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Evolution of catches and variability in the life history traits of the bonga shad, *Ethmalosa fimbriata* (Bowdich, 1825*)*, a highly targeted small pelagic fish in West African coastal waters

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Abstract
An updated study of the main life history traits of the bonga shad, *Ethmalosa fimbriata* (Bowdich, 1825), was undertaken in Senegalese coastal waters, together with an evaluation of the captures and fishing effort over the past 33 years. Captures varied considerably over the years, with a peak in 2001. The condition factor varied irregularly between the years. The reproductive period mainly occurred from January to July, the size at first sexual maturity was similar for both sexes (≈180 mm), and the absolute fecundity was very variable (133,000 ± 70,000 eggs, mean ± SD). Growth was rapid and variable with longevity of 6-7 years. These updated biological parameters indicated that the bonga shad is full-exploited in the area and that the fishing effort should be reduced and the permitted mesh size reviewed for conservation management measures.

Keywords: *Ethmalosa fimbriata* captures life history traits otolith

1. Introduction

The bonga shad (*Ethmalosa fimbriata,* Bowdich, 1825) is a pelagic clupeid species that inhabits the coastal waters in the Gulf of Guinea [1, 2]. It is a brackish or marine species, usually found along the coast at a depth of 0 to 50 m, as well as in lagoons and inshore waters [3, 4]. This species feeds by filtering phytoplankton, mainly diatoms, and breeds throughout the year in waters with salinity usually ranging from 3 to 38, with seasonal peaks in some areas, spawning in the sea or in estuaries. Bonga shad is one of the main pelagic fish species captured along West African coasts and total captures were around 250,000 tons in 2011 [5]. Studies to evaluate the stocks in this area have shown that it is over-exploited [5]. A reduction in catches would have a devastating effect on fisheries and food security. In Senegal, some aspects of the bonga shad biology were discussed for the first time by Blanc [6], and some reproduction and growth parameters were published later in the early1970s for estuarine environments where the species is common [7, 8]. Other studies assessed fishing effort, catches and catch composition in relation to hydrological parameters such as temperature and salinity [9]. Empirical observations have shown that the biological characteristics of the species are influenced by seasonal and inter-annual climate variations [10-12].

It is, therefore important, to update the main biological parameters of the bonga shad to give a better indication of the stocks and their management. First, this study assesses the current stock status by producing a comparative analysis of how landings and the fishing effort have changed over the past 33 years in Senegal (1981-2013). Second, it updates the knowledge of the main biological characteristics of the bonga shad along the Senegalese coast including the condition factor, reproduction (sexual cycle, size of first sexual maturity, fecundity and oocyte sizes), and age and growth (using otolith growth marks). Third, these data are compared with previous data from the same area and other areas to determine possible changes that may be related to significant biological or environmental pressures. Finally, this paper proposes some measures to sustainably exploit of the stocks.

2. Material and methods
2.1 Fishery data
The annual records of bonga shad catches (in tons) and fishing effort (trips by fishing units), between 1981 and 2013, in Senegalese waters were provided by the Oceanographic Research Center, Dakar-Thiaroye (CRODT). These data were obtained mainly from the landing surveys at Saint Louis, northern Thiès, Cape Verde and southern Thiès, based on catches by local fishermen using canoes.

2.2 Sampling
Samples of bonga shad were collected monthly, from July 2012 to June 2013, at the two main landing locations of Mbour and Joal in southern Thiès, Senegal (Fig. 1). Sampling was stratified by percentage of mature fish in each fork length class, FL is the central value of each fork length class, and (W_e) in g), and the sex and gonad maturity stage were determined using Fontana's [13] scale. The otoliths (sagittae) were extracted, cleaned in water, dried and stored dry in labeled microtube vials.

Fig 1: Sampling locations of bonga shad in Senegal (Mbour and Joal).

2.3 Weight-length relationship
The relationship between the fork length and the total weight was expressed using the formula:

$$W = a \times FL^b$$

where a and b are model parameters, b being the allometric coefficient. The condition factor was calculated for each fish using the formula:

$$Kc = \frac{W}{FL^3} \times 10^3$$

where Kc is the individual condition factor. The homogeneity of variance was checked using Bartlett's test before analysis of variance (ANOVA). If the variance was not homogeneous ($P<0.05$), the non-parametric Mann-Whitney test was used to compare monthly Kc averages.

2.4 Reproduction
The gonado-somatic index (GSI) was calculated monthly to determine the reproductive period, using the formula:

$$GSI = \frac{W_g}{W_e} \times 100$$

where W_g is the fish gonad weight. The mean GSI was compared between months for the same sex using a non-parametric Mann-Whitney test because conditions for using parametric tests were not respected.

The size at first sexual maturity (FL_{50}), for which 50% of individuals were observed to be mature during the reproductive season, was calculated using 50 mm size classes and a sexual maturity stage equal to or greater than III corresponding to an irreversible development of the gonad to reach maturity. FL_{50} was estimated using a logistic function fitted by non-linear regression (quasi-Newton method, Statistica ®):

$$\%M = \frac{100}{1 + e^{-a(FL - FL_{50})}}$$

where %M is the percentage of mature fish in each fork length class, FL is the central value of each fork length class, a and FL_{50} are constants.

Fecundity was calculated from female gonads of at least stage V during the spawning period. For each female, both gonads were weighed and a 0.05 g sub-sample was taken from one of the gonads and placed in Gilson liquid (100 ml ethanol, 9 ml glacial acetic acid, 20 ml of 60% nitric acid, 20 g mercury (II) chloride and 875 ml distilled water). The ovocytes were separated mechanically and then manually counted under a binocular microscope. The absolute fecundity (Abs. Fec.) was calculated as the number of ovocytes to be released at the next spawning and the relative fecundity (Rel. Fec.) as how many eggs g^{-1} of body weight were produced, i.e. the ratio between the absolute fecundity and the weight of the individual fish.

$$Abs.Fec. = \frac{W_g \times N_{ov}}{W_{gs}}$$

$$Rel.Fec. = \frac{Abs.Fec.}{W}$$

where N_{ov} is the number of ovocytes counted in the subsample, W_g is the total weight of the gonad and W_{gs} is the weight of the gonad subsample. To measure the dimensions of the ovocytes, five images were taken of each gonad (LAS-EZ software) and the diameter, perimeter and area of each oocyte were measured automatically using Image J. The means of these parameters were calculated for each fish and compared between sampling locations.

2.5 Growth
A standard protocol was used to interpret the otoliths. An image of the whole right otolith, submersed in 95% ethanol, was recorded (LAS-EZ software) under a binocular microscope under reflected light against a dark background. Each otolith was interpreted three times by the same reader, first from the core to the rostrum margin, and then from the core to the posterior margin, and from the posterior margin to the core. The seasonal translucent marks were identified and counted (Fig. 2). The last translucent mark was not counted if it was located on the otolith margin and therefore still being formed. If two of the three readings agreed, then this estimate was accepted as the final age. If there was no agreement between all three readings then the otolith was rejected from further analysis. The consistency of growth zone counts was assessed by calculating the coefficient of variation of Chang [14] following the formula:

$$CV = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - \bar{X}_j)^2}{R-1}}}{\bar{X}_j}$$

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 time each fish is aged. For determining the time when the translucent marks were deposited, the monthly percentage of the translucent margins of the otoliths was calculated over a year. The parameters of the Von Bertalanffy growth function were calculated using a non-linear regression (Statistica®):

$$FL = FL_{\infty}\left(1 - e^{-K(t-t_0)}\right)$$

where FL is the fork length at time t, FL_{∞} is the asymptotic fork length, K is the growth coefficient and t_0 is the theoretical age at which the length is null. These growth parameters were compared between locations using a likelihood ratio test [15] and applying the weighted sum of squares [16].

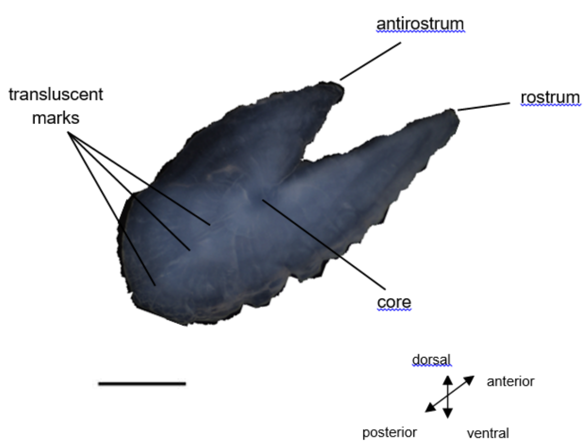

Fig 2: Bonga shad otolith viewed under a binocular microscope after immersion in 95% ethanol under reflected light against a dark background. The distal otolith face is shown. Three translucent marks are visible from the core, both along the rostrum and towards the posterior margin. Scale bar = 1.5 mm.

3. Results
3.1 Catches and fishing analysis
There were three phases in bonga catches in Senegal (Fig. 3a) during the last 33 years. From the early 1980s to the early 2000s, there was a rapid increase in landings. During this period, the catch volume increased by a factor of 9 from its 1981 level. There was a peak in 2001 (around 24,500 tons), and then a decline up to 2005. From 2005 to 2013 catches were relatively small (5,000 to 13,000 tons yr^{-1}), about a third of the 2001 level. Catches were dominated by encircling gillnets (62%) and purse seines (35%), the remainder (3%) covering other types of fishing gear. A comparison of the quantity of fish landed with fishing effort indicated that catches increased as the fishing effort increased up to 2001. After this period the annual number of trips was still high however catches had sharply declined (Fig. 3b). Breaking down the annual fishing effort into types of fishing gear showed that set gillnets were the main type of gear used (50% of the total number of trips), followed by purse seines and encircling gillnets (25% of the total number of trips). However, the use of beach seines for catching bonga shad decreased progressively and other types of fishing gear were very rarely used (1-2% of the total number of trips).

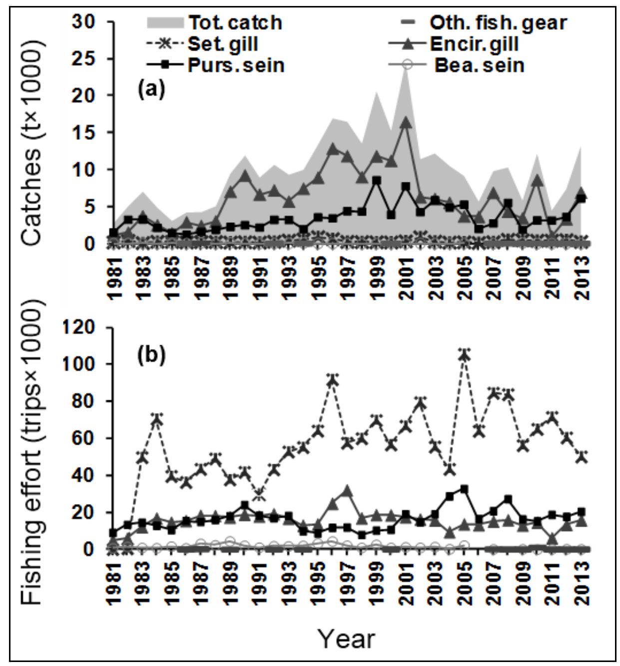

Fig 3: Annual catches (a) and fishing effort (b) for bonga shad in Senegalese coastal waters between 1981 and 2013. Tot. catch = total catch; Set. gill = set gillnets; Purs. Sein = purse seines; Oth. fish. gear = other types of fishing gear; Encir. gill = encircling gillnets; Bea. sein = beach seines.

3.2 Weight-length relationship and condition
For the fish sampled, FL varied from 114 to 304 mm for Mbour and from 124 to 300 mm for Joal. Weights ranged from 25 to 556 g for Mbour and 27 to 471 g for Joal. The relationship between length and weight was a power function with a very significant positive correlation (Mbour: $W = 1E^{-05} \times FL^{3.11}$, $r^2 = 0.98$; Joal: $W = 1E^{-05} \times FL^{3.10}$, $r^2 = 0.98$). The allometric exponent calculated for both locations was close to the isometric value i.e. 3. For both locations, the Kc trends were similar, with high values at the beginning of the dry season, a peak in January, a decrease thereafter, and high values at the beginning of the rainy season (June-July). There were two Kc cycles per year, but the differences between extreme monthly values were greater for Mbour (Fig. 4). The interval between minima was not the same between the two locations, five months for Mbour (October to February) and

seven months for Joal (September to March). For Mbour, the mean Kc in January was significantly higher than all other months, except June, and Kc in September was significantly lower than other months, except March (Fig. 4a & Table 1, Mann-Whitney, $P<0.05$). For Joal, the mean Kc in January was also significantly higher than all other months, except July (Fig. 4b & Table 1, Mann-Whitney, $P<0.05$).

Table 1: Comparison of the monthly condition factors (Kc) of bonga shad for Mbour and Joal using a Mann-Whitney U-test. Significant differences between the months are shown in bold (P <0.05).

Month	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Mbour											
Aug	0.00										
Sep	0.00	0.00									
Oct	0.00	0.18	0.00								
Nov	0.16	0.00	0.00	0.02							
Dec	0.00	0.35	0.00	0.69	0.16						
Jan	0.01	0.00	0.00	0.00	0.00	0.00					
Feb	0.00	0.60	0.00	0.13	0.00	0.18	0.00				
Mar	0.00	0.00	0.45	0.00	0.00	0.00	0.00	0.01			
Apr	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.28	0.07		
May	0.00	0.92	0.00	0.18	0.00	0.29	0.00	0.71	0.00	0.12	
Jun	0.29	0.00	0.00	0.00	0.01	0.00	0.29	0.00	0.00	0.00	0.00
Joal											
Aug	0.00										
Sep	0.00	0.03									
Oct	0.00	0.16	0.20								
Nov	0.00	0.08	0.63	0.65							
Dec	0.55	0.00	0.00	0.00	0.00						
Jan	0.12	0.00	0.00	0.00	0.00	0.01					
Feb	0.25	0.01	0.10	0.02	0.07	0.50	0.01				
Mar	0.00	0.04	0.91	0.41	0.80	0.00	0.00	0.12			
Apr	0.00	0.62	0.00	0.01	0.00	0.00	0.00	0.00	0.00		
May	0.00	0.46	0.01	0.24	0.07	0.00	0.00	0.00	0.04	0.03	
Jun	0.00	0.01	0.47	0.06	0.29	0.00	0.00	0.13	0.78	0.00	0.00

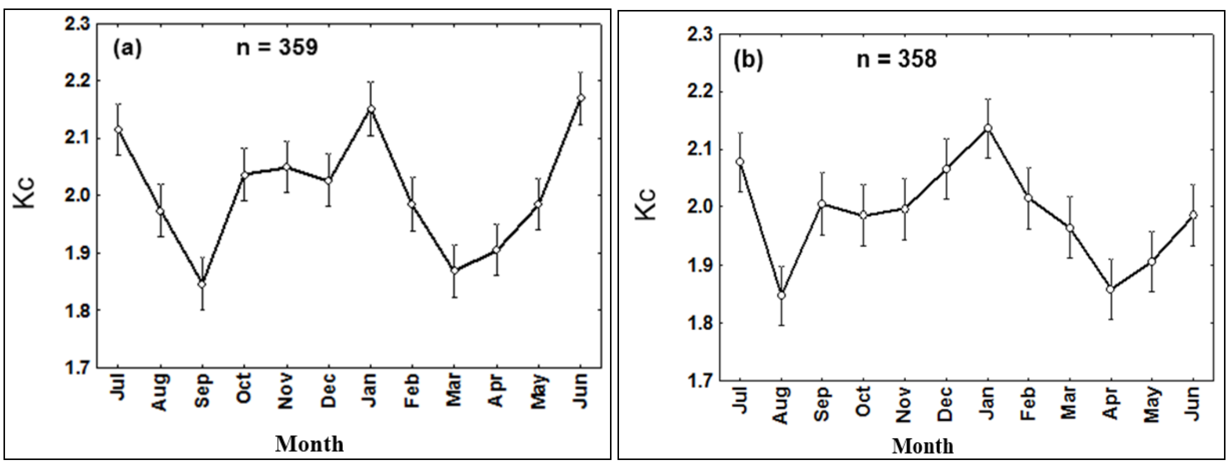

Fig 4: Monthly condition factor of bonga shad (mean Kc ± SD) for Mbour (a) and Joal (b).

3.3 Reproduction

For Mbour, there were two reproductive cycles per year, as shown by both GSIs, the first with a peak at the beginning of the dry season (January), and a second in June for female and in July for male at the beginning of the rainy season with a slowdown in February and October and December, respectively (Fig. 5a). From August to December the females GSIs were low (less than 4%), which could correspond to a sexual rest. For Joal, the females and males GSIs were synchronous. There was only one reproductive cycle per year with the females GSIs remaining high for several months, February to June, and a peak in May, corresponding to the end of the dry season and beginning of the rainy season (Fig. 5b). This reproductive period corresponded to the second period observed for Mbour. For Mbour, comparing the mean GSIs values of the females between months using Mann-Whitney U test was inconclusive but showed that the GSIs in January and June were similar ($P=0.50$), and were different from most other months (except March and May). For Joal, comparisons of the mean GSIs of the females between months were clearer, with May being statistically different from all other months ($P<0.05$). For both locations, the mean values of the GSIs of the males were relatively low along all sampled months and no clear seasonal pattern was evident. In conclusion, bonga shad probably had one prolonged reproductive period in both locations, between January and June, even though two peaks were identified for Mbour, in January and June, whereas the main peak for Joal was in May.

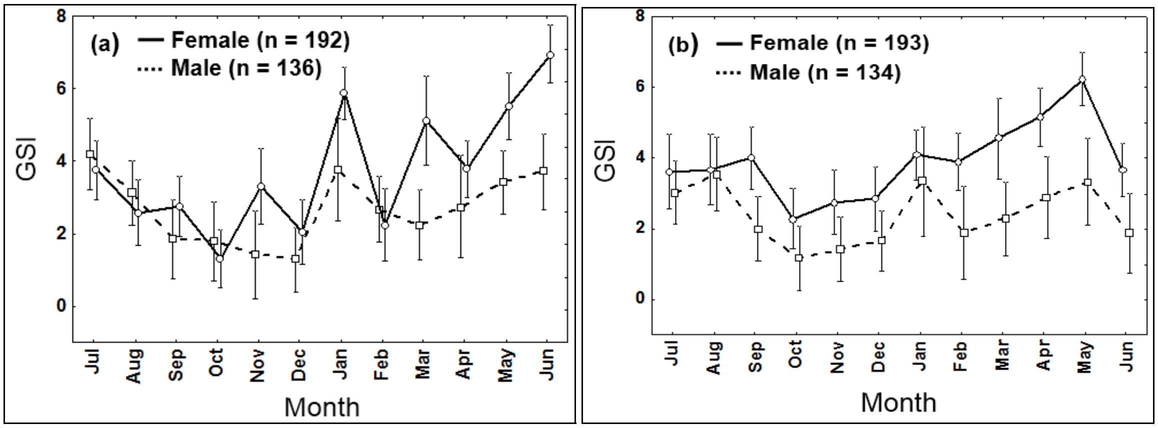

Fig 5: Monthly gonado-somatic index of bonga shad (mean GSI ± SD) for Mbour (a) and Joal (b).

During the sexual resting period, spawning individuals (gonads at stage V) were found but these were rare and were usually large in size. For Mbour, mature fish ranged from 178 mm to 304 mm for females and 147 mm to 277 mm for males. The sizes at first sexual maturity for Mbour were 176 mm for females and 180 mm for males (Fig. 6a & b). For Joal, mature fish varied from 160 mm to 300 mm for females and 160 mm to 268 mm for males. The size at first sexual maturity for Joal was 177 mm for both sexes (Fig. 6c & d).

For Mbour, the mean absolute fecundity of bonga shad was estimated at 135,500 ± 88,300 ovocytes (n = 10), with a high variability (from 46,000 to 282,500 ovocytes). The relative fecundity ranged between 210 and 790 eggs g^{-1}, with a mean of 436 ± 190 eggs g^{-1} (n = 10). The ovocytes had a mean diameter of 0.61 ± 0.04 mm, a mean area of 0.29 ± 0.04 mm², and a mean perimeter of 2.04 ± 0.15 mm. For Joal, the absolute fecundity varied between 53 606 and 230 581 for females between 202 mm and 273 mm in length. The mean absolute fecundity was estimated at 131,000 ± 56,000 ovocytes. The relative fecundity was estimated at 396 ± 84 ovocytes g^{-1} for mature females and varied between 309 and 557. The average diameter of these ovocytes was 0.64 ± 0.04 mm, the mean area was 0.31 ± 0.04 mm² and the mean perimeter was 2.18 ± 0.23 mm. There were no statistical differences between any of these variables between the two locations (Table 2).

Table 2: Comparison of fecundity parameters of bonga shad for Mbour and Joal using parametric Student's t test, or non-parametric Mann-Whitney U-test. SD = standard deviation; Abs. fec. = absolute fecundity; Rel. fec. = relative fecundity; Area = ovocyte area; Perim = ovocyte perimeter; Diam = ovocyte diameter.

	Mbour		Joal		test		
Parameters	**Mean**	**SD**	**Mean**	**SD**	**U**	**t**	**P**
Abs. fec. (nb eggs)	135481	88295	131056	55960	45		0.74
Rel. fec. (egg g^{-1})	436	190	396	84	50		1.00
Area (mm²)	0.29	0.04	0.31	0.04		0.90	0.38
Perim (mm)	2.04	0.15	2.18	0.23	39		0.41
Diam (mm)	0.61	0.04	0.64	0.04		1.33	0.20

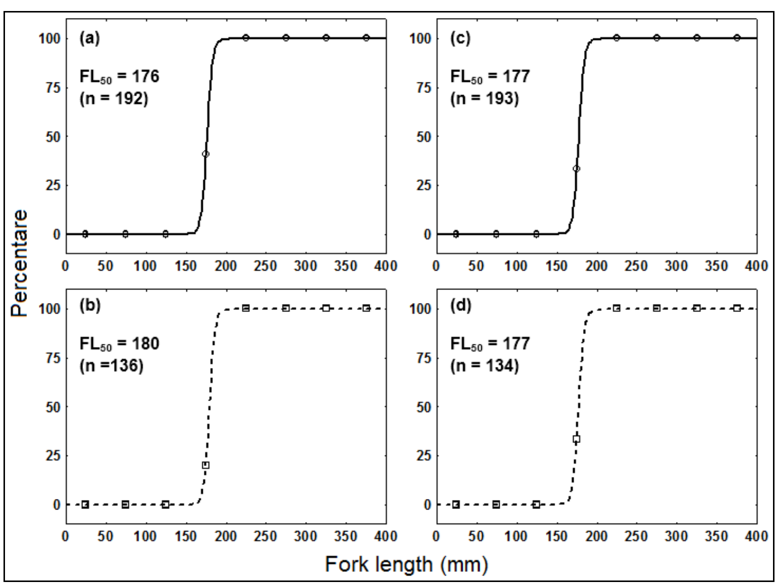

Fig 6: Logistic functions for estimating the fork length at the first sexual maturity (FL_{50}) of bonga shad for Mbour (a, females; b, males) and Joal (c, females; d, males).

3.4 Age and growth

The interpretation of the otolith growth marks was possible on the posterior face, from the core to the edge. Some otoliths were difficult to interpret (7.8%), mainly because they were completely opaque and their age was not given. It was sometimes difficult to interpret the edge because of the reflection of the light at this level, and the corresponding otoliths were then excluded from the analysis. The coefficients of variation of Chang (CV) were 3.18% for Mbour and 3.31% for Joal. Monthly percentages of the translucent edges of the otoliths showed that the translucent marks were formed annually (Fig. 7). This percentage reached a minimum in January and peaked in August, corresponding to the time when the translucent mark was deposited. The age in months was then calculated taking into account the average birth date obtained from the GSI (June for Mbour and May for Joal), the month when the translucent mark was formed (August), the date of capture and the number of translucent marks in the otolith. The growth curves were calculated by counting the seasonal translucent marks on the readable otoliths. These showed a high variability in growth (Fig. 8). The coefficients of determination (r^2) of the Von Bertalanffy growth function (VBGF) were 0.55 for Mbour and 0.57 for Joal. Growth was rapid for this species, especially at the beginning of life, with a low longevity (6-7 years). The asymptotic estimated fork lengths were 289 mm and 319 mm for Mbour and Joal respectively. The growth models were not significantly different between the two locations (SRv = -3154.61, $\chi^2 = 7.82$ for 3 df, $\alpha = 0.05$).

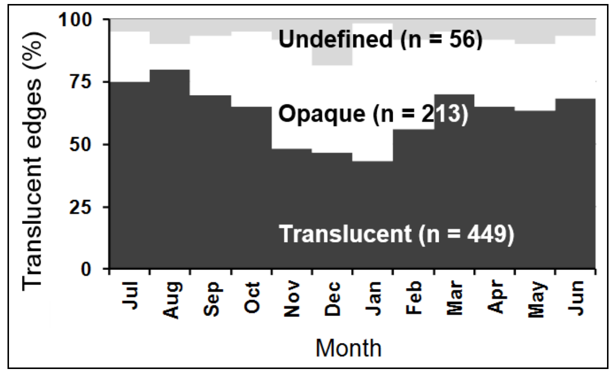

Fig 7: Monthly percentages of otolith translucent edges for bonga shad. The translucent edge percentage is shown in dark grey, the opaque edge percentage is shown in white and the undefined edge percentage is shown in grey.

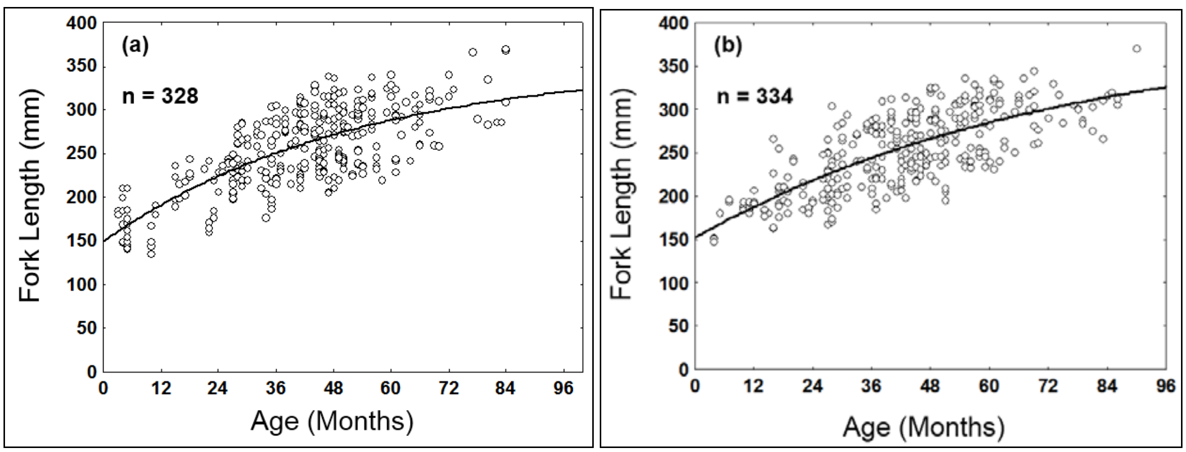

Fig 8: Von Bertalanffy growth functions of bonga shad for Mbour (a) and Joal (b) locations. n = number of otoliths read for both sexes combined.

4. Discussion

4.1 Catches and fishing effort

The combined analysis of catches and fishing effort showed that the current status of bonga stocks is worrying in Senegal waters. Captures have varied considerably over the years, with a peak in 2001, followed by a decrease at the beginning of the 2000s even though the fishing effort was increasing. This could be explained by the combination of a very strong demand for human consumption and the development of modernized local fisheries with powerful engines [17]. The decline in yields as well as in the fishing effort in recent years (2009-2013) may reflect a change in fishing tactics as a result of the decline in the initially targeted resource and/or an increasing interest in another resources which are more profitable and more easily available [18]. This change in target species may be due to the flexibility of local fisheries which catch a wide range of species [7, 19], but is unlikely to apply to bonga as this is a specialized fishery, particularly in Senegal, where the landings were continuous throughout the year.

On the other hand, many studies have suggested that the abundance of small pelagic fish resources is linked to the spatio-temporal variability of environmental factors such as sea temperature, salinity, chlorophyll-a variations and wind stress [20-22]. According to Diankha *et al.* [23], bonga landings and chlorophyll-a showed a decreasing trend from 1999 to 2009, with the sea surface temperature (SST) increasing which reduced larval survival and growth rates, and affected the timing of the reproductive peaks. However, it is unlikely that environmental conditions have been the main cause of the decrease in catches because bonga shad is a highly mobile pelagic species characterized by an extreme adaptability to environmental conditions [3, 9, 24]. Anthropogenic activities are more likely to be the main cause of the decrease in catches [25]. High fishing pressure can cause a decrease in the biomass, the abundance of predators, in the maximum size (fewer older fishes) and the growth and maturity rates in the population [26]. The current situation of bonga shad fisheries in West Africa has been the subject of great attention. This study shows that bonga shad is fully exploited in Senegalese coastal waters. Projections show that there will be a significant scarcity of large fish and a fall in catches because of a continued high fishing effort.

4.2 Weight-length relationship and condition

The weight-length relationships for bonga were isometric in Senegal. An isometric relationship was also reported for bonga in the Niger Delta [27], and previously in Senegal [9, 10]. However, these authors found highly significant differences between the populations off northern Senegal and those off southern Senegal, as well as highly significant differences between Gambia and mid-Senegal.

Two condition factor cycles per year, with a peak at the beginning of the dry season with cold waters in January, and another peak at beginning of the rainy season with warm waters (June-July) were also described many years ago by Mainguy and Doutre [28] in the same area, and Watts [29] in Sierra Leone. These authors linked the main phases of the adult condition cycle to the low food availability from January to May when the water was cold, followed by a fattening period from June to early October, when the water was warm and more saline, with a maximum in the food availability from October to December. The condition factor varies according to the seasons and is influenced by environmental conditions [11, 30, 31]. Bonga shad is well adapted to its environment and follows the changes in conditions in its habitat in West Africa, with the condition factor depending on the available food resources.

4.3 Reproduction

The reproductive period in 2012-2013 mainly occurred from January to July with a spawning peak during the transition between the cold and hot seasons (May-June), corresponding also to the end of the dry season. The start of reproduction in January coincided with the maximum condition factor (previous section). In both locations studied, the lowest values of the condition factor were measured in the middle or at the end of the reproductive season. This probably reflects the ability of bonga shad to draw on reserves for its energy needs during the breeding season. The most recent studies on its reproduction in Senegal were those undertaken by Panfili *et al.* [12] and Faye *et al.* [32] but in the Saloum Delta and, according to these authors, reproduction occurs during the cold season and early hot season, spread over six-eight months with the main spawning period in April-May. These results correspond to the results of the present study. Faye *et al.* [32] described a second reproductive period of short duration, from July to September (three months), not described in other studies, and also reported females spawning throughout the cold season. In the same area and further south, Blanc [6] distinguished two spawning areas: the Joal area from Palmarin to Pointe Sarène, and the "Banc rouge" at the mouth of the Djomboss river. In the first area, extended spawning continued from April to October. It began in April-May, peaked in June-July, declined in August and ended in September-October. Scheffers's [7] study showed that the GSI of Bonga shad in the Saint Louis area (north) increased rapidly from January to April with a maximum number of mature females (stage V) and an abundance of larvae in May and June, then decreased rapidly, reaching a minimum around September-October. In Gambian waters, reproduction continued throughout the year with the main reproductive period from January to May [9]. The reproductive pattern of bonga shad as described in Senegal has not changed for more than 50 years: reproduction always starts in the first quarter of the year and ends at the end of the rainy season. The start can shift from two to three months depending on the year, and last for at least five-six months but no more than nine months.

The reproductive period of the bonga has been studied in various West African countries (Table 3). In general, spawning occurs earlier in waters further from the Equator, and occurs mainly during the first half of the year in Senegal [8, 12, 32], from July to December-January in Sierra Leone [33, 34] and from October-November to May in the Ivory Coast [35], Ghana [36] and Nigeria [37]. Previous studies have shown that salinity is not a major factor in the reproduction of the bonga [38] which is able to reproduce in waters with very variable salinity ranging from oligohaline [8] to hypersaline [12]. However, temperature seems to play a limiting role below 22°C [38].

Table 3: Reproductive periods of bonga shad in West Africa. Crosses (×) represent the main reproductive months found in this study. The reproductive period is shaded.

	Reproductive periods												
Area	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	References
Mbour (Senegal)	×		×		×	×							Present study
Joal (Senegal)			×	×	×								Present study
Petite côte (Senegal)													Blanc (1951)[6]
Senegal river area													Scheffers *et al.* (1972)[8]
Petite côte (Senegal)													Faye *et al.* (2014)[32]
Saloum (Senegal)													Faye *et al.* (2014)[32]
Saloum (Senegal)													Panfili *et al.* (2004)[12]
Sierra Leone river													Salzen (1958)[34]
Aby lagoon (Ivory Coast)													N'goran (1991)[50]
Ebrie lagoon (Ivory Coast)													Albaret and Gerlotto (1976)[35]
Ghanaian coast													Blay and Eyeson (1982)[36]
Lagos lagoon (Nigeria)													Fagade and Olanyan (1972)[37]

The present results on the size at first sexual maturity confirmed the observations made by Faye *et al.* [32] in Senegal coastal waters and those in the Saloum Delta [10]. The values were between those calculated in the Senegal river [8] and in Gambia [9, 12]. Slight differences in size at first sexual maturity could be explained by the difference in food richness between the biotopes and their environmental parameters [39]. The analysis of the values obtained in different areas (Table 4) indicated that the size at first sexual maturity of fish living at sea or in open estuaries (Senegal, Gambia, Sierra Leone, Ghana) is larger than that of fish living in confined or narrow lagoons [12, 40]. The difference in size may also be explained by geographical distribution, which can activate a phenotypic plasticity and changes in size at first maturity [41-43], and human activities such as overfishing (intensification of fishing effort). Fish subjected to fishing pressure may show changes in growth or reproduction (dwarfism or early sexual maturity) [44, 45]. Other factors, such as pollution and high salinity, can lead to a reduction in size at first sexual maturity in estuarine Clupeidae [12, 40, 46].

The minimum catch size (150 mm) authorized by the Senegalese fisheries code [52] is less than the size at first sexual maturity found by most of the authors (170-180 mm), including the present study (176-180 mm). As a precautionary measure, this minimum size at capture should be revised upwards, based on the updated sizes at first maturity found in this study.

Like most clupeids, bonga shad is an oviparous species, egg fertilization and embryo development take place in the ambient environment [47], with the "r" reproductive strategy observed for the Clupeids of Senegal [48]. The fecundity of bonga shad was estimated by several authors for various West African countries where the species is more abundant. The results obtained in the present study were similar to those reported in the Lagos lagoon [37]: the average number of ovocytes ranged from 23,800 for fish measuring 143 mm to 187,000 for a specimen of 250 mm. These authors found a wide variation in fecundity for large fish (FL > 210 mm), while it was less variable for smaller sizes (143-210 mm), as observed in this study. A high condition factor enables efficient transfer of energy to gonad development and a high GSI should result in more eggs produced by females [49]. This was particularly clear for bonga at Mbour where the Kc peak in June coincided with the maximum spawning, but was less visible for Joal. Slight differences in fecundity were reported by other authors [32, 50]. In Ghana the number of eggs ranged from 16,000 for a 174 mm bonga to 51,800 for a 250 mm bonga [36]. The relative fecundity was estimated in the present study at 400 ovocytes g^{-1}. This was higher than any previous values for the area [12, 32], or values for the Ebrié Lagoon reported by Albaret and Gerlotto [35]. There are various possible explanations for this discrepancy, such as studying ovocytes in the pre-spawning stage rather than in the reproductive stages. Furthermore, the individual fecundity increases in general depending on the weight and size of the female [36, 37, 50] and on the gonad weight [51], or the stage of maturity which is relatively subjective.

4.4 Growth

Seasonal translucent growth marks were formed annually on the otoliths, the translucent mark being deposited during the hot rainy season (August) and the opaque zone during the cold, dry season (January). There are very few studies focusing on measuring the age of fish using calcified structures in West Africa. The analysis of size structures (Petersen method) is more often used for growth estimation, but such results are subject to considerable bias, mainly depending on the sampling strategy which is affected by the selectivity of the fishing gear. The high variability of individual growth and the long reproductive period [12, 32, 34, 37] can lead to overlap between cohorts and make it difficult to analyze the size distributions. For the bonga shad, the only available data on age measurement using calcified structures was published more than 10 years ago by Panfili *et al.* [12] in the Saloum and Gambia estuaries (Table 4). According to these authors, the translucent zone is formed in the second half or at the end of the rainy season (October), with, possibly, in September with a time lag. These results agree with those of the present study, and shows that, at sea or in estuarine environments, the translucent mark in the otolith appears during the rainy season.

Bonga shad has already been the subject of many growth studies in West Africa, but, as stated above, many were carried out using size distribution. In the Senegal River, Scheffers [7] decomposed the size distribution and identified three modes at 135-160, 210-245 and 330-340 mm. According to this author, the first two modes corresponded to fish aged 0-12 months old and 12 to 24 months old, respectively, and the third corresponded to older fishes. Compared to our results, where the bonga shad reached an average of 160 mm the first year and 190 mm the second, the growth rates were reported as slightly faster in the Senegal River. The differences between the methodologies used to estimate age may also explain the discrepancy. For Senegal coastal waters, there is no data on the estimation of the asymptotic size using a growth function, but recent values (314 mm) found in the same area as this study by Faye *et al.* [53] using size distribution are close to those of this study (290-320 mm), as are those found in the Saloum Delta using direct age estimation from otoliths by Panfili *et al.* [12]. These two observations do not make it possible to draw any conclusions about possible changes in asymptotic size. However, the maximum size observed in coastal water catches has decreased from 340 to 300 mm (Scheffers and Conand, 1976; present study). Furthermore, the maximum sizes found by Panfili *et al.* [12] (<300 mm) and Faye *et al.* [53] (260 mm) in the Saloum Delta are much lower than those recorded by Postel [54] (385 mm). This decrease is probably related to the lack of large fish in recent samples, probably resulting from the heavy fishing pressure during recent decades, as reported by Boude [55].

It appeared that the growth observed for Mbour and Joal was representative of bonga shad growth in Senegalese coastal waters, varying significantly from fish to fish. Reading the age from otoliths gave a good estimate of age and growth. There were, however, no large fish in the current catches. This could suggest overfishing, although this has not yet been confirmed. This hypothesis can only be verified by global studies of bonga shad population dynamics, which is the only means of determining the current status of the species.

5. Conclusion

These results highlighted the need for better management of the fisheries. The decrease in captures over recent years, together with increased fishing pressure, gives cause for alarm. The conservation and management of resources in Senegalese aquatic systems require a sound knowledge of the resources themselves and up-to-date biological data. Management measures should take account of the size at first maturity to determine the fishing gear selectivity (suitable mesh size) as well as taking account of the reproductive season. The current legal minimum size at capture should be increased from 150 to 180 mm, the approximate size at maturity which would provide better conditions for this species to reproduce. Biological data such as the reproductive period, the size at first maturity, and the modeled growth have not changed over time, but there are increasingly fewer large size individuals in the captures. Fishing for the species should be prohibited during the main reproductive period (May-June) to encourage higher spawning levels and consequently better recruitment. Further research should be undertaken to improve estimates of juvenile growth using for example daily otolith increments. The size spectrum would need to be studied for several years, in relation to the size at first sexual maturity, to determine the most suitable mesh size for bonga shad fisheries.

Table 4: Age and sizes for bonga shad in various waters in West Africa. Leng. freq = length frequency, FL∞ = asymptotic fork length; Max. FL = maximal fork length observed; Max. age = maximal age calculated by differ authors; F = female; M = male; FL_{50} = size at first sexual maturity; F = female; M = male; Age. FL_{50} = mean age at first sexual maturity; NA = not available; Lag. restr = lagoon and sea contact is very low.

Area	Methods	FL∞ (mm)	Max. FL (mm)	Max. age (months)	Sex	FL_{50} (mm)	Age. FL_{50} (months)	Environment	References
Mbour (Senegal)	Otolith	289	300	84	F	176	18-20	Marine	Present study
					M	180			
Joal (Senegal)	Otolith	319	300	90	F	177		Marine	Present study
					M	177			
Senegal river	Leng. Freq	NA	340	NA	F	170	18	Estuarine	Scheffers *et al.* (1972) [8]
					M	160			
Petite Côte (Senegal)	Leng. Freq	314	290	96	F	187	NA	Marine	Faye *et al.* (2014) [32, 53]
					M	172			
Saloum (Senegal)	Leng. Freq	291	260	96	F	175	NA	Estuarine	Faye *et al.* (2014) [32, 53]
					M	162			
Saloum (Senegal)	Otolith	270-276	< 300	60	F	153	NA	Estuarine	Panfili *et al.* (2004) [12]
					M	173			
Gambia	Otolith	407	< 300	60	F	192	NA	Estuarine	Panfili *et al.* (2004) [12]
					M	202			
Gambia area	Leng. Freq	NA	340	NA	F	185	18	Estuarine	Scheffers and Conand (1976) [9]
Sierra Leone river	Leng. Freq	NA	290	36	F	170 to 205	12	Estuarine	Salzen (1958) [34]
Bietry bay (Ivory Coast)					F	84		Polluted bay	Albaret and Charles-Dominique (1982) [40]
					M	81			
Ebrie lagoon (Ivory Coast)	Leng. Freq	244.8	< 250	17	F	140	< 12	Lag. restr	Albaret and Gerlotto (1976) [35, 56]
					M	130			
Ghanaian coast	Leng. Freq		250		F	147		Marine	Blay and Eyeson (1982) [36]
					M	154			
Lagos lagoon (Nigeria)	Leng. Freq	312	255	40	F	140	12	Lag. restr	Ama-abasi *et al.* (2004) [37, 57]
					M	100			

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