Demography of the Agassiz's parrotfish *Sparisoma frondosum* (Agassiz, 1831) in north-eastern Brazil

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Age and growth of Agassiz's parrotfish Sparisoma frondosum *captured off Brazil (Pernambuco) were estimated using sagittal otoliths from 251 specimens. Sex of each specimen was determined and showed that 130 specimens were females (13.1 to 36.8 cm TL) and 121 were males (17.5 to 36.6 cm TL). The otolith marginal increment analysis indicated a single translucent ring formed every year. Parameters of growth curves were derived for the von Bertalanffy (VBGF) and Gompertz models. Based on the Akaike information criterion (AIC), both models were suitable for describing the growth of this species. VBGF parameters were estimated for males $L_\infty = 39.74$ cm TL, $K = 0.22$, $t_o = -1.63$ years, females $L_\infty = 32.38$ cm TL, $K = 0.44$; $t_o = -0.23$ years; and for the sexes combined $L_\infty = 33.66$ cm TL, $K = 0.41$, $t_o = -0.27$ years. The study showed that 55% of individuals were 3 and 4 years of age, with maximal age of 9 years. Mature females (>17.6 cm TL) accounted for 45% of the sample. The age at first maturity for females was 1.6 years. For males the size at first maturity was not determined as immature individuals were not present in the overall sample. Also, primary males (PM) and specimens with gonads undergoing sexual transition were not found. The age structure and growth parameters for* S. frondosum *are an important contribution to the assessment of the state of exploitation of this species.*

Keywords: otolith, Scaridae, hermaphroditism, reef fish, north-east coast of Brazil

INTRODUCTION

The Agassiz's parrotfish, *Sparisoma frondosum* (**Actinopterygii**: Labridae), occurs along the Brazilian coast from the Manoel Luiz reef (00°50′S 44°15′W) to Santa Catarina State (27°30′S 48°31′W), including the oceanic islands of Fernando de Noronha (3°54′S 32°25′W), Rocas Atol (3°52′S 33°49′W), the Archipelagos Saint Peter and Saint Paul (00°56′N 29°22′W) and Trindade (20°31′S 29°19′W). Moreover, the species has been recorded in Venezuela, in the Dutch Antilles, Grenada, Trinidad and Tobago (Moura *et al.*, 2001; Nelson, 2006; Padovani-Ferreira *et al.*, 2012) and at the Cape Verde Archipelago (00°56′N 29°22′W) (Freitas *et al.*, 2014). Overall, along the Brazilian coast it is the second most abundant parrotfish species (Padovani-Ferreira *et al.*, 2012), locally called *budião*. The reclassification in 2001 of this parrotfish as a separate species from that which occurs in the Caribbean, suggests that the records of occurrence of this species in the Caribbean islands may be misidentifications – as this species is in fact endemic to Brazil (Freitas *et al.*, 2014).

Sparisoma frondosum occupies reef areas located in depths from 1 to 54 m where it reaches sizes of 38 cm of length (total length – TL) (Moura *et al.*, 2001; Ribeiro, 2004). Males and females show different patterns of colours, displaying in the upper caudal peduncle a dark spot, which is a distinctive feature from other western Atlantic species from the same family. In north-eastern Brazil, this is the most frequent species of the *Sparisoma* genus (*sensu* Westneat & Alfaro, 2005) in catches of fish-traps, which also include other reef species such as the parrotfish *S. axillare* and the spotted goatfish *Pseudupeneus maculatus* (Ribeiro, 2004).

Analysing official catch data annual average landings of *Sparisoma* species were estimated around 200 t in Pernambuco for the period 1996 to 2001 (Lessa & Araújo, 2009) as well as for 2002 and 2005 (136.5 and 280.5 t, respectively) (Véras, 2008). The number of gear annually employed for obtaining those captures ranged from 150 traps day^{-1} in April to 4500 traps day^{-1} in September/October and January (Ribeiro, 2004).

There are indications of overfishing for this species in south-eastern Brazil, which is worrying since fishing pressures have been steadily increasing throughout the distribution range of the *Sparisoma* species (Padovani-Ferreira *et al.*, 2012). Because of this, the Agassiz's parrotfish was included in the IUCN red list as Data Deficient (DD) (Padovani-Ferreira *et al.*, 2012), and was classified in the Vulnerable (VU) category in recent regional assessments in Brazil (Brazil, Ordinance 445 of 17.12.2015) in recognition of the threats that include fisheries.

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In addition to the fishing pressure, the continuing degradation and loss of coral reef habitat on which this species is dependent for shelter and food (Padovani-Ferreira *et al.*, 2012) is a matter of concern. Furthermore, based on life history, ecological characteristics and extinction vulnerability of marine fishes, Cheung *et al.* (2005) developed an index of intrinsic vulnerability for 835 species, among them some species from the *Sparisoma* genus, which obtained the index 48 (10 being the least vulnerable and 88 being the most vulnerable). Therefore, it is clear that the assessment of fisheries that allows the population age structure as well as the sizes most heavily impacted by fisheries to be known, are important in order to contribute meaningfully to fishing management (Longhurst & Pauly, 1987).

Aside from the general lack of knowledge about age distribution, reproductive aspects of this species are also unknown. *Sparisoma frondosum* is assumed to be a functional hermaphrodite, presenting a diandric protogynous pattern (Robertson & Warner, 1978), similar to other species of the same genus studied in the Caribbean. This hermaphrodite strategy encompasses a change in gender from female to male that may occur either from mature females or directly from the juvenile phase (Shapiro, 1987; Sadovy de Mitcheson & Liu, 2008). However, in this species the pattern of protogyny has not yet been ascertained.

The impact of fishing in hermaphroditic species is complex and dependent on mating systems. Selective pressures on adult individuals can significantly alter sex change dynamics (Taylor, 2014). One concern is that sexual inversion in a long-lived and large-body species may be hindered by fisheries, which reduce the average length of the fish (Sparre & Venema, 1997), preventing individuals from reaching the minimum size for sex reversal (Warner, 1984; Francis, 1992). On the other hand, in contexts with less intensive fishing pressure, protogynous hermaphroditism may increase sufficient resiliency to prevent stock depletion (Petersen & Warner, 2002) – and it may be a better strategy than that of gonochorism (Bannerot, 1984).

The knowledge that the inversion of sex in hermaphrodites can be triggered by social stimuli, has led to an increasing number of studies on behavioural, ecological and evolutionary aspects of hermaphroditism (Sadovy & Shapiro, 1987; Alonso-Fernández *et al.*, 2011; Collins & McBride, 2011). However, overall information on this species is scarce and restricted to secondary literature.

Our aim in the current study was to estimate age through otolith analysis, fitting a first growth curve for *S. frondosum*. With this, we intend to provide information on size and sex composition of samples through microscopic analyses, so that size at first maturity can be estimated – which is essential for fisheries management.

MATERIALS AND METHODS

Monthly samples of *S. frondosum* were randomly collected in landings of vessels at Itamaracá Island (Pernambuco) from May 2009 to April 2010 (Figure 1). Daily fishing trips were conducted using hexagonal unbaited fish traps, 1 cm mesh size, measuring 90 cm in length and 72 cm in height (the largest diameter of aperture being 24 cm and the smallest 9 cm). Small motorized vessels of 8.5 to 12 m in length operating in depths of up to 60 m were used (IBAMA, 2005).

The total length (TL, cm) and gutted weight (GW, g) of each specimen caught were recorded and the gonads were removed and stored in 4% formaldehyde solution. Sections of the anterior, medium and posterior areas of gonads were taken for ascertaining the sexes. They were dehydrated in alcohol series of different concentrations, diaphanized in xylene, embedded in paraffin at 60°C, sectioned at 6 μm and finally stained with haematoxylin-eosin. After this, sections were examined under a light microscope and gender was assigned following the descriptions of Sadovy & Shapiro (1987) for males, Kume *et al.* (2010) for females, and Hastings (1981) for transitional individuals. Female gonads were also inspected for classification into maturity phases based on the relative proportions of the various development stages of germ cells in the ovary, following Shapiro *et al.* (1993) and Sadovy & Colin (1995) (Table 1).

The overall ratio of males to females in the catches and the monthly frequencies of length classes by sex were tested using two-tail Chi-square tests (χ^2; gl = 1; $\alpha = 0.05$) (Zar, 1999). The relationship between gonad weight (GW) and TL of males and females was estimated, linearized and tested to show differences between sexes (ANCOVA, $\alpha = 0.05$). Comparisons of mean length by sex were performed using the Mann–Whitney *U*-test (Zar, 1999) through the two-tail Chi-square test (Zar, 1999).

An estimate of the length at 50% of maturity for males and females (TL, cm), divided in class intervals of 2 cm, were obtained from a logistic equation. Parameters of the model were derived by linearization of the curve through the use of the least-squares method (King, 1995):

$$P = \frac{1}{1 + e^{[-r \times (L - L_m)]}}$$

where: *P* is the proportion of mature fish in length class; *L* is the midpoint of the length class, *r* is the slope of the curve and L_m is the size at 50% maturity derived from |*a/b*|.

The pair of the *sagittae* was removed, soaked in a solution of bleach (sodium hypochlorite) and rinsed in distilled water and ethanol. The left otolith of the pair was embedded in transparent polyester resin and transversally cut using a metallographic saw, preserving the core (Panfili *et al.*, 2002). The sections were affixed with crystalbond on glass slides, sanded and polished in alumina powder of different granulations (0.33 to 3.0 μm). Two independent readings along the major axis of the otolith were made by the same reader under 25 × magnifications using a binocular dissecting microscope and transmitted light. On each occasion the reader was unaware of the length of the individual or the result of the previous reading.

To estimate the accuracy of the readings, the average percentage error (APE) (Beamish & Fournier, 1981) for comparing the reproducibility of age determination between the readings was used:

$$\text{APE} = 100\% \times \frac{1}{R} \times \sum_{i=1}^{R} \frac{|X_{ij} - \overline{X}_j|}{\overline{X}_j}$$

where *N* is the number of samples; *R* is the number of age determinations for the sample; X_{ij} is the estimated age; and $\overline{X}_j$ is the average of estimations.
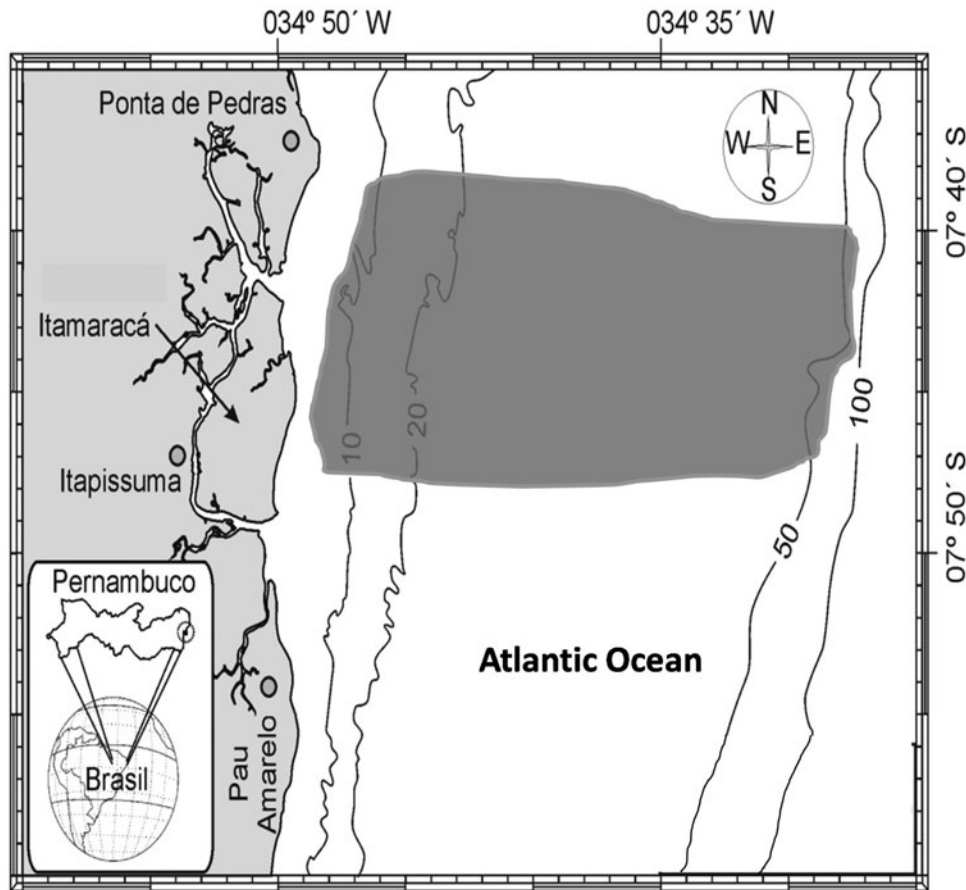
Fig. 1. Location of the the area (shaded in dark grey) of collection of Agassiz's parrotfish *S. frondosum* in north-eastern Brazil from 2009 to 2010.

The periodicity of ring deposition was inferred through Cadvallader's (1978) equation. Statistical differences in monthly marginal increment ratios (MIR) were tested using the non-parametric Kruskal–Wallis test, and the *post-hoc* Dunn's test was employed to examine the differences among individual months ($\alpha = 0.05$) (Zar, 1999):

$$\mathrm{MIR} = \frac{RO - R_n}{R_n - R_{n-1}}$$

where RO is the distance from the core to the otolith edge; R_n is the distance from the core to the last ring; and R_{n-1} is the distance from the core to the penultimate ring.

The relationship between the length of the otolith and individual fish length was examined through linear regression and ANCOVA ($\alpha = 0.05$) was used for examining statistical differences between regression lines by sex. Distances from the otolith core to each ring were back-calculated through the Monastyrsky formula:

$$L_i = \left(\frac{S_i}{S_c}\right)^b \times L_c$$

where L_i is the back-calculated length at the moment of ring deposition; L_c is the length at capture; S_i is the distance between the core to each ring; S_c is the otolith radius; and b is the slope of regression between otolith radius and L_c.

The VBGF (von Bertalanffy, 1938) and Gompertz (1825) models were adjusted to total length *vs* age data. Parameters were estimated through the SOLVER routine of the Excel program, using the least squares method: VBGF: $L_t = L_\infty \times [1 - e^{-k \times (t - t_o)}]$ and Gompertz: $L_t = L_\infty \times e^{[-a \times e^{(-k \times t)}]}$, where L_t is length at age t; L_∞ is the asymptotic length; k is the growth coefficient; t_o is the theoretical age for L_t zero; and a is a parameter of the equation.

Then, the Akaike's information criterion AIC $= 2\log(\theta) - 2k$ (Akaike, 1974), differences in *AIC* values (Δ_i) and the weight of evidence (w_i) (Burnham & Anderson, 2002) in favour of each model were computed to select the most suitable: $Log(\theta)$ being the maximal likelihood; and k being the number of parameters of the model.

The maximum longevity achieved was estimated from the size-at-age distribution (Choat *et al.*, 2003). Moreover, the age at first maturity was estimated through the inverted VBGF:

$$t_m = t_o - \left[\left(\frac{1}{K}\right) \times \left(1 - \frac{L_m}{L_\infty}\right)\right]$$

Using the inverted von Bertalanffy growth function on individual total length, the catch curve (King, 1995) was used for estimating the total mortality rate (Z). The Hewitt & Hoenig (2005) equation was used for estimating natural mortalities (M) for male, female and both sexes.

$$M = \frac{4.22}{t_{\max}}$$

Table 1. General histological description of the maturity stages of the functional males and females of *Sparisoma frondosum* from north-eastern Brazil.

Stage	Description
♂	
Primary juvenile	Germinal epithelium with scattered spermatocysts; presence of synchronous developing germ cells
Primary adult – mature	Lobules filled with sperm
Primary adult – spent	Peripheral sperm sinuses both partial or totally empty
Secondary juvenile	Presence of ovarian lumen; prevalence of germinal epithelium with developing germ cells
Secondary adult – mature	Presence of ovarian lumen; lobules filled with sperm
Secondary adult – spent	Presence of ovarian lumen with no signs of occlusion; peripheral sperm sinuses both partial or totally empty
♀	
I (immature)	Prevalence of unyolked and initial perionuclear oocytes, with basophilic cytoplasm; and presence of oogonia
II (maturing)	Prevalence of advanced perinucleolar oocytes, with cortical alveoli and small oil droplets (lipidic vitellogenesis)
III (mature)	Presence of advanced perinucleolar and vitellogenic oocytes, with eosinophilic protein granules
IV (hydrated)	Presence of migrating germinal vesicle or hydrated oocytes, with yolk coalescence
V (spawned/spent)	Presence of post ovulatory follicles and possible co-occurrence of atresic oocytes

Throughout the text all statistical inferences were made at a significance level of 0.05.

RESULTS

Population structure: size, sex and size at first maturity

From the 251 parrotfish analysed, 121 were males and 130 were females, resulting in an overall male:female sex ratio of 1:1.07, not significantly different from 1:1 ($\chi^2 = 0.256$; g.l. = 1; $P > 0.05$). Conversely, when monthly proportions were considered, significant differences were found in April ($\chi^2 = 4.263$; g.l. = 1; $P < 0.05$), with significantly more females being captured (Figure 2A).

Males of 17.5 to 36.6 cm (mode 27–31 cm) and females of 13.1 to 36.8 cm (mode 25–31 cm) were captured (Figure 2B). Mean length of males in the sample was 27.7 ± 3.1 cm TL, whereas mean length of females was slightly smaller (25.8 cm ± 2.3 cm TL), thus there was no significant difference between sexes (Mann–Whitney U-test = 0.067, g.l. = 248, $P > 0.05$).

However, the ratio between males and females did differ significantly among length classes. In length class 23–25 cm TL females were more numerous than males (67.6% females) ($\chi^2 = 4.000$, g.l. = 1, $P < 0.05$) (Figure 2B), whereas length class 33–35 cm TL was dominated by males (78.6% of examined
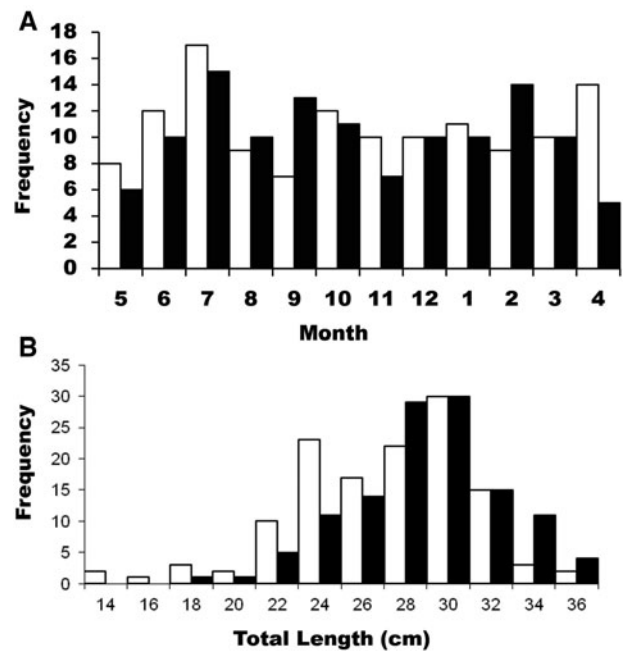
Fig. 2. Monthly frequency of males and females (A) and length frequency distribution (B) of males (black columns) and females (white columns) of the parrotfish *S. frondosum* caught in north-eastern Brazil (Pernambuco) from 2009 to 2010.

individuals). The stages of development of germ cells in ovaries were assigned as shown in Table 1.

Secondary males were observed; both mature and spent (Figure 3A, B). The gonadal morphology was similar, presenting the ovarian lumen and a lamellar organization with peripheral sperm sinuses, but in the spent secondary males the peripheral region presented residual sperm (Figure 3).

The estimated size at first maturity (L_m) was 17.6 cm (SE = 3.6 cm) for females (Figure 4). For males it was not possible to determine the size at first maturity due to the absence of immature individuals in the overall sample. However, the smallest mature males were found in size class 17.0–18.0 cm (TL).

Age, growth and age composition of samples

A total of 251 otoliths had the ventral region inspected along an axis drawn from the nucleus to the edge of the structure. Alternate opaque and translucent zones considered as growth rings were counted and measured (Figure 5). In the whole sample 1 to 9 rings were recorded in individuals from 13.1 to 36.8 cm TL. The percentage of error among readings ranged from 0 to 3.3%, with an overall sample average of 1.1%.

The mean relative marginal increment was lowest in January (Figure 6), suggesting that the otolith growth ring is laid down during this month. The Kruskal–Wallis test showed significant differences ($H = 10.512$; g.l. = 11; $P < 0.05$) among monthly median values that were caused by January and May.

The relationship between otolith radius and individual fish length (TL) was not significantly different between the sexes (ANCOVA; $P > 0.05$); it was represented by the potential regression $TL = 8.390 \, RO^{1.0801}$ (N = 178, $r^2 = 0.7293$, SE = 0.16) for both sexes combined.
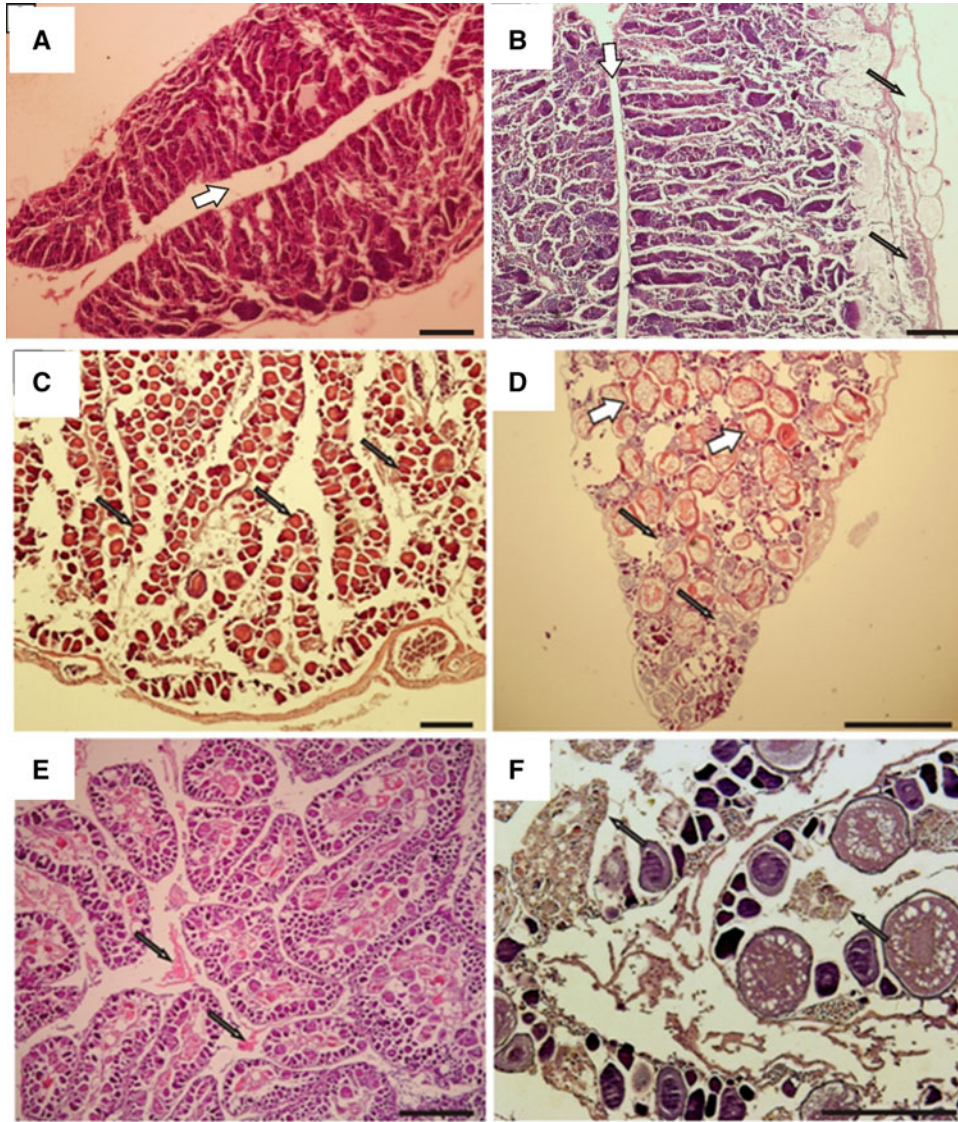
Fig. 3. Photomicrographs of male and female gonads of *S. frondosum*, in various reproductive stages stained with haematoxylin and eosin. (A) Transverse section of a secondary mature testis showing central lumen (white arrow); (B) Longitudinal section of a secondary spent testis showing central lumen (white arrow) and empty areas with residual spermatozoids (black arrows) in peripheral region. (C) Transverse section of functional ovary in initial development/immature stage showing initial perinucleolar oocytes (arrows); (D) Mature stage of functional ovary, showing cells in lipid vitellogenic phase (black arrows), with prevalence of vitellogenic oocytes (white arrows); € Hydrated, with residuals of hydrated oocytes (arrows); (F) Spent ovary showing atresic oocytes (arrows). Scale bars: 200 μm (A, B, C, D), 400 μm (E, F).
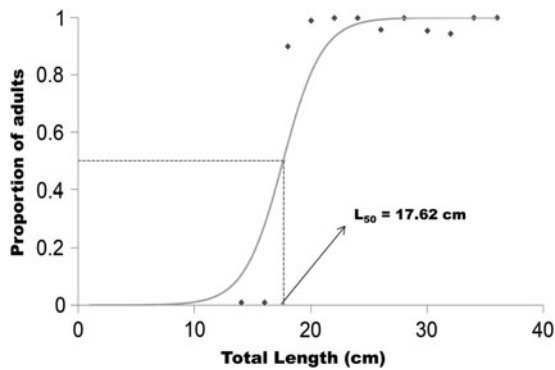
Fig. 4. Relationship between the proportion of adults and total length of females of *S. frondosum* caught in north-eastern Brazil (Pernambuco) from 2009 to 2010.
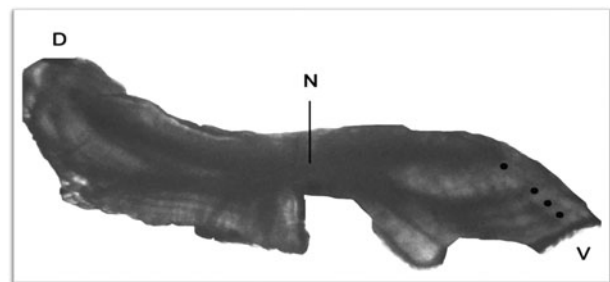
Fig. 5. Transverse section of an otolith of a 26 cm TL female of *Sparisoma frondosum*, caught in north-eastern Brazil from 2009 to 2010 under transmitted light showing four rings (black dots). D: dorsal edge, N: nucleus, V: ventral edge.
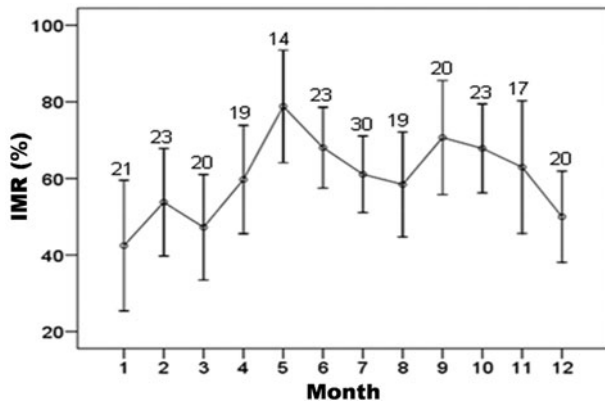
Fig. 6. Monthly relative marginal increment (IMR) of otoliths of *S. frondosum* caught in Pernambuco, Brasil. Vertical bars are mean values with standard deviations and numbers are the sample size per month.

Mean length at observed and back-calculated ages were similar (Table 2). However, the lowest value for the sum of squares of residuals was obtained for mean observed lengths (OL), therefore, whenever age is mentioned hereafter, we refer to OL.

Growth parameters were estimated adjusting the von Bertalanffy and Gompertz models on the basis of relative observed ages (Table 3; Figure 7). Slightly lower *AIC* and higher w_i values were obtained for the von Bertalanffy model, that was chosen for describing growth for this species (Table 3).

Growth curves for separate sexes of *S. frondosum* were different according to the likelihood test ($\chi^2 = 73.46$, $P > 0.05$), so the parameters of VBGF for each sex separately indicated that both males ($L_\infty = 39.7$ cm TL, $K = 0.22$, $t_0 = -1.63$ years) and females ($L_\infty = 32.3$ TL cm, $K = 0.44$; $t_0 = -0.23$ years) display rapid growth in the early years of life, reaching about 50% of their maximum length (L_∞) at 2 years of age (Figure 7A). At 5 years of age, 75% of the maximum length was attained after which growth slows considerably.

Parameters of VBGF estimated for combined sexes were: $L_\infty = 33.6$ cm TL, $K = 0.41$ and $t_0 = -0.27$ years (SE = 0.15) (Figure 7B). Age composition for the overall sample (N = 251) (Figure 8) showed that 55% of individuals were 3 and 4 years of age, the maximal age being 9 years. Females were present in all age classes from 1 to 9 years whereas males occurred in age classes from 2 to 7 years only. Mature females represented 45% of catches, since the age at first maturity was 1.6 years (17.6 cm TL), estimated on the basis of the inverted VBGF. A female from the age class 8–9 was the oldest specimen in the whole sample whereas the oldest male was estimated to be 7–8 years of age (Figure 8).

The natural mortality estimated using the Hewitt & Hoenig's equation for *S. frondosum* resulted in $M = 0.469$, whereas total mortality was $Z = 0.739$, estimated through the catch curve.

DISCUSSION

The *Sparisoma* species follow two patterns of sexuality, gonochorists or diandric protogynous hermaphrodites (Robertson *et al.*, 2006; Sadovy de Mitcheson & Liu, 2008), and this information is important to properly investigate how sexes are allocated throughout the range of sizes. An example of this is the current study, where sexes were microscopically assigned.

Corroborating with Robertson & Warner (1978), who only found secondary males in samples, in the current study PM weren't detected in the whole sample (although smaller females starting at 13 cm TL were collected), suggesting that males were derived from females (Reinboth, 1967; Alonso-Fernández *et al.*, 2011).

Furthermore, features observed in *S. radians* and *S. chrysopterum* (Robertson & Warner, 1978; Robertson *et al.*, 2006) were also found in *S. frondosum*, such as similarity of sex-ratios (with females prevailing by only 3.5%, not significantly different), females as large as males and females barely attaining identical maximal sizes. Therefore, considering that *S. frondosum* follows the same diandric protogynous hermaphroditism as the species above, the smallest individuals in the sample were a 13.1 cm TL female and a male of 17.5 cm TL. The latter also exhibited characteristics of a secondary mature male (SM), supposedly having changed sex at an undetermined smaller class, since only females were smaller than 17 cm. Results by Sadovy de Mitcheson & Liu (2008) on *S. aurofrenatum*, suggest that the lack of gonads undergoing sexual transition in *S. frondosum* – a feature considered the strongest evidence of sex change in fishes – requires further investigation.

Table 2. Mean observed (obs) and back-calculated (BC) lengths for age class, for sexes combined of *S. frondosum*, caught in north-eastern Brazil (Pernambuco) from 2009 to 2010.

t	n	1	2	3	4	5	6	7	8	9
1	1	10.97								
2	19	15.90	19.18							
3	58	16.91	20.87	23.66						
4	82	17.69	21.93	24.72	26.68					
5	45	18.35	22.21	24.98	27.18	28.62				
6	30	18.38	22.65	25.78	28.23	30.09	31.27			
7	13	16.51	20.21	23.13	25.66	27.57	29.06	30.35		
8	1	17.12	21.29	24.35	27.24	29.30	31.30	33.24	33.87	
9	2	16.14	20.48	23.45	26.10	27.75	29.85	31.04	32.22	31.90
Mean BC		16.44	21.10	24.30	26.85	28.67	30.37	31.54	33.04	31.90
SD		2.23	1.15	0.94	0.91	1.06	1.11	1.51	1.17	–
Mean obs		13.1	20.9	25.0	27.9	30.2	31.8	30.9	33.7	34.5
SD		–	3.39	2.34	2.38	1.79	2.51	2.85	–	1.80

SD = standard deviation, *n* = number of individuals.

Fig. 8. Age distribution of males (black columns) and females (white columns) of *S. frondosum*, caught in north-eastern Brazil (Pernambuco) from 2009 to 2010.
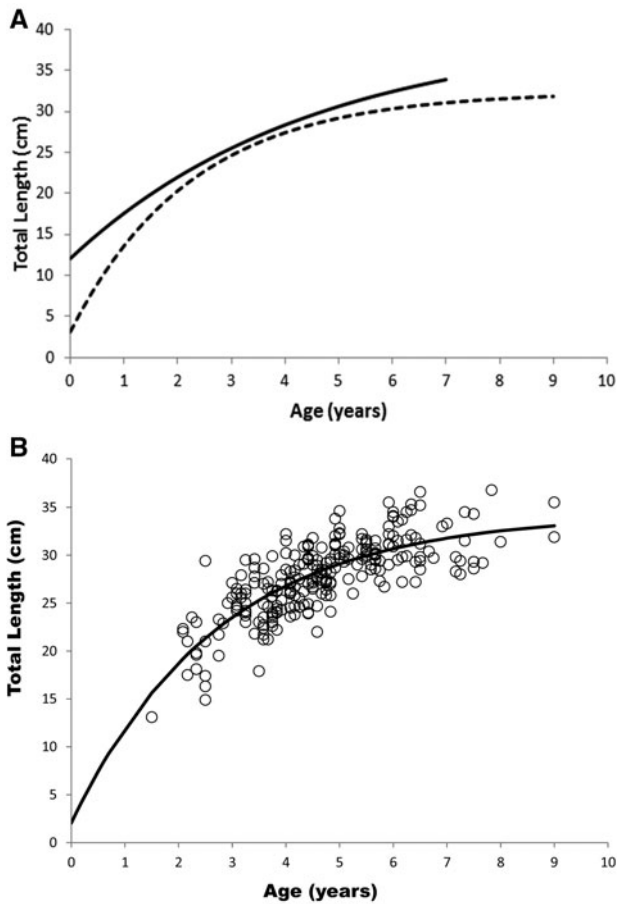
Fig. 7. Growth curve estimated using the von Bertalanffy model (VBGF) for males (solid line) and females (dashed line), separate (A) and combined sexes (B) for *S. frondosum* caught in north-eastern Brazil (Pernambuco) from 2009 to 2010.

17 cm (SL) off the coast of Pernambuco (Véras, 2008). Thus, 17 cm TL was assumed as a speculative first maturity size for males.

In the present study sagittal otoliths of *S. frondosum* were sectioned with the objective of obtaining more accurate estimates, a requirement especially important for older fish (Crabtree *et al.*, 1996) – which are more prone to the stacking of rings on the otolith edge (Lou, 1992). It is essential to know the periodicity of increments for the accuracy of age estimates. Growth rings were clearly observed along the reading axis of otoliths with annual periodicity inferred through marginal increment analyses, as was also shown for *S. viride* in the Caribbean (Choat *et al.*, 2003). In addition, the average percentage error (*APE*) indicated that errors of readings were within the recommended limits (Campana, 2001), meaning that otoliths are suitable for age estimations and readings can be repeated.

The lowest value of the marginal increment in January (summer) was due to the deposition of the translucent ring with the new band forming from that month onwards. It may be related to the reproductive period, as suggested for species of this family which have peaks of spawning in summer (Jonna, 2003; Kume *et al.* 2010), when the greatest reproductive activity occurs and most of the energy of the body is assigned to reproduction (spawning period), not to somatic growth (Takada & Tachihara, 2009).

Overall, ages ranged from 2 to 7 years in males and from 1 to 9 years in females, with maturity of females being 1.6 years of age. The maximal age for *S. frondosum* corroborates with Choat *et al.* (2003) for *S. viride* in four populations of the Caribbean. Such a result may be an attempt by the fish to maximize reproductive success, where some females do not

With respect to size at maturity, females in the overall sample were either clearly immature (under 17 cm TL) or fully mature in classes larger than 17 cm TL. Hence, the expected gradual increase of the percentage of mature individuals, with the increase of body size, was not perceived. The allocation of mature females throughout the range of sizes may have caused biases in the estimate. Still, in females of the largest fully mature sizes, the sex inversion is likely to result from a socially determined process driven by a decrease in the number of males, for instance, due to fisheries (Pauly *et al.*, 1998). The absence of males smaller than 17 cm TL (although females were recorded starting at 13 cm TL), hampered the estimation of the size of maturity for males, which in another study using a different approach was suggested at
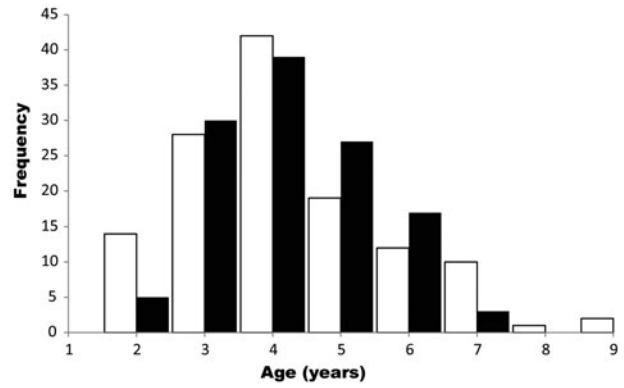
Table 3. Growth parameters estimated for separate and combined sexes adjusting the von Bertalanffy (VB) and Gompertz (G) models to observed lengths for *S. frondosum* from north-eastern Brazil (Pernambuco) caught from 2009 to 2010.

Sexes	Model	L_∞(cm)	K	t_o(years)	a	AIC	Δ_i	w_i
Males	VB	39.7	0.22	−1.63	–	91.20	0.00	50.2
	G	37.8	−0.31	–	1.00	91.22	0.02	49.8
Females	VB	32.3	0.44	−0.23	–	102.66	0.00	68.0
	G	31.9	−0.55	–	1.36	104.17	1.51	32.0
Combined	VB	33.6	0.41	−0.27	–	204.79	0.00	50.2
	G	33.0	−0.52	–	1.34	204.81	0.02	49.8

change sex, aiming to achieve higher fertility in larger classes when compared with other females of her social group. Thus, the postponement of sex reversal could be deemed as an advantage for the population (Muñoz & Warner, 2003; Hixon *et al.*, 2014).

The Akaike information criterion (*AIC*) has parsimony as its tenet, which implies that models with a smaller number of parameters are the most appropriate, expressing a satisfactory balance between bias and variance (Burnham & Anderson, 2002). Thus, even if the lowest *AIC* value and the highest w_i were estimated for the VBGF, the Gompertz model also had a performance that adequately described the growth of this parrotfish. However, the VBGF was chosen because it has described the growth of similar species, having a stronger biological basis and allowing parameters to be used in stock assessments (Campana, 2001).

Considering the reliability of the parameters of VBGF regarding the L_∞, observed lengths provided a result that was closer to the maximal recorded length for the species ($L_{max} = 36.8$ cm TL), thus it was chosen as the most accurate for the growth curves of *S. frondosum*. The L_∞ for both sexes combined conforms to this upper limit of maximal size in the sample, whereas the lower limit agrees with the maximal sizes recorded in other places of the species' distribution range (Vaske *et al.*, 2006). The overall rapid growth in the early years of life, reaching about 50% of their maximum length (L_∞) at 2 years of age, complies with findings for other *Sparisoma* species of the Caribbean (Choat & Robertson, 2002; Choat *et al.*, 2003).

The *S. frondosum* species is referred to as a sister species of *S. chrysopterum*, from the Caribbean (Moura *et al.*, 2001), which may suggest similar growth parameters (Choat & Robertson, 2002). However, higher longevity (t_{max}) and faster growth (*K*) were estimated for *S. frondosum*, revealing different growth patterns. Moreover, the largest specimen of *S. frondosum* ever recorded was a 34.5 cm SL (Moura *et al.*, 2001) (~38 cm TL), which corresponds with the largest size in the current study. Also, the L_∞ estimated for females and both sexes combined are compatible with the largest sizes for the species. Finally, the L_∞ estimated for males exceeded the largest size in the sample by about 5% being quite acceptable according to Campana's criterion (2001). Overall, the VBGF for combined sexes (Figure 7B) provided a *K* parameter compatible with the values estimated for the *Sparisoma* species from the Caribbean as shown by Choat *et al.* (2003).

In the current study natural mortality >0.45 was estimated, which together with the index of intrinsic vulnerability to fisheries (estimated for *S. cretensis* – 48 in a rank ranging from 10 to 88) (Cheung *et al.* 2005) suggests that *S. frondosum* deserves attention to keep the population stable. However, according to Petersen & Warner (2002) the protogynous hermaphroditism, which has not yet been completely ascertained in *S. frondosum*, may be a strategy that increases resiliency to fishing depletion when stocks are submitted to moderate fishing pressure, as seems to be the case in the study area.

In spite of that, in Brazil several species of the *Sparisoma* genus (including *S. frondosum*) were classified as vulnerable (VU) using the IUCN criteria (Brazil, Ordinance 445 of 17.12.2014), which demands the adoption of conservation measures, such as reduction of fishing efforts, among others (not necessarily related to fisheries). In this context, information on gonad maturation, growth rates, age structure and longevity is important for the assessment of the state of exploitation of this parrotfish in years to come.

REFERENCES

Akaike H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716–723.

Alonso-Fernández A., Alós J., Gran A., Domingues-Petit R. and Saborido-Rey F. (2011) The use of histological techniques to study the reproductive biology of the hermaphroditic Mediterranean fishes *Coris julis*, *Serranus scriba* and *Diplodus annularis*. Special Section: Fisheries Reproductive Biology. *Marine and Coastal Fisheries: Management and Ecosystem Science, American Fisheries Society* 3, 145–159.

Bannerot S.P. (1984) *The Dynamics of Exploited Groupers (Serranidae): an investigation of the Protogynous Hermaphroditic Reproductive Strategy.* PhD dissertation, University of Miami, FL.

Beamish R.J. and Fournier D.A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 982–983.

Brazil, Ministério do Meio Ambiente. Portarias No. 445, de 17 de Dezembro de 2014, Diário Oficial da União–Seção 1, 245, 110 (18 December 2014); http://pesquisa.in.gov.br/imprensa/jsp/visualiza/index.jsp?data=18/12/2014&jornal.

Burnham K.P. and Anderson D.R. (2002) *Model selection and multimodel inference. A practical information – theoretical approach*, 2nd edn. New York, NY: Springer.

Cadvallader P.L. (1978) Age, growth and condition of common river galaxias, *Galaxias vulgaris* Stolkell, in the Glentni river, Canterbury, New Zealand. *Fishery Research Bulletin* 17, 15–20.

Campana S.E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59, 197–242.

Cheung W.W.L., Pitcher T.J. and Pauly D. (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* 124, 97–111.

Choat J.H. and Robertson D.R. (2002) Age-based studies. In Sale P.F. (ed.) *Coral reef fishes. Dynamics and diversity in a complex ecosystem.* New York, NY: Academic Press, pp. 57–80.

Choat J.H., Robertson D.R., Ackerman J.L. and Posada J.M. (2003) An age-based demographic analysis of the Caribbean spotlight parrotfish *Sparisoma viridae*. *Marine Ecology Progress Series* 246, 265–277.

Collins A.B. and McBride R.S. (2011) Demographics by depth: spatially explicit life-history dynamics of a protogynous reef fish. *Fishery Bulletin* 109, 232–242.

Crabtree R.E., Harnden C.W., Snodgrass D. and Stevens C. (1996) Age, growth, and mortality of bonefishes, *Albula vulpes*, from the waters of the Florida Keys. *Fishery Bulletin* 94, 442–451.

Francis R.C. (1992) Sexual lability in teleosts: developmental factors. *Quarterly Review of Biology*, 67, 1–17.

Freitas R., Osmar J.L., Silva P.N., Floeter S.R., Bernardi G. and Ferreira C.E.L. (2014) The occurrence of *Sparisoma frondosum* (Teleostei: Labridae) in the Cape Verde Archipelago with a summary of expatriated Brazilian endemic reef fishes. *Marine Biodiversity* 44, 173–179.

Gompertz B. (1825) On the nature of the function expressive of the law of human mortality and on a new method of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London* 115, 513–585.

Hastings P.A. (1981) Gonad morphology and sex succession in the protogynous hermaphrodite *Hemanthias vivanus* (Jordan and Swain). *Journal of Fish Biology* 18, 443–454.

Hewitt D.A. and Hoenig J.M. (2005) Comparison of two approaches for estimating natural mortality based on longevity. *Fishery Bulletin* 103, 433–437.

Hixon M.A., Johnson D.W. and Sogard S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71, 2171–2185.

IBAMA (2005) Boletim estatístico da pesca marítima e estuarina do Nordeste do Brasil- 2004. *ESTATPESCA/Centro de Pesquisa e Gestão de Recursos Pesqueiros do Litoral Nordeste Tamandaré, PE: CEPENE*, 152 pp.

Jonna R. (2003) "Scaridae" Animal Diversity Web. Available at http://animaldiversity.ummz.umich.edu/site/accounts/information/Scaridae.html (last accessed 4 May 2013).

King M. (1995) *Fisheries biology, assessment and management.* Oxford: Blackwell Science.

Kume G., Kubo Y., Yoshimura T., Kiriyama T. and Yamaguchi A. (2010) Life history characteristics of the protogynous parrotfish *Calotomus japonicus* from northwest Kyushu, Japan. *Ichthyological Research* 57, 113–120.

Lessa R. and Araújo B.M. (2009) Resultados: Séries históricas. In Lessa R., Bezerra J.L. Jr and Nóbrega M.F. (eds) *Dinâmica das frotas pesqueiras da Região Nordeste do Brasil.* Fortaleza, Brazil: Martins & Cordeito LTDA, pp. 35–58.

Longhurst A.R. and Pauly D.E. (1987) *Ecology of tropical oceans.* San Diego, CA: Academic Press.

Lou D.C. (1992) Validation of annual growth bands in the otolith of tropical parrotfishes (*Scarus schlegeli* Bleeker). *Journal of Fish Biology* 41, 775–790.

Moura R.L., Figueiredo J.L. and Sazima I. (2001) A new parrotfish (Scaridae) from Brazil, and revalidation of *Sparisoma amplum* (Ranzani, 1842), *Sparisoma frondosum* (Agassiz, 1831), *Sparisoma axillare* (Steindachner, 1878) and *Scarus trispinosus* (Valenciennes, 1840). *Bulletin of Marine Science* 68, 505–524.

Muñoz R.C. and Warner R.R. (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size–fecundity skew. *American Naturalist* 161, 749–761.

Nelson J.S. (2006) *Fishes of the world*, 4th edn. New York, NY: John Wiley and Sons.

Padovani-Ferreira B., Rocha L.A., Ferreira C.E., Francini-Filho R., Moura R., Gaspar A.L., Feitosa C., Choat J.H., Myers R. and Russell B. (2012) *Sparisoma frondosum.* The IUCN Red List of Threatened Species. Version 2014.2. Available at www.iucnredlist.org (last accessed 27 July 2014).

Panfili J., de Pontual H., Troadec H. and Wright P.J. (2002) *Manual of fish sclerochronology.* Brest: IFREMER-IRD Coedition.

Pauly D., Christensen V., Dalsgaard J., Froese R. and Torres F. Jr (1998) Fishing down marine food webs. *Science* 279, 860–863.

Petersen C.W. and Warner R.R. (2002) The ecological context of reproductive behavior. In Sale P.F. (ed.) *Coral reef fishes: dynamics and diversity in a complex ecosystem.* New York, NY: Academic Press, pp. 103–118.

Reinboth R. (1967) Diandric Teleost species. *General and Comparative Endocrinology* 9, abstract 146.

Ribeiro F.P. (2004) Composição da biocenose e abundância relativa de peixes capturados com covos nos Estados do Rio Grande do Norte e Pernambuco (BRASIL). *Boletim Técnico Científico do CEPENE* 12, 115–128.

Robertson D.R. and Warner R.R. (1978) Sexual patterns in the labroid fishes of the western Caribbean. II. The parrotfishes (Scaridae). *Smithsonian Contributions to Zoology* 255, 1–26.

Robertson R.D., Karg F., Moura R.L., De Victor B.V. and Bernardi G. (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular Phylogenetics and Evolution* 40, 795–807.

Sadovy de Mitcheson Y. and Liu M. (2008) Functional hermaphroditism in teleosts. *Fish and Fisheries* 9, 1–43.

Sadovy Y. and Colin P.L. (1995) Sexual development and sexuality in the Nassau grouper. *Journal of Fish Biology* 46, 961–976.

Sadovy Y. and Shapiro D.Y. (1987) Criteria for the diagnoses of hermaphroditism in fishes. *Copeia* 1987, 136–156.

Shapiro D.Y. (1987) Differentiation and evolution of sex change in fishes: a coral reef fish's social environment can control its sex. *BioScience* 37, 490–497.

Shapiro D.Y., Sadovy Y. and McGehee M.A. (1993) Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bulletin of Marine Science* 53, 1151–1162.

Sparre P. and Venema S.C. (1997) *Introdução à avaliação de mananciais de peixes tropicais.* Rome: FAO Documento técnico sobre as pescas, No. 306/1.

Takada M. and Tachihara K. (2009) Comparisons of age, growth, and maturity between male and female, and diploid and triploid individuals in *Carassius auratus* from Okinawa-jima Island, Japan. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19, 806–814.

Taylor B.M. (2014) Drivers of protogynous sex change differ across spatial scales. *Proceedings of the Royal Society B* 281: 20132423. http://dx.doi.org/10.1098/rspb.2013.2423.

Vaske T. Jr, Lessa R.P.T., Ribeiro A.C.B., de Nóbrega M.F., Pereira A. de A. and de. Andrade C.D.P. (2006) A pesca comercial de peixes pelágicos no Arquipélago de São Pedro e São Paulo, Brasil. *Tropical Oceanography* 34, 31–41.

Véras D.P. (2008) *Biologia reprodutiva dos budiões-batata*, Sparisoma axillare *e* Sparisoma frondosum *(Actinopterygii: Scaridae), capturados na costa central do estado de Pernambuco.* MSc dissertation. Universidade Federal Rural de Pernambuco, Recife, Brazil.

von Bertalanffy L. (1938) A quantitative theory of organic growth (inquiries on growth laws). *Human Biology* 10, 181–213.

Warner R.R. (1984) Mating behaviour and hermaphroditism in coral reef fishes: the diverse forms of sexuality found among tropical marine fishes can be viewed as adaptations to their equally diverse mating systems. *American Scientist* 72, 128–136.

Westneat M.W. & Alfaro M.E. (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Molecular Phylogenetics and Evolution* 36, 370–390.

and

Zar J.H. (1999) *Biostatistical analysis*, 4th edn. Upper Saddle River, NJ: Prentice Hall.

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