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Reproduction Traits and Strategies of Two *Sardinella* Species off the Southwest Coast of Africa

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Abstract: Small pelagic fishes such as *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) are key intermediate-level components of the marine food web of the southwestern African coast. Their biomass off Angola has shown significant interannual variability, and information about their reproduction is insufficient in the region for adequate stock management. Thus, we aimed to unveil the reproduction period and reproductive traits of these two *Sardinella* species and establish a link with the prevailing ocean temperature conditions. Adult fish samples were obtained monthly from artisanal and semi-industrial fleets, and the ichthyoplankton samples were collected with a Hydro-Bios Multinet off southwest Angola by Instituto Nacional de Investigação Pesqueira (Angola). The macroscopic inspection of gonads showed that females of both species were more abundant than males. The gonadosomatic index and maturity stages indicate that *S. aurita* spawns during the Austral summer (December through March), while *S. maderensis* has a longer spawning period, from October to April. The spawning peak occurs in February for *S. aurita* and *S. maderensis*. The mean monthly condition factor of both species was high before and after spawning seasons. The females of *S. aurita* reach sexual maturity at a smaller size than males, and 50% of the population reaches sexual maturity at a total length of 31.3 cm. The males of *S. maderensis* reach sexual maturity at a smaller size than females, and 50% of the population reaches sexual maturity at a total length of 28.4 cm. We also found that both species use the southern coast of Angola as a spawning area during the Austral summer and avoid the area during periods of intense upwelling. Currently, these species are managed as a single unit, and the minimum capture size is set at 22 cm, well below the size at sexual maturity registered in the study area. Therefore, we strongly recommend increasing the minimum capture size to guarantee long-term stock viability.

Keywords: *Sardinella aurita*; *Sardinella maderensis*; reproduction; ichthyoplankton; spawning timing; sexual maturity; sea surface temperature; Angola

Key Contribution: This study provides new insights into the reproduction and spawning strategies of two *Sardinella* species. Their reproduction occurs mainly during the austral summer, and they avoid the coast off southern Angola during periods of intense upwelling. Sexual maturity occurs at bigger sizes than the minimum capture size for commercial fisheries, which prompts concern regarding long-term stock viability.

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1. Introduction

Understanding the reproductive biology of fish plays a crucial role in effective fisheries management, particularly in estimating stock size and tracking population trends [1]. For instance, knowing the size distribution of mature individuals informs gear design and supports more accurate estimates of spawning stock biomass, a key indicator of reproductive capacity [2–4]. Furthermore, reproductive traits such as spawning season, frequency, and size at maturity are essential for applying egg-based stock assessment techniques, including daily and annual egg production methods [5].

Small pelagic fishes such as *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) are crucial components of the food web off the southwestern coast of Africa by linking higher and lower trophic levels [6]. These species are found in tropical and subtropical regions of the Atlantic Ocean and Mediterranean Sea [7–9], thriving in productive upwelling areas [10]. They are fast-growing species with short lifespans (5–8 years) [9,11,12] and early sexual maturation [13]. *Sardinella* spp. are multiple spawner species [1,14] with protracted spawning seasons [1]. *Sardinella aurita* typically spawns twice yearly [12,15–17], and sexual maturity is reached at around 27.7 cm for males and 28.1 cm for females [9]. *Sardinella maderensis* reproduces continuously throughout the year [18], and sexual maturity is reached at 15.5 cm for males and 16.7 cm for females [19–21]. Differences in the reproduction traits between the species are probably related to overall habitat and environmental conditions [22].

There are three main stocks of *Sardinella* spp. along the west coast of Africa, which are influenced by sea surface temperature variations, including those induced by upwelling, and the associated shifts in productivity [23]. The southern stocks of *Sardinella* are shared between the Democratic Republic of the Congo and Angola, and are heavily exploited by artisanal and semi-industrial fishing fleets [24]. Off Angola, their migration along the coast is shaped by the upwelling regime and the Angola current [25,26]. These species contribute significantly to the local fisheries, accounting for over 88% of the total catch [27]. Their biomass has significant interannual variability [25,28,29], averaging $401 \pm 126 \times 10^3$ tonnes from 1985 to 2017 [30]. The mechanisms behind the biomass variability of *Sardinella* spp. off Angola are unclear, but recent observations suggest an expansion of these species into Namibian waters in the south linked to rising ocean temperatures. This migration occurs mainly during the austral summer due to an intensification of the warm Angola current, shifting the Angola–Benguela front to the south [31–33].

Despite several studies about their life history and spawning strategies throughout their distribution range, there is a substantial knowledge gap for the populations inhabiting and migrating along the southern Angolan coast. Their migrations are linked to reproductive activity during warm periods [30,34,35]; however, the pressing question is whether seasonal movements occur to avoid periods of intense upwelling. Hypothesizing that their southward aggregation pattern during the austral summer is related to reproductive activity, this study aims to characterize local oceanographic processes with spawning timing and reproductive traits of both *Sardinella* species.

2. Materials and Methods

2.1. Study Area

This study was conducted off the coast of Namibe in southern Angola (13°–17° S) (Figure 1). This region delineates the northern and southern boundaries of the cold Benguela Current and warm Angola Current. The high biological productivity of the region is driven by the nutrient-rich waters of the cold Benguela Current and the warm Angola Current, further enhanced by riverine nutrient inputs. The area where these currents meet is the Angola–Benguela front [36]. The coast of Namibe is one of the most important spawning and nursery grounds for small pelagic fish [34]. The southern limit of the Namibe coast, specifically Baía dos Tigres, is an important nursery area for fish species and has been designated as a special conservation zone.

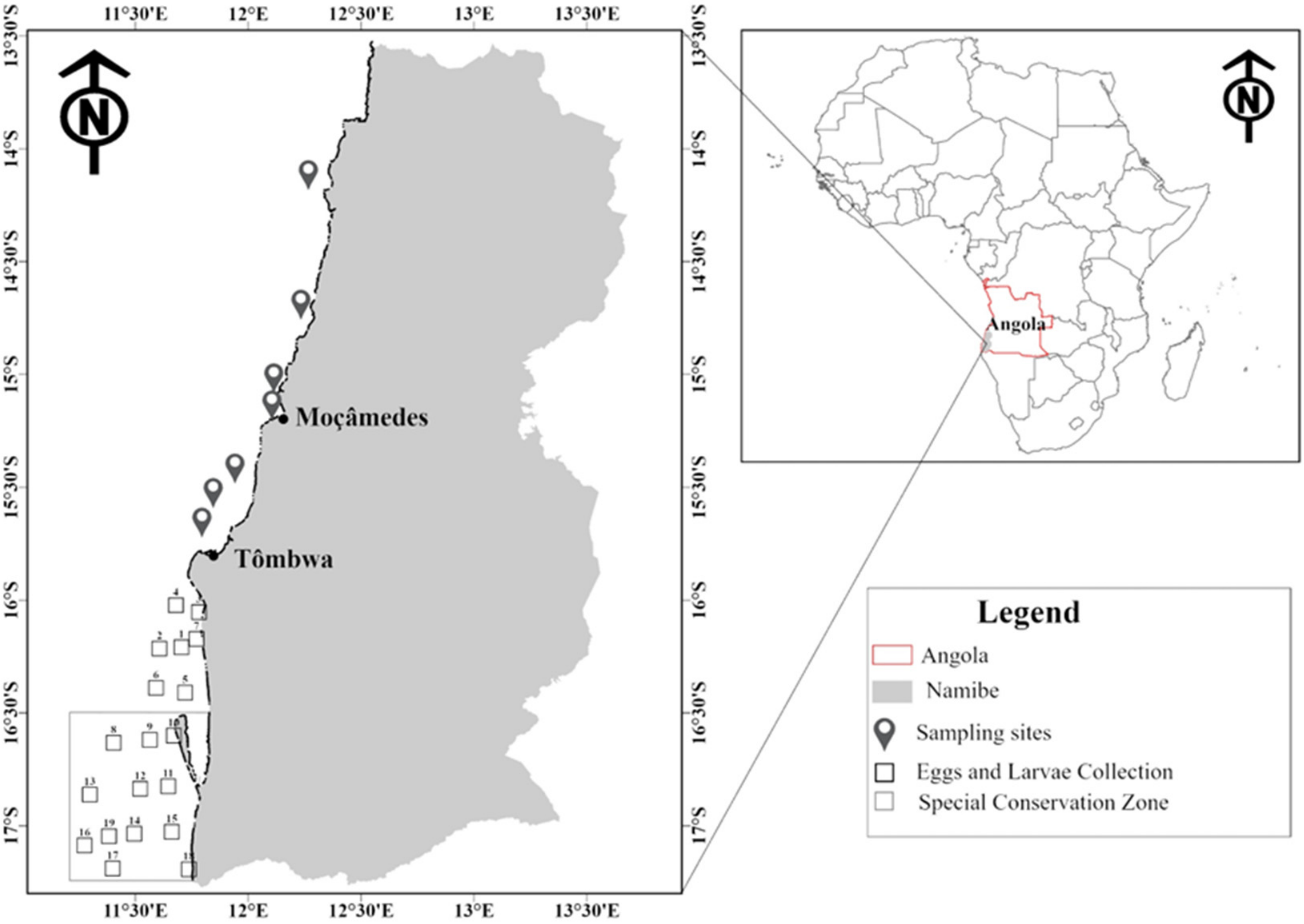


Figure 1. Map of the Namibe coast (south Angolan) showing the sampling sites of *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) (black pin marks) adult specimens, as well as the sites where ichthyoplankton samples were collected (small grey boxes). The larger grey box indicates the boundaries of the Special Conservation Zone at Baía dos Tigres.

2.2. Sea Surface Temperature Data

The sea surface temperature (SST) registered in 2016 and 2017 was linked with the spawning of *Sardinella* spp. The monthly average SST for the period between January 2010 and December 2020 was obtained from NASA's GIOVANNI visualization portal for the area off the coast of Angola (12° W, -17°2′ S; 15°5′ E and -5° S) and a box on the coast of Namibe (11°0′ E, 17°2′ S, 13°0′ E, 13°3′ S) [37]. Data were extracted from the MODerate-resolution Imaging Spectroradiometer (MODIS-Aqua) nighttime mapped product (Level 3) at a 4 km spatial resolution. An averaged Hovmöller plot for the 10-year period was made using NASA's GIOVANNI visualization portal to analyze the latitudinal variation off Namibe.

2.3. Sampling Process

Biological samples were collected from commercial purse-seine fleet landings operating along the Namibe coast and from the port of Namibe fish market. *Sardinella aurita* (n = 480) and *S. maderensis* (n = 357) were sampled monthly between January 2016 and December 2017 to investigate interannual variations in spawning timing and duration [14,38], size at maturity, and sex ratio. Due to their migration patterns along the coast, samples were not consistently available throughout the year, resulting in non-uniform sample frequency in terms of the number of specimens for both species (Table 1). After collection, specimens were transported to the Namibe Center of Marine Research to determine total length (TL, ±0.01 cm) and total weight (TW, ±0.01 g). After dissection, the sexes were macroscopically identified, and the gonads were weighed (±0.001 g).

Table 1. Descriptive statistics—sample size (n), average total length (TL), average total weight (TW), and their respective standard deviations (SD)—of *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) samples collected off the coast of Namibe in southern Angola from January 2016 to December 2017.

		Sardinella aurita			*Sardinella maderensis*		
	Month	**n**	**TL ± SD (cm)**	**TW ± SD (g)**	**n**	**TL ± SD (cm)**	**TW ± SD (g)**
2016	January	37	29.5 ± 1.9	323.6 ± 154.3	19	31.7 ± 0.9	329.8 ± 17.8
	February	24	31.9 ± 1.7	330.5 ± 53.2	13	32.2 ± 1.3	307.6 ± 26.6
	March	33	29.6 ± 2.1	292.0 ± 143.7	26	30.2 ± 1.6	293.8 ± 193.2
	April	40	23.4 ± 3.6	170.0 ± 127.4	16	31.1 ± 1.5	301.0 ± 196.3
	May	35	22.7 ± 1.3	187.1 ± 108.6	21	32.2 ± 1.3	427.1 ± 242.9
	June	24	22.9 ± 1.1	168.9 ± 102.0	33	25.2 ± 2.6	161.8 ± 73.0
	July						
	August						
	September						
	October	41	28.6 ± 2.5	405.9 ± 247.5	41	29.2 ± 1.2	369.0 ± 206.0
	November						
	December	28	31.0 ± 2.4	337.4 ± 145.5	23	31.6 ± 1.4	364.0 ± 163.0
2017	January	21	28.7 ± 1.1	326.7 ± 167.3	21	31.5 ± 1.2	552.5 ± 345.4
	February				18	32.6 ± 0.8	435.7 ± 149.8
	March	22	29.4 ± 1.3	298.2 ± 129.0	20	31.3 ± 1.9	260.1 ± 58.4
	April	42	22.9 ± 1.4	183.6 ± 108.8	16	25.0 ± 0.8	135.8 ± 11.7
	May	18	22.6 ± 1.2	125.7 ± 52.7	18	22.4 ± 0.7	129.9 ± 101.1
	June	25	19.1 ± 1.1	73.3 ± 27.4			
	July	26	21.5 ± 1.5	100.3 ± 31.7	21	23.4 ± 2.2	105.8 ± 42.8
	August						
	September	20	25.0 ± 0.7	193.3 ± 88.0			
	October				20	32.4 ± 1.0	475.1 ± 234.4
	November	23	27.0 ± 1.5	202.5 ± 62.6	13	31.6 ± 0.9	350.8 ± 136.1
	December	21	31.0 ± 1.0	442.0 ± 228.5	18	31.3 ± 0.7	361.6 ± 149.1

2.3.1. Sex Ratio and Sexual Maturity Stages

Based on the hypothesis that males and females occur in equal proportions in nature [38,39], the sex ratio was calculated as a proportion of females to males (F:M), with a theoretical sex ratio of 1:1. Differences between sexes were assessed through a chi-square test with the main hypothesis of proportionality between sexes with a significance level of 0.05. Sexual maturity was determined macroscopically by considering the structure, color, and relative size of the gonads [1]. Maturity stages were classified using a five-stage scale developed by the FAO (Table 2) [40]. Individuals at stages I and II were classified as immature, while those at stages III and above were classified as mature.

Table 2. Sexual maturity classification criteria using a five-stage scale developed by FAO [40] to determine the evolution of sexual maturity stages for *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) from the south coast of Angola.

Stage	State	Description
I	Immature	The ovary and testis are about one-third the length of the body cavity. The ovaries are pinkish and translucent. The testes are whitish, and the ova are not visible to the naked eye.

Table 2. *Cont.*

Stage	State	Description
II	Maturing virgin and recovering spent	The ovary and testis are about half the length of the body cavity. The ovary is pinkish and translucent. The testes are whitish and symmetrical, and the ova are not visible to the naked eye.
III	Ripening	The ovary and testis are about two-thirds of the length of the body cavity. The ovary is pinkish-yellow with a granular appearance. The testes are whitish to creamy. No transparent or translucent ova are visible.
IV	Ripe	The ovary and testis occupy two-thirds to the full length of the body cavity. The ovary is orange-pink with conspicuous superficial blood vessels. The ripe ova are large and transparent. The testes are whitish-creamy and soft.
V	Spent	The ovary and testis have shrunk to about half the length of the body cavity. The cavity walls are loose. The ovary may contain remnants of disintegrating opaque and ripe ova, darkened or translucent. The testes are bloodshot and flabby.

2.3.2. Length at Maturity

Length at sexual maturity was estimated for males, females, and combined sexes, using maturity ogives by fitting a logistic curve, considering the proportion of mature individuals (P) (stages III–V) per 1 cm length class (TL). The logistic regression was based on the equation proposed by [41,42] (Equation (1)),

$$P = \frac{1}{1 + e^{-(a+b\times L)}} \tag{1}$$

where P corresponds to the mature proportion by class size, L is the total length (cm), a is an intercept, and b is a slope. This formula was linearized using the natural logarithm, resulting in Equation (2).

$$\ln\left(\frac{1-p}{p}\right) = a + bTL \tag{2}$$

The regression between Ln $[P/(1-P)]$ and total length (cm) allowed the finding of parameters a and b (Equation (3)).

$$L_{50} = \frac{-a}{b} \tag{3}$$

2.3.3. Gonadosomatic Index

The gonadosomatic index (GSI) represents the ratio of gonad mass to total body mass and was used as a descriptor of spawning activity [43] (Equation (4)),

$$GSI = \left(\frac{GW}{W}\right) \times 100 \tag{4}$$

where GW is the gonad weight (g), and W (g) is the total fish weight. Thus, the spawning period was assessed through qualitative (monthly percentage of mature-stage individuals) and quantitative (monthly mean of the gonadosomatic index) approaches.

2.3.4. Condition Factor

The Fulton's condition factor (K) is used to indicate a fish's physiological condition [44] (Equation (5)),

$$K = \frac{EW}{(TL)^3} \times 100 \tag{5}$$

where *EW* is the eviscerated weight (g), and *TL* is the total length (cm), considering isometric growth (isometry is equal to 3). *K* values higher than 1 indicate good physiological condition [45].

2.3.5. Ichthyoplankton Collection

Ichthyoplankton data were obtained by the Instituto Nacional de Investigação Pesqueira (INIP, Angola) during pelagic survey cruises conducted in February and March 2016 and from October to December 2016 [46]. However, only samples from the first period (February and March 2016) were made available. Sampling for fish eggs and larvae was obtained from the super-stations (see black boxes in Figure 1) with a Hydro-Bios Multinet with a mesh size of 405 µm. The net was towed obliquely from ~10 m above the bottom or from a maximum depth of 100 m to the surface, with a speed of ~1.5 m s^{-1}. The fish larvae were preserved in a 4% formaldehyde solution buffered with borax, prior to identification in the laboratory. All fish eggs and larvae were placed on a Petri dish and identified under a stereomicroscope using an identification guide for the early life stages of clupeiforms [47,48].

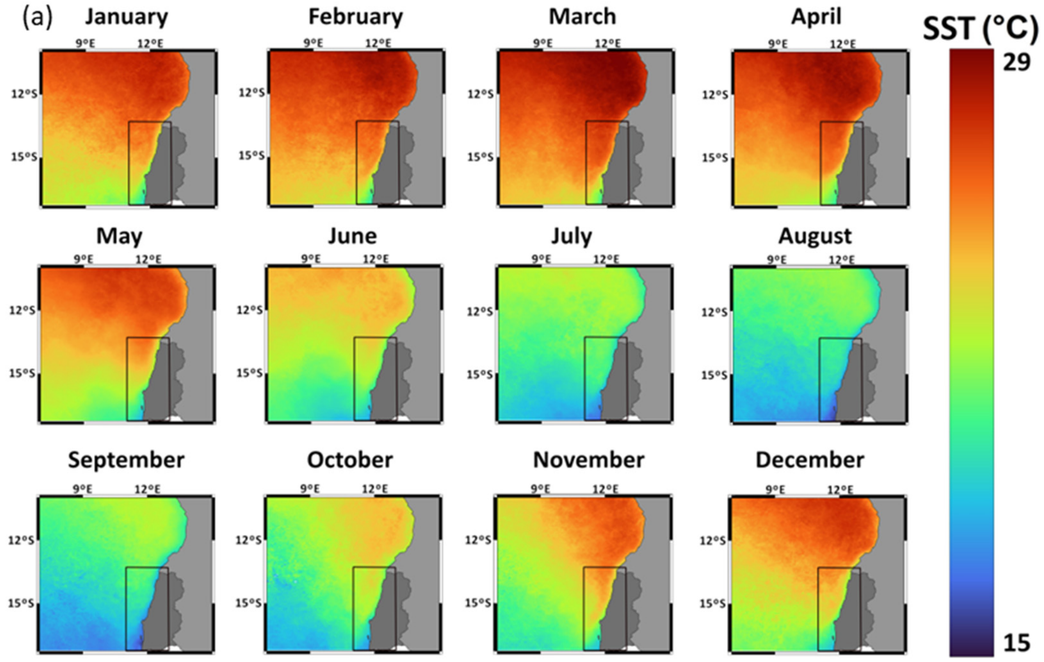
2.3.6. Statistical Analysis

Differences between the monthly mean values of the GSI and condition factor were determined with Kruskal–Wallis tests with a 0.05 significance level because the assumptions for an ANOVA test were unmet. A t-Student test was also performed to check interannual differences of mean GSI and K with a significance level of 0.05.

3. Results

3.1. Sea Surface Temperature Patterns

Due to limited local oceanographic data, monthly climatology off Angola (January 2010–December 2020) was used to provide regional context and compare with the sampling period. The coast off Angola shows a strong latitudinal temperature variation, with the lowest temperatures (<20 °C) being observed throughout the year off Namibe (black box), which is located between 16.0° S and 17.2° S (Figure 2).



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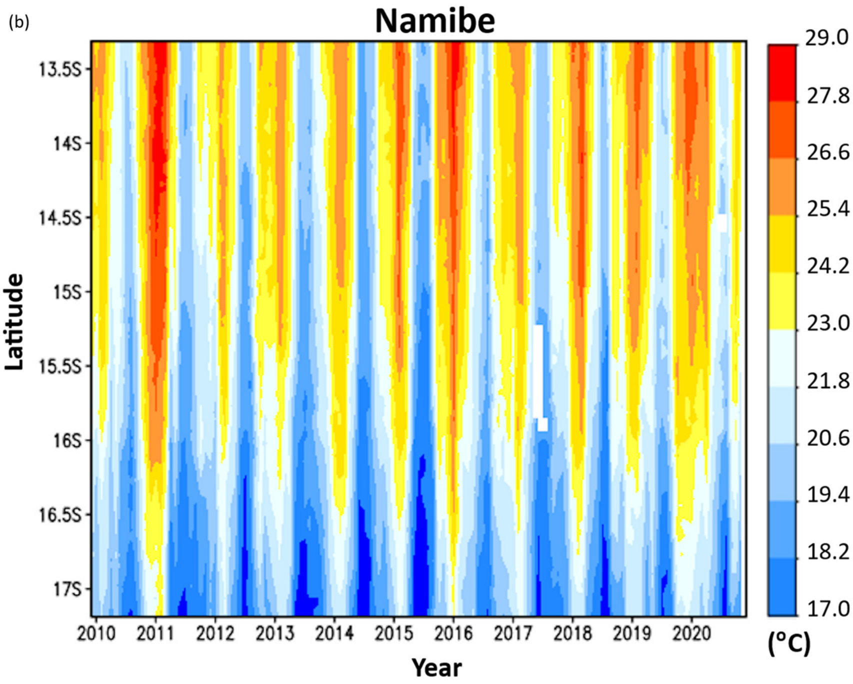
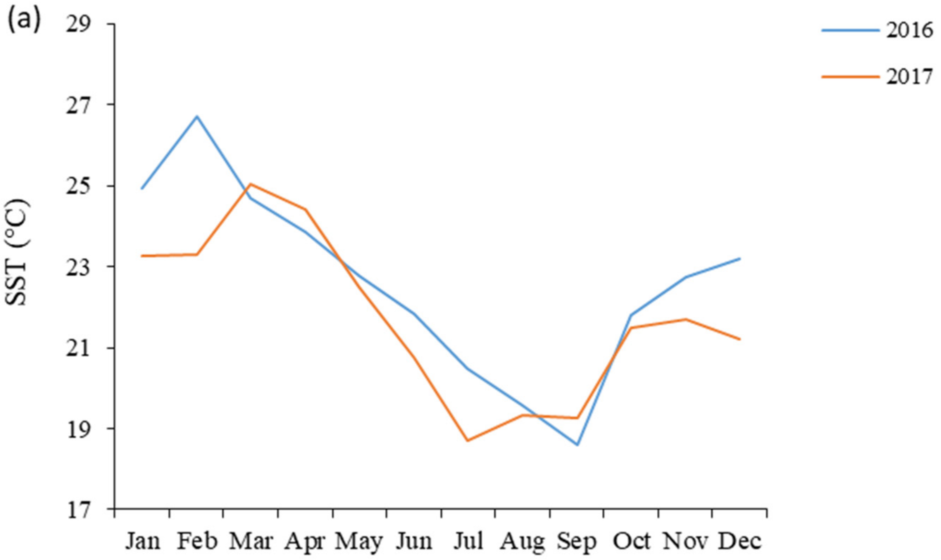


Figure 2. Monthly sea surface temperature (°C) composite off the coast of Angola (Africa) between 2010 and 2020 (**a**) and longitudinal-averaged Hovmöller plot of sea surface temperature for the Namibe coast (black box in panel (**a**)) for the period between January 2010 and December 2020 (**b**).

During the two sampling years, February (2016) and March (2017) were the periods with the highest SST values (26.7 °C and 25.2 °C, respectively) (Figure 3a). However, considering the whole period (10 years), the highest SST values were recorded in March (24.9 °C) and the lowest in August (18.8 °C). The year with the lowest temperature was observed during the Austral winter of 2015 (SST below 17.0 °C down to 16° S). Overall, June–September is the period with the lowest temperatures in the area. The black line is the monthly mean, and the grey area highlights the minimum and maximum values for the respective months (Figure 3b).



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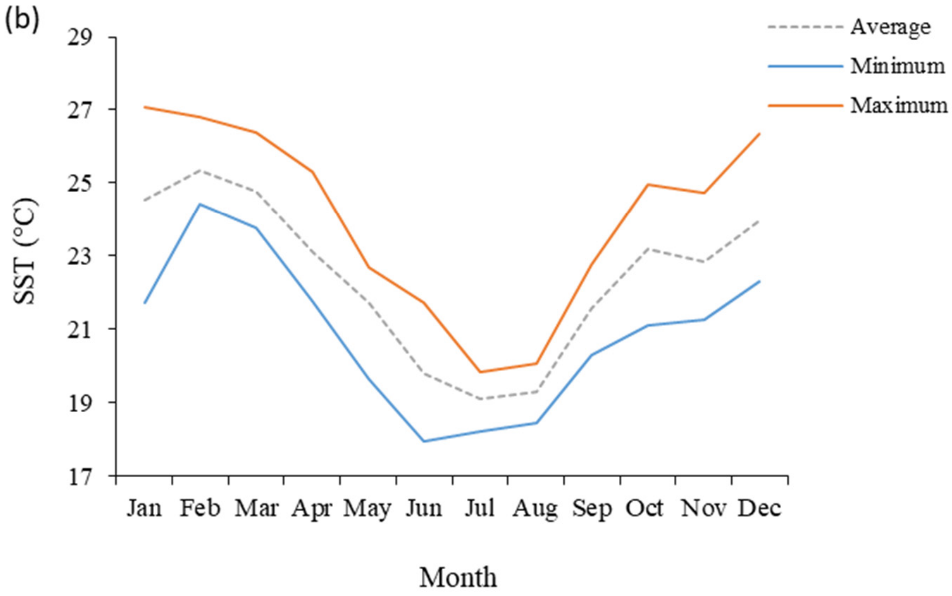
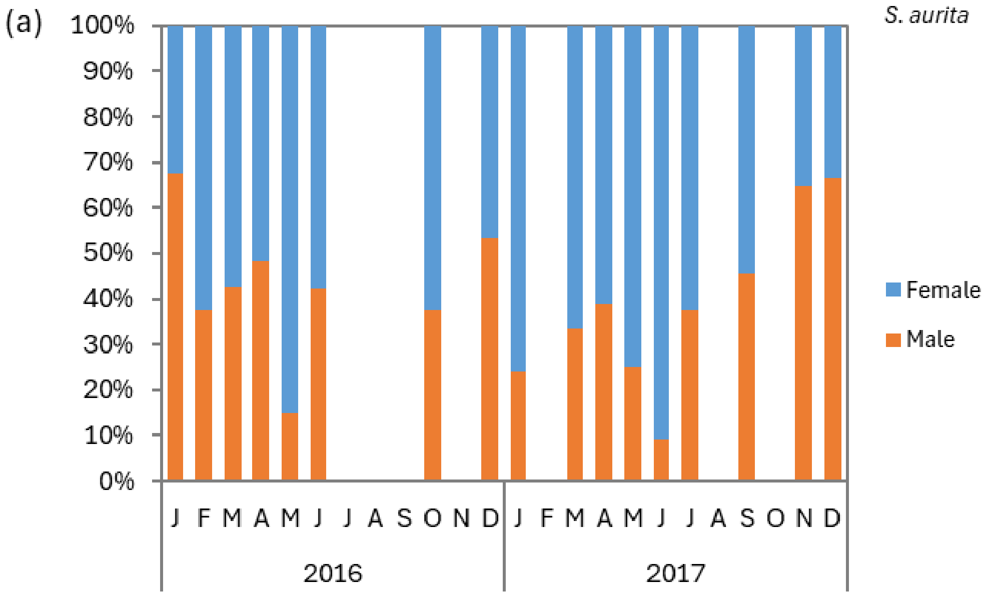


Figure 3. Average sea surface temperature for the period 2016–2017 (**a**), and minimum, average, and maximum sea surface temperature off the Namibe coast in southern Angola (Africa) (black box in Figure 2) for the period between 2010 and 2020 (**b**).

3.2. Sex Ratio and Size Distribution

Overall, the sex ratio variation shows a predominance of *S. aurita* females over males, 278 females (57.9%) and 202 males (42.1%), with a sex ratio of 1:1.4. The length class was higher for males (19–38 cm), which dominated the sample in January and December 2016 and November and December 2017 (Figure 4a). Similarly, females were more abundant in *S. maderensis*, comprising 191 individuals (53.5%) compared to 166 (46.5%) males, with a sex ratio of 1:1.2 for females. The dominance of males was notable in March, May, and December 2016 and in May and July 2017 (Figure 4b).



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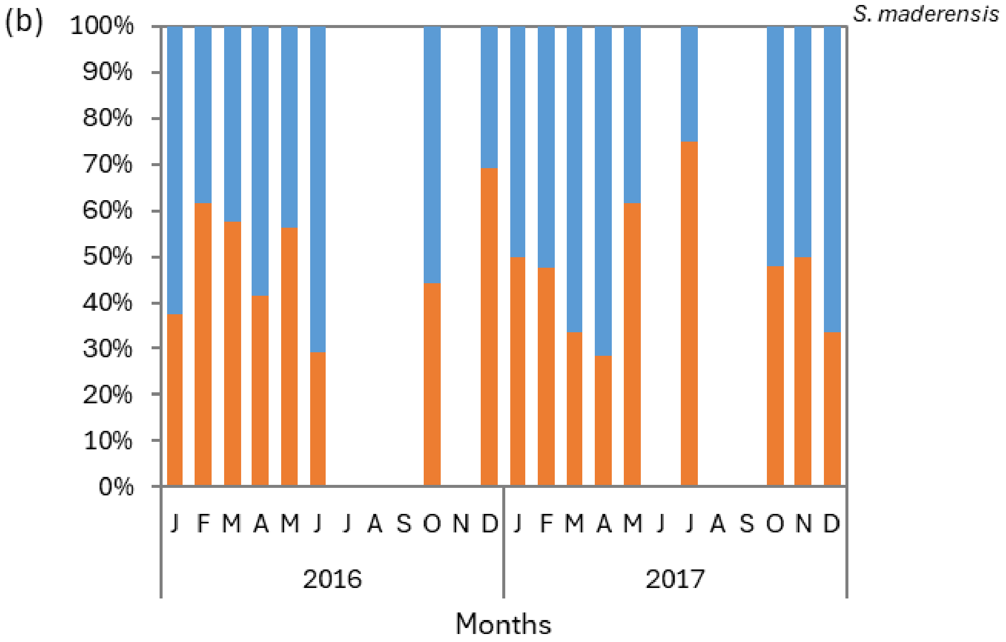

Figure 4. Monthly fluctuation in the sex distribution of (**a**) *Sardinella aurita* (Valenciennes, 1847) and (**b**) *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) during 2016 and 2017.

Regarding size classes, males dominated the larger classes, while females were more abundant in the smaller classes for *S. aurita*. For *S. maderensis*, however, females dominated most of the size classes except the 27 cm, 29 cm, and 34 cm classes (Figure 5). For *S. aurita*, there was strong evidence of differences in the monthly sex ratio between females and males in 2016 (χ^2 = 26.042; p = 0.006; df = 11) and moderate evidence for 2017 (χ^2 = 19.905; p = 0. 047; df = 11), while *S. maderensis* showed there was no evidence of differences in monthly sex ratio in 2016 (χ^2 = 13.103; p = 0.26; df = 11) and 2017 (χ^2 = 8.269; p = 0.69; df = 11).

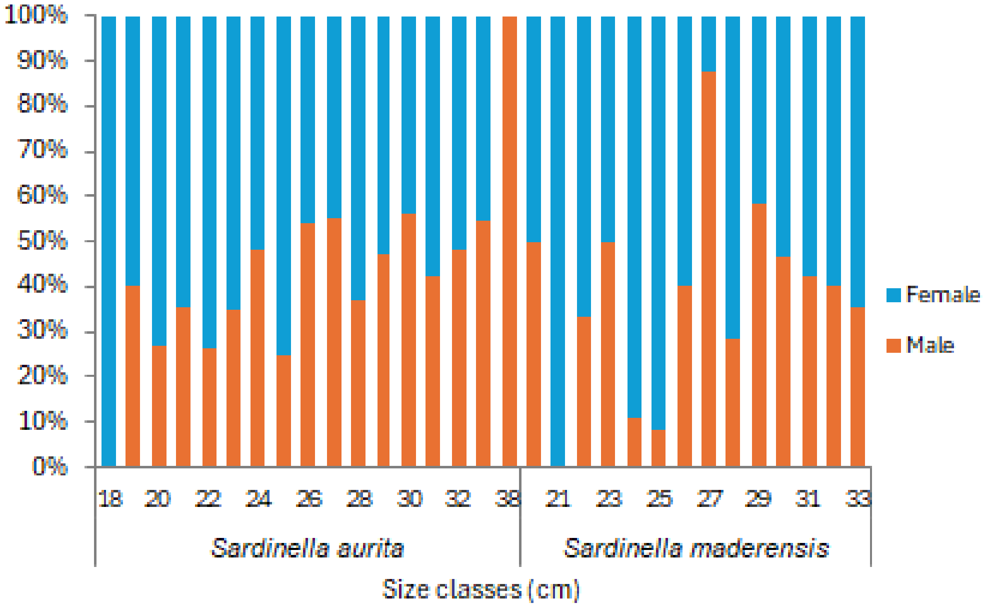

Figure 5. Relative composition of sex distribution across size classes for *Sardinella aurita* (Valenciennes, 1847) and *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) during 2016 and 2017.

3.3. Size at First Sexual Maturity

Size at first sexual maturity, determined from the percentage of mature individuals in the sample, indicates that 50% of the *S. aurita* population reaches sexual maturity at 31.3 cm. Females and males reached sexual maturity at 30.9 cm and 31.8 cm, respectively (Figure 6a). In *S. maderensis*, the total length at which 50% of the population reached first sexual maturity is 28.4 cm, while males matured at a smaller size than females, at 27.9 cm and 28.8 cm, respectively (Figure 6b).

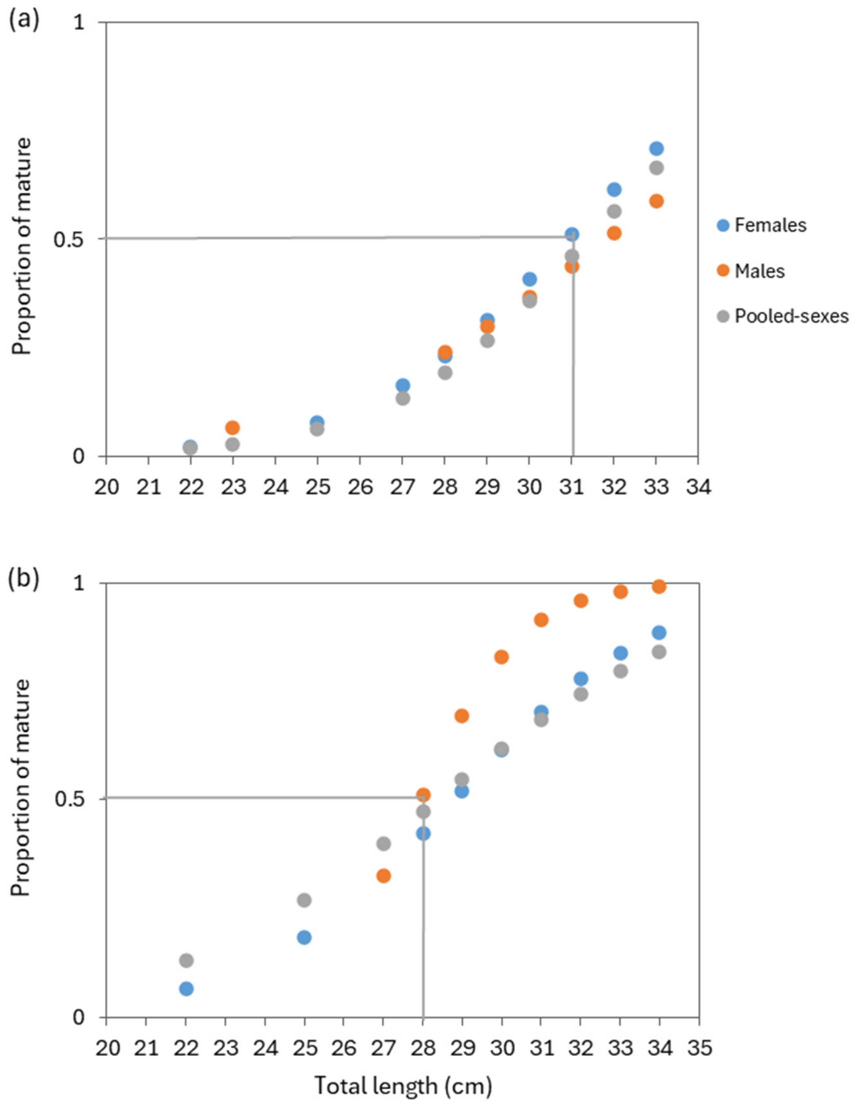

Figure 6. Size at sexual maturity for (**a**) *Sardinella aurita* (Valenciennes 1847) and (**b**) *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) between 2016 and 2017.

3.4. Sexual Maturity Stages

In 2016, an analysis of the average monthly maturity stages of *S. aurita*, based on macroscopic observation of gonads, suggested two spawning seasons: one from February to March, with spawning individuals representing 25% and 21% (stage IV), respectively, and another in December, with spawning individuals representing 27% of the sampled individuals. Post-spawning individuals (stage V) were predominant in February and March 2016, while immature individuals (stages I and II) were prevalent in the remaining months. In 2017, immature stages were prevalent throughout the year, stage IV individuals were only observed in March (10%) and December (27%), and stage V individuals were not registered (Figure 7a).

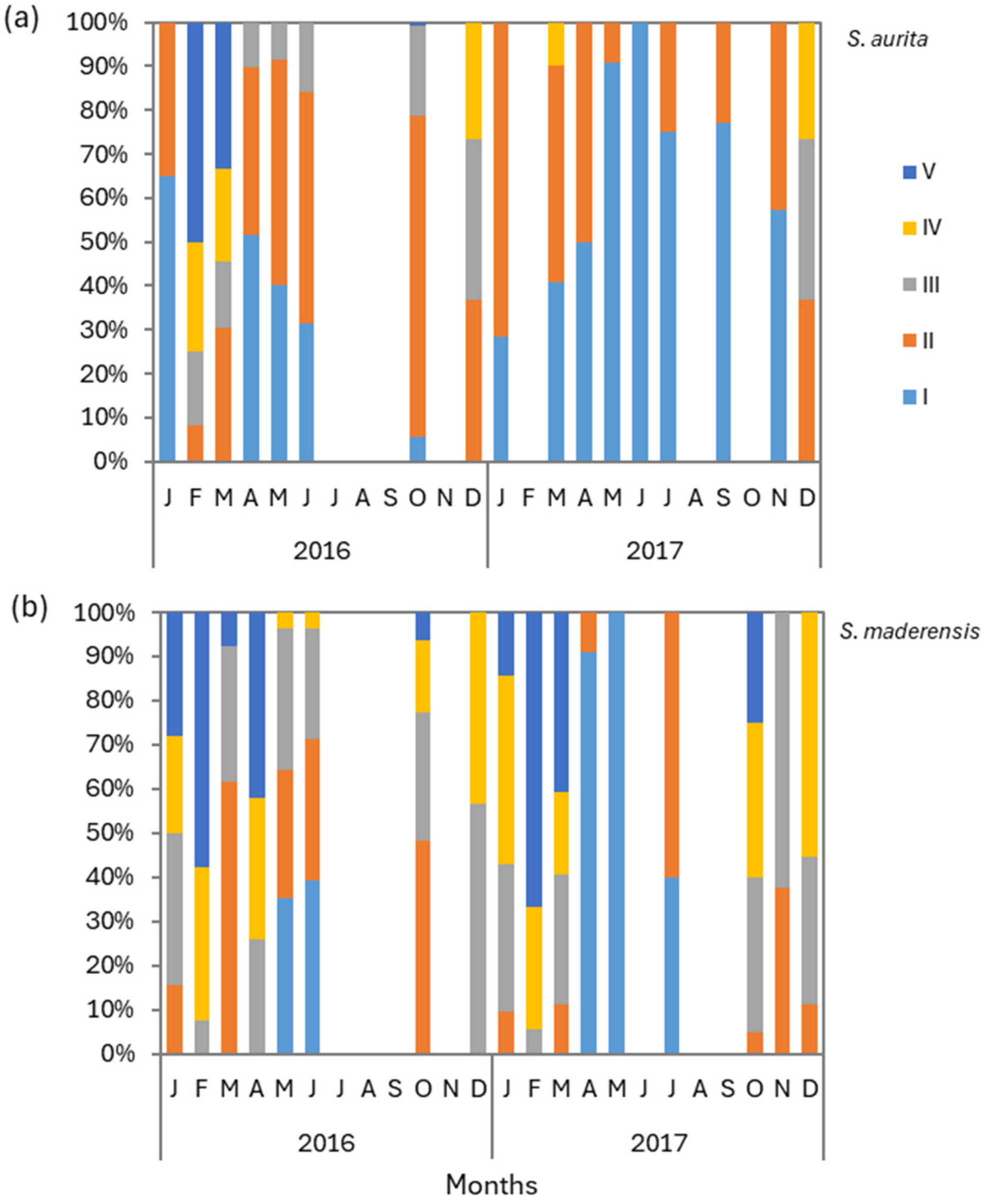

Figure 7. Monthly variation in sexual maturity stages of combined sexes for (**a**) *Sardinella aurita* (Valenciennes, 1847) and (**b**) *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) between 2016 and 2017.

For *S. maderensis*, an overall analysis suggests that this species matures between October and April. Mature individuals were present in the months sampled in 2016, with higher percentages of spawning individuals from January to April (except in March) and October and December (Figure 7b). In February and December 2016, 35% and 43% of individuals were in stage IV (spawning), respectively, while stage V (post-spawning) reached its highest percentage in February (58%), followed by April (42%). Immature individuals were absent only in February, April, and December, with the highest percentage in June (71%). In 2017, the highest proportion of spawning individuals (stage IV) was registered in December (56%), January (43%), and October (35%), while post-spawning individuals (stage V) dominated in February (67%). Immature individuals were most abundant in April, May, and July 2017.

3.5. Gonadosomatic Index

In 2016, the highest average GSI for *S. aurita* was observed in December (3.1), followed by 0.95 in February and March (Figure 8a). The same pattern was observed in 2017, with the highest GSI average recorded in December (2.75) and March (0.95), while the lowest average was observed in May (0.21). In 2016, the highest GSI average for *S. maderensis* was registered in January (4.91), followed by October (4.05), while the lowest average was observed in March (0.36) (Figure 8b). On the contrary, in 2017, October was the month with the highest GSI average (7.79), followed by February (5.8), but the lowest GSI average was registered in April (0.28). There was evidence of the monthly variation of GSI for *S. aurita* (2016: $H = 108.5$, $p < 0.001$; 2017: $H = 47.1$, $p < 0.001$) and *S. maderensis* (2016: $H = 106.3$, $p < 0.001$; 2017: $H = 79.5$ $p < 0.001$). Similarly, there was no evidence of differences in the mean GSI between 2016 and 2017 for *S. aurita* (t-test = 0.441; $p = 0.333$) and *S. maderensis* (t-test = -0.554; $p = 0.294$).

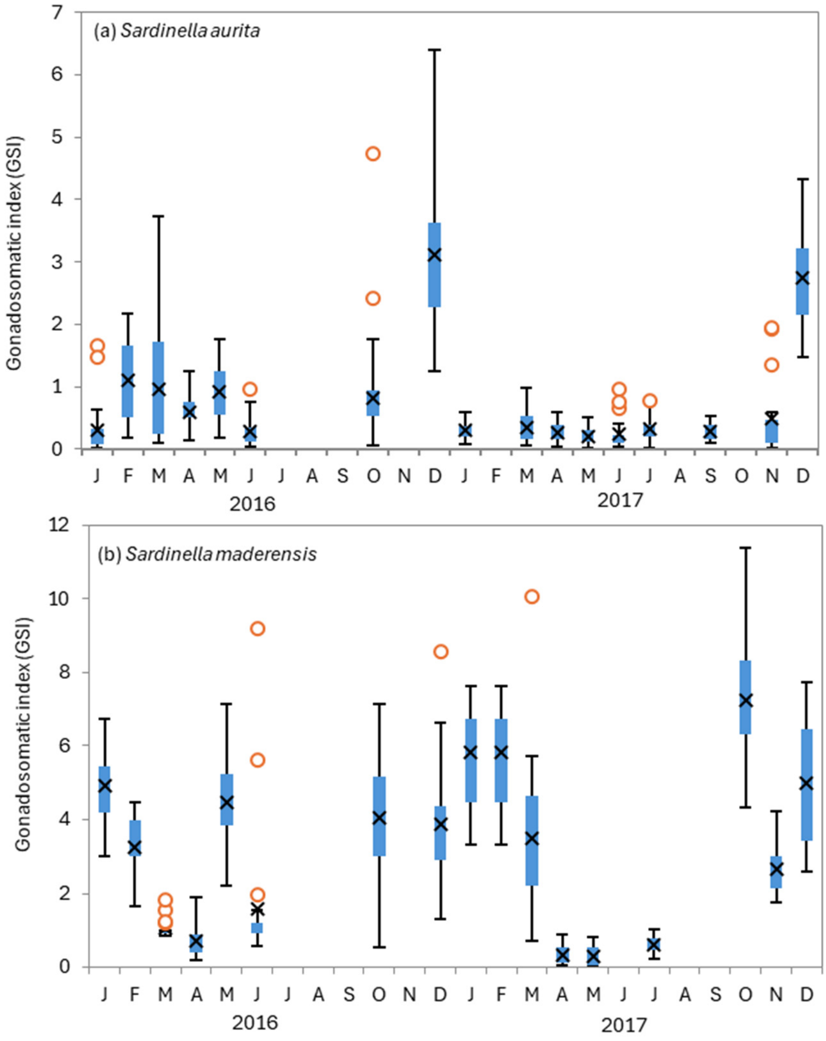

Figure 8. Monthly evolution of the gonadosomatic index (GSI) for (**a**) *Sardinella aurita* (Valenciennes, 1847) and (**b**) *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) between 2016 and 2017.

3.6. Condition Factor

The monthly average condition factor (K) for *S. aurita* in 2016 was highest in February and October (0.95) and lowest in June (0.84). In 2017, the highest mean K for *S. aurita* was recorded in February (0.97) (Figure 9a). In contrast, the K average for *S. maderensis* showed its highest value in May and October (0.91) (Figure 9b) and the lowest average in April (0.73). In 2017, the highest condition factor average of *S. maderensis* was observed in January (1.08) and the lowest average in June (0.72). For *S. aurita*, there was evidence of monthly variation in condition factor (2016: H = 197.5; $p< 0.001$; 2017: H = 123.1, $p < 0.001$) and in *S. maderensis* (2016: H = 82.1, $p < 0.001$; 2017: H = 68.8, $p < 0.001$). On the other hand, there was no evidence of differences in the mean condition factor between 2016 and 2017 for *S. aurita* (*t*-test = 0.181; $p = 0.429$) and *S. maderensis* (*t*-test = 0.496; $p = 0.314$).

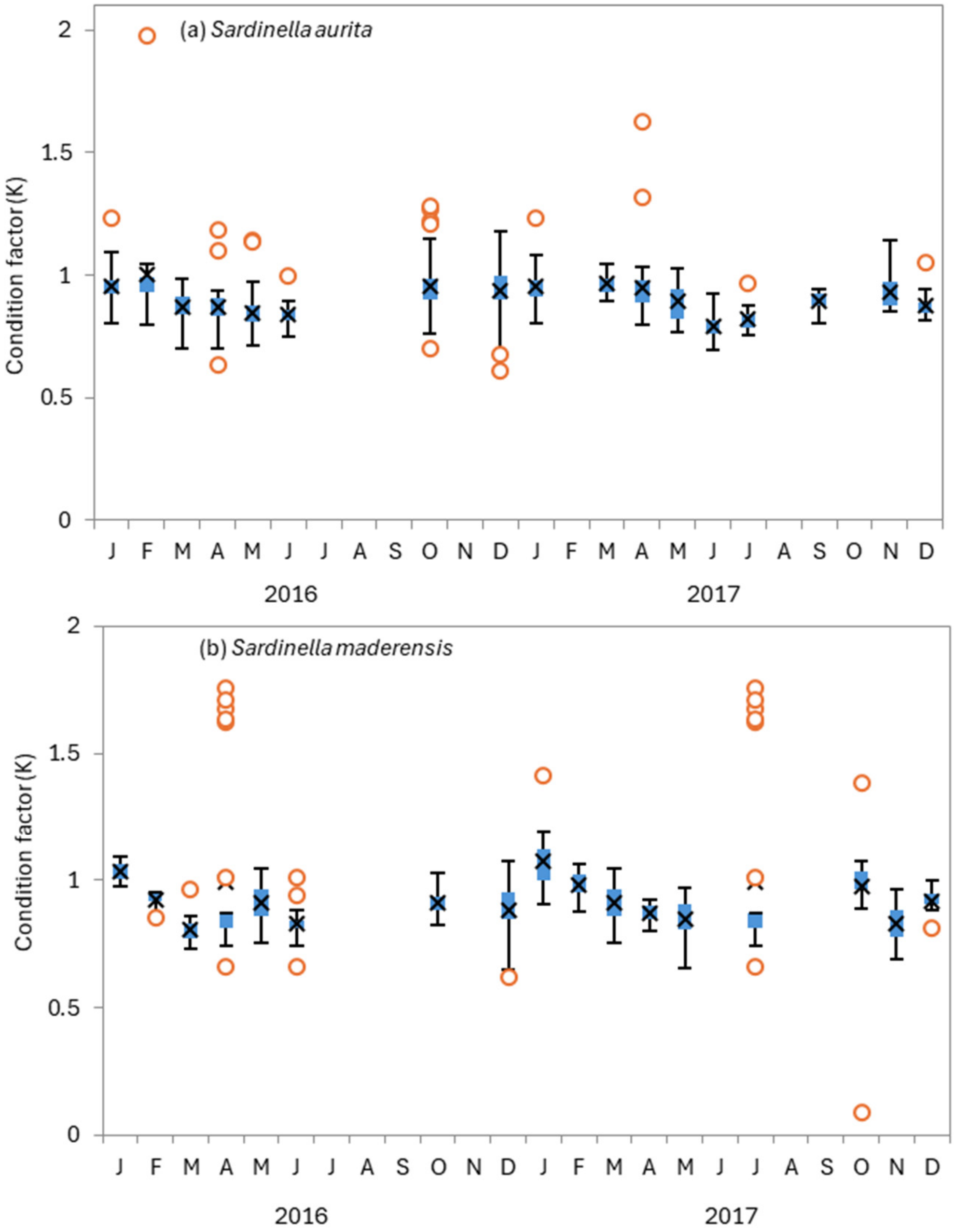

Figure 9. Monthly evolution of the condition factor (K) for (**a**) *Sardinella aurita* (Valenciennes, 1847) and (**b**) *Sardinella maderensis* (R. T. Lowe, 1838) from the southern coast of Angola (Africa) between 2016 and 2017.

3.7. Ichthyoplankton Collection

Ichthyoplankton samples were collected at 18 stations between February and March 2016, when *Sardinella* spp. migrates to the southwest coast of Angola. In total, 228 and 157 eggs and larvae of *Sardinella* spp. were counted, respectively (Table 3).

Table 3. Total number of eggs and larvae of *Sardinella* spp. collected off the southern Angola coast in February and March 2016 between the Tômbwa Bay and the Cunene River.

Station	Eggs	Larvae	Latitude	Longitude
1	15	35	17° 11′ 34″ S	11° 35′ 28″ E
2	7	5	17°11′ 21″ S	11° 23′ 56″ E
3	4	16	17° 13′ 78″ S	11° 21′ 06″ E
4	11	2	17° 05′ 14″ S	11° 16′ 23″ E
5	14	11	17° 06′ 60″ S	11° 17′ 50″ E
6	1	2	17° 02′ 46″ S	11° 22′ 58″ E
7	0	11	17° 16′ 07″ S	11° 29′ 42″ E
9	35	0	17° 01′ 36″ S	11° 39′ 38″ E
10	28	14	16° 59′ 79″ S	11° 40′ 95″ E
11	7	3	16° 50′ 42″ S	11° 41′ 06″ E
12	0	0	16° 49′ 30″ S	11° 38′ 43″ E
13	17	0	16° 50′ 10″ S	11° 03′ 74″ E
14	2	0	16° 51′ 42″ S	11° 17′ 51″ E
15	18	1	16° 36′ 09″ S	11° 18′ 09″ E
16	12	24	16° 21′ 96″ S	11° 43′ 12″ E
17	12	11	16° 22′ 80″ S	11° 35′ 28″ E
18	36	0	16° 23′ 97″ S	11° 35′ 12″ E
19	9	22	16° 09′ 80″ S	11° 45′ 74″ E
Total	228	157		

4. Discussion

4.1. Sex Ratio and Size Distribution

It has been proposed that the sex ratio of *Sardinella* species is likely influenced by stock size and composition [12] and environmental conditions [49]. Females of *S. aurita* and *S. maderensis* were more dominant than males, but differences were only evident for *S. aurita*. It has been proposed that females become more abundant in regions with high food availability, as feeding activity promotes hormonal activity and higher metabolism, leading to high production [50,51]. For *S. aurita*, this result is consistent with reports made elsewhere [16,21,52,53] but contrasts with male dominance in the Canary Islands (Spain) [54]. For *S. maderensis*, female dominance was reported off the south coast of Morocco [18] but not off Sierra Leone [21]. Furthermore, male concentration in the larger classes of *S. aurita* is probably related to adult dominance in the region, while smaller sizes are commonly concentrated on the central coast of Angola [25]. However, this contrasts with previous findings where females were dominant in all size classes [16,18].

4.2. Spawning Period

The populations of *S. aurita* and *S. maderensis* migrating along the southern coast of Angola spawn and reproduce during the austral summer and when SST is higher, as suggested by the maturity stage, GSI, and satellite data. *Sardinella aurita* reproduces between December and March, with the peak of maturation occurring in February. *Sardinella maderensis* reproduces between October and April, and the peak of maturation happens in February. The two spawning events of both species and the year-round presence of mature individuals of *S. maderensis* may suggest multiple spawning events [1,14]. Still, this strategy should be confirmed with a more robust dataset.

Although we did not characterize the spawning habitat with in situ environmental data (e.g., SST and salinity), it is reasonable to assume that SST can be used to indicate the spawning period for both species in this region, as performed for the Pacific sardine *Sardinops sagax* (Jenys, 1842) and the European anchovy *Engraulis encrasicolus* (Linnaeus,

1758) [55–57]. Such information has even allowed the simulation of an environmental homing for reproductive strategy and the prediction of climate change's effect on spawning habitat.

Overall, *S. aurita* has been described to spawn seasonally [12,40,58], particularly in summer [16,21]. However, *S. aurita* spawns during the cold season off Senegal [16]. Other works [2] reported that this species spawns throughout the year, in contrast to the single spawning season reported by other authors [9,12,58]. Similarly, two spawning seasons have been reported for *S. maderensis* [18]. However, *S. maderensis* reproduces throughout the year off Congo, with a peak in the cold season [10], coinciding with our observations. Differences in spawning periods have been attributed to the seasonality of environmental conditions and oceanographic features and environmental conditions such as the upwelling season [50], SST [16,59], and the transition from warm to cold seasons before upwelling [12]. In areas where *Sardinella* spp. co-occur, the spawning period peak differs in timing and duration. Off the coast of Ghana, *S. aurita* spawns from February to September and peaks between July and September, whereas *S. maderensis* spawns from July to September and peaks in September [58]. In Morocco, *S. aurita* spawns from February to July and from November to December, with a peak in April, while the reproduction period of *S. maderensis* reproduction period is shorter, spawning in February, March, and July, with a peak in the latter month [18].

4.3. Spawning Area

We could not obtain a comprehensive ichthyoplankton data set from the study area; however, the presence of eggs and larvae of *Sardinella* spp. confirms the existence of spawning activity off the southern Angolan coast. The study area—the Namibe coast—is the most productive area of the Angolan coast and comprises a convergence zone between the Angola and Benguela currents [60], which are oceanographic features critical for the spawning success of small pelagic fishes [1,16,22].

Further north, in the Congo–Angola region, nursery areas are located over broader areas of the continental shelf [61], similar to the area between the Tômbwa Bay and the Cunene River [62]. Further south, along the southern African coast, adult fish appear to spawn against the food gradient at the edge of current systems [34]. This is the case for the European sardine *Sardina pilchardus* (Walbauem, 1792) and Cape horse mackerel *Trachurus capensis* (Castelnau, 1861) spawning from the Lüderitz upwelling cell to the Angola–Benguela front [33], with the sardine *Sardina pilchardus* using the Angola–Benguela front for spawning in mid-austral summer [33,63].

High larval concentrations of *S. aurita* were reported from the convergence zone at its northern limit in the western Mediterranean [64]. In Mauritania, the spawning strategy of *S. aurita* results from a trade-off between retention patterns associated with seasonal circulation and food availability [65]. In Venezuela, significant spawning activity of *S. aurita* occurred during periods of intense upwelling [15]. However, off Senegal and Mauritania, *S. aurita* larvae have been found during cold and warm seasons but under low upwelling conditions [66]. Similarly, small pelagic fishes in the western Iberian upwelling ecosystem avoid upwelling conditions for spawning [67]. Therefore, the strategy of *Sardinella* spp. to spawn before and after upwelling events in the study area suggests an adaptive response to environmental conditions to maximize the survival of eggs and larvae.

4.4. Condition Factor

The higher condition factor (K) values in comparison with pre- and post-spawning periods for both species almost match those of maturity stages and the GSI, which agrees with the general hypothesis that, before and during the spawning period, fish should be in a better physiological condition [1,68,69]. This result corroborates those reported in Mauritania, where the condition of *S. aurita* increased synchronously in the months before the rise and during the spawning activity [2]. Small pelagic fish are expected to have better physiological conditions in periods of high food availability, and these are associated with upwelling conditions and spawning seasons [12], which decrease in post-spawning periods. This means that reproductive activity does not change the conditions of *S. aurita* and *S. maderensis*.

4.5. Size at Sexual Maturity

The females of *S. aurita* mature at a smaller size than males, which is consistent with studies in Mauritania [2] and contrary to what was observed off Senegal [16,52], Morocco [59], Ghana (16.34 cm and 16.55 cm for males and females, respectively) [58], and Mauritania [9], which might be attributed to the stock composition of each region.

The males of *S. maderensis* reached sexual maturity at a smaller size than females, as observed in south Morocco (20.7 cm for males, 21.7 cm for females) [18] but not off Ghana, where males reached sexual maturity at 15.3 cm, while females matured at 15.1 cm [58]. The overall size at first sexual maturity for both species is larger than those reported elsewhere for *S. aurita* [12,16,53] and for *S. maderensis* [19,58,70]. However, from Morocco to south Senegal, half of the population of *S. aurita* attained sexual maturity at 27.7 cm and 28.1 cm for females and males, respectively [9]. This difference could be explained by the high proportion of mature individuals in the sample, catch composition (from limited commercial sizes), and length composition, where smaller individuals were absent. Furthermore, these differences also highlight the plasticity of *Sardinella* spp. in coping with and responding to different environmental conditions.

4.6. Fishery Management

The *Sardinella* spp. fisheries off Angola are managed as a single unit, and the stock is shared with Congo [26]. Management is based on biomass estimates and the minimum landing size is 22 cm, which is substantially smaller than the maturity size estimated in this study for both species—*S. aurita*: 31.3 cm, *S. maderensis*: 28.4 cm. Thus, we recommend increasing the minimum capture size to guarantee reproduction and safeguard stock sustainability in the long term. We also recommend that future studies cover Angola's entire coast with samples gathered from commercial catches and scientific research programs. It is also critical to understand whether the population migrates massively along the coast or if population contingents remain in certain areas.

5. Conclusions

This study provides new information on the reproductive traits and spawning strategy of *S. aurita* and *S. maderensis* off the coast of Namibe in southern Angola. Spawning peaks during the austral summer for both species during their southward migration and they mature at larger sizes than in other regions, and *S. maderensis* has a more extended spawning period. The presence of eggs and larvae of *Sardinella* spp. highlights the region's importance as a spawning area and supports the implementation of egg-based stock assessment and recruitment estimates. Finally, we recommend developing a long-term stock assessment plan along the Angolan coast and advise increasing the minimum capture size for both species, since they are managed as a single stock unit.

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editing, P.M., M.A.T., and L.A.K.; supervision, M.A.T. and P.M.; remote sensing data analysis, L.A.K. All authors have read and agreed to the published version of the manuscript.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author.

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