

Statistical model of variable allometric growth: otolith growth in *Micropogonias furnieri* (Actinopterygii, Sciaenidae)

G. BERVIAN*, N. F. FONTOURA*† AND M. HAIMOVICI‡

**Faculdade de Biociências; Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Av. Ipiranga, 6681, P. O. Box. 1429, 90619-900, Porto Alegre, RS, Brazil* and ‡*Departamento de Oceanografia, Universidade Federal do Rio Grande, P. O. Box 474, 96201-900, Rio Grande, RS, Brazil*

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The main objective of this study was to develop a statistical model for accurate estimates of relative growth. The method was based on identifying patterns of the residuals obtained from the Huxley's allometric equation. Three different approaches were applied: (1) growth with variable proportionality and constant allometry coefficient, (2) growth with constant proportionality and variable allometry coefficient and (3) distinct growth phases in which proportionality and allometry coefficients remained constant. The proposed statistical models were applied to the relationship of the otolith size and fish size of whitemouth croaker *Micropogonias furnieri*. The best fit was obtained when using approach (3). A change in the growth parameters was associated with the attainment of sexual maturity.

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Key words: *Micropogonias furnieri*; otolith; relative growth; statistical models; variable allometric growth.

INTRODUCTION

The power-function model ($y = a x^b$), originally proposed by Huxley (1924) for the description of allometric growth (variation in form related to variation in size) has been conventionally used in studies of animal growth. According to this equation, body dimensions increase relative to each other according to a constant defined as b , the allometric coefficient. When $b > 1$, the y structure is growing relatively faster than the x structure, and allometry is positive. When $b < 1$, allometry is negative. The case in which $b = 1$ is known as isometry and implies that y and x are proportional to each other. The a parameter is the proportionality coefficient between the two variables and corresponds to the value of y when $x = 1$ (White & Gould, 1965).

†Author to whom correspondence should be addressed. Tel.: +55 51 3320 3500 ext. 4146; fax: +55 51 3320 3568; email: nfontoura@puers.br

Huxley's (1924) model is frequently used for description of relative growth and determination of sexual maturity in crustaceans, fish length estimates through backcalculation from scales and otoliths and for the statistical description of the relationship between mass and length (Le Cren, 1951; Hartnoll, 1978; Francis, 1990).

The condition factor is generally determined through the power-function model, considering the a parameter as constant ($a = y x^{-b}$). This parameter is important for the comparison of populations living in specific food and climatic conditions, the identification of reproductive cycles, and also for the follow-up of the feeding activity of a species, evaluating the efficiency of the use of food sources (Weatherley, 1972; Ricker, 1975).

Although frequently used, the Huxley (1924) model has shown limited capacity for the adequate description of relative growth as b , assumed to be constant, may change during the life cycle (Lovett & Felder, 1989).

The study of calcareous structures such as otoliths, scales and opercular bones has been important for the determination of the relationship between length and age in fishes, through backcalculation (Casselman, 1990; Francis, 1990). Estimations of length based on annuli spacing, however, can result in significant error if the mathematical model employed is not appropriate for the description of the allometric variation of the structures throughout ontogeny (Campana, 1990; Zivkov, 1996).

Micropogonias furnieri (Desmarest) is a marine demersal species, which has a wide distribution along the Atlantic coast, from Mexico to Argentina (Isaac, 1988). Movements into estuaries are related to its life cycle. Young individuals use these areas for feeding and growth, returning to the ocean when adults, although some individuals may remain inside an estuary throughout their whole life cycle (Vazzoler, 1991). Total length (L_T) at first maturation (L_{T50}) was estimated at 200 mm for the estuarine resident group (Castello, 1986; Vizziano *et al.*, 2002) and 330–350 mm for the those that migrate as juveniles to the adjacent coastal waters and mature at a higher age in marine waters (Vazzoler, 1971). The large size at maturity and large otoliths makes this species particularly suitable for allometric studies of its growth pattern. Volpedo & Echeverría (2003) classified the ecomorphological pattern of the sagitta of several species of the Argentine continental shelf, grouping *M. furnieri* with other bottom-related species.

This work investigated a mathematical model for a more accurate description of relative growth, by considering ontogenetic variation of growth parameters and using *M. furnieri* as a model species.

HYPOTHESES FOR CONSTRUCTING THE MODEL

The hypotheses for creating a mathematical model were based on the analysis of the distribution of residuals after applying Huxley's allometric equation (Huxley, 1924). As shown in Fig. 1, a random distribution of residuals after adjusting the Huxley regression model suggests that the equation is adequate and that the relative growth is well described. If there is no random distribution of residuals the model is not adequate, and more complex equations are necessary for a better description of relative growth. In this case, development of the

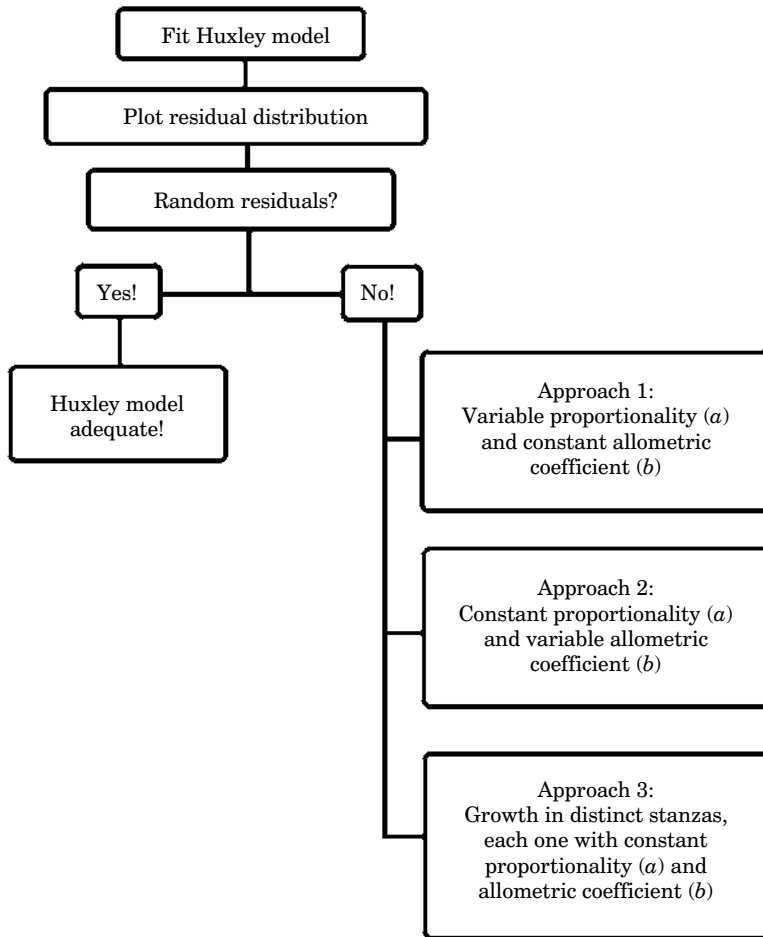


FIG. 1. Methodological approach for improving the general model of relative growth of Huxley (1924), considering complex allometric patterns.

equations is based on the interpretation of the behaviour of parameters a and b of Huxley's equation, using three different approaches described in Fig. 1.

APPROACH 1: VARIABLE PROPORTIONALITY AND CONSTANT ALLOMETRY

Approach 1 transfers all the unexplained variability to the proportionality coefficient (a), considering parameter b as constant and parameter a as a function of x : $y = f(x)x^b$. From the fishery point of view, this approach is not relevant, since variation of parameter a as a function of x has no biological meaning (White & Gould, 1965). On the other hand, keeping parameter a constant is important proceeding since it is generally used as an indicative of the condition factor (Le Cren, 1951). Approach 1 was therefore abandoned.

APPROACH 2: CONSTANT PROPORTIONALITY AND COMPLEX ALLOMETRY

Several authors have applied different approaches (Strauss, 1993) with complex allometry patterns. In this approach, all the variability is transferred to b , considering parameter a constant and parameter b as a function of x [$b = f(x)$]: $y = a x^{f(x)}$. This approach is convenient since the distribution of b values as a function of variable x , besides representing the relative growth rates between variables x and y , is also indicative of the animal's growth pattern. This pattern can be: (1) constant isometric, characterized by the random distribution of b along a horizontal line where $f(x) = 1$ (Fig. 2, A), (2) constant allometric, characterized by the random distribution of b along a horizontal line where $f(x) = \text{any constant different from 1}$ (Fig. 2, B), or (3) variable allometric, in which the distribution of b follows a pattern different from that of a horizontal line, where $f(x) = \text{any mathematical function}$ (Fig. 2, C).

APPROACH 3: GROWTH IN DISTINCT STANZAS, EACH ONE WITH CONSTANT A AND B

Approach 3 considers a growth pattern with different phases or stanzas, separated by a stanza changing point (SCP), which indicates the value of x at the moment when the animal growth pattern changes. Huxley (1924) already identified the presence of different growth phases. Strauss (1993) calls this approach as polyphasic allometry. For simplicity, a model with only two stanzas will be described, although the general model accepts the use of several stanzas.

Each growth phase is described through different power equations, one for animals with a size smaller than the SCP and another for animals larger than the SCP: stanza 1, $y_1 = a_1 (x)^{b_1}$ and stanza 2, $y_2 = a_2 (x)^{b_2}$ where a_1 and b_1 are the

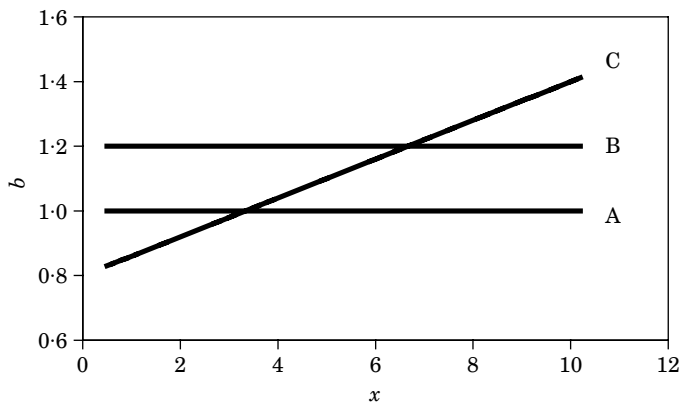


FIG. 2. Patterns of animal growth indicated by distribution of allometry coefficient (b) against x . A, Constant isometric growth ($b = 1$); B, constant allometric growth ($b < \text{or} > 1$); C, variable allometric growth [$b = f(x)$].

parameters of the allometric equation of stanza 1, and a_2 and b_2 are the parameters of the allometric equation of stanza 2.

The polyphasic growth pattern can be mathematically described by two different procedures, which are described below.

POWER-EQUATIONS SWITCHED ON AND OFF BY A LOGISTIC FUNCTION: APPROACH 3A

This approach integrates stanzas 1 and 2 equations into a single mathematical function by the introduction of an empirical logistical equation acting as a switch function (F_w). By multiplying any function by a logistic (F_w), the function could be turned on, when F_w value is near one, or off, when F_w value is near zero: $F_w = [1 + e^{R_{sc}(x-P_{sc})}]^{-1}$, where R_{sc} is the stanza changing rate and P_{sc} is the value of the variable x that corresponds to the SCP.

Using a logistic function as a switch is an interesting tool because the function can generate y values that change from zero to one or from one to zero with any x values. The P_{sc} indicates the average midpoint from where the growth pattern is changing and the R_{sc} controls how fast the change occurs. Using a set of logistic functions as switches, complex patterns could be described by a single equation. For two stanzas, the resulting mathematical function is as follows:

$$y = [(a_1 x^{b_1})F_w] + [(a_2 x^{b_2})(1 - F_w)]. \quad (1)$$

POWER-EQUATION WITH a AND b PARAMETERS SWITCHED INTO DIFFERENT VALUES BY LOGISTIC FUNCTIONS: APPROACH 3B

This approach considers the power-function as a general growth rule where parameters a and b could be modified together to specific values for each stanza, regulated by ontogenetic or environmental factors (Swain & Foote, 1999). A growth pattern with a polyphasic allometry with three or more stanzas could be described by this approach, but at the cost of increased mathematical complexity, with a switch function for each additional stanza necessary. To keep the model simple, only two states will be considered (a_1 and a_2 ; b_1 and b_2), before and after the SCP, following a logistic function:

$$y = f(a)x^{f(b)} \quad (2)$$

where $f(a) = a_1 + (a_2 - a_1)[1 + e^{R_{sc}(x-P_{sc})}]^{-1}$, $f(b) = b_1 + (b_2 - b_1)[1 + e^{R_{sc}(x-P_{sc})}]^{-1}$, and a_1 and a_2 are values of a in the first and second stanzas, and b_1 and b_2 are values of b in the first and second stanzas, respectively.

MATERIALS AND METHODS

RELATIONSHIP BETWEEN OTOLITH LENGTH AND TOTAL LENGTH OF *M. FURNIERI*

The relationship between otolith length (L_{OT}) and L_T in *M. furnieri* was used as an example to analyse the behaviour of the allometric coefficient. The data used in this analysis are derived from samples collected on Rio Grande do Sul coast, between 1987

and 1992, comprising a total of 1321 specimens of *M. furnieri*. Using the empirical function for backcalculation, L_{OT} was established as the predictor variable:

$$L_T = a L_{OT}^b \quad (3)$$

Parameters a and b of equation (3) were estimated by the least squares from ln-transformed data:

$$\ln L_T = \ln a + b \ln L_{OT} \quad (4)$$

To minimize the effects of data concentration in particular size classes, as well as decreasing the error of ln-transformation resulting from natural variability (Smith, 1993), data were grouped into L_T class intervals of 1 mm, and the average L_{OT} were calculated for each size class. The dispersion of individual data, however, was not omitted.

Knowing a , an allometric coefficient for each size class (b_{sc}) was isolated through the following expression, derived from equation (4):

$$b_{sc} = \ln(L_T a^{-1})(\ln L_{OT})^{-1} \quad (5)$$

To identify the presence of any pattern, each value of b_{sc} was plotted as a function of L_{OT} . Once a non-linear pattern was identified, it was empirically described through a polynomial equation of the minimum degree that adequately fitted the data. Polynomial adjustment was performed using Microsoft Excel 5.0:

$$b_{sc} = c_n L_{OT}^n + c_{n-1} L_{OT}^{n-1} + \dots + c_1 L_{OT} + c_0 \quad (6)$$

where c represents the parameters of the polynomial equation.

Polynomial models can be useful to express complex relationships, as in variation in the allometric coefficient, but the method is solely empirical, making almost impossible any biological interpretation of the parameters (Needham, 1950; Gould, 1966). Nevertheless, polynomials are simple to use and fit, and could be used as empirical functions describing the allometric coefficient (b_{sc}) for approach 2:

$$y = a x^{(c_n L_{OT}^n + c_{n-1} L_{OT}^{n-1} + \dots + c_1 L_{OT} + c_0)}$$

As a by-product, the polynomial model works as a tool to identify changes in the allometric coefficient throughout ontogenetic development. By definition, a derivative equation describes the pattern of how the instantaneous rates (dy/dx) of any function are changing through a range of x values. By using the first order derivative of the polynomial equation (6), the P_{sc} , necessary for approach 3, could be identified as the x value where the function crosses the x -axis. More than just theoretical information, the P_{sc} is indicative of different growth phases and represents important information to be used in model development.

Once the P_{sc} is identified, independent power equations could be adjusted to data below and above this point (approach 3): $y_1 = a_1 (x)^{b_1}$; $y_2 = a_2 (x)^{b_2}$. Equations (1) (approach 3a) and (2) (approach 3b) were then adjusted using previous estimates of a_1 , b_1 , a_2 , b_2 and P_{sc} as starting values. The R_{sc} was initiated as one as the starting value. Model fitting was performed by SPSS 11.5 Non-linear Regression Routine, using least squares as loss function, Sequential Quadratic Programming as estimation method and bootstrap estimates of s.e. At this point, as ln-transformation was not necessary, model adjustment was performed using all individual data.

After fitting the solutions (equations) describing growth pattern with complex or polyphasic allometry, each one following a different approach, the problem was which solution to choose. The criteria could be: (1) just numerical (or statistical), by minimizing the residual variance (S^2) for measuring the fitness or maximizing the coefficient of determination (r^2) for measuring the relationship, (2) visual, with no identifiable pattern in residual distribution, (3) by parsimony, choosing the model with least parameters, or (4) theoretical, selecting the model in which the parameters or most of them present biological meaning. To decide which model to use based in all these criteria goes beyond the scope of the present work.

RESULTS

The relationship between L_{OT} and L_T for *M. furnieri* was described as follows [Fig. 3(a)]: $L_T = 19 \cdot 9 L_{OT}^{1.061}$ ($S^2 = 767 \cdot 4$). The Huxley (1924) equation did not fit the distribution of mean L_T and L_{OT} points. The non-random pattern of the standardized residuals [Fig. 3(b)] shows the inadequacy of the simple power-function. Further, the allometric coefficient (b_{sc}) for each otolith length class was isolated (equation 5). Instead of presenting a linear horizontal distribution, the allometric coefficient varied as a function of size, presenting a complex pattern. To this pattern a polynomial function of the third degree was fitted [Fig. 3(c)]: $b_{sc} = 0 \cdot 00003011 L_{OT_m}^3 - 0 \cdot 001950 L_{OT_m}^2 + 0 \cdot 03685 L_{OT_m} + 0 \cdot 8756$ ($r^2 = 0 \cdot 937$), where m is the mean. This polynomial function can be used as a substitute for the

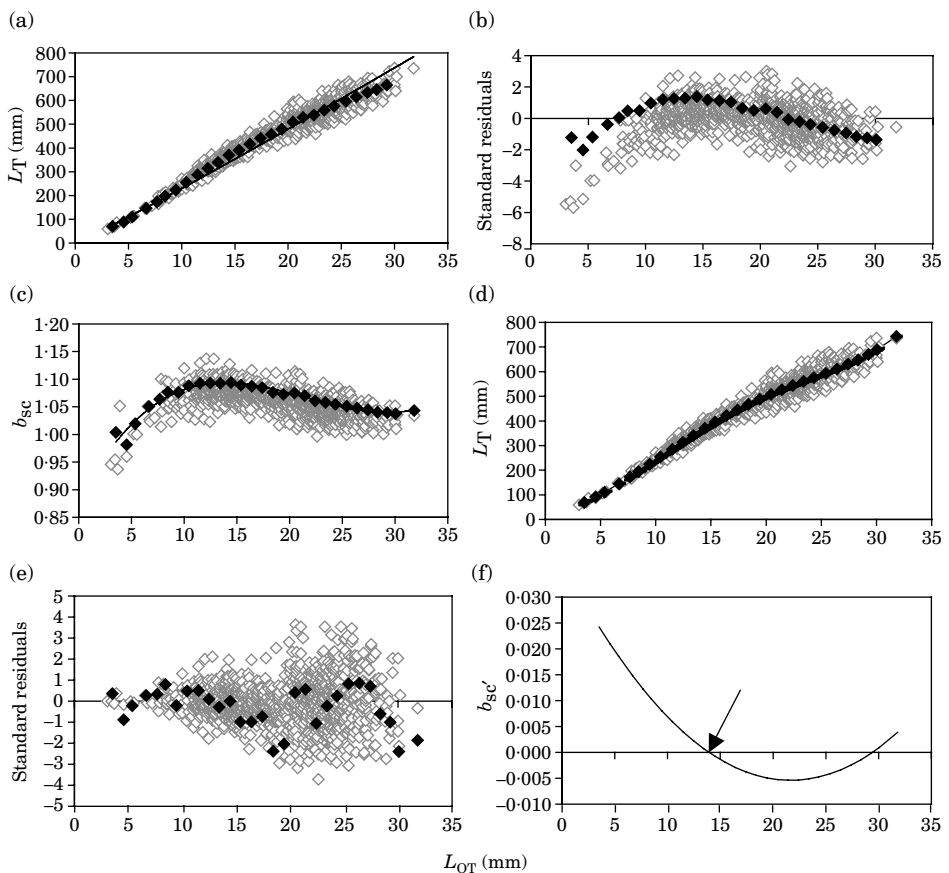


FIG. 3. Total (L_T) and otolith (L_{OT}) lengths of *Micropogonias furnieri*. (\diamond , individual measurements; \blacklozenge , average values for 1 mm size class). (a) Relationship between L_{OT} and L_T estimated from the allometric equation (Huxley, 1924), (b) standardized residuals estimated from allometric equation (Huxley, 1924), (c) distribution of allometry coefficient against L_{OT} (trend line described by a polynomial function), (d) relationship between L_{OT} and L_T estimated from the allometric equation with variable allometry coefficient ($b = \text{polynomial}$), (e) standardized residuals of relationship between L_{OT} and L_T estimated from allometric equation with variable allometry coefficient ($b = \text{polynomial}$) and (f) first derivative of the polynomial function (\rightarrow , the stanzas changing point, P_{sc}).

allometric coefficient (*b*) in the Huxley’s model (approach 2), which results in [Fig. 3(d)]: $L_{T_m} = 19.9L_{OT_m}^{(0.0003011L_{OT_m}^3 - 0.001950L_{OT_m}^2 + 0.03685L_{OT_m} + 0.8756)}$ ($S^2 = 555.8$) The adequacy of the new model for relative growth description could be seen through the residuals distribution [Fig. 3(e)].

As a by-product, as described above, the b_{sc} polynomial function could be used as a first approach to estimate the stanzas changing point of polyphasic allometry (approach 3).

By making y' equal to zero in the first derivative of the b_{sc} function ($y' = 0.00009x^2 - 0.0039x + 0.03685$) and isolating x , the P_{sc} was estimated as 14.4 mm [Fig. 3(f)]. Simple power functions were then calculated for each growth stanza (approach 3). Stanza 1 was calculated including otolith average lengths up to 14.4 mm while stanza 2 was calculated with higher values, resulting in the following equations: stanza 1, $L_{T_{m_1}} = 14.7L_{OT_m}^{1.212}$ ($r^2 = 0.998$) and stanza 2, $L_{T_{m_2}} = 42.1L_{OT_m}^{0.820}$ ($r^2 = 0.996$).

These preliminary values of the parameters a_1, b_1, a_2, b_2 and P_{sc} were then used as starting values for the adjustment of the mathematical models proposed in approach 3. Results are summarized in Tables I and II. The proposed models resulted in the following equations for the relationship between the L_{OT} and L_T in *M. furnieri*: approach 3a (growth with power-equations in stanzas) [Fig. 4(a)], $L_T = (14.8L_{OT}^{1.202})F_w + (42.0L_{OT}^{0.820})(1 - F_w)$, ($S^2 = 562.3$), $F_w = [1 + e^{(L_{OT} - 14.1)}]^{-1}$ and approach 3b (growth with parameters in stanzas [Fig. 4(b)], $L_T = [14.7 + (42.5 - 14.7)(1 + e^{-(L_{OT} - 13.3)})^{-1}]L_{OT}^{[0.817 + (1.214 - 0.817)(1 + e^{(L_{OT} - 13.3)})^{-1}]}$, ($S^2 = 556.7$).

Estimated values, s.e. and 95% CI of the parameters are given in Tables I and II and coefficients of determination and residual variances for the Huxley’s power function and approach 3 proposed models are presented in Table III. The distribution of standardized residuals resulting from approach 3a and 3b are shown in Fig. 4(c), (d).

TABLE I. Statistical summary of non-linear regression, estimated by SPSS 11.5 software, according to approach 3a (equations in phases with switch function) (equation 1) where a_1 and a_2 are the proportionality coefficients for the first and second growth stanzas, b_1 and b_2 are the allometric coefficients for the first and second growth stanzas, R_{sc} is the stanza changing rate, indicating the speed of changing from stanza 1 to stanza 2, and P_{sc} is the value of the variable x that corresponds to the stanza changing point. Model fitted to total length (y) and otolith length (x) of *Micropogonias furnieri*

Parameter	Estimate	Asymptotic S.E.	Asymptotic 95% CI	
			Lower	Upper
a_1	14.8	1.994	10.9	18.7
a_2	42.0	1.824	38.4	45.6
P_{sc}	14.1	1.321	11.5	16.7
R_{sc}	1.0	0.527	-0.033	2.032
b_1	1.202	0.0574	1.090	1.315
b_2	0.820	0.0137	0.794	0.848

TABLE II. Statistical summary of non-linear regression, estimated by SPSS 11.5 software, according to the mathematical approach 3b (parameters in phases) (equation 2) where a_1 and a_2 are the proportionality coefficients for the first and second growth stanzas, b_1 and b_2 are the allometric coefficients for the first and second growth stanzas, R_{sc} is the stanza changing rate, indicating the speed of changing from stanza 1 to stanza 2 and P_{sc} is the value of the variable x that corresponds to the stanza changing point. Model fitted to total length (y) and otolith length (x) of *Micropogonias furnieri*

Parameter	Estimate	Asymptotic S.E.	Asymptotic 95% CI	
			Lower	Upper
a_1	14.7	2.576	9.6	19.7
a_2	42.5	1.810	38.9	46.0
P_{sc}	13.3	1.556	10.2	16.3
R_{sc}	1.0	0.8011	-0.572	2.571
b_1	1.214	0.0755	1.066	1.362
b_2	0.817	0.0135	0.791	0.843

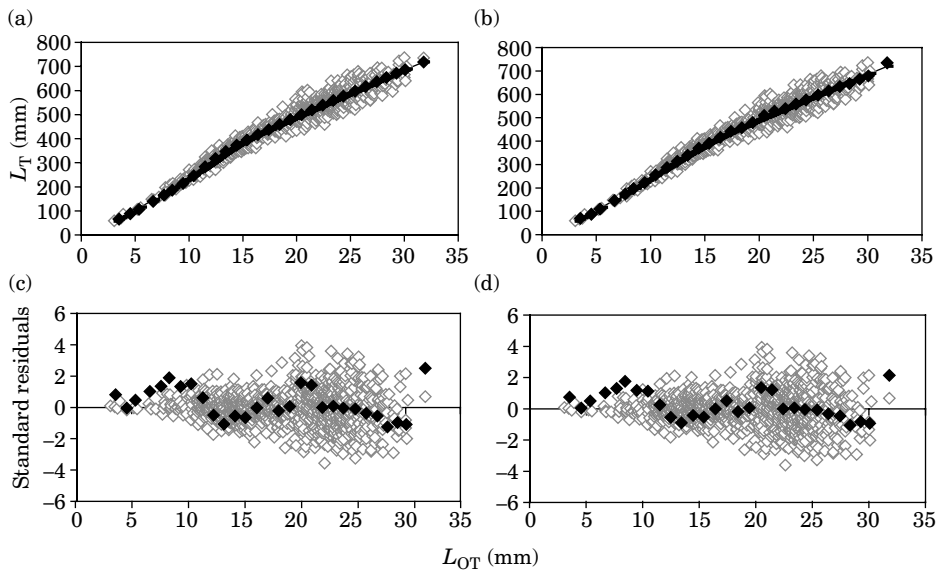


FIG. 4. Total length (L_T) and otolith length (L_{OT}) of *Micropogonias furnieri*. (\diamond , individual measurements; \blacklozenge , average values for 1 mm size class). (a) Relationship between L_{OT} and L_T estimated following approach 3a (equations in two stanzas), (b) relationship between L_{OT} and L_T following approach 3b (parameters in two stanzas), (c) standardized residuals of relationship between L_{OT} and L_T estimated following approach 3a and (d) standardized residuals of relationship between L_{OT} and L_T estimated following approach 3b.

TABLE III. Statistical summary of residual variances (S^2) and coefficient of determination (r^2), for each of the mathematical models employed. Models fitted to total length (L_T) and otolith length (L_{OT}) of *Micropogonias furnieri*

Mathematical model	General equation	r^2	S^2
Huxley power-function	$L_T = aL_{OT}^b$	0.991	767.4
Equations in stanzas (equation 1)	$L_T = (stanza_1 F_w) + (stanza_2 (1 - F_w))$	0.960	562.3
Parameters in stanzas (equation 2)	$L_T = f(a)L_{OT}^{f(b)}$	0.960	556.7

F_w , switch function.

DISCUSSION

Huxley's (1924) allometric model, originally formulated based on the comparison of volumetric measurements, was later expanded to be used for the comparison of linear dimensions. It has been considered as a kind of biological law determining the growth of parts of an organism in relation to each other (Smith, 1980; Lovett & Felder, 1989). The ease of calculation and interpretation of the allometric coefficient made the model generally useful, but there is some question about the capacity of a power function of the type $y = ax^b$ to describe relative growth (Hartnoll, 1982; Lovett & Felder, 1989; Strauss 1993, Leonart *et al.*, 2000).

Relationships between calcareous structures and body size in fishes are characterized by variability, generally as a function of external factors such as temperature, salinity and food availability (Casselman, 1990; Swain & Foote, 1999). Most estimates of fish length by backcalculation are based on hypotheses which assume a proportional growth of the structures under study (Francis, 1990). Growth of calcareous structures in relation to body size, however, is variable, which results in error in the estimates of backcalculated body length (Fukuwaka & Kaeriyama, 1997). Zivkov (1996) considers that proportional hypotheses do not have a biological meaning, since growth is a complex self-regulating process, which changes continually during ontogeny, so that adequate equations are necessary for a better description of the process.

Recent studies have shown differences between ontogenetic phases in the otolith-body size relationship, through the finding that otoliths grow in increments non-proportional to somatic growth (Reznick *et al.*, 1989; Secor & Dean, 1989; Hare & Cowen, 1995). Mosegaard *et al.* (1988) reported that the somatic and the otolith growth of *Salvelinus alpinus* (L.) were different at high temperatures, which corroborates the observation that otolith and somatic growth respond differently to environmental factors.

In the case of *M. furnieri*, although changes in the length and mass relationship were not observed (Haimovici & Velasco, 2000), the curve resulting from the otolith and total length relationship, initially described through a simple power-function [Fig. 3(a)], revealed an inadequacy of this model. Although the average y value for each x size class was employed, aiming to reduce the ln-transformation bias, this procedure did not change the general behaviour of the resulting curve, as can be observed in the distribution of the residual values [Fig. 3(b)].

The complex ontogenetic pattern of the allometry coefficient [Fig. 3(c)], derived by isolating parameter b_{sc} and keeping parameter a constant, corroborates the idea that non-constant allometry was present. Nevertheless, was the pattern of the parameter b_{sc} necessarily too complex to be described by a polynomial function (or any other complex function) as proposed by approach 2? This approach was already proposed, using different equations and general methods, by Jolicoeur (1989) for different data sets concerning several taxonomic groups. Although the proposed model described the data set with enough quality, polyphasic allometry was not tested.

For the present data, polyphasic allometry (approach 3a and 3b), applying just two distinct phases or stanzas in which parameters a and b remained constant, adequately expressed growth as a whole. This simpler and more parsimonious pattern suggests that the complex behaviour of b in approach 2 is a mathematical artefact produced by the transfer of all variability to a single parameter. Nevertheless, as a by-product, approach 2 can be viewed as a new methodological tool for determining the stanza changing points (P_{sc}), also called inflection point of polyphasic (log-log) growth models (Sommerton, 1980; Forbes & Lopez, 1989). This method is neither better nor worse than the previous ones, and is just a new tool for identifying it. Once a method to identify P_{sc} is chosen, even if identified by eye, the parameter is used only as a starting value in non-linear fitting routines.

Models 3a and 3b can be used for the description of growth as a whole, since both take into account the existence of allometric variation during ontogeny. Model 3b, however, besides resulting in little residual variance in the data, is more elegant, since it keeps the Huxley's (1924) power-function as a general biological law, in which parameters a and b change during ontogeny. Model 3a just connects two different power-equations by a switch-function and is a mathematical tool to merge different functions (Sommerton, 1980; Forbes & Lopez, 1989).

The residuals distribution [Figs 3(e) and 4(c), 4(d)] did not show homocedasticity, as is necessary to adjust equations by regular least-squares. This heterocedastic pattern results from regular variability, where absolute variation is larger in bigger animals. Although it could be corrected using average y values for x size classes, as shown in the figures, heterocedasticity did not interfere with the fitting models, as the scatter-plot of residuals were absolutely symmetric above and below the x axis.

Tables I and II show the calculated P_{sc} at otolith lengths of *c.* 14.1 and 13.3 mm (models 3a and 3b, respectively). Converting these measurements to the corresponding L_T , values of 363 and 337 mm are obtained. Considering the size at first gonadal maturation of *M. furnieri* estimated for the Brazilian south coast ($L_{T50} = 312$ mm; the size at which 100% of females are mature, $L_{T100} = 400$ mm; Vazzoler, 1971), the P_{sc} could be related to a change in the growth pattern associated with the reproductive biology of the species. In spite of variations in the first maturation sizes estimated for estuarine regions (190–200 mm; Castello, 1986; Vizziano *et al.*, 2002), the data analysed in the present work were derived from coastal samples. The P_{sc} is thus a factor, which included in the equation, allows an increase in the level of biological information, besides providing a better description of relative growth.

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