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Can otoliths of *Genidens genidens* (Cuvier 1829) (Siluriformes: Ariidae) reveal differences in life strategies of males and females?

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Abstract Determination of the growth parameters of a species is an indispensable requirement for understanding its biology and consequently the management of its fishery. In fisheries science, calculations of longevity, mortality rates and stock-assessment models depend on the availability of growth data. *Genidens genidens*, one of the most common ariid species in Brazil, is a potential sentinel species for biomonitoring in Guanabara Bay, one of the country's most degraded estuarine ecosystems. The present study investigated the growth parameters of *G. genidens*, providing supporting information for its management. Individuals were measured, sexed, and the number of rings in the *lapillus* otolith counted. The periodicity in the formation of the rings was determined by the monthly ratio of the edge type. Individuals from 0 to 11.5 years old were captured, including some that were older than previously reported. Our results showed that this species forms two growth rings per year, one in summer and the other in winter; the summer ring is formed one month later in males than in females, due to the period of oropharyngeal incubation of the offspring. Sexual dimorphism was also observed in the growth rate: males grow faster, and consequently reach smaller sizes than females. We can conclude that the parental care carried out by males and the high energy expenditure in forming the large oocytes by females mark the otoliths and reveal life-cycle particularities differently in each sex.

Keywords Growth parameters · Sexual dimorphism · *Lapillus* otolith · Catfish

Introduction

The family Ariidae is widely distributed along the Brazilian coast (Araújo 1988; Fischer et al. 2011), where their members are an important resource in artisanal fisheries, mainly the estuarine (Reis 1986b; Gomes and Araújo 2004a; Silva-Junior et al. 2013). The catfish *Genidens genidens* (Cuvier 1829) is one of the most common ariid species along the eastern coast of South America from the Guianas to the La Plata River in Argentina (Marceniuk and Menezes 2007; Fischer et al. 2011). This catfish is highly abundant in estuarine systems (Araújo et al. 1998; Azevedo et al. 1999; Silva-Junior et al. 2013) and is a possible sentinel species for biomonitoring in Guanabara Bay, since it completes its entire life cycle within the estuary and is resistant to eutrophication and other anthropogenic impacts (Silva-Junior et al. 2013). The estuary of Guanabara Bay, the second-largest bay on the Brazilian coast, is one of the most degraded estuarine systems in Brazil (Meniconi et al. 2012; Begot and Vianna 2014), but still supports the most productive estuarine fishery in the region

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(Prestrelo and Vianna 2016). Although the vulnerability of *G. genidens* to overfishing is recognized in management regulations for the state of São Paulo and southern Brazil (SUDEPE 1984; MMA 2004), no specific regulations for this catfish have been developed for Guanabara Bay or for the rest of Brazil.

Effective fishery management depends on accurate information on species biology, especially the age and growth pattern (Conand et al. 1995; Vaz-dos-Santos 2015a). Age information is the basis for calculating growth rates, productivity and mortality (Campana 2001). Age and growth are fundamental to understanding a species' biology (individual development), population dynamics (how the set of individuals grows and their abundance), community structure (how each population grows) and ecosystem functioning (age brackets that are preyed on or fished, etc.) (Labropoulou and Papaconstantinou 2000; Vaz-dos-Santos 2015a).

Birth time, growth rate, and interruptions of growth or transitions reflecting migration, reproductive activities, and changes in life history can be recognized in otoliths, allowing them to be widely used to evaluate the demographics of various species of fishes and answer questions about ecology, evolution and fisheries (Bell 2001). Otoliths are calcareous structures in the inner ear of teleost fishes, and function in balance and hearing (Campana 1999; Panfili et al. 2002; Vaz-dos-Santos 2015a). Fish have three pairs of otoliths, *sagitta*, *lapillus* and *asteriscus*, which are metabolically inert, do not act as calcium reserves, are not reabsorbed, and maintain a complete sequence of growth marks (Panfili et al. 2002). The *lapilli* otoliths are the least studied (Morales-Nin et al. 1999; Fuchs and Volpedo 2009; Oliveira et al. 2014). However, in the Siluriformes (catfishes) these otoliths are larger than the other pairs, differentiating this group from other teleosts (Fuchs and Volpedo 2009). Therefore, most of the work with this pair was conducted with Siluriformes, for example, studies of age and growth (Reis 1986a; Amaral et al. 1999; Oliveira and Novelli 2005; Velasco et al. 2007), otolith description (Carvalho et al. 2014), habitat use (Avigliano et al. 2015, 2016, 2017a) and stock identification (Avigliano et al. 2017b).

Investigation of sexual dimorphism in exploited species is essential for adequate fishing management, since this depends on the accuracy of the calculated growth parameters, which may be influenced by differing environmental and biological pressures on males and females. Ariids, including *G. genidens*, possess a peculiar

reproductive biology in which females produce large oocytes (Wallace and Selman 1981) and males carry out oral incubation of the offspring, during which time they do not feed (Chaves 1994; Garcia et al. 2006; Silva-Junior et al. 2013). Since in the ariid *Genidens barbus*, reproductive effort is one of the main factors influencing changes in growth rates (Reis 1986a; Velasco and Reis 2004; Velasco et al. 2007) and sexual dimorphism in growth parameters has been detected in other siluriform species (Reis 1986a; Alonso and Fabré 2003; Pérez and Fabré 2009), this aspect of their biology suggests that the species may show sexual dimorphism in growth, which should be detectable by a change in the pattern of formation of growth rings. Therefore, the present study analyzed the otoliths of *G. genidens*, generating information on the age and growth pattern, and verifying the existence of sexual dimorphism throughout development as a function of the reproductive strategy.

Methods

Collection and processing of material

Specimens of *G. genidens* were obtained biweekly from artisanal fishery landings in the Guanabara Bay estuary (Fig. 1), caught with various types of gear including fish corral, longline, gillnet and bottom-trawl. In the laboratory the individuals were measured (total length – LT, precision of 1 mm) and sexed by observation of the gonads.

The age of individuals was determined as proposed by Panfili et al. (2002) and Vaz-dos-Santos (2015a). The otolith pair was removed by sectioning the cranial cavity. The otoliths were cleaned of adherent tissue in 70% ethanol, air-dried, and stored dry. For the growth analysis, whenever possible five left *lapilli* were selected for each sex, length class (2-cm interval) and sampling month. The *lapilli* were embedded in crystal-clear epoxy resin and cross-sectioned through the core, using a low-speed metallographic saw (IsoMet™), to obtain a 1.5 mm thick section. The otolith sections were immersed in water and photographed with a camera attached to a stereoscopic microscope (Fig. 2).

To determine the age of individual fish, three independent blind readings were performed by the same observer. The set consisting of a hyaline zone and an opaque zone were considered as one growth ring. The radius of each ring (R_n) and the radius of the otolith (R_o)

Fig. 1 Guanabara Bay, Rio de Janeiro, Brazil, indicating the sampling stations: 1- Bancários, 2- Magé, 3- Paquetá Island, 4- Fundão Island, 5- central channel
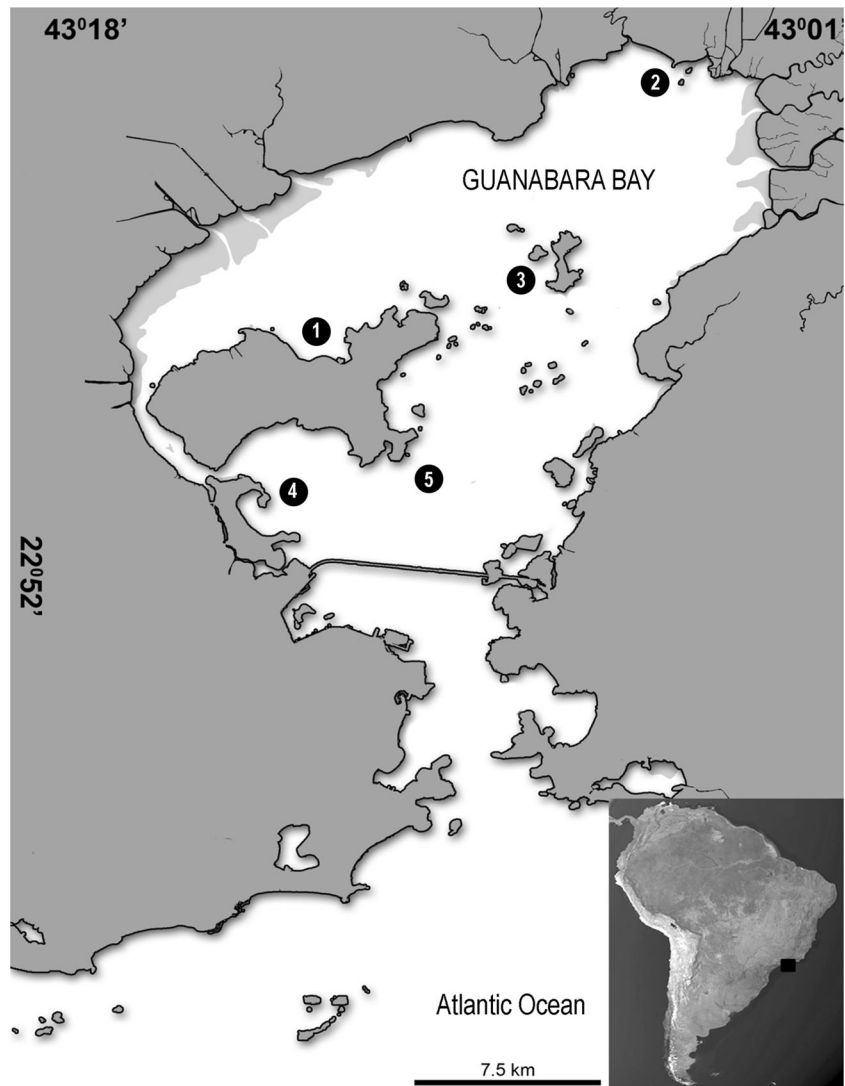
were measured from the nucleus to the opaque margin of the growth ring, using the AxioVision LE 4.8 program. The opaque or hyaline border type of each otolith was recorded (Fig. 2).

Data analysis

The accuracy of the readings was determined by calculating the average percent error (APE) (Beamish and Fournier 1981) and Coefficient of Variation (CV) (Chang 1982). The coincidence percentage of the border type between the three readings was also determined (Vaz-dos-Santos 2015a). Individual otoliths with discrepant ring numbers or types of edges among the readings were reanalyzed and a final reading was

determined. With this reading, the difference in the position of the rings (ring radius) between males and females was tested by two-way ANOVA with repeated measures (F; $\alpha = 0.05$), with assumptions verified through residue analysis (Zar 2010). Sex and ring were considered random variables.

For the validation and subsequent determination of an individual's age, the relative border-type method was used for each sex individually, taking care to use the numerically and temporally most important ring groups (Beamish and McFarlane 1983; Campana 2001), in this case ring groups 10 to 15 together. The large dark hyaline zones were considered fast-growing zones, and the narrow white opaque zones were considered slow-growing zones. The significance between the
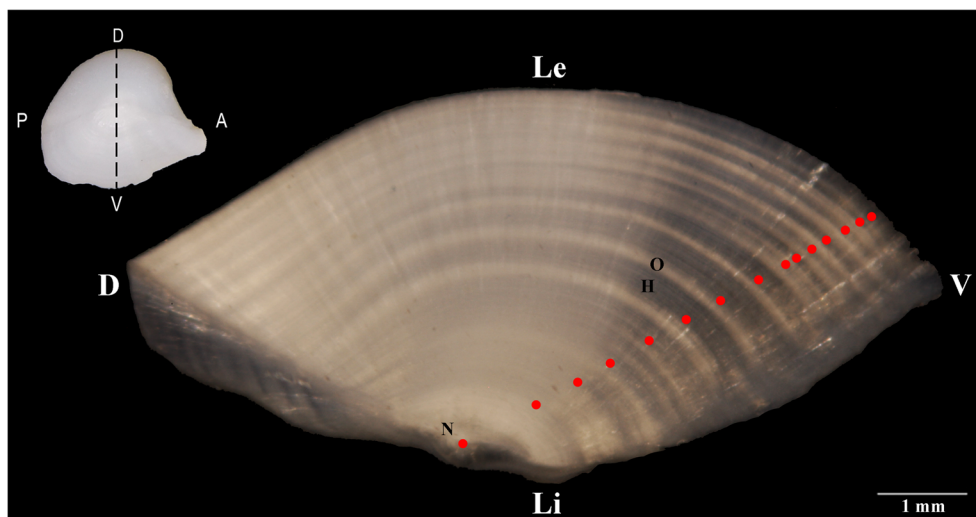
Fig. 2 Cross section of left *lapillus* of *Genidens genidens* under reflected light. Structures: nucleus (N), hyaline zone (H), opaque zone (O), and dorsal (D), ventral (V), posterior (P), anterior (A), internal lateral face (Li), external lateral face (Le) positions relative to the fish. Dashed black line indicates the orientation of the otolith section. Red dots indicate the growth rings and the measured axis

proportions of border types was tested by a log-likelihood ratio goodness-of-fit test with Williams correction (G; $\alpha = 0.05$) (Zar 2010). Based on the reproductive biology and frequency of formation of opaque zones, the average date of birth of individuals was fixed as March, when occurs the peak period of oral incubation by males (Chaves 1994; García et al. 2006). The proportion of each sex by age was tested in relation to the expected ratio of 1:1, with the chi-square test (χ^2; $\alpha = 0.05$) with Yates correction (Zar 2010). Back-calculated lengths were estimated using the model of Monastyrsky (Vigliola and Meekan 2009):

$$L_{BC} = (R_n/R_o)^b \, LT$$

where, L_{BC} is the back-calculated length, R_n is the radius of the ring, R_o is the radius of the otolith, b is the coefficient from the relationship between total length and otolith radius ($LT = a \, R_o{}^b$), adjusted by the non-linear least-squares iterative method, and LT is the total length. To quantify the growth of individuals, the age-length relationship was adjusted by the von Bertalanffy growth model. Several different simulations were conducted, using observed and back-calculated lengths and different combinations and seed parameters (Velasco et al. 2007). The best fits were obtained based on back-calculated lengths using the fixed value of L_∞ calculated with the formula $L_\infty = Lmax/0.95$ (Taylor 1958), where Lmax is the maximum total length observed in the sample. The non-linear least-squares iterative method was used for adjustments, performed for both sexes together and for males and females separately (Vaz-dos-Santos 2015b). This procedure was applied twice, the first time to detect and remove residuals (values <-1.96 and $> +1.96$) and the second time to make the final adjustments. The consistency of the final adjustments was checked by means of the standard errors of the regressions (SE) (Zar 2010; Vaz-dos-Santos 2015b). The significant difference between the models for males and females was assessed by comparing the residual analysis for growth curves (Haddon 2011).

Results

A total of 1107 individuals of *G. genidens* were obtained, including 730 females with LT of 6–47 cm and 377 males with LT 5–38 cm. Based on the criteria used to compose the subsample for the study of age and growth, a total of 428 left otoliths were read, 240 from females and 188 from males. All otoliths were legible, with their opaque and hyaline zones quite visible. The readings were self-consistent, with APE of 9.99 and 8.3% and CV of 13.52 and 11.46% (mean and median).

The coincidence in the classification of the opaque and hyaline edges was high in all the readings and increased from the first to third reading (86.95% between readings 1 and 2 and 89.51% between readings 2 and 3).

The maximum number of rings observed per otolith ranged from zero to 23 rings for females and zero to 22 rings for males. The mean radius of each ring, which determines its position in the otolith, was also highly coherent with growth, with a difference between the position of each ring (ANOVA, F = 3520.93, $p < 0.001$) and between males and females (ANOVA, F = 4.06, $p = 0.044$). The ring radii reflected the dimorphism in the growth of females and males. However, the interaction between factors was not significant (ANOVA, F = 0.63, $p = 0.893$) (Fig. 3).

The O:H ratio varied significantly for females (G = 26.842, $p = 0.0081$) along the period analyzed, but not for males (G = 20.548, $p = 0.0574$), whose p value was slightly above the cut line (0.05). Opaque edges were more frequent in January through March, beginning to increase in December, and from June through August in females, and in February through March and August through October in males. Therefore, this species forms two rings per year, one in summer and one in winter, with the males forming both rings one month later than the females (Fig. 4). Based on this diagnosis, the age of each individual of G. genidens could be assigned.

Table 1 shows the age structure of G. genidens in Guanabara Bay. Most of the population was composed of individuals aged 5 to 7 years, and the oldest and youngest age groups were composed of fewer individuals. Up to about two years, the majority of individuals were males, with females predominating in the older age groups (Fig. 5).

The von Bertalanffy growth models fitted were: $L_t = 49.47 [1 - e^{-0.123 \ (t + 0.198)}]$ (N = 2828, S = 2.716) for females, $L_t = 40 [1 - e^{-0.185 \ (t + 0.002)}]$ (N = 2013, S = 2.708) for males and $L_t = 49.47 [1 - e^{-0.124 \ (t + 0.210)}]$ for both sexes (N = 4830, S = 2.772) (Table 2 and Fig. 6). The models for females and males were different (F = 502.63; $p < 0.0001$), indicating sexual dimorphism in the growth of the species, with males having a faster growth rate (K) than females and a lower maximum theoretical size (L_∞).

Discussion

Although lapilli are not the most commonly used otoliths in the age-estimation studies, in this case the growth rings were quite visible in all otoliths of G. genidens examined, making it possible to determine the age of all the specimens. Lapilli proved to be good indicators of age, since the three blind readings, performed independently for each otolith, showed low APE and CV values, indicating that the readings were adequate (Campana 2001; Vaz-dos-Santos 2015a). Although these values are slightly higher than the reference values for precision (APE ~5% and CV 6–7% sensu Campana 2001), they are empirical and were derived from studies with sagitta, whereas the pattern for lapillus may be different. The use of lapilli otoliths for estimates of age and growth in teleosts is extremely rare, accounting for less than 10% of the studies in Brazil (Oliveira et al. 2014). Due to this lack of information, studies with lapilli generally adopt the methods proposed for sagittae. However, this practice may not
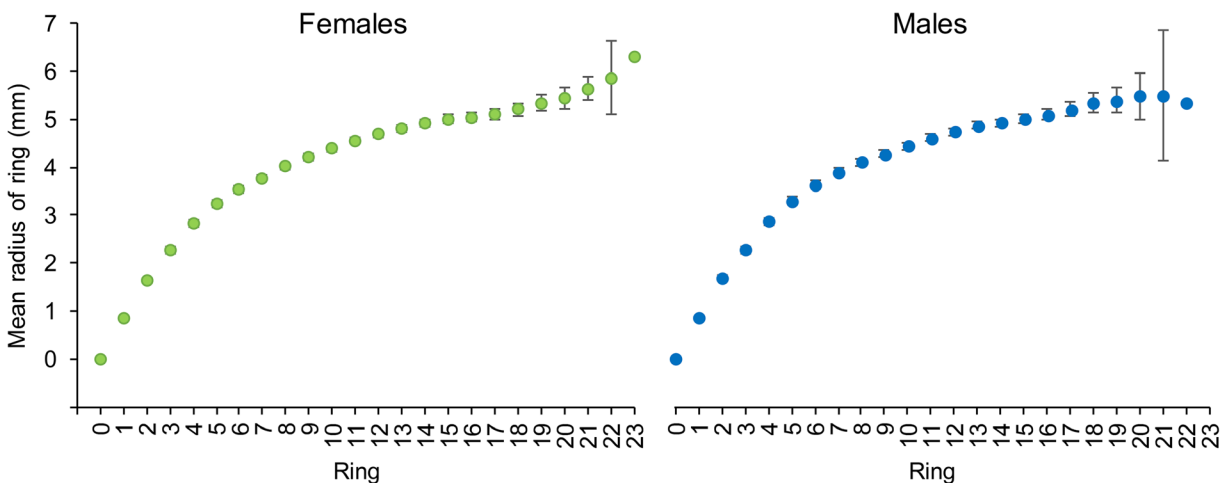

Fig. 3 Ring radius (mean ± 95% CI) of *lapillus* of females and males of *Genidens genidens*, from Guanabara Bay, Brazil
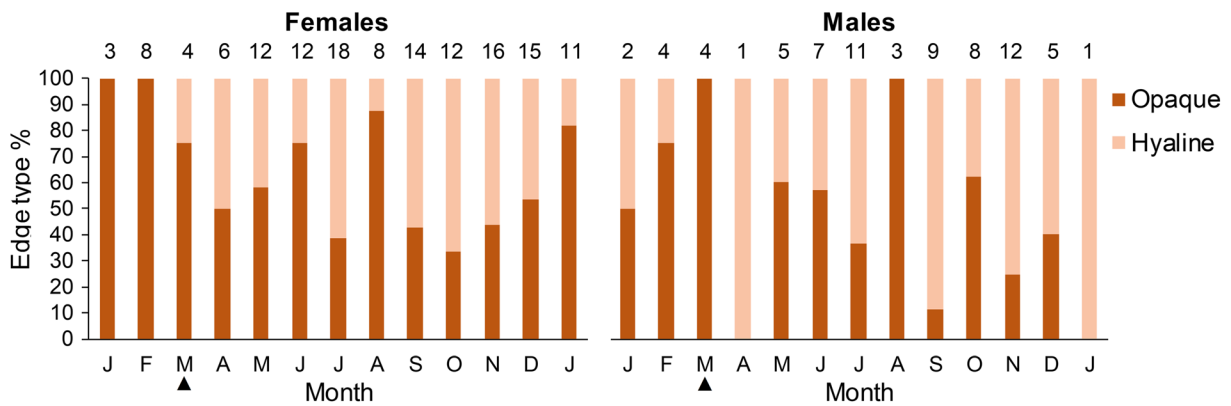
Fig. 4 Monthly percentage of opaque and hyaline edges of *Genidens genidens* male and female *lapilli* in Guanabara Bay, Rio de Janeiro, Brazil. (▲) birth month; upper numbers indicate the number of otoliths analyzed monthly

always be appropriate and further studies on *lapilli* are needed in order to develop an own standard.

For the *lapillus* otolith of *G. genidens,* the narrow opaque zones represent slow growth, while the wide hyaline zones represent rapid growth, since the daily increments in the thickness of the otolith are directly

related to body growth (Bell 2001). This pattern was also observed in the *lapillus* otoliths of other species of Siluriformes. Reis (1986a) considered wide zones as fast-growing and narrow zones as slow-growing for *Genidens barbus*, and Gibbs et al. (2013) also observed narrow opaque zones related to periods of slow growth

Table 1 *Genidens genidens* age-length key in the Guanabara Bay, Rio de Janeiro, Brazil. Percentage (from the total) of individuals by length class and age

LT class (cm)	Age (years)												Total
	0	1	2	3	4	5	6	7	8	9	10	11	
4	100%												1
6	100%												2
8			100%										1
10	50%	50%											2
12													0
14		40%	40%	20%									10
16			50%	35.7%	7.1%		7.1%						14
18	5.9%	17.6%	17.6%	29.4%	17.6%	5.9%	5.9%						17
20		6.7%	20%	6.7%	46.7%	20%							15
22		3.8%	15.4%	23.1%	19.2%	26.9%		7.7%	3.8%				26
24			7.1%	19%	19%	31%	14.3%	4.8%	4.8%				42
26			2.5%	7.6%	6.3%	16.5%	30.4%	20.3%	10.1%	6.3%			79
28					6.5%	11.7%	27.3%	28.6%	16.9%	5.2%	3.9%		77
30				10.9%	4.3%	6.5%	19.6%	28.3%	21.7%	6.5%		2.2%	46
32					7.9%	13.2%	18.4%	26.3%	10.5%	18.4%	5.3%		38
34					3.4%	17.2%	24.1%	20.7%	13.8%	6.9%	6.9%	6.9%	29
36						18.8%	25%	25%	18.8%	6.3%	6.3%		16
38						11.1%	11.1%	33.3%	11.1%	33.3%			9
40								50%		25%	25%		4
Total	5	10	27	38	40	60	80	80	47	28	9	4	428

Fig. 5 Age structure of males and females of *Genidens genidens* in Guanabara Bay, Rio de Janeiro, Brazil. (*) = significant difference (χ^2; $p < 0.05$)
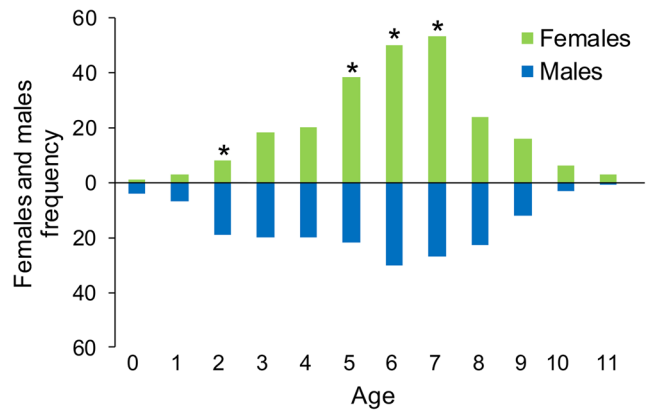
and wide hyaline zones related to periods of rapid growth for *Pterygoplichthys disjunctivus*.

In the present study, this pattern reported for *lapillus* otoliths was confirmed by comparing the frequency of formation of opaque and hyaline edges (Fig. 4) with the information available in the literature on the biology of the species (Barbieri et al. 1992; Chaves 1994; Gomes and Araújo 2004a, b; Garcia et al. 2006; Silva-Junior et al. 2013, 2016). The percentage of border type was the most suitable method for the validation, since the marginal increment would not be appropriate because the *lapilli* did not show the progressive reduction of ring radii in older fish that is indispensable for using this method, originating from studies with *sagittae* (Panfili et al. 2002). Although it was not possible to apply this technique for each ring group separately (cf. Beamish and McFarlane 1983; Campana 2001; Vaz-dos-Santos 2015a), the analysis of ring groups 10 to 15 together was enough to reach a correct diagnosis.

G. genidens formed two growth rings per year. One ring was formed in the summer, related to the reproduction in the same period (Barbieri et al. 1992; Chaves 1994; Gomes and Araújo 2004a, b; Garcia et al. 2006), which is a critical factor for decreases in growth rate in ariids, given the high energy expenditure (Reis 1986a; Velasco et al. 2007). The other ring was formed in the

winter, perhaps because of a slower metabolism due to the cooler water temperature in the inner bay at this time of year (Silva-Junior et al. 2016). The formation of two rings per year, with the ring formed in the summer also related to the reproductive effort, has been described in calcified structures of other tropical species of Siluriformes, such as *Brachyplatystoma flavicans* (Alonso and Fabré 2003), *Hypophthalmus marginatus* (Cutrim and Batista 2005) and *Calophysus macropterus* (Pérez and Fabré 2009). In addition, the average date of birth of individuals was fixed as March, i.e., the peak of oral incubation of the offspring by males (Chaves 1994; García et al. 2006), thus allowing attribution of individual ages.

Comparing the data obtained here with previously published information suggest that the time when the rings are formed differs between females and males. The opaque edges, formed in females from January through March, beginning to increase in December, coincided with the spawning peak (Barbieri et al. 1992; Gomes and Araújo 2004a, b) as a consequence of energy diversion to form the large oocytes. In males, the opaque edges appear most often formed in February–March, i.e., one month later than in females and coinciding with the peak period of oropharyngeal incubation of offspring, when the males may pass two to three months

Table 2 Growth parameters of *Genidens genidens* in Guanabara Bay, Rio de Janeiro, Brazil. L_∞ is the theoretical maximum size, K is the growth constant, and t_0 is the theoretical zero-length age. SE = standard error

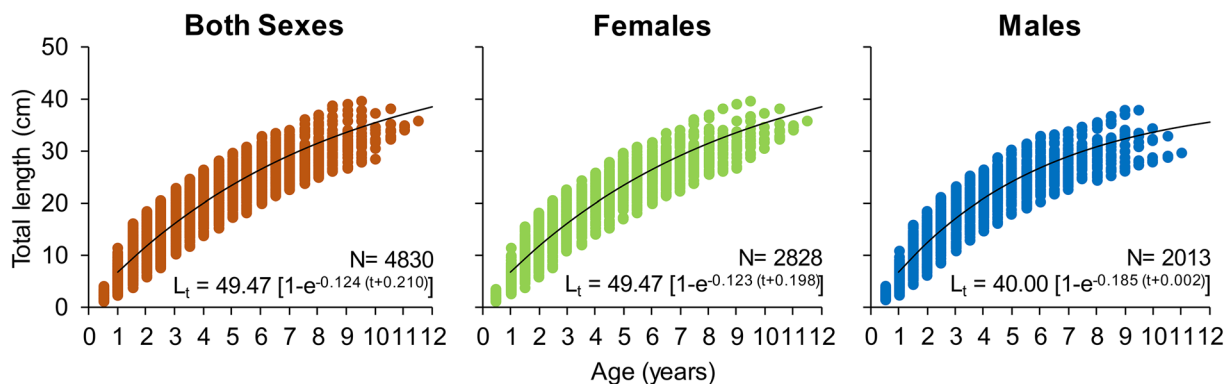| Growth parameters	Both sexes	Females	Males
L_∞	49.47	49.47	40.00
$K \pm SE$	0.124 ± 0.001	0.123 ± 0.001	0.185 ± 0.002
$t_0 \pm SE$	-0.210 ± 0.017	-0.198 ± 0.023	-0.002 ± 0.022

Fig. 6 Growth curve for grouped sexes, and for females and males of *Genidens genidens* in Guanabara Bay, Rio de Janeiro, Brazil, based on back-calculated lengths

without feeding (Barbieri et al. 1992; Chaves 1994; Garcia et al. 2006). We also identified a delay in the formation of the winter rings, i.e., in June through August in females and in August through October in males, although the cause of this delay is unknown.

The individuals of *G. genidens* analyzed in Guanabara Bay reached a maximum age of 11.5 years, with a predominance of intermediate ages, from 5 to 7 years. This age structure results from the natural rarity of older individuals in the population and the unlikelihood that younger individuals will be caught by fishing gear (Coggins et al. 2013). These age values are higher than those observed for the species by Oliveira and Novelli (2005) in Barra do Açu Lagoon (RJ), where the maximum age was 5 years, with individuals from 2 to 4 years predominating. This difference can be attributed to the capture of larger individuals in the present study, which may indicate that the population of Guanabara Bay is more stable, with more size classes and age groups.

The parameters L_∞ and K obtained adequately represented the growth of *G. genidens* in Guanabara Bay. The individuals showed a low growth rate (K) and reached large values of asymptotic length (L_∞), as expected, since low growth rates are associated with larger body sizes and vice-versa (Vaz-dos-Santos 2015a). Regarding the theoretical age at zero length, obviously the values obtained have no biological significance, as they do not reflect development time before hatching (Ricker 1975). However, the initial growth of larvae and young-of-the-year is usually different from that of adults (Pauly 1984), and in the present case, the estimate of t_0 has statistical significance, to adjust the beginning of the curve. The marked reduction in length increase with increasing age and the few specimens in the larger length classes indicate that the

asymptotic length fixation, calculated from the formula of Taylor (1958), was a suitable strategy for fitting the model. This strategy allowed the representation of dimorphism between males and females with very different maximum lengths (47 cm for females and 38 cm for males), associated with the low growth rates common in ariids (Reis 1986a; Conand et al. 1995; Velasco et al. 2007). This is an acceptable and efficient procedure for siluriforms (Velasco and Oddone 2004; Cutrim and Batista 2005; Velasco et al. 2007). Besides, the largest *G. genidens* ever recorded (47 cm LT) were caught in this study.

The present study also identified sexual dimorphism in absolute growth. Males grow faster and consequently reach a smaller body size than females. Converting the calculated values for the size at first gonadal maturation of this catfish in Guanabara Bay, 15.9 cm for females and 17.6 cm for males (Maciel et al. 2018), to age indicates that females mature at 2.9 years and males at 3.1 years. However, Maciel et al. (2018) reported that *G. genidens* females smaller than 20 cm skipped spawning. Therefore, although females reach L_{50} at 15.9 cm, they begin to divert energy to reproductive activity at 20 cm, which converted into age represents 4 years. This allows females to reach larger sizes, probably as an adaptation to increase fecundity, since larger and older females are more fecund (Haimovici and Reis 1984; Pandian 2010; Wootton and Smith 2015). For the males, due to the parental-care behavior that prevents the fish from feeding for a long period (Chaves 1994; Garcia et al. 2006; Silva-Junior et al. 2013) and makes them more susceptible to predation (Wootton and Smith 2015), even younger fish reach larger sizes because they can fit more eggs and young in the oral cavity, and the risk of predation is lower because of their greater length.

For this catfish, we identified the occurrence of sexual dimorphism in the growth, the ring radius in the otoliths, the ring-formation period, the age structure, and the growth parameters, as a consequence of the different reproductive energy expenditure of females and males, demonstrating that otoliths can be used as tools in distinguishing life-cycle patterns between the sexes of the same species.

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