

Original article

Sexual dimorphism in the catfish *Genidens genidens* (Siluriformes: Ariidae) based on otolith morphometry and relative growth

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Genidens genidens is a species susceptible to population declines in view of their reproductive biology peculiarities. Morphometric differences between sexes are observed in the literature, and these differences should also be evident in otolith development. Growth patterns are one of the most important biological characteristics regarding population dynamics and management. In this context, the aim of the present study is to describe this species relative growth and identify differences between sex life cycles. Somatic growth-otolith growth relationships and somatic length-weight relationships were estimated based on two methodologies; the Huxley and the polyphasic allometric models. Both models demonstrated different growth patterns between sexes. The three axes of otolith growth were adequate descriptors of growth, and the results of the Huxley model demonstrated distinct growth patterns between sexes, with male otoliths larger in all three measured axes. In the polyphase model, male otoliths were thicker, while female otoliths were longer and higher. Both sexes presented similar length-weight relationships, which may indicate that oocyte production and parental care lead to similar costs for this species.

Keywords: Biphasic growth, Energy allocation, Growth models, *lapillus* otoliths, Morphometric relationships.

Genidens genidens é uma espécie suscetível a declínios populacionais, tendo em vista as peculiaridades de sua reprodução. Diferenças morfométricas entre os sexos são observadas na literatura, e essas diferenças também devem ser evidentes no desenvolvimento dos otólitos. O padrão de crescimento é uma das características biológicas mais importantes no que diz respeito à dinâmica populacional e manejo. Assim, nosso objetivo é descrever o crescimento relativo da espécie e identificar diferenças entre os ciclos de vida dos sexos. A relação crescimento somático-crescimento do otólito e a relação comprimento-peso somáticos foram estimados com base em duas metodologias, os modelos alométricos de Huxley e polifásico. Ambos os modelos demonstraram diferentes padrões de crescimento entre sexos. Os três eixos dos otólitos descreveram adequadamente o crescimento, e os resultados do modelo de Huxley demonstraram padrões de crescimento distintos entre os sexos, com os otólitos dos machos sendo maiores em todos os três eixos medidos. No modelo polifásico os otólitos dos machos foram maiores em espessura, enquanto os otólitos das fêmeas exibiram maior comprimento e altura. Ambos os sexos apresentaram relações de comprimento-peso semelhantes, o que pode indicar que a produção de ovócitos e o cuidado parental apresentam custos semelhantes para essa espécie.

Palavras-chave: Alocação de energia, Crescimento bifásico, Modelos de crescimento, Otólitos *lapillus*, Relações morfométricas.

Introduction

The catfish *Genidens genidens* (Cuvier, 1829) is distributed throughout the eastern coast of South America, from the Guianas to Rio de la Plata, in Argentina, and is one of the most common ariids on the Brazilian coast (Marceñiuk, Menezes, 2007). This species is especially abundant

in coastal lagoons and estuaries (Andrade-Tubino *et al.*, 2008; Schmidt *et al.*, 2008; Silva-Junior *et al.*, 2013), including Guanabara Bay, one of the most degraded estuarine systems on the Brazilian coast (Meniconi *et al.*, 2012). Despite this condition, Guanabara Bay supports the most productive estuarine fishery in the state of Rio de Janeiro (Prestrelo, Vianna, 2016). Silva-Junior *et al.* (2013) su-

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gest that *G. genidens* exhibits significant potential as a sentinel species for Guanabara Bay biomonitoring, since it completes its entire life cycle in this estuary, exhibits commercial importance, and demonstrates high tolerance to eutrophication and other anthropic impacts.

Growth is an important component of fish life history (Vaz-dos-Santos, 2015; Weatherley, 1966). The energy intake of an individual is directed to body mass development in the juvenile stage and both body mass and reproductive elements in adults (King, 1995). Consequently, different developmental patterns are observed throughout fish life cycles, detected through both length and weight growth rates and biometric ratios between different body parts (Bervian *et al.*, 2006; Vaz-dos-Santos, 2015). Age variations in individual shape can be expressed through variations between the different somatic magnitudes of an organism, called relative growth (Bagenal, Tesch, 1978; Huxley, Teisser, 1936; Vaz-dos-Santos, 2015). Many fish species may exhibit differences between female and male growth rates (Martins, Haimovici, 2000; Newman *et al.*, 2000; Yoneda *et al.*, 2002; Vaz-dos-Santos, 2015). Paiva *et al.* (2015) demonstrated that, although *G. genidens* does not present evident sexual dimorphism body biometry, significant differences are observed, mainly in head and mouth measurements, related to the oropharyngeal incubation of offspring carried out by males. Additionally, Maciel *et al.* (2018b) found differences between growth parameters for males and females for this species. Thus, growth differences between males and females are also expected in other representative development elements, such as otoliths. Fish present three otolith pairs (Panfili *et al.*, 2002) and, in Siluriformes, *lapilli* otoliths are larger than the other pairs, distinguishing these fish from other teleosts (Fuchs, Volpedo, 2009).

In particular, morphometry applications to otolith development provide a powerful and accurate tool by combining allometric model advantages and relative growth evaluations (Campana, 2001; Perin, Vaz-dos-Santos, 2014; Vaz-dos-Santos, 2015). The power function ($y = a x^b$), originally applied by Huxley (1924) to describe allometric growth (shape variations related to size variations), has been conventionally applied to animal growth studies (Bervian *et al.*, 2006), establishing a conceptual framework for the use of size relationships in morphometric studies (Perin, Vaz-dos-Santos, 2014). However, in spite of its frequent use, the Huxley model is limited in some cases regarding the adequate description of relative growth, since the b coefficient can change during the organisms' life cycle (Bervian *et al.*, 2006). These authors emphasize the importance of a residual analysis to verify the adequacy of the adjusted model and the constancy (or not) of the b coefficient throughout development, proposing methodological alternatives to the model when growth is polyphasic. Given otolith usefulness as a record of individual (and hence population) growth, somatic growth-otolith growth relationship evaluations may indicate factors that affect this

proportionality throughout fish life cycles (Hare, Cowen, 1995), such as differences between male and female development.

Considering that growth patterns are one of the most important biological population dynamic characteristics, also important in the management of exploited species (Alós *et al.*, 2010a), and based on the premise of marked differences between male and female life cycles, the hypothesis presented herein is that these differences are reflected in sexual dimorphism concerning otolith morphometry and relative growth. Therefore, the aim of this study was to describe the relative growth of the catfish *Genidens genidens* based on *lapilli* otoliths, identifying possible differences between development of males and females.

Material and Methods

Genidens genidens individuals were obtained every 15 days from artisanal fishing landings at five points distributed throughout the Guanabara Bay estuary, RJ (22°50'S and 43°10'W), between January 2014 and January 2015 (Fig. 1). Specimens were deposited at the National Museum of Rio de Janeiro collection (voucher specimens: MNRJ 42040). Individual biometry was carried out, determining total length (Lt, 0.1 cm precision) and total weight (Wt, 0.001 g precision). An abdominal incision was performed for macroscopic sex identification. In immature individuals, sex identification was confirmed by histological analyses according to Brown-Peterson *et al.* (2011).

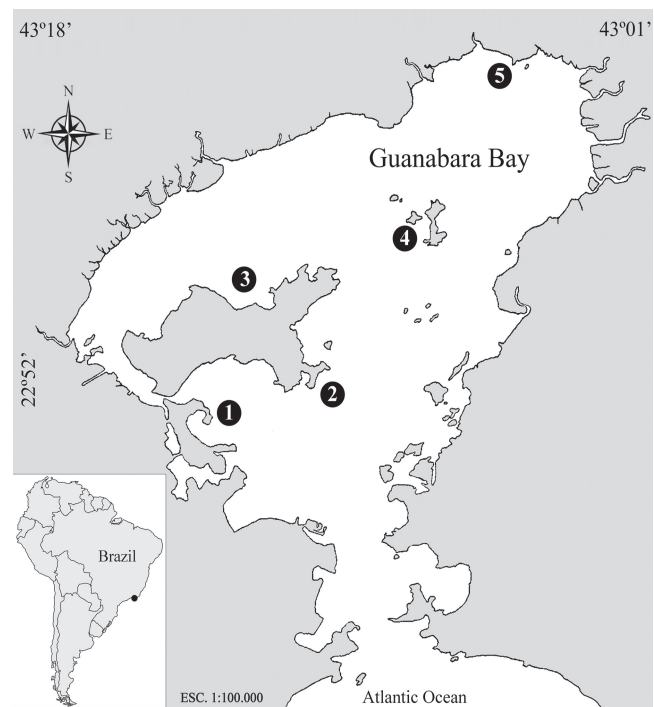


Fig. 1. Guanabara Bay, Rio de Janeiro, Southeastern Brazil, indicating the sampling sites: 1- Bancários, 2 - Magé, 3 - Paquetá Island, 4 - Ilha do Fundão, 5 - central channel.

For otolith pair removal, cranial cavity sectioning was performed and maximum length (Lo), height (Ho) and thickness (To) were obtained for each left *lapillus* otolith (Fig. 2), using a digital caliper (0.01 mm accuracy), while weight (Wo) was determined using an electronic balance (0.0001 g accuracy).

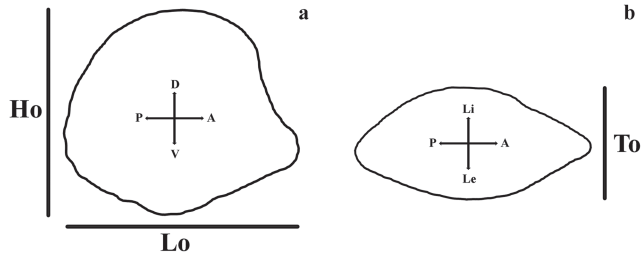


Fig. 2. Schematic representation of *Genidens genidens* otolith measurements: maximum length (Lo), maximum height (Ho) and maximum thickness (To). **a.** Lateral view; **b.** lateroventral view. Structures: dorsal (D), ventral (V), posterior (P), anterior (A), internal lateral face (Li) and external lateral face (Le) position relative to the fish.

To support interpretations regarding changes in morphometric otolith patterns, the otoliths were photographed, and an illustrative schematic of male and female *lapilli* otoliths during different development stages was elaborated. The relationships between somatic and otolith growth for *G. genidens* males and females were estimated based on two methodologies, by adjusting the traditional power model (Huxley, 1924) and the polyphasic model (Bervian *et al.*, 2006, modified by Barradas *et al.*, 2016). The latter approach considers a growth pattern comprising two distinct phases, separated by a stanza changing point (SCP), which indicates the Lt at the time individual growth pattern changed.

The Huxley allometric model ($y = a x^b$) was adjusted using Lt as the independent variable and Lo, Ho, To, Wo as dependent variables. The nonlinear least squares method was applied to the proportional residuals to y through the Levenberg-Marquardt algorithm using the nlsLM function present in the minpack.lm (Elzhov *et al.*, 2016) package of the statistical platform R (R Core Team, 2017). Due to the naturally occurring heteroscedasticity of this data set, homocedastic residues were used for model fit, instead of gross residues (Barradas *et al.*, 2016).

For the polyphasic model analysis, the moving average of the residuals was used to verify the somatic length range in which changes in male and female growth patterns occur, by observing the trends for each point. Each growth phase was described by a power equation. Both growth phases were described by:

$$W = [(a_1 L^{b_1}) \cdot F_w] + [(a_2 L^{b_2}) \cdot (1 - F_w)]$$

where W is the weight, a_1 and a_2 are the proportionality coefficients relative to each growth stage, L is the length, b_1 and b_2 are the allometry coefficients relative to each growth stage and F_w is the switch function.

The switch function is a logistic function that varies between 0 and 1 and that acts by “turning on” and “turning off” equations referring to growth. It is a phase multiplier, described by:

$$F_w = \frac{1}{1 + e^{R_{sc} \cdot (L - SCP)}}$$

where F_w is the switch function, R_{sc} is the stage change rate - which indicates the transition speed between phase 1 and phase 2, L is the length and SCP is the length corresponding to the stanza changing point.

Model evaluation was based on residual significance, tested by a linear regression between the homocedastic residual and length, which are expected to be randomly distributed, and by the Akaike Information Criterion (AIC), which varies according to the sum of the least squares of the residual and the number of parameters in each tested model. The Huxley and polyphasic models were also applied as described above to compare the somatic length-weight relationship (LWR) between males and females.

Results

Biometric data was obtained for the left *lapillus* otolith of 730 *G. genidens* females, with Lt ranging from 6.0 to 37.0 cm, and 377 males, with Lt between 5.0 and 36.0 cm. The general *lapilli* shape variation pattern throughout male and female development was similar for different sizes (Fig. 3), where *lapilli* in individuals up to 28.0 cm in total length acquire their “adult” form and when fish grow to greater lengths, and a higher increase occurs in a three-dimensional perspective, visually revealed by thickness increases.

Tables 1-2 exhibit the results of the relative growth analyses by the Huxley and the polyphasic allometric models. Graphic representations can be consulted in supplementary material (S1 - S10 - Available only as online supplementary file accessed with the online version of the article at <http://www.scielo.br/ni>). The residual analysis for the polyphasic model ensured the adequacy of the adjusted model and the identification of fish life stages, except for the Lt-Wo ratio in females, as residual exhibited a trend ($p < 0.05$). The model presenting the lower AIC, and, consequently, representing the best otolith growth, was the Lt-Lo ratio for both sexes in both the Huxley and polyphasic models. AIC values were high for both male and female Lt-Wo ratios, indicating that this relationship is not the most adequate to describe *G. genidens* growth.

The stanza changing rate (R_{sc}), which controls the rate at which the change in growth patterns occurs, was higher in males (7.2 to 12.0) compared to females (between 1.2 to 9.6), indicating that this change may be more pronounced in males. Female SCP was calculated between 26.8 and 31 cm, while male SCP ranged between 26 and 29.2 cm. This indicates that males alter their growth pattern to a smaller body size compared to females. Regarding *G. genidens* ontogenetic development, otolith growth was more pronounced in smaller individuals for all somatic growth-otolith growth relationships, and was decreased in larger fish ($b_1 > b_2$).

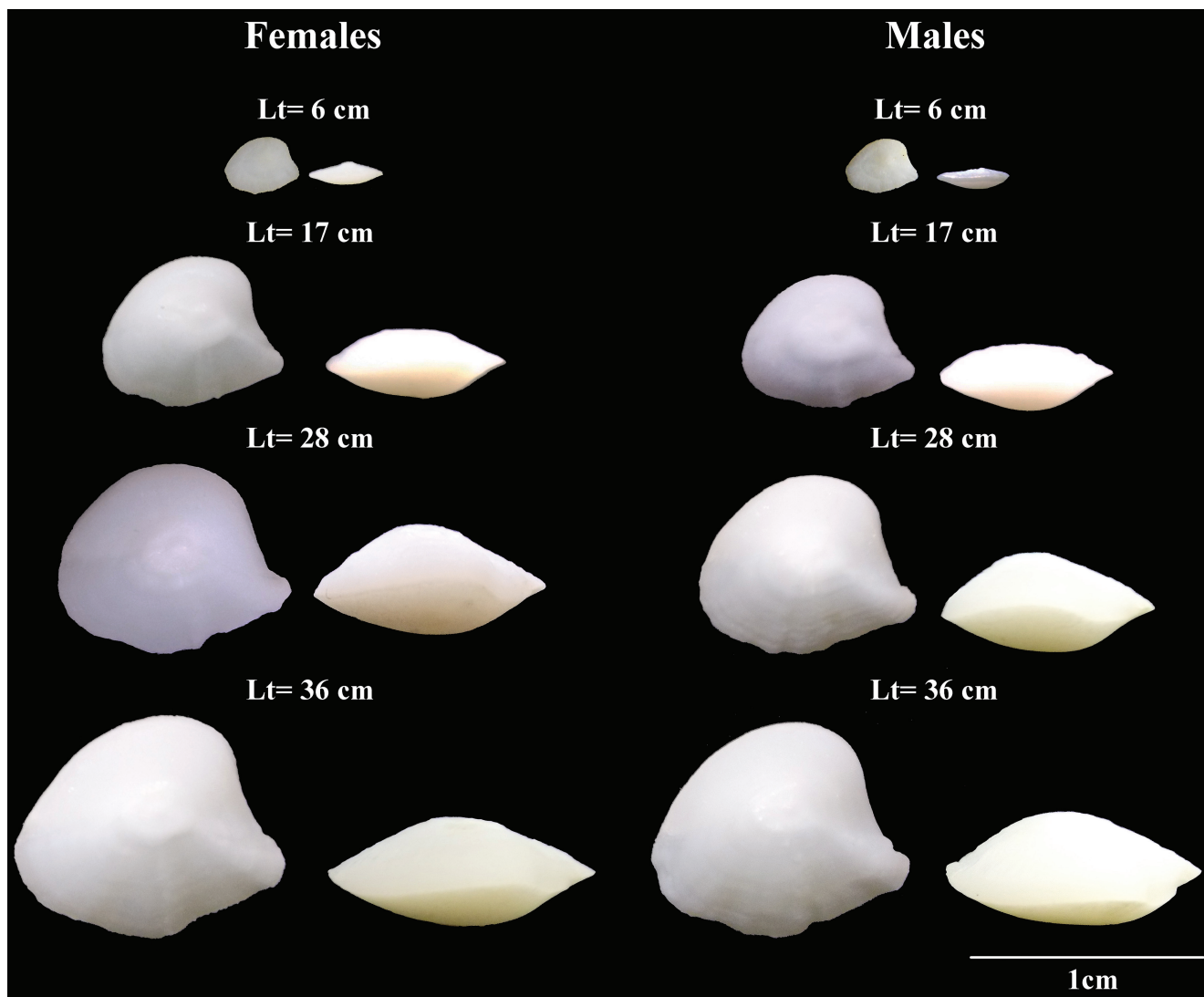


Fig. 3. Lapilli otoliths from *Genidens genidens* females and males from Guanabara Bay, Rio de Janeiro, southeastern Brazil.

Tab. 1. Relative *Genidens genidens* females growth ratios, calculated by the Huxley (1924) and the polyphasic allometric models (SE = standard error), in specimens obtained from Guanabara Bay, Rio de Janeiro, southeastern Brazil.

| Number | Females | | | | |
|-----------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | Lt-Lo | Lt-Ho | Lt-To | Lt-Wo | Lt-Wt |
| | 651 | 653 | 652 | 637 | 645 |
| Lt max | 37 | 36 | 36 | 37 | 37 |
| a (Huxley) \pm SE | 1.6147 \pm 0.0622 | 1.1565 \pm 0.0513 | 0.4140 \pm 0.0281 | 0.0017 \pm 0.0003 | 0.0020 \pm 0.0002 |
| b (Huxley) \pm SE | 0.5549 \pm 0.0115 | 0.5939 \pm 0.0132 | 0.7117 \pm 0.0202 | 1.6532 \pm 0.0436 | 3.4352 \pm 0.0352 |
| AIC (Huxley) | -981916.2500 | -901178.2100 | -627931.7600 | 353969.2000 | -2154674.7000 |
| a_1 (polyphasic) \pm SE | 0.9834 \pm 0.1005 | 0.6231 \pm 0.0740 | 0.2049 \pm 0.0213 | 0.0001 \pm 0.0001 | 0.0019 \pm 0.0030 |
| b_1 (polyphasic) \pm SE | 0.7077 \pm 0.0318 | 0.7846 \pm 0.0370 | 0.9270 \pm 0.0315 | 2.5197 \pm 0.1704 | 3.4735 \pm 0.5024 |
| $R_{sc} \pm$ SE | 1.2 \pm 0.7 | 1.2 \pm 0.6 | 9.6 \pm 1720.6 | 1.5 \pm 0.8 | 2.4 \pm 2.4 |
| SCP \pm SE | 29.4 \pm 0.8 | 29.6 \pm 0.7 | 31.0 \pm 8.1 | 29.9 \pm 0.5 | 26.8 \pm 0.6 |
| a_2 (polyphasic) \pm SE | 1.5953 \pm 0.5271 | 0.9045 \pm 0.3882 | 0.3304 \pm 0.2028 | 0.0011 \pm 0.0010 | 0.0012 \pm 0.0002 |
| b_2 (polyphasic) \pm SE | 0.5551 \pm 0.0935 | 0.6600 \pm 0.1216 | 0.7676 \pm 0.1738 | 1.7572 \pm 0.2584 | 3.5681 \pm 0.0566 |
| AIC (polyphasic) | -981885.5800 | -901124.1500 | -627719.4800 | 356380.3000 | -2157331.6000 |
| Significance of residuals | 0.7058 | 0.1452 | 0.3464 | 0.0082 | 0.0818 |

Tab. 2. Relative *Genidens genidens* males growth ratios, calculated by the Huxley (1924) and the polyphasic allometric models (SE = standard error), in specimens obtained from Guanabara Bay, Rio de Janeiro, southeastern Brazil.

| Males | | | | | |
|-----------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| Number | Lt-Lo | Lt-Ho | Lt-To | Lt-Wo | Lt-Wt |
| | 334 | 340 | 334 | 330 | 334 |
| Lt max | 36 | 36 | 36 | 36 | 36 |
| a (Huxley) \pm SE | 1.3570 \pm 0.0546 | 0.9954 \pm 0.0455 | 0.3114 \pm 0.0216 | 0.0009 \pm 0.0002 | 0.0012 \pm 0.0002 |
| b (Huxley) \pm SE | 0.6065 \pm 0.0121 | 0.6379 \pm 0.0137 | 0.7946 \pm 0.0207 | 1.8231 \pm 0.0496 | 3.5836 \pm 0.0468 |
| AIC (Huxley) | -254309.7700 | -239601.8600 | -159013.3200 | 105201.5700 | -558365.4700 |
| a_1 (polyphasic) \pm SE | 0.9940 \pm 0.0957 | 0.6696 \pm 0.0719 | 0.1954 \pm 0.0225 | 0.0002 \pm 0.0002 | 0.0050 \pm 0.0052 |
| b_1 (polyphasic) \pm SE | 0.7041 \pm 0.0310 | 0.7621 \pm 0.0345 | 0.9415 \pm 0.0356 | 2.2441 \pm 0.2901 | 3.1529 \pm 0.3216 |
| $R_{sc} \pm$ SE | 12.0 \pm 769.8 | 12.0 \pm 39305.1 | 12.0 \pm 3148.7 | 7.2 \pm 333.9 | 12.0 \pm 14631.0 |
| SCP \pm SE | 26.4 \pm 27.4 | 27.0 \pm 120.3 | 29.2 \pm 61.4 | 26.0 \pm 1.1 | 27.2 \pm 184.2 |
| a_2 (polyphasic) \pm SE | 2.2639 \pm 0.2263 | 1.9475 \pm 0.2158 | 0.2615 \pm 0.1023 | 0.0028 \pm 0.0008 | 0.0006 \pm 0.0002 |
| b_2 (polyphasic) \pm SE | 0.4571 \pm 0.0291 | 0.4421 \pm 0.0323 | 0.8412 \pm 0.1119 | 1.5093 \pm 0.0807 | 3.7591 \pm 0.0802 |
| AIC (polyphasic) | -254293.4000 | -239565.2400 | -158904.1600 | 106643.5200 | -560660.6000 |
| Significance of residuals | 0.9205 | 0.0586 | 0.1215 | 0.6854 | 0.3223 |

The b coefficient values in both allometric model equations show that the Lt-Lo, Lt-Ho and Lt-To relationships present negative allometry ($b < 1$). This indicates that increases in somatic length were proportionally greater than otolith growth in the three measured axes (Lo, Ho and To). Based on the Huxley model results, males exhibit larger otoliths concerning length, height and thickness compared to females (b males $>$ b female). The polyphasic model, however, indicates that female otoliths are larger than male otoliths regarding length and height (b_1 females $>$ b_1 males; b_2 females $>$ b_2 males), but thinner (b_1 females $<$ b_1 males; b_2 females $<$ b_2 males) during both, the first and second growth stages.

Concerning the somatic length-weight relationship, growth presented a positive allometry ($b > 3$), indicating that weight increases are proportionally greater than length increases. Throughout ontogenetic development, weight gain is proportionally lower in small individuals, increasing with individual growth ($b_1 < b_2$), for both sexes. Both models indicate that males exhibit greater somatic weight (Wt) at the same length as females (b females $<$ b males; b_2 females $<$ b_2 males).

Discussion

Genidens genidens lapilli otoliths reflect polyphasic growth in relation to body growth, and a differentiated growth pattern between males and females was identified. Traditionally, growth pattern studies between body and otoliths consider these relationships to be constant throughout fish development, limiting interpretations regarding life cycle events that affect otolith development (Bervian *et al.*, 2006). Ontogenic growth pattern changes are well documented, emphasizing the importance of considering this variable in growth studies. For example, Hare, Cowen

(1995) detected changes in the relationship between otolith size and body size throughout different *Pomatomus saltatrix* (Linnaeus, 1766) (Pomatomidae) ontogenetic stages, while Alós *et al.* (2010a) and Alós *et al.* (2010b) identified ontogenetic changes in *Diplodus annularis* (Linnaeus, 1758) (Sparidae) and in *Serranus scriba* (Linnaeus, 1758) (Serranidae) growth rates, respectively, inferring that this change is related to different energy allocations between reproductive and somatic activities at different ages. Alós *et al.* (2010a) emphasize that neglecting ontogenetic changes in individual life history parameters can lead to serious issues, especially in growth studies, suggesting the inclusion of an initial and final growth rate in the von Bertalanffy model, representing different growth energy allocations before and after sexual maturity, while Bervian *et al.* (2006), identifying the same problem, suggest the application of a polyphasic model to describe growth.

Relative *G. genidens* body and otolith growth presented negative allometry ($b < 1$), similar to that described for other teleost species (*e.g.* Labropoulou, Papaconstantinou, 2000; Perin, Vaz-dos-Santos, 2014), indicating that somatic length growth is proportionally greater than otolith growth.

Maciel *et al.* (2018b) observed differences between male and female *G. genidens* concerning growth parameters and age, estimated from otoliths, while Paiva *et al.* (2015) observed intersex differences for morphometric body measurements. The results reported herein indicate that these intersex morphometric differences also apply to otoliths, since the Huxley model demonstrated that male otoliths are proportionally larger in all three measured axes, while the polyphasic model indicates that female otoliths are larger in length and height, and that male otoliths are thicker in both developmental stages. Since otolith shape may reflect body shape (Perin, Vaz-dos-Santos, 2014), thicker otoliths in males may reflect higher body growth rates in this dimension,

while females may exhibit greater body growth in length and height. Sexual dimorphism in otolith growth patterns has also been described for other teleosts, such as species belonging to the Ophidiidae family (Schwarzahns, 1994), *Prionotus nudigula* Ginsburg, 1950 (Triglidae) (Volpedo, Thompson, 1998), *Coryphaena hippurus* Linnaeus, 1758 (Coryphaenidae) (Morales-Nin *et al.*, 1999) and *Porichthys notatus* Girard, 1854 (Batrachoididae) (Bose *et al.*, 2016).

Ontogenetic changes in intersex growth parameters were also detected. The polyphasic allometric model data indicated that *G. genidens* undergoes two growth stages, in both sexes, between 26.0 and 29.2 cm for males and between 26.8 and 31.0 cm for females. Several factors can affect fish growth patterns, such as migration, sexual maturity and food availability, among others (Weatherley, Gill, 1987; Wootton, 1998; Busacker *et al.*, 1990; Saborido-Rey, Kjesbu, 2005; Vaz-dos-Santos, 2015). Particularly, reproductive efforts negatively affect growth, as more energy is directed to somatic growth during the juvenile phase, leading to rapid length growth, which decreases when fish become adults, since energy is divided between two processes (reproduction and growth) (Haimovici, Reis, 1984; Vazzoler, 1996; Pandian, 2010). For *G. genidens*, who presents a very complex reproductive cycle, with females producing among the largest oocytes in all teleosts (Wallace, Selman, 1981) and males performing oral offspring incubation, when they maintain a fasting state (Chaves, 1994; Garcia *et al.*, 2006), reproductive activity seems to be the determining factor for the growth pattern changes observed herein.

Considering that the L_{100} value for *G. genidens* males was calculated at 28.2 cm (Maciel *et al.*, 2018a), the SCP seems to be related to the size in which all males in a given population become mature. For females, although Maciel *et al.* (2018a) calculated that all females of a given population were already adults at 19.3 cm (L_{100}), the same study shows they skip spawning and only begin to spawn at 20 cm, and from 28 cm a considerable increase in fecundity is detected, suggesting that these females reabsorb produced oocytes and skip the reproductive period in order to invest energy in growth, beginning actual reproductive activities when they reach larger body sizes and are more fecund. Folkvord *et al.* (2014) demonstrated that immature fish or those who skipped the spawning season exhibited more pronounced growth rates than individuals carrying out reproduction activities. Thus, SCP size in females seems to be related to a reproductive strategy aiming at increased fertility, rather than sexual maturation. Since fecundity is related to size increases in this species (Maciel *et al.*, 2018a), the changes in growth pattern occur when individuals are at the peak of their reproductive activity.

The somatic length-weight relationship in *G. genidens* exhibited positive allometry ($b > 3$), demonstrating that weight increases are greater than somatic growth, as described by Oliveira, Novelli (2005) for the same species at Lagoa do Açú (RJ). Weight gain was proportionally higher during the second growth stage for both sexes, when individuals invest less in length growth, probably due to reproductive

activity costs (Perin, Vaz-dos-Santos, 2014). The data reported herein also suggest that females presented lower weights at the same length as males, in contrast to what was reported by Araújo *et al.* (1998). However, the b values generated by both models for each sex are close, suggesting that weight gains for both males and females are similar. Since the somatic length-weight relationship reflects individual living conditions related to feeding, migration and reproduction (King, 1995), this may indicate that the parental care process performed by males, which can last from two to three months (Barbieri *et al.*, 1992), is almost as energetically costly as the production of large oocytes by females, since males remain in fasting conditions throughout this period, as their oropharyngeal cavity remains blocked by offspring (Araújo, 1988; Chaves, 1994; Garcia *et al.*, 2006).

This study demonstrates the importance of otolith morphometry in determining the occurrence of sexual dimorphism in *G. genidens*, related to the reproductive biology of the species. The Huxley and polyphasic allometric models were adequate in revealing differential growth patterns between males and females, with the latter doing so in more details. These results are relevant to a better understanding of the ontogenetic development of the species, also serving as subsidy for age estimation studies.

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