Iranian Journal of Fisheries Sciences

http:doi.org/ 10.22092/ijfs.2025.133396 2025, 24(3) 505-525

Research Article

Growth and reproduction parameters estimation of *Octopus vulgaris* in the Moroccan Mediterranean by size frequency analysis

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Keywords

Growth,
Reproduction,
Octopus vulgaris,
Moroccan Mediterranean,
Modal progression analysis

Article info

Received: April 2024
Accepted: December 2024
Published: May 2025

Abstract

A study of growth and reproductive parameters of *Octopus vulgaris* in the Moroccan Mediterranean (between Fnideq and Jebha) was carried out based on size frequency data of a sample of 14919 specimens (7891 females and 7028 males) from fishing trawlers and artisanal boats during 2015-2019. Different methods of FISAT II software including Powell-Wetherall, ELEFAN I, Shepherd, and Modal Progression Analysis were tested. Based on the annual sex ratio, females were slightly more abundant than males (1.06:1.00). Mature females were most abundant between June and September. Throughout the year, 53% of the males caught were mature on average. Length $L_{50\%}$ and Weight $TW_{50\%}$ were 15.56 cm, 2602.16 g for females and 10.77 cm, 991.30 g for males respectively. Compared with those found by other authors in the Mediterranean and Atlantic, and after the most appropriate growth parameters were selected, the Von Bertalanfy equation was estimated to be $L(t)=28.76\ (1- e^{-1.06(t - 0.386)})$ for combined sex. The size-age data obtained using the direct method and Bhattacharya's approach were substantially similar. The study of size frequencies from commercial data, even for octopus, would be a useful substitute to estimate size-at-age data required for stock assessment and fishery management.

Introduction

The Moroccan octopus fishery plays a significant socio-economic role in Morocco through its predominant contribution to exports. Octopus landings accounted for 9.2% in value and 10.3% in weight of all fishing product landings in the Moroccan Mediterranean (Maritime Fishing Department, 2018). This fishery is managed along the Moroccan Atlantic and Mediterranean coasts under a national plan that was adopted in 2001 and established two activity seasons (Winter and Summer) and two closed seasons (Spring and Autumn), with the primary goal of protecting the octopus stock.

In parallel, individual growth is a fundamental process used in describing the dynamics of populations, and is a vital element in the formulation of management policies (Francis, 2016; Maunder *et al*. 2016; Punt *et al*. 2016). Growth can often vary spatially, temporally, between cohorts, between individuals, and within individuals (Quinn and Deriso, 1999; Wang, 1999; Morrongiello and Thresher, 2015). Moreover, cohort effects can vary to a lesser or greater extent depending on the species and have been linked to environmental changes (Baudron *et al.*, 2014; Morrongiello and Thresher, 2015). Even for the common octopus *Octopus vulgaris*, a short-lived species (12-14 months) characterized by generations with only one or two cohorts present in the fishery at any time (Pierce and Guerra, 1994), the study of growth based on the analysis of length frequency distributions has been widely used (Arregun-Sanchez *et al.*, 1993; Nepita and Defeo, 2001; Storero *et al.*, 2010). However, the use of this indirect method has been questioned (Jackson *et al.*, 2000; Doubleday *et al.*, 2006) since length is not a good measure of size in soft-bodied organisms and size is not a good indicator of age due to the high inter-individual variability in cephalopod growth rate (Semmens *et al.*, 2004). Easy to apply and inexpensive for fisheries without financial resources or limited scientific capacity to carry out direct methods (López-Rocha *et al.*, 2012), this method continues to be applied despite criticism (Storero *et al.*, 2010; Jabeur *et al.*, 2012).

The robust maximum likelihood-based estimation approach MULTIFAN, which is incorporated into a length-based statistical catch at age stock assessment model, is probably the most well-known length frequency method in the literature (Fournier *et al.*, 1990, 1998). The non-parametric ELEFAN procedure (Pauly, 1987) is also widely used and has recently been extended into the R environment where modern optimization algorithms are used to improve its performance (Mildenberger *et al.*, 2017; Taylor and Mildenberger, 2017).

This study aims to estimate and select the most suitable growth and reproductive parameters of the *Octopus vulgaris* population in the Moroccan Mediterranean by analysing the size frequencies 2015-2019 using various methods from the FISAT II software.

Materials and methods

Materials and measurements

The 14919 *Octopus vulgaris* specimens (7891 females and 7028 males) used in this study were randomly collected from coastal trawlers using the atomic bottom trawl and artisanal boats using ordinary octopus jigs, which are made up of a plumb piece with three to six hooks, at the M'diq port between 2015 and 2019. Typically taking place in January-February-March, June-July-August, and December, the weekly sample period covered from six months (2018) to seven months (2015, 2016, 2017, and 2019). Unfortunately, because octopus fishing is prohibited during the biological rest periods of April-May, October-November, and occasionally June and September, it was unlikely to cover these months.

The average monthly sea surface temperature during 2019 along Morocco's Mediterranean coast based on estimations from Reynolds *et al*. (2002) NOAA database ranged from 15.5°C to 23°C. The surface salinity was 36.6 psu, rising from the coast towards the open sea (INRH, 2014). According to Faiki *et al.* (2023), the depth area ranged from 5.5 to 73.2 m (mean=24.7 m) for artisanal boats while it varied from 73 to 219.5 m (mean=124 m) for trawlers. The biometric measurements included dorsal mantle length (DML) measured with an ichthyometer to the nearest 1 cm on a table to stretch samples, total weight (TW) using a scale to the nearest 1 g, sex and stage of sexual maturity determined by eye. The study area extends from Fnideq to Jebha (Fig. 1).

Figure 1: Study area between Fnideq (35.86°N 5.34°W) and Jebha (35.20°N 4.59°W) in the Moroccan Mediterranean.

Sex ratio, sexual maturity stages, and size $L_{50\%}$

The sex ratio was calculated by month and size class. Sexual maturity was based on naked-eye observation of the relative size, color, and appearance of oviduct glands and ovary for females, the presence of spermatophores, and the Needham's sac appearance for males (Gonçalves, 1993). The adopted sexual maturity scale consists of 3 stages (immature, maturing, and mature) for males and females (Sanchez and Obarti, 1993) and a post-spawning stage for females (Idelhaj, 1984). The logistic regression model was used to determine the length ($L_{50\%}$) at which 50% of the individuals are mature (Hunter *et al.*, 1992; Roa *et al.*, 1999). It was calculated using the following expression: $Pi=1/1+\exp[-(a+bLi)]$, where Pi is the relative frequencies of fully mature individuals in the length class Li, and a and b are the regression constants: $L_{50\%}=-a/b$. The body weight at maturity ($TW_{50\%}$) was also estimated using the same approach. For these calculations, mature specimens (stage 3) were grouped into interval classes of 1 cm DML (Li) and 250 g TW (TWi). No post-spawning female specimens were encountered.

Size-Weight relationship

This kind of relationship allows the conversion of measured sizes into weight data: $TW=a\times DML^b$ (Ricker, 1980). TW: weight per specimen (g), DML: dorsal length (mm), a: constant of proportionality, and b: growth coefficient that reflects allometry.

Linear and weight growth

Growth was studied by the Von Bertalanffy (1938) model: $L(t)=L\infty(1-e^{(-K(t-t_0))})$, Lt: Length of the fish at time t, L∞: Theoretical asymptotic length, K: Growth coefficient and t_0: Theoretical age at which the fish length is zero (years). Fisat II has allowed to test of several approaches, namely the Electronic Length Frequency Analysis (ELEFAN) I, and the Powell (1979) and Wetherall (1986) methods, to determine growth parameters (asymptotic length L∞ and growth rate K) from the analysis of size frequencies. While the first approach combines Petersen's method and Modal Progression Analysis (MPA), which defines growth from the change in modes or means in a time series of length-frequency samples, the second one suggests applying the Beverton and Holt (1956) equation (Gayanilo *et al.*, 2005). Since *O. vulgaris* is a short-lived species, it was suitable to use seasonal size frequency distributions rather than monthly ones. Bhattacharya (1967) and NORMSEP techniques were used to separate size frequency distributions to identify age group averages. The latter technique was not employed as mean sizes with a separation index SI < 2, which are considered unreliable (Abrahamson, 1971; Pauly and Caddy, 1985), disappear once refined and consequently reduce the likelihood of cohort formation (linking mean size of age groups). Growth rates and size-age data from the MPA were analysed using Munro and Appeldoorn methods to estimate growth parameters and curves that best suit the size-frequency distribution.

Munro (1982) suggested a method using growth rate data to estimate L∞ and K or K alone with L∞ fixed, based on a function that minimizes the coefficient of variation of the ratio=$[\ln(L\infty-Lm)-\ln(L\infty-Lr)]/(tr-tm)$ where Lm is marking length (initial reading), Lr is recapture length, and tm and tr the corresponding dates.

The seasonal oscillation version of the VBGF 's parameters can be estimated using growth rate data owing to Appeldoorn (1987) and Soriano and Pauly's (1989) approach. It applies the non-linear

Marquardt curve algorithm to minimize the following functions:

$SSE = \sum \{Li + \Delta t - (L\infty - (L\infty - Li)\ e^{(-(K\Delta t - S_t + S_{t+\Delta t}))}\}^2$

Where, $S_t = (CK/ 2\pi).\ \sin(2\pi\ (t - t_s))$, $S_{t+\Delta t} = (CK/2\pi).\ \sin(2\pi\ ((t + \Delta t) - ts))$ and $t_s = 0.5 + WP$ (C and WP were set to 0 to estimate the standard VBGF parameters without taking into account the seasonal oscillation of growth). The growth performance index Ø' (Munro and Pauly, 1983) is calculated by the formula: $Ø' = \log K + 2\log L\infty$.

Theoretical age t_0 was estimated from Pauly's (1980) empirical equation: $\log10(-t_0) = -0.3922 - 0.2752\log_{10}L\infty - 1.038\log_{10}k$ and Von Bertalanffy's graph, using linear regression $Y = a + bt = -\ln(1 - (Lt /L\infty))$:

- t: arbitrary age corresponding to each mean length calculated assuming that the birth date of spring and autumn cohorts was 15 May and 15 October, respectively,
- Lt: average length of each cohort at time t,
- L∞: asymptotic length (Y calculated based on L∞ from the ELEFAN I, Shepherd and Powell-Wetherall methods).
- $t_0 = -a/b$.

The growth curve equation $DML = 0.185\ age^{1.188}$ (Faiki *et al.* 2023) was used to compute additional estimates of ages corresponding to age group mean sizes (TM) in addition to the size-age data from the MPA. This growth equation, which was derived from a recent ageing study, involved reading 128 *Octopus vulgaris* beaks (56–239 mm DML, 121–5974 g TW) collected from artisanal boats and trawlers landing on the Moroccan Mediterranean coasts between Fnideq and Jebha in 2019,

The Von Bertalanffy weight growth model was generated by combining the size-weight relationship with the Von Bertalanffy linear growth model: $W(t)= W\infty[1 - e^{-k(t - to)}]^b$, where W∞ : asymptotic weight (g), and W(t), specimen weight at time t (g).

Statistics

The $\chi 2$ Goodness-of-fit test was used to check the deviation from the 1:1 sex ratio between males and females. To examine the variations in the slopes of males and females TW-DML relationship, an analysis of covariance (ANCOVA) was performed. The Kruskal-Wallis test was used to see whether males and females differed in DML and TW. The paired Wilcoxon test was used to compare the two age distributions, which were calculated using the MPA (Age-Bhatta) and the growth curve equation (Age-beak).

Results

Sample

Dorsal mantle length was 4-25 cm (mean=9.98±2.62), and 4-25 cm (mean=9.81±2.66) while TW was 59-10960 (mean=904±772.4) g, and 53-8200 g (mean=826±664.6) respectively for males and females (Fig. SI 1). The Kruskal-Wallis test showed that there were significant differences between males and females in DML (H=21, P=0.000004) and TW (H=41.12, $p<0.000001$).

Sex ratio, stages, and size at sexual maturity

Females were slightly more abundant than males with an average annual sex ratio of 1.06:1 (1.02:1 in 2018, 1.09:1 in 2015). The χ2 test showed that the deviation from the 1:1 annual sex ratio was significant (*p*<0.01) except for the year 2018 (0.50<*p*<0.25). The average annual sex ratio was 1.06:1, meaning that there were slightly more females than males (1.02:1 in 2018, 1.09:1 in 2015). Except for the year 2018 (0.50<*p*<0.25), the χ2 test revealed that the annual sex ratio deviation from 1:1 was significant (*p*<0.01). For 19 out of the 34 months of the study period, which mostly coincided with the winter and summer seasons, the deviation was non-significant (*p*>0.05) on a monthly basis (Table SI 1).

According to Figure 2A, the average female sex ratio was highest in July (1.15:1) and lowest in September (0.89:1). In general, females dominated the 5-21 cm classes while males dominated classes > 21cm (Fig. 2B).

Table 1: The annual sex ratio (female) χ2 test result of the Moroccan Mediterranean common octopus (2015-2019).

Year	Observed F	Observed M	Expected F/M	χ2	P value	Sex ratio (female)
2015	1364	1128	1246	22.35	< 0.005	1.09
2016	1818	1545	1681.5	22.161	< 0.005	1.08
2017	1420	1273	1347	7.912	< 0.005	1.05
2018	1433	1382	1407.5	0.924	0.50< P< 0.25	1.02
2019	1856	1700	1778	6.844	< 0.01	1.04
Total	7891	7029	7460			1.06

$\chi^2_{critical}$=3.84. F: female, M: male.

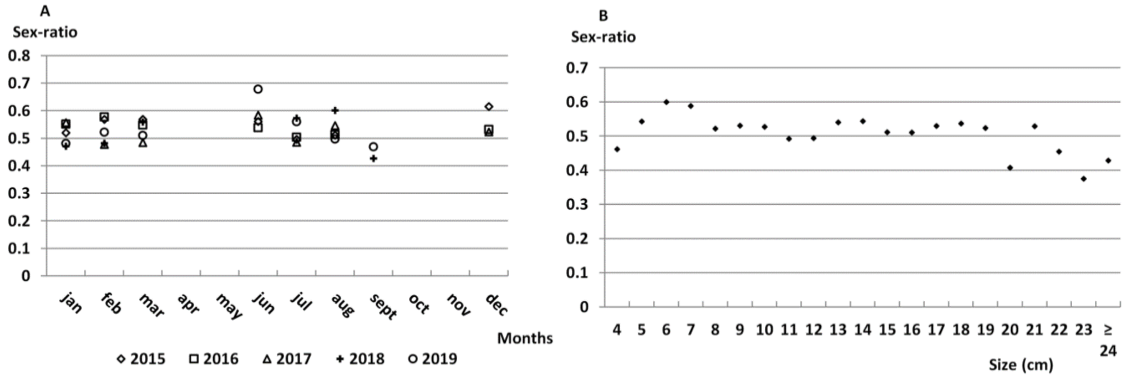

Figure 2: Common octopus monthly female sex ratio (A) and by size class (B) in the Moroccan Mediterranean during 2015-2019.

The average frequency of mature females is shown in Figures 3A and B to be low in January and March and high between June and September, mostly in July and August: 17.3% ± 9.9 (5.5% Min to 36.7% Max). Males are mature at 53% ± 19.4% (16.3% Min to 82.2% Max) throughout the year.

The smallest adult specimen measured 7 cm DML, 234 g TW for females, whereas it measured 6 cm DML, 161 g TW for males. For females and males respectively, the $L_{50\%}$ was 15.56 cm, 10.77 cm (13.21 cm for combined sex) and the $TW_{50\%}$ was 2602.16 g, 991.30 g (2075.9 g for combined sex) (Fig. 4). The determination coefficients of the logistic models DML and TW ranged from 0.74 to 0.98 (Table 2).

Size-weight relationship

The ANCOVA test revealed significant heterogeneity in the b slopes between males and females ($p<0.001$). The growth is negatively allometric with b coefficient <3 for males, females, and combined sex (Table 3, Fig. 5). Therefore, Moroccan Mediterranean *Octopus vulgaris* grows faster in length than in weight.

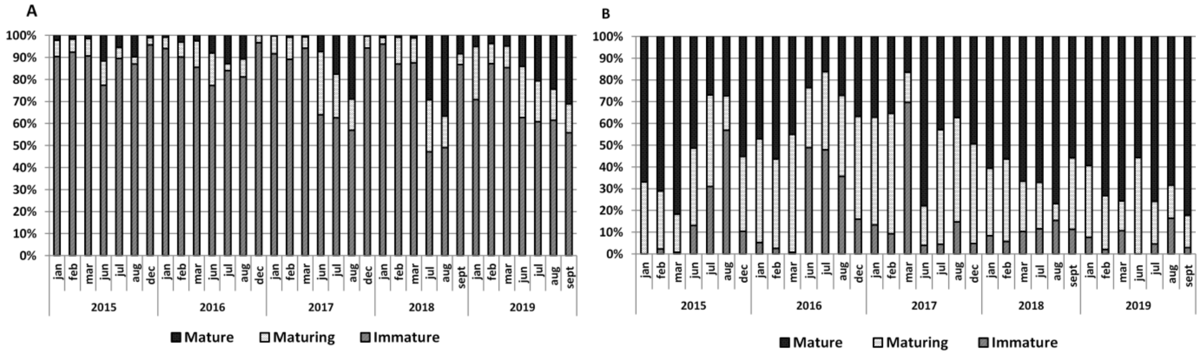

Figure 3: *Octopus vulgaris* sexual maturity stages in the Moroccan Mediterranean during 2015-2019. A. Females. B. Males.

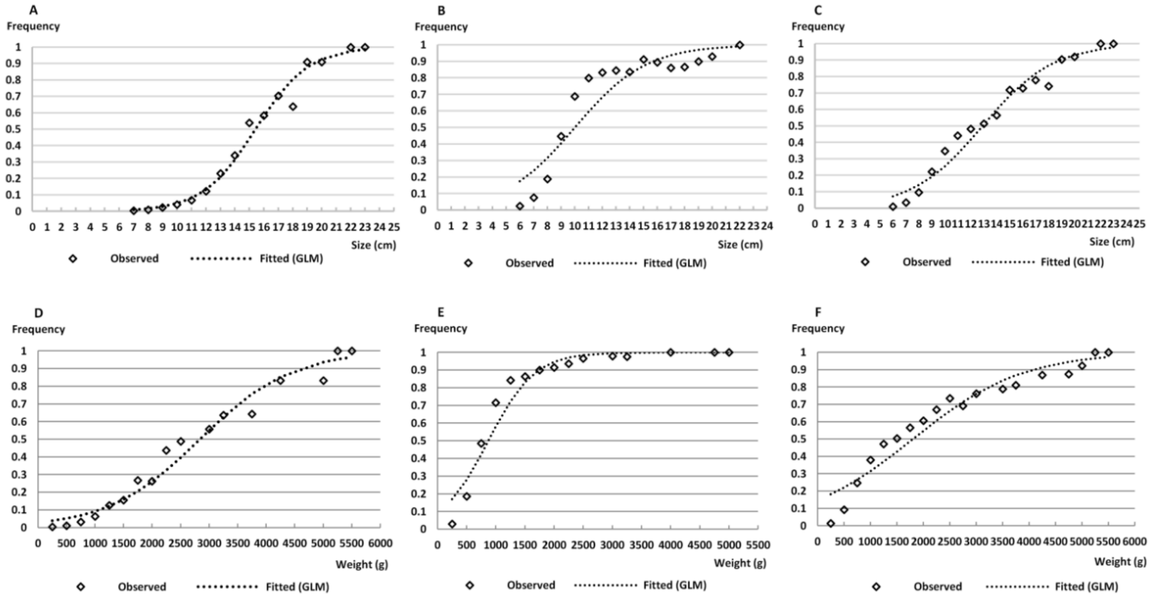

Figure 4: Observed and GLM-fitted frequencies of mature *Octopus vulgaris* individuals by size (A. females, B. males, C. combined sex) and weight (D. females, E. males, F. combined sex) in the Moroccan Mediterranean.

Table 2: Logistic model parameters (a, b, r^2) for DML (cm) and TW (g) of the Moroccan Mediterranean *Octopus vulgaris*.

		a	b	r^2
Females	DML	-9.0548	0.5818	0.98
	TW	-4.9441	0.0019	0.92
Males	DML	-3.9367	0.3655	0.74
	TW	-2.28	0.0023	0.86
Combined sex	DML	-4.8673	0.3685	0.92
	TW	-2.0759	0.001	0.78

N: sample size.

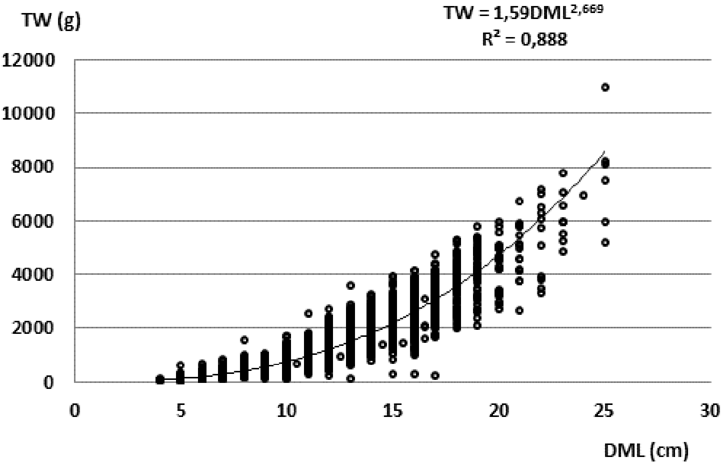

Figure 5: *Octopus vulgaris* (combined sex) size-weight relationship (DML-TW) in the Moroccan Mediterranean (2015-2019).

Linear and weight growth

The monthly size class distribution was generally uni-modal in winter (January-March) (Fig. SI 2). The appearance of the two peak recruitment periods was hindered by missing data from the biological rest periods of April–May and October–November. However, the fact that immature females dominated in February and March (Fig. 4A) and the proportion of size <10 cm (mostly immatures as $L_{50\%}$=13.21 cm combined sex), dominated from 54 to 83% suggested that there was likely a recruitment peak resulting from the spawning period April-May. Moreover, the size class distribution was mostly bi-modal in June and August-September with a first large mode of immatures (6-10 cm) and a second smaller mode of matures (12-16 cm). Growth parameters were estimated by the Powell-Wetherall method (Fig. SI 3), the ELEFAN I, and Shepherd methods (Table 4, Table SI 2). The choice of $L\infty$, k pairs (ELEFAN I) was made based on the growth performance index Ø'. The monthly growth rate estimated by ELEFAN I for combined sex individuals was low-medium (0.31 to 0.59) between June and September and generally large between December and March (0.59 to 1.01) (Fig. SI 4).

Table 4: Growth parameters estimated by ELEFAN I, Shepherd, and Powell-Wetherall methods of the Moroccan Mediterranean common octopus (2015-2019).

Parameters	ELEFAN I			Shepherd			Powell-Wetherall		
	L∞	k	Ø’	L∞	k	Ø’	L∞	Z/k	r
Combined sex	25.7	1.01	2.824	26	0.94	2.803	28.76	3.743	-0.948
Females	25.6	0.94	2.790	25.4	1.08	2.843	29.87	4.486	-0.884
Males	27.2	0.38	2.449	27.8	0.94	2.861	27.06	2.535	-0.969

Table 5 displays the mean size age groups (TM) determined by the Bhattacharya approach. The seasonal distribution of size frequencies enabled the identification of two (7 times) to three (10 times) age groups.

For the years 2014, 2015, 2016, 2017, and 2018, Table 6 and Figure 6 illustrate the possible linking of mean sizes (and related s.d.) to retrace the spring and autumn cohorts.

Table 5: The Bhattacharya method's seasonal size frequencies decomposition in age groups (G) and their mean size (cm).

Date /Groups	G 1	G2	G3
15/02/2015	10.03	14.43	21.5
15/06/2015	8.38	14.51	16.5
01/08/2015	8.48	17.54	-
15/12/2015	7.61	12.13	-
15/02/2016	9.4	15.43	-
15/06/2016	8.9	14.36	20.93
01/08/2016	8.84	14.77	16.5
15/12/2016	8.91	11.75	15.59
15/02/2017	9.36	14.61	18.62
15/06/2017	10.79	14.5	-
01/08/2017	9.83	14.8	16.5
15/12/2017	9.83	16.1	20.53
15/02/2018	9.01	13.03	-
15/08/2018	10.66	18.41	21.5
15/02/2019	10.64	19.6	23.5
15/06/2019	8.71	13.42	-
15/08/2019	11.48	19.71	-

Table 6: Spring (S) and autumn (A) cohort mean sizes evolution (MS) and corresponding standard deviations (s.d.) for the years 2014, 2015, 2016, 2017, and 2018.

Cohorts/ Date	S 2014		A 2014		S 2015		A 2015		S 2016		A 2016		S 2017		A 2017		S 2018		A 2018	
	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d	MS	s.d
15/02/2015	10.0	1.7																		
15/06/2015	14.5	0.7																		
01/08/2015	17.5	1.2	8.5	1.9																
15/12/2015			12.1	1.8																
15/02/2016			15.4	2.6	9.4	1.6														
15/06/2016			20.9	0.6	14.4	2.6														
01/08/2016					16.5	1.0	8.8	1.7												
15/12/2016							15.6	1.2												
15/02/2017							18.6	1.0	9.4	2.0										
15/06/2017									14.5	0.8										

Table 6 continued:

01/08/2017	16.5	1.5	9.8	1.8								
15/12/2017	20.5	3.2	16.1	0.9								
15/02/2018					9.0	1.7						
15/08/2018					18.4	1.1	10.7	2.0				
15/02/2019							19.6	0.9	10.6	2.0		
15/06/2019									13.4	1.1		
15/08/2019									19.7	1.6	11.5	2.2

The growth rate (k) from the Munro and Appeldoorn data analysis was relatively similar, notably for the spring cohorts. The Munro and Appeldoorn models both match the cohort data reasonably well. By cohort type, data analysis revealed that spring cohorts had an extremely good fit (r2=0.86) to the Appeldoorn model (Table 7, Fig. 7). The t_0 estimation was based on the Von Bertalanffy plot (Fig. 8), using the Age-Bhatta, Age-beak, and L∞ distributions estimated by the Powell-Wetherall method (Table 8).

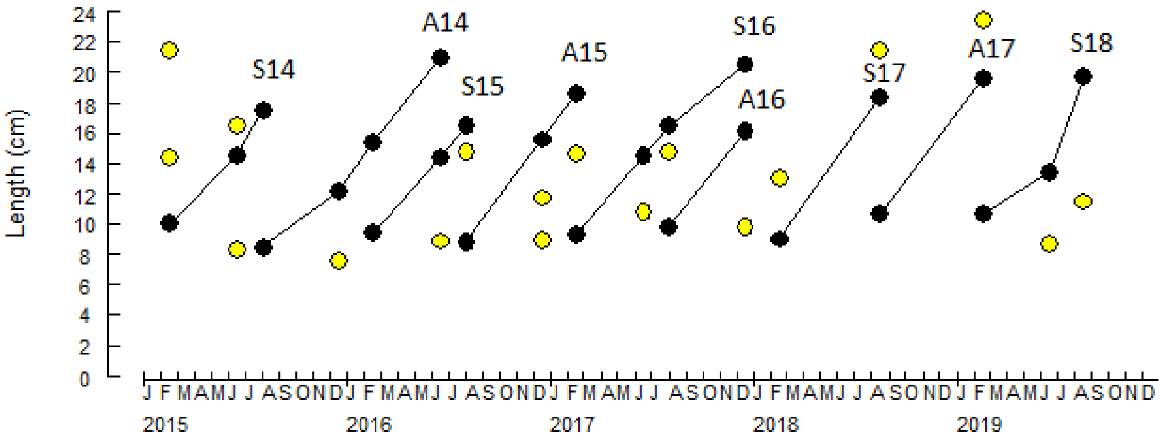

Figure 6: Age group linking means of common octopus spring (S) cohorts from 2014 to 2018 and autumn (A) cohorts from 2014 to 2017.

Table 7: Growth rate (k) estimation of the common octopus spring (SC) and autumn (AC) cohorts during 2015-2019 using Munro and Appeldoorn methods.

Parameters	**Munro**			**Appeldoorn**		
	SC	**AC**	**All cohorts**	**SC**	**AC**	**All cohorts**
k	1.165	1.219	1.278	1.06	1.08	1.06
ø'	2.984	3.004	3.024	2.943	2.951	2.943
R^2	-	-	-	0.86	0.49	0.46

Fixed L∞ =28.76 cm.

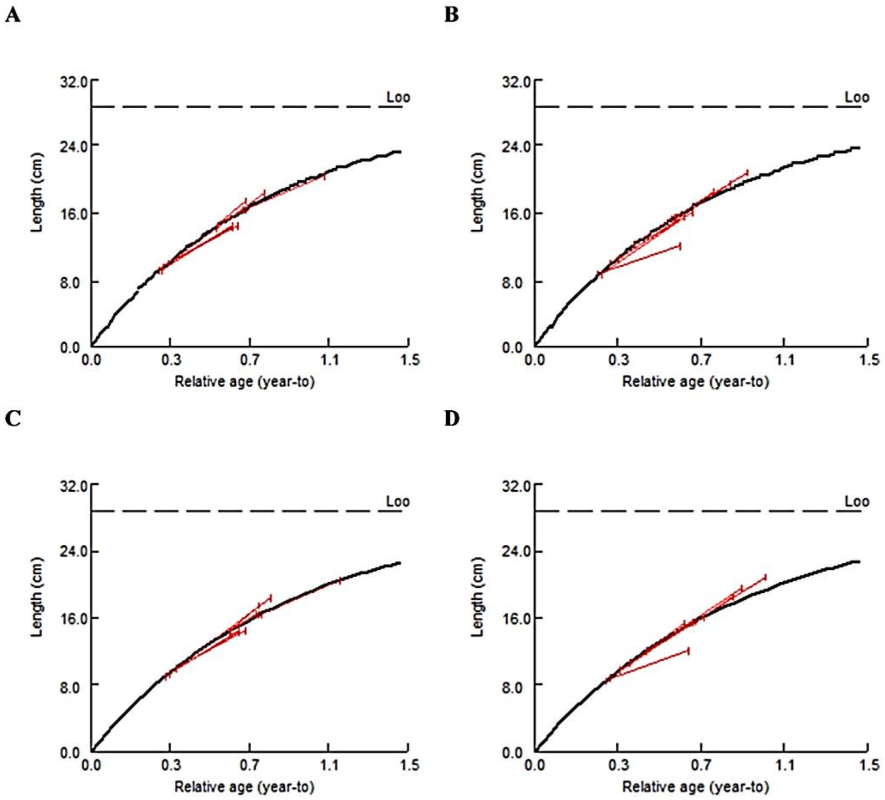

Figure 7: Common octopus growth curves using Munro (A: spring cohort, B: autumn cohort) and Appeldoorn (C: spring cohort, D: autumn cohort) methods.

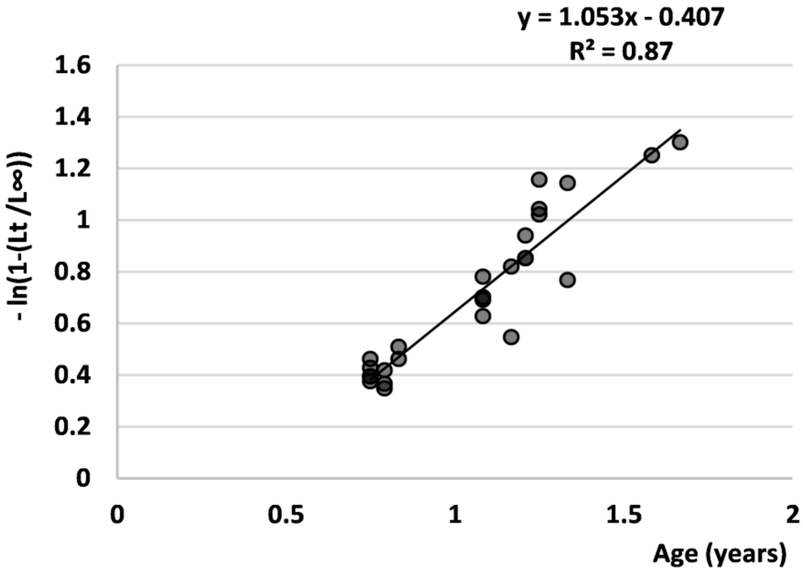

Figure 8: Theoretical age estimation at Lt=0 (t_0=-a/b) using the Von Bertalanfy equation.

Table 8: Theoretical age t_0 estimation using the Von Bertalanfy equation for both Age-Bhatta and Age-bec distributions.

	t_0	Equation	R^2
Age-bec	0.394	y=1.094x -	0.98
Age-Bhatta	0.386	y=1.053x -	0.87

L∞ derived from the Powell-Wetherall method.

Generally, t_0 of the two distributions was quite similar. The non-parametric Wilcoxon paired test (V=157, P=0.449) showed that there was no significant difference in mean between the two age distributions (Table SI 3). Furthermore, t_0 was based on the Pauly (1980) method using the growth parameters estimated by ELEFAN I (-0.089), Shepherd (-0.059), Munro (0.365), and Appeldoorn (0.137).

The following equation of Von Bertalanfy for combined sex could be useful for later applications in octopus stock assessment models: $L(t) = 28.76(1 - e^{-1.06(t - 0.386)})$. The weight growth model: $W(t) = 12484 (1 - e^{-1.06(t - 0.386)})^{2.67}$ was generated by combining this equation with the relationship $TW = 1.59DML^{2.67}$.

Discussion

Sample

There were significant differences between males and females in the size and weight of the sample (N), in contrast to the findings of Hernandez-Garcia *et al.* (2002) on the coast of the Canary Islands (N=760) and González *et al.* (2011) in the Gulf of Alicante-northwestern Mediterranean (N=1176) (no significant differences).

Sex ratio, stages, and size of sexual maturity

Females were slightly more abundant than males (1.06:1). Caverivière (1982) pointed out that a higher natural mortality rate for males and a higher catchability of females might explain female dominance in older individuals. This finding is consistent with those reported by the authors Otero *et al.* (2007) (1:0.88 in the northwest Atlantic of the Spanish coast) and Carvalho and Sousa Reis (2003) (1.28:1 in Cascais, 1.17:1 in Santa Luzia, and 1.04:1 in Viana do Castelo of the Portuguese coast). However, it differs from those reported by the authors for which males dominate, namely Silva *et al.* (2002) (1.06:1 in the Gulf of Cadiz) and Ajana *et al.* (2021) (1:0.91 in the Moroccan Mediterranean. This latter study whose number of samples was small (365 specimens) could explain this difference in results compared to the current one.

The annual sex ratio (4 years/5) showed a significant deviation from the 1:1 ratio compared to the findings reported by authors Carvalho and Sousa Reis (2003), Otero *et al.* (2007), and Ajana *et al.* (2021). For the monthly sex ratio, it was non-significant (19 months/34) which is similar to the results of Quetglas *et al.* (1998), Silva *et al.* (2002), and Carvalho and Sousa Reis (2003).

Some variations in the spawning season and maturity size were observed in different areas of the Mediterranean where the common octopus reproduction was studied (Mangold-Wirz, 1963; Guerra, 1978; Mangold, 1983, 1989; Sanchez and Obarti, 1993; Quetglas *et al.*, 1998; Tirado-Narvaez *et al.*, 2003; González *et al.*, 2011; Cuccu *et al.*, 2013). A major spring spawning peak has been noted in the Atlantic Ocean (Hatanaka, 1979; Gonçalves, 1993; Hernandez-Garcia *et al.*, 2002; Silva *et al.*, 2002), or in the Mediterranean Sea (Sanchez and Obarti, 1993; Katsanevakis and Verriopoulos, 2006; Otero *et al.*, 2007). A second (smaller) spawning peak was observed primarily in the autumn in Atlantic waters (Hatanaka, 1979; Gonçalves, 1993; Hernandez-Garcia *et al.*, 2002), or even in the south of the Iberian Peninsula (Silva *et al.*, 2002; Rodriguez-Rua *et al.*, 2005).

Figure 2 shows that males live a little longer than females. This matches the maximum age results (12.7 months for males and 12.3 months for females) of *O. vulgaris* reported by Faiki *et al*. (2023). The high percentage of mature females observed from June to September (Fig. 3A) may strengthen the autumnal peak existence of spawning. This is consistent with the following findings: May-July and November in Cascais and Santa Luzia of the Portuguese Atlantic coast (Carvalho and Sousa Reis, 2003), April-August in Sardinia Central West Mediterranean (Cuccu *et al*. 2013), and February-August with two peaks in April and August in the Moroccan Mediterranean (Ajana *et al*. 2021). It seemed that missing data in April and May prevented the appearance of spring spawning peak. The fact that 53% of males were mature throughout the year (Fig. 3B) was consistent with the results of Silva *et al*. (2002), Carvalho and Sousa Reis (2003), Otero *et al*. (2007), Cuccu *et al*. (2013), and Ajana *et al*. (2021).

Considering the continuous presence of mature females and males in September 2019, these results, along with those found by other scientists in the Mediterranean, suggest that the peak spawning periods could likely occur in April and September (Fig. 3). In order to get a starting point, assuming that egg incubation lasts an average of 30 days (Mangold, 1983), the most likely cohort birth dates would be 15th May for the spring cohort and 15th October for the autumn cohort (Wyatt, 1983; Sparre and Vienema, 1996).

The $ML_{50\%}$ and $TW_{50\%}$ results were consistent with those found by Silva *et al.* (2002), and Gonzalez *et al*. (2011). They did nevertheless vary mostly from those of Cuccu *et al*. (2013) and Ajana *et al*. (2021) likely as a result of the small sample size of these two studies (Table SI 4).

Size-weight relationship

Other authors in the Mediterranean including the coasts of Tunisia (Jabeur *et al*., 2012), Gulf of Alicante (González *et al*., 2011), Gulf of Cadiz (Silva *et al*., 2002), Catalan Sea (Sánchez and Obarti, 1993) and Aegean Sea (Lefkaditou *et al*., 2007) have also recorded the result of negative growth allometry ($b<3$).

Growth parameters

The overestimation of $L\infty$ generates an underestimation of K and together they will be in equilibrium. The comparison of different growth parameters could not be based on a single parameter individually but on the resulting growth curve (Sparre and Vienema, 1996).

The presence of mature males and females (Fig. SI4) and the recruitment of immature individuals from the spring cohort may account for the high growth rate recorded between December and March and the low to medium monthly growth rate observed between June and September, respectively.

For the common octopus, which is a semelparous species, monthly frequencies might be applied to track the evolution of a cohort, provided that regular samples were collected within the framework of research campaigns that covered a well-defined geographic area for at least of one year. The Bhattacharya method's size frequency analysis based on commercial catches, which was first conducted for each month in the current study, produced modes that represented age groups: one mode (once), two (16 times), and three (17 times). The absence of data during the biological rest months hindered the ability to trace the mode's evolution. Additionally, considering the high individual variability and rapid growth of cephalopods, particularly *Octopus vulgaris* (Domain *et al.*, 2000; Semmens *et al*., 2004), the slight difference (0.2 to 2 cm) between the monthly first modes (cm) that constituted each season for the entire 2015–2019 period (Table 5) likely meant that the first modes belonged to the same cohort. In this case, it would be appropriate to use size frequencies that cover the entire season in order to benefit from a sufficient number of samples, minimize the intensity of this significant individual growth variability, and improve the possibility of tracking the cohort's evolution.

According to Gayanilo *et al*. (2005), the growth rate TM/t declines with length reaching 0 at L∞. This growth rate was frequently increasing, respectively with an average of 1.41 and 1.42 cm/month (min=0.81, max=2.02) for the spring and autumn cohorts. It started to decrease when the TM exceeded 15 cm. Indeed, the cases of AC 2014 and SC 2016 (Table SI5) matched Guerra’s (1978) findings for octopus in the Mediterranean. This seems to be the case since octopuses of this size are typically in the spawning phase ($L_{50\%}$=13.21 cm combined sex), during which the growth rate is normally slowed down, and the senescence begins at the end of sexual maturity (Vidal and Shea, 2023).

The growth rate data analysis yielded the following results respectively for spring, autumn, and all cohorts: L∞=22.18/23.35/22.6 cm, k=2.38/2.16/2.48 for r^2=0.58/0.81/0.69 by the Munro approach and L∞=33.28/41.86/41.86 cm, k=0.81/0.58/0.57 for r^2=0.87/0.62/0.54 by the Appeldoorn approach. In order to estimate only the growth rate k, it became obvious to adopt a constant L∞ as it was either <Lmax (25 cm). Sparre and Vienema (1996) state that the Powell-Wetherall approach (L∞=28.76 cm) is still likely the most accurate method for estimating L∞. Comparing this growth rate to those reported by other authors namely Jabeur *et al*. (2012) in the Mediterranean, k=1.06 determined by the Appeldoorn method remained the most appropriate growth rate. Similarly, the growth rate data for spring and autumn cohorts suited effectively the Appeldoorn model. The common octopus growth of autumn and spring cohorts was nearly similar, in agreement with the findings of Idelhaj (1984) and Dia (1988) in the Atlantic. In fact, temperature has a major impact on early octopus growth during the planktonic and early benthic life phases, but not during the sub-adult or adult phases, as pointed out by Semmens *et al*. (2004). The significantly similar means of the Age-Bhatta and Age-beak distributions suggest that the size frequency analysis-based indirect method for estimating octopus age in the Moroccan Mediterranean was as reliable as the direct approach of upper beaks increment counting. Furthermore, it might support the choice of May 15th and October 15th as the most probable birth dates, respectively, for

the spring and autumn cohorts. For the current study, the Von Bertalanfy equation from the MPA provided the most relevant t_0. This theoretical age t_0 (Table 8) was quite similar to those calculated by Pauly's method (Munro and Appeldoorn). The outcome (t_0=0.386) is in agreement with Guerra's (1978) results for octopus in the Atlantic. However, t_0 found by other authors in the Atlantic, Mediterranean, and Caribbean (Table 9) was similar to those estimated by Pauly's method (ELEFAN I, Shepherd).

Table 9: Common octopus growth parameters found by other authors using indirect methods.

Authors and areas	Method	Cohorts	L∞ (cm)	k	t_0	Lmax
Guerra, 1978 Atlantic (26°10’N-23°30’N)	Size frequencies, Peterson's methods, Harding(1949) and Cassie (1954), Bhattacharya (1967)	-	39.81	0.72	0.33	27
Hatanaka (1979), Mauritanian coast (Atlantic)	-	-	27.68	0.48	-	-
Idelhaj (1984), Atlantic (26°N-22°N)	Size frequencies, Pauly's method (1980).	SC AC All cohorts	37 33 36	0.32 0.35 0.33	0.066 -0.025 -0.03	35
Dia (1988), Mauritanian coast (Atlantic)	Weight frequencies, Method of successive maximums (Daget et Le Guen, 1975).	SC AC All cohorts	29.78 25.49 28.8	0.74 0.94 0.69	-0.07 - 0.13 -0.13	24
Jabeur *et al.* (2012) East coast of Tunisia (Mediterranean)	Size frequencies, Bhattacharya method (1967) Fisat.	-	28.3	1.12	0.008	24
Walter González *et al.* (2015), coast of Nueva Esparta State, Venezuela, Caribbean Sea	Size frequencies, Powell-Wetherall, ELEFAN, Fisat II.	-	26.26 (M) 24.28 (F)	2.3 (M) 1.8 (F)	-0.015 (M) -0.09 (F)	25 (M) 23 (F)
Current study, Moroccan Mediterranean	Fréquences de tailles, Powell-Wetherall, MPA (Bhattacharya, Appeldoorn) Fisat II.	SC AC All cohorts	28.76 (fixed)	1.06 1.08 1.06	0.386	25

C: cohort, S: spring, A: autumn, M: male, F: female.

The asymptotic weight value (W_∞=12484 g) estimated by the weight growth model was similar to that found by Guerra (1978) (10840 g) and different from that found by Jabeur *et al.* (2012) (6801 g) in the Mediterranean. To sum up, size frequency analysis appears to be a viable method for accurately estimating common octopus growth parameters, despite the lack of data from the April–May and October–November periods in this case. Without requiring a fixed L∞, an exhaustive monthly database of size frequencies from random sampling might provide a reliable estimation of growth parameters (L∞, k) with the Munro and Appeldoorn models. Size frequency analysis from commercial data could be a useful substitute for estimating the size-at-age data that stock assessment and fishery management require. It might furthermore adjust these size-at-age data with those estimated by a direct method as well when logistic resources enable it.

Acknowledgments

I would like to thank deeply people of the National Institute of Fisheries Research - Regional Center of Tangier: Said Ait Taleb, Chaib El Fanichi and Meryem Benziane responsible for taking biometric measurements of the octopus sample collected in the M’diq port between 2015 and 2019. No special funding was received for conducting this study.

Conflict of Interests

The authors have no financial or proprietary interests in any material discussed in this article.

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