

Article

Growth Patterns of Small Pelagic Fish in West Africa

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Abstract: Small pelagic fishes play important ecological roles in marine ecosystems, constitute some of the most economically valuable fisheries resources, and play a vital role in West African food security. Often living in upwelling regions, these species appear to have developed mechanisms to cope with environmental variability, such as opportunistic reproductive tactics, enhancing their growth performance, or increasing their egg production by following the more predictable system attributes of seasonal cycles. To test this hypothesis, we investigated size-dependent patterns of the two growth mechanisms (i.e., growth rate) of two West African small pelagic populations (*Ethmalosa fimbriata* and *Sardinella maderensis*) in upwelling environments. These results were discussed with other areas in African tropical Atlantic waters. The monthly mean length of both species showed a large variation over the study period. Based on the fish length-frequency data and a coastal upwelling index, we found that the growth peaks of the species tended to occur during the most intense periods of upwelling (March–April). This study showed a significant decrease in size compared with other species found in other regions. It demonstrates how the geographical distribution of the same species, together with location-specific variation in temperature and food, can combine to determine local and regional growth responses in pelagic fish. Changes in growth rate may be an adaptive tactic in response to environmental change, as well as phenotypic plasticity in fish. This knowledge is essential to predict future changes in fish productivity and distribution vs. climate and to provide effective advice for ecosystem-based management.

Keywords: Bonga shad; *Sardinella*; body size; environmental changes; exploited species; population dynamics; West Africa



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1. Introduction

Growth is a physiological process that influences the status and dynamics of fish stocks [1–3]. Adult fish size is often an important factor in fitness (e.g., distribution, fecundity, recruitment, and offspring survival [4–6]). Female fecundity (the number of eggs in a batch) increases (either exponentially or linearly) with increasing body size in small pelagic fish [7–9]. This indicates that growth rates, as an age structure, have a marked impact on the reproductive quality of small pelagic fish [5]. However, many correlative analyses have invoked environmental factors as important in influencing the growth rate of these small pelagic species [7,10,11]. Thus, there is a clear need to study intraspecific variation in which age at maturity, fecundity, and longevity may be related to factors such as temperature, food availability, and population density [5,7]. Therefore, a better understanding of the underlying factors affecting fish growth is needed to inform and improve current stock assessments for sensible fisheries management [5,6,12]. In this work,

the focus was on two species of clupeids living in the Guinea Bissau waters (West Africa): *Sardinella maderensis* and *Ethmalosa fimbriata*.

Fishing is an essential economic, social, and cultural activity in West Africa. In 2017, the total catch of small pelagic fish in West Africa was around 1,300,000 tons (t), with 65% in Mauritania, 28% in Senegal, and 7% in Gambia and Guinea Bissau, respectively [13]. Guinea Bissau is part of the Canary Current Large Marine Ecosystem, one of the world's major upwelling systems. This system is characterised by a high production of plankton, which favours the presence of a high biodiversity and biomass of marine species, especially small pelagic fish [14,15]. In Guinea Bissau, the fishery-dependent population is estimated at 68,658 individuals, more than 60% of whom are involved in artisanal fisheries targeting small coastal pelagic fish [13]. Small pelagic fish are the most accessible source of animal protein for Guinea Bissau's low-income population [16]. In Guinea Bissau, the annual availability fluctuates between 25,000 and 2000 t of small pelagic for a per capita consumption of between 16 and 18 kg [13].

Sardinella maderensis is a species with tropical affinity tolerating temperature ranges from 20 to 23 °C [17]. It breeds throughout the year in Senegal. The first breeding season extends from April to October, while the second breeding season, with continuous reproduction (more intense than during the first period), takes place from January to the end of February [18]. *Sardinella maderensis* was considered one of the most important small-sized pelagic species in the coastal waters of West Africa and the eastern central Atlantic region [19,20]. In Guinea Bissau, catches of *S. maderensis* were relatively low from 1970 to 2008 (around 500 t) before increasing from 2009 to 2019, with peaks in 2010 (3500 t), 2012 (4200 t), and 2017 (6000 t) (Figure 1). The latest stock assessment of *Ethmalosa fimbriata* and *Sardinella aurita* in the sub-region considers that it is overvalued [20] and that it is classified as a vulnerable species by the IUCN [21]. *Ethmalosa fimbriata* is a tropical species also dependent on estuarine environments for parts of its life cycle, distributed from Mauritania to Angola [22], and is the most common clupeid in brackish waters (salinity between 5 and 90 psu) of West African estuaries [22]. In Sine Saloum (Senegal), the reproduction of *E. fimbriata* is possible throughout the year and the main breeding periods are during the cold season in the estuary and the hot season at sea [23]. This species reacts dramatically and rapidly to changes in the ocean climate and has biological characteristics that make it very sensitive to environmental fluctuations [7]. Catches of *E. fimbriata* in Guinea Bissau increased between 1970 and 1985 (peak in 1972 with 10,500 t) and 1987 and 2005 (peak 1999 with 29,000 t), with a slight decrease between 2008 and 2019 (peak in 2010 with 11,927 t; Figure 1). Despite its overexploited status according to the FAO [20], it is considered by the IUCN to be of least concern [21]. Studies of the key parameters of *E. fimbriata* and *S. maderensis* are scattered across numerous sources and indicate a dynamic research field. Several studies on growth and population dynamics have been documented for the Gulf of Guinea (i.e., off Nigeria) [24,25], Congo [26], off the Ivory Coast [27], Sierra Leone [28] Cameroon [29], and Senegal [18,30]. Despite the importance of these small pelagic species, studies exploring key parameters (e.g., growth parameters) and the size structure of *E. fimbriata* and *S. maderensis* have never been conducted in Guinea Bissau. Reproduction and growth data, when available, are useful information for management purposes e.g., [7,21]. Thus, knowledge on growth and reproduction in Guinea Bissau will help managers to sustainably manage these resources.

This study analyses and compares the growth of *E. fimbriata* and *S. maderensis*, integrating data from the existing literature with findings specific to the African tropical Atlantic Ocean. By focusing on growth parameters within the same geographical area, we aim to highlight the environmental factors influencing these species. Our discussion emphasises the implications for stock management of *E. fimbriata* and *S. maderensis* in Guinea Bissau's waters, providing insights into sustainable practices that can help maintain healthy populations in the face of environmental changes. Through this analysis, we hope to contribute to effective fisheries management strategies that consider both ecological dynamics and the socioeconomic importance of these species.

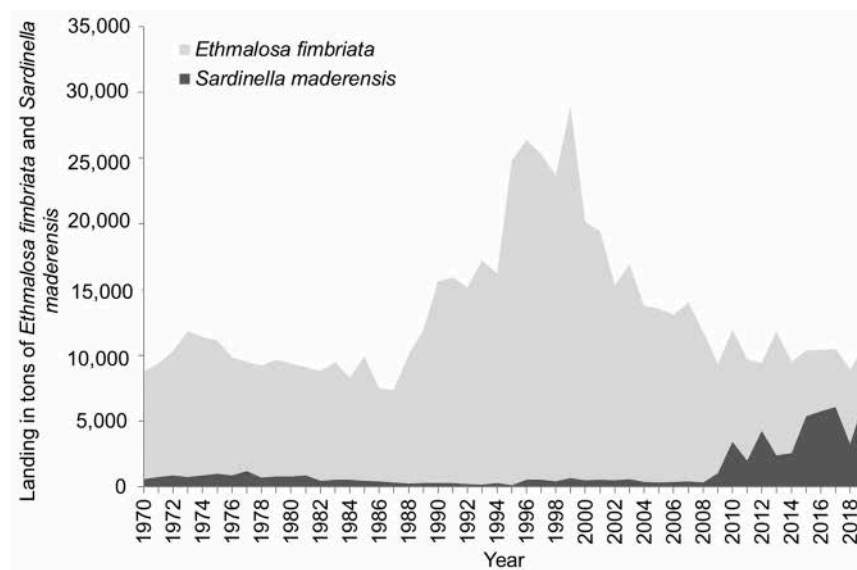


Figure 1. Landings of *Ethmalosa fimbriata* (grey fill) and *Sardinella maderensis* (black fill) by artisanal fisheries in Guinea Bissau (1970 to 2019). Source: Data obtained from the Sea Around Us (<https://www.seaaroundus.org/>; last visited: 30 September 2022). The data we present ('reconstructed data') combine official reported data and reconstructed estimates of unreported data (including major discards).

2. Materials and Methods

2.1. Study Area

The marine ecosystem of Guinea Bissau is characterised by the presence of a tropical climate with two distinct seasons (dry and rainy season). The dry season (November to May) is characterised by the effect of the Canary Current and the rainy season (June to October) by the Guinea Current [31]. Sea surface temperature (SST) and salinity (SSS) vary from 26 to 30 °C and from 36 to 30 psu in the dry and rainy seasons, respectively [32]. The input of organic matter from rivers, coupled with the effect of currents, leads to an increase in productivity [14,15,33]. The coastline is 274 km with a continental shelf of 45,000 km. The coastal area of Guinea Bissau is mainly covered by mangroves [16,34,35]. These mangrove areas play a regulating role in the ecosystem, protecting the coastline, and, among other things, provide nutrients for the surrounding fauna [36–38]. They are also a nursery area for several small pelagic species [34,39].

Guinea Bissau also has important rivers, such as the Geba, Cacheu, Buba, and Cacine, and an island part that forms the Bijagós archipelago [16,35]. The Cacheu River is located in the extreme northwest of Guinea Bissau, in the administrative region of Cacheu, in the area of Cacheu and São Domingos. It is bounded to the north by the Suzana/S. Domingos area and the Antoninho and Djopa Rivers, to the south by the Cobia River, and to the west by the Bolol and Defeneme Rivers [40,41]. The Buba River covers an area of 271 km², with a width of about 4 km from the mouth to Farancunda and a length of 52 km from the source to the mouth [42]. The Cacine River is located in the Tombali region, Quitafine sector, and consists of about 18 river branches [43].

2.2. Environmental Data

Remotely sensed environmental data were analysed to test the effects of sea surface salinity (SSS), sea surface temperature (SST), and coastal upwelling index (CUI) on the growth of *S. maderensis* and *E. fimbriata*. Monthly data were compiled for the area of Guinea Bissau (August 2020 to July 2021; Figure 2). The sea surface salinity, derived from SMOS (Soil Moisture and Ocean Salinity satellite, <https://earth.esa.int/eogateway/missions/smos>, last visited: 22 February 2024), were averaged in the first 100 km of the Guinea Bissau coast. SST data were obtained from the U.S. National Aeronautics and

Space Administration (NASA) (<http://oceancolor.gsfc.nasa.gov>, last visited: 17 August 2022). Original SST data were acquired with a 5 km resolution and averaged from the coastline to the 200 m isobath, where upwelling-induced SST anomalies are generally maximal [44]. The CUI was computed as the Ekman transport [45] ($\text{m}^3 \text{s}^{-1} \text{m}^{-1}$) as in Jacox et al. [46], deduced from wind speed data obtained from the U.S. National Oceanic and Atmospheric Administration (NOAA) (<https://oceanview.pfeg.noaa.gov/projects>, last visited: 17 August 2022). The CUI was computed by CRODT (Centre de Recherches Oceanographiques Dakar-Thiaroye).

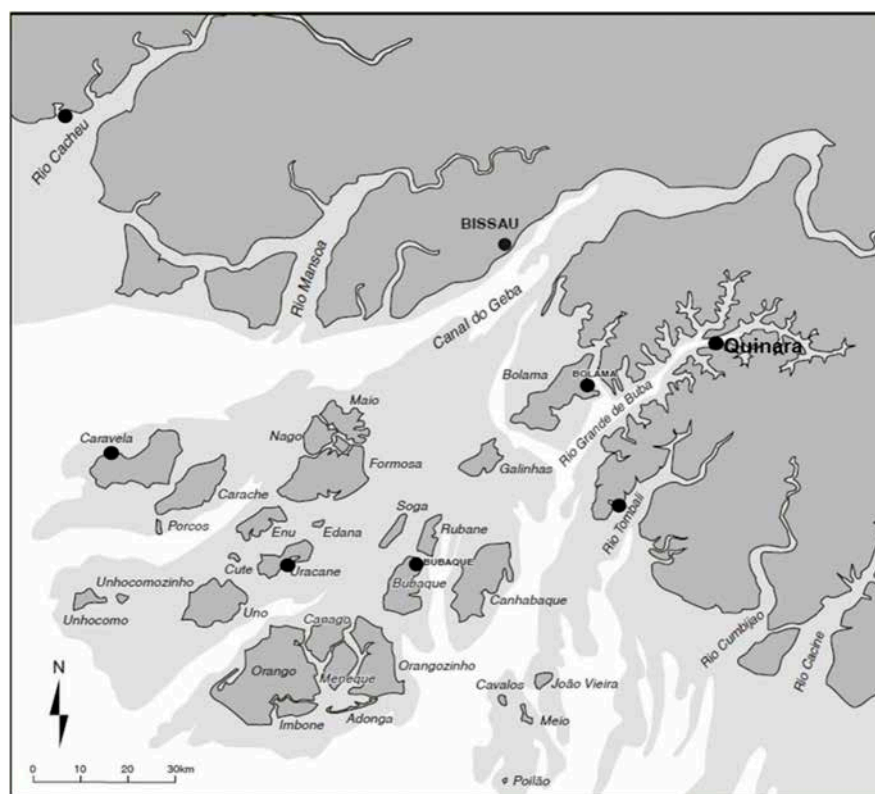


Figure 2. Map of the study area with the localisation of sampling stations corresponding to the main landing ports along the Guinea Bissau coast.

2.3. Biological Data

Data on *E. fimbriata* (n = 46,465 individuals) and *S. maderensis* (n = 776) were obtained from fish that landed at the main artisanal fishing harbours along the Guinea Bissau coast (Bissau, Cacheu, Bubaque, Boloma, Caravela, Uracane, Quinara, and Tombali) from August 2020 to July 2021 (Figure 2). Length frequency data were collected randomly for about five days per week (Table 1). To have the same fishing gear selectivity for monthly comparisons of the length distribution, only specimens caught in encircling gillnets (EGNs; [47]) were used. Fish total length (TL in cm) was measured to the nearest 1 mm, while body weight (W) was determined to the nearest 0.01 g. Sampled individuals were grouped into 1 cm interval size classes to calculate length–frequency distributions and estimate growth parameters.

Table 1. Growth variables for *Ethmalosa fimbriata* and *Sardinella maderensis* collected from various tropical locations in coastal West Africa (Tropical Atlantic Ocean). The locations are near several large marine ecosystems: the Canary Current (south of Senegal (i.e., off Sierra Leone)) and the Guinea Current off Nigeria, Côte d’Ivoire, Congo, and Cameroon. Data was obtained from length-frequency (LF) data and otoliths. Abbreviations: L_{∞} (L_t value when the growth rate is zero), K (coefficient of growth rate), and ϕ' (variation of performance index). t_0 (time “t” when the fish length is zero).

Species	Area	Method	L_{∞}	K	t_0	ϕ'	References
<i>Ethmalosa fimbriata</i>	Côte d’Ivoire	LF	24.5	0.79	−0.21	2.68	Gerlotto [27]
	Mean		24.5	0.79	−0.21	2.68	n/a
	Nigeria	LF	26.3	0.43	−0.39	2.47	Moses [48]
	Nigeria	LF	29.2	0.36	−0.46	2.49	Essen [49]
	Nigeria	LF	31.2	0.90	−0.17	2.94	Ama-Abasi et al. [50]
	Mean		28.9	0.56	−0.34	2.63	n/a
	Sierra Leone	LF	40.8	0.25	−0.61	2.62	Showers [28]
	Mean		40.8	0.25	−0.61	2.62	n/a
	Senegal	Otolith	27.0	0.48	−0.35	2.54	Panfili et al. [51]
	Senegal	LF	31.4	0.47	−0.34	2.67	Faye et al. [52]
	Senegal	LF	38.1	0.31	−0.50	2.65	Baldé et al. [30]
	Mean		32.1	0.42	−0.40	2.62	n/a
	Guinea Bissau	LF	36.2	0.61	−0.25	2.91	Present Study
	Mean		36.2	0.61	−0.25	2.91	n/a
<i>Sardinella maderensis</i>	Cameroon	LF	32.5	0.59	−0.26	2.79	Gabche et al. [29]
	Cameroon	LF	27.2	1.26	−0.13	2.97	Gabche and Hockey [53]
	Cameroon	LF	27.2	0.48	−0.35	2.55	Gabche et al. [29]
	Cameroon	LF	29.1	0.83	−0.19	2.85	Djama et al. [54]
	Mean		29.0	0.79	−0.23	2.79	n/a
	Congo	Otolith	24.4	0.08	−2.35	1.68	Ghéno and Le Guen [55]
	Congo	Otolith	24.9	0.99	−0.17	2.79	Ghéno and Le Guen [55]
	Congo	Otolith	39.6	0.28	−0.55	2.64	Rossignol [26]
	Mean		29.6	0.45	−1.02	2.37	
	Nigeria	LF	37.5	0.34	−0.46	2.68	Marcus [24]
	Mean		37.5	0.34	−0.46	2.68	
	Senegal	LF	37.5	0.30	−0.52	2.63	FAO [56]
	Senegal	LF	39.5	0.45	−0.34	2.85	Samb [57]
	Senegal	Otolith and LF	30.3	0.49	−0.33	2.65	Camarena Luhers [58]
	Senegal	Otolith	35	0.61	−0.25	2.87	Postel [59]
	Senegal	LF	33.4	0.35	−0.45	2.59	Ba et al. [18]
	Mean		35.1	0.44	−0.38	2.72	
	Sierra Leone	LF	29.6	0.35	−0.47	2.49	Showers [28]
	Mean		29.6	0.35	−0.47	2.49	
	Guinea Bissau	LF	27.1	0.1	−1.78	1.87	Present study
	Mean		27.1	0.1	−1.78	1.87	

2.4. Estimation of Growth Parameters

The von Bertalanffy [60] growth parameters (K , L_∞) were estimated from monthly length–frequency data using the ‘TropFishR’ (Tropical Fisheries Analysis with R) package (v1.1.3) [61]. These software packages contain many promising new features, but still include the Powell–Wetherall (P–W) method [61] as a central component of the proposed analyses [38]. The P–W method allows for the estimation of L_∞ from a linearised transformation of the annual length frequency data (LFD) (i.e., the “catch curve”). For this, the mean lengths (L_{mean}) of all fish larger than the catch length (L_c) are calculated. As the value of t_0 (the time “ t ” when the fish length is zero) cannot be estimated from length–frequency data, approximate value of t_0 was estimated by substituting L_∞ (in cm) and K (year^{-1}) in the equation of Pauly [62]. The growth performance index was calculated from the formula given by Pauly and Munro [63]:

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty \quad (1)$$

This equation can be used to compare growth rates between species and to evaluate the growth performance potential under various environmental stresses [64]. The growth index is a species-specific constant related to the shape and gill surface area of the species [65].

All growth parameters used were converted to total length (TL) according to the relationship provided by Sylla et al. [66]:

$$LF(\text{cm}) = 1.08264 + 0.08066 TL(\text{cm}) \quad (2)$$

Or

$$TL = (LF - 1.08264) / 0.08066 \quad (3)$$

2.5. Statistical Analysis

All statistical analyses were performed using the “stats”, “pgirmess”, and “agricolae” R packages, with a significance level of $\alpha < 0.05$ [67,68]. To compare the monthly length variations, the data were analysed either using one-way parametric analysis of variance (ANOVA) or the nonparametric method of Tukey’s honest significant difference (HSD) post hoc test or the Kruskal–Wallis test depending on whether the data were normally distributed. The Pearson test was used to study the correlation between the annual value mean length of *E. fimbriata* and *S. maderensis* with the mean annual of each environmental parameter, SST, SSS, and CUI [69]. We also used analyses of variance (ANOVA) to compare the growth performance index (ϕ') of different countries (Nigeria, Cameroon, Congo, Sierra Leone, Ivory Coast, Senegal, and Guinea Bissau; Table 1) where *E. fimbriata* and *S. maderensis* were found, followed by Kruskal–Wallis tests. These populations represent the entire geographical range of *E. fimbriata* and *S. maderensis*’s distribution. The growth performance index (ϕ') was used to compare growth rates and to assess growth potential under different environmental stresses [7,30,70].

3. Results

3.1. Size Spectra vs. Environmental Parameters

The annual size distribution of *E. fimbriata* and *S. maderensis* in the sea off Guinea Bissau peaked at 25 ± 1 cm (Figure 3). The mean monthly lengths of *E. fimbriata* are different (Figure 4; ANOVA; $F = 660.9$; $p < 0.05$). The Kruskal–Wallis pairwise comparison test showed that the length did not vary among the months of January–February, January–July, February–July, February–November, March–May, March–June, March–December, May–June, May–July, May–December, and June–December. For *S. maderensis*, the mean monthly lengths were different (Figure 4; ANOVA; $F = 13.5$; $p < 0.05$) for the period of study (August 2020 to July 2021). The Kruskal–Wallis pairwise comparison test showed that the length did not vary except for January–March, January–August, February–March, February–August, March–April, March–June, and March–September. The peaks of the monthly average were obtained in August (25.6 cm) and July (27 cm) for *E. fimbriata* and *S. maderensis*, respectively.

The increase in the mean monthly length of *E. fimbriata* and *S. maderensis* corresponded to a period of high upwelling intensity (CUI), sea surface salinity (SSS), and low sea surface temperature (SST).

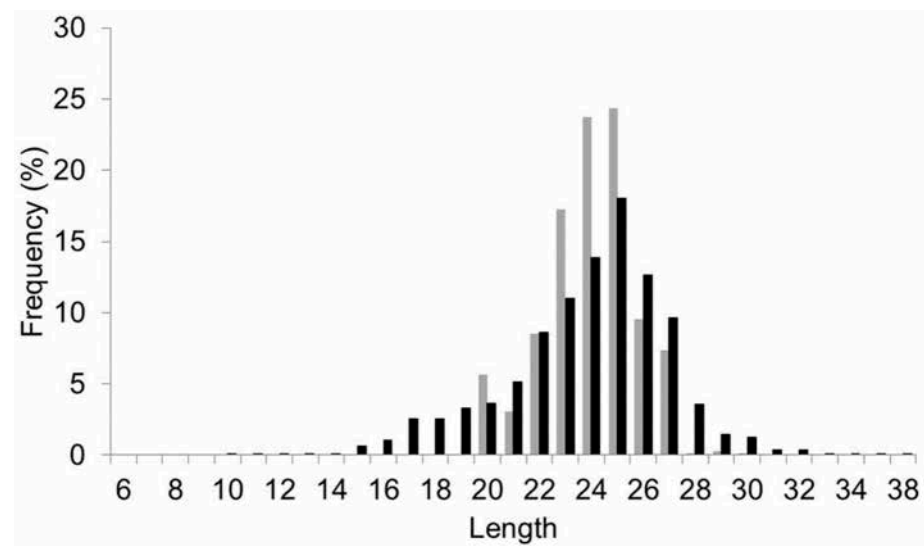


Figure 3. Annual size frequency distributions for *Ethmalosa fimbriata* (black, n = 46,465) and *Sardinella maderensis* (grey, n = 776) caught off the Guinea Bissau coast from August 2020 to July 2021. Total length was used.

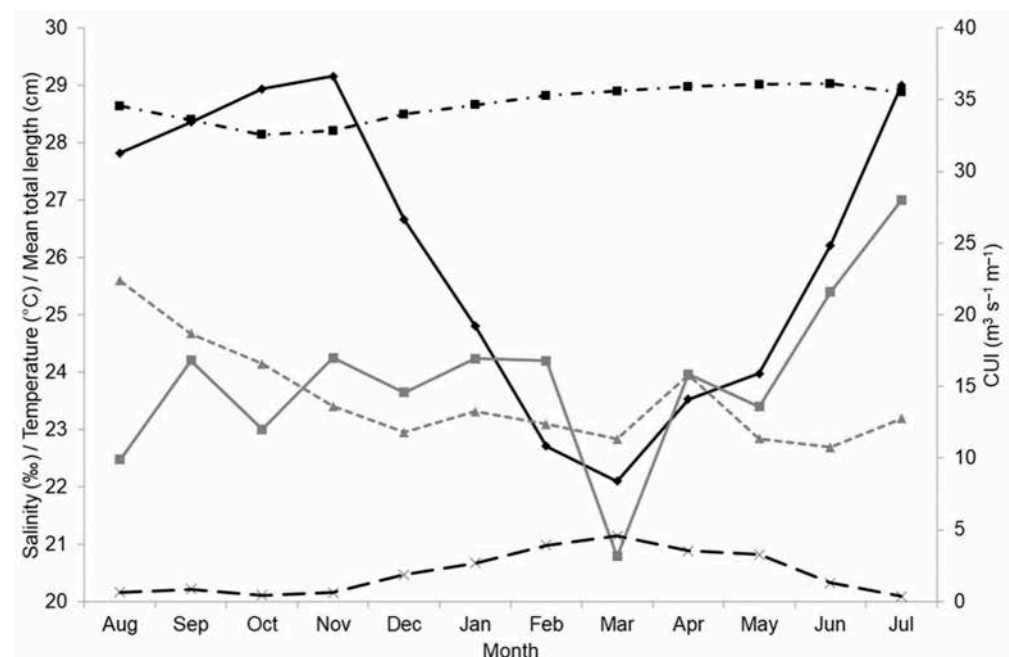


Figure 4. *Ethmalosa fimbriata* (grey line, dashed line with triangle) and *Sardinella maderensis* (grey line, solid line with square) mean total length (in cm) data (black line), combined with seasonal environmental components for Guinea Bissau coastal waters (August 2020 to July 2021): coastal sea surface temperature (black, solid line with triangle) (Modis AVHRR), coastal upwelling index (black, long dashed line with cross), and sea surface salinity (black, dot-dash with square).

The seasonal cycle of declining SST coincides with an increase in CUI because strong offshore wind-induced upwelling in winter brings cold water to the surface. Coastal surface temperature is high from July to November (maximum in November) and low from December to June (minimum from February to March). The seasonal cycle of SST was therefore opposite to the SSS and CUI cycles (Figure 4). Thus, there were decreases in

SSS (minimum in October) and CUI (minimum in July) from August to January and from August to November and July, respectively (maximum in April), followed by increases in SSS (maximum in June) and CUI (maximum in March) during the rest of the study period. No positive correlations were found between environmental parameters and mean lengths of *E. fimbriata* and *S. maderensis*, except between CUI and the mean length of *S. maderensis* (Table 2), which were positively correlated (Figure 5, $y = 100x - 9 \times 10^{-13}$; $R^2 = 1$; p -value < 0.05).

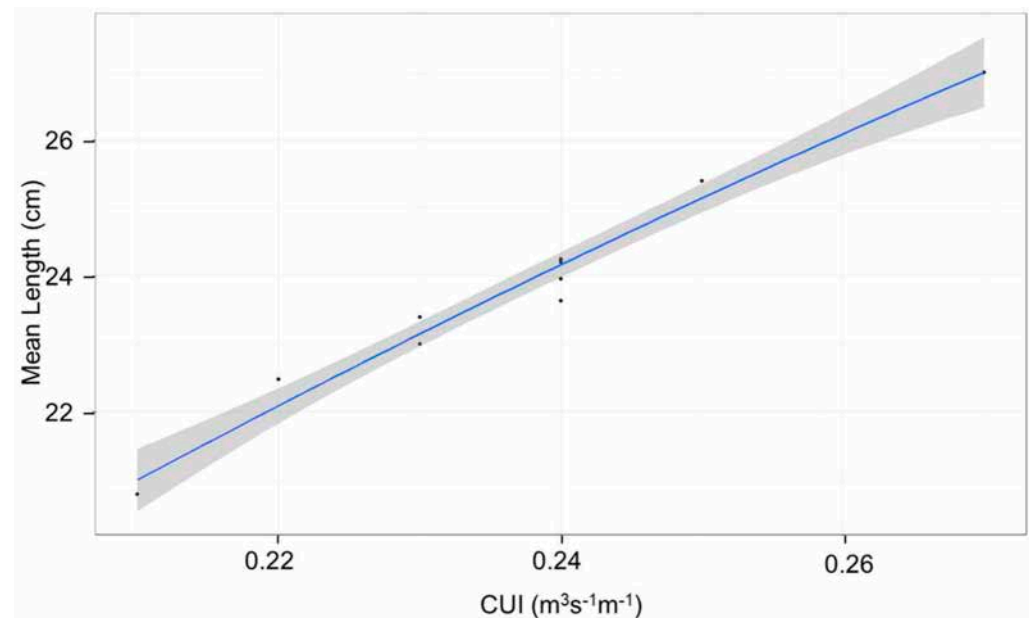


Figure 5. *Sardinella maderensis* mean length (cm) as a function of coastal upwelling index (CUI), August 2020 to July 2021. The solid lines (blue) represent the best-fit estimates; the grey shaded regions represent the confidence intervals.

Table 2. Results of Pearson tests between mean monthly length (TL_m) of *Ethmalosa fimbriata* and *Sardinella maderensis* vs. environmental parameters (CUI: coastal upwelling index, SST: sea surface temperature, Chl-a: chlorophyll-a concentration) observed in Guinea Bissau's waters (August 2020 to July 2021). N: Number of variables; df degrees of freedom; R² coefficient of correlation. * significant p -value.

Species	Variables	N	t	df	R ²	p-Value
<i>Ethmalosa fimbriata</i>	TL _m yr ⁻¹ vs. CUI	12	−0.85158	10	−0.26	0.4144
	TL _m yr ⁻¹ vs. SST	12	1.5404	10	0.44	0.1545
	TL _m yr ⁻¹ vs. Chl-a	12	−1.0084	10	−0.30	0.337
<i>Sardinella maderensis</i>	TL _m yr ⁻¹ vs. CUI	12	18.386	10	0.98	<0.05 *
	TL _m yr ⁻¹ vs. SST	12	1.4159	10	0.41	0.1872
	TL _m yr ⁻¹ vs. Chl-a	12	−1.9038	10	−0.51	0.08608

3.2. Growth Parameters

Based on the length frequency data of *E. fimbriata*, L_{∞} , K , and ϕ' for August 2020 to July 2021 caught off the Guinea Bissau coast were estimated to be 36.2 cm, 0.61 year⁻¹, and 2.91, respectively. The growth parameters (L_{∞} , K , and ϕ') obtained from the LFs of *S. maderensis* were estimated as 27.1 cm, 0.1, and 1.87, respectively, for the period of August 2020 to July 2021.

4. Discussion

Small pelagic fishes are renowned for their notable and swift population oscillations [14,71]. Consequently, it is imperative to consider adaptive alterations in life history when projecting population reactions to climate change [7,72,73]. During the study period (2020–2021), intermonth variability was observed in the length distributions of *E. fimbriata* and *S. maderensis* in Guinea Bissau's waters. This variability could be attributed to fluctuations in environmental parameters. For instance, adverse environmental conditions and limited food availability early during the stages of life may lead to slower growth, decreased energy reserves, and subsequently diminished fitness throughout a fish's lifespan [74]. In response to these environmental fluctuations, certain pelagic fish species exhibit permanent or conditional migrations to different regions during specific life stages to enhance their life success (e.g., achieving rapid growth and high reproductive success) [75–77].

We observed a positive correlation between the monthly growth of *S. maderensis* and the CUI. The relationship between growth rates and feeding rates has been quantified in various small pelagic fish species [73,78,79]. Ba et al. [18] proposed an adaptation of the biological parameters of *S. maderensis* to environments with varying upwelling intensities. Similarly, Baldé et al. [7], also in Senegal, revealed a connection between the growth of *S. aurita* and CUI. In the eastern Pacific, herring growth declined due to a reduction in zooplankton availability [80]. In the case of European anchovy (*Engraulis encrasicolus*) fry, growth has been linked to higher phytoplankton values [81]. The body condition, encompassing factors like growth and weight, of sardines and anchovies may reflect bottom-up controls influenced by changes in plankton composition and/or concentrations [71]. Nonetheless, in certain small pelagic species such as *Clupea pallasii*, *Engraulis japonicus*, and *Sprattus sprattus*, growth has been observed to correlate with a combination of SST and zooplankton abundance [82–84]. Despite this, while no direct positive correlation has been identified between the growth of *E. fimbriata* and *S. maderensis* and SST, several studies have demonstrated that temperature plays a role in various life stages of small pelagic fish [73,85,86]. Sea temperature can interact with other key physical factors, such as light, salinity, pH, and dissolved oxygen, as well as biotic factors, including prey availability and size/quality influencing the environmental windows that support the growth and survival of small pelagic fish [85,87–89]. For instance, Dorval et al. [12] highlighted that, in the California Current large marine ecosystem, a decrease in sea temperature is associated with an increase in zooplankton production. Temperature exerts control over the rates of metabolic processes that directly regulate growth energetics by altering the rates of digestion, gut evacuation, enzyme activity, swimming activity, and overall catabolism [90–92]. Notably, Takahashi et al. [83] showed that elevated temperature leads to an accelerated growth rate during the early life stages of small pelagic fish, provided there is an adequate food supply. Furthermore, in certain small pelagic fish, studies have shown that temperature has promoted faster hatching and enhanced growth rates of post-larvae [93–95]. Consequently, elevated temperatures have the potential to exert an influence on and bolster the growth of small pelagic species, particularly when the abundance of prey zooplankton diminishes and temperature-related energy losses, such as respiration, become more pronounced [82,95]. This interplay suggests that a rise in temperature over a given season can influence the development trajectory of pelagic fish. This thermal influence may prompt them to transition from a linear growth pattern during specific stages of their life cycle to the manifestation of an exponential growth pattern [95]. It is important to acknowledge that other parameters, including food quality and predator abundance, have the potential to exert an influence on growth. However, due to the absence of available data to quantify these parameters across different seasons or on an annual basis, their consideration was precluded in our analysis. Notably, previous studies have also underscored the significance of salinity and *E. fimbriata* growth [23,51]. In particular, Panfili et al. [51] showed that growth rates were reduced in the hypersaline environment in Saloum (Senegal). This phenomenon may lead to a decrease in size at maturity and an increase in the fecundity of *E. fimbriata* under high-salinity conditions [23,51].

For *E. fimbriata* and *S. maderensis*, a gradient in Sierra Leone and Nigeria appeared, respectively, with larger body sizes and longer life spans observed. However, growth was slower with shorter life spans in Cameroon and Guinea Bissau for *E. fimbriata* and *S. maderensis*, respectively (Figure 6a,b). Populations from Guinea Bissau, Côte d'Ivoire, Congo, Sierra Leone, and Senegal for *E. fimbriata* and those from Cameroon, Congo, Senegal, and Sierra Leone for *S. maderensis* were generally larger and longer-lived, suggesting that there is at least an intermediate growth pattern between the two extremes. These differences and gradients were most clearly visible when the growth curves of all populations were plotted together (Figure 6a,b). No statistical differences between the growth performance index (ϕ') of historical data collected off the West African coast of *E. fimbriata* and *S. maderensis* (Table 1; ANOVA: F value = 0.362, $p = 0.8$ and ANOVA: F value = 1.87, $p = 0.2$, respectively). The coefficient of the growth rate (K) of *E. fimbriata* in Nigeria was higher than in the other countries, while in Sierra Leone, an increase in L_{∞} was observed. The asymptotic length (L_{∞}) was lower in Côte d'Ivoire (Figure 7a). The coefficient of the growth rate (K) of *S. maderensis* in Cameroon was higher than in the other countries, while in Congo, an increase in L_{∞} was observed (Figure 7b).

Variations in growth patterns can indeed be observed among species within the same environment or across different regions [7,30]. In this study, it is noteworthy that the calculated K and L_{∞} values for *E. fimbriata* and *S. maderensis* were found to be lower than those reported in studies conducted in other regions (Figure 7a,b). This disparity raises the possibility that observed shifts in life history traits (such as slower growth and reduced size) alongside associated trade-offs, could result from population adaptation to either natural factors (environmental fluctuations) or anthropogenic pressure (e.g., fishing) [96]. The disparate growth rates exhibited by *E. fimbriata* and *S. maderensis* serve as a reminder that distinct growth trajectories can emerge within the same small pelagic fish species, contingent upon the specific system, region, year, and study context. It is plausible, for instance, that individuals may undergo slower growth in their initial year, potentially due to environmental constraints or late-season hatching, and subsequently exhibit accelerated growth in their second year [97]. The manifestation of changes in growth rate variance resulting from non-linear selection can also occur [98], particularly in response to variance in environmental conditions that can constrain or reinforce phenotypic changes [99]. Thus, possible mechanisms for such an anomaly may be related to either anthropogenic pressure, like fishing, or a shift in environmental factors [100,101]. The causal mechanism thus appears to be involved in changes in growth rates for small pelagic species [5,73]. Notably, the selective disappearance of fast-growing individuals has often been attributed to fishing which, by targeting large individuals, increases the mortality rate of fast-growing individuals [19,97,102]. Thus, a high removal of older and larger individuals can lead to a change in species growth dynamics (e.g., population age structure and reproductive capacity [7,19,103]). This results in the selective disappearance of large individuals within cohorts with the effect of decreasing size at age [104,105], leading to a decline in the biomass of small pelagic species [101,106]. This has profound management implications, particularly for small, fast-growing species where rapid changes in growth, maturation, and fecundity largely determine the size of the spawning stock biomass, the number of recruits produced, and, therefore, the potential harvest achievable from a given stock.

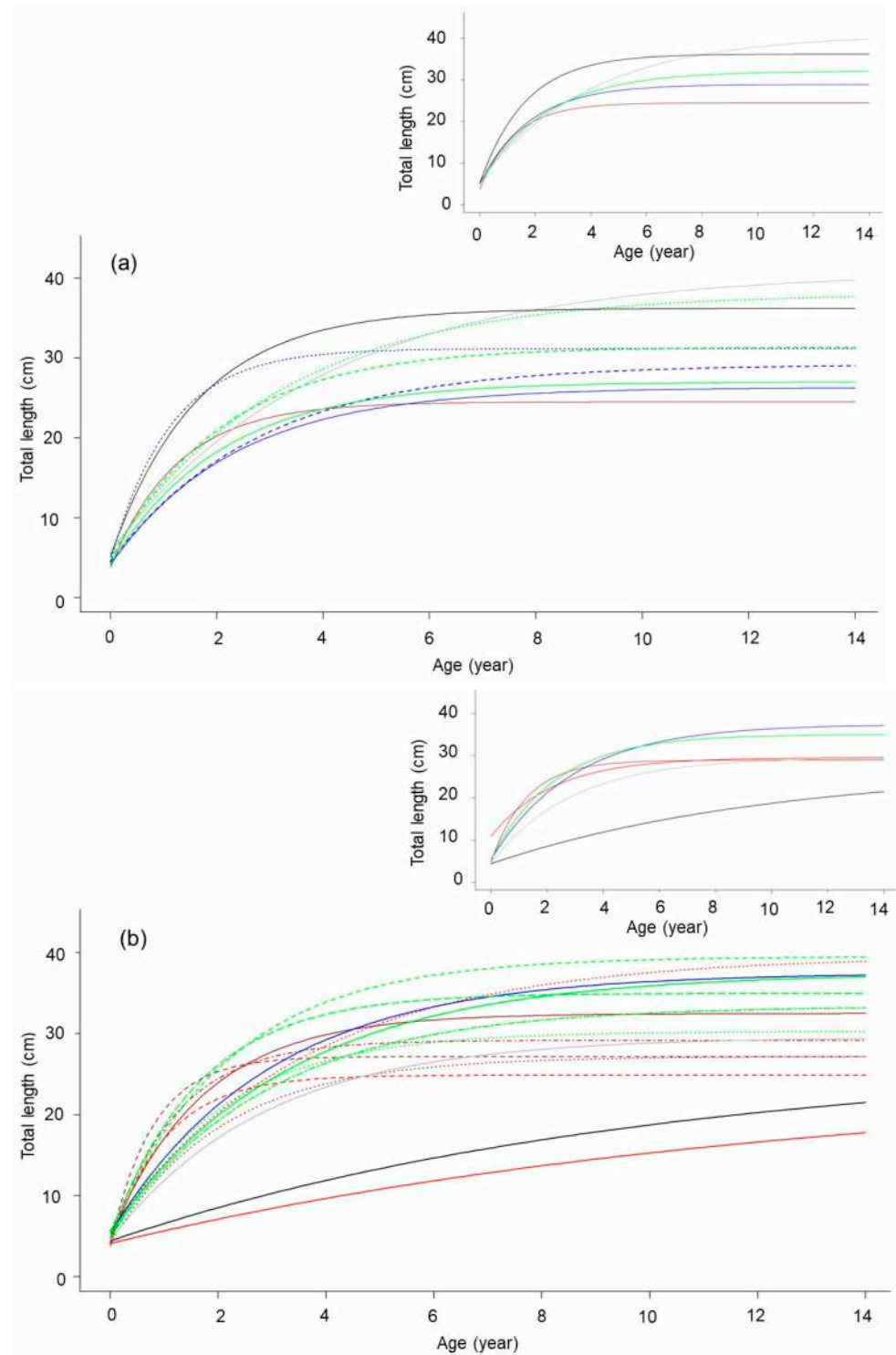


Figure 6. Growth curves of (a) *Ethmalosa fimbriata* and (b) *Sardinella maderensis* listed in Table 1. The growth curves are marked with different colours on an area basis (Cameroon and Côte d'Ivoire: brown; Congo: red; Guinea Bissau: black; Senegal: green; Sierra Leone: grey; Nigeria: purple). The panel on the top-right shows the average growth curves per area.

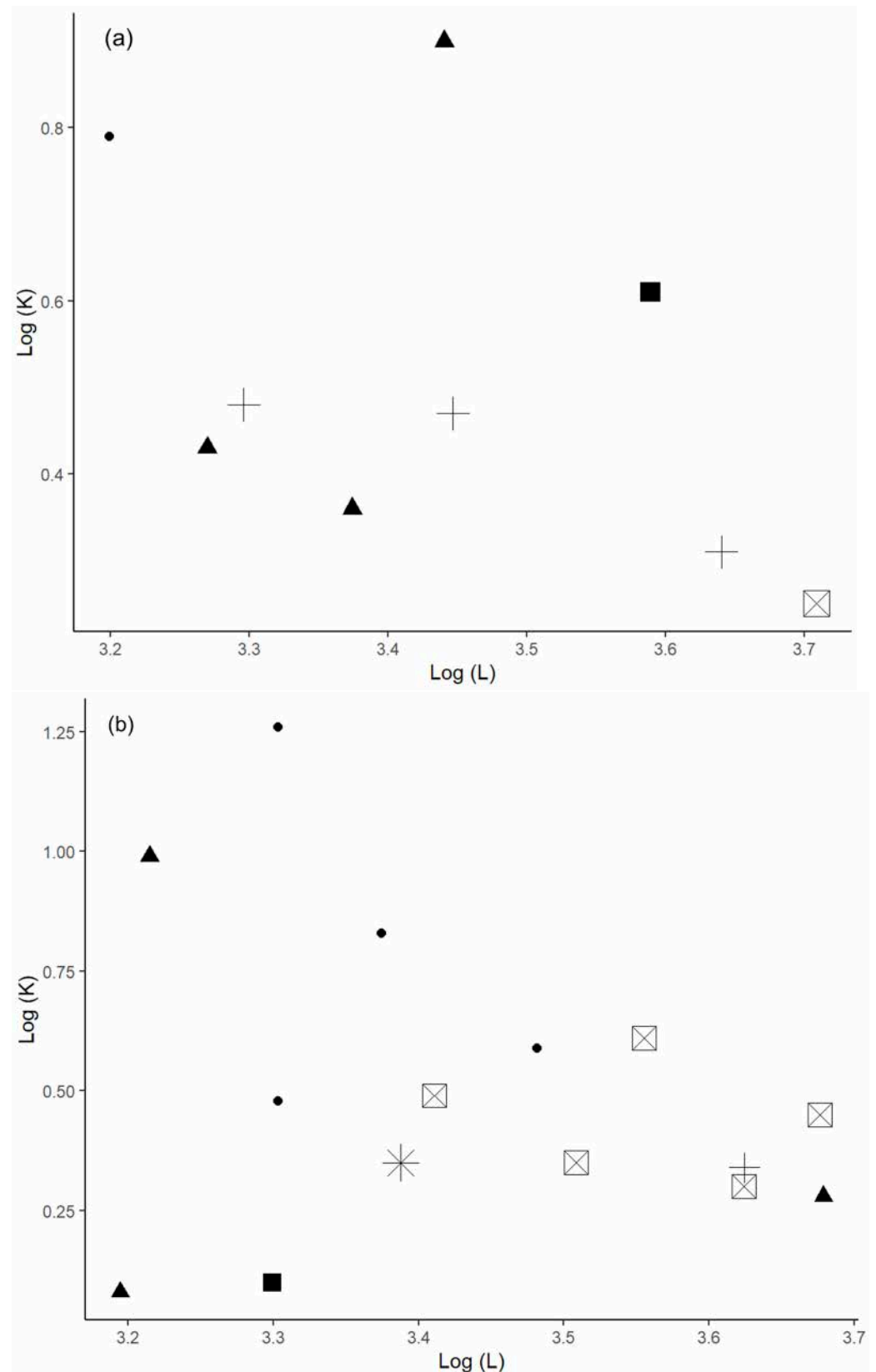


Figure 7. Auximetric plot (double logarithmic plot of parameters K and L_{∞}) for (a) *Ethmalosa fimbriata* populations for five (5) coastal areas. Data from this study in Guinea Bissau (square) and from a literature review of Nigeria (triangle), Sierra Leone (square with cross), Côte d'Ivoire (circle), and Senegal (plus) and (b) *Sardinella maderensis* populations for six (6) coastal areas. Data from this study in Guinea Bissau (square) and from a literature review of Nigeria (plus), Sierra Leone (cross), Cameroon (circle), Congo (triangle), and Senegal (square with cross). Abbreviations: L_{∞} : (asymptotic length, in cm) and K : (coefficient of growth rate (by year)).

5. Conclusions

The biological characteristics of *E. fimbriata* and *S. maderensis* (e.g., growth), are significantly influenced by environmental conditions (e.g., intensity of CUI and SST). Both species respond dramatically and rapidly to changes in ocean climate and have biological characteristics that make them highly sensitive to environmental fluctuations. Based on fish size frequency data and the CUI, we observed that recruitment of small pelagic fish tends to occur during the most intense upwelling periods (March–April). Environmental changes appear to have a significant positive effect on the growth of *E. fimbriata* and *S. maderensis* in Guinea Bissau, confirming a more general trait of their high phenotypic plasticity [96]. Understanding the growth tactics of a fully exploited fish species is important for understanding how climate change might affect fisheries, especially in countries where fisheries are essential to the social fabric and economy, as is the case in Guinea Bissau. Better information on the population biology of *E. fimbriata* and *S. maderensis* in variable environments with complex interactions will help fishery managers to plan and adapt to environmental change.

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