

Article

Population Biology and Reproductive Characteristics of *Pseudotolithus elongatus* in the Cacine River Estuary, Guinea-Bissau

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Abstract

Pseudotolithus elongatus is one of the most commercially important species supporting artisanal fisheries in Guinea-Bissau; however, its population biology and reproductive characteristics remain poorly understood, particularly in estuarine ecosystems. This study provides the first integrated biological characterisation of *P. elongatus* in the Cacine River Estuary, Guinea-Bissau, based on 1776 specimens collected through three independent sampling programmes. Length at first sexual maturity (L_{50}) was estimated using binomial generalised linear models (GLMs); length–weight relationships were assessed by ordinary least squares regression and analysis of covariance (ANCOVA); sexual size dimorphism was evaluated using a battery of parametric and non-parametric tests (ANOVA, Welch's *t*-test, Kruskal–Wallis, Kolmogorov–Smirnov); and sex ratio was tested using chi-square goodness-of-fit tests with Yates' continuity correction. Females attained sexual maturity at a significantly smaller size than males ($L_{50} = 224.9$ mm vs. 306.8 mm), and both sexes exhibited positive allometric growth. Females attained larger body sizes and predominated in the largest length classes, confirming pronounced sexual size dimorphism. Reproductive activity occurred throughout the year, with a distinct spawning peak during the dry season (February–April), and the overall sex ratio remained close to parity despite significant variation among length classes and months. These findings provide a biological baseline to support evidence-informed fishery management of *P. elongatus* in Guinea-Bissau and highlight the need for long-term, standardised monitoring in the Cacine River Estuary.

Keywords: *Pseudotolithus elongatus*; population biology; reproductive biology; length at first sexual maturity; length–weight relationship; sexual size dimorphism; sex ratio; allometric growth; artisanal fisheries; Guinea-Bissau

Key Contribution: This study provides the first integrated assessment of the biological and reproductive characteristics of *Pseudotolithus elongatus* in the Cacine River Estuary, Guinea-Bissau. It establishes the first scientific baseline for this species in this estuarine ecosystem, providing essential information to support sustainable fishery management and future monitoring programmes.



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1. Introduction

Pseudotolithus elongatus is a demersal species of the family Sciaenidae, commonly known in Guinea-Bissau as djoto. It has a wide distribution along the West African coast, from northern Senegal to southern Angola [1–3], and is considered native to the Gulf of Guinea region, which extends from southern Guinea-Bissau to the Congo, where its abundance and catch levels are high [4]. Among the main species of the genus *Pseudotolithus*, namely *P. senegalensis*, *P. typus*, and *P. senegallus*, *P. elongatus* is one of the most important in terms of economy and fisheries in several West African countries [5–8].

P. elongatus, along with other species of the genus *Pseudotolithus*, constitutes a heavily exploited demersal resource, targeted by both artisanal and industrial fisheries [9–11]. However, stock assessment studies on demersal resources in the marine and coastal waters of Guinea-Bissau indicate that populations of these species show signs of overfishing, highlighting the urgent need for effective fishery management measures [12,13].

Recent studies on *P. elongatus* populations from West African estuarine systems have further highlighted the importance of assessing morphological variability and population structure to improve fishery management strategies [8,14,15].

In Guinea-Bissau, the main areas of *Pseudotolithus* spp., occurrence and exploitation are located in the southern (Cacine) and northern (Cacheu) regions. In these areas, catches are predominantly from artisanal fisheries, with efforts concentrated in coastal areas, estuaries, and adjacent rivers. In contrast, within the exclusive economic zone (EEZ), catches of these species are limited, as industrial fleets target other species.

In recent years, the commercial exploitation of *P. elongatus* has significantly increased in Guinea-Bissau. Between 2013 and 2021, exports by South Korean companies showed a rising trend, with two main peaks: the first in 2016–2017, reaching approximately 300 metric tons, and the second in 2020, with approximately 400 metric tons exported. Fishing activity is most intense in January, February, October, and November, corresponding to the periods of greatest fishing effort [13].

Despite the recognized economic importance of *P. elongatus* in Guinea-Bissau, studies on its biology remain scarce and fragmented, particularly in estuarine systems such as the Cacine River, which plays a crucial role as a habitat for shelter, feeding, and reproduction for several commercially important species [16–18].

Recent studies from West African coastal and estuarine environments have shown that biological traits, including population differentiation and morphological characteristics, may vary among local populations, reinforcing the need for region-specific assessments of commercially exploited species [14,15].

Existing published studies have focused primarily on populations from Nigerian estuaries (Cross River and Bonny Estuary) and the Ebrié Lagoon in Côte d'Ivoire, with only limited biological information available for Guinean waters. Furthermore, recent advances in *Pseudotolithus* research indicate that otolith-based approaches can provide valuable complementary information for species discrimination and population studies within this genus [19].

Consequently, no study has yet provided an integrated biological characterisation of *P. elongatus* in the Cacine River Estuary the principal artisanal fishing ground for this species in southern Guinea-Bissau combining estimates of length at first sexual maturity, length–weight relationships, sexual size dimorphism, reproductive seasonality, and sex ratio within a single multi-programme dataset. These biological parameters are widely recognized as key indicators for evaluating population resilience and supporting evidence-based fishery management of exploited marine fishes [20,21]. This study addresses this knowledge gap by providing the first comprehensive biological characterisation of *P. elongatus* in the Cacine River Estuary, based on 1776 specimens collected through

three independent sampling programmes (2013–2022), thereby establishing the biological baseline required to support evidence-based fishery management in Guinea-Bissau.

Accordingly, this study aims to characterise the population biology and reproductive characteristics of *P. elongatus* in the Cacine River Estuary, Guinea-Bissau, and to provide the first comprehensive biological characterisation of this species in the Cacine River Estuary, thereby establishing the scientific baseline needed to support evidence-based fishery management and conservation. Specifically, we tested the following a priori biological hypotheses: (i) females and males differ in length at first sexual maturity; (ii) the length–weight relationship exhibits positive allometric growth; (iii) females and males differ in body size, indicating sexual size dimorphism; (iv) sex ratio varies among length classes and sampling months; and (v) reproductive activity exhibits seasonal variation associated with the dry and wet seasonal cycle in the Cacine River Estuary.

2. Materials and Methods

2.1. Study Area

The Cacine River estuary, located in the southernmost part of Guinea-Bissau in the Tombali region, is one of the most productive estuarine systems in the country. It is characterized by a complex network of approximately 18 main channels, with bottoms composed of mud, coarse sand, and gravel [22,23]. The environmental dynamics of the estuary are influenced by the tropical climate of the region, which has two well-defined seasons: the dry season (November to April) and the rainy season (May to October).

The characteristics of the marine and aquatic environment of the Cacine River vary considerably across its channels, ranging from shallow areas of less than 5 m to deeper channels exceeding 10 m [22]. These habitats are frequented by a diverse assemblage of fish species, including both pelagic and demersal, as commonly observed in mangrove-dominated estuarine systems [24,25]. The study area and the fishing sampling stations are shown in Figure 1.

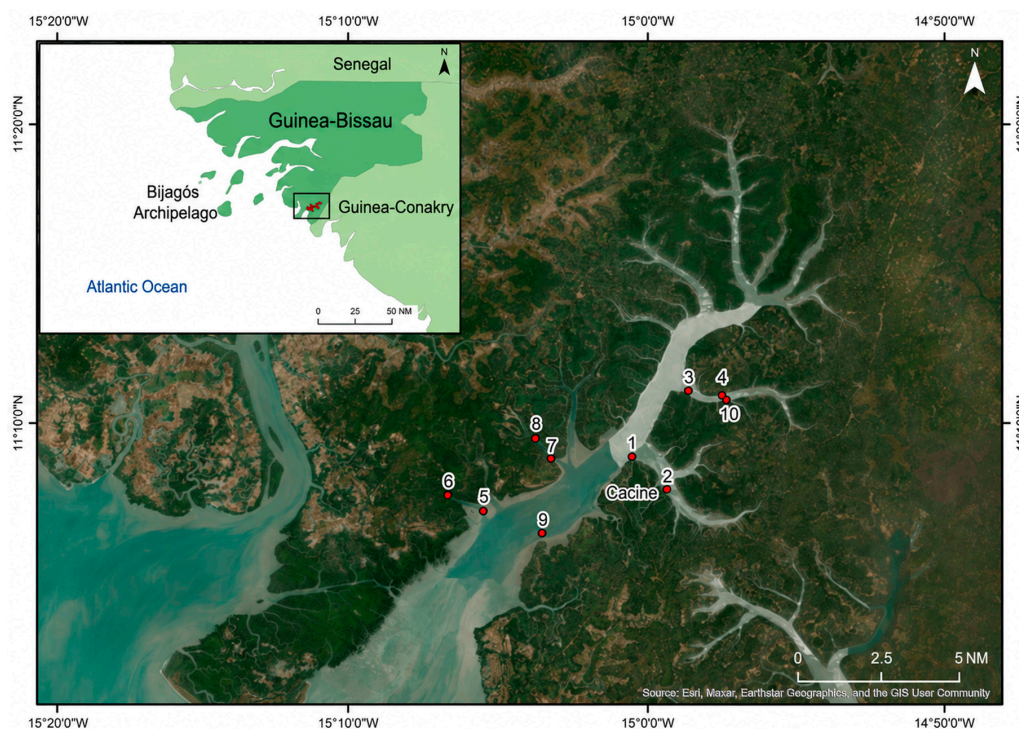


Figure 1. Map of the Cacine River and fishing sampling stations. (1) Cacine main channel; (2) Cacine secondary channel; (3) Calaxe main channel; (4) Calaxe secondary channel; (5) Canamine North main

channel; (6) Canamine North secondary channel; (7) Canamine South main channel; (8) Canamine South secondary channel; (9) Pampeira; (10) Poilão.

The estuary's banks are dominated by extensive mangrove ecosystems, locally known as “tarrafes.” These ecosystems play an extremely important role, particularly in the purification and filtration of organic matter and provide nutrients for various marine species. In addition, they create an ideal habitat for the reproduction and growth of small juvenile fish species, significantly contributing to the region's biodiversity [26,27].

2.2. Data Collection

The data used in this study were obtained from three independent sources: (i) scientific fishing surveys conducted in the Cacine River Estuary, Guinea-Bissau, between 2013 and 2017 (Table 1); (ii) monthly biological sampling conducted by the National Institute for Fisheries and Oceanography Research (INIPO) in 2022 (Table 2); and (iii) annual biological sampling conducted under DEMERSTEM Project between 2019 and 2020 (Table 3).

Table 1. Summary of *P. elongatus* sampling data collected during scientific surveys in the Cacine River estuary (2013–2017). TN = total number of individuals; TW = total weight (g); Gear type: Surface = surface-set gillnet, Bottom = bottom-set gillnet; Mesh size (mm) = mesh sizes deployed per sampling set; -- = zero observations recorded.

Year	Site	Species	TN	TW (g)	Gear Type	Mesh-Size (mm)									
						14	25	26	27	28	29	30	50	60	80
2013	Cacine	<i>P. elongatus</i>	69	12,498	Surface/ Bottom	14	25	--	--	--	--	--	--	--	--
2014	Cacine	<i>P. elongatus</i>	30	2760	Surface/ Bottom	14	25	--	--	--	--	--	--	--	--
2015	Cacine	<i>P. elongatus</i>	48	6138	Surface/ Bottom	14	25	--	--	--	--	--	--	--	--
2016	Cacine	<i>P. elongatus</i>	21	3509	Surface/ Bottom	14	25	--	--	--	--	--	--	--	--
2017	Cacine	<i>P. elongatus</i>	2	314	Surface/ Bottom	14	25	--	--	--	--	--	--	--	--
Total		1	170	25,219											

Table 2. Monthly biological data of *P. elongatus* collected in the Cacine River estuary by the National Institute for Fisheries and Oceanographic Research (INIPO), Guinea-Bissau, in 2022. TN = total number of individuals; TW = total weight (g); Length = total length (mm); M = males; F = females; UI = unidentified sex; Maturity stage 1–5 = macroscopic gonadal maturity stages; -- = zero observations recorded.

Month	Species	TN	TW (g)	Length (mm)		Sex			Maturity Stage					
				Max	Min	M	F	UI	1	2	3	4	5	UI
June	<i>P. elongatus</i>	48	16,635	330	170	20	28	--	4	15	10	19	--	--
July	<i>P. elongatus</i>	46	6329	300	150	6	40	--	2	8	32	4	--	--
August	<i>P. elongatus</i>	18	2029	270	190	--	18	--	--	--	9	8	1	--
September	<i>P. elongatus</i>	54	5943	290	170	10	42	2	1	10	17	11	13	2
October	<i>P. elongatus</i>	77	9912	300	210	31	46	--	46	26	5	--	--	--
November	<i>P. elongatus</i>	35	5324	310	210	7	28	--	12	19	3	1	--	--

Table 2. Cont.

Month	Species	TN	TW (g)	Length (mm)		Sex			Maturity Stage					
				Max	Min	M	F	UI	1	2	3	4	5	UI
December	<i>P. elongatus</i>	64	6320	320	170	26	38	--	38	26	--	--	--	--
Total	1	342	52,492	330	150	100	240	2	103	104	76	43	14	2

Table 3. Biological sampling data for *P. elongatus* collected in the Cacine and Cacheu rivers under the DEMERSTEM Project (2019–2020). TN = total number of individuals; TW = total weight (g); Length = total length (mm); M = males; F = females; UI = unidentified sex; Maturity stage 1–5 = macroscopic gonadal maturity stages; -- = zero observations recorded.

Year	Site	Species	TN	TW (g)	Length (mm)		Sex			Maturity Stage					
					Max	Min	M	F	UI	1	2	3	4	5	UI
2019	Cacine	<i>P. elongatus</i>	280	25,889	356	109	201	67	12	25	155	27	43	18	12
	Cacheu	<i>P. elongatus</i>	280	30,061	330	115	180	100	--	18	142	52	47	21	--
2020	Cacine	<i>P. elongatus</i>	517	92,602	356	149	162	350	5	53	150	143	158	8	5
	Cacheu	<i>P. elongatus</i>	226	20,679	311	110	128	97	1	18	80	55	67	5	1
Total		1	1303	169,231	356	109	671	614	18	114	527	277	315	52	18

2.2.1. Scientific Fishing Surveys

Scientific fishing surveys were conducted annually over a ten-day period and covered ten sampling stations distributed along the estuary. At each station, three fishing sets were performed using wooden dugout canoes (6 m in length, 70 cm in width, and 45 cm in height) equipped with surface and bottom gillnets measuring 25 m in length and 2 m in height, with mesh sizes of 14, 25, 26, 27, 28, 29, 30, 50, 60, and 80 mm (stretched mesh). The nets were set in the late afternoon and retrieved the following morning. During each survey, environmental parameters, including temperature, salinity, dissolved oxygen, and pH, were recorded at each sampling station using an HI 9828 multiparameter meter equipped with an HI 769828 multisensor probe (Hanna Instruments, Woonsocket, RI, USA) [13,22]. Although the scientific surveys employed gillnets with mesh sizes ranging from 14 to 80 mm, only *P. elongatus* specimens captured with the 14 and 25 mm gillnets were included in the present study, as these were the only mesh sizes that captured this species during the scientific surveys.

2.2.2. Monthly Biological Sampling

The monthly biological sampling conducted by INIPO between June and December 2022 was based on catches from the local artisanal fishery. For each individual, total length (mm), total and individual weight (g), sex, and gonadal maturity stage were recorded. Sex and maturity stage were determined by macroscopic examination of the gonads. Measurements were obtained using an iK2 ichthyometer (Aquatic BioTechnology S.L., El Puerto de Santa María, Cádiz, Spain) and an HCB 1502 precision balance (Adam Equipment Co., Ltd., Milton Keynes, UK), with a precision of 0.05 g.

2.2.3. Annual Biological Sampling

Annual biological sampling data were collected between 2019 and 2020 under the DEMERSTEM project, covering the estuaries of Cacine and Cacheu in Guinea-Bissau. Samples were obtained monthly from artisanal fishery catches landed at the main ports of both regions. The sampling protocol aimed to collect 70 individuals per month; however, operational constraints prevented full compliance with this effort, and some samples were

supplemented with frozen specimens obtained from authorized commercial vessels. In the laboratory, individuals were analyzed for total length (mm), total and individual weight (g), and sex, which was determined by macroscopic examination of the gonads. Across all data sources, sex identification and sexual maturity stage was also assessed through macroscopic inspection based on a specific identification guide, ensuring methodological standardization across analyses.

2.3. Data Analysis

The data were organized into two databases: one containing biological information from the DEMERSTEM Project and the INIPO sampling programme, and another containing data from the scientific fishing surveys conducted in the Cazine River estuary. Statistical analyses of length at first sexual maturity (L_{50}), length–weight relationships, population structure, sex ratio, and sexual dimorphism were performed using R software (v4.4.3; R Foundation for Statistical Computing, Vienna, Austria). Additional statistical analyses, including generalized linear models (GLMs), chi-square tests, Student's *t*-tests, one-way analysis of variance (ANOVA), Kruskal–Wallis tests, Kolmogorov–Smirnov tests, and assumption diagnostics (Shapiro–Wilk, Levene's, and Breusch–Pagan tests), were conducted using Python (v3.11; Python Software Foundation). The assumptions of normality and homogeneity of variance were assessed before each analysis, and appropriate parametric, robust, or non-parametric methods were applied whenever these assumptions were not met. Statistical significance was accepted at $\alpha = 0.05$.

2.3.1. Estimation of Length at First Sexual Maturity (L_{50})

Gonadal maturity stages (I–V) were used to classify each individual based on the macroscopic characteristics of the gonads, following established criteria for reproductive development in fishes [27,28]. Individuals classified as stages I–II were considered immature, whereas stages III–V were considered mature. The length at first sexual maturity (L_{50}) was estimated separately for each sex by fitting a binomial generalised linear model (GLM) with a logit link to the maturity status (mature = 1, immature = 0) as a function of total length (CT): $\text{logit}[P(\text{mature})] = \beta_0 + \beta_1 \cdot \text{CT}$, from which $L_{50} = -\beta_0 / \beta_1$. The statistical significance of the length effect was assessed with a likelihood-ratio (LR) test comparing the fitted model against an intercept-only null model (χ^2 distribution, 1 df). Goodness-of-fit was evaluated using the residual deviance-to-degrees-of-freedom ratio, McFadden's pseudo- R^2 , and the Hosmer–Lemeshow test (decile-of-risk grouping, χ^2 distributed). Because the sampling distribution of $L_{50} = -\beta_0 / \beta_1$ is a non-linear function of the model coefficients, 95% confidence intervals were obtained using three complementary approaches: (i) the Delta method, based on a first-order Taylor expansion of the variance-covariance matrix of β_0 and β_1 ; (ii) a non-parametric bootstrap (2000 resamples with replacement of individuals, model refitted at each iteration, percentile method); and (iii) profile-likelihood confidence intervals, obtained by inverting the likelihood-ratio statistic across a grid of fixed L_{50} values. The three approaches were compared to assess the sensitivity of the L_{50} estimate to the asymptotic normality assumption underlying the Delta method, which can be unreliable for non-linear ratio statistics, particularly with skewed sampling distributions or smaller sample sizes. A sex-by-length interaction term was additionally tested in a combined GLM to formally assess whether the slope of the maturity ogive differed significantly between sexes.

2.3.2. Estimation of the Length–Weight Relationship

The length–weight relationship was estimated using the allometric power model $W = aL^b$, where W is the total weight (g), L is the total length (mm), and a and b are the regression constants [29]. To allow linear regression, the equation was linearised through

logarithmic transformation of both variables, yielding $\log(W) = \log(a) + b \cdot \log(L)$, where $\log(a)$ is the intercept and b is the slope of the regression line. The parameters a and b were estimated separately for each sex by ordinary least squares (OLS) regression applied to the log-transformed data. The nature of the growth pattern was assessed by testing whether b differed significantly from the isometric value of 3 using a two-tailed Student's t -test on the regression slope, following [30] if $b = 3$, growth is isometric; if $b > 3$, growth is positively allometric (weight increases faster than length); and if $b < 3$, growth is negatively allometric. The quality of fit was evaluated using the coefficient of determination (R^2). Model adequacy was further examined through the Shapiro–Wilk test for normality of residuals and the Breusch–Pagan test for heteroscedasticity; given the large sample sizes ($n = 960$ females, $n = 816$ males), minor departures from normality detected by these tests were not expected to materially bias slope estimates, consistent with the asymptotic robustness of OLS under the central limit theorem, although confidence intervals for b should be interpreted with this caveat in mind. To formally test for sex-specific differences in the length–weight relationship, an analysis of covariance (ANCOVA) was performed on the linearised model ($\log W \sim \log L \times \text{Sex}$), with the $\log L \times \text{Sex}$ interaction term testing for homogeneity of slopes between sexes. When the interaction was not significant, a reduced parallel-lines model ($\log W \sim \log L + \text{Sex}$) was fitted to test for differences in intercepts (i.e., in condition/weight-at-length) between sexes.

2.3.3. Population Structure

Population structure was assessed by grouping individuals into 10 mm total length classes and analysing length-frequency distributions separately for each sex. A class width of 10 mm was selected because it provided sufficient resolution to describe size-frequency patterns while maintaining consistency with the analyses of sex ratio by length class and the corresponding graphical presentation. The modal length class for each sex was identified as the class with the highest frequency of individuals. Length-frequency distributions were illustrated using histograms constructed separately for males and females.

2.3.4. Determination of the Reproductive Season

Reproductive seasonality was examined based on monthly variation in the proportion of mature individuals (gonadal stages III–V). For each sex, the association between month and maturity status was tested using a Pearson χ^2 test of independence on the month $\times$ maturity-stage contingency table (5-stage classification) and, as a more robust complementary test given expected-count limitations in some maturity stage $\times$ month cells, on the corresponding binary contingency table (mature vs. immature $\times$ month). The percentage of cells with expected counts below five was reported for each contingency table as a check on the validity of the χ^2 approximation (Cochran's rule). The month with the highest proportion of mature individuals was identified as the peak reproductive month for each sex.

2.3.5. Analysis of Sex Ratio

Sex ratio (SR) was determined as the proportion of males to females using the formula $SR = M/F$, where M is the number of males and F is the number of females. A chi-square goodness-of-fit test was applied to assess whether the observed sex ratio of *P. elongatus* differed significantly from the expected 1:1 (female:male) proportion, both for the overall dataset and separately within each sampling programme (scientific fishing surveys, monthly biological sampling, and annual biological sampling). To evaluate whether sex ratio varied with body size or sampling period, chi-square tests of independence were performed using the sex $\times$ 10 mm total length class and sex $\times$ month contingency tables, respectively. In addition, chi-square goodness-of-fit tests with Yates' continuity correction

were performed within each 10 mm total length class ($df = 1$) to compare the observed and expected 1:1 female:male proportions. The overall chi-square tests of independence for the complete sex $\times$ length-class ($df = 24$) and sex $\times$ month ($df = 11$) contingency tables were performed without Yates' continuity correction because they involved more than one degree of freedom. Statistical significance was assessed at $\alpha = 0.05$.

2.3.6. Sexual Dimorphism

Sexual size dimorphism was assessed by comparing the total length of males and females using a one-way analysis of variance (ANOVA). Prior to the ANOVA, the normality of the length distribution within each sex was examined with the Shapiro–Wilk test, and homogeneity of variance between groups was assessed with Levene's test (median-centred). Because both assumptions were violated, three complementary tests were applied alongside the classical ANOVA to assess the robustness of the conclusion: Welch's t -test (which does not assume equal variances and uses the Welch–Satterthwaite approximation for degrees of freedom), the Kruskal–Wallis rank-based test (a non-parametric alternative that does not assume normality), and the two-sample Kolmogorov–Smirnov test (which compares the entire length distribution between sexes rather than only central tendency). Effect size was quantified using Cohen's d . Length distributions were visualised using boxplots, in which the central line represents the median, the box indicates the interquartile range (IQR; 25th–75th percentiles), whiskers extend to $1.5 \times$ IQR, and individual points represent outliers.

3. Results

3.1. Length at First Sexual Maturity (L_{50})

For *P. elongatus* (Figure 2), the logistic curve indicates that females and males reach the length at first sexual maturity (L_{50}) at different sizes. Females attained 50% maturity at 224.9 mm (95% CI: 211.7–238.2 mm, Delta method; 209.0–237.2 mm, bootstrap, $n = 2000$; 209.4–236.4 mm, profile likelihood), whereas males reached 50% maturity at a larger size of 306.8 mm (95% CI: 277.2–336.4 mm, Delta method; 284.1–348.6 mm, bootstrap; 284.3–350.3 mm, profile likelihood) (Table 4). The agreement among the three interval-estimation methods indicates that the L_{50} estimates are stable and not strongly distorted by the asymptotic-normality assumption of the Wald-type Delta method. In both sexes, the relationship between length and maturity probability was highly significant (likelihood-ratio test against the null model: females, $\chi^2(1) = 66.03$, $p < 0.001$; males, $\chi^2(1) = 32.73$, $p < 0.001$, Table S2), and the fitted logistic models showed adequate goodness-of-fit (Hosmer–Lemeshow test: females, $p = 0.886$; males, $p = 0.037$, indicating a somewhat weaker fit for males, consistent with the greater observed variability noted below). The residual deviance-to-degrees-of-freedom ratio was close to 1 for both sexes (females: 1.29; males: 1.15), indicating no marked overdispersion. There was nonetheless some scatter around the fitted ogives, particularly for males, plausibly reflecting inter-observer differences in the macroscopic classification of maturity stages across the three sampling programmes.

A combined GLM testing the length $\times$ sex interaction showed no significant difference in the slope of the maturity ogive between sexes ($p = 0.987$), indicating that the steepness of the maturation transition is comparable for males and females, and that the marked difference in L_{50} reflects a shift in the position rather than the shape of the ogive.

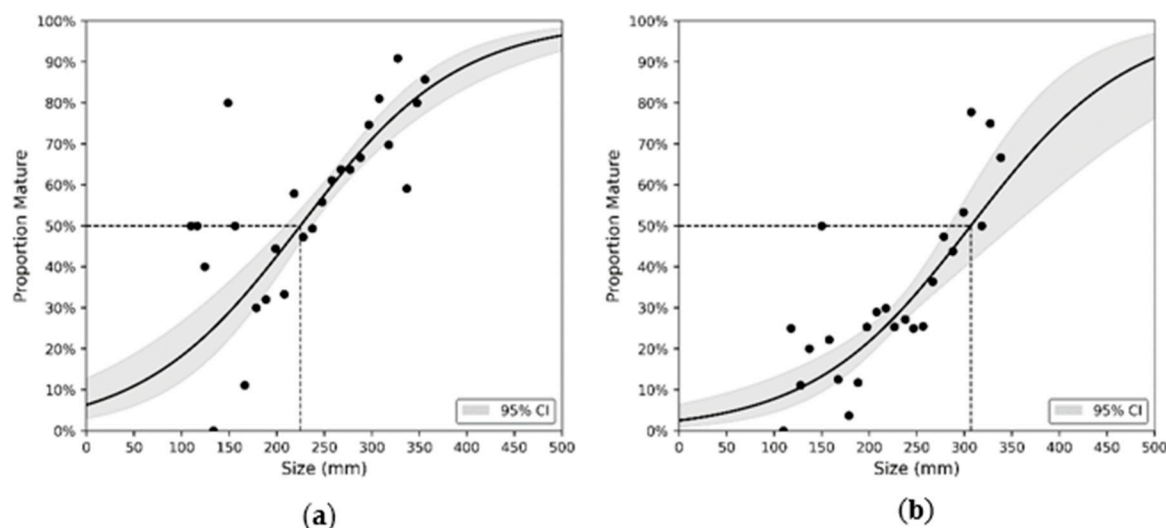


Figure 2. Logistic maturity ogives for *P. elongatus* showing the relationship between total length (mm) and the proportion of mature individuals. Solid lines represent fitted logistic models, shaded areas indicate 95% confidence intervals, and dashed lines show the estimated length at first maturity (L_{50} : 224.9 mm for females and 306.8 mm for males). (a) Females. (b) Males.

Table 4. Length at first sexual maturity (L_{50}) for male and female *P. elongatus*, with 95% confidence intervals obtained by three complementary methods, and goodness-of-fit diagnostics for the binomial GLM. LR = likelihood-ratio test of the length effect ($df = 1$); HL = Hosmer–Lemeshow test; Dev/df = residual deviance-to-degrees-of-freedom ratio.

Sex	n	L_{50} (mm)	95% CI—Delta	95% CI—Bootstrap	95% CI—Profile	LR χ^2 (p)	HL (p)	Dev/df
Females	960	224.9	211.7–238.2	209.0–237.2	209.4–236.4	66.03 (<0.001)	0.886	1.29
Males	816	306.8	277.2–336.4	284.1–348.6	284.3–350.3	32.73 (<0.001)	0.037	1.15

3.2. Length–Weight Relationship

The length–weight relationship of the *P. elongatus* population shows that both females and males exhibit positive allometric growth $b > 3$ (Figure 3). This is expressed by the following equations: $W = 3.85 \times 10^{-6} L^{3.134}$ for females and $W = 3.89 \times 10^{-6} L^{3.13}$ for males. These results indicate that individuals of both sexes tend to gain proportionally more body mass as they grow in length.

The length–weight relationship was estimated separately for females and males of *Pseudolithus elongatus* (Table 5). Both sexes exhibited positive allometric growth, with allometric exponents significantly greater than the isometric value of 3 (females: $b = 3.134$, $t = 7.241$, $df = 958$, $p < 0.001$; males: $b = 3.130$, $t = 5.623$, $df = 814$, $p < 0.001$), indicating that body mass increases proportionally faster than length in both sexes. Residual diagnostics indicated significant departures from normality (Shapiro–Wilk: females, $W = 0.945$, $p < 0.001$; males, $W = 0.978$, $p < 0.001$) and significant heteroscedasticity (Breusch–Pagan: females, $p < 0.001$; males, $p < 0.001$). Given the very large sample sizes in both groups, these departures are not expected to bias the OLS point estimates of b materially, but they indicate that the reported confidence intervals for b , which assume homoscedastic, normally distributed residuals, are likely to be conservative approximations rather than exact intervals.

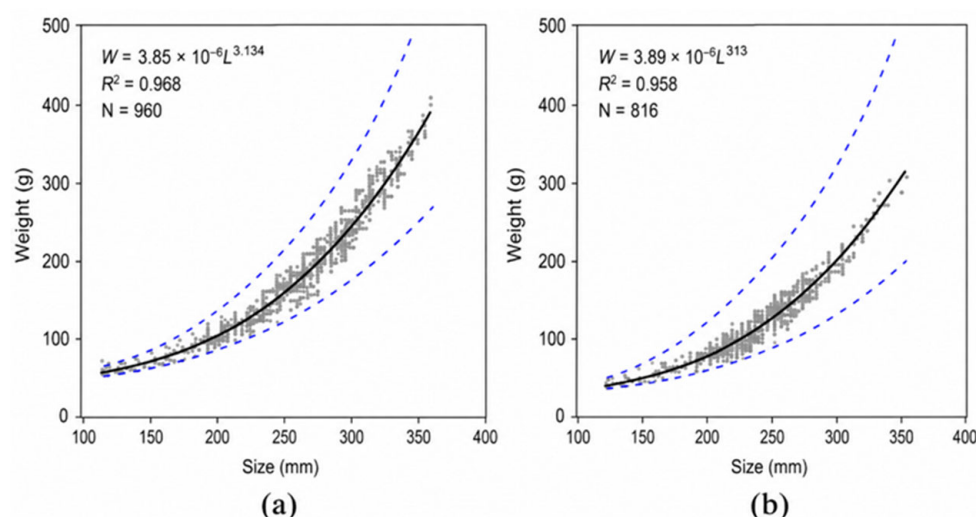


Figure 3. Length–weight relationships of *P. elongatus* in the Cacine River estuary. Points represent individual fish, solid black lines represent the fitted length–weight regression models, and blue dashed lines indicate the corresponding 95% confidence intervals. (a) Females ($N = 960$). (b) Males ($N = 816$).

Table 5. Length–weight relationship parameters for *P. elongatus* by sex. a = allometric coefficient; b = allometric exponent; 95% CI (b) = 95% confidence interval of b ; R^2 = coefficient of determination. Growth type determined by t -test against the isometric value $b = 3$.

Sex	n	$a (\times 10^{-6})$	b	95% CI (b)	R^2	Growth Type
Females	960	3.8521	3.1343	3.0979–3.1707	0.9675	Positive allometric
Males	816	3.8910	3.1296	3.0844–3.1748	0.9577	Positive allometric

ANCOVA revealed no significant difference in allometric slopes between sexes ($F(11772) = 0.025$, $p = 0.874$; Table 6), indicating that the rate of weight gain relative to length does not differ between females and males. Accordingly, a parallel-lines model was fitted, which revealed a significant difference in intercepts between sexes ($F(1,1773) = 7.184$, $p = 0.007$), indicating that females are significantly heavier than males at any given body length.

Table 6. Results of Student's t -test for the allometric exponent b against the isometric value of 3, for each sex of *P. elongatus*. b = observed allometric exponent; t = t -statistic; df = degrees of freedom; p -value = two-tailed significance.

Sex	b	t	df	p -Value	Interpretation
Females	3.1343	7.2414	958	<0.001	Significantly positive allometric ($b > 3$)
Males	3.1296	5.6231	814	<0.001	Significantly positive allometric ($b > 3$)

3.3. Population Structure and Sexual Dimorphism

The population structure of *P. elongatus* shows that individual lengths, for both females and males, range from 109 to 349 mm (Figure 4). However, there is a difference in age structure between the sexes, with a higher concentration of individuals in the modal class: for females, it is between 289–299 mm, while for males, it is between 209–219 mm.

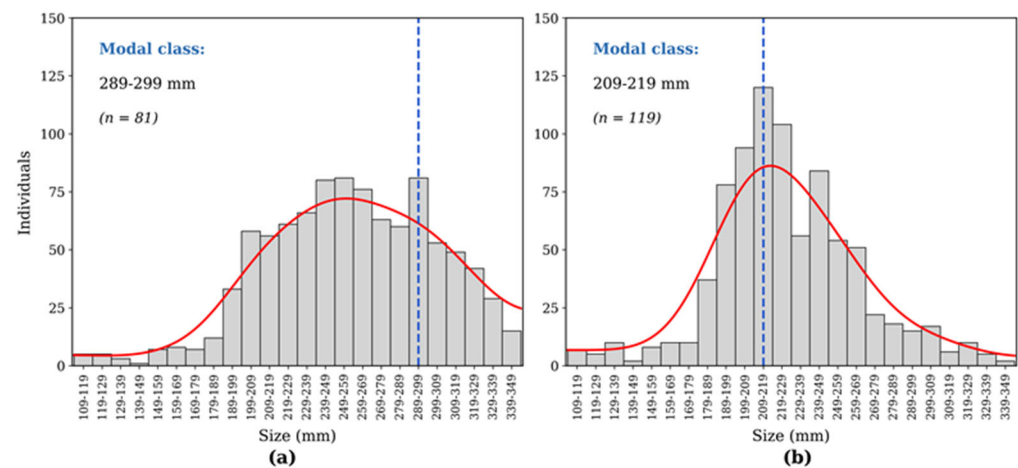


Figure 4. Population structure of female (a) and male (b) *P. elongatus* based on length-frequency histograms grouped into 10 mm total length classes. The dashed blue line indicates the modal length class, and the red curve represents the kernel density estimate.

Length distributions departed significantly from normality within each sex (Shapiro–Wilk: females, $W = 0.988$, $p < 0.001$; males, $W = 0.978$, $p < 0.001$), and variances differed significantly between sexes (Levene’s test, median-centred: $F(1,1774) = 50.67$, $p < 0.001$) (Table 7). Sexual size dimorphism was nonetheless statistically significant across all tests applied, with females attaining greater total lengths than males: one-way ANOVA, $F(1,1774) = 253.23$, $p < 0.001$; Welch’s t-test (not assuming equal variances), $t = 16.16$, $df = 1772.3$, $p < 0.001$; Kruskal–Wallis test, $H(1) = 237.58$, $p < 0.001$; and two-sample Kolmogorov–Smirnov test, $D = 0.342$, $p < 0.001$ (Table 8). The consistency of this result across parametric, variance-robust, rank-based, and full-distribution tests indicates that the conclusion of significant sexual size dimorphism is not an artefact of the assumption violations detected above. The magnitude of the difference was moderate-to-large (Cohen’s $d = 0.76$). The median total length was 258.5 mm for females (IQR: 224.0–291.3 mm) and 220.0 mm for males (IQR: 200.0–248.0 mm), corresponding to mean lengths of 257.0 ± 46.4 mm (SD) and 224.6 ± 38.2 mm (SD), respectively (Figure 5; Table 9). The size distributions of both sexes were approximately symmetric, as indicated by the central position of the median within the interquartile range in the boxplot.

Table 7. ANCOVA of the length–weight relationship ($\log W \sim \log L \times \text{Sex}$) Sequential (Type II) analysis of covariance testing for differences between sexes in the slope ($\log L \times \text{Sex}$ interaction) and, in a reduced parallel-lines model, in the intercept (Sex) of the log-linearised length–weight relationship.

Model Term	df	F	p-Value	Interpretation
$\log L \times \text{Sex}$ (slope test)	1, 1772	0.025	0.874	Slopes do not differ
Sex (intercept test, parallel-lines model)	1, 1773	7.184	0.007	Intercepts differ ($F > M$)

Table 8. Descriptive statistics and full battery of dimorphism tests for total length by sex. Descriptive statistics of total length (mm) for each sex, and results of the parametric (one-way ANOVA, Welch's *t*-test) and non-parametric (Kruskal–Wallis, Kolmogorov–Smirnov) tests used to assess sexual size dimorphism, together with the assumption checks (Shapiro–Wilk, Levene's test) that motivated the use of multiple complementary tests. Referenced in Section 3.3 of the main text.

Sex	<i>n</i>	Mean	SD	Median	IQR (25–75%)	Range
Females	960	257.0	46.4	258.5	224.0–291.3	110–356
Males	816	224.6	38.2	220.0	200.0–248.0	109–340
Test	Statistic	<i>df</i>	<i>p</i> -value	Conclusion		
Shapiro–Wilk (females)	W = 0.988	—	<0.001	Departs from normality		
Shapiro–Wilk (males)	W = 0.978	—	<0.001	Departs from normality		
Levene's test (median-centred)	F = 50.67	1, 1774	<0.001	Unequal variances		
One-way ANOVA	F = 253.23	1, 1774	<0.001	Significant dimorphism		
Welch's <i>t</i> -test	t = 16.16	1772.3	<0.001	Significant dimorphism		
Kruskal–Wallis	H = 237.58	1	<0.001	Significant dimorphism		
Kolmogorov–Smirnov	D = 0.342	—	<0.001	Distributions differ		
Cohen's <i>d</i> (effect size)	d = 0.76	—	—	Moderate to large effect		

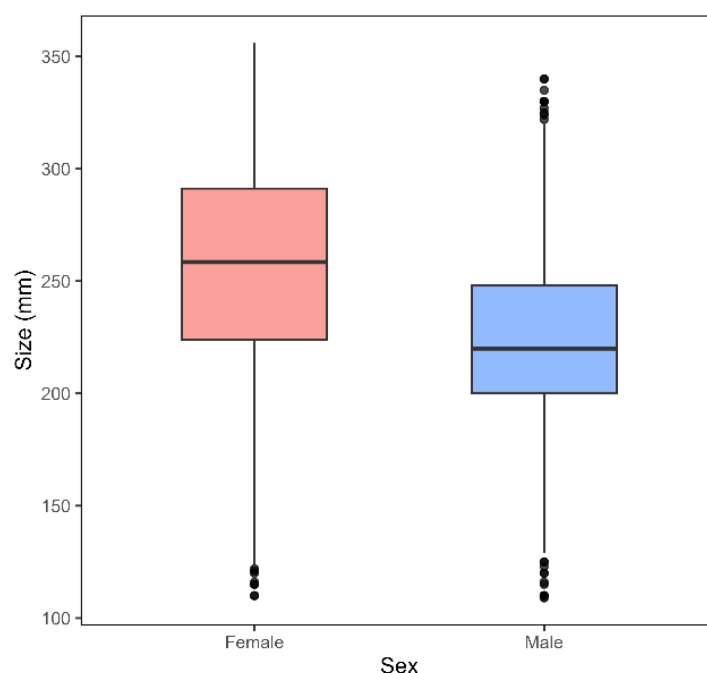


Figure 5. Distribution of total length (mm) by sex in *Pse elongatus* from the Cacine River estuary. Boxplots show the median (horizontal line), interquartile range (box), whiskers extending to 1.5× the interquartile range, and outliers (points). Sample sizes were 960 females and 816 males.

Table 9. Results of chi-square goodness-of-fit tests comparing the observed and expected 1:1 female:male proportions of *P. elongatus* for each sampling programme and for the overall dataset. *n* (F) = number of females; *n* (M) = number of males; *N* = total sample size; M/F = male-to-female ratio; χ^2 = chi-square statistic (*df* = 1); *p*-value = probability associated with the chi-square test. Statistical significance was assessed at α = 0.05.

Sampling Programme	<i>n</i> (F)	<i>n</i> (M)	<i>N</i>	Females (%)	Males (%)	M/F	χ^2	<i>p</i> -Value
Scientific fishing surveys (2013–2017)	106	45	151	70.2	29.8	0.42	24.64	<0.001
Monthly biological sampling—INIPO (2022)	240	100	340	70.6	29.4	0.42	57.65	<0.001

Table 9. Cont.

Sampling Programme	<i>n</i> (F)	<i>n</i> (M)	<i>N</i>	Females (%)	Males (%)	M/F	χ^2	<i>p</i> -Value
Annual biological sampling—DEMERSTEM (2019–2020)	614	671	1285	47.8	52.2	1.09	2.53	0.111
Overall	960	816	1776	54.1	45.9	0.85	11.68	0.0006

3.4. Reproductive Season

The reproductive cycle of *P. elongatus* seems to occur continuously throughout the year, from January to December (Figure 6), with marked seasonal variation in the proportion of mature individuals. The association between month and maturity status was highly significant for both sexes (χ^2 test of independence on the month $\times$ maturity-stage table: females, χ^2 (44) = 646.48, $p < 0.001$; males, χ^2 (44) = 291.01, $p < 0.001$; confirmed on the binary mature/immature table: females, χ^2 (11) = 270.85, $p < 0.001$; males, χ^2 (11) = 126.09, $p < 0.001$, the latter with 12.5% of cells showing expected counts below five, indicating that the male result should be interpreted with some caution). For females, the proportion of mature individuals exceeded 85% from February to May, peaking in March (97.8% mature, $n = 46$), and fell to its annual minimum in December (19.2% mature, $n = 73$); contrary to a previous interpretation of these data, females sampled in May were predominantly mature (87.2%, $n = 47$), indicating that reproductive activity does not cease at any point in the annual cycle. For males, the proportion of mature individuals was comparatively lower throughout the year, peaking in February (63.0%, $n = 73$) and reaching a minimum in May (5.0%, $n = 20$) (Table S3). One main peak of reproductive activity is therefore evident during the dry season, particularly from January to April, and is most pronounced in females.

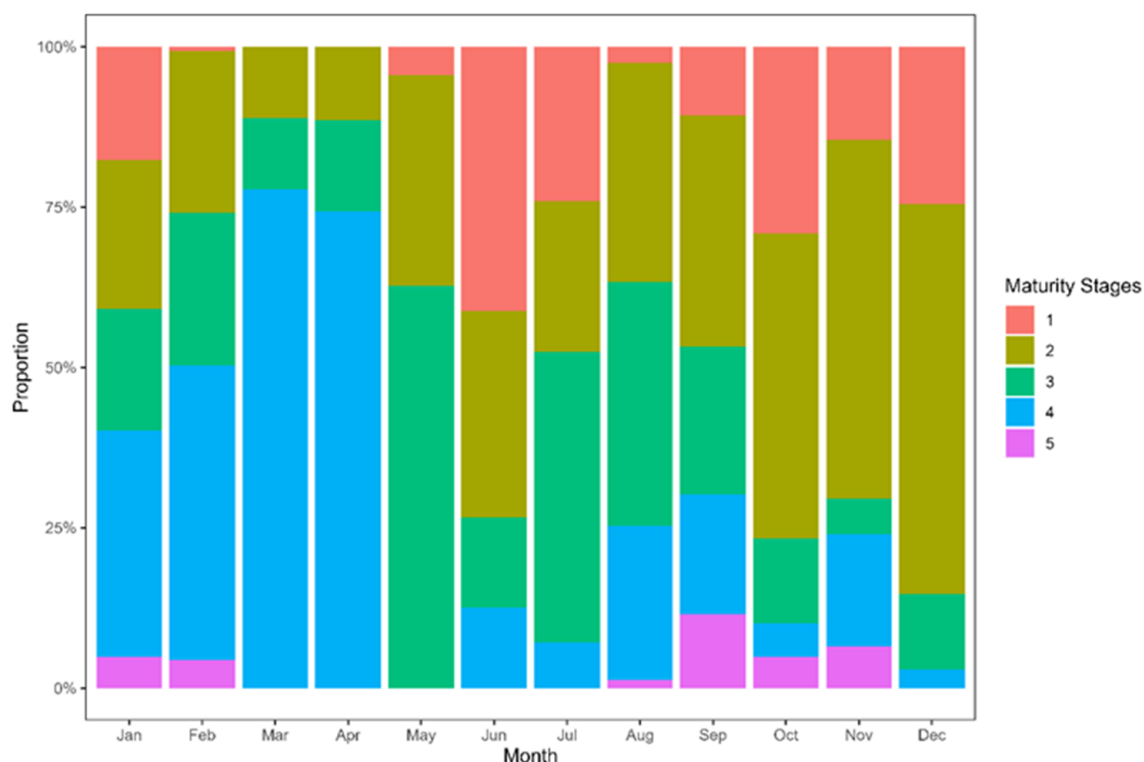


Figure 6. Monthly variation in the proportional distribution of gonadal maturity stages of *P. elongatus* in the Caciné River estuary. Stacked bars represent the percentage of individuals in each macroscopic maturity stage (1–5) for each month.

3.5. Sex Ratio

The sex ratio of the *P. elongatus* population indicated a slightly higher proportion of females (54.1%) than males (45.9%), remaining relatively close to the expected 1:1 ratio. Examination of the sex ratio across 10 mm total length classes (Figure 7) revealed a progressive shift in sex composition with increasing body size. Although males were generally more frequent in the smaller length classes, a significant male predominance was observed only between 189 and 229 mm. The 239–249 mm length class showed an equal proportion of females and males, whereas females predominated significantly in all length classes from 249 mm onwards (Table S1).

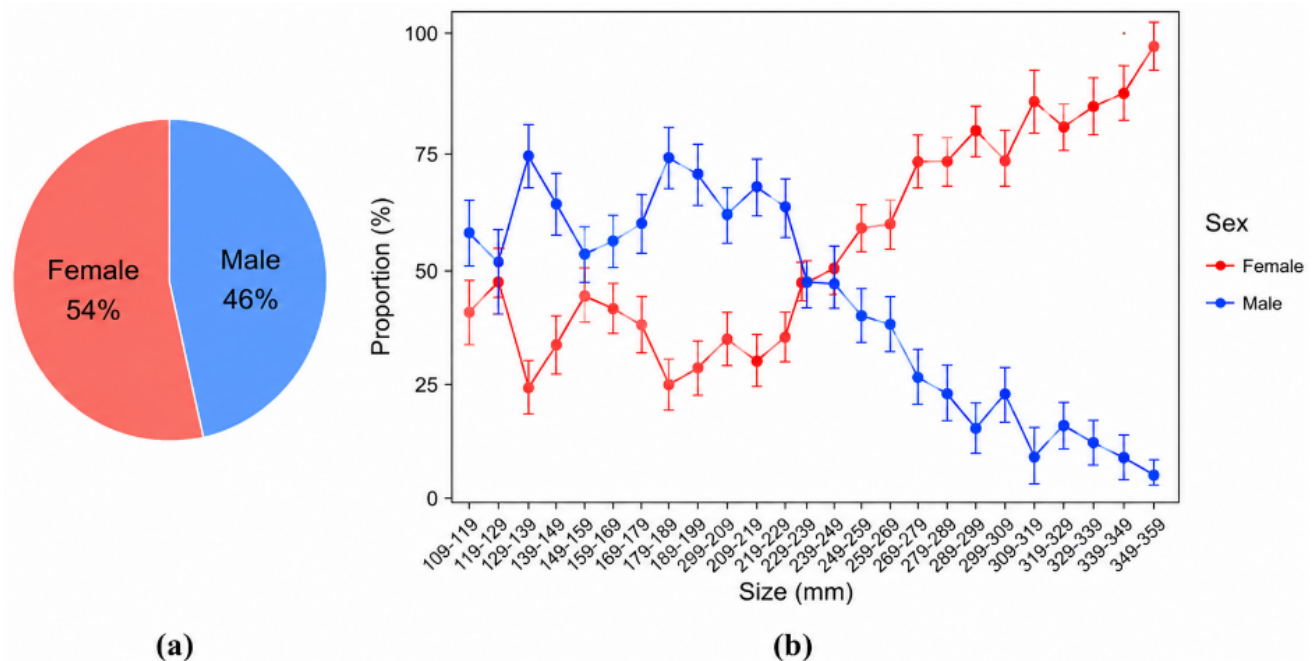


Figure 7. Sex ratio of *P. elongatus* in the Cacine River Estuary. (a) Overall sex composition. (b) Female and male proportions (%) by total length class (mm). Error bars indicate 95% Wilson confidence intervals.

The overall sex ratio differed significantly from the expected 1:1 ratio ($\chi^2 = 11.676$, $df = 1$, $p = 0.001$), with females representing 54.1% ($n = 960$) and males 45.9% ($n = 816$) of the total sample ($n = 1776$). However, sex ratio varied substantially among the different sampling programmes (Table 9). A significant female predominance was observed in the scientific fishing surveys (70.2% females; $\chi^2 = 24.64$, $df = 1$, $p < 0.001$) and monthly biological sampling (70.6% females; $\chi^2 = 57.65$, $df = 1$, $p < 0.001$), whereas the annual biological sampling showed a sex ratio close to parity (47.8% females and 52.2% males; $\chi^2 = 2.53$, $df = 1$, $p = 0.111$). Sex ratio also varied significantly across 10 mm total length classes ($\chi^2 = 279.269$, $df = 24$, $p < 0.001$), with a significant predominance of males between 189 and 229 mm, an equal proportion of males and females in the 239–249 mm class, and a significant predominance of females in all length classes from 249 mm onwards (Table 10). A significant association was also found between sex and month of capture ($\chi^2 = 202.93$, $df = 11$, $p < 0.001$), reflecting seasonal variation in the relative abundance of males and females during the reproductive cycle.

Table 10. Results of chi-square goodness-of-fit tests with Yates continuity correction ($df = 1$), comparing the observed and expected 1:1 female:male proportions within each 10 mm total length class of *elongatus*. $n(F)$ = number of females; $n(M)$ = number of males; χ^2 = chi-square statistic with Yates continuity correction; p -value = probability associated with the chi-square test. Statistical significance was assessed at $\alpha = 0.05$.

Length Class (mm)	n Females	n Males	χ^2 Yates	p -Value	Significant ($\alpha = 0.05$)
109–119	5	7	0.083	0.773	No
119–129	2	7	1.778	0.182	No
129–139	5	8	0.308	0.581	No
139–149	2	2	0.000	1.000	No
149–159	7	12	0.842	0.359	No
159–169	10	6	0.563	0.454	No
169–179	7	15	2.227	0.135	No
179–189	13	18	0.516	0.471	No
189–199	36	86	19.607	<0.001	Yes (M > F)
199–209	58	97	8.929	0.003	Yes (M > F)
209–219	59	115	17.471	<0.001	Yes (M > F)
219–229	59	101	10.556	0.001	Yes (M > F)
229–239	67	52	1.681	0.195	No
239–249	77	77	0.000	1.000	No
249–259	83	49	8.273	0.004	Yes (F > M)
259–269	78	44	8.885	0.003	Yes (F > M)
269–279	62	25	14.598	<0.001	Yes (F > M)
279–289	58	18	20.000	<0.001	Yes (F > M)
289–299	78	17	37.780	<0.001	Yes (F > M)
299–309	53	17	17.469	<0.001	Yes (F > M)
309–319	49	9	25.931	<0.001	Yes (F > M)
319–329	45	7	26.404	<0.001	Yes (F > M)
329–339	28	6	12.559	<0.001	Yes (F > M)
339–349	16	2	9.389	0.002	Yes (F > M)
349–359	13	0	11.077	<0.001	Yes (F > M)

4. Discussion

Females of *P. elongatus* reached sexual maturity at a significantly smaller body size than males ($L_{50} = 224.9$ mm versus 306.8 mm), indicating clear sex-specific differences in maturation schedules. This pattern suggests that females begin reproducing earlier in life, whereas males continue investing in somatic growth before reaching sexual maturity. Such differences are consistent with sex-specific life-history strategies commonly reported in teleost fishes, in which the allocation of energy between growth and reproduction differs between sexes. The maturation pattern observed in the present study agrees with previous findings for *P. elongatus* in Guinea-Bissau [13], although contrasting patterns have been reported in other West African populations [31,32]. Geographic variation in L_{50} is likely associated with differences in environmental conditions, fishing pressure, and population-specific life-history characteristics. In particular, size-selective fishing may alter maturation

schedules by disproportionately removing larger individuals from the population [9,33,34]. Likewise, variation in salinity, temperature, and food availability among estuarine systems may influence endocrine processes involved in gonadal development, contributing to regional differences in the size at first maturity [25,35]. Methodological differences in gonadal staging among studies may also account for part of the variability reported in the literature [36]. These findings emphasise that maturation schedules are not fixed across populations and reinforce the importance of considering sex-specific biological characteristics when establishing minimum landing sizes and other management measures intended to protect the reproductive capacity of exploited populations.

The length–weight relationship indicated positive allometric growth in both sexes ($b > 3$), demonstrating that body mass increased proportionally faster than body length throughout ontogeny. This growth pattern suggests that, as individuals increase in size, they allocate proportionally more energy to somatic tissue accumulation than to linear growth, resulting in progressively heavier fish for a given increase in length. Such a strategy is generally associated with favourable feeding conditions, adequate energy reserves, and good physiological condition, particularly in productive estuarine environments where food resources remain relatively abundant throughout the year. Positive allometric growth has also been reported for *P. elongatus* in other West African estuarine systems [6,37,38], although both positive and negative allometry have been documented in neighbouring coastal areas [39,39]. These regional differences probably reflect spatial and temporal variation in environmental conditions, prey availability, population density, reproductive investment, and fishing pressure. According to Froese [28], the allometric coefficient is influenced by nutritional status, gonadal development, season, and habitat characteristics, emphasising that growth patterns represent the combined effects of biological and environmental processes rather than fixed species-specific traits. In the Cacine River Estuary, seasonal hydrological dynamics, including the alternation between dry and rainy seasons and the influence of coastal upwelling along the Senegalo–Guinean shelf, probably enhance nutrient availability and primary productivity, ultimately increasing prey availability for *P. elongatus* [12,18,40]. Although environmental variables were not incorporated directly into the statistical analyses, these ecological processes provide a plausible explanation for the positive allometric growth observed in the present study and should be evaluated explicitly in future investigations.

The population structure revealed pronounced sexual size dimorphism, with females dominating the larger size classes and males predominating among smaller individuals. This pattern suggests that males and females follow different life-history trajectories after maturation despite exhibiting similar allometric growth patterns. The larger body size attained by females is consistent with sex-specific patterns of energy allocation, whereby females may continue investing proportionally more in somatic growth after maturation, while males allocate a greater proportion of available resources to reproductive functions. Similar patterns have been widely reported for *Pseudotolithus* species across West African estuaries [9,41,42] and are broadly consistent with fecundity selection theory, which predicts that larger females achieve higher reproductive output because body size is positively associated with egg production and spawning capacity [43,44]. The transition from male dominance in the smaller length classes to female dominance in the larger classes is therefore likely to reflect the combined influence of sex-specific growth trajectories, differential mortality, and size-selective fishing [32]. Although fishing preferentially removes larger individuals, the persistence of female dominance in the largest size classes suggests that intrinsic biological differences between the sexes contribute substantially to the observed population structure. In particular, continued somatic growth in females may represent an adaptive strategy that increases lifetime reproductive potential, whereas earlier maturation

in males may favour reproductive participation at smaller body sizes. Despite these differences in body-size distribution, the overall sex ratio remained close to parity, consistent with previous studies of *P. elongatus* from other West African estuaries [6,30]. This finding suggests that the observed sexual size dimorphism is more likely to result from differences in growth, maturation, and survival after recruitment than from persistent deviations in the primary sex ratio.

The reproductive biology of *P. elongatus* indicates continuous spawning activity throughout the year, with a pronounced spawning peak during the dry season (January–April). Continuous reproduction is a common life-history strategy among tropical estuarine Sciaenidae and is generally considered an adaptive strategy that reduces the risks associated with environmental variability by distributing reproductive effort over an extended period [45,46]. Nevertheless, the marked increase in reproductive activity during the dry season suggests that spawning is synchronised with seasonal environmental conditions that are more favourable for successful reproduction. Similar reproductive patterns have been reported for *Pseudotolithus* populations in other West African estuaries, although the timing and intensity of spawning peaks vary geographically according to local hydrological conditions [10,40,47,48]. In the Cacine River estuary, the dry season is characterised by reduced freshwater discharge, greater salinity stability, lower turbidity, and increased marine productivity associated with seasonal coastal upwelling along the Senegalo–Guinean shelf [12,18,39]. Collectively, these environmental conditions are likely to improve habitat quality and food availability, thereby creating favourable conditions for reproductive activity and the early life stages of the species. The coincidence between peak reproductive activity and periods of greater environmental stability suggests that the reproductive timing of *P. elongatus* is closely linked to predictable seasonal changes in the estuarine environment. Such synchronisation may increase reproductive efficiency by concentrating spawning during periods that provide more suitable conditions for egg development, larval growth, and juvenile establishment. Similar associations between reproductive timing and seasonal environmental conditions have been described for numerous tropical estuarine fishes, highlighting the important role of environmental seasonality in shaping reproductive strategies [45,46].

Several methodological limitations should be acknowledged when interpreting the present findings. The three data sources differed in temporal coverage, sampling design, fishing gear, sampling objectives, and specimen handling protocols. The INIPO biological sampling programme covered only June–December 2022, leaving the January–May period unrepresented, which may have affected the characterisation of reproductive seasonality because the principal spawning peak occurred between February and April. In addition, a proportion of the specimens analysed under the DEMERSTEM project originated from commercial fishing vessels, where market-driven size selection may have introduced bias into the observed length distribution and, consequently, the estimation of the length–weight relationship and population structure. The marked differences in sex ratio among the different data sources (70.2% females in the scientific fishing surveys versus 47.8% in the DEMERSTEM project) probably reflect a combination of biological variation and methodological heterogeneity that could not be fully disentangled. Consequently, the biological parameters presented here should be regarded as integrated baseline estimates derived from multiple complementary data sources rather than precise estimates representative of a single year or sampling period. Future studies incorporating age determination, histological validation of gonadal maturity, environmental covariates, and long-term fishery-independent monitoring would improve understanding of the mechanisms regulating the growth, reproduction, and population dynamics of *P. elongatus*. Likewise, integrating environmental variables with biological indicators would allow direct

evaluation of the ecological processes hypothesised to influence reproductive timing and population structure. Overall, the biological patterns observed are consistent with the potential influence of environmental variability, fishing pressure, and species-specific life-history characteristics reported for other West African populations. However, because these drivers were not directly evaluated, they should be interpreted as biologically plausible hypotheses rather than demonstrated causal mechanisms. From a fishery management perspective, the present findings provide an important biological baseline for developing evidence-based management measures, including the evaluation of appropriate gillnet mesh-size regulations, the protection of peak spawning periods, and the implementation of long-term monitoring programmes capable of detecting temporal changes in recruitment, environmental conditions, and population structure.

5. Conclusions

This study provides the first integrated biological characterisation of *P. elongatus* in the Cacine River estuary, Guinea-Bissau, based on 1776 individuals. Females reached sexual maturity at a smaller size than males, indicating distinct maturation patterns between sexes. Both sexes exhibited positive allometric growth, demonstrating that body weight increased proportionally faster than total length. Pronounced sexual size dimorphism was observed, with females attaining significantly larger body sizes and dominating the larger length classes, whereas males predominated in the smaller ones. Reproductive activity occurred throughout the year, with a marked spawning peak during the dry season (February–April), suggesting that reproductive timing is closely associated with seasonal environmental conditions. Although the overall sex ratio remained close to parity, it varied significantly among length classes, reflecting sex-specific differences in growth, maturation, and population structure. These findings provide an important biological baseline for the sustainable management of *P. elongatus* in the Cacine River estuary and support evidence-informed fishery management measures, including the evaluation of appropriate gillnet mesh-size regulations to reduce size-selective mortality, the protection of peak spawning periods, and the implementation of long-term monitoring programmes to detect temporal changes in population structure, reproductive characteristics, and environmental conditions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fishes11080493/s1>: Table S1: Detailed sex-ratio analysis by 10 mm length class of *P. elongatus*, including female proportions with 95% Wilson confidence intervals, effect sizes (Cohen's *w*), and false discovery rate (FDR)-adjusted *p*-values; Table S2: Binomial GLM results for estimation of L_{50} ; Table S3: Monthly proportion of mature individuals by sex.

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Institutional Review Board Statement: Not applicable. The present study did not involve animal experimentation or the maintenance of organisms in captivity.

Data Availability Statement: Part of the data supporting this study (aggregated data) is presented in the main text of the article. The remaining data are available from the corresponding author upon reasonable request. The data are not publicly available due to ethical and/or privacy restrictions associated with the data-sharing agreement between the institutions involved.

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Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

EEZ	Exclusive Economic Zone
GLM	Generalized Linear Model
L ₅₀	Length at first sexual maturity
SR	Sex Ratio

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