Research Article



Age, growth, and maturity of little tunny, *Euthynnus alletteratus* (Rafinesque, 1810) in southeastern Brazil

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ABSTRACT. This is the first attempt to assess life parameters of little tunny *Euthynnus alletteratus* in the southwestern Atlantic. Fin spines, liver, and gonad information from 345 fishes (330-780 mm fork length) sampled from artisanal landings between March 2018, and February 2019 were used to analyze age, growth, and sexual maturity. Age was estimated by counting and measuring increments in sectioned spines, and the von Bertalanffy growth function was used to fit length-at-age data. There was no significant difference between male and female size distributions. Gonadosomatic index peaked from November to February in both sexes, associated with the South Atlantic Central Water (SACW) upwelling in temperatures between 15-18°C. Reproduction in cold waters has never been reported before and is possibly related to a richer environment for feeding and growth of larvae. The coefficient of variation among successive readings was 9.2%. The oldest fish was 5 years, and one annual increment for 2 and 3-year-old fish was observed to form associated with SACW. Little tunny growing in southeastern Brazil shows a higher growth rate and smaller asymptotic length when compared to most stocks in Mediterranean waters. Growth was not significantly affected by sex, and the von Bertalanffy growth parameters for all fish were L_∞ = 791.9 mm, k = 0.42, and t₀ = -0.97 yr⁻¹. Length at first maturity is attained by 1-year-old fish of either sex (423-492 mm), suggesting that a small proportion (8%) of juveniles was recorded from fishery landings.

Keywords: *Euthynnus alletteratus*; little tunny; age; growth; reproduction; size; age structure; southwestern Atlantic

INTRODUCTION

Tuna and tuna-like fish consist of several species of worldwide economic importance, belonging to the Scombridae family, and are responsible for 7.9 million metric tons produced in 2018 (FAO 2020). There are more than 10 species of small-bodied tunas, but only five of these account for about 88% of the total reported catch by weight (ICCAT 2009). The little tunny *Euthynnus alletteratus* (Rafinesque, 1810) is an epipelagic, neritic, small-bodied tuna and one of three species of the genus *Euthynnus* found in tropical and

subtropical waters of the world (Manooch III et al. 1985). It is distributed on both sides of the Atlantic Ocean, including the Mediterranean, Black Sea, Caribbean Sea, and Gulf of Mexico (Collette & Nauen 1983).

E. alletteratus is reported as the most abundant scombrid in the epipelagic zone of the Gulf of Mexico (Pruzinsky et al. 2020) and one of the most abundant small tuna species in the Mediterranean Sea (Macías et al. 2009), where it is commercially exploited off the Spanish coast together with bullet tuna *Auxis rochei* and the Atlantic bonito *Sarda sarda* (Baéz et al. 2019).

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Like the Atlantic bonito and frigate tuna (Auxis thazard), little tunny is also among the most captured small scombrid in the Atlantic Ocean (ICCAT 2018). It is captured seasonally in western Africa and the Mediterranean Sea (Gaykov & Bokhanov 2008), considered a secondary target species, and captured mainly as bait in the Gulf of Mexico (Cabrera et al. 2005). Located in southeast Brazil (20-23°S), Rio de Janeiro State is one of the main locations for the skipjack tuna (Katsuwonus pelamis) fishery in Brazil, from where little tunny has been reported to be caught as one of the most frequent secondary targets alongside other tunas (Thunnus spp.), the common dolphinfish (Coryphaena hippurus) and the frigate tuna (Auxis thazard) (Da Silveira-Menezes et al. 2010). Little tunny's production in 2018 (9 t) represented 0.8% of the monitored rod and live-bait production (Martins et al. 2020). However, capturing E. alletteratus along the Brazilian coast is not subjected to fishing control or management policies due to the lack of valid data (Lucena-Frédou et al. 2017).

Small tuna species are relatively understudied (Juan-Jordá et al. 2013) and are expected to be subjected to increasing fishing pressure as several stocks of valuable large-bodied tunas are overfished (Pruzinsky et al. 2020). Despite its wide distribution and economic importance, E. alletteratus is classified as least concern by the IUCN (Juan-Jordá et al. 2013), and most studies regarding its biology have been conducted in Mediterranean waters (Rodriguez-Roda 1979, Kahraman & Oray 2001, Macías et al. 2006, 2009, Falautano et al. 2007, Kahraman et al. 2008, Hajjej et al. 2010, Mohamed et al. 2014, Saber et al. 2018). The southwest Atlantic (SWA) studies are scarce and mostly outdated (Menezes & Aragão 1977, Matsuura & Sato 1981, Chatwin & Matsuura 1998). Life traits such as age, growth, feeding ecology, and reproduction are completely unknown in SWA (Lucena-Frédou et al. 2017, Pons et al. 2019).

Like other scombrids, *E. alletteratus* is a multiple spawners, with an asynchronous development of oocytes resulting in numerous intermittent spawning seasons (Schaefer 2001). Estimates of length at first maturity (L_{50}) ranged from 350 to 448 mm fork length (FL) in Tunisia and Egypt, where the species is exploited by small-scale or recreative fisheries (Hajjej et al. 2010, Mohamed et al. 2014). The smallest L_{50} value (343 mm) was recorded in the Gulf of Mexico (Cruz-Castán et al. 2019) and the largest (570 mm) in Spanish waters (Rodriguez-Roda 1966). Little tunny is mainly caught in both places as a secondary target in artisanal multispecific fisheries, despite being abundant in Spanish waters (Cabrera et al. 2005, Macías et al. 2006).

Little tunny's maximum age is mostly estimated at 5 years (Rodriguez-Roda 1979, Valeiras et al. 2008, Adams & Kerstetter 2014) and occasionally eight (Cayré & Diouf 1983) and 9 years (Kahraman & Oray 2001). In Mediterranean waters (Rodriguez-Roda 1979), Senegal (Diouf 1980), and Gulf of Mexico (Cruz-Castán et al. 2019), age at first maturity is estimated at around 2 years. Among calcified structures, dorsal fin spines were the most utilized to investigate age and growth of *E. alletteratus* as it has a good relationship between radius and FL (Diouf 1980, Cayré & Diouf 1983, Johnson 1983, Valeiras et al. 2008). Studies using fin spines and vertebrae have reported a formation of one annual growth increment (Rodriguez-Roda 1979, Kahraman & Oray 2001, Valeiras et al. 2008), while two annual growth increments were observed in otoliths from Florida (Adams & Kerstetter 2014). There have been reports of paired increments in fin spines and vertebrae, referred to as "doublets," but they were considered one annual growth mark (Cayré & Diouf 1983, Johnson 1983).

The Cabo Frio upwelling system is the most intense of the upwelled areas along the Brazilian coast and has a rich pelagic fauna that includes large populations of Brazilian sardine Sardinella brasiliensis and skipjack tuna (Kampel et al. 1997, Matsuura & Sato 1981, Valentin 2001). The upwelling process happens throughout austral spring-summer when E-NE wind prevails, and the proximity of the 100 m isobath leads to a topography that promotes an upwelling of the cold (6-18°C) and less saline (34.5-36) South Atlantic Central Water (SACW) from a depth of 300 m (Silva et al. 1984, Gonzalez-Rodriguez et al. 1992). In contrast, when the NE wind velocities are reduced, or polar fronts are present, the direction of the wind changes and the thermocline depth fluctuates until the superficial area up to 300 m depth is occupied by the Coastal Water, characterized by the higher temperature (20-24°C) and salinity (>36) (Emílsson 1961, Silveira et al. 2000).

Surface water temperature is one of the most important and used predictors of abundance and distribution of tunas as it regulates physiology, behavior, reproductive activity, and growth (Fonteneau & Soubrier 1996, Worm et al. 2005). Although there are exceptions, spawning generally occurs at sea surface temperatures of about 24°C or higher (Schaefer 2001). Scombrid's physical adaptations (e.g. vascular current heat exchangers) made them capable of displaying wide temperature tolerance, i.e. bigeye and the yellowfin tuna can be found in water temperatures ranging between 3 and 31°C (Boyce et al. 2008). Little tunny has been reported in water temperatures between 18 and 30°C (Cayré & Diouf 1980, Cruz-Castán et al. 2019). Like other small-bodied tropical tunas such as *Euthynnus affinis* and *K. pelamis*, it has a higher tolerance for warmer waters when compared to cold-tolerant tuna species (e.g. *Thunnus* sp.) (Boyce et al. 2008).

In this paper, the age, growth, and maturity of *E. alletteratus* are described for the first time in the SWA through investigation on transversal sections of fin spines, monthly gonad development, reproductive cycle, and physiological indexes. Additionally, we examined the influence of sea surface temperature on reproductive activity and the formation of growth increments on the first dorsal fin spine.

MATERIALS AND METHODS

Sampling

Samples of *Euthynnus alletteratus* were collected monthly from March 2018 to February 2019 on the southeastern Brazilian coast. Fishes were sampled from artisanal beach seine fisheries in Arraial do Cabo and purse seine fishing landings in the Port of Cabo Frio to cover as much of the size structure and age structure as possible. Beach seine is selective for smaller sizes, while purse seine favors large sizes.

FL was measured to the nearest mm, and total weight (TW) was recorded to the nearest 0.1 g. After that, gonad weight (GW) and liver weight (LW) were recorded to the nearest 0.001 g, and sex was registered. During the sampling period, the sea surface temperature (SST) was continuously recorded by a data logger (HOBO Tidbit UTBI-001), fixed at a rocky shore at Arraial do Cabo in 1 m water depth (Fig. 1). SST records were used to assess seasonal changes of physiological indicators and the periodicity of formation of growth marks in *E. alletteratus*' spines.

The length-frequency distribution between sexes by fishing gear comparison was performed by a Kolmogorov-Smirnov test (D). An analysis of covariance (ANCOVA) was used to compare the length-weight relationship parameters of both sexes and the proportion of fishes among fisheries and sex-ratio were analyzed by the chi-squared test (χ^2).

Sexual maturity was visually classified by macroscopic gonad examination following Brown-Peterson et al. (2011) description, which included five phases: immature, developing, spawning capable, regressing and regenerating. Fishes under one of the four latter phases were considered sexually mature (adults). After the macroscopic classification, a sub-sample of gonads was removed, fixed in a solution of alcohol (76.5%), distilled water (8.5%), formaldehyde (10%), and glacial



Figure 1. Map of the Cabo Frio region in southeastern Brazil showing the position of sea surface temperature measurements (\bigstar) and landing samplings (\bullet).

acetic acid (5%) for 24 h and preserved in 70% alcohol. They were subsequently dehydrated in different series of alcohol concentrations and included in paraffin. Transverse sections (5 μ m thick) of tissue were removed with a microtome, mounted on glass microscope slides, stained with hematoxylin-eosin for histological analysis, which was used to validate the macroscopic classification.

The spawning period was evaluated using two physiological indexes, the gonadosomatic index (GSI), calculated as $GSI = (GW / (TW - GW)) \times 100$, and the hepatosomatic index (HI), calculated as HI = ((TW - TW))LW) / LW) \times 100. Monthly changes in the condition factor (K) were also recorded to follow the welfare condition of the specimens and calculated as K = (TW) $/ \text{FL}^{\text{b}}$ × 10⁴, where b is the allometric coefficient from the length-weight relationship. Monthly data of the physiological and conditional indexes were tested using Shapiro-Wilk and Levene's tests to verify the normality and homogeneity of the variance of the data before applying an analysis of variance (ANOVA). When restrictions were not met, a Kruskal-Wallis (H) nonparametric test followed by a Mann-Whitney's (U) post-hoc test was used (Zar 2010).

Size at first maturity (L₅₀) was estimated as $P = 1 / [1 + \exp^{-r(L-L_{50})}]$, where *P* is the proportion of mature individuals in the length class, r is the parameter determining the slope of the maturity curve, L is the lower limit of the length class and L₅₀ is the fork length

at which 50% of the fish are mature. Estimates of the model parameters were performed by non-linear regression, using Solver's quasi-Newton algorithm available in the Microsoft Excel software (Sparre & Venema 1997). Solver optimizes the best combination of parameters, minimizing the differences between mature individuals' predicted and observed proportions.

The first dorsal fin spine obtained from the specimens was extracted and used for age determination. Two cross-sections of 0.8 mm of thickness were taken successively along the length of each spine with a low-speed Buehler-Isomet metallographic saw as close as possible to the condyle. Transversal sections were examined under a stereomicroscope equipped with a micrometer scale and a digital image capture system (Zeiss Stemi 508[®]), applying transmitted light at 40x to 100x magnification. Translucent growth marks were counted, and each section was read twice by one reader, without information on the size or sex of the fish. A third was performed if there was a disagreement between the readings, and specimens whose age estimates still disagreed were removed from further analyses. In several sections was observed the presence of double or triple thinner growth marks with a smaller distance between one another that formed an opaque or translucent band, also reported by Cayré & Diouf (1983), Johnson (1983), and Valeiras et al. (2008). When present, annuli consisting of multiple bands were carefully considered to assess the age. The accuracy of the readings was determined by the average coefficient of variation (CV, Chang 1982) and by the index of average percentage error (APE, Beamish & Fournier 1981).

A translucent band of clear aspect (related to lower growth rates) intercalated with an opaque band of dark aspect (related to higher growth rates) was considered one increment. The spine radius (Rt) and each increment radius (Ri) was measured to the nearest 0.001 mm from the center of the spine (Fig. 2). The radius estimate for the missing initial rings in larger fishes was performed following Hill et al. (1989). A statistical summary of the first two rays of the smaller and younger fish that still had the increments visible was compiled, and a *t*-test was applied to compare the radii of the fishes with the first two increments visible and compare the increments' radii between sex. Final corresponding ages were assigned when the radii of at least two successive increments of the first three or four were within the confidence interval limits of the increments' compiled data. Finally, a corrected age estimate was assigned to spines missing up to the second increment by comparing the radii of the first three or four visible increments to the means and the confidence interval limits at 95% of the summarized data.



Figure 2. A transversal section of the first spine of a 3^+ year female specimen (634 mm fork length) showing the spine radius (Rt) measured from the focus to the edge and each increment identified (R1, R2, R3).

The edge aspect of each section (translucent or opaque) was recorded along with the readability of the section, which was classified as 0 (unreadable), 1 (low readability), and 2 (high readability). The precision among readings and the Rt per ring position were analyzed. An ANOVA was performed in order to test mean Rt values. The periodicity in increment formation was assessed by marginal increment analysis (Panfili & Morales-Nin 2002) and by the percentage of edge aspect calculated for fishes of 2 and 3 years, as they were the most frequent among samples. The marginal increment was calculated as MI = $(R_t - R_n) / (R_n - R_{n-1})$, where Rt is the spine radius, and R_n and R_{n-1} are the distance from spine focus to the outermost and the penultimate increment identified, respectively. Differences in marginal increment were tested using Shapiro-Wilk and Levene's tests to verify the normality and homogeneity of the data variance before applying an analysis of variance (ANOVA). When restrictions were not met, a Kruskal-Wallis (H) non-parametric test followed by a Mann-Whitney's (U) post-hoc test was used (Zar 2010). Edge aspect proportion (translucent/ opaque) during upwelling (SACW) and non-upwelling (CW) was tested using a chi-square test (χ^2) .

Von Bertalanffy growth curves were fitted to the observed data applying the standard von Bertalanffy growth function (VGBF): $FL = L_{\infty} [1 - e^{-k (t-t0)}]$, where FL is the fork length at age t; L_{∞} is the asymptotic length; k is the growth coefficient, and t_0 is the theoretical age at zero length. The likelihood ratio test (LRT) was used to estimate the growth parameters (L_{∞} , K, t_0), according to Aubone & Whöler (2000). Curves of females and males were compared using Kimura's likelihood ratio test (Kimura 1980, Haddon 2001).

RESULTS

Size distribution

A total of 345 specimens were sampled, including 174 females (409-780 mm), 169 males (330-780 mm) and two unsexed specimens (361-363 mm). Length classes <400 mm were underrepresented. Size-related distribution did not change between sex according to Kolmogorov-Smirnov test (D = 0.11; df = 1; P = 0.22; Fig. 3a), but it was significantly affected by the fishing gear (D = 0.79; df = 1; P < 0.01; Fig. 3b), although samples were taken from the same population. When size distribution was compared, the chi-squared test pointed towards a significant difference between proportions among fisheries ($\chi^2 > 3.84$; df = 1; P < 0.00).

Parameters of the length-weight relationship did not point to significant difference between sexes (ANCOVA: F = 0.40; df = 1; P = 0.52) or between slopes' angular coefficients (F = 0.363; P = 0.54). The equations that describe LWR were TW = 0.0003 × FL^{2.8711} (R² = 0.97) for females and TW = 0.0003 × FL^{2.8737} (R² = 0.98) for males (Fig. 4). For all fishes grouped the equation was TW = 0.0003 × FL^{2.8760} (R² = 0.98).

Histological analysis

Females and males of all maturity stages were observed. Euthynnus alletteratus ovaries were strongly characterized by oocytes exhibiting asynchronous and discontinuous secondary growth. Primary growth oocytes (PG) were exhibited by immature phase females (Fig. 5a). After reaching sexual maturity, ovaries entered the first phase of the reproductive cycle, the developing phase, with oocytes in the germinative stages of PG and CA (cortical alveolar) present (Fig. 5b). Ovaries in the capable spawning phase had numerous oocytes in the vitellogenic stage (Vit) as well as mature oocytes (MO) with pre-ovulatory hydration distortions, a common aspect after the dehydration process during histological processing (Figs. 5c-d). The "regressing" phase of females, which can be considered as a "partially spent" phase for this species, was characterized by the presence of post-ovulatory follicle complexes (POF) (Fig. 5e). Ovaries in the "regenerating" phase (Fig. 5f) exhibited fibrous nodules (FN) as well as numerous oocytes in PG. Fibrous connective tissue was also observed.

Despite observing males in all maturity stages, testicles' histology micrographs were obtained only for developing and spawning capable phases (Figs. 5g-h). "Developing" testicles exhibited several testicular ducts (TD) with sperm cysts (SCy) in different stages of development along the ducts' walls, and a low number



Figure 3. Length-frequency by a) sex and b) gear of *Euthynnus alletteratus* landed in the southeastern Brazilian coast between March 2018 and February 2019.



Figure 4. Length-weight relationship for females (0) and males (•) of *Euthynnus alletteratus* landed in the southeastern Brazilian coast between March 2018 and February 2019.

of spermatozoa (Sz) present. In contrast, Sz cells were observed greatly occupying the testicular lobules and ducts of testicles in the "spawning capable" phase.

Spawning period and maturity

The overall female-male proportion didn't change significantly from the equilibrium ($\chi^2 = 0.02$, df = 1; *P* = 0.88). When separated among size classes, however,



Figure 5. Micrographs from gonad section of females (a-f) and males (g-h) of *Euthynnus alletteratus* stained with hematoxylin-eosin. a) Immature ovary, b) ovary in developing phase, c) ovary in the capable spawning phase, d) ovary in spawning capable phase, e) ovary in the regressing phase, f) ovary in the regenerating phase, g) testicle in the developing phase, h) testicle in the capable spawning phase. PG: primary growth; CA: cortical alveolar; MO: mature oocyte; Vit: oocyte in vitellogenic stage; POF: post-ovulatory follicle complex; BV: blood vessel; TD: testicular duct; SCy: sperm cysts; Sz: spermatozoa.

most fishes by class were females ($\chi^2 < 3.84$; df = 1; *P* < 0.05), especially in sizes between 600 and 690 mm. Mean GSI values for females and males of *E. alletteratus* indicated maximum gonad weight corresponding to 1.2 and 1.8% of the body mass, respectively. Monthly mean changes in GSI were significantly different for females (H = 126.9; df = 11; *P* < 0.01) and males (H = 125.1; df = 11; *P* < 0.01) (Fig. 6). GSI peaked after a long period of temperature decrease, from 22°C in July to 15°C in November and was significantly higher during upwelling periods (SST < 18°C) (Fig. 6), as were HI and K values (Figs. 7a-b). Monthly values of HI (females: H = 111.2; df = 11; *P* < 0.01; males: H = 53.5; df = 11; *P* < 0.01) and K (females: H = 37.17; df = 11; P < 0.01; males: H = 23.69; df = 11; P < 0.01) were also significantly different, with HI increasing from December, after spawning period, in a clearer relationship with gonad development when compared to condition factor.

The monthly variation on sexual maturity stages (Figs. 8a-b) showed that most developing females were observed from May to October. Testicles in this phase occurred throughout the year. Spawning capable ovaries were most frequent in November and December, matching the period of higher GSI mean values. Partially spent ovaries and testicles increased from winter to the beginning of summer (June-October). Ovaries in the regenerating phase occurred



Figure 6. Monthly means of gonadosomatic index (GSI) of a) females and b) males of *Euthynnus alletteratus* in the southeastern Brazilian coast. Open circles (\circ) correspond to monthly sea surface temperature (SST, $^{\circ}$ C). Vertical bars show the 95% confidence interval.

almost year-round, except November when most fish were spawning. Regenerating testicles occurred in May-September and March, associated with warm, coastal waters (SST >18°C). Immature males (<28%) occurred in low frequencies in June and October, in waters above 17° C.

Length at first sexual maturity (L_{50}) was attained by one-year-old fish of either sex and was 423.7 mm FL for females and 492.8 mm FL for males (Fig. 9). Out of 345 fishes, only 3.47% were below the estimated L_{50} . The results suggest that a small proportion (8%) of juveniles came from beach-seine catches.

Validation

As Rt and FL relationship was similar in females and males (ANCOVA: F = 0.297; df = 1; P = 0.58), data were grouped in marginal increment analysis to reduce variability and increase sample size. A significant correlation between Rt and FL was obtained (F = 1901.226; df = 1; P < 0.01; R² = 0.88) (Fig. 10). Few 0+ fish were sampled, resulting in a high variance. Spine radius was significantly different for all ages (Fig. 11: H=136,4; P < 0.00), except 0+ and 1. Marginal increment variation was significantly associated to lower temperatures at age 2 (ANOVA: F = 4.163; DF =



Figure 7. Monthly means of a) hepatosomatic index (HI), and b) condition factor (K) of females and males of *Euthynnus alletteratus* in the southeastern Brazilian coast. Vertical bars show the 95% confidence interval.

1; P = 0.04). At age 3, however, water temperature had no effect in marginal increment (Kruskal-Wallis: H = 0.001; df = 1; P = 0.9). The edge aspect indicated that, for both ages, one increment is formed during springsummer (upwelling of SACW), when frequency of opaque edges was significantly higher than translucent ones ($\chi^2 = 5.64$; df = 1; P = 0.018) (Fig. 12b). During CW, translucent edges were statistically more frequent ($\chi^2 = 4.94$; df = 1; P = 0.026).

Readability, age composition, and growth

Readability of the 314 sectioned spines was classified mostly as high (53.1%) and low (44.2%); only 2.7% of spines were unreadable. The APE was 9.3%, and the CV was 9.2%. Assigned ages on spine sections ranged from 0+ to 5 years. Ages 2 (43.3%) and 3 (28.5%) predominated, and males were the most frequent in ages 1, 2, and 5 (60, 52, and 83%, respectively). When analyzed separately, 78% of males and 80% of females were 2-3 years old. Beach seine and purse seine's selectivity overlapped at 575 to 644 mm FL, corresponding to ages 2-3. Individuals between 425-574 mm FL and young one-year-old fish were captured only by beach seine. Larger (645-754 mm FL) and older (4-5 years) fish were restricted to purse seine catches. A wide range of lengths within the same age



Figure 8. Monthly frequency distribution of maturity phases: a) female and b) male of *Euthynnus alletteratus* in the southeastern Brazilian coast. A: immature; B: developing; C: spawning capable; D: regressing/spent; R: regenerating. The numbers above bars correspond to the number of samples per month.

was observed, especially between ages 2 and 3. Growth parameters were not significantly affected by sex according to Kimura's likelihood test (Table 1). The von Bertalanffy growth coefficients of all fish combined with confidence intervals were: $L_{\infty} = 791.9 \pm 33.4$ mm, $k = 0.42 \pm 0.09$ and $t_0 = -0.97 \pm 0.33$ yr⁻¹ (Fig. 13).

DISCUSSION

The onset of *Euthynnus alletteratus* spawning in the Cabo Frio region was observed in late spring-summer, from November to February, associated with the upwelling of deep colder waters ($<18^{\circ}$ C) near the coast. The spawning period during summer is in accordance with previous studies in Mediterranean waters (Mohamed et al. 2014, Saber et al. 2018), Gulf of Mexico (Cruz-Castán et al. 2019), and the western coast of Africa (Diouf 1980, Gaykov & Bokhanov 2008). According to Matsuura & Sato (1981), little

tunny larvae have been observed in offshore oceanic waters during late spring-summer (December-January), associated with warmer waters (25°C). In a similar condition, larvae of little tunny were recorded in temperatures from 24.1 to 25.4°C in the Gulf of Gabes (Koched et al. 2013). Present results show that water temperature tolerance of little tunny is not only lower than previously reported (Boyce et al. 2008), but also that spawning can happen in cold waters (<18°C), a first-time documented aspect for the species. Spawning periods related to upwelling events introduce the larvae into a rich habitat (Bakun & Parrish 1990). For some smaller warm-water tunas, adult feeding and spawning grounds greatly overlap (Collette & Nauen 1983, Reglero et al. 2014), and the highest productivity in the Cabo Frio region during the summer favors zooplankton as well as clupeids, an important food group for adults of E. alletteratus (Menezes & Aragão 1977, Manooch III et al. 1985, Valentin & Coutinho 1990, Falautano et al. 2007). Spawning period of the



Figure 9. The proportion of mature a) females and b) males *Euthynnus alletteratus* landed in the southeastern Brazilian coast.



Figure 10. Relationship between spine radius (Rt) and fork length (FL) of *Euthynnus alletteratus* landed in the southeastern Brazilian coast.

skipjack tuna (Martins et al. 2020), sailfish *Istiophorus* platypterus (Mourato et al. 2018), silver porgy Diplodus argenteus (David et al. 2005), red porgy Pagrus pagrus (Costa et al. 2021), anchovy Engraulis anchoita (Bakun & Parrish 1991), the Argentine hake Merluccius hubbsi (Costa et al. 2018) and the Brazilian sardine (Matsuura 1971, Matsuura 1998) are also associated with late spring and summer coastal upwe-



Figure 11. Spine radius (Rt) per number of increments identified.



Figure 12. a) Marginal increment (MI) and b) mean frequency of edge aspect in sectioned spines of selected 2and 3-years-old *Euthynnus alletteratus* during upwelling (SACW) and non-upwelling (CW) period.

lling in southeastern Brazil. Additionally, *Thunnus thynnus* in Mediterranean waters has also been reported to spawn in temperatures considerably lower than optimal, matching the offspring with ocean productivity and prey availability, in a trade-off between foraging and survival, when higher food abundance increases larval survival (Reglero et al. 2018).

E. alletteratus gonads were also strongly characterized by germinative cells in different developmental stages, resulting from multiple spawner species with an

	Hypothesis	Chi-squared	df	P-value
$H_0 vs. H_1$	$L_{\infty(F)}$ vs. $L_{\infty(M)}$	1.94	1	0.16
H ₀ vs. H ₂	K _(F) <i>vs.</i> K _(M)	2.30	1	0.12
H ₀ vs. H ₃	$t_{0(F)} vs. t_{0(M)}$	0.79	1	0.37
H ₀ vs. H ₄	$L_{\infty(F)}$; $K_{(F)}$; $t_{0(F)}$ vs. $L_{\infty(M)}$; $K_{(M)}$; $t_{0(M)}$	1.04	3	0.11



Figure 13. Observed lengths by fishing gear (symbols) and von Bertalanffy growth curve for combined sexes (all data) of *Euthynnus alletteratus* in the southeastern Brazilian coast.

asynchronous oocyte development and indeterminate fecundity (Schaefer 2001, Kahraman et al. 2008). This aspect was observed as all developmental phases occurred simultaneously along the year. Fishes in the capable spawning phase were associated with upwelled waters (<18°C). Spent and regenerating gonads were mostly observed in warm waters, especially during the year's first half, coinciding with low GSI values. Mean GSI values for females and males of *E. alletteratus* were compatible with those recorded for the species in previous studies, where the gonad weight corresponded from 0.8 to 1.2% of the body mass (Kahraman et al. 2008, Hajjej et al. 2010, Mohamed et al. 2014, Cruz-Castán et al. 2019).

Estimates of length at first maturity for *E. alletteratus* in the literature greatly differ and have been given for separated and combined sexes (Table 2). Our findings (females: 423 mm; males: 492 mm) are close to estimates from Senegal (400 mm; Diouf 1980), Tunisia (females: 448 mm; males: 428 mm; Hajjej et al. 2010), Egypt (~430 mm; Mohamed et al. 2014) and Spain (females: 500 mm; males: 434 mm; Saber et al. 2018). Sample classes were similar between these previous studies and ours, although some specimens of 97, 100, and 101 cm were sampled by Hajjej et al. (2010), Mohamed et al. (2014), and Saber et al. (2018), respectively. Fishing gears were similar to those used

in our sampling, consisting of gill nets, drift nets, and beach seine. The lowest mean L_{50} for the species (346-343 mm, F-M; Cruz-Castán et al. 2019) was recently recorded in the Gulf of Mexico due to smaller fishes (360-400 mm FL) caught by gill nets. The authors suggested that little tunny reproduces in smaller lengths in the Gulf of Mexico due to tropical fishes being smaller than those of greater latitudes and places of higher productivity.

This study is the first attempt to interpret increments in sectioned fin spines as a satisfactory method for age assessment of *E. alletteratus* in the southwestern Atlantic. The age composition was the same as the stocks from Mediterranean waters near Spain (Valeiras et al. 2008) and East Atlantic, near the Strait of Gibraltar (Rodriguez-Roda 1979). Ages were also close to those estimated by Kahraman & Oray (2001) in the Aegean Sea (6 years), Cayré & Diouf (1983) in the Senegalese coast (7 years), and by Kahraman & Oray (2001) in Mediterranean waters (7 years).

As the little tunny otoliths are very small and difficult to process, we found thin transversal sections of dorsal fin spines to be the easiest technique to apply with satisfactory results, as only 2.7% of the spines were classified as unreadable. The difficulties in reading fin spines included the reabsorption of the first two annuli in older fishes, making it necessary to estimate the radius of those lacking these growth marks and the existence of multiple thinner bands, which constituted an opaque or translucent band. These problems were reflected in the relatively high CV (9.18%) and APE (9.32%) results, although APE estimates were lower than those by Cayré & Diouf (1983) for the coast of Senegal (10.5%).

Even though it is the most commonly used age validation method, validation by marginal increment analysis is still difficult to interpret and is not an absolute validation method (Campana 2001). According to Cayré & Diouf (1983), the formation of growth marks in tunid spines is probably related to several factors, including migration, spawning, and environmental conditions such as temperature, that work both in combination and separately, affecting physiology, reproduction, and growth. Lower mean marginal incre-

Reference	FL	L ₅₀ (M-F)	Aging method	L_{∞}	k	to	T_{max}	Area
Rodriguez-Roda (1979)	400-900	570*	V	1.150	0.19	-1.71	5	Spain
Diouf (1980)	200-900	400*	S	995	0.30	-	-	Senegal
Cayré & Diouf (1983)	264-860	-	S	1.120	0.12	-	8	Senegal
Johnson (1983)	315-741	-	S/V					GOM
Kahraman & Oray (2001)	550-850	-	S	1.270	0.10	-4.10	6	Turkey
Kahraman & Oray (2001)	520-970	-	S	1.230	0.12	-3.80	9	Turkey
Valeiras et al. (2008)	480-840	-	S	915	0.39	-0.40	5	Spain
Hajjej et al. (2010)	367-978	448-428	-	-	-	-	-	Tunisia
Mohamed et al. (2014)	320-100	420*	-	-	-	-	-	Egypt
Adams & Kerstetter (2014)	250-832	-	0	779	0.60	-0.69	5	USA
Saber et al. (2018)	306-101	434-500	-	-	-	-	-	Spain
Cruz-Castán et al. (2019)	282-807	343-346	-	-	-	-	-	GOM
This study	330-780	492-423	S	791	0.42	-0.97	5	Brazil

Table 2. Size-range of fork length (FL, mm), length at maturity (L_{50}), aging method, growth parameters (L_{∞} , k, t_o), maximum age (T_{max}), sea surface temperature (SST, °C) during spawning, and area reported for *Euthynnus alletteratus*. M: male, F: female. V: vertebrae, S: spine, O: otolith. *Sex combined, GOM: Gulf of Mexico.

ments and highest frequencies of opaque edges in spines for fishes of 2 and 3 years occurred associated with cold upwelled waters (<18°C). Adams & Kerstetter (2014) observed the formation of two translucent increments annually, during summer and winter, in otoliths of little tunny captured in Florida. The authors suggest that one of the increments' formations could be related to changes in fish metabolism for gonad development as little tunny is a tropical and subtropical species and would not face drastic environmental changes. However, in the Cabo Frio system, the water temperature decreases up to 10°C during the upwelling season, affecting fish metabolism, growth, and reproduction. In Brazilian waters, the red porgy (Costa et al. 2021) has been reported to form an annulus during summer, from November to February, also associated with SACW upwellings and the reproductive tract activity. The Argentine hake is also known to form a growing mark during spring-summer. However, the formation of increments in juveniles and adults at the same time suggested that the regulating mechanism is not related exclusively to somatic growth or to reproductive activity (Costa et al. 2018).

Previous and present estimates confirm that little tunny is a fish of slower growth when compared to other species of the genus (Juan-Jordá et al. 2013), and capable of attaining larger sizes, with several reports of specimens around 1 m FL and growth coefficient values between 0.1-0.39 yr⁻¹ (Rodriguez-Roda 1979, Diouf 1980, Cayré & Diouf 1983, Kahraman & Oray 2001, Valeiras et al. 2008, El-Haweet et al. 2013). The faster growth (0.6 yr⁻¹) and smaller maximum sizes (779 mm) reported for the species off the coast of

Florida appeared to reflect the size composition of the samples, as most fishes were around 700 mm FL (Adams & Kerstetter 2014). The addition of any amount of data from smaller individuals is recommended to reduce the bias in VBGF parameter estimates, and the only situation when combining samples from two or more gears to achieve this goal may not be preferable to single-gear approaches is when both gears miss smaller individuals (Wilson et al. 2015).

In agreement with the hypothesis that fishes in tropical, subtropical, and high productivity areas (e.g. upwelling systems) grow faster and attain smaller sizes when compared to temperate areas counterparts (Pörtner et al. 2005, Watt et al. 2010), our southeastern Brazil results suggest that little tunny has higher growth rates (0.42 yr⁻¹) when compared to stocks in other areas of the Atlantic, as well as the Mediterranean. Furthermore, attain smaller asymptotic lengths (791.9 mm FL) (Table 2), a condition also suggested by Cruz-Castán et al. (2019) for little tunny in the Gulf of Mexico.

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