

Research Article

Age, growth and mortality of white grouper *Epinephelus aeneus* from the Senegalese coast (West Africa)

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Abstract

The objective of the study is to describe the length-frequency distribution, (2) to estimate the growth parameters by counting growth bands deposited on whole otolith (3) to determine the white grouper natural mortality. White grouper (*Epinephelus aeneus*) sampled from Soumbédioune, Mbour, and Joal along the southwestern coast of Senegal in 2020 (n = 973) were aged by counting opaque bands on whole sagittal otoliths. Total length (TL) ranged from 179.0 to 948.0 mm with an average of 422.48 ± 133.79 mm. Analysis of otolith edge type (opaque or translucent) revealed that annuli formed in July-January with a peak in November. White grouper was aged up to 8 years, and the largest fish measured 948 mm in total length (TL). The von Bertalanffy function provided the following parameters: $L_{\infty}=1042$ mm, $K=0.13$ year⁻¹ and $t_0= -1.48$ year. Natural mortality (M) estimated by Hewitt & Hoenig's longevity-based method which integrates all ages was 0.50. Because this is a species with a low growth rate, the population of *E. aeneus* in Senegalese coast requires prudent management. Furthermore, fishery managers need to consider as part of any harvest strategy for these fish the preservation of significant levels of the spawning stock by reducing the numbers of juvenile fish captured in the shrimp trawls and for sale in the market.

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Introduction

The groupers (Family: Epinephelidae) are represented by several species of great importance in marine ecosystems and play a fundamental role in maintaining the trophic chain and its equilibrium because they often act as top predators in their ecosystems (Reñones *et al.*, 2002). The different grouper species exhibit K-strategist species characteristics such as a complex reproductive mode, late sexual maturity, and a slow growth rate (Manooch, 1987). These characteristics, along with the large commercial value of groupers throughout their range of occurrence (Heemstra and Randall, 1993), make these species vulnerable to overfishing (Huntsman *et al.*, 1999; Coleman *et al.*, 2000).

The white grouper *Epinephelus aeneus* (Actinopterygii, Epinephelidae), is an important commercial marine fish teleost distributed along the Atlantic west coast of Africa and the southern Mediterranean Sea (Heemstra and Randall, 1993). Like many other groupers, the white grouper is a promising candidate for intensive aquaculture due to its high market value, excellent taste, and rapid growth rate (Hassin *et al.*, 1997; Glamuzina *et al.*, 2000). White grouper is caught with hooks and lines and in trawls, is utilized fresh and smoked, and is highly prized in the market of West Africa. This species inhabits regions with temperatures between 15–25°C (Caverivière, 1994). Its bathymetric distribution goes from 20 to 200 m in depth, but it is mainly fished at depths of between 30 and 60 m (FAO, 2006). This grouper mainly feeds on bony fish and crustaceans with a preference for crabs (Kouassi *et al.*,

2010). The largest fish found from the Tunisian population was 115 cm L_T, and was estimated to be 17 years old (Bouain, 1986).

In Senegal, this species is found along the whole of the continental shelf. Here, as elsewhere, besides its ecological importance, it is a prized catch for recreational and commercial line fishermen because it can reach a large size (for trophies) and has a high market value. *E. aeneus* is undoubtedly the most sought-after on the market (Cury and Roy, 1988), the Senegalese vernacular name being “thiof” as it is the most popular fish for the main traditional dish in the area (“thiéboudiène”, literally “rice with fish”). *E. aeneus* is, therefore, heavily fished throughout its range using various methods ranging from small-scale to industrial fishing.

Not surprisingly, the white grouper is assessed as a near threatened species in the IUCN Red List (<http://www.iucnredlist.org/apps/redlist/details/132722/0>) as a result of overexploitation in many areas of its range and is listed as overexploited in Senegal (Froese, 2004).

A study of the size structure (length-frequency) in marine fish reveals many ecological and life history traits such as the sea health, stock conditions and breeding period of the fish. The size structure of a fish population at any point in time can be considered a ‘snapshot’ that reflects the interactions of the dynamic rates of recruitment, growth and mortality (Neumann and Allen, 2001). Growth information provides a lot of tools that are used in fishery management (Rahman *et al.*,

2024). The data on the age of a fish can provide tools in fishery management such as the general background information needed for management decisions. It aids in the diagnosis of management needs such as the recognition of overcrowding and stunting (Deekae and Abowei, 2010).

Age and growth studies provide information on population structure and effects of fishing on the stocks, assist in understanding life history events, and provide information on population responses to environmental changes (Jones, 1992; Islam *et al.*, 2024). For this reason, there has been a large amount of research and controversy about the best way to measure fish growth and determine age. Information on fish growth is obtained through growth studies where growth parameters like length-frequency distribution, length-weight relationship and condition factor are determined. Length-frequency distribution gives information on specific fish sizes and their corresponding frequency within a given population (Cunha *et al.*, 2007; Rahman *et al.*, 2023).

While various methods have been employed to age fish and measure growth, Jones (1992) advocates for most fish, otoliths are the most reliable indicator of age. She outlines the advantages of otoliths over other calcified structures be that they show the early life history of fish and there is no reabsorption under stress conditions. Therefore, only otoliths were used for aging in this study.

This study aimed (1) to describe the length-frequency distribution, (2) to estimate the growth parameters by counting growth bands deposited on whole otolith (3) to determine the white grouper natural

mortality in order to provide precise information to guide fishery management and conservation plans for this endangered marine species.

Materials and methods

Sampling collection

Samples of *E. aeneus* were collected monthly by a random method (≈ 30 individuals by month and by location) along the Senegalese coast from commercial landings from January to December 2020 at Soumbédioune; Joal and Mbour locations (Fig.1).



Figure 1: Map of the study area showing the location of fishing sites (Soumbédioune, Mbour, and Joal).

Each fish was measured to the mm for total length (L_T), and weighed to the g for total body weight (W_T). Sex was determined by

macroscopic observation of the gonads. Sagittal otoliths were removed, cleaned and stored dry in labelled envelopes for later examination and age determination (Campana, 2001). The length-frequencies were grouped into classes of 50 mm intervals.

Age and growth

Whole otoliths were immersed in 95% alcohol in a black watch-glass and examined at 70× magnification using a binocular microscope with reflected light. The opaque bands were counted as annuli. The otolith samples were read in a random order without knowing the meristic information. Each otolith was read twice by two independent readers with no prior knowledge of either fish size. The agreement between readings and readers were evaluated by calculating the percent agreement. Disagreements in age estimates were resolved by both readers examining the otoliths simultaneously. The index of average percent error (APE) (Campana, 2001) and the mean coefficient of variation (CV) (Chang, 1982) were calculated to estimate the relative precision of age estimates between readers.

$$APE = 100\% R^{-1} \sum_{i=1}^k |X_{ij} - \bar{X}_j| \bar{X}_j^{-1}$$

Where X_{ij} is the i^{th} age estimation of the j^{th} fish; \bar{X}_j is the mean age of the j^{th} fish, and R is the number of times each fish is aged (Campana and Jones, 2001):

$$CV = 100\% \left[\left(\sqrt{\sum_{i=1}^R \left((X_{ij} - \bar{X}_j)(R-1)^{-1} \right)^2} \right) \bar{X}^{-1} \right]$$

A total of 33 otoliths (8%) were excluded from age determination because they were crystallized or if the growth rings were difficult to interpret and a consensus between readers could not be achieved. To assess the yearly pattern of deposition of otolith annuli, the appearance of each otolith margin was recorded as opaque or translucent. To validate the seasonality of deposition of opaque and translucent zones, the relative frequency of an opaque zone on the otolith margin was plotted by month (Beckman and Wilson, 1995; Panfili and Morales-Nin, 2002). The cycle in the formation of the opaque and translucent zones should equal 1 year in true annuli (Campana and Jones, 2001).

A von Bertalanffy growth curve was fitted to the age and length data for each and for the whole sample using a non-linear regression with least-squares estimation as the loss function (Statistica® software) as:

$$L_t = L_{\infty} \left[1 - e^{-k(t-t_0)} \right]$$

Where, L_t is the total length (mm) at age t ; L_{∞} is asymptotic length (mm); k is the Brody growth coefficient and t_0 is the theoretical age at zero.

The estimated L_{∞} and K were used to calculate the growth performance index (ϕ') using the equation of (Pauly and Munro, 1984):

$$\phi' = 2 \log L_{\infty} + \log K$$

Where, K and L_{∞} are VBGF parameters.

The maximum longevity of individuals (t_{\max}) was calculated through Pauly's equation (1983) defined as follow:

$$t_{\max} = \frac{3}{K} + t_0$$

Where, K and t_0 are VBGF parameters.

Natural mortality

Estimates of the instantaneous rate of natural mortality (M) were obtained using 2 methods.

(1) Hewitt and Hoenig (2005) longevity mortality relationship:

$$M = \frac{4.22}{t_{\max}}$$

Where, t_{\max} is the maximum age of the fish in the sample.

(2) Charnov *et al.* (2013) method, which uses the von Bertalanffy growth parameters:

$$M = \left[\frac{L}{L_{\infty}} \right]^{-1.5} \times K$$

Where, L_{∞} and K are the VBGF parameters and L is fish length at age. The newer Charnov *et al.* (2013) method, which incorporates growth parameters, is an improvement to the empirical equation of

Gislason *et al.* (2010) and is based on evidence that M decreases as a power function of body size.

Statistical analysis and graphics were performed with Excel and STATISTICA® version 6. After checking normality, the nonparametric Kruskal-Wallis test was used to verify the significance of certain results between sites.

Results

Length-frequency distribution

The length-frequency distribution (LFD) for all specimens was shown in Table 1. During the sampling, a total of 973 fish were measured. The LFD showed that specimens which sizes ranged from 250 to 499 mm L_T were more common in the landings for all stations (Fig. 2).

Table 1: Length-frequency data for *Epinephelus aeneus* from the southwestern coast of Senegal.

L_T (mm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
150 - 199	1										1	3
200 - 249	3	6	6	2	1	2	12	4	1	5	9	4
250 - 299	11	6	11	14	12	15	16	9	6	12	15	7
300 - 349	10	10	7	11	9	9	16	15	15	12	11	10
350 - 399	9	13	6	9	13	6	9	29	24	17	11	18
400 - 449	10	10	8	9	8	9	9	8	12	15	12	16
450 - 499	8	9	11	9	5	10	4	7	10	5	12	16
500 - 549	7	4	8	5	9	7	3	3	6	6	5	3
550 - 599	6	7	10	9	6	5	3	4	5	6	4	4
600 - 649	3	3	1	6	4	7	5	2	1	3	2	
650 - 699	3	4	10	3	5	3	1		4	4	4	3
700 - 749	3		2	1	3	1	1	1	1	2	2	1
750 - 799	1	1			1				1	1	1	1
800 - 849	1								1	1		2
850 - 899												1
900 - 949										1		
Total	76	73	80	78	76	74	79	82	87	90	89	89

The fish collected in Soumbédioune ranged from 217 to 774 mm L_T (mean \pm SD=495.5 \pm 115.3 cm, n=358), and the dominant size-classes were 250-299 mm and 550-599 mm. Mbour and Joal showed two identical modal size-classes at

350-399 mm and 650-699 mm but these stations differed in sizes distribution. In Mbour, the sizes ranged from 184 to 948 mm (mean \pm SD=566.1 \pm 135.4 cm, n=302) and in Joal between 179-816 mm (mean \pm SD= 497.5 \pm 118.3 cm, n=313).

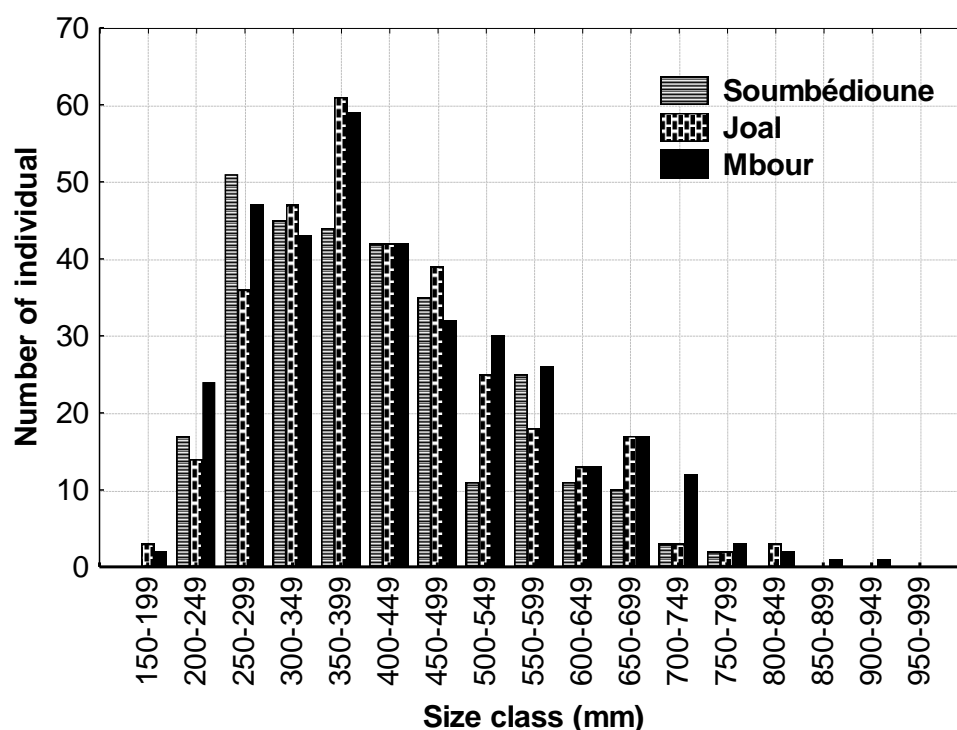


Figure 2: Length-frequency distribution for *Epinephelus aeneus* captured from the Senegalese coasts (Soumbédioune, n = 296; Mbour, n = 354 and Joal, n = 323).

The smaller-sized fish was caught in Joal (179 mm) while the larger one was from Mbour (948 mm). Fish larger than 750 mm constituted a small part of the total catch. The length-frequency distribution throughout the study period showed a prominent peak with a preponderance total length ranging from 350-399 mm on the Senegalese coast, except for Soumbédioune where the prominent peak with a preponderance total length ranged from 250-299 mm. There was no significant difference between the total length of

species from the three stations sampled (Kruskal-Wallis test, $p>0.05$).

Precision and bias

The index of average percent error (APE) and the mean coefficient of variation (CV) were 4.3% and 7.5%, respectively for the data. Otoliths that were deformed, crystalized, or extremely cloudy were eliminated without assigning an age estimate (n=21 in Soumbédioune, n=18 in Mbour and n=17 in Joal). After eliminating the otoliths that were hard to read or for which agreement could not be reached

between readers, there was a 96% agreement between readers in Mbour and Joal and 94% in Soumbédioune, indicating a high-level consistency. Disagreements in age estimates between readers were more frequent for fish >5 years.

Age and growth parameters

Under polarized transmitted light, alternate, concentric opaque and hyaline bands were observed in the anterior area of the otolith, which facilitated the reading of growth markers (Fig. 3).

For whole otolith, monthly changes of the opaque percentage edge gradually

increased from July to January, and appeared to peak at 87% in November followed by a gradual decrease to 12% in July (Fig. 4). Significant differences were found in percentage edge type among months (one-way ANOVA, $F=11$, $p<0.001$). The Kruskal-Wallis test comparisons revealed that the opaque percentage edge between May and September significantly differed from that from October to April ($p<0.05$). These results indicated that the opaque band of the otoliths was laid down once a year between October and January.

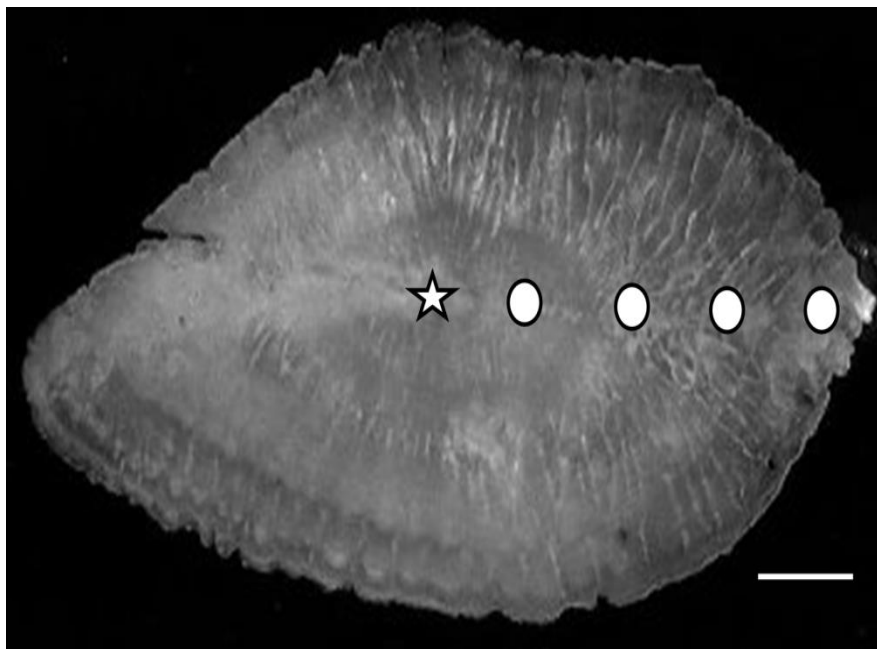


Figure 3: Whole sagittal otolith of *Epinephelus aeneus* showing the annuli in a 4-year-old fish with an opaque margin. Star indicates the otolith core, dots indicate the opaque annuli and the scale bar = 2 mm.

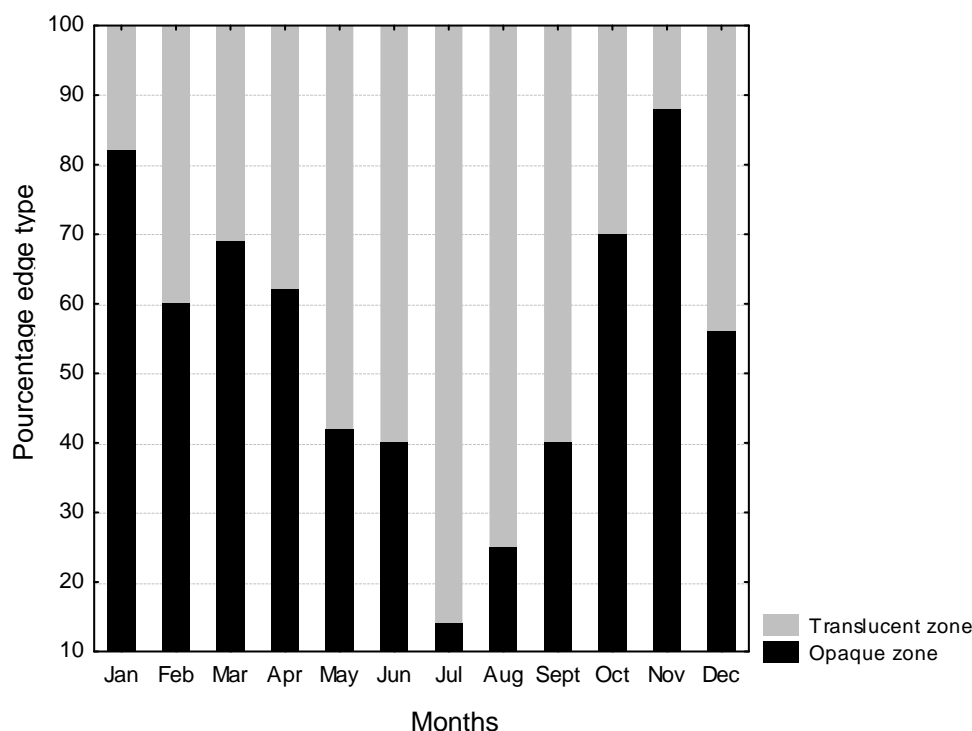


Figure 4: Percentage of occurrence of opaque margin of whole sagittal otoliths of the white grouper, *Epinephelus aeneus* sampled in Senegalese coasts.

Results of the von Bertalanffy growth model for white grouper were presented in Table 2 and Figures 5 A-D. Separate growth curves for males and females were not plotted because of the lack of males in the samples. Based on the annual growth ring counts of 940 (96.6%) readable otoliths, white grouper ages ranged from 0

to 8 years. Most of the fish were 1-5 years old, accounting for 82.32% of the total sample. Results showed there was no significant difference in the growth indices between locations for this species (Kruskal-Wallis test, $p > 0.05$).

Table 2: Comparison of growth parameters derived from the von Bertalanffy growth function for *Epinephelus aeneus* from the Senegalese coasts.

Site	n	L_{∞} (cm)	K (year ⁻¹)	t_0 (year)	(Φ')	Age Range
Soumbédioune	358	133.05	0.13	-1.42	3.36	2-7
Mbour	302	134.02	0.14	-1.48	3.40	0-8
Joal	313	132.75	0.15	-1.50	3.42	0-7
Combined	973	134.68	0.14	-1.53	3.40	0-8

n, number of individuals, L_{∞} , asymptotic length; K, growth coefficient, t_0 , theoretical age at zero and Φ' , growth performance index.

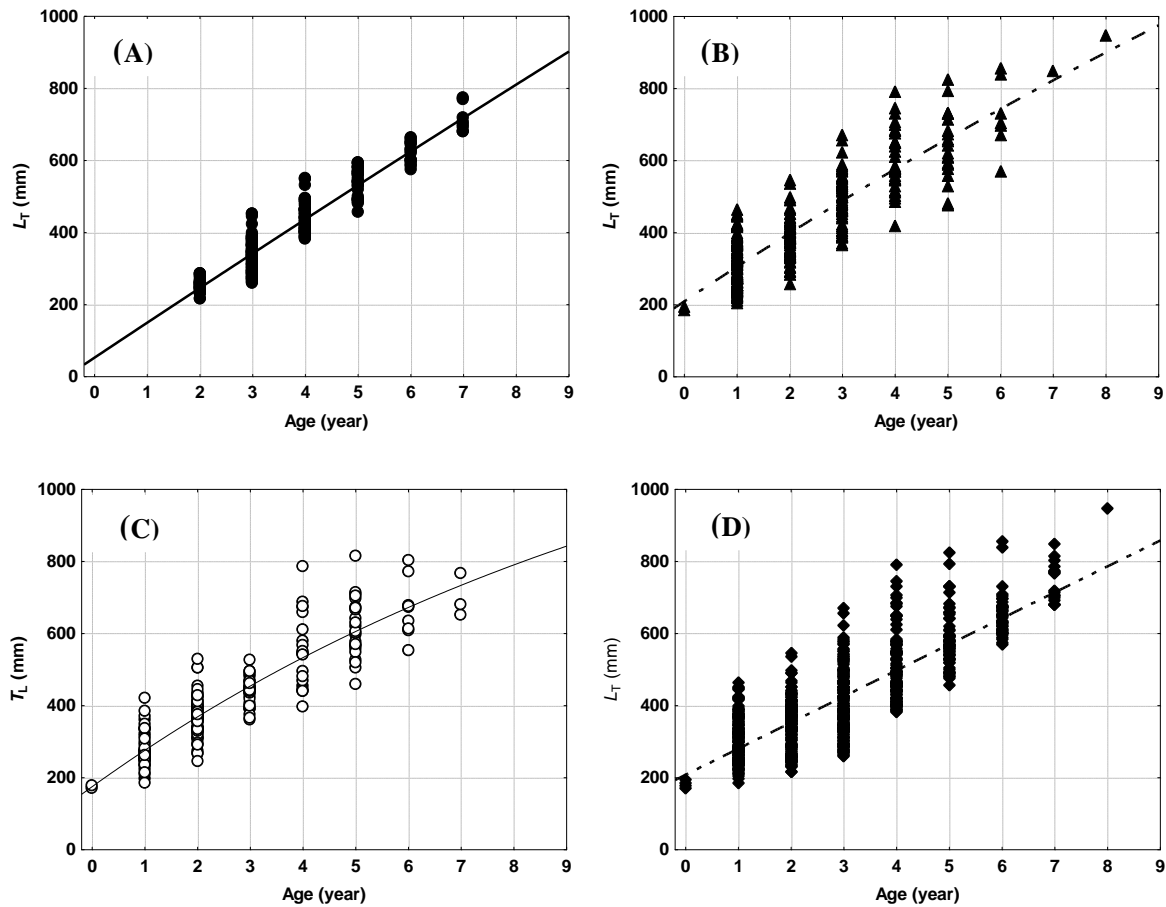


Figure 5: Total length at age and fitted von Bertalanffy growth curves for *Epinephelus aeneus* sex combined in Soumbédioune (A), Mbour (B), Joal (C), and Combined (D).

Natural mortality

The natural mortality rate M estimated from Hewitt and Hoenig's method was 0.52, 0.60, and 0.60 for Mbour, Soumbédioune, and Joal respectively. The method of Charnov, which produces age-specific estimates of M with the use of von Bertalanffy growth indices, resulted in estimates of 0.23 for age-8 fish in Mbour, 0.30 for age-7 fish in Soumbédioune and 0.35 for age-7 fish in Joal.

Discussion

Age determination of fish is needed to study the growth, abundance, and fluctuations of fish species. Such studies represent the main way by which the research can assist and develop the fishery.

This study used the analysis of annual otolith marks to evaluate the growth rates of white grouper along the southwestern coasts of Senegal. There was difficulty in estimating growth parameters for separate sexes because the number of males was very low.

There are no published studies that fully validate the yearly deposition of annuli in *E. aeneus*. Age estimation based on whole otoliths was conducted successfully for the specimens investigated in this study. For the three locations the majority of fish were between 1 and 3 years. The oldest age estimated in this study was 8 years and the stacking phenomenon of growth rings towards the otolith margin was not evident. For the dusky grouper (*Epinephelus*

marginatus), Mario *et al.* (2014) revealed that the ages ranged from 1 to 40 years, and 85% of samples were aged between 2 and 8 years. Morales-Nin *et al.* (2005) proved that *E. caninus* might reach 55 years old in the western Mediterranean, a similar longevity than in *E. marginatus* (Heemstra and Randall, 1993). In a scale-based study on the age of *E. marginatus* in the Mediterranean Sea, the maximum determined age was 19 years, an age superior to 50 years for a captive fish (Bouchereau *et al.*, 1999). Therefore, owing to the translucency of the otolith, its observation provided easy age estimation without having to prepare a thin section. *E. aeneus* showed the common ring pattern of teleost fishes with concentric growth marks composed of an opaque and a translucent zone, corresponding to rapid and slow growth, respectively (Paula *et al.*, 2024). The opaque zone of the first annulus was larger than the translucent one. After the second ring, the two components of the annulus had the same width, although their width slowly decreased towards the otolith margin. The validity of the estimates was supported by the low values of the APE (4.3%) and CV (7.5%) indices. It was observed in this study that the otoliths exhibited a well-defined pattern. In addition, because the marginal increment analysis clearly showed that annual growth increments were formed once per year, we were convinced that interpreting annual growth rings in otoliths was a valid method of age determination in this white grouper. A dark fast opaque zone (organic-rich component) was deposited in the wet season while the clear slow translucent growth zone (calcium-rich component) was

deposited in the dry season. These results were similar to those found by Artero *et al.* (2015) in French Guiana. The authors found that the Atlantic goliath grouper deposits a single annulus each year, with the translucent zone initiated at the start of the dry season (July) and the opaque zone prominent from September through December. The formation of alternating opaque and translucent zones in the otoliths is controlled by a combination of endogenous and environmental factors (Beckman and Wilson, 1995) which vary at different ages and between sexes. The physiological changes are produced mainly by the influence of temperature, photoperiodism, reproductive cycle, and food availability (Pannella, 1980). The fast growth in the otoliths of *E. aeneus*, occurred at the end of wet season (November) when the sea temperature reached its highest values, and the slow growth at the end of dry season (July) when the sea water reached its lowest values. This significant rise in water temperature could involve changes in the metabolic activity of the individuals during the wet (hot) season and could be the main factor responsible for opaque zone deposition. The determination of otolith nature margin was easier for the small size individuals. However, with the increase of ring numbers it became thin and sometimes the incidental light reflection on the otolith could be confused with an opaque margin. It was observed also many false rings and they should “be gathered” for the reading of the age.

Based on the growth rate values, white grouper has a relatively slow growth rate along the Senegalese coasts. The white grouper growth studies are very few. They

were carried out starting from the reading of osseous parts (thorny rays) and scales. No validation confirmed the results advanced by the various authors. In Senegal, two studies gave different results. Cadenat work (Bruslé, 1985) starting from scales reading, gave a growth twice lower than Cury and Worms (1982) work carried out starting from the thorny rays of the dorsal fin ($L_{\infty}=144.96$ cm and $K=0.17$ year⁻¹). In comparing fish age and growth among structures, scale annuli appear to be the most inconsistent which produces the most variable results. It can be difficult to distinguish annuli once they become condensed at the outer edge in older fish. The Cadenat results were very close to those of Bouain (1986) carried out in Tunisia ($L_{\infty}=204.34$ cm, $K=0.03$ year⁻¹ and $t_0=-0.76$ year). Under a JICA (2006) project, estimation of white grouper growth was carried out by reading the scales. The following parameters were obtained: $L_{\infty}=99.29$ cm; $K=0.14$ year⁻¹ and $t_0=-0.23$ year. In Mauritania waters, Meissa and Gascuel (2014) found $L_{\infty}=100.00$ cm and $K=0.23$ year⁻¹. Kouassi *et al.* (2010) found in Ivory Coast littoral, $L_{\infty}=194.25$ cm and $K=0.94$ year⁻¹. The growth parameters found in Senegal by Laurans *et al.* (2003) in two studies were respectively $L_{\infty}=109.25$ cm, $K=0.17$ year⁻¹ and $L_{\infty}=109.25$ cm, $K=0.12$ year⁻¹. A Study of the Sea Around Us Project found a L_{∞} as 120.0 cm and K as 0.23 year⁻¹. The method used in both cases was the multimodal decomposition. The values of the growth parameters obtained in this study were ($L_{\infty}=133.05$ cm, $K=0.13$ year⁻¹ and $t_0=-1.42$ year; $L_{\infty}=134.02$ cm, $K=0.14$ year⁻¹ and $t_0=-1.48$ year; $L_{\infty}=132.75$ cm, $K=0.15$ year⁻¹ and $t_0=-1.50$

year in Soumbédioune, Mbour, and Joal respectively). The greatest values of L_{∞} (204.34 cm) and K (0.94 year⁻¹) were thus those found in Tunisia and Ivory Coast waters. This would be explained by a more favorable environment for growth in these areas and less strong fishing pressure. The growth parameters, estimated in this study by the direct reading of the age on the otoliths, were lower than those found by Cury and Worms (1982) in Senegal ($L_{\infty}=143.96$ cm, $K=0.17$ year⁻¹). These authors worked on the counting of marks of growth, specifically on the thorny rays of the dorsal fin. Differences found in the values of the growth parameters could be explained by the difference in sampling periods, the difference in the numbers of sampled fish, or in the used reading methods such as otolithometry or scalimetry (Keznine *et al.*, 2020). The pressure of the fishing activity has also an influence: if there is growth in overfishing, the older age groups will disappear (Espino-Barr *et al.*, 2010; Gallardo-Cabello *et al.*, 2011). Ages at zero length (t_0) were found to be negative (-1.42, -1.48 and -1.50 year in Soumbédioune, Mbour, and Joal respectively) indicating that juveniles grew more quickly than the predicted growth curve for adults (King, 1995). The growth performance index value (ϕ') was the result of the relation between L_{∞} and K and should present close values for species phylogenetically related (Gayanilo *et al.*, 1997). Thus, its values constitute a reference to validate the growth parameters estimate.

The low value of the growth performance index ($\phi'=3.36, 3.40$, and 3.42 in Soumbédioune, Mbour, and Joal

respectively) in the present study indicated slower growth for the species in Senegal. The value of the growth coefficient was of the same order as those found by Ezzat *et al.* (1981) and by Cury and Worms (1982). However, Cadenat (1935) and Erzini (1991) found higher values. On the other

hand, the growth performance indexes were of the same order as all those recapitulated in Table 3. In this study, it was estimated that *E. aeneus* might live as long as 8 years in the coastal waters.

Table 3: Comparison of growth parameters for white grouper (*Epinephelus aeneus*) from various studies.

Countries	L_{∞} (cm)	K (year ⁻¹)	t_0 (year)	(Φ')	Authors
Senegal	133.05	0.13	-1.42	3.36	Present study
	134.02	0.14	-1.48	3.40	
	132.75	0.15	-1.50	3.42	
Senegal	144.0	0.17		3.55	Cury and Worms (1982)
Morocco	85.0	0.25		3.25	Erzini (1991)
Morocco	100.0	0.23		3.35	Cadenat, J. (1935)
Egypt	136.0	0.15		3.44	Ezzat <i>et al.</i> (1981)
Ivory Coast	194.2	0.94			Kouassi <i>et al.</i> (2010)
Mauritania	100.0	0.23			Meissa and Gascuel (2014)
Senegal	99.29	0.14	- 0.23		JICA (2006)
USA	120.00	0.23			Anonym (2012)
Tunisia	204.3	0.04	-0.76	3.21	Bouain (1986)

L_{∞} , asymptotic length; K, growth coefficient and Φ' , growth performance index.

Values of natural mortality (M) are essential for the assessment and management of fish populations but are notoriously difficult to estimate once exploitation begins (Ricker, 1975). Errors in the estimation of mortality affect the outcome of various models used in stock assessments. Mertz and Myers (1997) show that an error in cohort reconstruction (cohort analysis) occurs when an inaccurate estimate of natural mortality is provided. Clark (1999) determines that an erroneous natural mortality estimate creates a bias in the estimates of stock size provided by an age-structured model. Williams and Shertzer (2003) state that policy based on mortality is particularly sensitive to the estimation of model parameters. Changes in M at age can be interpreted as a consequence of physiological requirements and predation rates, among other factors,

which act differently in time and space for each developmental stage (Ramírez-Rodríguez and Arreguín-Sánchez, 2003). Natural mortality of wild populations of fishes is difficult to measure. A single estimate of M for the entire life span of a fish is unreasonable, except for fish that have attained a size that renders them invulnerable to high predation rates. The Hewitt and Hoenig (2005) estimate of M is based on the maximum age attainable in an unfished population. In this sense, the point estimate of M, derived using the method of Hewitt and Hoenig (2005), can serve as a lower boundary on the estimate of M derived for older ages by an age-varying method. The maximum observed age for *E. aeneus* in our study was 8 in Mbour and 7 in Soumbédioune and Joal using whole otolith. Our estimates seem reasonable given that our age-specific estimate of M

(0.23, 0.30, and 0.35 respectively in Mbour, Soumbédioune, and Joal) for the older ages that were derived using Charnov *et al.* (2013) compares lowly with the point estimate of M (0.52 in Mbour and 0.60 in Soumbédioune and Joal) found using the method of Hewitt and Hoenig (2005). The natural mortality found in Mauritania by Meissa and Gascuel (2014) was ($M=0.25$). Cury and Worms (1982) found in Senegal a natural mortality $M_{2-3\text{years}}=0.2$; $M_{4-5\text{years}}=0.2-0.3$ and $M_{6\text{years}}=2.5$.

One limitation of this study was the lack of fish smaller than about 179 mm, because of the fishery-dependent nature of our samples, the selectivity of fishing gear, and the minimum size limits in place for white grouper. Lack of smaller fish is common in studies dominated by fishery-dependent samples and can lead to problems in estimating the growth curve for the youngest ages. The clusion of fishery-independent samples usually corrects this problem, as fishery-independent gear such as traps will catch smaller fish. Younger fish were unavailable to us to help define the trajectory of the growth curve at the earliest ages, and this section of the growth curve should be interpreted with caution.

This study provides the first age, growth and natural mortality estimates for a commercially important large grouper species. It showed the length frequency variation and the growth parameters in Senegalese coasts. The species exhibit slow rates of growth, highlighting the potential vulnerability of *E. aeneus* in the southwestern Senegal region, and the need to assess their resilience to the current level of fishing pressure. This information, together with studies of reproduction will

allow the management of the fishery by suggesting fishing gears such as the size of the mesh opening, closed seasons to the fishing, and catches quotas, which will avoid the overexploitation of the natural resources. The results from this study will provide crucial information to parameterize demographic models of this species, which is critical considering the high levels of exploitation in Senegal (Ndiaye *et al.*, 2013).

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Conflicts of interest

The authors have declared that no conflicts of interest exist.

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