

Original article

# Management proposal based on the timing of oral incubation of eggs and juveniles in the sentinel species *Genidens genidens* (Siluriformes: Ariidae) in a tropical estuary

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Ariids such as *Genidens genidens* are particularly susceptible to overfishing because of their complex reproductive mechanisms, which result in slow replenishment of stocks. In this study, we obtained data about the reproductive ecology of the catfish *G. genidens* in the Guanabara Bay estuary, Rio de Janeiro, Brazil, providing supporting information for management of its fishery. The sex ratio, mean size of each sex at first sexual maturation, and female fecundity were determined and the reproductive period was characterized. The males:females ratio was 1:2. The fecundity is low and increases proportionally to the females' growth in total length and weight. The breeding season occurs during the warmest months of the year, with spawning extending from October through March and incubation from December through April. Sexual maturation is late, with males maturing at a larger size than females. Skipping spawning was also identified in females. Based on the reproductive biology, it is suggested that the catch be restricted to individuals larger than 20 cm, considering the  $L_{75}$  of the males, and that fishing be prohibited from December through March, to include the main period of spawning season by females and oropharyngeal incubation by males.

**Keywords:** Catfish, Fishery management, Guanabara Bay, Parental care, Reproductive strategy.


Ariídeos, como *Genidens genidens*, são particularmente suscetíveis à sobrepesca devido a seus complexos mecanismos reprodutivos, que resultam em uma reposição lenta dos estoques. Neste estudo, obtivemos dados sobre a ecologia reprodutiva do bagre *G. genidens* no estuário da Baía de Guanabara, Rio de Janeiro, Brasil, fornecendo subsídios para seu manejo pesqueiro. A proporção sexual, o tamanho médio de primeira maturação sexual de cada sexo e a fecundidade das fêmeas foram determinados e o período reprodutivo caracterizado. A proporção machos:fêmeas foi de 1:2. A fecundidade é baixa e aumenta proporcionalmente ao crescimento das fêmeas em comprimento total e no peso. O período reprodutivo ocorre durante os meses mais quentes do ano, com a desova se estendendo de outubro a março e a incubação de dezembro a abril. A maturação sexual é tardia, com machos amadurecendo em tamanho maior que as fêmeas. Também foi identificado nas fêmeas adiamento da desova. Com base na biologia reprodutiva, sugere-se que a captura seja restrita a indivíduos maiores que 20 cm, considerando a  $C_{75}$  dos machos, e que a pesca seja proibida de dezembro a março, para incluir o período principal de época de desova das fêmeas e incubação orofaríngea dos machos.

**Palavras-chave:** Bagres, Baía de Guanabara, Cuidado parental, Estratégia reprodutiva, Gestão pesqueira.

## Introduction

In tropical and subtropical regions, catfishes of the Ariidae family occur in marine, estuarine and freshwater environments, usually in shallow coastal waters with mud bottoms (Araújo, 1988; Azevedo *et al.*, 1999; Schmidt *et al.*, 2008; Silva Junior *et al.*, 2013). Estuarine and coastal

regions are especially important areas for breeding, feeding and growth (Araújo, 1988; Schmidt *et al.*, 2008; Silva Junior *et al.*, 2013, 2016; Maciel *et al.*, 2018). Food and Agriculture Organization of the United Nations (FAO) data describe landings of 49,600 to 72,900 tons of ariids in the Western Central Pacific and 14,885 to 26,630 tons in the Western Central Atlantic from 1995 through 1999 (Kailola, 1999;

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Aceró, 2002). In Brazil, ariid catfishes are widely distributed along the coast and have high economic importance for artisanal fisheries, especially in estuaries (Gomes, Araújo, 2004; Silva Junior *et al.*, 2013).

One of the most common species of Ariidae is the catfish *Genidens genidens* (Cuvier, 1829), which occurs on the eastern coast of South America, from the Guianas (8°40'N) to the Río de La Plata, Argentina (35°95'S) (Marceniuk, Menezes, 2007). This species is especially abundant in estuaries and coastal lagoons (Andrade-Tubino *et al.*, 2008; Schmidt *et al.*, 2008; Silva Junior *et al.*, 2013). This great abundance and the estuarine-resident behavior caused *G. genidens* to be selected as a sentinel species to monitor the environmental quality of Guanabara Bay (Silva Junior *et al.*, 2013), which makes the study of its biology a priority. Guanabara Bay is a tropical estuary of high social, economic and environmental importance (Silva Junior *et al.*, 2013; Begot, Vianna, 2014; Prestrelo, Vianna, 2016; Silva Junior *et al.*, 2016). Even though this bay is considered the most degraded estuarine system on the Brazilian coast (Meniconi *et al.*, 2012), it still maintains the essential ecological characteristics to harbor a diversified ichthyofauna (Andrade *et al.*, 2015; Corrêa, Vianna, 2016; Silva Junior *et al.*, 2016), supporting the most productive estuarine fishery in the region (Prestrelo, Vianna, 2016).

The reproductive ecology of the Ariidae is peculiar, considering the fishes sexual plasticity (Pandian, 2010). The family includes demersal fish, whose males incubate the eggs and embryos in the oropharyngeal cavity (Wootton, 1990; Hostim-Silva *et al.*, 2009; Silva Junior *et al.*, 2013; Paiva *et al.*, 2015). Similarly to all other Ariidae, *G. genidens* is particularly susceptible to overfishing because of its complex reproductive mechanisms, which result in slow stock replenishment (King, 1995). Therefore, the management of the *G. genidens* fishery is based on obtaining reliable population data, since the peculiarities of their reproductive behavior make these fish highly dependent on population density (*e.g.* Chaves, 1994).

The goal of conventional fishery management is to regulate fishing mortality of a given stock in a way that produces sustainable, near-maximum yields (O'Farrell, Botsford, 2006). However, the factors that affect reproductive success and resilience in exploited marine fish are extremely complex and poorly understood, and not all these factors can be managed (Lowerre-Barbieri *et al.*, 2016). There is growing awareness that we need to better understand the species' reproductive biology and its effects on recruitment. The reproductive success of a species is determined by the probability that the offspring will survive to reproductive age, on the basis of reproductive production and the survival of the young (Stearns, 1992; Lowerre-Barbieri *et al.*, 2016). Studies on the ecology of teleost reproductive processes make it possible to understand not only the mechanisms that enable the perpetuation of the species, but also their vulnerability to overfishing and the evolution induced by fishing pressure (Dias *et al.*, 1998; Lowerre-Barbieri *et al.*, 2016).

Knowledge of biological variables such as adult abundance, sex ratio, spawning areas and period, fecundity, and number of eggs and larvae of a species is essential for use in predictive models applied to managing the fishery (Dias *et al.*, 1998; Lowerre-Barbieri *et al.*, 2016). The mean length at first gonadal maturity is also an important parameter for population management, as it guides the determination of the minimum catch and net mesh sizes (*e.g.* King, 1995; Vazzoler, 1996).

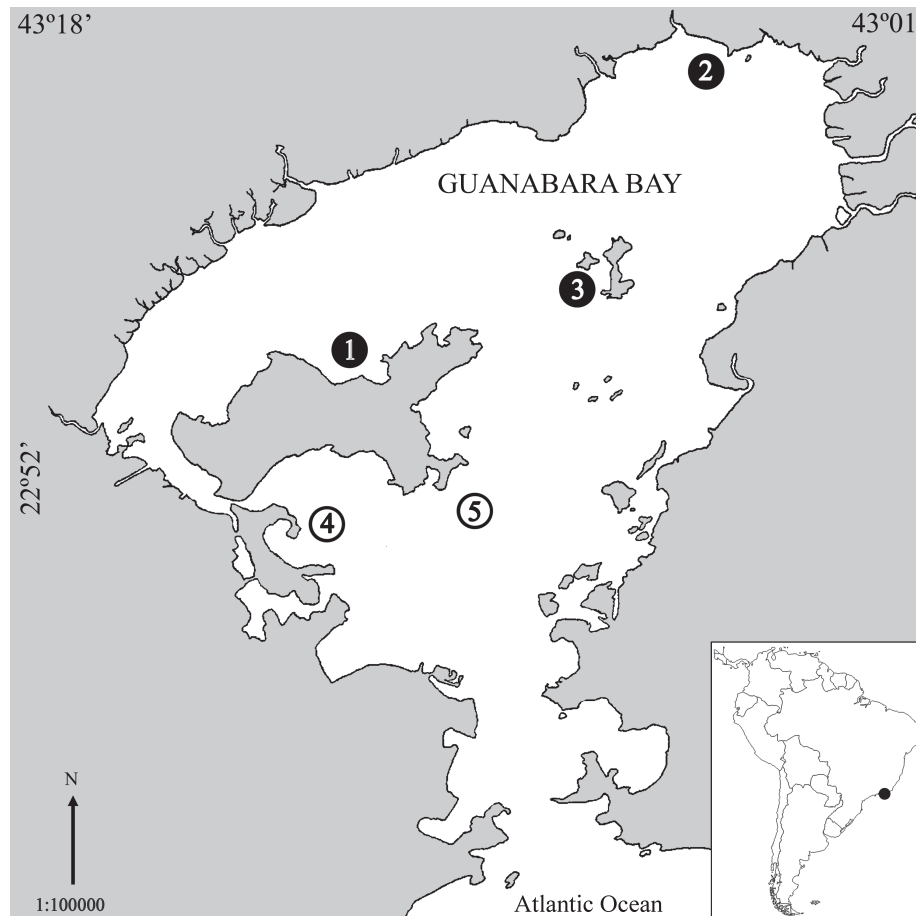
In this study we acquired objective data on the reproductive ecology of the catfish *G. genidens* in the Guanabara Bay estuary, for the purpose of fishery management. This contributes to a tropical estuarine fishery that is still lacking in information to enable proper management (Blaber, 2013), and which should be defined by specific legal regulations according to the biological characteristics of the populations in each region (Begot, Vianna, 2014).

## Material and Methods

**Study area.** Guanabara Bay (Fig. 1), the second-largest bay on the Brazilian coast (Meniconi *et al.*, 2012), is located in the state of Rio de Janeiro, at 22°50'S and 043°10'W, with an area of 384 km<sup>2</sup>, mean water volume of  $1.87 \times 10^9$  m<sup>3</sup> and maximum depth of 50 m at the bay entrance (Kjerfve *et al.*, 1997). The climate is tropical-humid, with a warm rainy season (December through March) and a cold dry season (July through August) (Castro *et al.*, 2005). This estuary is important socioeconomically and supports a productive fishery (Meniconi *et al.*, 2012; Begot, Vianna, 2014; Prestrelo, Vianna, 2016). It is extremely degraded, due to large inputs of untreated solid waste, organic matter, heavy metals and hydrocarbons from a densely populated area, with about 11 million inhabitants and approximately 10,000 industries, as well as intense port activity and a petrochemical hub (Meniconi *et al.*, 2012; Silva Junior *et al.*, 2016).

**Biological sampling.** Specimens of *G. genidens* were obtained biweekly from artisanal fishery landings, with different types of fishing gear, from January 2014 to January 2015, in the localities of Paquetá, Bancários and Magé. In order to improve the sampling of small individuals, experimental sampling was conducted monthly at two stations in the bay, one near Fundão Island and the other in the central channel (Fig. 1), where, in each month, 30-min bottom trawls were conducted. The collected catfish were stored on ice for transport to the laboratory. Specimens were deposited in the collection of the Museu Nacional, Rio de Janeiro, Brazil (Voucher specimens: MNRJ 42040).

In the laboratory, the fishes were measured (total length – Lt, cm) and weighed individually with an electronic balance (total weight – Wt, g). An incision was made in the abdominal region for inspection, removal and weighing of the gonads (gonad weight – Wg, g). The gonadal development stages of males and females were identified macroscopically, considering oocyte size (for females), color, vascu-



**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. Black circles indicate artisanal fishing landing sites and white circles indicate experimental sampling sites.

larization, and percentage of abdominal-cavity occupancy. The gonad stages were classified as immature, developing, spawning-capable, regressing, and regenerating, as proposed by Brown-Peterson *et al.* (2011). For the fecundity analyses, the total number of hydrated vitellogenic oocytes (ready-to-spawn), recognized by their translucent appearance, was counted from each pair of gonads classified as spawning-capable (Vazzoler, 1996).

For small individuals for which macroscopic analysis of the gonads was inconclusive, the classification was later confirmed by histological analysis (Vazzoler, 1996). The gonads were fixed in 20% buffered formaldehyde and preserved in 70% ethanol. They were then gradually dehydrated and embedded in histological resin, cross-sectioned in 5  $\mu$ m-thick sections, and stained with hematoxylin-eosin. The sections were observed under an optical microscope, and the stages of gonadal maturation were determined according to the development stage of the germ cells. Immature ovaries were characterized by the presence of only oogonia and oocytes in primary growth, with little space between the oocytes; and immature testes by a predominance of primary, non-organized spermatogonia in the seminiferous tubules (Brown-Peterson *et al.*, 2011).

**Data analysis.** The monthly sex ratio was compared to the expected ratio of 1:1 with the chi-square test ( $\chi^2$ ;  $\alpha = 0.05$ ) and Yates correction (Zar, 2010). To characterize the reproductive cycle and determine the spawning period, the relative frequency of individuals at different gonadal development stages, and the monthly mean values of the gonadosomatic index (GSI) and gonad condition factor ( $\Delta K$ ) were calculated for each sex separately (Vazzoler, 1996; Hostim-Silva *et al.*, 2009),  $GSI = (Wg/Wt) \times 100$ , where:  $Wg$  = gonad weight and  $Wt$  = total weight and  $\Delta K = (Wg/Lt^b) \times 10^5$ , where:  $Wg$  = gonad weight,  $Lt$  = total length, and  $b$  = the angular coefficient of the length-weight relationship, that was adjusted by the least-squares method (Zar, 2010). Juveniles were removed from the GSI and  $\Delta K$  analyzes, but maintained in the analysis of frequency of the gonadal development stages to illustrate the recruitment period. After assumptions checking, the monthly series of GSI and  $\Delta K$  values were compared with a Kruskal-Wallis test followed by a Mann-Whitney test for pairwise comparisons (Zar, 2010). We also calculated the monthly frequency of adult males incubating eggs and juveniles in order to define parental care period. The relationships between the length or weight of males and the number or weight of eggs and ju-

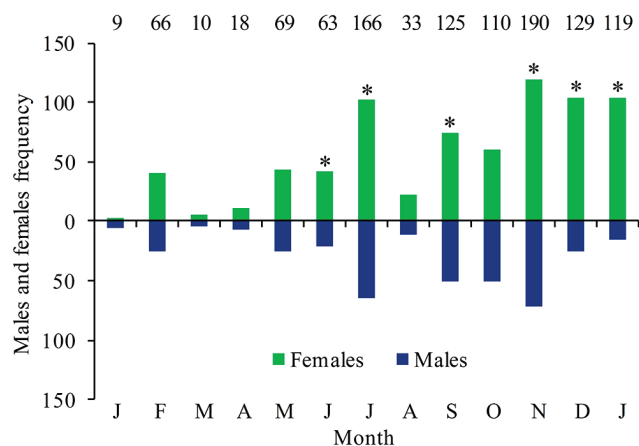
veniles that they were incubating were determined and adjusted using the least-squares method (Zar, 2010).

To estimate the transition from the juvenile to the adult status, individuals were classified as young (immature) or adult (all other gonadal maturation stages) from the histological analyses of the gonads. The proportion of mature individuals per size class ( $P$ ) was calculated, estimating the mean size at first gonadal maturation ( $L_{50}$ ) and applying a logistic curve according to the method of King (1995). The  $P$  values were estimated using the parameters  $a$  and  $b$  of the regression. The  $L_{50}$  was calculated from the ratio of  $a$ : $b$ . The  $L_{25}$ ,  $L_{75}$  and  $L_{100}$  values were calculated based on the estimated  $P$  values of the logistic curve, from the following mathematical expression (King, 1995):  $P = 1 / \{1 + e^{-r(L_t - L_{50})}\}$ , where,  $P$  = proportion of adult individuals expected in the length class ( $L_t$ ),  $r = -b$  and  $L_t$  = total length class. The parameters  $a$ ,  $b$  and  $L_{50}$  were adjusted by the least-squares method (Zar, 2010). In addition, to evaluate the maturation of females we calculated the relative frequency of females at each stage of gonadal maturation by length class (intervals of 2 cm).

Absolute fecundity was calculated as the mean number of oocytes released per female during the spawning period (Vazzoler, 1996). The relationships between fecundity ( $F$ ) and total length, total weight, and gonad weight were determined (Pandian, 2010). The residues from the initial adjustment were removed and the coefficients recalculated using the least-squares method (Zar, 2010).

### Results

A total of 1,107 individuals of *G. genidens* were collected, with total lengths ranging from 5 to 47 cm, including 377 males and 730 females (sex ratio 1:2). The number of females was higher than that of males in the months of June, July, September, November, December and January (Fig. 2).



**Fig. 2.** Monthly distribution of *Genidens genidens* males and females in Guanabara Bay, Rio de Janeiro, Brazil from January 2014 to January 2015. The values at the top indicate the number of individuals caught each month. (\*) Significant difference ( $p < 0.05$ ).

We observed males and females in all five stages of gonad development and the monthly proportion varied in both sexes (Fig. 3). From September on, the number of females with developing gonads increased, and the number of females with regenerating gonads decreased. Males and females with spawning-capable gonads were captured from October through March. A similar pattern was apparent for the GSI, which was higher from November through March in females and from December through March in males, indicating that this species reproduces in the warmer period, from spring to summer. Monthly values of GSI showed significant differences both for males ( $H = 149.4$ ,  $p < 0.001$ ) and females ( $H = 465.5$ ,  $p < 0.001$ ), related to those periods with remarkable differences ( $p < 0.05$  in the pairwise Mann-Whitney tests). A predominance of females with regenerating gonads extended from April through August. In addition, individuals with developing gonads were caught throughout the year.

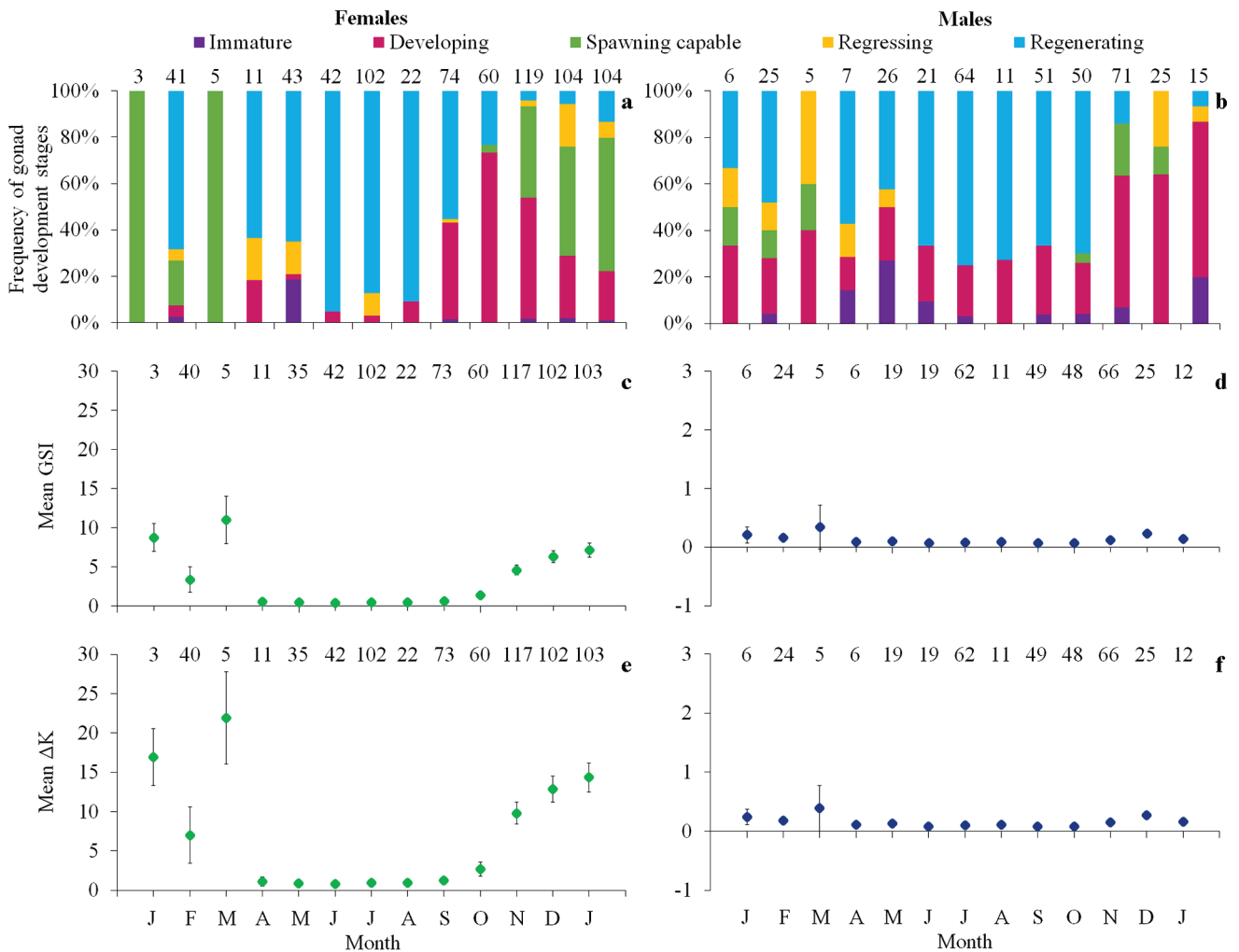
The highest  $\Delta K$  values of the females ( $H = 453.0$ ,  $p < 0.001$ ) and males ( $H = 137.9$ ,  $p < 0.001$ ) coincided with the months of higher frequency of gonads capable of spawning (Figs. 3-4). The months whose  $\Delta K$  values showed remarkable differences also presented statistical differences ( $p < 0.05$  in the pairwise Mann-Whitney tests).

Males incubating eggs ( $N = 10$ ) were recorded from December through March, and males incubating juveniles ( $N = 3$ ) from January through April (Fig. 4). Both eggs and juveniles incubated by the same male were in similar stages of development. The smallest incubating male caught measured 22 cm, and the largest 38 cm. Individual males incubated 1 or 2 juveniles and 4 to 25 eggs (mean 10.6 eggs per male). No linear relationships were observed between the length or weight of males and the number or weight of eggs and the number of juveniles incubated. However, the juveniles weight was higher when incubated by larger and heavier males (Tab. 1). Fig. 5 shows the reproductive cycle of the species throughout the year based on spawning and parental care period.

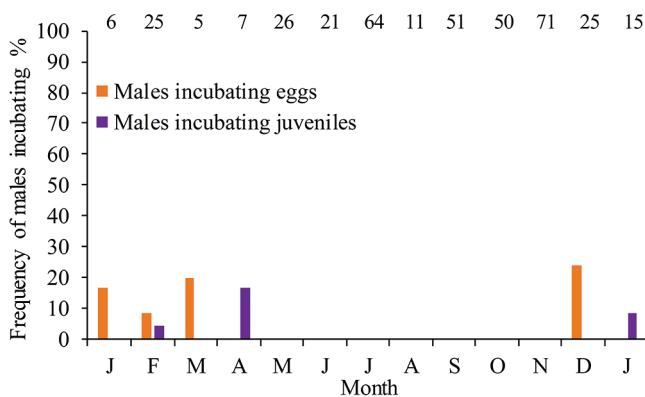
The calculated values of  $L_{25}$ ,  $L_{75}$ ,  $L_{50}$  and  $L_{100}$  for females were 15.2 cm, 15.9 cm, 16.6 cm and 19.3 cm, and for males 15.3 cm, 17.6 cm, 19.8 cm and 28.2 cm respectively (Fig. 6).

Although all females became adults at about 19 cm, females with gonads capable of spawning were only observed from 20 cm and above (Fig. 7), indicating that these smaller individuals are reabsorbing the oocytes produced. This supposition was confirmed by the histological analysis of the gonads, where atretic follicles and yellow bodies were present in the ovaries of adult females smaller than 20 cm (Fig. 8).

The absolute fecundity was 25 oocytes per female (minimum 8, maximum 52). A more pronounced increase in female mean fecundity was observed from 28 cm and above (Fig. 9a). The number of eggs produced per female showed linear and potential relationship with the total length increase and total weight increase, respectively, but low relationship to the increase in the weight of the gonads (Fig. 9).



**Fig. 3.** Monthly distribution of the gonad development stages, GSI (mean ± CI) and ΔK (mean ± CI) of *Genidens genidens* females and males in Guanabara Bay, Rio de Janeiro, Brazil from January 2014 to January 2015. **a.** frequency of gonad development stages of females (N = 730); **b.** frequency of gonad development stages of males (N = 377); **c.** females GSI (N = 715); **d.** males GSI (N = 352); **e.** females ΔK (N = 715); **f.** males ΔK (N = 352). The values at the top of the graphs indicate the number of individuals caught each month. The juveniles were excluded from GSI and ΔK analyzes.

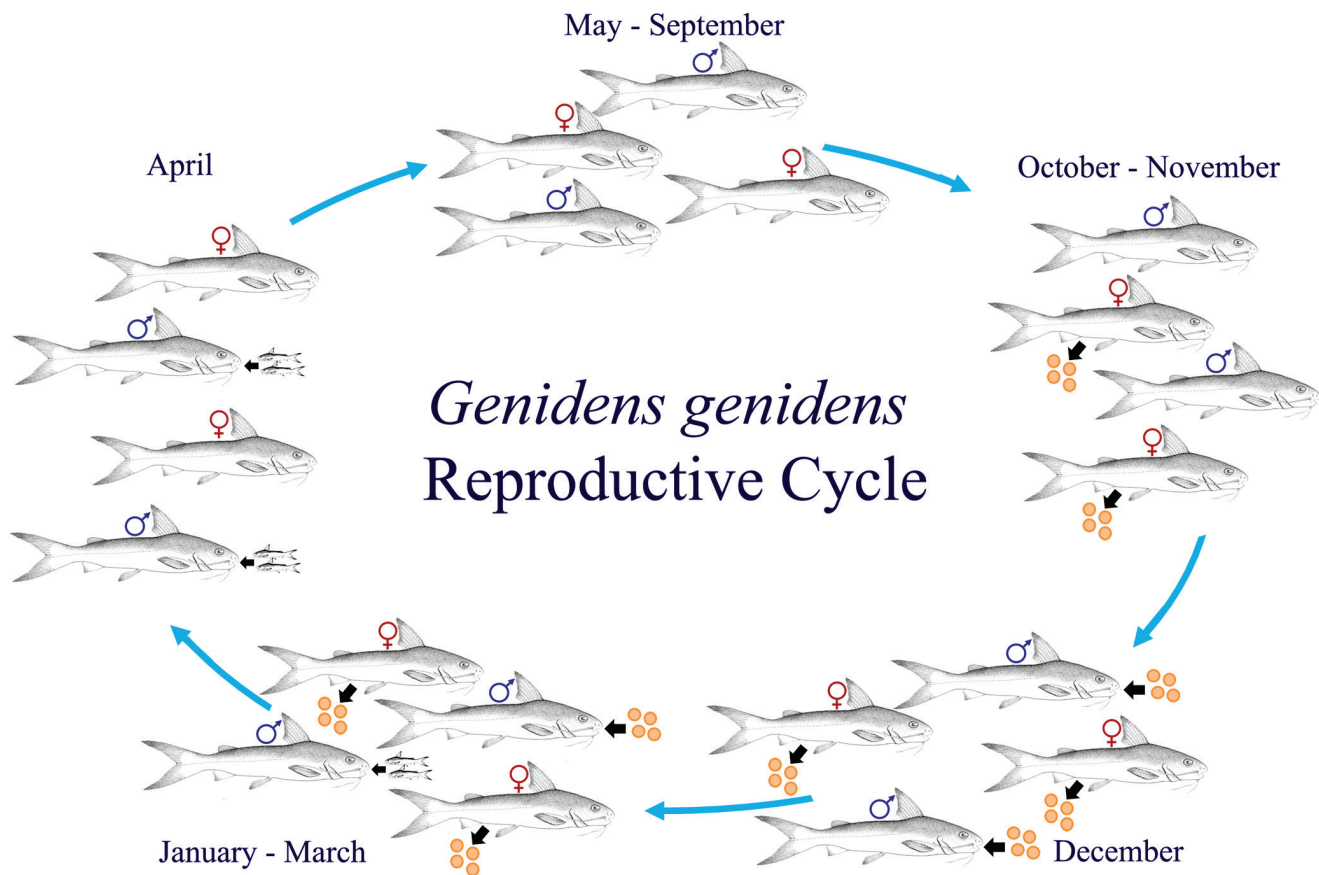


**Fig. 4.** Monthly distribution of the relative frequency (%) of *Genidens genidens* males (N = 377) performing oral incubation of eggs and juveniles in Guanabara Bay, Rio de Janeiro, Brazil from January 2014 to January 2015. The values at the top indicate the total number of adult males caught each month.

**Discussion**

This study confirmed the reproductive cycle of *G. genidens* occurred completely within the Guanabara Bay estuary, reinforcing the estuarine-resident character attributed to this population (Silva Junior *et al.*, 2013). The length structure and the presence of fish in all stages of development, as well as individuals in reproductive activity, demonstrated that the species does not depend on other adjacent environments to complete its life cycle (Elliott *et al.*, 2007).

In the Guanabara Bay estuary, the number of females of *G. genidens* exceeded that of males. This pattern seems to be related to resident estuarine populations that travel between the upper, middle and lower estuaries, as was previously observed for *G. genidens* in Guanabara Bay (Silva Junior *et al.*, 2013) and in Sepetiba Bay, another tropical estuary, approximately 305 km<sup>2</sup> in area (Gomes *et al.*, 1999). However, in smaller more heterogeneous environments the proportion of



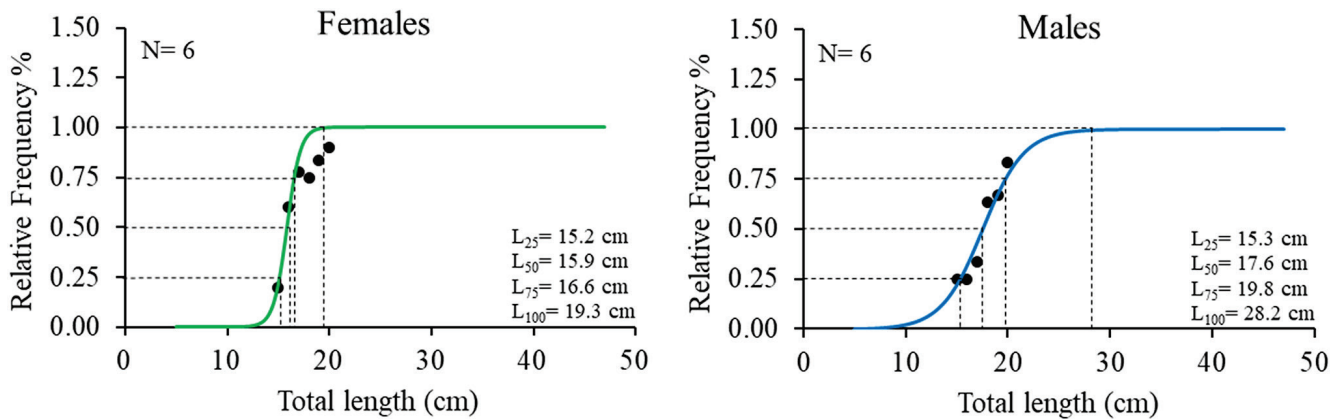
**Fig. 5.** *Genidens genidens* reproductive cycle in Guanabara Bay, Rio de Janeiro, Brazil. Fishes images are a modification of Fischer *et al.* (2011).

**Tab. 1.** Linear relationship between number and weight of offspring, and length and weight of *Genidens genidens* males in Guanabara Bay, Rio de Janeiro, Brazil.

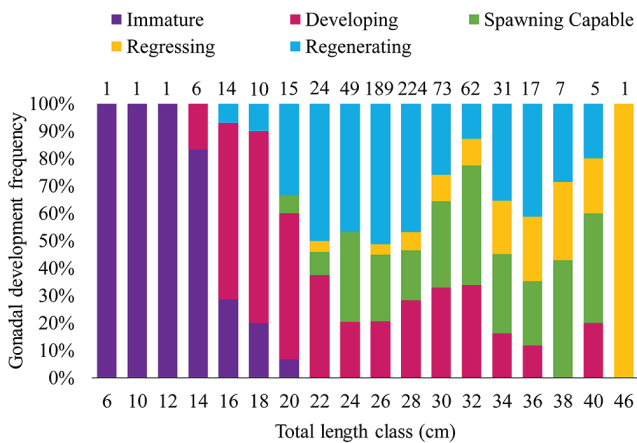
| Relationship                                   | #offspring | #males | <i>a</i> | <i>b</i> | R <sup>2</sup> |
|--|------------|--------|----------|----------|----------------|
| Total length of males – number of eggs         | 106        | 10     | 0.1821   | 5.0107   | 0.0235         |
| Total weight of males – number of eggs         | 106        | 10     | 0.0081   | 8.4572   | 0.0237         |
| Total length of males – average weight of eggs | 106        | 10     | -0.0039  | 1.1814   | 0.0081         |
| Total weight of males – average weight of eggs | 5          | 3      | -0.0003  | 1.1359   | 0.0210         |
| Total length of males – number of juveniles    | 5          | 3      | -0.1154  | 4.6667   | 0.5192         |
| Total weight of males – number of juveniles    | 5          | 3      | -0.0053  | 2.4750   | 0.3620         |
| Total length of males – weight of juveniles    | 5          | 3      | -0.1057  | 4.1563   | 0.9561         |
| Total weight of males – weight of juveniles    | 5          | 3      | -0.0055  | 2.2701   | 0.9459         |

males tends to be higher, as observed by Barbieri *et al.* (1992) in Jacarepaguá Lagoon (Rio de Janeiro, Brazil) and by Hostim-Silva *et al.* (2009) in the mouth of the Itajaí-Açu River (Santa Catarina, Brazil). The authors do not relate this to a population attribute, but as result from the seasonal migration mainly of females to adjacent marine coastal areas, with males remaining longer in the estuary to incubate the eggs and juveniles. In our study, the number of females was higher than that of males during six months of the year and there was no difference in sex ratio in the other months, demonstrating that individuals from Guanabara Bay complete their life cycle within the estuary and do not migrate to adjacent regions.

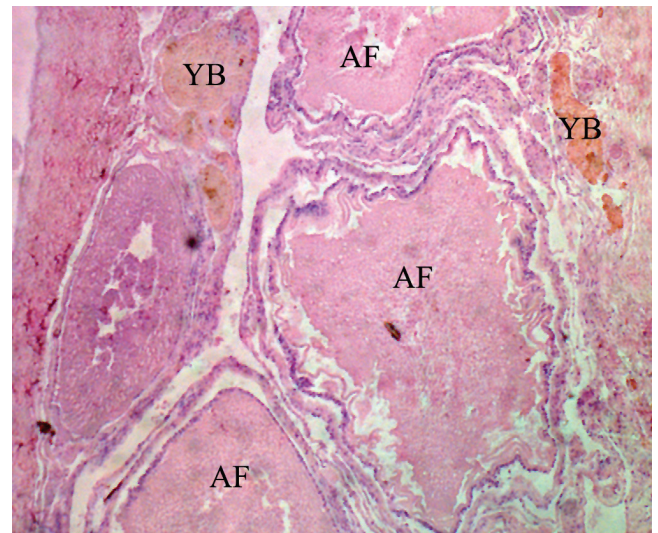
The spawning season identified in the present study resulted from the biological coherence between the analyses of the monthly frequency of individuals with spawning-capable gonads and the mean values of the GSI and ΔK indices. Dias *et al.* (1998) suggested that macroscopic analysis, since it is a simple and immediate classification, can be applied if it is accompanied by a previous survey of information on the reproductive biology of the species, an analysis of other indicators, such as quantitative indices, and a determination of the mean length of first gonadal maturation from microscopic analysis are also convenient. All these measures were adopted in the present study and supported the results of the



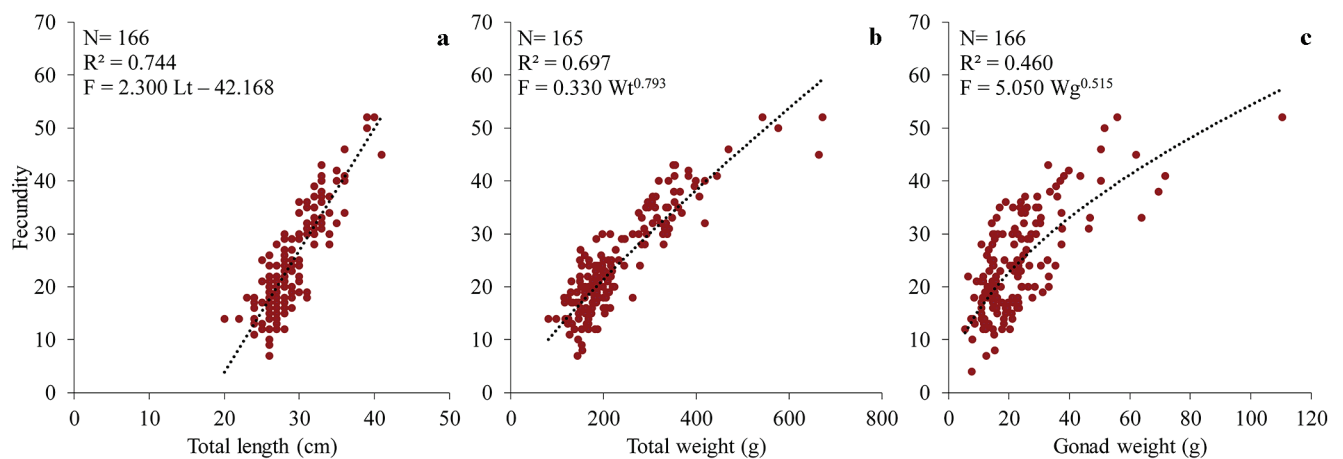
**Fig. 6.** Lengths of sexual maturation for males and females of *Genidens genidens* in Guanabara Bay, Rio de Janeiro, Brazil. Points are the observed values and the continuous line the calculated values.



**Fig. 7.** Frequency of gonad development stages of *Genidens genidens* females (N = 730) per total length class in Guanabara Bay, Rio de Janeiro, Brazil. There was no capture of females on lengths classes 8 cm, 42 cm and 44 cm. The values at the top indicate the number of females caught in each length class.



**Fig. 8.** Histological section of ovary of adult female smaller than 20 cm of *Genidens genidens* in Guanabara Bay, Rio de Janeiro, Brazil. Where: AF – atretic follicles; YB – yellow bodies.



**Fig. 9.** Relationship between fecundity and **a.** total length, **b.** total weight and **c.** gonad weight of *Genidens genidens* females, in Guanabara Bay, Rio de Janeiro, Brazil.

macroscopic analysis. Criticisms of macroscopic classification of gonadal development stages, due to the subjectivity of the researcher in recognizing characteristics (e.g. Gomes, Araújo, 2004; Honji *et al.*, 2006), are less important in the case of *G. genidens*, since the large size of the gonads, especially the ovaries, facilitates the visual diagnosis.

For *G. genidens*, the spawning period coincided with the warm months, beginning in spring (October) and extending into late summer (March), with a single annual spawning event. Similar information on *G. genidens* has been recorded in other areas along the Brazilian coast as Rio de Janeiro (Barbieri *et al.*, 1992; Araújo *et al.*, 1998; Mazzoni *et al.*, 2000; Gomes, Araújo, 2004; Silva Junior *et al.*, 2013), São Paulo (Mishima, Tanji, 1983; Schmidt *et al.*, 2008) and Santa Catarina (Hostim-Silva *et al.*, 2009), indicating that this is a general pattern for the species. In addition, the presence of individuals with developing gonads throughout the year suggests that a portion of the population is always prepared for a possible atypical reproduction (Hostim-Silva *et al.*, 2009).

The peak reproductive period indicated by the GSI and  $\Delta K$  values was supported both by the frequency of gonads spawning-capable, and by other studies (e.g. Barbieri *et al.*, 1992; Gomes, Araújo, 2004; Hostim-Silva *et al.*, 2009). Both indices are indicative of reproduction (West, 1990) and reflect the amount of energy being directed toward it (Vazzoler, 1996). However, the values of GSI and  $\Delta K$  of males were much lower than those obtained for females, since much less energy need be allocated for sperm production than for oocytes, especially in species such as *G. genidens* that reproduce in closed environments with little tidal variation (Wootton, 1990). Despite this, an increase in these rates for males was apparent one month after the beginning of the increase observed for females, which may reflect a small delay in the beginning of reproductive activity of the males. Therefore, the values of GSI and  $\Delta K$  for the males are not good indicators of the reproductive period (Hostim-Silva *et al.*, 2009).

The record of males carrying out oropharyngeal incubation was important, since their frequency of occurrence can also be used as indicator of the reproductive period of the species (Hostim-Silva *et al.*, 2009). The incubation period of *G. genidens* occurred from early summer to early autumn, coinciding with the period during and soon after the peak frequency of females capable of spawning, as recorded by Barbieri *et al.* (1992) and Hostim-Silva *et al.* (2009).

Few males were captured while incubating eggs or juveniles, and fewer incubated eggs and juveniles were collected, compared to the results obtained by Barbieri *et al.* (1992), who obtained 53 males incubating, and by Silva Junior *et al.* (2013), with males incubating up to 34 eggs or juveniles. In addition, a linear increase in the number and weight of eggs and juveniles was expected as a function of the size of the males (Barbieri *et al.*, 1992), but this was only observed for the weight of juveniles in Guanabara Bay. Chaves (1994) stated that in this species, larger adults incubate more eggs and juveniles, as well as larger juveniles, but did not

find a similar relationship for egg weight. One possible explanation for the low number of incubating males caught is that these individuals do not feed when they are performing parental care (Chaves, 1994) and hide themselves, which reduces the chance of being caught. In addition, during capture, it is possible that males release the eggs and juveniles into the water as a last attempt to protect the offspring, which would explain the few eggs and juveniles sampled. This suggestion is based on the observation of males with an empty oral cavity but with the mandible dilated, which is indicative of incubation (Gomes *et al.*, 1999; Paiva *et al.*, 2015).

The mean lengths at first gonadal maturation ( $L_{50}$ ) and the sizes in which all individuals are mature ( $L_{100}$ ) recorded in the literature for *G. genidens* are quite dissimilar. Mishima, Tanji (1983) described  $L_{50}$  of 15.5 cm for females and 16 cm for males in the Cananéia estuary (São Paulo). Barbieri *et al.* (1992) found  $L_{50}$  of 18.0 cm and  $L_{100}$  of 25.0 cm for females in the Jacarepaguá Lagoon (Rio de Janeiro). Araújo *et al.* (1998) obtained the  $L_{50}$  of 13.3 cm and 16.0 cm and  $L_{100}$  of 16.0 cm and 18.5 cm for females and males, respectively, in Sepetiba Bay (Rio de Janeiro). Mazzoni *et al.* (2000) estimated the  $L_{50}$  of 5.5 cm for females and 8.5 cm for males in the Maricá Lagoon (Rio de Janeiro), while Hostim-Silva *et al.* (2009) recorded  $L_{50}$  and  $L_{100}$  of 13.4 cm and 21.3 cm for females and 16.8 cm and 23.9 cm for males at the mouth of the Itajai-Açú River (Santa Catarina).

The calculated values in this study (Fig. 6) were, in general, higher than most of the values found in the literature for the species in other localities. Independently of small methodological differences in parameter estimation among studies, this variation could be explained by intraspecific genetic differences (Vazzoler, 1996). Different fishing pressures along the area of occurrence of the species may explain this variability, since they may trigger density-dependent compensatory changes (Trippel, 1995; Law, 2000; Lowerre-Barbieri, 2009). Selective capture leads to changes in the evolutionary regime, causing a decrease in the first-maturation size, due to plastic responses resulting from the decreased competition for food, leading to faster growth, and genetic responses resulting from greater survival of individuals that tend to mature at a smaller body size, to the detriment of individuals that mature later, since early-maturing individuals are more likely to reproduce before being captured, thus increasing their genetic contribution to the population (Law, 2000; Roos *et al.*, 2006). Therefore, the relatively small sizes at first maturation estimated by the other studies may indicate a decrease in stock sizes (Trippel, 1995). At the same time, Maciel *et al.* (2018) showed that *G. genidens* from Guanabara Bay reach older ages, suggesting that this population is more stable, with more size classes. This variation primarily shows that, although the calculated values are important references, they can change due to fishing pressure and therefore should not be used as a static reference (Lowerre-Barbieri, 2009).

In Guanabara Bay, the high values of  $L_{50}$  and  $L_{100}$  indicate later maturity, allowing individuals to reach larger sizes



by allocating more energy to growth for longer periods. This will increase fecundity, in females due to the larger space in the abdominal cavity, and in males due to the larger space in their oral cavity to carry more juveniles (Mazzoni *et al.*, 2000; Paiva *et al.*, 2015). In all regions where the reproductive biology of *G. genidens* has been studied, the  $L_{50}$  and  $L_{100}$  values of males are always higher than those of females (Barbieri *et al.*, 1992; Araújo *et al.*, 1998; Mazzoni *et al.*, 2000; Hostim-Silva *et al.*, 2009), showing that males reach sexual maturity at a larger size than females, a sexual dimorphism inherent to the species (Hostim-Silva *et al.*, 2009). This dimorphism was also evident in the analysis of morphometry of the head of adult males (Paiva *et al.*, 2015) and in the growth of the species (Maciel *et al.*, 2018).

The results also suggest that *G. genidens* females are skipping spawning. The skipped-spawning strategy is defined as postponement of spawning for the following year, with no negative consequences for future reproduction (Rideout, Tomkiewicz, 2011). This plastic response is modeled as a trade-off between current and future reproduction (Rideout *et al.*, 2005). Skipping spawning may have advantages for survival and growth of individuals in the current year, to maximize their reproductive success in later years (Secor, 2008).

Adult females of *G. genidens* had gonads classified as spawning-capable only from 20 cm and larger. The presence of atretic follicles and yellow bodies in the ovaries of adult females smaller than 20 cm showed that they are reabsorbing their oocytes (Miranda *et al.*, 1999; Santos *et al.*, 2008; Rideout, Tomkiewicz, 2011). This suggests that these young individuals are skipping spawning as an adaptive strategy, which allows greater investment in growth to increase their fertility in later years (Rideout *et al.*, 2005; Jørgensen *et al.*, 2006; Folkvord *et al.*, 2014). Jørgensen *et al.* (2006), who studied skipped spawning in *Gadus morhua* (Linnaeus, 1758), and Rideout, Tomkiewicz (2011), that reviewed skipping spawning in several species, showed that it is more common in the first years after maturation. The reason is that reproduction costs are disproportionately higher for young individuals that are reproducing for the first time (Secor, 2008). For *G. genidens* the probable reason is that the number of eggs produced is limited both by the quantity of resources for oocyte production and by the space available for eggs in the females' body cavity (Barbieri *et al.*, 1992; Gomes, Araújo, 2004; Pandian, 2010), since species from the family Ariidae produces the largest oocytes among teleosts (Wallace, Selman, 1981).

The recorded fecundity for *G. genidens* in Guanabara Bay (8-52 oocytes) is low in comparison to other teleosts. However, it is higher than that observed by other authors for the species: 7-30 (Barbieri *et al.*, 1992), 13-24 (Gomes *et al.*, 1999), 6-24 (Gomes, Araújo, 2004) and 7-38 oocytes (Schmidt *et al.*, 2008). This can be explained by the large specimens captured in our study, since larger females are more fecund (Palumbi, 2004). Our results also showed that the fecundity of the species was linearly correlated with

length, proving this positive relationship between the size of the females and the increase of the fecundity. Barbieri *et al.* (1992) stated that although the fecundity in teleosts is generally expressed as a potential relationship with length, the linear relationship in *G. genidens* is in agreement with observations for other ariids, due to their large oocytes (Wallace, Selman, 1981). Therefore, a cubic increase in fecundity would be limited by the space in the abdominal cavity of females, as well as by the energy available to produce oocytes. Although the fecundity showed a potential correlation with weight increase, as expected, the same did not occur for gonadal increase.

Studies on the reproduction of *G. genidens* are highly important for the conservation of the species, since for effective management it is essential to understand the reproductive processes of the exploited stocks and the effects of these processes on recruitment (Lowerre-Barbieri, 2009; Lowerre-Barbieri *et al.*, 2015, 2016). Although Guanabara Bay is one of the most degraded estuarine ecosystems on the Brazilian coast (Meniconi *et al.*, 2012), it supports intense fishing activity (Prestrelo, Vianna, 2016) in which this species is widely caught. In this study, the number of specimens caught was high and the reproductive characteristics of the species, such as time and type of spawning, as well as size at first maturation and fecundity of the females, do not seem to be affected by anthropic pressures. These results corroborate the high tolerance of *G. genidens* to adverse environmental conditions, reported by Silva Junior *et al.* (2013) showing that this population has high reproductive resilience, considering its capacity to maintain reproductive success, resulting in its long-term stability, despite disturbances such as environmental degradation and fishing pressure (Lowerre-Barbieri *et al.*, 2015, 2016).

Although its apparent resistance to adverse conditions, low fecundity coupled with intensive parental care make this catfish quite susceptible to population decreases due to fishing pressure. Its vulnerability has already been recognized nationally, generating fishing-regulation measures for São Paulo State and for the southern coast of Brazil, defining the closed-season and minimum catch size (MMA, 2004; SUDEPE, 1984). However, despite its importance in the regional fishery (Silva Junior *et al.*, 2013), there is no management measure for the ariid fishery in Guanabara Bay, nor specifically for *G. genidens*, as well as in all the regulations promulgated by the state of Rio de Janeiro (Begot, Vianna, 2014). Therefore, considering that the resilience of a stock is directly connected to factors related to its reproductive success (Lowerre-Barbieri, 2009), the results obtained by this study produced important supporting information for the management of the species. We propose the following restrictive measures for the *G. genidens* commercial fishery: (1) establish a minimum catch size of 20 cm, considering the  $L_{75}$  of males and the better consumer acceptance of larger fish; (2) total fishing prohibition during a closed-season from December through March, to include the reproductive peak and the main period of oropharyngeal incubation. Im-

plementation of these two measures will contribute significantly to the conservation of the species, and this strategy can be replicated in the other estuaries and areas of occurrence of this catfish.

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