

## Can weight/length relationship predict size at first maturity? A case study with two species of Characidae

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A weight/length relationship was established for *Astyanax jacuhiensis* (Cope, 1894) (n = 370) and *Cheirodon ibicuihensis* Eigenmann, 1915 (n = 701), from samples taken monthly in Fortaleza Lagoon, Cidreira, Rio Grande do Sul, from December 1991 through November 1992. Both species showed a polyphasic allometric growth pattern, each stanza described by an independent power equation controlled by a switch function. For *C. ibicuihensis*, this change in the growth pattern occurred at 2.948 cm standard length (SL), close to published sizes for the attainment of female maturity. The change in the growth pattern of *A. jacuhiensis* (SL = 3.481 cm) was below the predicted size at first maturity, and merits further investigation. Although not conclusive, our data suggest that a complex growth pattern is frequent in nature, and perhaps is not usually identified because trends are obscured by natural variability. Despite the increased complexity resulting from the application of a more-complex equation, the identification of a change in the growth pattern could indicate important aspects of fish biology, including the attainment of sexual maturity.

A relação peso/comprimento para *Astyanax jacuhiensis* (Cope, 1894) (n = 370) e *Cheirodon ibicuihensis* Eigenmann, 1915 (n = 701) foi estimada a partir de amostras mensais efetuadas na lagoa Fortaleza, Cidreira, Rio Grande do Sul (dezembro de 1991 a novembro de 1992). As espécies analisadas apresentaram padrão de crescimento alométrico polifásico, sendo cada fase descrita por uma equação potência independente controlada por uma função interruptora. Para *C. ibicuihensis* foi identificada uma modificação no padrão de crescimento com 2,948 cm de comprimento padrão (CP), valor próximo à dados publicados relativos ao início da maturação sexual. A alteração observada no padrão de crescimento de *A. jacuhiensis* (CP = 3,481 cm) encontra-se abaixo do tamanho previsto para a primeira maturação e sugere a necessidade de investigação adicional. Embora não conclusivos, nossos dados sugerem que padrões complexos de crescimento são frequentes na natureza e, talvez, não identificados porque tendências sutis acabam por ser obscurecidas pela variabilidade natural dos dados. Apesar do aumento de complexidade resultante da aplicação de uma equação complexa, a identificação de mudanças no padrão de crescimento pode apontar para aspectos relevantes da biologia de peixes, incluindo a maturação sexual.

**Key words:** Allometric growth, Polyphasic growth, Growth stanza, Reproduction, Fish.

### Introduction

The weight/length relationship is an important tool to analyze fish populations. Its applications range from simple estimates of an individual's weight to indication of fish body condition factor or inferences regarding sexual development (Le Cren, 1951). Knowledge on this relationship also helps to identify energy investments for growth or reproduction as a natural cyclic phenomenon of natural populations (Bolger & Connolly, 1989).

The weight/length relationship is adjusted through a power equation described by Huxley (1924):  $W = a.L^b$ , where W is the individual weight, L is the length, a is the proportionality coefficient or condition factor, and b is the allometric

coefficient. As a simple model, the weight/length relationship is widely applied for descriptive purposes. Bervian *et al.* (2006), however, revised the Huxley relative growth function and proposed a polyphasic model in which the growth pattern can be divided into different stanzas connected by switch equations. Through analyses of the relative growth of otoliths in *Micropogonias furnieri* (Desmarest, 1893) (Sciaenidae), Bervian *et al.* (2006) identified a change in the growth pattern related to the attainment of the size at first maturity.

Because weight/length data are available for many fish species, extracting additional information from regular weight/length relationships may be useful. The present study aimed to identify the existence of polyphasic growth by means of analysis of the weight/length relationship of fish, and its

possible linkages to the attainment of sexual maturity, following the general model proposed by Bervian *et al.* (2006). As a study case, data from two species of Characidae were applied. *Cheirodon ibicuihensis* Eigenmann, 1915 is found in the Uruguay River basin, the Patos Lagoon basin, and the Tramandaí River system, and attains a maximum standard length (SL) of 4.2 cm (Lima *et al.*, 2003). Reported minimum sizes of mature females range from 2.7 to 3.2 cm SL (Braun *et al.*, 2000; Oliveira *et al.*, 2002). *Astyanax jacuhiensis* (Cope, 1894) is found in the Jacuí and Uruguay River basins and the coastal drainages of southern Brazil, and can reach 11 cm SL (Lima *et al.*, 2003). No published data concerning size at first maturity are available for this species. Using the general model proposed by Binohlan & Froese (2009), the size at first maturity for *A. jacuhiensis* is estimated as 6.8 cm SL, based on a maximum length of 11 cm SL.

Although few data are available for comparison, Table 1 presents data on maximum length and estimates of size at first maturity ( $L_{50}$ ) for species of small characids.

### Material and Methods

Monthly samples were taken from December 1991 through November 1992 in the Fortaleza Lagoon (Tramandaí basin, Coastal Drainage, southern Brazil, 30°08'S 50°13'W) by means of a beach seine net 15 m long, 3 m high, and with 5 mm mesh size. The hauls were made from a sandy beach and near the stands of macrophytes. All captured fish were preserved in 4% formalin. In the laboratory, fish were identified, weighed (W, to the nearest 0.001 g) and measured (SL, to the nearest 0.01 cm). Because gender information is not available (the data analyzed were obtained from the laboratory data bank), the data set was analyzed as a whole (merged gender). Voucher specimens for *A. jacuhiensis* and *C. ibicuihensis* are respectively deposited in the Fish Collections of the Universidade Federal do Rio Grande do Sul (UFRGS 2003) and Museu de Ciências e Tecnologia da PUCRS (MCP 13893).

For each species, the first procedure was to adjust a regular weight/length relationship:  $W=a.L^b$ ; where W is the expected weight (g) for a specific length, a is the proportionality coefficient, L is the standard length (cm), and b is the allometric

coefficient. The objective was to identify possible trends (residual not evenly distributed along the y-axis zero baseline) by plotting proportional residuals as a function of the observed standard length. Proportional residuals ( $[\text{observed weight} - \text{predicted weight}] / \text{predicted weight}$ ) were used instead of regular residuals (observed weight - predicted weight) to minimize bias from heteroscedasticity. Also, to avoid bias from log-transformation (Smith, 1980), the standard Huxley allometric equations were adjusted by using the Solver routine of the Microsoft Excel (loss function using least squares of proportional residues, Newton search algorithm).

If the weight/length data follow a regular power function, proportional residuals should distribute randomly along the y-axis zero baseline. Any residual pattern different from zero-centered horizontal distribution indicates the model's inability to describe the growth pattern, and suggests the presence of a growth anomaly such as polyphasic growth. In this case, a break in the residual pattern is an indication of a point of change in the growth cycle.

Following Bervian *et al.* (2006), polyphasic growth can be divided into different stanzas, each stanza described by a regular power function. According to these authors, the Huxley power function is appropriate to describe relative growth, but due to environmental pressures or development strategy, a change in the growth pattern could be expected in the life history of animals. Therefore, a polyphasic growth function is no more than a series of regular power functions ( $Y = a.X^b$ ), each one controlled by a switch function that turns a growth segment on or off:  $S_w = 1/(1+e^{(T_x*(L-SCL)})}$ ; where  $S_w$  is the interruption factor (ranging from one to zero),  $T_x$  is the rate of change, L is the standard length, and SCL is the mean length at which individuals switch from one stanza to the next.

Considering a growth pattern with two stanzas, the weigh/length relationship can be described as follows:  $W = (a_1.L^{b_1}).(1/(1+e^{(T_x*(L-SCL))})) + (a_2.L^{b_2}).(1/(1+e^{(-T_x*(L-SCL))}))$ ; where W is the expected weight for a specific length L,  $a_1$  and  $a_2$  are the proportionality coefficients for the first and second stanzas,  $b_1$  and  $b_2$  are the allometric coefficients for the first and second stanzas,  $T_x$  is the rate of change from the first to the second stanza, and SCL is the Stanza Changing Length.

As a first approximation, each growth stanza was visually identified as a clump of residuals presenting any particular trend, and the Stanza Changing Length (SCL) established as the middle-point between two successive growth stanzas. Then a new weight/length relationship was individually adjusted for each stanza, below and above the Stanza Changing Length. Next, the parameters a and b for each growth stanza, as well as the size at the Stanza Changing Length (SCL) were used as seed values to adjust the function as a whole. In the absence of a known biological value, the rate of change ( $T_x$ ) was set at 1.0 as the initial value. The function adjustment was made by using the Microsoft Excel Solver routine using Least Squares (proportional residues) as the loss function and the Newton search algorithm. Considering the large sample size, Standard Errors for each parameter were estimated by adjusting the polyphasic models

**Table 1.** Size at first maturity ( $L_{50}$ ) and maximum recorded length (Lmax) for characid species.

Species	$L_{50}$	Lmax	Source
<i>Astyanax altiparanae</i>	3.2	10.6	Andrade, 2003
<i>Astyanax aurocaudatus</i>	4.0	7.7	Román-Valencia & Ruiz, 2005
<i>Astyanax bimaculatus</i>	6.9	19.5	Vazzoler, 1996
<i>Astyanax fasciatus</i>	5.2	13.2	Vazzoler, 1996
<i>Astyanax fasciatus</i>	11.0	16.4	Fontoura <i>et al.</i> , 2009
<i>Astyanax fasciatus</i>	12.2	16.4	Marques <i>et al.</i> , 2007
<i>Astyanax janeiroensis</i>	5.5	11.4	Mazzoni <i>et al.</i> , 2005
<i>Astyanax scabripinis paranae</i>	5.0	9.5	Veregue & Orsi, 2003
<i>Astyanax schubarti</i>	4.1	10.6	Vazzoler, 1996
<i>Hemigrammus marginatus</i>	1.7	4.2	Andrade, 2003
<i>Hypheosobrycon eques</i>	2.0	3.6	Andrade, 2003
<i>Hypheosobrycon poecilioides</i>	5.5	8.0	García-Alzate & Román-Valencia, 2008
<i>Piabina argentea</i>	2.4	5.8	Andrade, 2003
<i>Serrapinnus notomelas</i>	2.2	3.6	Andrade, 2003

20 times, each time with only half of the data set, using random resampling without replacement, *i.e.*, emulating a bootstrap procedure. Parameter Standard Errors were estimated as the Standard Deviations of all the 20 different computations. The Coefficient of Determination,  $R^2$ , was calculated for regular and polyphasic models as follows:  $R^2 = 1 - (\text{residual Sum of Squares} / \text{total Sum of Squares})$  (Zar, 1999).

Considering that reproduction can change dramatically the energy budget directed for body growth, and could be reflected in the growth pattern, we suppose that the presence of a Stanza Changing Length (SCL) could be indicative of the size at first maturity ( $L_{50}$ ). So, for comparison purpose, estimates of the Stanza Changing Length were compared to published values of  $L_{50}$  for *A. jacuhiensis* and *C. ibicuihensis*, and to  $L_{50}$  estimated values according to the general model proposed by Binohlan & Froese (2009):  $L_{50} = 10^{-0.1189+0.9157 \cdot \text{Log}(L_{\text{max}})}$ , where  $L_{50}$  is the size at first maturity and  $L_{\text{max}}$  is the maximum recorded size of a species.

## Results

The captured specimens of *A. jacuhiensis* ( $n = 370$ ) showed standard lengths ranging from 1.8 to 9.2 cm. Figure 1a shows the weight/length relationship for the species ( $a = 0.01264$ ;  $b = 3.464$ ; residual Sum of Squares = 4.954) according to Huxley's traditional model. It is apparent that the species has two independent spot clusters, which characterize at least two age groups, and no fish were captured with standard lengths around 4 cm SL. Figure 1b represents the proportional residuals resulting from the Huxley adjustment for *A. jacuhiensis*. The proportional residuals of animals smaller than 4 cm were predominantly negative, clearly demonstrating the inadequacy of the applied model. There was also a concentration of positive residues in animals with lengths between 4 and 6 cm SL, and a new concentration of negative residues in animals larger than 6 cm SL, following a complex diagonal pattern. With distinct trends but with no obvious indication of a breakdown in the residual pattern, the Stanza Changing Length (SCL) was initially adjusted using 4.0 as the seed value.

Figures 1c-d show, respectively, the weight/length relationship and distribution of proportional residuals according to the polyphasic model for *A. jacuhiensis*. The adjusted parameters with their confidence intervals (1.96 SE) are presented in Table 2. The Stanza Changing Length (SCL) was estimated as 3.841 cm. Below this size the species shows a positive allometric growth pattern ( $b_1 = 3.112$ ), changing to negative allometry for larger animals ( $b_2 = 2.939$ ). Although at least two age groups were clearly identified as two data clouds (Fig. 1d), each group was well distributed around the zero line, which represents the predicted function. Nevertheless, the first group was still unbalanced, perhaps because of asymmetrical data distribution, as there was no pattern related to size. For the second group, even considering a well-balanced residual distribution for animals with lengths between 4 and 8 cm SL, large animals ( $> 8$  cm SL) are clearly underestimated concerning weight to length.  $R^2$  for both models was close to 0.99, indicating that this statistical parameter is not robust to

identify minor differences in the model's descriptive power. On the other hand, the Proportional Residuals Sum of Squares decreased from 4.954 to 2.537 in the polyphasic model, indicating a better adjustment.

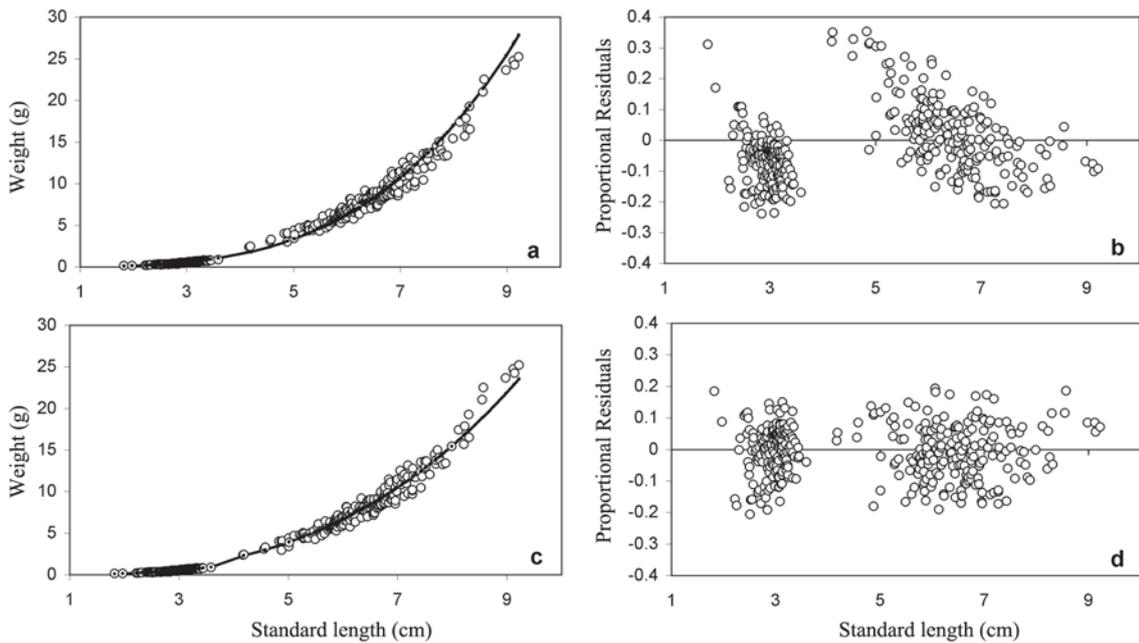
The 701 collected specimens of *C. ibicuihensis* ranged from 1.7 to 4.5 cm SL. The weight/length relationship according to the Huxley model is shown in Fig. 2a ( $a = 0.01600$ ;  $b = 3.287$ ; residual Sum of Squares = 3.925). Although the trend line appears to fit the data set, fish longer than 4 cm SL clearly showed an overestimated weight (Fig. 2a). Proportional residuals derived from Huxley's adjustment for *C. ibicuihensis* are shown in Fig. 2b. Proportional residuals are distributed apparently in a random pattern, except for larger animals ( $> 4$  cm SL), which had negative residuals. Besides this anomaly, a clear breakdown in the residual pattern was not identified for *C. ibicuihensis*. With no obvious indication, the Stanza Changing Length (SCL) was initially adjusted using 3.0 as the seed value. This value was chosen because of the bottleneck in the residual distribution as identified through Fig. 2b, suggesting a concentration of data derived from at least two age groups.

The weight/length relationship and the distribution of proportional residuals according to the polyphasic growth model are presented in Figs. 2c-d respectively. The adjusted parameters are given in Table 2. The SCL was estimated as 2.948 cm. Below this size, the species shows a positive allometric growth pattern ( $b_1 = 3.319$ ), changing to an unexpected very slight negative allometry for larger animals ( $b_2 = 1.224$ ), following an almost straight line but correcting the identified anomaly of larger animals (Fig. 2d). Determination Coefficients ( $R^2$ ) were not informative, close to 0.99 for both models. The Sum of Squares of Proportional Residuals decreased slightly in the polyphasic model, but no more than 10%.

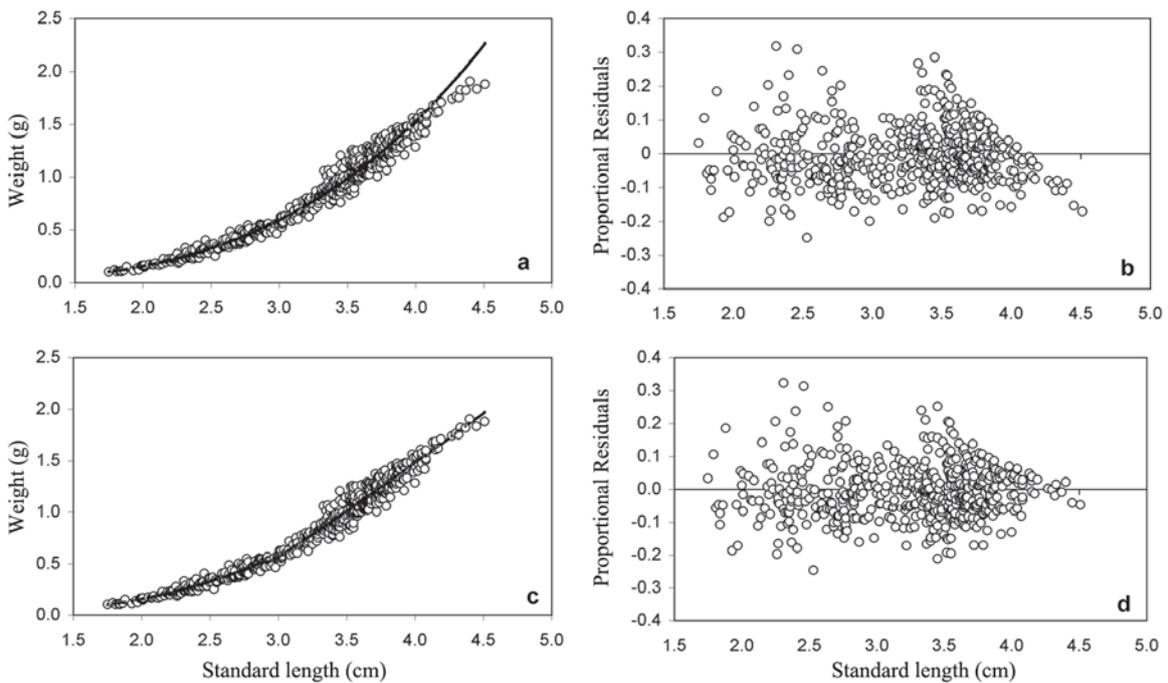
Figure 3 shows a general relationship between the maximum size of small characid species and the estimated sizes at first maturity. As can be seen, there is a clear trend, as described by Binohlan & Froese (2009). Nevertheless, the general model proposed by these authors does not fit the available information for small characids ( $< 15$  cm SL), and is biased to increase estimates of  $L_{50}$ . As an empirical approach, a simple line passing through the origin (Fig. 3, dark line, gray spots) was adjusted to literature available data (Table 1), showing that the size at first maturity is around 50% (inclination = 0.5079) of the maximum length, with a determination coefficient of 0.6754. The Stanza Changing Lengths (SCL) as a function of Standard length for *A. jacuhiensis* and *C. ibicuihensis* are presented as black spots in Fig. 3. From the general pattern showed by small characids with available data concerning size at first maturity (gray spots), it appears that the estimated SCLs are a good approximation for size at maturity.

## Discussion

A change in the growth pattern of *A. jacuhiensis* and *C. ibicuihensis* were identified through the weight/length relationship. Is this change related to the attainment of sexual



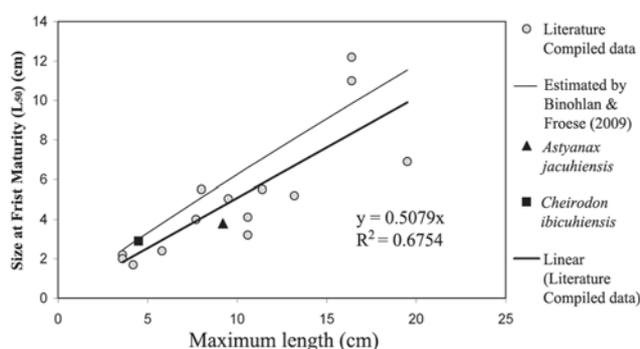
**Fig. 1.** Weight/length relationship for *Astyanax jacuhiensis* (a); proportional residuals resulting from Huxley's adjustment (b); weight/length relationship and proportional residuals distribution according to the polyphasic growth model (c and d, respectively).



**Fig. 2.** Weight/length relationship for *Cheirodon ibicuiensis* (a); proportional residuals resulting from Huxley's adjustment (b); weight/length relationship and proportional residuals distribution according to the polyphasic growth model (c and d, respectively).

maturity? Concerning *A. jacuhiensis*, there are no published values for  $L_{50}$ . The general model proposed by Binohlan & Froese (2009) estimates  $L_{50}$  for *A. jacuhiensis* as 5.8 cm SL if used the maximum species size of 9.6 cm SL of the present work. This value is well above the 3.8 cm estimate for the Stanza Changing Length (SCL) of the polyphasic growth model, and direct estimates of  $L_{50}$  for the species are necessary.

For *C. ibicuiensis*, mature females are found from 2.7 (Oliveira *et al.*, 2002) to 3.2 cm SL Braun *et al.*, 2000). These values are compatible with the Stanza Changing Length estimated by the polyphasic growth model (SCL = 2.948 cm). This suggests that, similarly to *M. funieri* (Bervian *et al.*, 2006), a change in the growth pattern of *C. ibicuiensis* can be related to a change in energy allocation related to the start of reproductive activities. It is also interesting the



**Fig. 3.** Relationship between size at first maturity ( $L_{50}$ ) and maximum reported size for small characids (grey spots, bold line; data from Table 1). The thin line represents  $L_{50}$  values estimated from maximum size following the general function of Froese & Binohlan (2000). Black spots are original data from the present study (SCL values).

negative allometry of the second stanza of *C. ibicuhiensis* ( $b_2 = 1.224$ ). According to Oliveira *et al.* (2002), *C. ibicuhiensis* has a long reproductive period from September through February, although Braun *et al.* (2000) reported mature females throughout the year. The species has also partial spawning (Oliveira *et al.*, 2002), suggesting high energy allocation for reproduction, and perhaps decreased energy for somatic growth.

Although the  $L_{50}$ /SCL association is apparently clear for *C. ibicuhiensis*, other biological factors could be related to the observed change in the growth pattern of *A. jacuhiensis*. Unfortunately, there is no published information concerning the biology of *A. jacuhiensis* that could explain the identified change in the growth pattern. Even the two-stanza growth model does not perfectly describe the full data series, as positive residuals above 8 cm suggest the need for a third growth stanza. Because of the few data available for this size (only nine animals), we decided not to model a more complex function.

From Fig. 3, it is apparent that the predicted trend line (thin line) of Binohlan & Froese (2009) is well above the  $L_{50}$  estimates for most small characids. In reality, this model is a correction of an older one proposed by these same authors (Froese & Binohlan, 2000), with inflated  $L_{50}$  values especially for small species. Nevertheless, for small characids, the empirical linear relationship of  $L_{50}$  as half of the maximum size is also simple and apparently fits better than the general proposition for all teleosts, as the Binohlan & Froese (2009) model, explaining 68% of  $L_{50}$  variability. This “rule”, however, requires corroboration from a larger data set. Applied to *A. jacuhiensis*, this pattern indicates an  $L_{50}$  of 4.8 cm, only one centimeter above the estimated Stanza Changing Length (3.8). In this case, a relationship between the estimated change in the growth pattern (SCL) and the attainment of sexual maturity of *A. jacuhiensis* could only be matched if, in some way, the species anticipates the change in the growth pattern as a way to allocate energy for the demands of reproduction.

**Table 2.** Estimated parameters (mean±1.96 SE) for polyphasic weight/length relationship for *Astyanax jacuhiensis* and *Cheirodon ibicuhiensis* in Fortaleza Lagoon, Cidreira, Rio Grande do Sul, according to the general function:  $W = (a_1 \cdot L^b) \cdot (1/(1+e^{(T_x \cdot (L-SCL))})) + (a_2 \cdot L^b) \cdot (1/(1+e^{-T_x \cdot (L-SCL)}))$ ; where  $W$  is the expected weight (g) for a specific length,  $a$  is the proportionality coefficient,  $L$  is the standard length (cm);  $b$  is the allometric coefficient,  $T_x$  is the changing rate from the first to the second stanza, and SCL stanza changing length.

	<i>Astyanax jacuhiensis</i>	<i>Cheirodon ibicuhiensis</i>
$a_1$	0.01724±0.00143	0.01513±0.00297
$b_1$	3.112±0.0778	3.319±0.240
$a_2$	0.03451±0.00670	0.7217±0.4143
$b_2$	2.939±0.099	1.224±0.501
$T_x$	40.00±0.00	49.96±0.20
SCL	3.841±0.016	2.948±0.322
Sum of Squares	2.537	3.631

Although not conclusive, our data suggest that a complex growth pattern is frequent in the natural environment, and perhaps is not usually identified because small trends are obscured by natural variability. Nevertheless, there is a trade-off when using sophisticated models: any additional parameter can improve the adjustment at a cost of increased complexity. In this respect, there are several methods to support model selection, as the adjusted  $R^2$ , the likelihood ratio test, the Akaike information criterion, or the Schwarz criterion (for revision in this subject, see Johnson & Omland, 2004). Despite the increased complexity, the key factor by choosing to apply the polyphasic model is not strictly statistical, but the possibility to identify a change in the growth pattern that could indicate relevant biological aspects, such as sexual maturity. In this respect, the increased complexity of the polyphasic growth model should not be viewed as a way to merely describe the weight/length relationship. The practical gain in terms of adjustment quality could be minimal. The key factor is that some important biological facts could be reflected in the growth trend. Besides the attainment of sexual maturity, a diet shift, a change of habitat occupation, or the start of a migratory process are all biological facts that may cause a change in the energy budget of a species, what could be reflected in the weight/length relationship. These biological facts, however, could not be identified if simple data adjustments are applied. Therefore, the application of a more complex function, as polyphasic growth model, could point out to unknown anomalies and inspire new insights, guiding research programs to understand fish biology in detail.

Concluding, can weight/length relationship predict size at first maturity? The present study supports our previous hypothesis that the energetic demands related to reproduction could be reflected in the growth pattern of fish species, as for *C. ibicuhiensis* and maybe for *A. jacuhiensis*. Yet, any change in the growth pattern could also be reflecting a neglected aspect of fish biology, and the application of the proposed methodology should be encouraged as an additional tool to depict the complex biology of fish.

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