is proportional to a power of the body weight equal or very close to 2/3 (O'Shea et al., 2006; Ling et al., 2008; Frederick et al., 2017; Li et al., 2018). Thus, the instantaneous TGC seems to refer to the quotient between dW/dt and a quantity proportional to the body area, whereas the instantaneous expression of SGR refers to the quotient between dW/dt and body weight itself. To our knowledge, this meaning of TGC has not been previously noticed.

From Equations 2, 5, it is possible to define the relationship between IGR and ITGC for a given individual,

$$ITGC = \frac{1}{3\ T} \cdot \frac{dW}{W^{2/3}\ dt} = \frac{1}{3\ T}\ \frac{W}{W}\ \frac{dW}{W^{2/3}\ dt} = \frac{1}{3\ T}\ W^{1/3}\ IGR$$

$$ITGC = \frac{1}{3\ T}\ W^{1/3}\ IGR \qquad (6)$$

Therefore, the ontogenetic pattern for ITGC can be based on Equation 5 and, if it is empirically known, on the relationship between IGR and weight. Although instantaneous growth rates cannot be directly measured, previous literature about the effect of body weight on the SGR is abundant. The usual methodology consists in measuring the SGR for different initial weights, W_1, and over a finite weight interval, (W_1, W_2), and attributing the measured value to the mean weight in the interval (usually the geometric mean) (Kaufmann, 1981; Björnsson and Steinarsson, 2002; Handeland et al., 2008). Although this protocol implies a bias with respect to the true value of the SGR at the mean W, the bias is usually very small (Kaufmann, 1981). Data from different species support a power relationship between SGR and mean body weight of the type SGR ≈ A (mean body weight)$^{-B}$, with A, B > 0 (Jobling, 1983; Björnsson and Steinarsson, 2002). On the other hand, there are also experimental evidence indicating that the temporal trajectory of body weight in juvenile fish follows a power function of time (Iwama and Tautz, 1981; Dumas et al., 2007). This type of weight trajectory implies a power relationship between the IGR and the body weight (Kaufmann, 1981), similar to that found for the finite-interval index, SGR,

$$IGR \approx a\ W^{-b} \qquad a,\ b > 0 \qquad (7)$$

Thus, according to Equations 6, 7, it is possible to find the relationship between ITGC and W in juvenile fish,

$$ITGC \approx \frac{a}{3\ T}\ W^{(\frac{1}{3}\ -\ b)} \qquad a,\ b > 0 \qquad (8)$$

3 Estimated relationship between finite-interval growth indexes applied to juvenile fish

Since instantaneous indexes cannot be directly measured, it is necessary to extend the already discussed relationship between IGR and ITGC to finite, experimentally measurable indexes. Bearing the theoretical basis presented in the previous section in mind, we are going to approximate the values of TGC and SGR for a given individual, assuming the approximations $(W_2/W_1)^{1/3} \approx 1+(1/3)(\Delta W/W_1)$, and $\ln(W_2/W_1) \approx (\Delta W/W_1)$, which are accurate when W_2/W_1 is close to 1,

$$SGR = \frac{\ln\ W_2 - \ln\ W_1}{\Delta t} = \frac{\ln(W_2/W_1)}{\Delta t} \approx \frac{\Delta W}{W_1\ \Delta t}$$

$$TGC = \frac{W_2^{1/3} - W_1^{1/3}}{T\ \Delta t} = \frac{[(W_2/W_1)^{1/3} - 1]\ W_1^{1/3}}{T\ \Delta t} \approx \frac{\Delta W}{3W_1} \cdot \frac{W_1^{1/3}}{T\ \Delta t}$$

Based on these two approximations, it is possible to write an approximate relationship between TGC and SGR,

$$TGC \approx \frac{1}{3\ T}\ W_1^{1/3}\ SGR \qquad (9)$$

Equation 9 is very similar to Equation 6, barring that instantaneous indexes have been replaced by finite-interval indexes. Equation 9 applies when the periodicity of consecutive samplings is short enough, and/or growth is not too fast, which can be the case of the sampling frequency during an experiment about fish growth.

In order to put Equation 9 to the test, it has been applied to data about fish growth published by Kantserova et al. (2020). The first two consecutive samplings reported by those authors comprised 32 individuals of rainbow trout growing for 18 days in the control treatment, with ratios W_2/W_1 ranging from 1.07 to 1.70. In this case, the estimation of TGC from SGR according to Equation 9, let us call it TGC', showed a direct correlation with the true TGC, expressed by the regression line (TGC'/TGC) = 1.000 $(W_2/W_1)^{-0.169}$ (n=32, p<0.001). Thus, TGC' was always somehow below the true value, but TGC' became a useful approximation to TGC when the ratio W_2/W_1 was close to 1. For example, for fish sampled every 10 days, and growing with a mean SGR up to 2.0% day^{-1} (a value compatible with growth rates in juvenile fish), the ratio W_2/W_1 for two consecutive samplings will be below 1.22, and the ratio TGG'/TGC will be always above 0.967.

For a group of fish, we will assume sampling frequency makes all or nearly all individuals meet the condition $W_2/W_1 \leq 1.2$ (or any other value below 1.2), thus Equation 9 can be applied to nearly all individuals. Under this condition, the average values for the first and second members in Equation 9 are related as follows (Equation 10),

$$\overline{TGC} \approx \frac{1}{3\ T} \overline{W_1^{1/3} \quad SGR} \tag{10}$$

Where the overlined variables represent arithmetic means. Since the mean of a product of two variables depends on the mean of each variable, and on the covariance between them, the following equation is obtained,

$$\overline{TGC} \approx \frac{\overline{W_1^{1/3}} \cdot \overline{SGR} + Cov[(W_0^{1/3})_i \ , \ SGR_i]}{3\ T} \tag{11}$$

To apply Equation 11, each animal should be tagged in some way, otherwise it will be impossible to associate pairs of values (W, SGR), and covariance could not be calculated. On the other hand, if the variation in W within a single population of fish is small, the covariance term will most probably not introduce any important correction. In such a case, Equation 11 could be simplified as follows,

$$\overline{TGC} \approx \frac{1}{3\ T} \overline{W_1^{1/3}} \cdot \overline{SGR} \tag{12}$$

It is always possible to calculate or estimate the mean values of $W_1^{1/3}$ and SGR, thus, the estimation of the average TGC presented in Equation 12 can be worked out for any group of fishes, provided that consecutive samplings are not too distant.

To ascertain the limitations of Equations 11, 12, they will be tested on the data published by Kantserova et al. (2020). Those authors provided individual body weights of 16 fish for 6 consecutive samplings in the control treatment, with a variable period of time between samplings. Thus, it was possible to calculate five averaged ratios (W_2/W_1) ranging from 1.1 to 1.7 (one for each pair of consecutive samplings), five consecutive TGC [true indexes according to Equation 3], and ten estimations of TGC, five of them based on Equation 11, and the other five ones based on Equation 12. As a result, when the average TGC was estimated from Equation 11, let us call it TGC', the following power regression line was obtained (TGC'/TGC) = 0.999 $(W_2/W_1)^{-0.172}$ (n=5, p<0.001). This is practically the same relationship found when testing Equation 9 on individual fish data, and it is useful to stablish the connection between SGR and TGC when the ratio W_2/W_1 is not close enough to 1.0 (see Supplementary material Table 1). On the other hand, when the estimation of TGC was calculated according to Equation 12, let us call it TGC", the resulting regression line was (TGC"/TGC) = 1.014 $(W_2/W_1)^{-0.196}$ (n=5, p<0.001). In both cases, the bias of the estimated average TGC with respect to the true average TGC was less than 3% when the ratio W_2/W_1 was below 1.19 and 1.25, respectively.

4 Discussion

The present work shows that the instantaneous index ITGC can be expressed as a direct function of the product $W^{1/3}$ IGR (Equation 6). This is an interesting finding, because it implies that ITGC and IGR rest on different power functions of body weight, $W^{(1/3)-b}$ and W^{-b}, according to Equation 7, 8, respectively. Thus, the variation of those two indexes with body weight (or time) does not necessarily go in the same direction. For example, when -b is larger than -(1/3), IGR decreases with body weight (and time), whereas ITGC increases with body weight. Indeed, three possibilities remain,

i) If $0< b< 1/3 \Longrightarrow (1/3 - b) > 0$, IGR decreases with W whereas ITGC increases.

ii) If $b = 1/3 \Longrightarrow (1/3 - b) = 0$, IGR decreases with W, but ITGC remains constant.

iii) If $b > 1/3 \Longrightarrow (1/3 - b)< 0$, both indexes decrease with body weight.

Since Jobling (1983) found that the parameter b was equal to or, more frequently, larger than 1/3 in juvenile specimens of seven fish species (0.33< b< 0.63), ITGC is expected to be constant or, more frequently, to drop as body weight increases. Even more important, if TGC and ITGC are redefined by substituting $W^{1/3}$ by W^b in Equation 4, 5, respectively, the so redefined indexes will not depend on fish body weight. Thus, the relationship between IGR and ITGC expressed in Equation 6 provides with a systematic way to redefine ITGC and TGC towards body weight independence.

Let us now discuss the range of application of the equations for the average TGC of a group of juvenile fish (Equation 11, 12). As already stated, those equations are expected to produce good approximations when samplings are conducted every 7-10 days, and the average growth rate is below 2.0% day^{-1}. These conditions are generally met in juvenile fish cultured under experimental conditions. For example, the SGR of Atlantic salmon post-smolts fed commercial pellets in excess is below 2.0% day^{-1} when growing in the temperature range 6-18°C (Handeland et al., 2008). In the case of the rainbow trout growing at the optimum temperature of 17°C, a size above 47 g assures an SGR below 2.0% day^{-1} (Jobling et al., 1993). In the Atlantic cod *Gadus morhua* fed a commercial diet in excess, body weights heavier than approx. 35 g always show SGR values smaller than 2.0% day^{-1} in the whole thermal range of the species (Björnsson and Steinarsson, 2002; Björnsson et al., 2007). Therefore, empirical data support the utility of TGC/SGR relationships when applied to juvenile fish cultured under experimental conditions, although the sampling periodicity can be a limitation when it is longer than 7-10 days. The larger the body weight of juvenile fish used in the experiment, the smaller the growth rate, what relaxes the requirement for sampling periodicity, and improves the accuracy of the relationships between TGC and SGR herein proposed.

As a conclusion, the formal expressions of the TGC and SGR growth indexes allows to disclose an approximate relationship between them with some limitations. When the mean increase in body weight between samplings is less than 20-25%, the average TGC can be estimated, with very good accuracy, as a value directly proportional to the SGR multiplied by the 1/3 power of the mean initial body weight. This finding is generally applicable to experimental cultures of juvenile fish sampled with a periodicity of 7-10 days. Therefore, there is a relationship between both indexes previously unnoticed. In addition, the formal relationship between SGR and TGC herein presented provides with a systematic way to redefine TGC towards body weight-independence, which can be applied to future works dealing with growth models in juvenile fish.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: Kantserova et al. (2020). Data in Brief 32, 106184. Data have been obtained from previous literature cited in the bibliography section.

Author contributions

LM: Conceptualization, Formal Analysis, Writing – original draft, Writing – review & editing. EA: Conceptualization, Writing – review & editing. NR: Conceptualization, Writing – review & editing. MD: Conceptualization, Writing – review & editing. FM: Conceptualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1332912/full#supplementary-material

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