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Research Article

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Age, growth and maturity of frigate tuna (*Auxis thazard* Lacepède, 1800) in the Southeastern Brazilian coast

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Abstract – Age, growth and maturity of frigate tuna (*Auxis thazard*) were studied for the first time in Southeast Brazil. A total of 650 fish (265–494 mm Fork Length) were sampled from beach-seine landings between March 2018 and February 2019. Sectioned fin spines from 548 specimens were processed and age was determined by counting and measuring of increments. Growth parameters were fitted to length-at-age data using the von Bertalanffy growth function and were compared to the literature using the growth performance index (Phi). Macro and microscopic characterization of gonads and physiological indexes were used for the analysis of the reproductive cycle. The length distribution did not differ by sex. Assigned ages were between 0+ and 4 years, with annual increments formed during winter. Coefficient of variation between readings was 11%. Growth differed by sex, and the von Bertalanffy growth parameters were $L_\infty = 471$ mm; $k = 0.47$ year^{-1}; and $t_0 = -1.46$ year^{-1} for females; $L_\infty = 498$ mm; $k = 0.35$ year^{-1}; and $t_0 = -2.01$ year^{-1} for males. Phi was 5.0 for both sexes. Estimated growth rate is among the lowest recorded for the species, possibly related to the method used for age and growth assessment. Gonadosomatic index peaked in December, associated with the upwelling of the South Atlantic Central Waters, at a temperature of approximately 16 °C. Spawning activity in colder waters has never been reported for this species and may be influenced by a richer habitat caused by the intrusion of more nutritive rich waters during spring-summer, which allows larval development. Length-at-first-maturity (L_{50}) was 345.4 mm for females and 329.8 mm for males.

Keywords: *Auxis thazard* / age / growth / reproduction / southeast brazil / upwelling

1 Introduction

Scombrids sustain some of the most important fisheries in the world due to their high catches, usually high economic value and extensive international trade (Juan-Jordá et al., 2013). They have a wide distribution that includes tropical, subtropical, and temperate oceans (Collette and Nauen, 1983). Among the group, there are the small–bodied tunas, which includes species of the genus Scomberomorus, as well as the wahoo (*Acanthocybium solandri*), the plain bonito (*Orcynopsis unicolor*), the blackfin tuna (*Thunnus atlanticus*), the skipjack tuna (*Katsuwonus pelamis*), the Atlantic bonito (*Sarda sarda*), the three species of little tunas (*Euthynnus affinis; E. alletteratus* and *E. lineatus*) and the frigate and bullet tunas (*Auxis thazard*; *A. rochei*) (Lucena-Frédou et al., 2021). Fish from this group are important socio-economic resources for industrial fleets as well as for artisanal fisheries, despite the lower economic value when compared to larger tunas (Arrizabalaga et al., 2011; Pons et al., 2017).

The frigate tuna (*Auxis thazard*, Lacepède, 1800) is a small, epipelagic, cosmopolitan scombrid found in tropical and subtropical oceans, around islands and occupying continental shelves (Collette and Nauen, 1983). It reaches sizes of approximately 500 mm and a maximum age of 4 years in India (Abdussamad et al., 2005; Lelono and Bintoro, 2019). In Iran,

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Indonesia and Taiwan ages of 5 years have been estimated, however, *A. thazard* attains lower maximum sizes (Tao et al., 2012; Darvishi et al., 2020). Length-at-first maturity records are variable throughout its distribution (269–349 mm) and spawning season is long, with indeterminate fecundity usually associated to warm months (Schaefer, 2001; Ghosh et al., 2012; Tao et al., 2012; Jude et al., 2002; Bahou et al., 2016; Tampubolon et al., 2016; Calicdan-Villarao et al., 2017; Herath et al., 2019; Zapadaeva, 2021). In the Atlantic Ocean, age and growth assessments are limited to the Northeast and Equatorial areas (Grudtsev and Korolevich, 1986; Zapadaeva, 2021), whereas there are no reproduction studies. According to Lucena-Frédou et al. (2021), the great morphologic similarities between *A. thazard* and *A. rochei* may create difficulties in obtaining parameter estimates for the species separately.

The frigate tuna in the Atlantic is among the most captured small scombrid alongside the Spanish mackerel *Scomberomorus maculatus*, the Atlantic bonito *Sarda sarda* and the little tunny *Euthynnus alletteratus* (ICCAT, 2021). *Auxis thazard* is often caught as a by-catch (non-targeted species) by industrial purse seines and associated with FADs (fish aggregating devices; Amandè et al., 2010; Lucena-Frédou et al., 2021). According to the Report of the 2021 Standing Committee on Research and Statistics (ICCAT, 2021), frigate tuna corresponded to 13% (12.723 ton) of all reports for small tunas in the Atlantic Ocean and Mediterranean waters for 2020. In Brazil, it is frequently caught by purse seine and pole-and-line together with the skipjack and other tunas (*Thunnus sp.*), although the latter two account for most of the landings (da Silveira Menezes et al., 2010). In 2018, frigate tuna also represented 3.1% (36.1 ton) of the monitored rod and live–bait production (Martins et al., 2020).

Located in Southwest Atlantic (SWA), the Cabo Frio upwelling system is the most intense of the upwelled areas in the Brazilian coast (Kampel et al., 1997). The upwelling process occurs throughout austral spring–summer, when E-NE wind prevails and the topography promotes an upwelling of the cold (6–18 °C), less saline (34.5–36) and nutrient rich South Atlantic Central Water (SACW) from a depth of 300 m (Gonzalez-Rodriguez et al., 1992). As a result, a rich pelagic fauna that includes highly economic important species, such as the Brazilian sardine *Sardinella brasiliensis* and the skipjack tuna, is frequently observed in the area (Matsuura and Sato, 1981; Valentin, 2001).

Life history information such as age, growth and maturity are fundamental indicators of population dynamics and essential for the sustainable management of species (King, 2008). Many approaches have been developed in order to support the correct management of species lacking long-term fisheries, with some based on basic life history information (Lucena-Frédou et al., 2017; Pons et al., 2019). However, except for the skipjack tuna, knowledge on the biology of the small tunas remains incomplete or missing for most species of SWA, even if they are expected to suffer from higher fishing pressure as several valued tuna stocks are overfished (Juan-Jordá et al., 2013; Pons et al., 2017).

Although economically important, catches of frigate tuna off the Southeastern (SE) Brazilian coast are not subjected to fishing control or management policies, as the life parameter data for this species in SWA is not available (Lucena-Frédou et al., 2017). Therefore, our objectives are to investigate age and growth through assessment of increments on transversal sections of fin spines, and describe the maturity using physiological indexes and histological records of gonads. Additionally, we evaluate the relationship between sea surface temperature and the growth and reproductive activity of the species.

2 Material and methods

2.1 Sample processing

Biological samples were collected monthly from the artisanal beach seine fishery in Arraial do Cabo (Rio de Janeiro State, SE Brazil) between March 2018 and February 2019. Fresh fish were kept on ice before fork length (FL, mm), total weight (TW, g), gonad weight (GW, g), and sex were registered. Length-frequency distribution between sexes was compared by Kolmogorov–Smirnov test (D) and an analysis of covariance (ANCOVA) was performed to compare the parameters of the length–weight relationship (LWR) of both sexes. A *t* test was performed to test the b values estimated against isometry ($b = 3$), using the FSA package in R (Ogle, 2017).

Sea surface temperature (SST, C°) from March 2018 to January 2019 was also recorded by a Data logger (HOBO Tidbit UTBI-001) fixed on the shore at 1 m depth, where records were obtained every two/four hours (Fig. 1). This information was used to determine seasonal patterns of spawning activity and the periodicity of increment formation on the spines.

2.2 Age and growth

The first spine of the first dorsal fin was extracted and used for age assessment. Spines were cleaned and embedded in polyester resin before two thin transversal sections (0.5–0.65 mm) near the condyle were removed using a Buehler–Isomet metallographic saw. The photographic registry of the sections was performed using a stereomicroscope (Zeiss STEMI 508), with transmitted light at 40× to 100× magnification. A translucent band (associated with periods of low growth rates) and an opaque band (associated with periods of high growth rates) were considered to be an increment and the radius of each spine (R_t), as well as the radius of each increment (R_i), was measured to the nearest 0.001 mm (Fig. 2). Opaque bands were counted and each section was read two times, four months apart, by the same reader with no prior knowledge on size, sex, or capture date. When the first two readings differed, a third was performed and in cases of further disagreement the specimen was discarded from subsequent analysis. Reading accuracy was determined by the Coefficient of Variation (CV, Chang, 1982) and sections were classified as "Legible", "Low legibility" and "Illegible".

Age frequencies between females and males were compared using a Chi-square test (χ^2) and the periodicity of increment formation was investigated using marginal increment analysis (MI), calculated as $MI = (R_t - R_n)/(R_n - R_{n-1})$ where R_t is the spine radius and R_n and R_{n-1} are the radius of the outermost and penultimate increments, respectively. Monthly MI data for fish of 1 and 2 years, the most frequent, was tested for normality using a Shapiro–Wilk test and for homoscedasticity using a Levene's test. Thereafter, when restrictions were met, data was compared using an ANOVA followed by a Tukey's pairwise *post-hoc*. When the restrictions were not met,

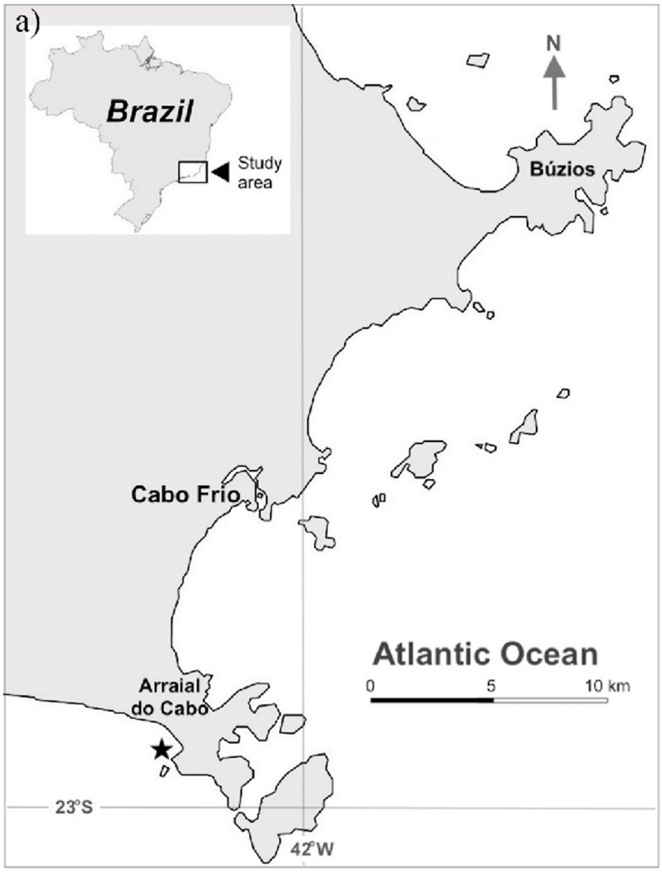

Fig. 1. Map of the Cabo Frio region, Southeastern Brazil. (★) corresponds to sea surface temperature measurements.

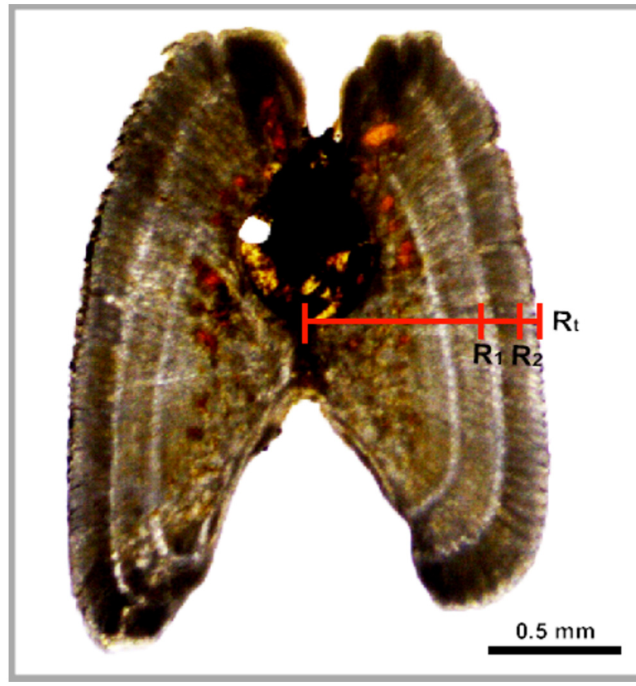

Fig. 2. Dorsal fin spine's transversal cut showing the spine radius (R_t) and identified increment (R_1; R_2) measurement position of a 2+ years old female specimen (422 mm FL).

a non-parametric Kruskal–Wallis analysis (*H*) was applied before a Mann–Whitney (*U*) post hoc (Zar, 2010).

Growth parameters were adjusted for observed lengths on the terms of the von Bertalanffy growth function (VGBF): $FL = L_\infty \times [1 - e^{-k\,(t-t)}0]$, where L_∞ is the asymptotical length, k is the growth rate constant i.e., the rate of approaching L_∞ and t_0 is the age when fish length is theoretically zero (von Bertalanffy, 1938). The likelihood ratio test was used to estimate the growth parameters (L_∞, K, t_0) for fish from 1 to 4 years (Aubone and Wöhler, 2000). Fish of 0+ years were not included in the estimation as the data for added too much noise to the estimates. Growth curve estimates of females and males were compared using Kimura's likelihood test (Kimura, 1980; Haddon, 2011) and the growth performance index (Phi) was calculated as $\phi' = \log(k) + 2 * \log(L_\infty)$, and used to compare the obtained growth parameters with those from literature.

2.3 Gonad maturity, spawning period and length-at-first-maturity (L_{50})

Gonad maturation phases were assigned for each fish as described by Brown-Peterson et al. (2011): "Immature", "Developing", "Spawning capable", "Resting", and "Regenerating". All fish included in one of the latter four stages were considered as adult. After visual classification, gonad subsamples were fixed in a solution composed of alcohol (76.5%), distilled water (8.5%), formaldehyde (10%) and glacial acetic acid (5%) for 24h and preserved in 70% alcohol. Afterwards, each sample was dehydrated in different series of alcohol concentration and included in paraffin before transverse sections of tissue (5 µm-thick) were sectioned with a microtome, mounted on glass microscope slides and stained with hematoxylin–eosin. Microscopic analysis was used to validate the macroscopic assignment of sexes.

The spawning period was assessed using the gonadosomatic index (GSI), calculated as GSI = (GW/(TW − GW) × 100, and the percentage of maturity stage by month. Monthly data was tested using Shapiro–Wilk and Levene's tests to verify the normality and homogeneity of the variance of the GSI data. Subsequently, an ANOVA followed by a Tukey's pairwise *post hoc* was applied, if restrictions were met. When restrictions were not met, a Kruskal–Wallis (*H*) non-parametric test followed by a Mann–Whitney's (*U*) *post hoc* was applied (Zar, 2010). Sex ratio was calculated by month and by size class, and observed results were compared to expected results using a Chi–square test (χ^2).

Length-at-first-maturity (L_{50}) was estimated using the logistic regression in the SizeMat package in R (Torrejon-Magallanes, 2020).

3 Results

3.1 Size distribution and length–weight relationship (LWR)

A total of 650 frigate tuna were sampled, including 321 females, 300 males, and 29 specimens without assigned sex. Females ranged between 269 mm and 494 mm (Mean:

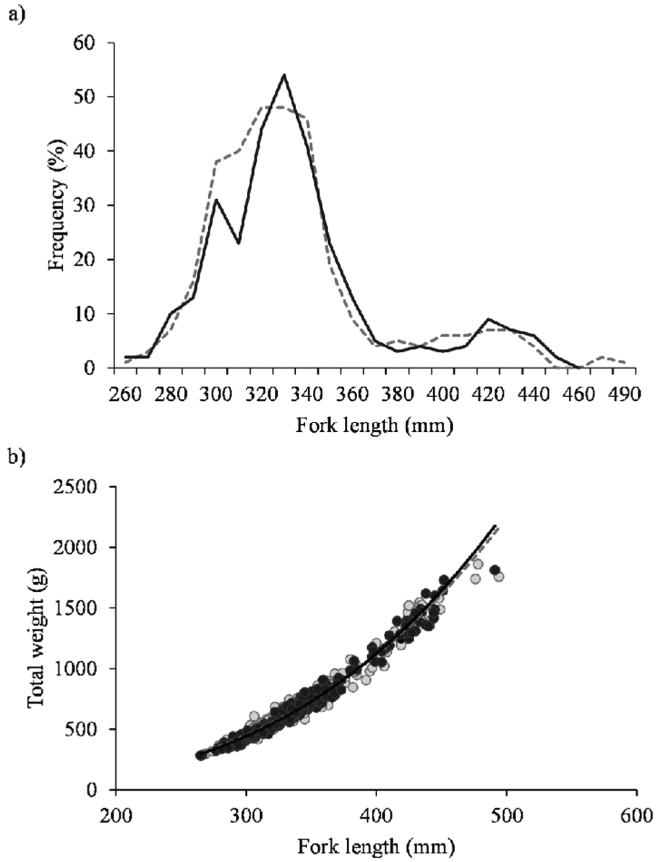

Fig. 3. (a) Fork length frequency for females (-----) and males (—) and (b) Length–Weight relationship and tendency lines for females (●; -----) and males (●; —) of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019.

338.2 mm) and males ranged between 265 mm and 452 mm (Mean: 340.5 mm). Length distribution was not different by sex (Kolmogorov–Smirnov: D: 0.074; $P = 0.34$) (Fig. 3a). Fish between 305 and 355 mm comprised 71% of the samples.

Comparison of LWR by sex did not indicate significant differences between parameters (ANCOVA: $F = 0.733$; DF = 1; $P = 0.39$) or regression's slopes (ANCOVA: $F = 2.459$; $P = 0.11$) (Fig. 3b). The equations that described LWR were $TW = 0.00007 \times FL^{3.14}$ for females ($R^2 = 0.96$), $TW = 0.00004 \times FL^{3.22}$ for males ($R^2 = 0.97$) and $TW = 0.00005 \times FL^{3.19}$ for all fish ($R^2 = 0.96$).

When tested against isometry, both sexes exhibited a positive allometric increase in weight by size ($P < 0.00$), with b between 3.06 and 3.24 for females and 3.17 and 3.32 for males, with 95% confidence.

3.2 Age determination and validation

A total of 548 spines were sectioned, with 495 (90.32%) successfully aged. From all ($n = 548$) sections analyzed, 327 (59.65%) were classified as legible, 168 (30.67%) with low legibility, and 53 (9.68%) as illegible. The coefficient of variation between readings was 11%.

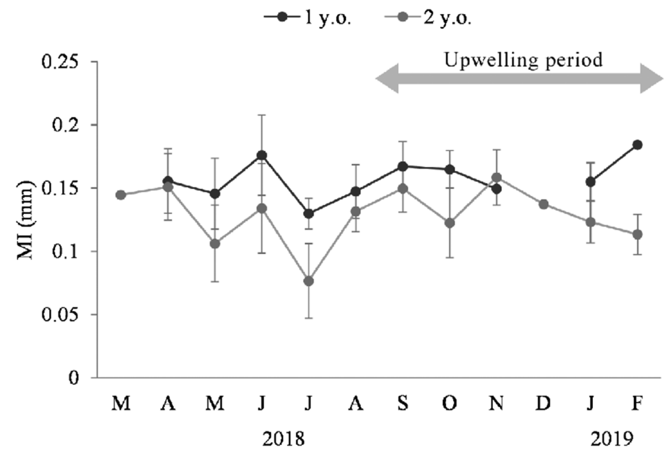

Fig. 4. Monthly means of marginal increment (MI) for 1 year (●) and 2 years–old (■) *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. Triangles (△) correspond to Sea surface temperature (SST, °C). Vertical bars denote 95% confidence interval.

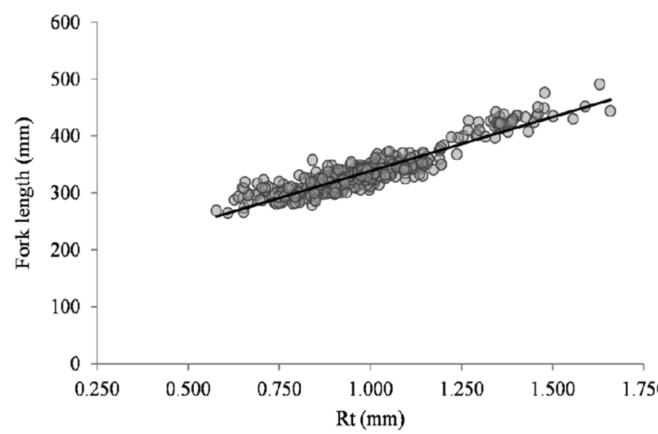

Fig. 5. Relationship between fork length and spine radius (R_t) of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019.

Increments were formed during winter, when Coastal Waters (CW) of SST > 18 °C were registered. MI values were significantly different for 1 y.o. (ANOVA: $F = 2.685$; DF = 9; $P < 0.005$) and for 2 y.o. fish ($H = 19.7$; DF = 11; $P = 0.03$) (Fig. 4).

The relationship between Rt and FL did not point towards differences in spine growth between sex (ANCOVA: $F = 2.133$; DF = 1; $P = 0.144$) so, as a mean to increase information and reduce variance, female and male data was grouped for the regression, which was significant ($R^2 = 0.84$; $F = 2413.4$; DF = 1; $P < 0.00$) (Fig. 5).

For females and males assigned age ranged from 0+ to 4 years (Fig. 6). The most frequent age class was 1 year for both sexes, which constituted of 54% of all aged fish. When analyzed separately, the frequency differed by sex ($\chi^2 = 0.02$; DF = 1; $P = 0.8$).

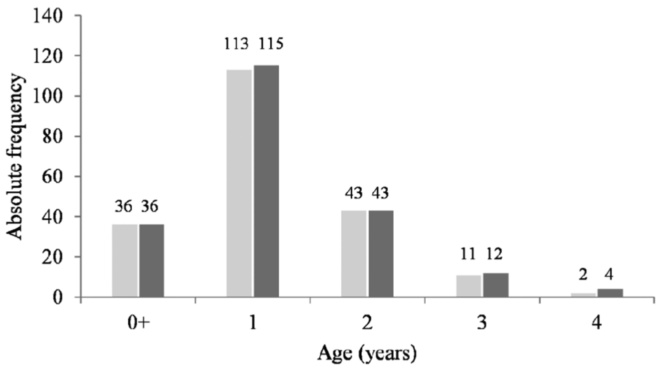

Fig. 6. Age composition of females (■) and males (-----) of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. Numbers above bars correspond to number of aged fishes.

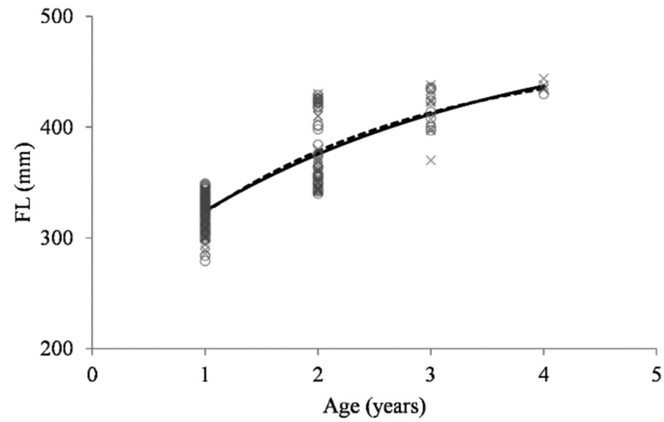

Fig. 7. von Bertalanffy growth curves for females (—) and males (—) of *Auxis thazard* landed in Southeastern Brazil between March 2018 and February 2019. Symbols represent observed lengths for females (○) and males (×).

Table 1. Kimura's likelihood test for *Auxis thazard* landed in Southeastern Brazil between March 2018 and February 2019. M – Male; F – Female.

Hypothesis		χ^2	*df*	*p*-value
H_0 vs H_1	$L\infty_{(F)}$ vs $L\infty_{(M)}$	4.48	1	0.03
H_0 vs H_2	$K_{(F)}$ vs $K_{(M)}$	4.25	1	0.04
H_0 vs H_3	$t_{0(F)}$ vs $t_{0(M)}$	3.75	1	0.05
H_0 vs H_4	$L\infty_{(F)}$; $K_{(F)}$; $t_{0(F)}$ vs $L\infty_{(M)}$; $K_{(M)}$; $t_{0(M)}$	4.63	3	0.20

3.3 Growth curves

Growth parameters estimated using the standard von Bertalanffy growth function (VBGF) were $L_\infty = 471$ mm; $k = 0.47$ year^{-1}; and $t_0 = -1.46$ year for females, $L_\infty = 498$ mm; $k = 0.35$ year^{-1}; and $t_0 = -2.01$ year for males (Fig. 7).

The Kimura likelihood test did not point towards differences between coincident curves ($\chi^2 = 4.63$; DF = 3; $P = 0.20$). However, when parameters were analyzed separately, L_∞ ($\chi^2 = 4.48$; DF = 1; $P = 0.03$) and k ($\chi^2 = 4.25$; DF = 1; $P = 0.04$) were different by sex, whereas t_0 was not ($\chi^2 = 3.75$; DF = 1; $P = 0.05$; Tab. 1). Females and males estimated growth performance index (ϕ') was 5.

3.4 Gonad characterization

Immature ovaries were strongly characterized by the presence of oocytes in primary development (PG; Fig. 8a). Ovaries at the beginning of the developing phase showed numerous PG oocytes, but also oocytes in the CA (Cortical–Alveolar) phase (Fig. 8b) and during final development CA oocytes were present in greater numbers, alongside oocytes in the Vitellogenic phase (Vit; Fig. 8c). "Spawning capable" ovaries had mature oocytes (MO) in bigger sizes and a displacement of the germinal vesicle to the animal pole (Fig. 8d), and when fish had partially spawned, ovaries exhibited postovulatory follicle complexes (POF) (Fig. 8e). Regenerating ovaries had fibrous nodules (NF) among numerous oocytes in PG and few CA oocytes (Fig. 8f).

Immature testicles exhibited spermatic cysts (SCy) on the walls of the testicular lobules (Fig. 9a). Developing testicles, however, had numerous testicular ducts (TD) with spermatic cysts in different development stages alongside its wall (Fig. 9b). Mature testicles showed spermatozoid cells occupying the testicular lobules and testicular ducts (Fig. 9c), and regenerating testicles displayed empty testicular ducts (Fig. 9d). Spermatic cysts were observed to occur only in the periphery of the testicles, restarting the spermatozoid production.

3.5 Sex ratio, reproductive cycle and length-at-first-maturity

The overall sex ratio (321:300) for *A. thazard* landed in Cabo Frio was 1:1 (Female:Male). The chi-square test did not indicate differences in sex ratio by month ($\chi^2 = 0.10$; $P = 0.75$) (Tab. 2), although there were a few significantly different months. Sex ratio between size classes also did not differ ($\chi^2 = 0.11$; $P = 0.74$), despite females dominating numerous classes (Tab. 3).

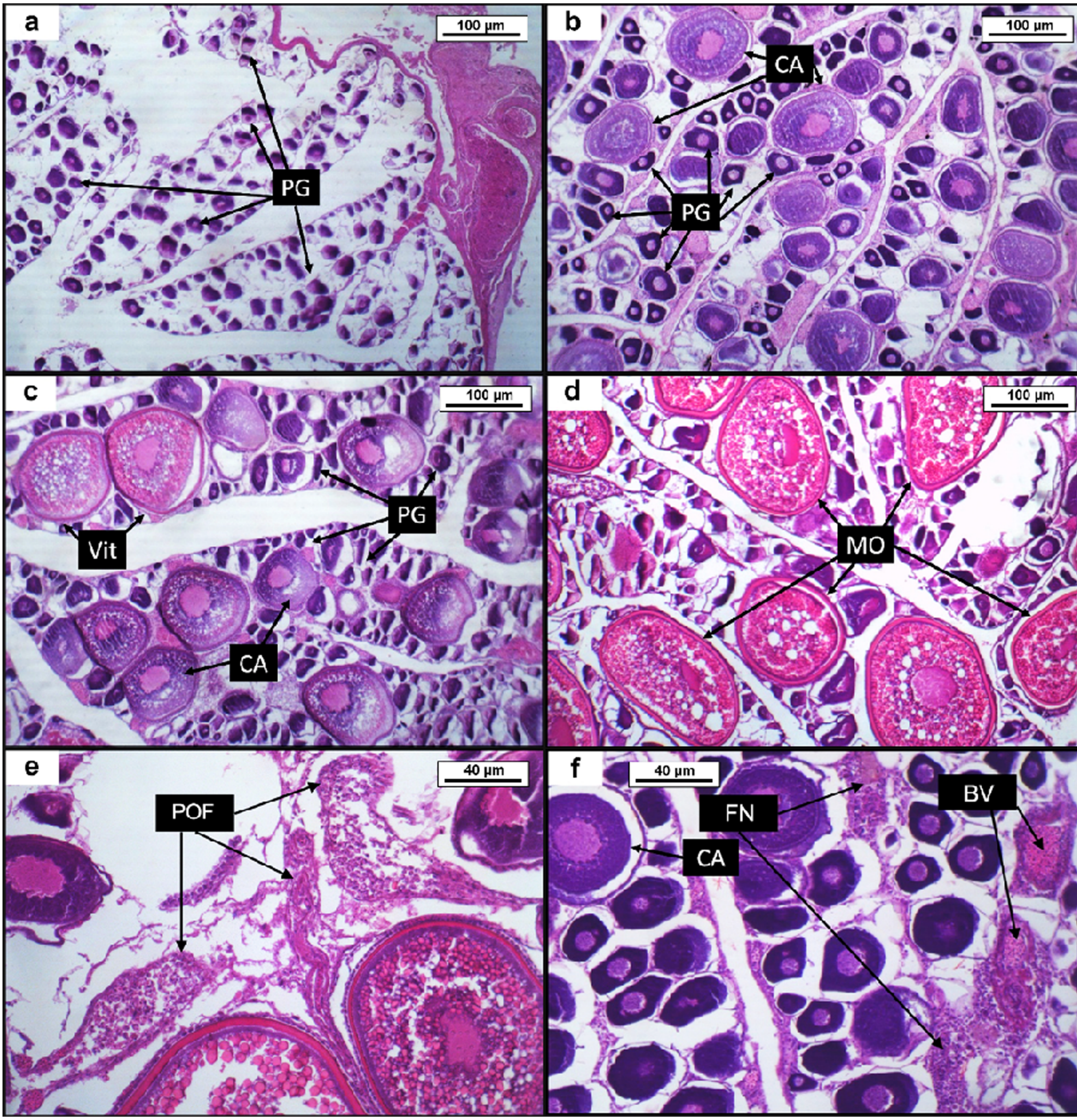

Fig. 8. Micrographs of the gonad section stained with hematoxylin–eosin from female *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019 (a–f). (a) Immature, (b) developing, (c) spawning capable, (d) spawning capable, (e) regressing/spent, (f) regenerating. PG: primary growth; CA: cortical alveolar; Vit: oocyte in vitellogenic stage; MO: mature oocyte; POF: post-ovulatory follicle complex; BV: blood vessel; FN: Fibrous nodule.

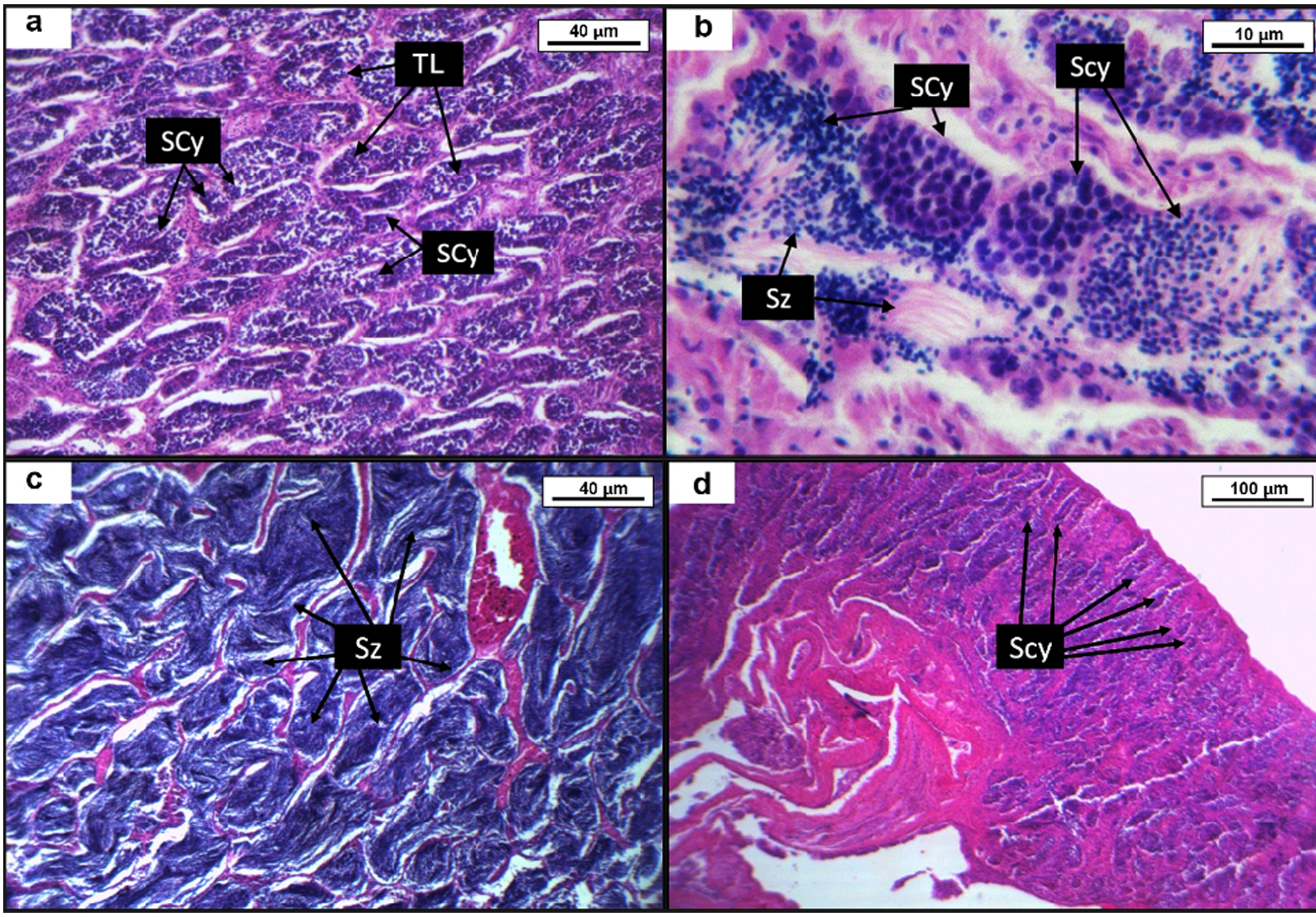

Fig. 9. Micrographs of the gonad section stained with hematoxylin–eosin from male *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. (a) Immature; (b) development phase; (c) spawning capable; (d) regeneration. TD: testicular duct; SCy: sperm cysts; Sz: spermatozoa.

Monthly data on gonadossomatic index showed that reproductive activity is inversely associated to SST progression for the frigate tuna in SE Brazil. Adults' GSI values increased from October onwards and maximum spawning activity was reached during spring–summer, when SST was at approximately 16 °C (Females: $H = 46.99$; DF = 1; $P < 0.00$; males: $H = 78.37$; DF = 1; $P < 0.00$; Figs. 10a and 10b).

Variation of gonad development stages showed that most sampled immature fish were associated to coastal waters (SST > 17 °C; Fig. 11). In contrast, developing and spawning fish were observed almost year-round, with no clear association with water temperature, despite spawning capable gonads constituting 84% of all gonads in November, right before maximum GSI values in December. Regressing (or partially spent) ovaries and testicles were the smallest fraction among samples (3.5%) and the highest frequency of gonads in this phase occurred in March, when only fish in spawning, regressing and resting phases were identified. Regenerating gonads were observed very sparsely.

Length-at-first-maturity was 345.4 mm for females (95% CI: 334.5–356.6 mm) and 329.8 mm for males (95% CI: 320.6–337 mm) (Fig. 12).

4 Discussion

The small-tunas are an important social and economic resource for coastal communities, having comprised 17% of the total catches of tuna and tuna-like species between 1950 and 2018, according to the ICCAT official catch statistics (Lucena-Frédou et al., 2021). Conversely, there are several gaps in their life history information, which are fundamental determinants of fish's population dynamics as well as essential to understand the impacts of fishing and to promote sustainable fishing practices (King, 2008; Juan-Jordá et al., 2013; Lucena-Frédou et al., 2021). The frigate tuna stock, in particular, has been identified as a priority to be evaluated by the ICCAT (Lucena-Frédou et al., 2017), and Pons et al. (2019) classified the data on life-history parameters of the species in the SWA as insufficient for a proper assessment of the stock.

In Brazilian waters, the scarce knowledge on *A. thazard* also hinders the management for the stock, even though it comprises of a target species for artisanal fisheries in SE Brazil (da Silveira Menezes et al., 2010; Martins et al., 2020). Additionally, the overexploitation of more valuable fish stocks

Table 2. Monthly variations in sex ratio of *Auxis thazard* landed in Southeastern Brazil between March 2018 and February 2019. χ^2=chi–square test.

	Number		Frequency (%)				
	F	M	F	M	χ^2	*p*-value	F:M
Mar	53	49	51.5	48.5	0.09	0.76	1.1:1
Apr	40	44	47.6	52.4	0.23	0.63	0.9:1
May	4	5	44.4	55.6	1.23	0.27	0.8:1
Jun	36	36	50.0	50.0	0.00	1.00	1:1
Jul	20	18	52.6	47.4	0.28	0.60	1.1:1
Ago	10	10	50.0	50.0	0.00	1.00	1:1
Sep	10	18	35.7	64.3	8.16	0.00	0.6:1
Oct	74	49	60.2	39.8	4.13	0.04	1.5:1
Nov	16	17	48.5	51.5	0.09	0.76	0.9:1
Dec	25	25	50.0	50.0	0.00	1.00	1:1
Jan	29	23	55.8	44.2	1.33	0.25	1.3:1
Feb	4	6	40.0	60.0	4.00	0.05	0.7:1
Mean	321	300	51.6	48.4	0.11	0.74	1.1

Table 3. Monthly variations by Fork length class (FL, mm) in sex ratio of *Auxis thazard* landed in Southeastern Brazil between March 2018 and February 2019. χ^2 = chi-square test.

	Number		Frequency (%)				
FL (mm)	F	M	F	M	χ^2	*p*-value	F:M
265	2	2	50.0	50.0	0.00	1.00	1:1
275	3	8	27.3	72.7	20.66	0.00	0.4:1
285	12	10	54.5	45.5	0.83	0.36	1.2:1
295	23	18	56.1	43.9	1.49	0.22	1.3:1
305	48	29	62.3	37.7	6.09	0.01	1.7:1
315	38	29	56.7	43.3	1.80	0.18	1.3:1
325	50	60	45.5	54.5	0.83	0.36	0.8:1
335	54	49	52.4	47.6	0.24	0.63	1.1:1
345	28	30	48.3	51.7	0.12	0.73	0.9:1
355	14	16	46.7	53.3	0.44	0.50	0.9:1
365	5	10	33.3	66.7	11.11	0.00	0.5:1
375	6	2	75.0	25.0	25.00	0.00	3.0:1
385	2	1	66.7	33.3	11.11	0.00	2.0:1
395	6	6	50.0	50.0	0.00	1.00	1:1
405	5	3	62.5	37.5	6.25	0.01	1.7:1
415	8	7	53.3	46.7	0.44	0.50	1.1:1
425	8	8	50.0	50.0	0.00	1.00	1:1
435	4	7	36.4	63.6	7.44	0.01	0.6:1
445	2	4	33.3	66.7	11.11	0.00	0.5:1
455	0	0	0.0	0.0	–	–	–
465	0	0	0.0	0.0	–	–	–
475	2	0	100.0	0.0	100	0.00	–
485	1	1	50.0	50.0	0.00	1.00	1:1
Mean	321	300	51.7	48.3	0.11	0.74	1.1

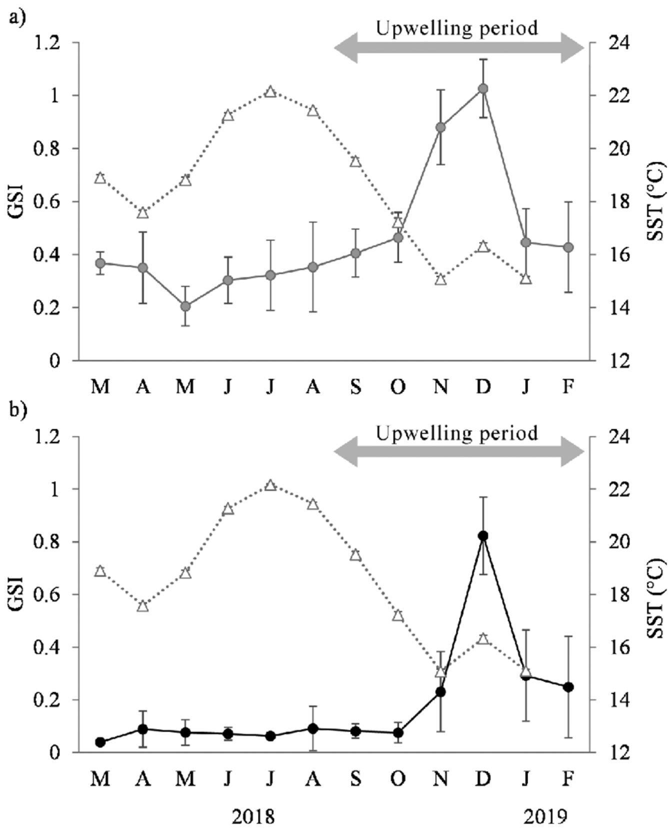

Fig. 10. Monthly means of Gonadosomatic index (GSI) for (a) females and (b) males of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. Triangles (△) correspond to Sea surface temperature (SST, °C). Vertical bars correspond to the standard deviation.

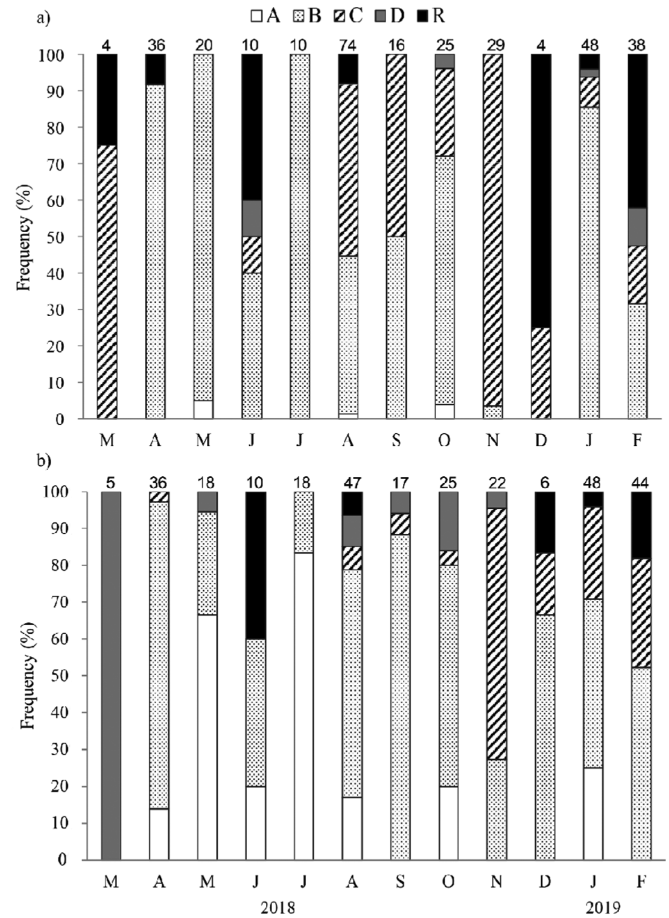

Fig. 11. Monthly frequency distribution of maturity phases for (a) females and (b) males of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. A: immature; B: developing; C: spawning capable; D: regressing/spent; R: regenerating. Numbers above bars correspond to the number of samples per month.

has resulted in their replacement by new target species, which includes some small-tunas (Fogliarini et al., 2021).

In line with these observations, this study provides new information regarding life–history parameters (age, growth, and maturity) of frigate tuna, which are essential for the assessment of the stock in SWA.

4.1 Length–weight relationship (LWR)

The positive allometric growth ($b > 3$) observed in our results suggests that frigate tuna in SE Brazil increases faster in weight rather than length. Likewise, frigate tuna in the Indian Ocean, Northeast Atlantic and Gulf of Guinea also exhibits positive allometric growth (Bahou et al., 2016; Tampubolon et al., 2016; Abekan et al., 2017; Herath et al., 2019, Darvish et al., 2020). For the North West Indian coast, Mudumala et al. (2018) calculated $b < 3$ for *A. thazard*, indicating a negative allometric growth, which the authors suggested to be caused by the absence of juveniles in the samples. Moreover, *A. thazard* caught on Veraval (India) was observed to have an isometric growth (Ghosh et al., 2010). The variations of the b parameter are possibly related to ecosystem and biological conditions such as temperature, salinity and food availability, and generalizations for the species should only be made after considering all the variables (Froese, 2006).

4.2 Increment formation

The completion of opaque bands occurred during winter when translucent increments, which reflect periods of slow somatic growth, started to deposit. Tropical fish growth is most likely to be influenced by temperature, as it directly affects metabolism (Morales-Nin and Panfili, 2005). However, the formation of increments in calcified structures (e.g., spines and otoliths) can also be influenced by spawning activity and/or food availability (Beckman and Wilson, 1995). Experiments on otoliths have shown that translucent material can be deposited in response to slow somatic growth caused by food restriction (Høie et al., 2008) and in the Cabo Frio upwelling system the wind direction changes during cold months (March to August, during autumn and winter), which leads the

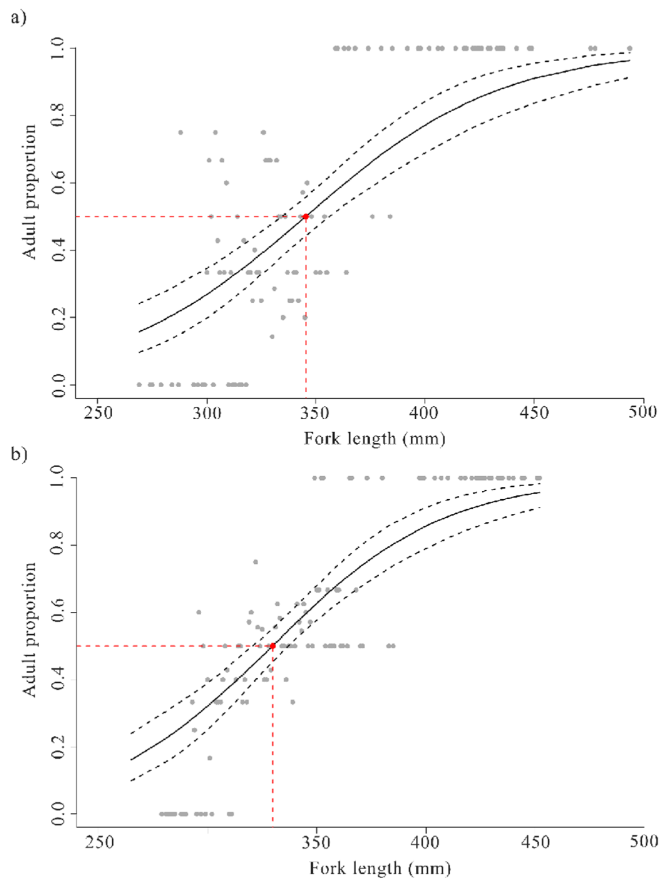

Fig. 12. Length-at-first-maturity (L_{50}) for (a) females and (b) males of *Auxis thazard* landed in the Southeastern Brazil between March 2018 and February 2019. Dotted lines (---) denote 95% confidence interval.

superficial depths to be occupied by warm, coastal waters that have less nutrients (Valentin, 2001).

Thus, the deposition of translucent material may be related to lower nutrient availability during winter, while more organic material is deposited due to the presence of highly productive waters of the SACW. This association was also corroborated by our samples' stomach content, as food was only present from September to February, during spring-summer (unpublished data). The formation of translucent growth marks during austral winter has also been reported for the little tunny *E. alletteratus* exploited off the Brazilian coast (Vieira et al., 2021).

4.3 Age and growth parameters

Reports of maximum age for the frigate tuna in the literature ranges from 3 to 5 years (Kasim, 2002; Abdussamad et al., 2005; Ghosh et al., 2010; Tao et al., 2012; Darvishi et al., 2020). Maximum age in our study was of 4 years, similar to recent observations in India (Mudumala et al., 2018); however, most studies in India have reported maximum ages of 3 years (Kasim, 2002; Abdussamad et al., 2005; Ghosh et al., 2010). Additionally, for Taiwan, Indonesia and Iran, the frigate tuna attains up to 5 years (Tao et al., 2012; Lelono and Bintoro, 2019; Darvishi et al., 2020).

Estimates of growth parameters (L_∞, k, t_0) from the literature are summarized in Table 4. Growth rate was similar and particularly high for maximum age in the Indian Ocean, where data was estimated using length frequency analysis (Kasim, 2002; Abdussamad et al., 2005; Ghosh et al., 2010; Mudumala et al., 2018). The exception is the most recent report by Lelono and Bintoro (2019), where the growth rate was 0.58 year^{-1} for frigate tuna caught in two landing sites off the Indonesian coast. Taiwanese estimates were also lower ($k = 0.50$–0.52) and similar to one another, despite using length frequency analysis and vertebrae, respectively (Lu et al., 1991; Tao et al., 2012). Regardless of variations, our estimates are among the lowest reported for growth rate, an aspect possibly related to the different methods and locations, since most assessments for the species have been conducted using length frequency analysis. This hypothesis is further corroborated by Grudtsev and Korolevich (1986), whose estimates for frigate tuna in Eastern Central Atlantic using spines were close to ours ($L_\infty = 514.5$ mm; $k = 0.32$). The growth performance index calculated herein ($\phi' = 5.0$) reflects the lower growth rates for asymptotic length obtained for *A. thazard* caught off SE Brazil. Our results were also among the lowest calculated values from previous studies' data, which varied from 4.8 to 5.6 (Tab. 4). The lowest value ($\phi' = 4.8$) was associated with the lower L_∞ (354 mm) estimated for the Indonesian population (Lelono and Bintoro, 2019).

4.4 Reproductive cycle

The onset of the frigate tuna's reproduction associated with cold waters was an unexpected result of our study, as most tunas are known to have a universal requirement for warm waters (>20 °C) to spawn (Schaefer, 2001). The *Auxis* genus has been observed to spawn throughout its range, in coastal to oceanic waters of tropical and subtropical areas (Collette and Nauen, 1983). Off the Indian coast, the reproduction occurs during summer, while in Gulf of Mexico it happens during spring, at SSTs above 20 °C (Ghosh et al., 2010). In Sri Lanka spawning season is from May to August, during autumn–winter, and in the Philippines reproductive activity peaks twice a year, in January and from March to April, in winter/spring (Calicdan-Villarao et al., 2017; Herath et al., 2019). In Côte d'Ivoire, spawning occurs from July to October, at temperatures between 22.14 and 25.15 °C, although gravid females were observed at temperatures between 27 °C and 28 °C (Bahou et al., 2016). In Brazilian waters, while previous data on the genus' reproduction is limited, Matsuura and Sato (1981) have described the distribution of *Auxis sp.* larvae along the SE Brazilian coast from samples collected in considerably varied SST (16–28 °C), but mostly from temperatures between 22 °C and 26 °C.

Spawning activity of *A. thazard* seems to favor more productive continental shelf and slope environments, and during spring–summer the intrusion of deeper and more nutritious waters of the SACW causes an enrichment of the habitat's productivity and enables the feeding and growth of larvae and adults (Valentin, 2001; Pruzinsky et al., 2020). This characteristic was also observed by Bahou et al. (2016)

Table 4. Size-range (FL, mm), ageing method, growth parameters (L_∞, k, t_0), maximum age (T_{max}), growth performance index (ϕ') and area reported for *Auxis thazard.* Ageing method: LF – Length frequency, V – Vertebrae, S – Spine; NE – Northeast; EC – Eastern Central.

References	FL	Method	L_∞	k	t_0	T_{max}	ϕ'	Area
Kasim, (2002) (Female)	–	LF	512.0	1.30	–0.00	3	5.5	India
Kasim, (2002) (Male)	–	LF	490.0	1.30	–0.00	3	5.5	India
Abdussamad et al., (2005)	180–300	LF	529.0	0.68	–0.28	3	5.3	India
Ghosh et al., (2010)	200–470	LF	466.0	0.93	–0.01	3	5.3	India
Mudumala et al., (2018)	160–500	LF	473.8	1.40	–0.23	4	5.5	India
Lu et al., (1991)	201–469	LF	484.4	0.50	–0.40	–	5.1	Taiwan
Tao et al., (2012)	198–456	V	481.8	0.52	–0.33	5	5.1	Taiwan
Calicdan-Villarao et al., (2017)	160–550	LF	409.5	0.60	–	–	5.0	Filipinas
Calicdan-Villarao et al., (2017)	160–550	LF	462.0	0.70	–	–	5.2	Filipinas
Lelono and Bintoro, (2019)	–	LF	354.0	0.58	–0.26	4.8	4.8	Indonesia
Darvishi et al., (2020)	210–490	LF	532.0	0.80	–1.17	5	5.4	Iran
Grudtsev & Korolevich (1986)	–	S	514.5	0.32	–0.83	–	4.9	EC Atlantic
Zapadaeva (2021)	–	LF	486	0.48	–	–	5.1	NE Atlantic
Present study (Female)	269–494	S	471.0	0.47	–1.46	4	5.0	Brazil
Present study (Male)	265–452	S	498.0	0.35	–2.01	4	5.0	Brazil

in Côte d'Ivoire, as peak spawning season occurred during main upwelling season. For some smaller tunas, adult feeding and spawning grounds considerably overlap, and sardines and anchovies, which are important food items for frigate tuna, are commonly found associated to upwelled waters in Brazil (Collette and Nauen, 1983; Valentin, 2001; Reglero et al., 2014; Herath et al., 2019). In SE Brazil, other tunas also seem to synchronize their reproductive activity with upwelling events, such as the little tunny *E. alletteratus* (Vieira et al., 2021) and the skipjack tuna *K. pelamis* (Soares et al., 2019).

The peak of spawning activity for frigate tuna was restricted to spring–summer; however, fish in developing and spawning phases were observed almost year-round, as illustrated by the monthly evaluation of gonad development, and the presence of germinative cells in different developmental stages simultaneously. Like other tunas, *A. thazard* has an asynchronous oocyte development that leads to long and multiple spawning seasons throughout the year, as observations in India and Gulf of Guinea suggest (Rudomiotkina, 1984; Schaefer, 2001; Ghosh et al., 2012; Abekan et al., 2017). Collette and Nauen (1983) have also mentioned the occurrence of adult fish throughout the year in the eastern Pacific, although spawning activity increases during some months.

4.5 Length-at-first-maturity (L_{50}) and sex-ratio

Length-at-first-maturity for *A. thazard* has been often estimated for combined sex. For other locations, L_{50} range between 269 and 349 mm, with most estimates under 330 mm (Ghosh et al., 2012; Jude et al., 2002; Tao et al., 2012; Bahou et al., 2016). Although within the range, our estimates (L_{50} = 329.6–345.6 mm) are among the highest for the species and are comparable to those of Tampubolon et al. (2016) (L_{50} = 348.9) and Jude et al. (2002) (L_{50} = 308–328) from Indonesia and India, respectively. When separated by sex, our results are similar to reports in India (Jude et al., 2002), where females of frigate tuna mature at greater sizes when compared to males. In contrast, the opposite has also been reported for the Taiwanese population (Tao et al., 2012).

The balanced sexual ratio (1:1, F:M) indicated the absence of sexual segregation in the area. Our findings were also similar to previous observations in other locations, such as Indonesia, Sumatra and the Philippines (Noegroho et al., 2013; Tampubolon et al., 2016; Calicdan-Villarao et al., 2017). When samples were analyzed by month, the number of females and males was not significantly different, despite fluctuations over time, in contrast to observations in the Gulf of Guinea, where males were dominant all year-round (Abekan et al., 2017). Conversely, when samples were divided by size, females were most numerous, although only a few classes significantly diverged from the 1:1 ratio. This suggests that both sexes are equally vulnerable to the fishery and that there is no size-related segregation for this species.

5 Conclusions

This study validated the use of fin spine as an age assessing method for the *A. thazard* caught in SE Brazil. The deposition of growth marks was completed during winter and the longevity of the frigate tuna (4 years) was close to observations in other areas, although the growth rate was among the lowest recorded for the species. Moreover, our observations of spawning gonads from fish in upwelled cold waters during spring-summer contradict the assumption that the frigate tuna only spawns at temperatures above 20 °C.

Small tunas such as the frigate tuna are important social and economic resources for coastal communities. However, the available data on this species is still scarce for management aims. Therefore, our study provides the ICCAT and other management institutions essential information on *A. thazard*'s biology in SWA, where no investigations on age, growth and maturity have been conducted. In Brazilian waters, particularly, there are no management policies for the frigate tuna's fishery and catches are underestimated, a problem aggravated by the deficiency of knowledge on the species.

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