



Age, growth, and population structure of the African cuttlefish *Sepia bertheloti* based on beak microstructure

Airam Guerra-Marrero¹ · Aurora Bartolomé² · Lorena Couce-Montero¹ · Ana Espino-Ruano¹ · David Jiménez-Alvarado¹ · José J. Castro¹ · Catalina Perales-Raya²

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Abstract

In this study, we explored the feasibility of using the beaks of the African cuttlefish *Sepia bertheloti* for age estimation and growth analysis. The rostrum sagittal section (RSS) of the lower beak was the most suitable region in the species. It was applied in samples caught off Morocco and Guinea-Bissau between June 2018 and January 2020. A maximum life expectancy of around 14 months was observed (specifically 419 days for cuttlefishes from Morocco and 433 from Guinea-Bissau). The males presented greater longevity, as the maximum age of the females was between 9 and 11 months. *Sepia bertheloti* showed a negative allometric growth; however, the exponential model better describes each population growth. By sexes, the males of both locations followed an asymptotic growth model while the females exhibited a non-asymptotic growth. The growth rates were different between locations, with the highest values in Guinea-Bissau. The males, in turn, grew faster for both study locations. In Guinea-Bissau, these growth differences were influenced by the hatching season since individuals born between autumn and winter were the fastest-growing. Samples from Morocco did not show growth differences between the hatching season and other seasons. These results indicate that the RSS of lower beaks are suitable for estimating the age, growth pattern, and population structure of *Sepia bertheloti*.

Keywords Increments · Lower beak · RSS · Daily growth · Cuttlefish

Introduction

The African cuttlefish *Sepia bertheloti* (Orbigny, 1839) is distributed in the Eastern Atlantic from the Canary Islands and Western Sahara to Angola, predominantly occupying sandy bottoms from 20 to 160 m (Jereb and Roper 2005; Guerra et al. 2014). It can reach sizes of a 180 mm mantle length for males and 130 mm for females (Guerra et al. 2014). This species is caught by bottom trawlers at depths between 70 and 140 m (Roper et al. 1984), with greater frequency in the fisheries operating off the West African coast

(FAO Fishing Area 34). It is one of the most productive regions of the world (Martos and Peralta 1995; Doumbouya et al. 2017) due to the upwelling systems off of the Western Sahara, Senegal, and Guinea-Bissau (Berrit and Rebert 1977).

There are no separate capture statistics for *S. bertheloti*, as it is often traded together with *S. officinalis* in Moroccan/Saharan waters, with *S. hierredda* in Guinean waters or treated as commercial by-catch. *Sepia bertheloti* accounts for 11–35% of reported by-catch and is marketed fresh and/or deep-frozen for export (Jereb and Roper 2005). The target cephalopod species for the Western Sahara/Morocco area are *Octopus vulgaris*, *S. officinalis*, and *Loligo vulgaris* (Hernández García and Castro 1994), while for the Guinea-Bissau fishing grounds, the target species are *O. vulgaris* and *S. hierredda* (FAO 2021). Furthermore, probably due to the low density and commercial value, the biological and fishery information about *S. bertheloti* is very limited in comparison to the fishing industry's cuttlefishes. Most of this information has been acquired by analyzing the stomach contents of its natural predators (Delgado de Molina et al.

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✉ Airam Guerra-Marrero
airam.guerra@ulpgc.es

¹ IU-ECOQUA, Universidad de Las Palmas de Gran Canaria, Edf. Ciencias Básicas, Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

² Centro Oceanográfico de Canarias (IEO, CSIC), Calle Farola del Mar. 38180, Santa Cruz de Tenerife, Spain

1993; Monzón-Argüello et al. 2018), by conducting exploratory fishing campaigns to assess the state of the resources (Balguerías et al. 1993; Rocha et al. 2017; García-Isarch et al. 2009; Perales-Raya et al. 2010a), or from the analysis of metal concentrations (Ama-Abasi and Akpan 2008). However, there is no information about age and growth of *S. bertheloti*, which are both key factors in estimating life history parameters and understanding its population dynamics in order to conduct an appropriate biomass estimation available for fishing (Arreguín-Sánchez et al. 1996).

The use of indirect methods off growth estimation based on length–frequency analysis is not suitable for age estimation in cephalopods since they are semelparous species with short life cycles and high variations among individuals, making their estimation imprecise (Jackson 2004). Direct methods using hard structures, such as statoliths, beaks, lenses, or gladius, based on the study of growth increments have proven to be the most useful method for estimating the absolute age and the growth of cephalopods. Growth increment analysis in jaws has been shown to be an appropriate technique for age determination, validated in other benthic cephalopods, such as *O. vulgaris* (e.g., Hernández-López et al. 2001; Canali et al. 2011; Perales-Raya et al. 2014b; Armelloni et al. 2020), *O. maya* (e.g., Rodríguez-Domínguez et al. 2013; Bárcenas et al. 2014), or *Sepia officinalis* (Guerra-Marrero et al. 2023). The recent revision of Xavier et al. (2022) provides detailed information on the attempted study of other cephalopod species using beak increment analysis, as well as those with confirmed daily deposition and validated ontogenetic stages.

The processing of cephalopod's hard structures is usually a time-consuming process, but it enables age estimates with a high rate of precision and is useful for identifying seasonal cohorts, an important component of cephalopod stock assessment. Nevertheless, the great variety of the growth rates (exhibited by individuals of the same age with different lengths) makes age-based models impractical for real-time stock assessment (Arkhipkin et al. 2021). Arkhipkin et al. (2021) propose a range of methodologies for assessing cephalopod populations, while warning that there is a high data requirement with a constant catch per unit effort report (CPUE) required. The abundance estimates of *S. bertheloti* in the area encompass other cuttlefish species, such as *S. officinalis* for Northwest Africa and *S. hierredda* for Central-West Africa (Jereb and Roper 2005); therefore, age analysis using hard structures is a suitable approach for future stock assessments.

Based on previous studies of other cuttlefish species, it is known that sepias have high growth rates (Perales-Raya et al. 1994; Perales-Raya 2001; Bettencourt and Guerra 2001; Guerra 2006) although size/weight differences have been observed between the populations of these species along the large Canary Current marine ecosystem (Hernández-García

and Castro 1994; Hernández-López 2000; Almonacid-Rioseco 2006; Jurado-Ruzafa et al. 2014).

This study contributes to (i) age and life span estimations of *S. bertheloti* in wild populations using the beak microstructure, (ii) the calculation of the hatching periods, (iii) determining the best model to describe the population growth pattern, and (iv) assessing the growth rates by seasons, with the final goal of obtaining these data for the future stock assessment of the African cuttlefish.

Materials and methods

The sample

A total of 1124 individuals of the African cuttlefish *Sepia bertheloti* were collected from June 2018 to January 2020 in two locations of Northwest Africa (449 individuals from Morocco and 625 from Guinea-Bissau) from commercial trawlers operating in each study location (Fig. 1). The subsequent data sampling is summarized in Table 1.

The cuttlefish were immediately frozen at -20°C after fishing and remained frozen until they were processed in the laboratory. Dorsal mantle length (DML) and body weight (BW) were measured to the nearest 1 mm and 0.01 g respectively. Sex was noted and maturity stages were identified according to the macroscopically maturity scale proposed by ICES (2010) for *Sepia officinalis* (namely, 0 is undetermined, 1 is Immature, 2a as Developing, 2b is Maturing, 3a is Mature/Spawning and 3b is Spent). Beak extraction and measurements were taken according to Perales-Raya et al. (2010b); Hernández-García (2003), respectively. The individuals caught in both locations were categorized according to the capture season (spring, summer, autumn, and winter).

Length–weight relationship

The length–weight relationship (LWR) was calculated using the equation $\text{BW} = a\text{DML}^b$ (power function), where a and b are the regression parameters estimated by linear regression of the data logarithmically transformed and adjusted by the least squares method. Student's t test was used to verify the 'b' values to determine whether they have isometric ($b=3$) or allometric (negative allometric $b < 3$, and positive allometric $b > 3$) growth.

Beak analysis

After dissection, the beaks were extracted, cleaned, and stored in distilled water at a temperature of 4°C , according to the procedure described by Perales-Raya et al. (2014b). A beak subsample of 78 specimens from Morocco and 128 from Guinea-Bissau were analyzed. A randomized

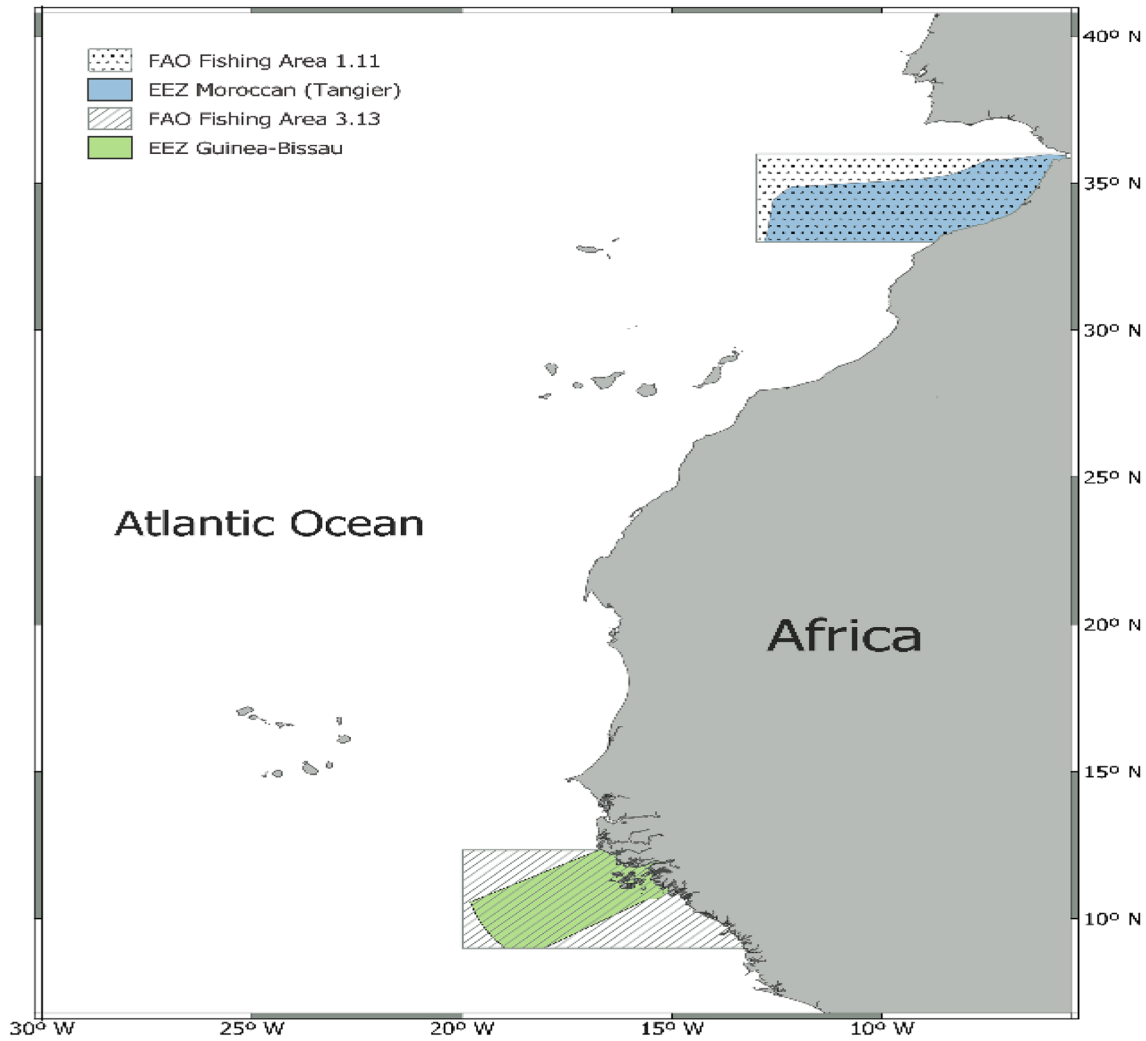


Fig. 1 Sampling areas (FAO Fishing Area 34) where the commercial trawlers caught *Sepia bertheloti* in Morocco (Tangier zone) (FAO 34.1.11) and Guinea-Bissau (FAO 34.3.13). Exclusive Economic

Zone (EZZ) for Morocco (Tangier zone) and Guinea-Bissau in the FAO Fishing Area 34 are shaded

Table 1 Number of individuals of *Sepia bertheloti* analyzed in two areas of West Africa caught from July 2018 to January 2020

Capture date	Morocco	Guinea-Bissau
July 2018	234	
August 2018	43	
September 2018	44	
July 2019		42
August 2019		36
September 2019		97
October 2019		78
November 2019		157
December 2019		155
January 2020	178	60
Total	499	625

categorizing process of the specimens was performed by size range within 5 mm of DML for both sexes.

After an analysis of the different regions of the upper and lower jaws was performed, the rostrum sagittal sections (RSS) of the lower beak were selected according to Perales-Raya et al. (2010b; 2014a). Once the beaks were processed, they were analyzed using a Nikon Microscope Multizoom AZ100 with a UV epi-illumination attachment (providing vertical reflected light) and different magnifications (100–400x) to observe the growth increments (Fig. 2).

The observed increments were counted twice by the same trained reader. The coefficient of variation (CV) was used to estimate the precision of the readings and the reproducibility of the method. The CV was calculated as the ratio of the standard deviation over the mean:

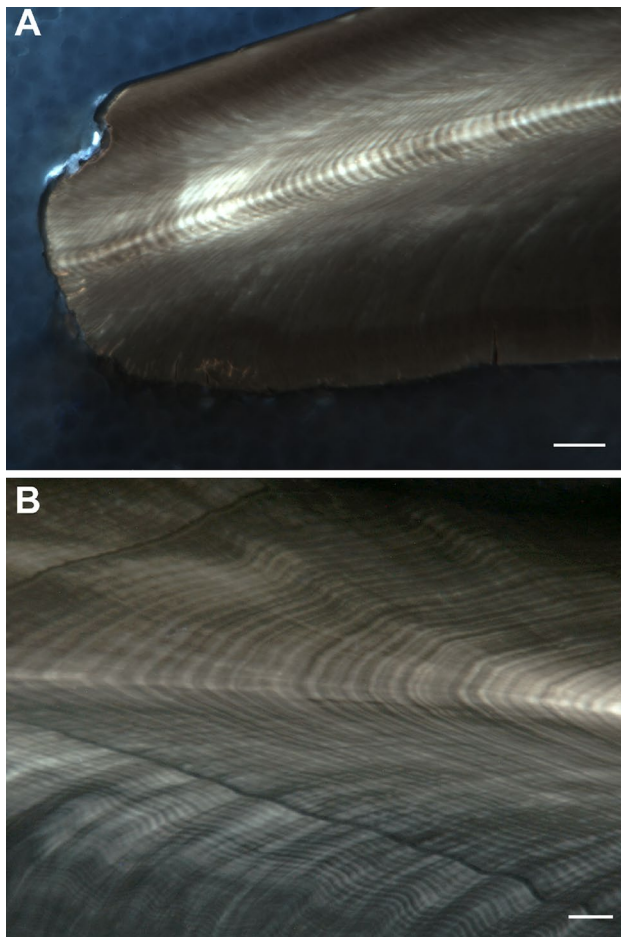


Fig. 2 Appearance of growth increments in the rostrum sagittal section (RSS) of lower beak in *Sepia bertheloti*. **A** tip region with older increments. **B** Detail of the growth increments in the posterior region of RSS with recent increments. Scale bar: 50 μm

$$\text{CV}(\%) = \frac{100 \times \sqrt{(R1 - R)^2 + (R2 - R)^2}}{R}$$

where $R1$ and $R2$ were the numbers of increments from the first and the second reading, respectively. R was the average of the number of increments of the two readings. According to Campana (2001), to avoid any bias, the mean of CV was averaged for each study location, and a $\text{CV} < 7.6\%$ was taken as valid, with higher values of CV being rejected.

The relationship between the rostral length of lower beak (LRL) and the number of increments (NI) was calculated to observe the growth of the reading area according to the estimated age. The analysis of covariance (ANCOVA) was carried out to determine possible significant differences in LRL–DML and LRL–NI relationships according to sex and study locations. These relationships and all the different analysis were performed using the second reading ($R2$) according to Perales-Raya et al. (2010b),

who postulate that $R2$ is more reliable since the reader has greater experience and practice.

Growth models and growth rate estimation

Length-at-age data of *Sepia bertheloti* were fitted into seven growth models (lineal, power, exponential, von Bertalanffy, Gompertz, logistic, and Schnute ($a \neq 0$ and $b \neq 0$) models). According to Bolser et al. (2018), model parameters for von Bertalanffy, Gompertz, logistic, and Schnute were estimated using a non-linear least squares regression and the Levenberg–Marquardt algorithm, and confidence limits were placed around parameter estimates in R studio (using the R packages Ogle 2017; Elzhov et al. 2015; Baty et al. 2015):

- von Bertalanffy growth model (Von Bertalanffy 1938):

$$L(t) = L_{\infty} \left[1 - e^{-K(t-t_0)} \right]$$
- Gompertz growth model (Gompertz 1825):

$$L(t) = L_{\infty} e^{-\left(\frac{1}{K}\right)e^{-K(t-t_0)}}$$
- Logistic growth model (Ricker 1975):

$$L(t) = L_{\infty} \left[1 + e^{-K(t-t_0)} \right]^{-1}$$
- Schnute growth model (Schnute 1981):

$$L(t) = \left[L_1^b + (L_2^b - L_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{1/b}$$

where $L(t)$ is length (in mm DML) at age t , L_{∞} is the maximum average length (in mm DML), K is the growth rate coefficient (in year $^{-1}$), and t_0 is the theoretical age at which length is zero (in years). For the Schnute growth model, $T1$ is the first specified age, $T2$ is the second specified age, $L1$ is length at age $T1$; $L2$ is length at age $T2$, a is the constant relative rate of relative growth (in year $^{-1}$), and b is the incremental relative rate of relative growth (dimensionless). Since the Schnute model does not calculate the parameter L_{∞} directly, the following equation must be used (Schnute 1981):

$$L_{\infty} = \left[\frac{e^{aT_2} L_2^b - e^{aT_1} L_1^b}{e^{aT_2} - e^{aT_1}} \right]^{1/b}$$

The parameters $L1$, $L2$, $T1$, and $T2$ are the same as used in the Schnute equation previously, while the parameters a and b are the resulting parameters of the growth model.

The best model for each sex and area was determined using the Akaike's information criterion (AIC) (Akaike 1974), transformed to Akaike weight (AICw) (Burnham and Anderson 2002) and the Bayesian Information Criterion (BIC) using the "AICcmodavg" package in R (Mazerolle and Mazerolle 2017). Akaike weights provide relative likelihood of each model from the tested set of models.

Estimated growth rates for length-at-age relationships were calculated for each 90-day age class according to the

following equations (Forsythe and Van Heukelem 1987; Gonzalez et al. 1996):

a. Instantaneous relative growth rate, G (% DML d^{-1})

$$G = \frac{\ln R_2 - \ln R_1}{t_2 - t_1} \times 100$$

b. Absolute growth rate, AGR (mm d^{-1})

$$AGR = \frac{R_2 - R_1}{t_2 - t_1}$$

Hatching date estimation

To study the influence of seasonality on growth, the hatching date of each cuttlefish was back-calculated according to estimated age and the date of capture. According to hatch dates, four seasonal hatching groups were defined: Spring

(March–May), Summer (June–August), Autumn (September–November), and Winter (December–February). Kruskal–Wallis test and post hoc Dunn test were used to describe possible differences between hatching seasons.

The normal distribution of the data was checked using the Shapiro–Wilk test in each analysis. When the data showed a normal distribution, a two-group independent t test was used to compare differences in age according to the location and differences in age by sex. ANCOVA was also used to analyze differences between locations and sexes. When a normal distribution was not achieved, a non-parametric Kruskal–Wallis test and a Dunn post hoc test were used. All statistical analyses were carried out using R v-4.1.1 (R Core Team 2022).

Results

Size–structure

Cuttlefish lengths and weights from Morocco and Guinea-Bissau are shown in Table 2. Mature males from Morocco ranged from 50 to 130 mm DML while mature females ranged from 60 to 110 mm (Fig. 3). Guinea-Bissau’s mature males fell within a range off 60–176 mm DML, while mature females ranged from 68 to 140 mm (Fig. 4). Immature and developing/maturing individuals were not

Table 2 Ranges of Dorsal Mantle Length (DML) and Body weights (BW) of *Sepia bertheloti* caught in Morocco and Guinea-Bissau

Area	Sex	DML (mm)	BW (g)
Morocco	Females	60–120	21.87–127.87
	Males	50–138	18.94–206.98
Guinea-Bissau	Females	32–168	20.03–314.00
	Males	60–176	28.44–456.61

Fig. 3 Dorsal Mantle Length (DML) frequency distribution for the sample of *Sepia bertheloti* females ($n = 102$) and males ($n = 397$) caught off Morocco

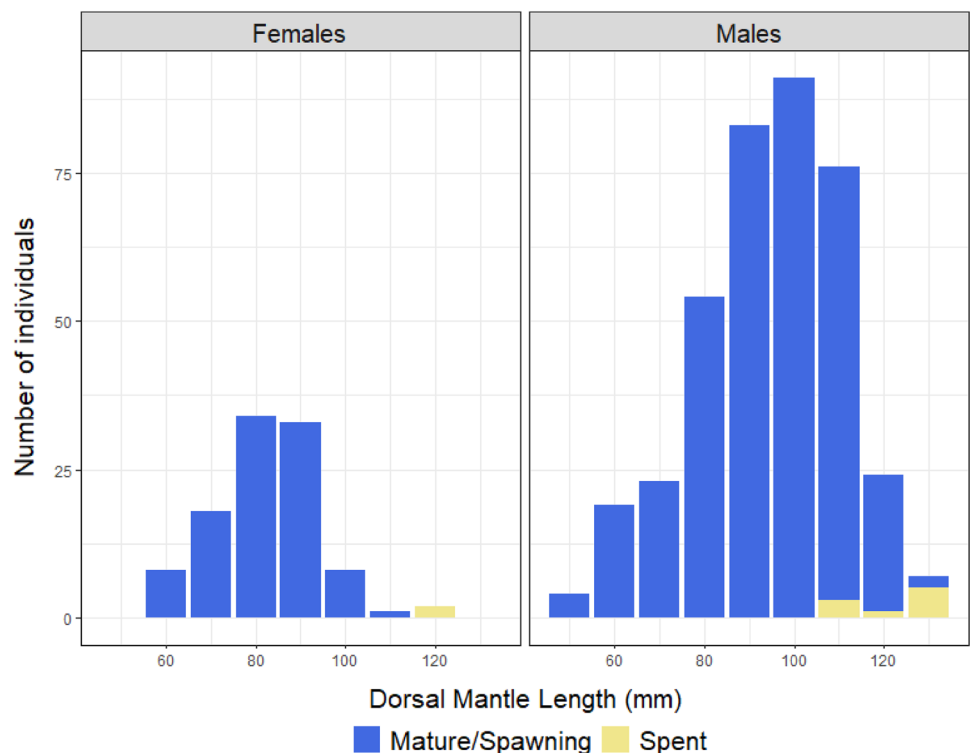
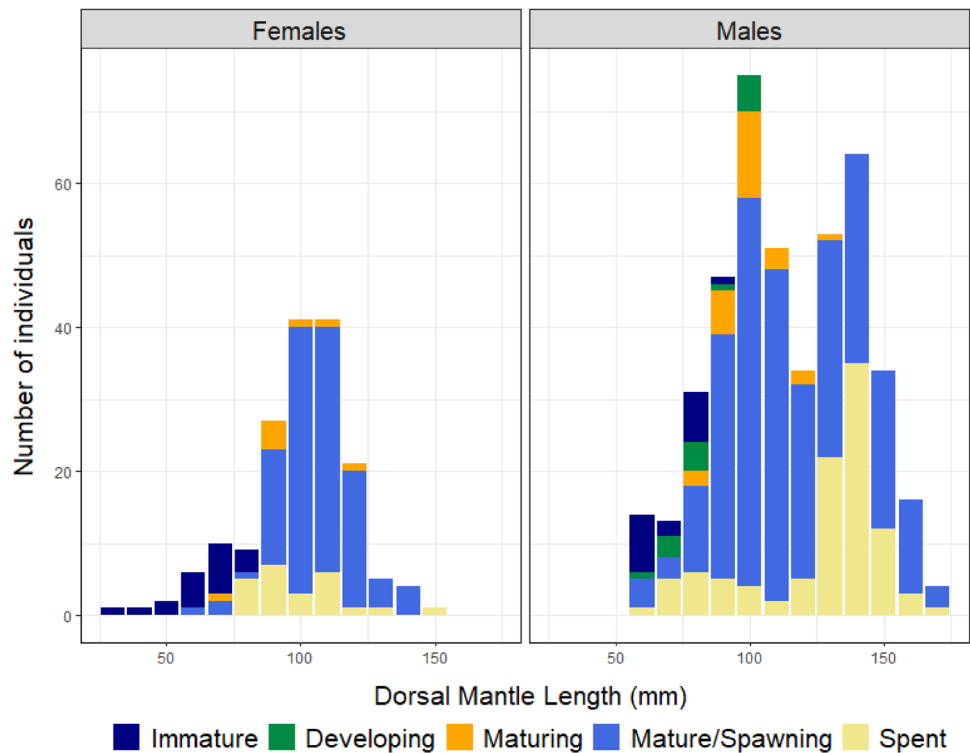


Fig. 4 Dorsal Mantle Length (DML) frequency distribution for the sample of *Sepia bertheloti* females ($n=194$) and males ($n=431$) caught off Guinea-Bissau



found in Morocco (Fig. 3), while all reproductive stages were found in Guinea-Bissau (Fig. 4).

The regression parameters of the DML–BW relationship (power equation) for males and females from Morocco and Guinea-Bissau are shown in Table 3.

The ANCOVA test showed significant differences in DML–BW relationships between sex and locations ($p < 0.0001$). Males of both locations were larger and heavier than the females, and the specimens from Morocco were smaller and lighter than those from Guinea-Bissau.

In terms of growth, the LWRs exhibited negative allometry (See Table 3) for both sexes and locations. This growth model implies a faster growth in DML than in BW.

Age analysis

Of the 206 beaks analyzed, 183 allowed a reliable reading. Twenty-three beaks (11.17%) were discarded due to malformations (see image in supplementary material) or severe damage during grinding that made a reliable reading impossible. Of the 183 beaks, 69 belonged to cuttlefish from Morocco (Table 4) with 114 belonging to specimens taken from Guinea-Bissau (Table 5).

From the Morocco sample, the youngest specimen was a female (111 days old, 60 mm DML), and the oldest specimen was male (419 days, 140 mm DML). No significant difference in age was found between sexes (t test: $p = 0.09034$), with the median age being 186 ± 41 days in females and 220 ± 70 days in males. The oldest specimen was caught in

Table 3 Statistical parameters of the Dorsal Mantle Length (DML) and Body Weight (BW) relationships for females, males and all individuals caught in Morocco and Guinea-Bissau

	DML–BW relationship	R^2	Confidence interval of b	Growth model*
Morocco				
Females	$BW = 0.4813DML^{2.3012}$	0.903	2.1701–2.4323	a–
Males	$BW = 0.414DML^{2.3576}$	0.934	2.2973–2.4179	a–
All	$BW = 0.4433DML^{2.3303}$	0.932	2.2774–2.3832	a–
Guinea-Bissau				
Females	$BW = 0.4619DML^{2.3183}$	0.922	2.2058–2.4308	a–
Males	$BW = 0.266DML^{2.5662}$	0.962	2.5147–2.6177	a–
All	$BW = 0.3296DML^{2.4757}$	0.952	2.4297–2.5216	a–

*a– negative allometry

Table 4 Descriptive statistics for *Sepia bertheloti* females, males and total sample collected throughout different seasons off Morocco

Capture season	N	NI (days)			DML (mm)			BW (g)		
		Min.	Max.	$\bar{X} \pm SD$	Min.	Max.	$\bar{X} \pm SD$	Min.	Max.	$\bar{X} \pm SD$
Morocco										
Females										
Summer '18	13	144	267	212.62 ± 39.12	70	110	88.31 ± 12.34	35.7	96.52	69.19 ± 19.14
Autumn '18	2	187	204	195.50 ± 12.02	90	96	93.00 ± 4.24	65.93	83.46	74.70 ± 12.40
Winter '20	8	111	240	184.75 ± 42.35	60	12	91.13 ± 20.88	30.82	127.87	80.75 ± 34.86
Males										
Summer '18	29	149	419	237.24 ± 65.34	75	140	106.62 ± 14.16	45.19	192.85	110.01 ± 36.04
Autumn '18	8	137	383	204.25 ± 76.81	82	133	106.38 ± 16.66	50.38	175.8	107.71 ± 40.14
Winter '20	9	114	410	231.13 ± 107.19	60	138	99.11 ± 28.03	26.29	202.37	104.04 ± 66.01
Total										
Summer '18	42	144	419	229.62 ± 59.13	70	140	100.95 ± 15.96	35.7	192.85	97.37 ± 36.87
Autumn '18	10	137	383	202.5 ± 67.96	82	133	103.70 ± 15.80	50.38	175.8	101.10 ± 38.26
Winter '20	17	111	410	207.94 ± 82.30	60	138	95.35 ± 24.50	26.29	202.37	93.08 ± 53.42

NI number of growth increments, DML dorsal mantle length, BW body weight, \bar{X} mean, SD standard deviation

Table 5 Descriptive statistics for *Sepia bertheloti* females, males and total sample collected throughout different seasons off Guinea-Bissau

Capture season	N	NI (days)			DML (mm)			BW (g)		
		Min.	Max.	$\bar{X} \pm SD$	Min.	Max.	$\bar{X} \pm SD$	Min.	Max.	$\bar{X} \pm SD$
Guinea-Bissau										
Females										
Summer '19										
Autumn '19	25	94	316	201.28 ± 57.04	70	152	103.2 ± 17.51	44.93	258.74	107.89 ± 44.32
Winter '20	12	102	301	213.16 ± 55.91	60	132	101.17 ± 20.25	21.8	174.65	105.22 ± 44.20
Males										
Summer '19										
Autumn '19	25	118	400	219.84 ± 77.35	60	173	114.84 ± 30.01	34.09	351.39	140.29 ± 86.49
Winter '20	21	122	372	234 ± 74.06	65	175	115.43 ± 29.74	30.04	383.86	151.13 ± 94.35
Total										
Summer '19	31	174	433	269.48 ± 75.60	126	170	145.29 ± 11.25	172	393.34	270.93 ± 57.94
Autumn '19	50	94	400	210.56 ± 67.91	60	173	109.02 ± 25.02	34.09	351.39	124.09 ± 69.96
Winter '20	33	102	372	226.48 ± 67.88	60	175	110.24 ± 27.25	21.8	383.86	134.43 ± 82.09

NI number of growth increments, DML dorsal mantle length, BW body weight, \bar{X} mean, SD standard deviation

summer 2018, while the youngest was caught during winter 2020 (see Table 4). Mature females were found between 111 and 234 days while the mature males were found between 11 and 370 days (see Fig. 5).

Cuttlefishes from Guinea-Bissau showed an estimated age between 94 and 433 days, with a mean age of 219 ± 74 days. The youngest specimen was a 94-day-old female (72 mm DML), and the oldest specimen was a 433-day-old male (160 mm DML). The youngest male was 122 days old (85 mm DML), and the oldest female was 316 days old (152 mm DML). Statistically significant difference in age was found between the sexes (t test: $p=0.0082$), with a mean age of 198 ± 56 days in females and 235 ± 78 days in males.

The oldest specimen was caught in summer 2019, while the youngest individual was caught during the fall of the same year (see Table 5). Mature females were found between 126 and 289 days while the mature males were found between 118 and 400 days (see Fig. 6).

No significant difference in age was found between locations (t test: $p=0.3285$) and sexes (t test: $p=0.784$ for females and $p=0.354$ for males). The mean reading precision value (CV) off the beaks readings was $2.72 \pm 3.95\%$ for specimens from Guinea-Bissau and $2.61 \pm 3.54\%$ for specimens from Morocco. Correlations between NI, LRL, and DML for both locations are shown in Table 6. In Morocco, the relationship between LRL and DML for both sexes was

Fig. 5 Age frequency distribution for females ($n=23$) and males ($n=46$) of *Sepia bertheloti* caught off Morocco

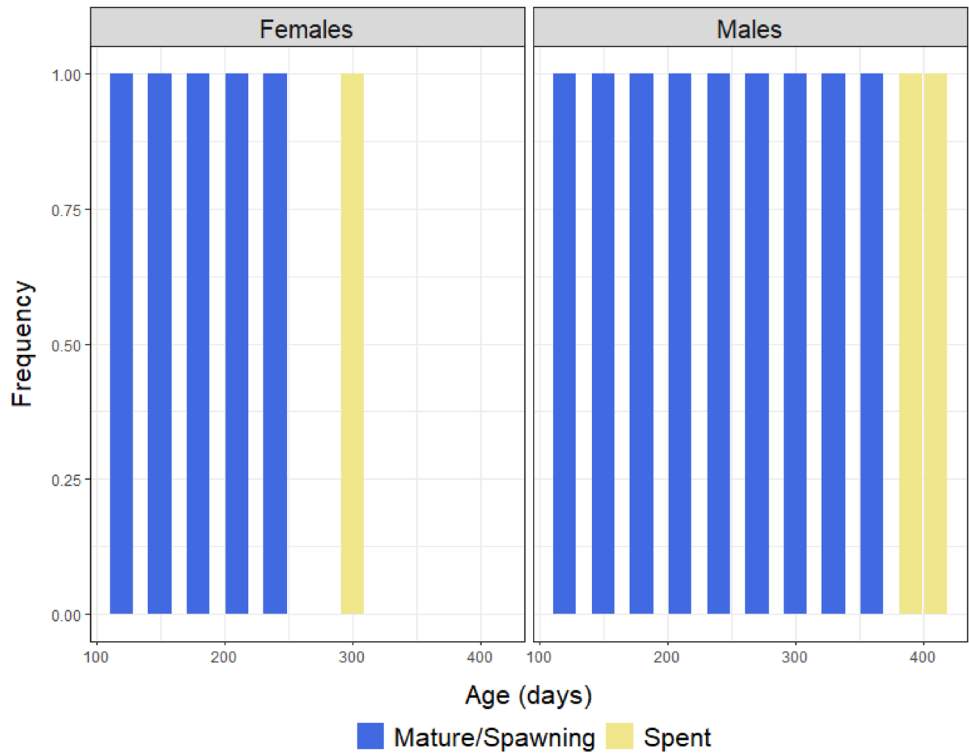


Fig. 6 Age frequency distribution for females ($n=37$) and males ($n=77$) of *Sepia bertheloti* caught off Guinea-Bissau



best fitted by the exponential model (Table 6). Moreover, the exponential model was the best model to describe the relationship between LRL and NI (Table 7). ANCOVA

showed that there were statistically significant differences between the sexes with respect to the DML–LRL relationship ($p=0.022$), but no significant differences were found in

Table 6 Pearson’s correlation coefficients for Morocco and Guinea-Bissau.

	Morocco			Guinea-Bissau		
	<i>R</i>	<i>p</i> value	Correlation	<i>r</i>	<i>p</i> value	Correlation
LRL–DML	0.45	<0.001	+	0.81	<0.001	+
NI–LRL	0.48	<0.001	+	0.66	<0.001	+
NI–DML	0.77	<0.001	+	0.84	<0.001	+

DML dorsal mantle length, *LRL* lower rostral length, *NI* number of increments

Table 7 Statistical parameters of the Dorsal Mantle Length (DML) and Lower Rostral Length (LRL) according to the numbers of increments (NI) observed in males and females caught in Morocco and Guinea-Bissau

Area	Equations	<i>R</i> ²
Guinea-Bissau		
Females	DML = 32.499LRL + 8.9974	0.600
	LRL = 0.0059NI + 1.7166	0.580
Males	DML = 32.114LRL + 25.17	0.630
	LRL = 0.2698NI + 0.4569	0.410
Morocco		
Females	DML = 36.36e ^{0.4235LRL}	0.563
	LRL = 1.414e ^{0.0023NI}	0.568
Males	DML = 34.297e ^{0.483LRL}	0.500
	LRL = 1.945e ^{0.0008NI}	0.430

the LRL–NI relationship (*p* = 0.587). Also, in the LRL–NI relationship, greater variability was observed in males than in females, which resulted in lower *R*² values. In the case of Guinea-Bissau for both sexes, the relationship between LRL and DML was best described by a linear model (Table 7). In the case of females, the best LRL–NI relationship fits the linear model, while this relationship in males was best described by the power model (Table 7). ANCOVA showed that there was a statistically significant difference in the DML–LRL relationship of both sexes (*p* = 0.001) but not in the LRL–NI (*p* = 0.155) relationship. A greater variability of the DML–LRL and LRL–NI relationships was observed in males than in females, which resulted in lower *R*² values observed in samples from Morocco.

Growth models and growth rates

The estimated statistical parameters for the different growth models are shown in Table 8. According to AIC parameters, the Schnute and the exponential models best described the

Table 8 Statistical parameters of different growth model fitted to *Sepia bertheloti* Dorsal Mantle Length–age data from Morocco and Guinea-Bissau

Model	Dorsal Mantle Length–age data								
	Males			Females			All		
	AIC	AICw	BIC	AIC	AICw	BIC	AIC	AICw	BIC
Morocco									
Logistic	412.32	0.02	420.27	233.80	0.17	239.27	655.50	0.10	665.18
Gompertz	411.49	0.03	419.44	234.13	0.14	239.60	654.81	0.14	664.18
von Bertalanffy	410.58	0.04	418.58	234.47	0.12	239.94	654.24	0.19	663.91
Schnute	404.55	0.86	410.52	234.95	0.09	239.05	660.96	0.01	668.22
Power	424.15	0.00	430.12	235.51	0.07	239.61	666.56	0.00	673.82
Linear	419.69	0.00	425.66	234.18	0.14	238.28	660.46	0.01	667.72
Exponential	410.28	0.05	416.24	232.86	0.27	236.96	652.09	0.55	659.35
Guinea-Bissau									
Logistic	564.01	0.13	572.89	229.41	0.10	235.02	833.29	0.06	843.67
Gompertz	562.61	0.27	571.49	229.25	0.10	234.85	832.25	0.10	842.63
von Bertalanffy	561.40	0.48	570.29	229.09	0.12	234.69	831.31	0.16	841.69
Schnute	577.82	0.00	284.48	253.98	0.00	258.19	858.34	0.00	866.13
Power	583.70	0.00	590.36	228.90	0.13	233.10	842.14	0.00	849.93
Linear	577.00	0.00	583.66	228.18	0.19	232.38	834.98	0.03	842.76
Exponential	564.21	0.12	570.88	226.84	0.36	231.04	828.54	0.65	836.33

AIC akaike’s information criterion, AICw akaike’s weight, BIC bayesian information criterion. K: number of parameters in each model. Best growth model fit is given in bold underlined

growth pattern of males and females, respectively, in the Morocco population. The exponential model was the best to describe the growth of the entire population (combining males and females). In the case of Guinea-Bissau's *Sepia bertheloti* population, the von Bertalanffy model best described the growth pattern of males and the exponential model for females, while for the entire population (males and females combined), the exponential model showed the best fit. Figure 7 shows the best growth curves for males and females of each study location.

The asymptotic length (L_{∞}), according to the Von Bertalanffy model for males from Guinea-Bissau, was 173 mm DML, and according to the Schnute model, the males from Morocco showed a L_{∞} of 140 mm DML.

The largest number of specimens was aged from 191 to 280 days (Table 8), for Morocco (51.47%) and Guinea-Bissau (41.22%), with the youngest age classes (< 100 days old) being the least present (Morocco: 0.00% and Guinea-Bissau: 0.88%). In the case of males, the lowest instantaneous relative growth rate (G) values were for the age classes of 281–370 and > 371 days old for Morocco and Guinea-Bissau, respectively. In the case of females, the lowest G values were for the 191–280 days old age classes for Guinea-Bissau. The fastest growth patterns were found in the lower age classes of 191–280 for males from Morocco and Guinea-Bissau, while for females, it was in the range of 101–190 days old for Guinea-Bissau. Females from

Morocco have not been compared since just obtaining a value of G could misrepresent their results. Even so, the age range available for Morocco females (191–280 days old) exhibited a lower G than individuals of the same age from Guinea-Bissau. This also occurs for males as, those from Guinea-Bissau show a higher G for all age classes, except for individuals > 371 days old, where cuttlefishes from Morocco show a value of 0.137% DML d^{-1} and those from Guinea-Bissau a value of 0.131% DML d^{-1} . In Table 9, all G and AGR data are summarized.

Significant differences in G and AGR growth rates between sexes (t test, $p < 0.0001$) and locations (t test, $p < 0.0001$) were found. The individuals from Guinea-Bissau showed a higher G value than the individuals from Morocco, showing faster growth at the same age (See Table 9). On the other hand, within each location, males had a higher growth rate than females. This is demonstrated by the fact that males showed larger sizes than females in both locations for the same age. The differences in G and AGR between locations are observed: individuals from Guinea-Bissau showed larger sizes than individuals from Morocco at the same age ranges.

Hatching season

The back-calculation method indicated that the cuttlefish hatched between June 2017 and September 2019 for Morocco, and between May 2018 and October 2019 for

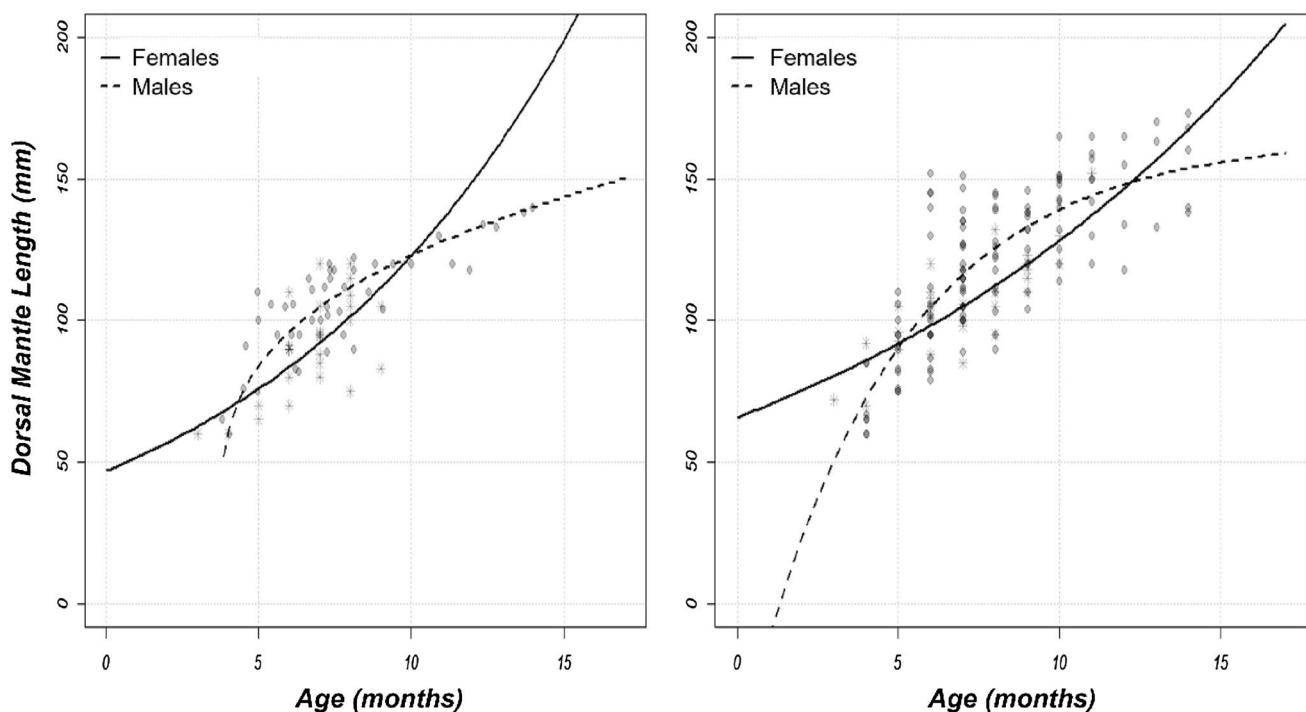


Fig. 7 Best growth models fitted to Dorsal Mantle Length at age data for females (asterisks), males (circles) and all individuals of *Sepia bertheloti* caught off Morocco (left) and Guinea-Bissau (right)

Table 9 Dorsal mantle length growth rates for each age class of *Sepia bertheloti* females and males from Morocco and Guinea-Bissau

Age class (Days)	Morocco			Guinea-Bissau		
	DML $X \pm SD$	G	AGR	DML $X \pm SD$	G	AGR
Females						
< 100				72.00 ± 0.00	–	–
101–190	81.78 ± 16.27	–	–	94.38 ± 15.24	0.402	0.332
191–280	100.71 ± 13.89	0.147	0.141	107.5 ± 12.29	0.182	0.183
281–370				129.25 ± 16.40	0.288	0.340
Males						
101–190	89.6 ± 15.51	–	–	93.52 ± 21.45	–	–
191–280	108.52 ± 9.97	0.281	0.277	130.42 ± 13.58	0.455	0.505
281–370	123.67 ± 6.62	0.129	0.149	146.79 ± 12.77	0.144	0.199
> 371	137.00 ± 3.61	0.137	0.179	166.50 ± 4.76	0.131	0.205

Highest value of G is given in bold

G instantaneous relative growth rate (% DML d⁻¹), AGR absolute growth rate (mm d⁻¹), X average, SD standard deviation

Guinea-Bissau. It was observed that cuttlefish hatched throughout the year in Morocco (Fig. 8A) and Guinea-Bissau (Fig. 8B); however, 45.59% of the total sample hatched in winter for Morocco, while Guinea Bissau's the hatchings had two marked peaks—one in summer (30.70%) and another in winter (35.08%). Kruskal–Wallis test ($W = 4.0462$, $p = 0.2565$) did not result in significant differences in length ranges according to season of hatching for individuals from Morocco. In contrast, individuals from Guinea-Bissau showed significant differences in length ranges (Kruskal–Wallis test; $W = 36.439$, $p < 0.0001$). The post hoc Dunn test ($p < 0.001$) showed that these differences were due to the fact that individuals born during warm seasons (spring and summer) were smaller than those born in the autumn/winter. Individuals hatched in winter exhibited the largest sizes.

Growth rates for each hatching season group were analyzed for females and males separately (see supplementary material). In Morocco, the highest values of G for males and females were found for specimens born in summer, and for Guinea-Bissau, the highest values of G were found in autumn for females and in spring for the males. In both locations and sexes, a decreasing trend in the growth rhythm was observed with age.

Discussion

In this study, the length ranges obtained from commercial fisheries did not enable us to separate the catches into different ontogenetic groups (juveniles and adults) due to the lack of consensus regarding definition the juvenile phase. Sweeney et al. (1992) assigned the category of “juveniles” to the stage of development between hatching and the subadult

stage (defining the category of “subadult stage” as that stage in which the morphological characteristics of cephalopod are sufficiently developed to determine the species and ending when sexual maturity is reached). Bellanger et al. (2005) defined the juvenile category for *Sepia officinalis* as individuals up to 3 months old.

Significant differences in mean length between the sexes have already been described for other cuttlefish, such as *Sepia latimanus*, *S. koilados*, *S. rhoda*, and *S. subplana* (Bettencourt and Guerra 2001; Dan et al. 2012), white males being larger than females. However, this is not a characteristic that can be extrapolated to the whole Sepiidae family since most species have a different growth pattern where females are larger than males (i.e., *S. orbignyana* and *S. elegans* among others; Jereb and Roper 2005).

Differences in growth conditioned by environmental factors (i.e., latitude, temperature, food, etc.) have been described in cephalopods (e.g., Arkhipkin et al. 1998; Semmens et al. 2004; Guerra 2006; Batista et al. 2021). In the case of *S. bertheloti*, it was observed that specimens from Guinea-Bissau (Central Africa) exhibited larger sizes than individuals captured in Morocco (North Africa) at the same age. The oceanographic differences of both zones, due to the influence of high productivity from the Western Sahara upwelling (Aristegui et al. 2009) and the different thermal ranges between the locations due to the seasonality of upwellings and winds (Aristegui et al. 2009; Pelegrí et al. 2017), might cause differences in the length frequency distribution. In relation to growth, males and females showed negative allometric patterns, growing faster in dorsal mantle length than in total weight, which is comparable to other species of cuttlefish such as *S. officinalis* (Vasconcelos et al. 2018).

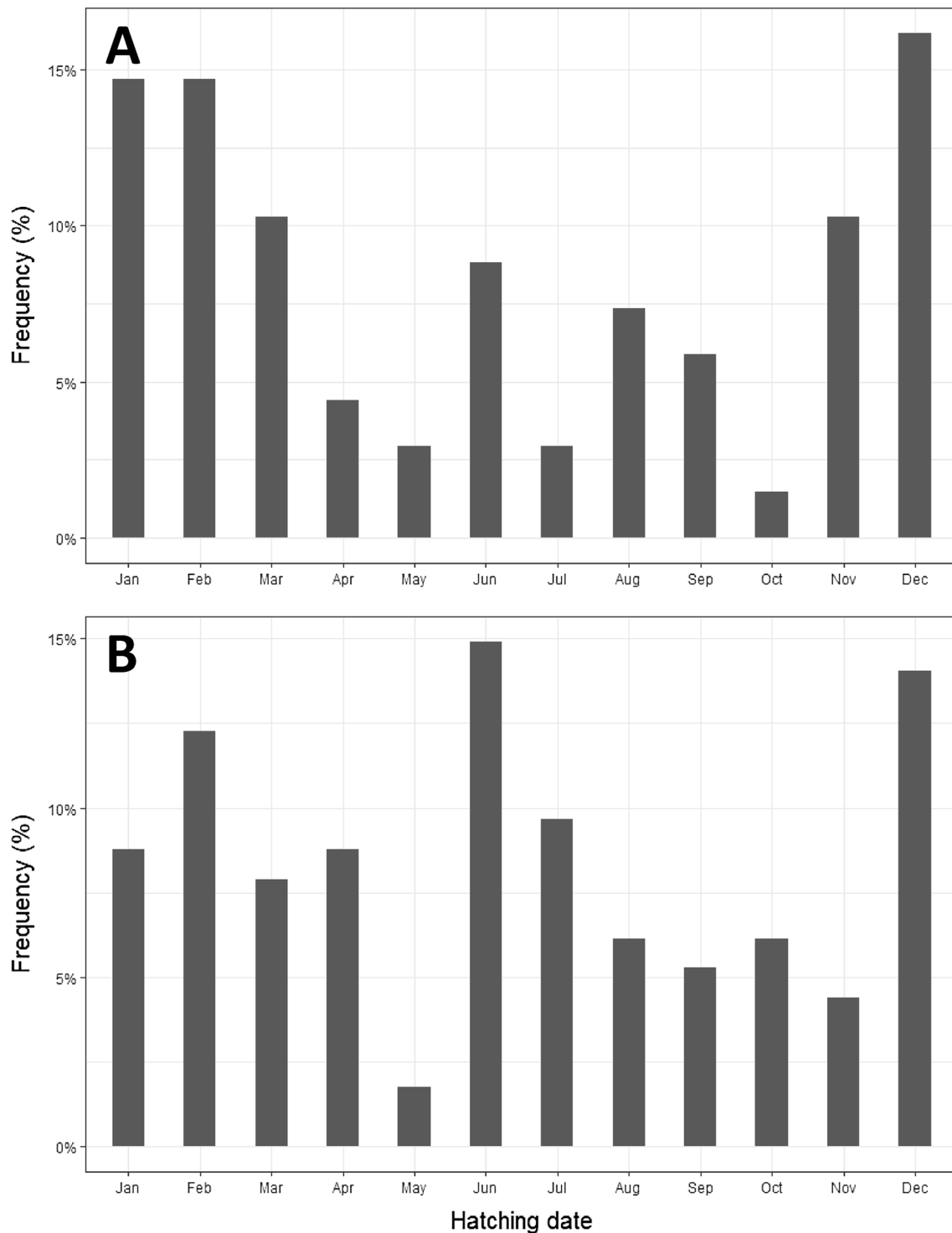


Fig. 8 Frequency distribution of back-calculated hatching months for *Sepia bertheloti* from **A** Morocco and **B** Guinea-Bissau

In this study, the analysis of beak microstructure for *Sepia bertheloti* used rostrum sagittal sections to determine age. This is in contrast to other benthic cephalopods, such as *Octopus vulgaris* (e.g., Perales-Raya et al. 2010b; 2014a, b; Canali et al. 2011; Cuccu et al. 2012), *O. insularis* (Batista

et al. 2021), or *O. maya* (Rodríguez-Domínguez et al. 2013) where the lateral wall surfaces (LWS) of upper beaks were successfully used for age estimation. In the case of *S. bertheloti*, and after exploring the RSS and LWS of several upper and lower jaws, the RSS of the lower beak showed the

clearest pattern of growth increments. On the contrary, no clear sequence of growth increments were observed for age estimation of *S. bertheloti* in the LWS of the upper beaks.

Although differences were observed among the length distributions of specimens within the same age classes of both studied locations, the maximum age recorded for *Sepia bertheloti* (14 months) did not differ between locations. Nevertheless, according to our data, males showed a higher life span than females in both locations. The maximum estimated age for males was 14 months, while females showed a maximum age of 9–10 months. As samples do not cover the entire year in the northern location, some of the largest individuals may not have been caught; therefore, the maximum age could be underestimated. In this context, using age data from statoliths, Perales-Raya (2001) obtained a maximum age of 223 days (over 7 months) for both sexes for *S. hierredda* from Western Sahara, with males reaching larger sizes than observed in this study. Bettencourt and Guerra (2001) showed that the maximum age of *S. officinalis* under culture conditions was 420 days (14 months), although the number of increments in the statoliths could have been underestimated due to the large number of narrow increments close to the nucleus, which were very dark and difficult to detect and discern. While working with samples from the English Channel, Challier et al. (2005) reported an approximate life expectancy of 2 years for *S. officinalis*. Similarly, Nabhitabhata and Nilaphat (1999) described the life expectancy of *S. pharaonis* as one year or over two years depending on the season of birth. This characteristic of life expectancy was also described by Hernandez-López (2000); life span variations in *O. vulgaris* are dependent on the hatching season. Our results indicate life span of around one year for *S. bertheloti* in both fishing locations, although it should be noted that this age range corresponds to specimens captured by commercial fishing fleets. Additionally, a deeper study of both populations would be advisable in order to observe possible differences in life expectancy and sexual maturity as reported for other species (Moreno et al. 2002).

The use of asymptotic models for the growth analysis in cephalopods is something that has been under discussion for years. Several studies, e.g., Jackson et al. (2000), describe the inefficiency of the von Bertalanffy model for cephalopods. In contrast, authors such as Uozumi and Shiba (1993) or Brodziak and Macy (1996) recommend the use of the Gompertz and Schnute asymptotic models (Petric et al. 2021). Arkhipkin and Roa-Ureta (2005); Arkhipkin et al. (2021) recommend using the Schnute model to describe growth since the use of von Bertalanffy parameters for assessment models is inappropriate for cephalopods' semelparous classification. In this study, seven growth models were tested, including four with asymptotic growth (Logistic, von Bertalanffy, Gompertz, and Schnute models). The absence of individuals of small and very large lengths means that

our growth models were adapted to the fished portion of the population. Forsythe and Van Heukelem (1987) indicated that cephalopods grow differently in each life stage, so the presence of extreme length ranges determines which model fits best. According to the length distributions in our sample, the exponential model was the one that best described the growth of the *S. bertheloti* population of Morocco and Guinea-Bissau, which has also been described as adequate for other cephalopods species during the early stages of their life cycles (Forsythe and Van Heukelem 1987). However, the exponential model was not the best model to consider to each sex separately. The females, with a shorter maximum age, showed an exponential growth pattern, but the asymptotic models (Schnute's for males from Morocco and Von Bertalanffy's for males from Guinea-Guinea) was a better fit for males. This variation in growth between males and females may be due to life expectancy factors, since males have a longer life span than females and are probably able to survive a longer after reproduction. Furthermore, an asymptotic model in the final phase of life would be expected as the growth rate slows.

The instantaneous growth rates generally showed high values in the early stages of life and are expected to decrease with age. Many authors have already observed this growth pattern in cephalopods (Richard 1971; Dominguez et al. 2006; Petric et al. 2021 among others). Cuttlefish from Guinea-Bissau showed higher growth rates than those from Morocco in the same age bracket, although differences in date of capture might affect this. By sexes, males from both locations exhibited a longer life span than females. These differences between sexes and geographic locations have also been observed in other cephalopods such as *Illex coindetii* (Arkhipkin 1996) where females grow faster than males and specimens from Central Africa (Sierra Leone) grow faster than those from the Western Sahara. These observations are in keeping with the hypothesis that individuals from colder waters (i.e., Morocco) have a longer life span, a slower growth rate and later reproduction than cuttlefish from warmer waters (i.e., Guinea-Bissau), as suggested by several authors (e.g., Hernández-García and Castro 1998; Pelegrí et al. 2017).

Regarding growth differences by hatching season, specimens from Guinea-Bissau born during the warmer seasons (spring and summer) had smaller lengths at a given age than individuals born during the autumn and/or winter periods. Conversely, in the cuttlefish *S. hierredda* from the Western Sahara, the specimens born in spring showed larger sizes at a given age than those born in autumn (Perales-Raya 2001), though it should be noted that the author also found inter annual differences. The back-calculation analysis showed that *S. bertheloti* from Morocco and Guinea-Bissau hatch continuously throughout the year. A peak of hatching was observed in the

winter off of Morocco, but two marked peaks were shown in Guinea-Bissau, one in summer and one in winter. These results should be considered with caution when managing these populations that are difficult to access as the sampled period does not cover the whole year, since a more complete study (> 18 months of sampling) would be necessary to confirm the hatching peaks. However, a continuous spawning has been observed for many benthic cephalopods, such as *O. vulgaris*, *S. officinalis*, and *S. hierredda*, in West Africa: however, like the Guinea-Bissau sample, they usually had two marked reproductive periods (Hatanaka 1979; Jurado-Ruzafa et al. 2014). In both locations, it was observed that the highest G values coincided with the greatest intensity of the upwellings (Ingham 1970; Arístegui et al. 2009), when the increased availability of nutrients at hatching makes cuttlefishes grow faster.

In conclusion, the RSSs of beaks are suitable structures for age estimation in cuttlefish. The results obtained from this study suggest that the life span of *S. bertheloti* is around 9–10 months for females and 14 months for males, with differences between the growth rates likely due to genetic, environmental and geographical factors, in keeping with observations off other cephalopod species (Guerra 2006). The growth of *S. bertheloti* showed a negative allometry following an exponential model in both study locations. By sex, this model was the best fit for all the females of the study. However, in the case of males, the Schnute model was the best adapted to Moroccan males with the von Bertalanffy model being best suited to the Guinea-Bissau sample. Growth rates were also different between locations and sexes. In both locations, males showed a faster relative instantaneous growth pattern than females. The population of Guinea-Bissau presented a higher overall growth rate than Morocco. In Guinea-Bissau, a sample's hatching season marked a difference in growth patterns with individuals born in spring and summer being smaller than those born in autumn–winter. In contrast, no size differences were observed in relation to the hatching season in Morocco. Future efforts should be focused on accessing a wider range of lengths, seasons, and maturity stages among *S. bertheloti* to enhance understanding of their life cycles in the region. This information may enable the analysis of potential differences related to the water temperature and the influence of upwellings. This knowledge is indeed essential for the sustainable management of cuttlefishes in the Central Eastern Atlantic.

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Data availability The datasets generated during and/or analyzed during the current study are not publicly available due to are being processed for further analysis but are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval No applicable.

Consent to participate No applicable.

Consent to publish Not applicable.

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