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Age, growth, and reproductive biology of the Atlantic spadefish *Chaetodipterus faber* in southern Brazil

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Abstract

This is the first study to investigate the age, growth and reproductive biology of the Atlantic spadefish *Chaetodipterus faber* in southern Brazil. A total of 625 individuals [total length (TL) ranging from 7 mm to 510 mm] were sampled at the Paranaguá Estuarine Complex (PEC) and adjacent coastal areas over a year (August 2015 to July 2016). Age estimation based on sagittal otolith cross section showed that *C. faber* has a 17-year longevity close to its southern distributional limit, two times greater than previously reported from the North Atlantic Ocean. Sexual growth dimorphism was not evident as the male:female sex ratio was 1:1.17. The species displayed asymptotic growth. Fitted von Bertalanffy growth function estimates for all individuals were $L_\infty = 508.81$ mm, $k = 0.22$ year^{-1}, and $t_0 = -0.05$ year. The histological gonadal examination and gonado-somatic index indicated that *C. faber* is a batch spawner with a main reproduction period from October to January in subtropical latitudes at 25°S. Postovulatory follicles were often recorded in the ovaries of spawning capable individuals indicating a high frequency of spawns over the reproductive period. The data also suggest that estuaries are important reproductive areas for this species that most likely exhibits a seasonal movement for spawning aggregation purposes. Females mature approximately 0.5 years later than males and are capable of spawning just prior to two years old. Fishery closures during the spawning season and fishing size restrictions should be used to manage the *C. faber* stock in southern Brazil. The effects of current harvest levels are unknown and warrant further investigation to assist management decisions.

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Introduction

The Ephippidae family comprises eight genera and 15 species distributed in coastal environments of the subtropical and tropical regions of the Indian, Pacific and Atlantic Oceans (Nelson 2006; Eschmeyer and Fong 2018). The only species that occurs along the western Atlantic Ocean is the Atlantic spadefish *Chaetodipterus faber* (Broussonet 1782). The species is distributed from Massachusetts (United States) to Santa Catarina, South Brazil, encompassing the Caribbean Sea and Gulf of Mexico (Burgess 2002; Soeth et al. 2014; Machado et al. 2017). In subtropical regions of the North Atlantic Ocean *C. faber* males and females exhibit early maturation at around 1 year old (Hayse 1990). The species is a pelagic spawner (Chapman 1978; Ditty et al. 1994) that forms reproductive aggregations that have been recorded during underwater observations (Chapman 1978; Heyman and Kjerve 2008). Pelagic larvae occur primarily in coastal waters and being their transition to the juvenile stage

after 25 days when individuals reach 8.0 to 8.5 mm standard length (Ditty et al. 1994; Castro et al. 2005). Demersal early juveniles are plant mimetics (Barros et al. 2015) and common in estuarine and coastal regions (Barros et al. 2013; Soeth et al. 2014; Possato et al. 2016). Adults change to a benthopelagic behavior and are known to be a reef-associated fish, frequently observed on rocky reefs, artificial reefs and other consolidated continental shelf structures up 30 meters deep (Hayse 1990; Burgess 2002; Simon et al. 2013; Daros et al. 2012). *Chaetodipterus faber* can reach over 6 kg in total mass (IGFA 2017) with longevity of at least 8 years (Hayse 1990). The species exhibits trophic plasticity throughout their life cycle, feeding on algae, benthic epifauna and planktonic cnidarians (Hayse 1990; Barros et al. 2013). *Chaetodipterus faber* is also an important food source for top predators such as *Tursiops truncatus* (Gurjão et al. 2004), *Epinephelus itajara* (Gerhardinger et al. 2006), and *Galeocerdo cuvier* (Bornatowski et al. 2007).

The Atlantic Spadefish recreational fisheries have grown in popularity and developed into a specialized and directed fishery in the United States waters (Bell 2005). In Brazil, *C. faber* is highly targeted by recreational fisheries (Pinheiro et al. 2010) but total catch is dominated by artisanal and industrial fleets that have landed around 250 tons per year along the Brazilian coast for the past decade (IBAMA 2007; MPA 2012). The species often congregates in large schools in coastal waters (Burgess 2002), mainly in the spring and summer at subtropical latitudes, which greatly increases its potential for harvest (Bell 2005; PMAP-BS 2017a, b). However, these aggregation periods appear to coincide with the peak spawning season for *C. faber* (Hayse 1990; Castro et al. 2005), which makes the species vulnerable to demographic overexploitation (Sadovy de Mitcheson et al. 2008; Sadovy de Mitcheson and Colin 2012; Chao et al. 2015). Additionally, the decline of many fish population globally (Myers and Worm 2003) has led to a gradual transition in fishery landings from long-lived, high-trophic-level fishes toward short-lived and low-trophic-level fishes (Pauly et al. 1998). In southern Brazil, this scenario is not different. The average annual industrial landings of *C. faber* has increased by 6 times, from 36 tons in 2000 and 2011 to 240 tons from 2012 to 2017 (UNIVALI/CTTMar 2010, 2013a, b, PMAP-SC 2018). The schooling behavior makes *C. faber* particularly vulnerable to purse seine vessels, typically used in the herring and mackerel fisheries (Misund 1993; PMAP-SC 2018). Currently there is no specific legislation to prevent the use of purse seine nets to target *C. faber* aggregations.

Fish life-history traits, including growth, maturity, and reproduction, are extremely diverse and species specific (Pauly 1980; Vazzoler 1996); understanding these traits is integral to the successful fishery management and conservation of exploited fishes (Harry et al. 2013; van Overzee and Rijnsdorp 2014; Aschenbrenner et al. 2017). For instance,

information about size at maturity and the timing of reproductive events can be used as biological reference points for management decisions on size limits and periodic fishery closures during spawning seasons (Yamahira 2004; Lowerre-barbieri 2009; van Overzee and Rijnsdorp 2014). In addition, length and age composition data are essential to the estimation of biological parameters including growth rates and natural mortality, which are fundamental to modelling population and biomass dynamics (Pauly 1980; Wartenberg et al. 2013; He et al. 2016; Aschenbrenner et al. 2017). However, biological and ecological information regarding population structure, feeding regimes and migratory behavior for *C. faber* in the SW Atlantic is scarce (Barros et al. 2013, 2015; Machado et al. 2017). Estimates of key life-history parameters are unknown for this region.

The objective of this study was to provide life-history information critical to the successful management of the *C. faber* stock in southern Brazil. The aims of this study were to (1) estimate individual fish ages based on sagittal otolith cross sections, (2) model population growth, (3) determine size frequency distributions and sex compositions, (4) determine reproductive cycles using histological analysis of gonads and the gonado-somatic index, and (5) estimate the size- and age-at-maturity for *C. faber* males and females.

Materials and methods

Study area and biological sampling. Fish sampling took place monthly between August 2015 and July 2016 at the Paranaguá Estuarine Complex (PEC) (25°30'S, 48°25'W) and adjacent coastal areas of the Paraná state, southern Brazil (Fig. 1). The PEC is characterized by a range of habitats including mangrove forests, tidal flats, tidal creeks, rivers, estuarine beaches, rocky reefs, and deep channels (Lana et al. 2001). The adjacent inner shelf is dominated by sandy bottom (> 99 %) and includes scattered rocky reefs, artificial reefs and islands (Veiga et al. 2004; Brandini 2014). The study area has a humid subtropical climate with an annual average rainfall of 2,500 mm (Lana et al. 2001), wet summers and dry winters, and subsurface water temperature varying from 18 °C to 28 °C (Soeth et al. 2015).

A total of 625 individuals were sampled (Table 1) using multiple gear types to provide a representative sample across size and age groups. About 50 % of the total (i.e., 307 individuals) were sampled by spearfishing that required approximately 10 hours per month of freediving effort on rocky reefs, artificial reefs and in marinas or around anchored ships in the study area. Additionally, seine nets were used in tidal estuarine beaches of the PEC; bimonthly from August 2015 to June 2016 with a 70 m x 2 m seine net and stretched mesh size of 2 cm (4.16 % of individuals); and monthly from January to July of 2016 with 15 m x 2 m seine net and stretched

Fig. 1 Sampling location of *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex (PEC) and adjacent coastal areas from August 2015 to July 2016 by spearfishing (black circles), seine nets (white squares) and acquisition from local fishermen (gray triangles)
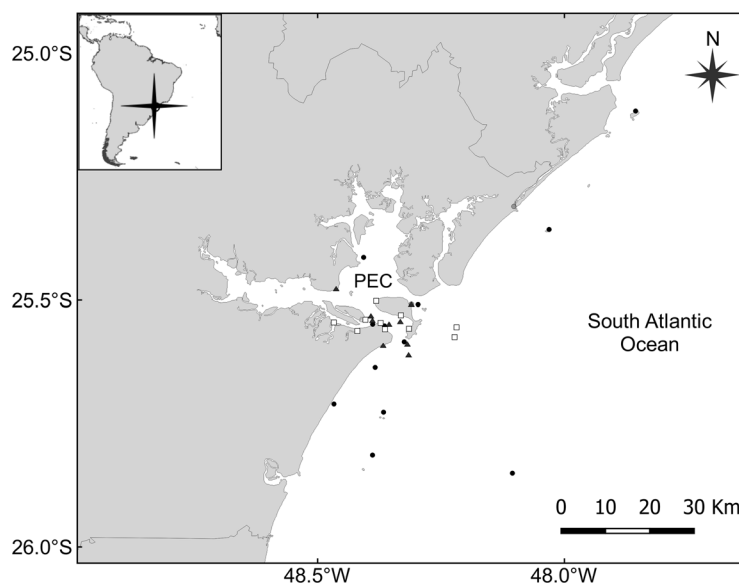

Table 1 Sample size (n), mean, minimum (Min) and maximum (Max) total length (millimeters) and sex ratio (males:females, M:F) by month for *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex and adjacent coastal areas from August 2015 to July 2016

Date		*n*	Mean	Min	Max	M:F
2015	August	54	181	134	510	1:0.82
	September	54	167	96	323	1:1.17
	October	30	288	73	508	1:1.42
	November	37	286	146	486	1:0.85
	December	104	306	84	493	1:1.46*
2016	January	63	174	20	479	1:1.06
	February	42	212	24	473	1:1.06
	March	71	161	7	380	1:1.20*
	April	37	179	18	445	1:1.17
	May	56	83	12	297	1:1.29
	June	43	145	24	400	1:1
	July	34	148	31	348	1:1.50

Superscript * indicates significant differences ($\chi^2 < 3.840$, $d.f. = 1$, $P < 0.05$) observed by χ^2 test

mesh size of 2 mm (16.29 % of individuals). Finally, remaining samples were obtained from local fishermen that used trammel and gill nets with stretched mesh sizes ranging from 90 mm to 250 mm (26.43 % of individuals) or demersal penaeid trawls (4 % of individuals).

Upon collection, fish were immediately preserved on ice and transported back to the laboratory for processing. All fish were measured for total length (TL, 1 mm), weighed (0.01 g) for total fish mass (TM), gonad mass (GM), and gutted fish mass (GFM). Sagittal otoliths were removed, cleaned of adherent tissues and stored dry in labeled Eppendorf tubes. The gonads were initially evaluated macroscopically for sex determination and development stages, which were later confirmed by routine histological analysis (see Reproductive biology section).

Sex ratio and mass-length relationship. Sex ratio was calculated by month and for each 50 mm TL size class according to Sturges rules (Sokal and Rolf 1981). Significant monthly deviations from the expected 1:1 sex ratio were determined by a χ^2 test ($\chi^2 < 3.840$, $d.f. = 1$, $P < 0.05$) for each class. The sex-specific mass-length (grams-millimeters) relationship was calculated by the equation: $TM = aTL^b$ where a is the linear coefficient and b is the slope (Le Cren 1951). The r-squared (r^2) values, in conjunction with residual plots, were used to assess the how well the model fitted the dataset. The mass-length relationship of males and females were compared using analysis of covariance (ANCOVA) in R (R Core Team 2017).

Age determination and validation. Age estimation of transverse otolith cross sections was made using an established protocol for *C. faber* (Davies et al. 2015). Left otoliths were embedded in transparent epoxy resin, and were cut near the nucleus (0.5 mm) with a Buehler Isomet Low-Speed Saw. Otolith cross sections were ground along the

transverse plane to expose the core with 400, 1,200 and 2,400 silicon carbide papers and further polished with alumina paste. Thereafter thin sections were immersed in a clearing agent (alcohol:glycerin, 1:1) for 48 hours. Microphotographs were obtained using a microscope with transmitted light coupled to a 5-megapixel Opticam (OPT5000 Power) at 40x magnification.

All cross sections were blind-counted (i.e., without the knowledge of capture date and fish size) three times by one experienced reader. Repeated readings were done with a minimum fifteen-day interval. Otoliths that showed discrepancies between counts were re-aged and the final age was assigned when at least two counts agreed. To improve the age estimation, the average radius from otolith cross sections of late young-of-the-year was used to determine the expected radius (1 mm) of the first annulus (Campana et al. 2001; Natanson et al. 2002). Individual age estimates for *C. faber* were assigned based on the opaque zone counts, starting from the nucleus towards the proximal edge, taking into consideration the date of capture and the assumed birth date for this population based on the peak spawning season identified in the results (Morales-Nin and Panfili 2002; Davies et al. 2015). The average coefficient of variation index (ACV) and the average percent error (APE) were calculated to measure precision among age estimates (Beamish and Fournier 1981; Chang 1982; Ogle 2016).

Analyses of edge type (expressed as percentage of opaque or translucent otolith edge) and the relative marginal distance (RMD) were used to validate the annual growth pattern increment deposition based on Panfili and Morales-Nin (2002). The quantification of the RMD was calculated according to the formula: $RMD = MD(LA)^{-1}$, where MD was the distance that separated the last opaque band from the edge of the otolith, and LA was the width of the last complete annulus. Fish age groups 0 and 1 and older than 5 were excluded from the RMD and edge-type analyses due to the difficulty in calculating the RMD for the age 0 group, the difficulty in visualizing the first annuli for the age 1 group and the low monthly frequency of older individuals. Otoliths with poor legibility of annuli (16.5 %) were also disregarded in these analyses (Aschenbrenner et al. 2017). Otolith measurements were taken using the software ImageJ (IJ 1.46r version). A non-parametric Kruskal–Wallis one-way ANOVA, followed by pairwise comparisons using Fisher's least significant difference test, was to identify differences among monthly mean RMD (Conover 1990).

Age and growth. The age-at-length dataset contained data for males, females, and all individuals pooled. Three length-at-age models were evaluated for goodness of fit: the von Bertalanffy growth function (VBGF), the Gompertz growth model (GM), and the Logistic model (LM) (Ogle 2016). The VBGF was fitted by the equation: $L_t = L_\infty \left[1 - e^{-k(t - t_0)}\right]$,

where L_t is the TL (mm) as a function of a given age, L_∞ is the theoretical asymptotic TL mm, *k* is the growth coefficient (year^{-1}), and t_0 is the theoretical age (years) at which the length is zero. The GM was given by the function $L_t = L_\infty e\left[-e^{-gi(t - ti)}\right]$, where *gi* is the instantaneous growth rate (year^{-1}) at the inflection point and *ti* is the age (years) at the inflection point. The LM was $L_t = L_\infty[1 + gninf(t - ti)]^{-1}$, where *gninf* is the instantaneous growth rate (year^{-1}) at negative infinity. A bootstrap method with 1000 iterations was applied to estimate the 95 % confidence intervals (C.I.) of the parameters. Akaike Information Criterion (AICc) was used to assess the best-fit model based on goodness of fit and parsimony for males, females and all individuals pooled (Hurvich and Tsai 1989). The model with the smallest AICc value was selected as the best among the candidates. The AICc difference ($\Delta AICc$ or Δ_i) was computed for candidate models to evaluate relative model support. Models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 7$ and models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration (Burnham and Anderson 2002). The likelihood ratio and extra sum-of-squares tests were used to compare results between VBGF parameters for males and females (Kimura 1980; Ritz and Streibig 2008; Ogle 2016). All age and growth analyses were performed using the *Agricolae, FSA*, *nlstools*, and *AICcmodavg* packages loaded into R (R Core Team 2017).

Reproductive biology. The gonado-somatic index (GSI) was calculated according to the formula: $GSI = [GM(GFM)^{-1}]100$. The transformation $[Log(GSI + 1)]$ was unsuccessful in transforming the data to a state of normality and homogeneity of variances. Thus, non-parametric Kruskal–Wallis one-way ANOVA tests, followed by pairwise comparisons using Fisher's least significant difference, were used to compare differences among monthly GSI means for adult males and females (Conover 1990).

For microscopic determination of development stages, the gonads were fixed in ALFAC, embedded in paraffin wax and sectioned at 5-7 µm. Slides were stained with haematoxylin-eosin and analyzed under a compound light microscope (Vazzoler 1996) to assign sex and reproductive phase: immature (phase I), developing [subphase early developing (II) and late developing (III)], spawning capable (IV), actively spawning capable subphase (V), regressing (VI), and regenerating (VII) (Brown-Peterson et al. 2011). Individuals with very small gonads (< 0.001 g) were considered as indeterminate since it was impossible to identify the sex and reproductive phase. The relative frequency distribution of each reproductive phase was calculated by month and analyzed together with the GSI to confirm the spawning season.

Maturity ogives were used to estimate the length- (L_{50} and L_{95}) and age- (A_{50} and A_{95}) at-maturity as the TL and

age at which 50 % and 95 % of the males and females were mature. Maturity stages were converted to binary maturity determinations (0 = immature, 1 = mature). The following logistic regression model was used to estimate length- and age-at-maturity for males and females as $PM = PMAX[1 + e^{-\ln(19)\{(1-\beta_1)(\beta_2-\beta_1)^{-1}\}}]^{-1}$, where PM is a proportion of mature at TL or age; β_1 and β_2 are fitted parameters corresponding to L_{50} and L_{95} or A_{50} and A_{95}, respectively; PMAX is the asymptote (Harry et al. 2013). A bias-reduction generalized linear model with binomial responses and logit-link (Kosmidis 2014) was used to estimate parameters β_1 and β_2 (Harry et al. 2013). A bootstrap method with 1000 iterations was applied to estimate the 95 % C.I. The presence of cortical alveoli oocytes was considered as an indication that *C. faber* was sexually mature and would spawn during that reproductive season (Brown-Peterson 2003). Therefore, only immature individuals (phase I) were not considered adult (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). Individuals collected outside of the reproductive period, when there were higher percentages of regenerating females, were excluded from maturity determination analysis (Hunter and Macewicz 2003; Lowerre-Barbieri et al. 2011). For immature fish smaller than 45 mm TL, for which sex was indeterminate, a double entry (once as female and then again as male) was added to the dataset used to construct maturity ogives (Boulcott et al. 2007). All reproductive analyses were performed using the *Agricolae, MASS, psyphy, brglm*, and *boot* packages loaded into R software (R Core Team 2017).

Results

Sample composition, sex ratio, and mass-length relationships. From the total of 625 *Chaetodipterus faber* samples, 274 were females, 237 were males and 114 individuals were indeterminate. Female TL ranged from 68 mm to 510 mm (mean TL 245 ± SD 120 mm), male TL ranged from 41 mm to 508 mm (mean TL 224 ± SD 110 mm), and indeterminate TL ranged from 7 mm to 48 mm (mean TL 28 ± SD 10 mm). The male:female sex ratio was 1:1.17 and did not differ significantly from the expected ratio of 1:1 ($\chi^2 = 2.69$; $P > 0.05$). The proportion of females was higher than males only in the 450–499 mm TL size class ($\chi^2 = 5.95$; $P < 0.05$) (Fig. 2). The sex ratio differed significantly from the expected 1:1 sex ratio in December ($\chi^2 = 5.96$; $P < 0.05$) and March ($\chi^2 = 4.36$; $P < 0.05$), where female dominance was recorded. Males and females demonstrated negative allometric growth and mass-length relationships were not significantly different between males $TM = 0.00009TL^{2.829}$ (n = 237; $r^2 = 0.990$) and females $TM = 0.0001TL^{2.811}$ (n = 274; $r^2 = 0.993$) (ANCOVA, $F = 0.488$; $P > 0.05$). Therefore, the relationship for pooled sexes was $TM = 0.00009TL^{2.821}$ (n = 511; $r^2 = 0.991$). In
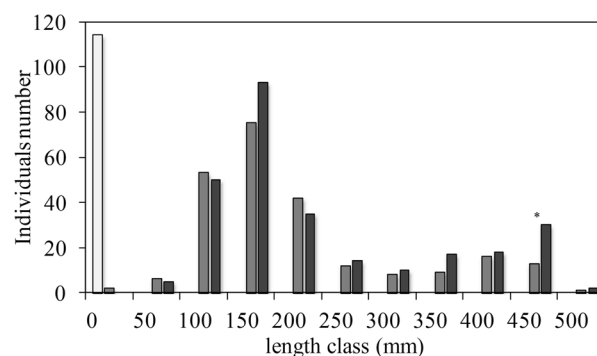

Fig. 2 Individual number of *Chaetodipterus faber* with indeterminate sex (white bars), males (black bars), and females (gray bars), by length classes, caught in the Paranaguá Estuarine Complex and surrounding areas in southern Brazil from August 2015 to July 2016. Superscript * indicates significant differences ($\chi^2 < 3.840$, $d.f. = 1$, $P < 0.05$) observed by χ^2 test

contrast, indeterminate individuals demonstrated positive allometric growth where $TM = 0.000007TL^{3.404}$ (n = 114; $r^2 = 0.992$).

Age determination and validation. The average coefficient of variation and the average percent error among age estimates were 3.07 % and 2.36 %, respectively. From the 625 *C. faber* samples, 90 % (562 individuals) were aged successfully. The remaining otoliths were discarded due to the variability in readings or because they were damaged during processing.

The Kruskal–Wallis test indicated significant differences in the RMD between months (Kruskal–Wallis $H = 89.39$; $P < 0.001$). The lower median RMD from September 2015 to December 2015 ($P < 0.05$) suggests that opaque bands are laid down during these months when higher proportions of opaque otolith edges were recorded. In May 2016, 100 % of the otolith edges were translucent. These results suggest that a single opaque zone is deposited each year (Fig. 3a). The deposition of the opaque bands was accompanied generally by a depression at the distal margin of the otoliths (Fig. 3b).

Age and growth. Age estimates from otoliths ranged from 0 to 17 years (Table 2). Individuals older than 11 years were rare and the oldest fish was a male of 508 mm TL sampled from the coastal beach adjacent to the PEC. The longest TL was 510 mm from a female of 10 years old caught inside the PEC. Although the growth models demonstrated some support ($\Delta_i < 2$), prediction varied according to the dataset and the model used. The VBGF exhibited the lowest AICc for males and all individuals pooled, while the GM exhibited the lowest AICc for females (Fig. 4; Table 3). The age at the inflection point (ti) for the GM was higher for females (1.96 years) than males (1.83 years). The LM was only suitable as an alternative model for modeling growth in females ($\Delta_i = 0.47$; $\omega i = 0.4$). The inclusion of small individuals in the pooled dataset produced more realistic t_0 estimates that
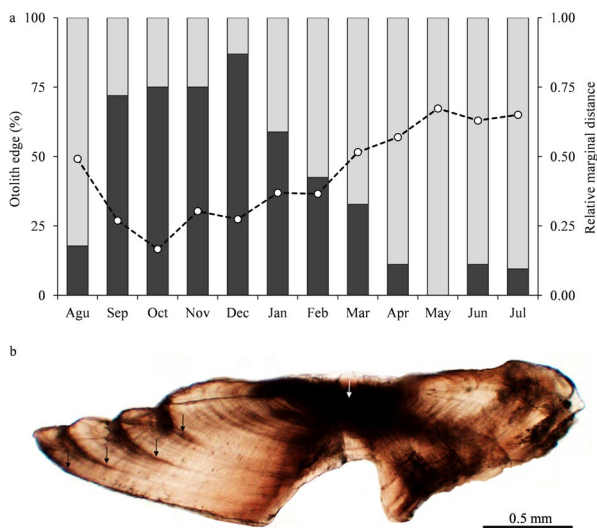
Fig. 3 (**a**) Monthly edge-type analysis expressed as percentages of opaque (black bars) or translucent (gray bars) otolith edges and average monthly relative marginal distance (RMD) (line and open circles) for *Chaetodipterus faber* (age 2 to 5 years pooled; n = 167) collected from the Paranaguá Estuarine Complex and surrounding areas from August 2015 to July 2016. (**b**) Transverse sections from the left sagittal otolith of a four-year-old *C. faber* (TL = 227 mm) collected in December 2015 from the Paranaguá Estuarine Complex. *Dark arrows* annuli (opaque zones), *white arrow* nucleus. Image viewed at 40x magnification

Reproductive biology. Both the monthly GSI average and relative frequency of the developmental sexual phases showed a peak during the reproductive season between October 2015 and January 2016. The GSI averages were significantly different among months for both adult females ($H = 125.20$; $P < 0.0001$) and males (Kruskal–Wallis $H = 138.44$; $P < 0.0001$) with higher mean values from October 2015 to January 2016 ($P < 0.05$) for both sexes (Fig. 5).

The ovarian histological examination demonstrated that *C. faber* sustains a constant reserve of primary growth oocytes throughout all development phases. Asynchronous oocyte development and multiple reproduction phases exhibited monthly within an extended reproduction season suggesting that *C. faber* is a batch spawner (Figs. 6 and 7). Primary oocytes were recruited for secondary growth in September 2015 and October 2015 when the relative frequency of females in the developing phase increased. Individuals in the spawning capable phase increased from October 2015 onwards (Fig. 7). The actively spawning subphase was highest in December 2016 (Figs. 6d and 7), coinciding with highest GSI values collected from the southern region of the PEC. Almost all spawning capable and actively spawning females presented postovulatory follicles (POFs) indicating an elevated spawning frequency at the study site (Fig. 6e). Males were reproductively active (Fig. 6b) slightly longer than females which ceased spawning from January 2016 to March 2016, as shown by the high relative frequency of regressing individuals (Fig. 6f and Fig. 7).

Immature males' TL (n = 14) ranged from 41 mm to 169 mm while immature females' TL (n = 39) ranged from 68 mm to 164 mm. All males < 99 mm TL and younger than 0.75 years, and all females < 120 mm TL and younger than 1 year were immature (Fig. 6a, c). The smallest sexually mature male and female were 99 mm and 120 mm TL, respectively. The youngest sexually mature male and female
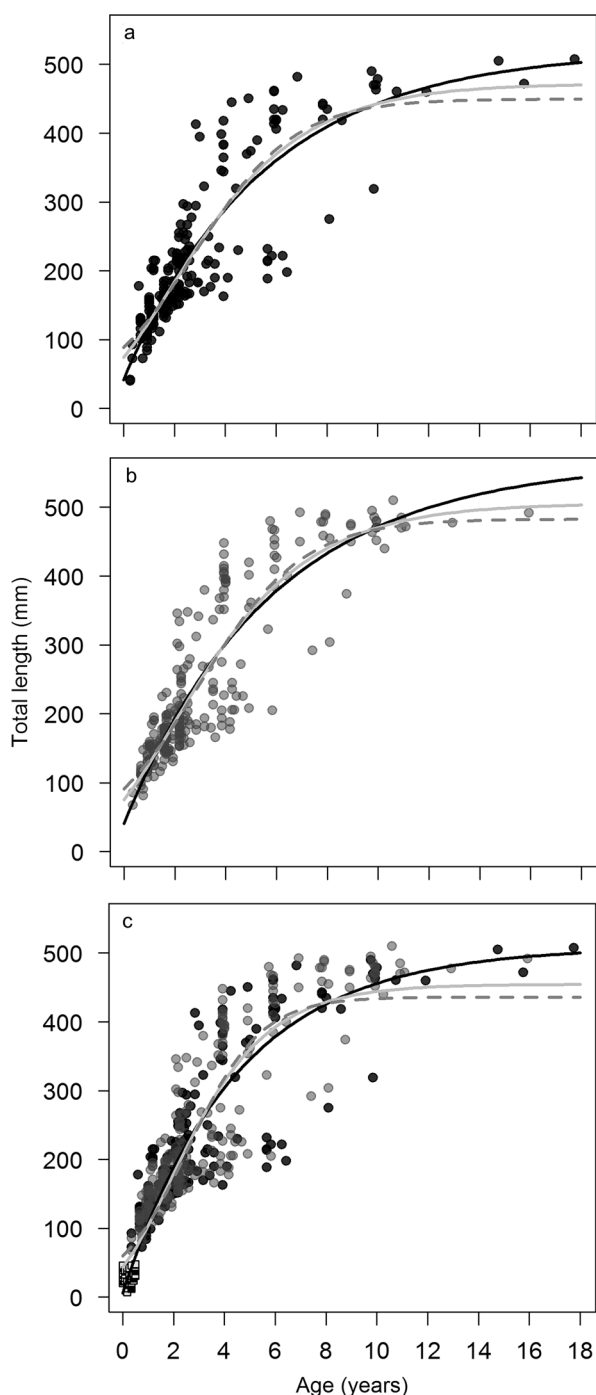
were closer to 0, conferring a bias reduction by the addition of these fish in the analyses (Table 3). Additionally, *k*, *gi* and *gninf* were higher in this dataset. Despite the different support levels exhibited by the AICc between males ($\Delta_i = 0$) and females ($\Delta_i = 3.53$), mean VBGF parameter estimates were compared between sexes. There were no significant differences in L_∞, *k*, and t_0 between males and females as shown by the likelihood ratio test ($\chi^2 = 5.60$; $P > 0.05$) and extra sum-of-squares test ($F = 1.853$; $P > 0.05$).

Table 2 Age-length distribution for all *Chaetodipterus faber* caught in southern Brazil from August 2015 to July 2016

TL (mm)	Age (years)																	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
0 - 49	107																	
50 - 99	7	5																
100 - 149	18	86	2															
150 - 199		71	53	11	4	1	1											
200 - 249		9	30	10	8	6	1											
250 - 299			16	3	1		1	1										
300 - 349			5	4	2	1		1	1									
350 - 399				7	11	4	1		1									
400 - 449			1	3	5	6	8	3	2	1	1							
450 - 499				1	5	2	4	3		10	7	4	1		2			
500 - 549											1			1				1
Total	132	171	107	38	32	23	13	8	8	12	9	4	1	0	1	2	0	1

Fig. 4 Age-at-length plot for *Chaetodipterus faber* (**a**) males (n = 215), (**b**) females (n = 243), and (**c**) all individuals (n = 562) collected from the Paranaguá Estuarine Complex and surrounding areas from August 2015 to July 2016. In each plot, the von Bertalanffy growth model (solid black line), Gompertz model (solid gray line) and Logistic model (dashed gray line) are shown. Points depict individual fish by age; males (black circles), females (gray circles), and individuals with indeterminate sex (white squares)

were 1-year-old fish. Males reached maturity at smaller size and younger age than females which took approximately 0.5 year longer to reach maturity (Table 3 and Fig. 8).

Discussion

This is the first study that provides information on age, growth and reproduction of *Chaetodipterus faber* in the South Atlantic Ocean. As previously recorded by Hayse (1990), no significant gender differences were found in the sex ratio of sampled population, despite the slight deviation in favor of females which is common in gonochoric fishes (Tsikliras et al. 2010). However, the proportion of females significantly outnumbered males in the 450 to 499 mm TL size class. This pattern was not consistent across months because it was observed in December 2015 and March 2016 only. The occurrence of shoals with unequal sex ratios during the spawning season has been recorded for several fishes (Morgan and Trippel 1996; Boudinar et al. 2016; Freitas et al. 2018). For fishes that form aggregations during spawning, sex ratio may be highly space-time variable due to spatial segregation by sex during spawning (Macchi et al. 2002) and gender differential movement into and out of the spawning sites, as observed for commercially important Atlantic cod (Morgan and Trippel 1996), Black drum (Macchi et al. 2002) and groupers (Freitas et al. 2018). However, several factors including differential longevity, mortality and catchability may also contribute to the observed gender differences (Hixon et al. 2014; Boudinar et al. 2016; Freitas et al. 2018). Little information is available on the reproduction of ephippids (Hayse 1990; Ditty et al. 1994; the present study) and further research is needed to address this.

Sexual growth dimorphism was not evident in length-mass relationships and the overall length-frequency distributions. The adult males and females demonstrated negative allometric growth because they grew slightly faster in length than in weight. There were no statistical differences in the mass-length relationships between sexes. Negative allometric growth was noted in previous work on *C. faber* (mean TL = 147 mm; $b = 2.75$) in southeastern Brazil (Dias et al. 2014). In the present study, however, the indeterminate individuals showed positive allometric growth because they grew slightly faster in weight than in length. This has been observed in smaller *C. faber* (mean TL = 25 mm; $b = 3.66$) from northern Brazil (Ferraz and Giarrizzo 2015). A size-dependent shift from early allometric positive growth to allometric negative growth may be a necessary step in the development of *C. faber* that will ultimately occupy a pelagic environment (Barros et al. 2015).

The otolith edge-type and RMD analyses showed an annual pattern in the deposition of opaque bands. The lowest RMD and the > 50 % proportions of opaque otolith edges

Table 3 Estimated von Bertalanffy growth function (VBGF), Gompertz model (GM), and Logistic model (LM) parameters describing the length-at-age relationship of *Chaetodipterus faber* males, females, and all individuals pooled. Logistic regression models (LRM) for the estimated proportion of mature *C. faber* relative to total length and age are also presented. Samples were collected from the Paranaguá Estuarine Complex and surrounding areas in southern Brazil from August 2015 to July 2016

Model	Parameter	Males		Females		All individuals	
		Estimates	C.I.	Estimates	C.I.	Estimates	C.I.
VBGF	L_∞ (mm)	520.87	466 - 598	567.2	509 - 664	508.81	483 - 537
	K (year^{-1})	0.18	0.13 - 0.24	0.17	0.12 - 0.22	0.22	0.20 - 0.25
	t_0 (year)	-0.46	-0.84 - -0.13	-0.44	-0.86 - -0.12	-0.05	-0.15 – 0.05
	AICc	2330.04		2641.16		6032.91	
	Δ_AICc	0		3.53		0	
GM	L_∞ (mm)	472.12	436 - 516	505.72	470 - 548	454.57	438 – 473
	gi (year^{-1})	0.34	0.27 - 0.41	0.33	0.27 - 0.39	0.46	0.42 - 0.51
	ti (year)	1.83	1.58 - 2.18	1.96	1.73 - 2.92	1.85	1.73 - 1.97
	AICc	2331.9		2637.63		6081.67	
	Δ_AICc	1.86		0		48.76	
LM	L_∞ (mm)	449.68	419 - 482	482.81	456 - 516	435.99	421 - 451
	$gninf$ (year^{-1})	0.51	0.43 - 0.60	0.49	0.42 - 0.57	0.71	0.66 - 0.78
	ti (year)	2.78	2.44 - 3.19	2.95	2.66 - 3.35	2.60	2.44 - 2.74
	AICc	2336.89		2638.10		6130.47	
	Δ_AICc	6.85		0.47		98.03	
LRM	L_{50} (mm)	98	91 - 108	144	133 - 158		
	L_{95} (mm)	147	122 -163	204	176 - 214		
	A_{50} (year)	0.89	0.74 - 1.06	1.37	1.11 - 1.62		
	A_{95} (year)	1.79	1.31 - 2.10	2.29	1.51 - 2.63		

C.I. = 95 % confident intervals; L_∞ (mm) = theoretical asymptotic TL; k (year^{-1}) = is the growth coefficient; t_0 (years) = theoretical age at which length is zero; AICc = Akaike information criterion; ΔAICc = AICc difference; gi (year^{-1}) = instantaneous growth rate at the inflection point; ti (years) = is the age at the inflection point; $gninf$ (year^{-1}) = is the instantaneous growth rate at negative infinity; L_{50}, L_{95}, A_{50}, A_{95} = TL (mm) and age (years) at which 50 % and 95 % of the individuals were mature

Fig. 5 Box plot of monthly variation in the gonado-somatic index (GSI) of adult *Chaetodipterus faber* (**a**) females (n = 228) and (**b**) males (n = 211) from the Paranaguá Estuarine Complex and surrounding areas in southern Brazil sampled from August 2015 to July 2016. Dark bands indicate median proportions, box edges indicate the 25 % and 75 % quartiles, whiskers represent maximum and minimum values and samples with values 1.5 times lower or bigger than the quartiles are shown as gray points. Dark points show monthly averages
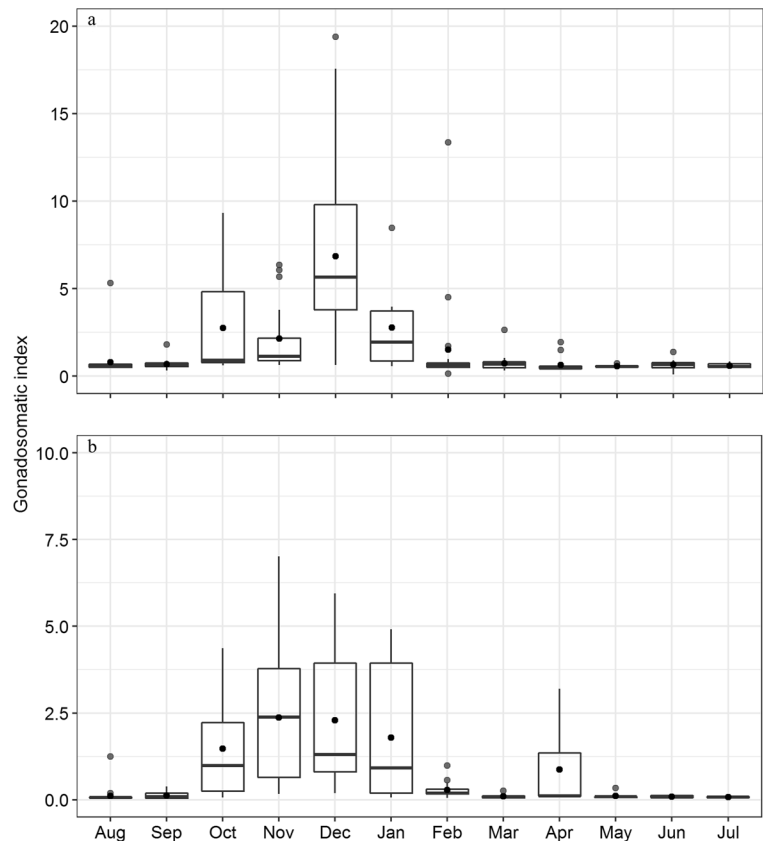
Fig. 6 Microphotographs of gonad histology of *Chaetodipterus faber* collected from the Paranaguá Estuarine Complex and surrounding areas. (**a**) Immature male (TL = 73 mm; GSI = 0.007); (**b**) spawning capable male (TL = 123 mm; GSI = 0.26); (**c**) immature female (TL = 68 mm; GSI = 0.12); (**d**) spawning capable female in active spawning condition (TL = 490 mm; GSI = 10.06); (**e**) spawning capable female (TL = 464 mm; GSI = 6.98); (**f**) regressing female (TL = 298 mm; GSI = 0.98). *At* follicular atresia, *CA* cortical alveolar oocyte, *Hy* hydrated oocytes, *PG* primary growth oocytes, *POF* postovulatory follicle complex, *Sg1* primary spermatogonia, *Sz* spermatozoa, *Vtg1* primary vitellogenic oocyte, *Vtg2* secondary vitellogenic oocyte, *Vtg3* tertiary vitellogenic oocyte
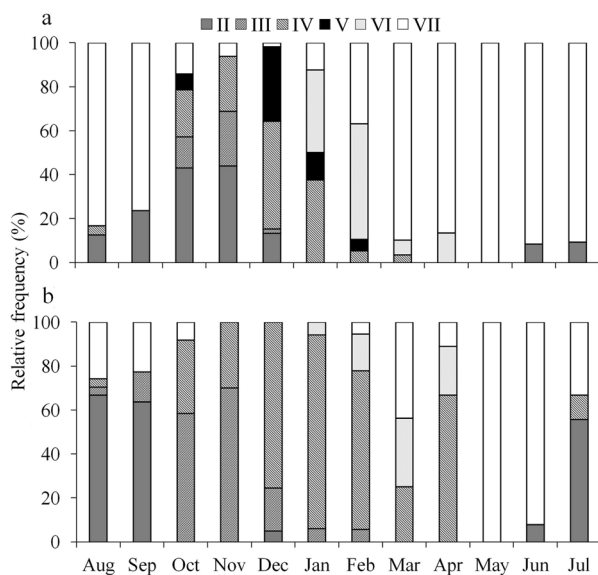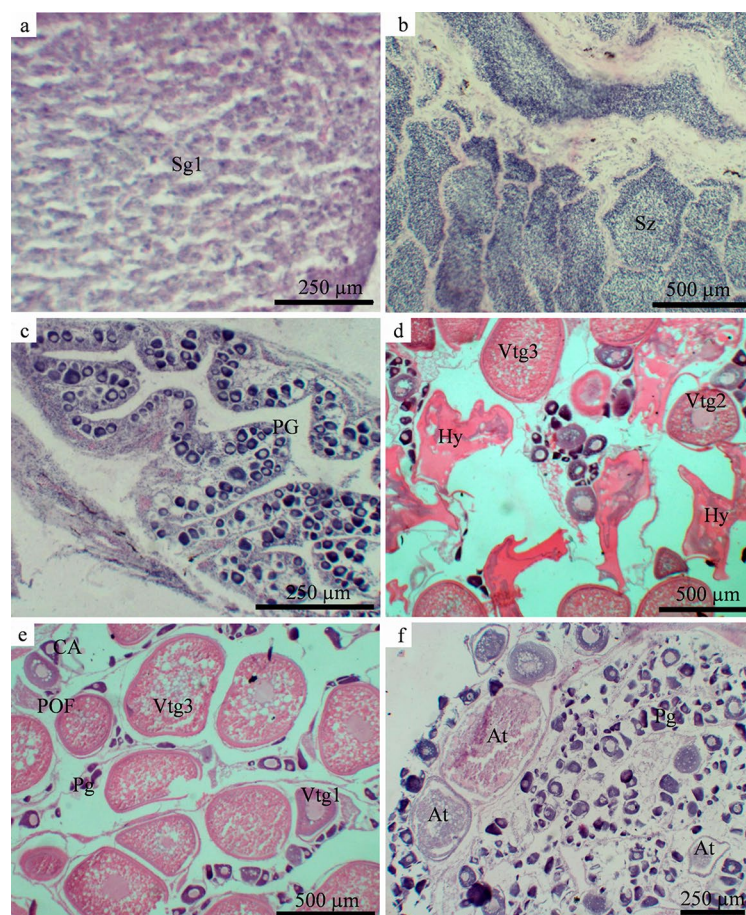
Fig. 7 Relative frequency of each reproductively mature phase and subphases by month for (**a**) females (n = 228) and (**b**) males (n = 211) of *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex and surrounding areas in southern Brazil from August 2015 to July 2016. *II* Early developing, *III* late developing, *IV* spawning capable, *V* actively spawning capable, *VI* regressing, *VII* regenerating

from September 2015 to January 2016 appear to be related to the period of rising water temperature in the study area (Soeth et al. 2015). In *C. faber* from North Atlantic Ocean, the opaque zone deposition in otoliths occurs from winter (January) to early summer (July) (Davies et al. 2015). Slight differences in the deposition period may be related to different age groups analyzed (Hyndes et al. 1992) and environmental factors, such as seawater temperature and variable feeding conditions (Geffen and Nash 1995; Pilling et al. 2007). The results of the present study show that spring and autumn appear to be a primary periods for the deposition of opaque and translucent zones in the otoliths of *C. faber* in subtropical environments.

The results presented in this study showed that small differences in the dataset can strongly influence the model of best fit in fish growth studies. The inclusion of small fish in the dataset favored the VBGF based on AICc selection mainly due to the lack of fit from the both S-shaped GM and LM that were less accurate for description of *C. faber* at all life stages. The GM and LM models underestimated the maximum asymptotic TL which, in turn, increased the relative growth rate estimates. Although the GM appeared less appropriate for describing male growth, the parameters were obtained by sufficient model support
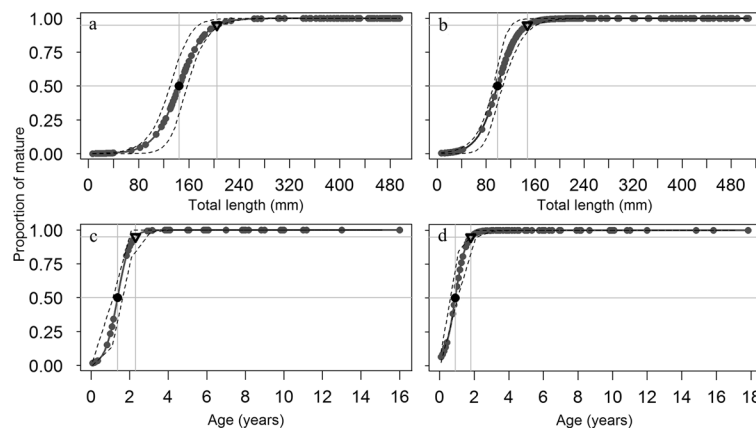
Fig. 8 Mean ± 95 % C.I. logistic regression models for the estimated proportion of mature *Chaetodipterus faber* relative to total length for females (**a**) and males (**b**) and relative to the age of females (**c**) and males (**d**) collected at the Paranaguá Estuarine Complex and surrounding areas in southern Brazil during August 2015 to July 2016. Sample sizes are 109 for females and 192 for males. Dark points and triangles indicate L_{50} and A_{50} and L_{95} and A_{95}, respectively

for both sexes ($\Delta i < 2$). The estimated inflection point from the Gompertz model for males ($ti = 1.83$ years old) and females ($ti = 1.96$ years old) was close to A_{95} (males $A_{95} = 1.79$ years old; female $A_{95} = 2.29$ years old). The inflection point in sigmoid functions can be biologically interpreted as a shift where growth stops increasing and begins to decrease (Thorson and Simpfendorfer 2009). This finding suggests some trade-off between growth and reproduction in *C. faber*, which appears to increase the proportion of energy allocated to reproduction in the post-maturation life stage (Roff 1983). However, changes in somatic growth can also occur as juveniles that emigrate from estuarine nursery grounds to continental shelf habitats (Secor 1999; King 2007; Daros et al. 2012).

The VBGF parameters obtained from the pooled dataset ($L_\infty = 508$ mm TL, $k = 0.22$ year^{-1}, $t_0 = -0.05$ year) were similar to those reported previously for *C. faber* from South Carolina (Hayse 1990: $L_\infty = 490$ mm TL, $k = 0.34$ years^{-1}, $t_0 = 0.18$ year) where seawater surface temperatures range from 8°C to 30°C in the central coast (Calder 1990). Direct comparisons among studies are difficult because differences in the sampling environment and datasets can strongly influence the model parameters (Thorson and Simpfendorfer 2009). In all datasets in the present study, k was smaller than that reported from the South Carolina study where the oldest fish was 8 years old and the age 0 group represented more than 50 % of the total sample modeled (Hayse 1990). In the present study, the oldest observed fish was 17 years old and age groups between 8 and 11 years old were well represented in the samples. These age-class differences are probably the main reason for the difference in k between studies due to the inverse relationship between L_∞ and k. The inclusion of small individuals into the dataset produced more realistic t_0 estimates ($t_0 = -0.05$), which in turn modified k and L_∞.

The maximum age recorded for *C. faber* in the present study was two times higher than previously reported from the North Atlantic (Hayse 1990). Large specimens of *C. faber* are common in United States waters (Bell 2005), where the world record specimen of 6,750 g was caught in Chesapeake Bay, Virginia (IGFA 2017). Thus, the observed age differences between studies could be explained by the low number of individuals that were larger than 450 mm TL and also the age estimation method which counted annual increments from whole otoliths (Hayse 1990). Counting whole otoliths tends to underestimate fish age due to the stacking of rings on the otolith edge (Hyndes et al. 1992). However, it is difficult to confirm the main reason for the observed latitudinal age differences as environmental and ecological factors play a role in longevity variation at both intraspecific and intrapopulation levels (Pauly 1980; Secor 1999). Genetic and environmental factors like temperature and salinity can strongly influence fish growth and longevity (Pauly 1980; Boeuf and Payan 2001; Yamahira and Conover 2002). Additionally, human exploitation rates can have a direct impact on the age and size structure of fish populations (Aschenbrenner et al. 2017).

The total length of *C. faber* showed a large variation within age groups which indicates wide variation in individual growth rates. Intrapopulation variability in the growth rates could be explained by genetic, ecological and environmental factors such as discontinuous polymorphisms involving growth rate in discrete populations (Nordeng 1983; Secor 1999), density-dependent intraspecific competition (Hamrin and Persson 1986), habitat quality (Schwartzkopf and Cowan Jr 2017) and other factors including behavior, function and performance (Jørgensen et al. 2016). In addition, large size-at-age variation is common in fishes which employ a multiple batch-spawn strategy (Lowerre-Barbieri

et al. 1998), by means of the match or mismatch between the reproduction time (i.e., birth months) and optimal conditions to juvenile fish growth, such as seawater temperature and food availability (Olson 1996; Lowerre-Barbieri et al. 1998, 2011). Such ecological trends could later drive divergent migration behavior or habitat use that also affect individual fish growth (Olson 1996; Secor 1999).

The *C. faber* population under analysis showed a protracted spawning period as reproductive active individuals were identified in samples from October 2015 to January 2016. This period coincides with rising seawater temperatures in the study area (Soeth et al. 2015). The relationship between spawning period and temperature is in agreement with research from the North Atlantic and the Gulf of Mexico which showed that *C. faber* spawns from mid-spring to summer (Hayse 1990; Ditty et al. 1994). In southern Brazil, reproduction peaks through spring and summer have been identified in several fish families, such as Gerreidae (Chaves and Otto 1998), Balistidae (Bernardes and Dias 2000), Tetraodontidae (Rocha et al. 2002), and Sciaenidae (Haluch et al. 2011). This period appears to be linked with favorable conditions for gonadal and initial fish development in estuarine and coastal habitats (Godefroid et al. 1999; Castro et al. 2005; Lowerre-Barbieri et al. 2011; Souza-conceição et al. 2013).

The histological examination of gonadal structure demonstrated that *C. faber* females sustained a constant reserve of primary growth oocytes during all sexual development phases. The presence of pre-vitellogenic and vitellogenic follicles at different development stages, in combination with the presence of postovulatory follicles (POFs), confirmed that *C. faber* is a batch spawner (Hayse 1990; Brown-Peterson et al. 2011). Postovulatory follicles were often recorded in the ovaries of spawning capable and actively spawning *C. faber* females which suggests a high frequency of spawning events across the primary reproductive period (Hunter et al. 1986; Ganias et al. 2007; Brown-Peterson et al. 2011). This protracted spawning period in conjunction with a high frequency of spawns would have a selective advantage, decreasing density-dependent intraspecific competition and increasing the likelihood that larvae or juveniles will find favorable conditions for growth (Johannes 1978; Lowerre-Barbieri et al. 1998).

The most actively spawning females were collected in the southern channel of the PEC, in December. In these individuals, several indicators of the imminent release of gametes (Brown-Peterson et al. 2011) were seen including oocyte hydration and newly collapsed POFs. Moreover, male samples from the same area showed spermiation during macroscopic observations of milt release. These findings suggest that the southern channel of the PEC could be a spawning site for this *C. faber* population. Since the sampling effort was conducted for a full year at this site, and the highest

number of larger individuals were collected between October 2015 and December 2015, the data suggest that *C. faber* may display a seasonal movement for spawning aggregation purposes, an event well known to occur in many fish species (Macchi et al. 2002; Sadovy de Mitcheson and Colin 2012; Bueno et al. 2016). These observations are in agreement with observations drawn from the landings of *C. faber* in the artisanal fisheries of SE-S Brazil because catch associated with large estuary systems increases by over 1,100 % from August to December annually (PMAP-BS 2017a, b). This spawning aggregation behavior could increase the level of local recruitment and further benefit demersal plant-mimetic juveniles through settlement in estuarine regions where they are abundant (Sadovy de Mitcheson and Colin 2012; Barros et al. 2013; Possato et al. 2016). In addition, the timing and location of fish spawning aggregations and variations in local recruitment are functions of different biological (e.g., pelagic larval duration and larval swimming) and physical (e.g., sea currents, coastline and bathymetric variability) processes and interactions (Siegel et al. 2008). To our knowledge, only two studies, which used underwater observations, have reported reproductive aggregations of *C. faber* from the entrance of Sapelo Sound, Georgia State, United States (Chapman 1978) and at the Belize Barrier Reef (Heyman and Kjerve 2008). Some speculation has been made about the potential for spawning aggregations of other Ephippidae, *Platax spp.* from the Republic of Palau, but this hypothesis has not been confirmed (Domeier and Colin 1997). Regarding the early life stages of *C. faber*, few studies have reported spatial and temporal distributions. However, most studies that have collected *C. faber* eggs and larvae have done so inside or at the entrance to bays and estuarine systems (Barletta-Bergan et al. 2002; Joyeux et al. 2004; Castro et al. 2005; Bonecker et al. 2009; Burghart et al. 2014), or in coastal waters and riverine frontal areas (Ditty et al. 1994). Although the data available are too limited to make conclusions on *C. faber* reproductive sites, the present study and all previous work suggests that *C. faber* spawning is associated with estuarine systems and costal bays. In addition, mixed schools of spawning capable and regressing *C. faber* females were collected from a shallow rocky reef (< 15 meters depth) and an artificial reef (< 27 meters depth) on 24 January 2016 and on 31 March 2016 in the present study. Although these individuals did not show oocyte hydration, the GSI values ranged from 0.9 to 8.4 in the presence of POFs. This suggests that, even at low percentages, some *C. faber* individuals may spawn for longer in coastal areas adjacent to the PEC until April.

The present study was in agreement with previous work from subtropical areas of the North Atlantic which showed that males reached maturity at a shorter length and younger age than females (Hayse 1990). While more than 50 % and 100 % (upper A_{95} C.I.) of males are mature by their first

and second birthdates, respectively, females spend approximately 0.5 more year than males to reach 50 % and 100 % maturity. These findings suggest that females would be capable of spawning just prior their second birthdate (second spring-summer) and would be 100 % mature just prior to their third birthdate. Thus, the catch of individuals under 250 mm TL must be restricted to ensure that all individuals have an opportunity to spawn at least once in their lifetime to guarantee stock replenishment.

This study demonstrated that *C. faber* shows early maturation with a life span of more than 15 years in the SW Atlantic Ocean. The observed trade-off between growth and reproduction, elevated GSI values, and an extended spawning season suggests that *C. faber* exhibits a high reproductive capacity in subtropical latitudes. *Chaetodipterus faber* may aggregate seasonally to facilitate spawning thereby increasing the susceptibility of the species to overexploitation (Macchi et al. 2002; Sadovy de Mitcheson et al. 2008). Fishery closures during the spawning season (van Overzee and Rijnsdorp 2014) should be used as a tool to manage the *C. faber* stock in southern Brazil. However, the effects of current harvest levels are unknown and require further study. The location of the main spawning/nursery areas and knowledge of the population dynamics are also necessary to fulfill the prerequisites for informed management of this important fishery resource.

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