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ORIGINAL ARTICLE



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Bonga shad (*Ethmalosa fimbriata*) spawning tactics in an upwelling environment

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Abstract

Successful recruitment in small pelagic fish populations inhabiting upwelling zones is subject to variation in fecundity and is driven by spatial and temporal fluctuations in environmental conditions, that is, mainly sea surface temperature, salinity and food availability. These fluctuations in abiotic factors have stimulated small pelagic fish populations to exhibit specifically adapted spawning tactics. To better understand to what extent a short-lived exploited fish species such as bonga shad *Ethmalosa fimbriata* has adapted to an upwelling environment, we have investigated the inter-relationship between upwelling intensity as a proxy for productivity and population fecundity by means of a virtual population analysis. We found that females of intermediate size contributed significantly more eggs to the population's fecundity than smaller or larger ones. Our model results further indicate that *E. fimbriata* exhibits a spawning preference at water temperatures of around 25°C and upwelling intensities of around $2.5 \text{ m}^3 \text{ s}^{-1} \text{ m}^{-1}$. Hence, we hypothesize that climate change-driven increases in sea temperatures and modifications of upwelling-favourable winds could significantly impact the species' reproductive biology. To understand how climate change might impact fisheries, spawning tactics of small pelagic fishes are important to assess as well as their recruitment success. Such information is particularly relevant in countries where the fishery is critical at socio-economic level, to better implement fisheries management addressing multiple stressors.

KEYWORDS

climate change, clupeid, data-poor fisheries, fecundity, optimal environmental window, reproductive adaptation, small pelagic fish

1 | INTRODUCTION

Successful reproduction in marine fishes requires a variety of energetic, ecological, physiological, anatomical and biochemical adaptations (Baldé et al., 2019; Rocha, Arukwe, & Kapoor, 2008). These parameters drive some species to develop reproductive strategies

that ensure the survival of their offspring (Peck, Reglero, Takahashi, & Catalán, 2013). A species-specific response to environmental factors, such as water temperature, salinity and food availability, determines the capacity of fish to react to environmental fluctuations.

The plasticity of small pelagic fish species in their growth, survival and other life history characteristics is key to their ability to

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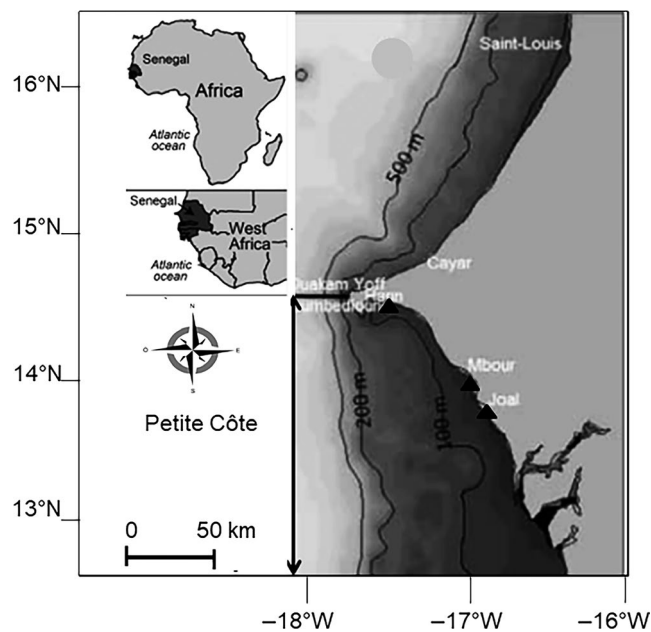


FIGURE 1 Map of the 'Petite Côte' of Senegal in West Africa, representing the important fishing grounds of *Ethmalosa fimbriata*. The main landing sites (where fish sampling took place) are marked by triangles. The Hann fish landing site is situated on the Cape Verde Peninsula. Arrows represent the study area

adapt to environmental changes and makes them a suitable index for gauging the impact of climate variability on marine ecosystems (Baldé et al., 2019; Brehmer et al., 2007). Maximum reproductive success is expected when spawning events match with optimal environmental window (OEW) conditions (Cury & Roy, 1989; Diankha et al., 2018). Certain temperatures favour the optimal development during early life stages, and/or the correct location ensures the feeding success of larval offspring (Cury & Fontana, 1988; Cushing, 1982). Fish fecundity (hereafter defined as the number of eggs a fish produces during each reproductive cycle) increases with size, condition, age and prey availability. Thus, in addition to environmental features, female body size and condition strongly influence the reproductive success in small pelagic fishes (Brosset et al., 2016; Peck et al., 2013).

While the reproductive strategy of a species encompasses the various phenotypic expressions of a reproductive trait (e.g. spawning behaviour, seasonality and frequency; size and age at first maturity, fecundity and egg size) over the full range of environmental settings, the term "reproductive tactic" describes the extent to which specific reproductive traits are expressed in a specific environmental situation (Green, 2008; Pavlov et al., 2009). The Eastern Boundary Upwelling System of the Canary Current Large Marine Ecosystem (CCLME) is located between 10°N and 35°N and is the most spatially and seasonally variable compared to the other three EBUS (California, Peru and Benguela) in terms of primary production (Auger, Gorgues, Machu, Aumont, & Brehmer, 2016; Carr & Kearns, 2003). Upwelling-induced nutrient supply is the main source primary production (Lathuilière, Echevin, & Lévy,

2008). Its variability plays an important role in the distribution and abundance of fish populations (Thiaw et al., 2017) and results in adaptive phenotypic responses in fish populations (Roy, Cury, Fontana, & Belvéze, 1989). These responses encompass specialized reproductive tactics to ensure the survival and recruitment of offspring (Peck et al., 2013).

In the waters of Senegal, which are located at the southern tip of the CCLME, small pelagic fishes are exploited intensively by artisanal fleets and dominate fishery landings by volume and value (Diankha et al., 2017). The bonga shad *Ethmalosa fimbriata* (Bowdich, 1825) is the third-most commercially important clupeid species for the fisheries along the southern coast of Senegal (after round sardinella *Sardinella aurita* and madeiran sardinella *S. maderensis* also known as flat sardinella) (Baldé et al., 2018), with catches reaching 18,400 tons in 2015 (Thiao, Sow, Thiam, Fall, & Thiam, 2016). *Ethmalosa fimbriata* inhabits hypersaline, marine, brackish and freshwater habitats Charles-Dominique, 1982 along the coasts of West Africa, from Mauritania to Angola (Charles-Dominique & Albaret, 2003). Reproduction occurs during the cold season (January to June) in the Senegalese shelf waters (Charles-Dominique, 1982; Döring & Ekau, 2018). During this timeframe, individuals of *E. fimbriata* neritic population exhibit little monthly variability in batch fecundity (Döring, Tiedemann, Stäbler, Sloterdijk, & Ekau, 2017) and in the progression of maturity stages (Döring, 2018).

Population fecundity represents the total number of eggs spawned by a population during the spawning season of a given year. The parameter is considered a fundamental indicator of a fish population's reproductive capacity and is therefore used to predict the population's future productivity (Serebryakov, 1990). The potential usefulness of this indicator is based on a conceptual model in which increased fecundity is assumed to increase the survival rate. In other words, the superabundance of eggs might increase the chances of first-feeding larvae often encountering limited spatio-temporal patches of adequate food resources (Rothschild, 2000; Winemiller & Rose, 1993). The concept should prove especially applicable to fish populations with low variability in the quality of the spawned eggs. In marine fishes, egg quality is positively correlated with hatching success and closely linked to maternal provisioning of oocytes with energy (i.e. proteins and lipids; Castro, Claramunt, Krautz, Llanos-Rivera, & Moreno, 2009) and essential fatty acids (Lane & Kohler, 2006). *Ethmalosa fimbriata*'s neritic population has previously been shown to express markedly low temporal variability in terms of oocyte energy content (Döring, Wagner, Tiedemann, Brehmer, & Ekau, 2019) and essential fatty acid composition (Döring & Ekau, 2018); hence, the species is predestined as a model organism for our study.

This study aimed to investigate factors which drive changes in population size (from VPA) of *E. fimbriata*, based on length measurements over one year and fixed fecundity for a given body length in the seasonal upwelling ecosystem of *Petite Côte* in southern Senegal (PCS). PCS extends from Dakar/Senegal to the border of The Gambia. We correlated the heterogeneous environmental conditions of the coastal waters of PCS from 2004 to 2012 with the estimated population fecundities of *E. fimbriata* based on fishery

landings from 2004 to 2012 and the fecundity characteristics of the species retrieved from our 2014 investigations. Specifically, we examined the following: (a) the effect of female size class on population fecundity; (b) temporal changes in population fecundity between 2004 and 2012; and (c) the effect of environmental conditions on population fecundity.

2 | MATERIALS AND METHODS

2.1 | Study area

The PCS (14° 36' N to 13° 36' N) (Figure 1) is geomorphologically and biologically highly diverse. It has barrier beaches, cliffs, bays, lagoons, estuaries and shores fringed with mangrove forests. Warm, salty, tropical waters circulate offshore from May to July under the influence of freshwater inflow during the monsoon season. Northerly and south-easterly winds (7 m/s) predominate during the dry season (November to May) along the PCS, while winds blow mainly from the west and southwest during the rainy season (June to October) at a reduced velocity (5 m/s) (Sakho et al., 2010). In most coastal regions with a narrow shelf, the core of the upwelling occurs at the shelf break; however, along the PCS, the upwelling core occurs on the shelf proper (Ndoye et al., 2017).

2.2 | Environmental data

Remotely sensed environmental data were analysed to test the effects of temperature and upwelling intensity on the reproductive tactics and productivity of *E. fimbriata*. Monthly environmental data [sea surface temperature (SST in °C), Chlorophyll-*a* (Chl-*a* in mg/m³) concentration and coastal upwelling index (CUI in m³ s⁻¹ m⁻¹)] were compiled for the area of the PCS over an eight-year period (Figure 1). SST and Chl-*a* data from January 2004 to December 2012 were obtained from the website of the U.S. National Aeronautics and Space Administration (NASA) (<http://oceancolor.gsfc.nasa.gov>, last visited: 12/11/2017). Mean monthly remote-sensed data were acquired at a 5-km resolution from the coastline to the 200-m isobath, where upwelling-induced SST anomalies are generally maximal (Thiaw et al., 2017). A CUI was deduced from wind speed data obtained from the website of the U.S. National Oceanic and Atmospheric Administration (NOAA) (<http://www.pfeg.noaa.gov>: Upwelling and Environmental Index Products, last visited: 20/11/2017). In order to calculate the CUI in the PCS, we have considered the Ekman hypothesis (Ekman, 1905) of the transport of surface water masses by wind in the north or north-east direction, coupled with the rotation of the earth. Thus, the CUI was estimated from the following equation (Diankha et al., 2018; Thiaw et al., 2017):

$$\text{CUI} = \frac{\tau}{\rho \omega f} \quad (1)$$

Where τ is the along-shore component of wind stress within 270 km of the coastline (positive southward), ρ is the seawater

density (1,025 kg/m³) and f is the Coriolis parameter ($=2 \Omega \sin(\theta)$), with Ω and θ equal to the Earth's angular velocity and latitude, respectively).

2.3 | Biological data

Landing data, by size class, were used to estimate abundance and recruitment of *E. fimbriata* by applying a virtual population analysis (VPA) (Jones, 1984; Lassen & Medley, 2001; Pope, 1972). Previously, this method was used to analyse population dynamics for several species from data-poor fisheries in Senegal (e.g. Diankha et al., 2018). Two data sets were combined to accomplish the VPA. The first data set was total landing of *E. fimbriata* by the Senegal artisanal fishery from 2004 to 2012. The study was limited to 2012 due to lack of biological data (length size spectra) for *E. fimbriata* after this year. The data set was extracted from the Centre de Recherches Océanographiques de Dakar-Thiaroye (CRODT) database, collected at three main landing ports along the PCS: Hann, Mbour and Joal (Figure 1). The number of trips per fishing gear was recorded on a daily basis, whereas fisheries landing data were collected randomly at about 5 days per week. After sorting the data by port, gear type and period (fortnightly intervals), total landings per port were estimated by multiplying the mean number of fish landed for the sampled trips by the total number of fishing trips (Diankha et al., 2018). The landings were summed by month for each landing port. A second data set, which was used only for VPA modelling, contained monthly size distributions of commercially landed *E. fimbriata* specimens by port over a 12-month period from July 2014 to June 2015. Weight (W) and total length (TL) were measured for 28,500 randomly sampled fish. To estimate abundance and recruitment using VPA modelling, the number of individuals per size class was first sorted into size frequency distributions (Figure 2). We then assumed that all monthly landings, by port, were distributed according to this average size frequency. We used a size-age key to convert size class data into seasonal age groups by applying the growth equation of von Bertalanffy (1938) using growth parameters we had obtained from size frequency data of *E. fimbriata* (from July 2014 to June 2015). Seasonal time steps [winter (January–March), spring (April–June), summer (July–September) and autumn (October–December)] were chosen to evaluate growth characteristics of *E. fimbriata*, by assuming a fast growth and short life cycle (Charles-Dominique, 1982).

Catch (numbers at age for each month) was estimated from:

$$C_{t,i} = \frac{F_{t,i}}{F_{t,i} + M} \times N_{t,i} \times (1 - e^{-(F_{t,i} + M)}) \quad (2)$$

The VPA was adjusted according to the approximation of Pope (1972). This approximation basically assumes that the entire catch was made instantly in the middle of the month. This approach simplifies the survival equation, allowing the numbers N to be calculated directly from the natural mortality data M and catches C .

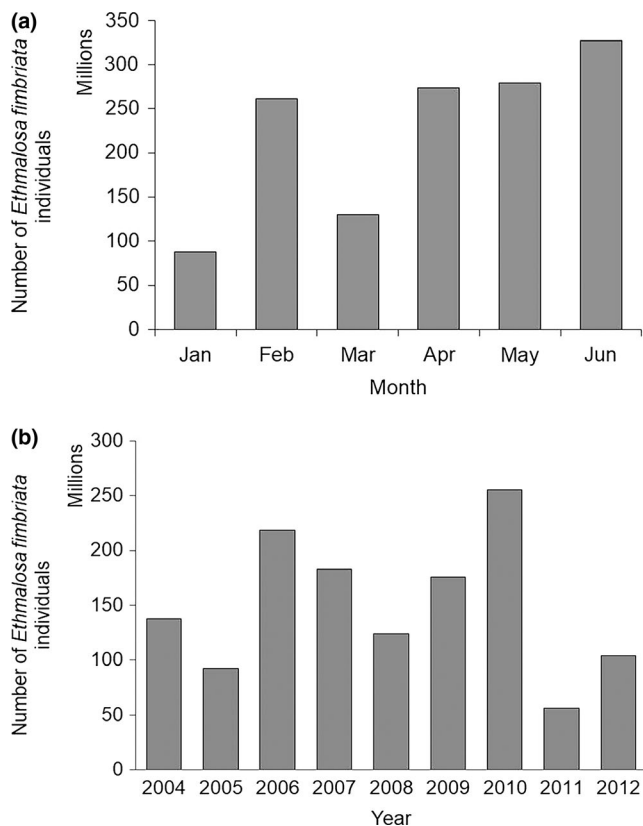


FIGURE 2 Variation in population size (number of individuals) of *Ethmalosa fimbriata* from the virtual population analysis models (2004–2012): (a) monthly and (b) annually

$$N_{t,i} = N_{t+1,i+1} \times e^{-M_{t,i}} + C_{t,i} \times e^{-\frac{M_{t,i}}{2}} \quad (3)$$

where “*i*” denotes the month, “*t*” denotes the age group, “*C*” denotes total catch (in numbers of individuals), “*F*” denotes fishing mortality, “*M*” denotes natural mortality [obtained from the McQuinn, Cleary, and O’Boyle (1990)] and “*N*” denotes the number of individuals.

2.4 | Population fecundity

For population fecundity studies in *E. fimbriata*, we were able to, first, comprehensively sample mature females from February to October 2014 to establish the biological reference points for absolute batch fecundity and sex ratio. Specimens were caught with gill nets (32–36 mm mesh size) by local fishermen in a 20-km radius from Joal. To assess the sex ratio and spawning fraction per length class of the species, the stages of maturity of 100 fish per month were determined by naked eye using a key developed by Blay and Eyeson (1982). To identify mature females with ovaries containing fully hydrated oocytes (stage V), further descriptions on maturity stages in clupeid fishes were taken into account (ter Hofstede, Dickey-Collas, Mantingh, & Wague, 2007; West, 1990).

A logistic function with an inflection point at 0.5 ($L_{50\%}$) was used to model the relationship between the per cent of mature females

($Ma \geq$ Stage III) and total length TL. The following equation was used, where *b* is a constant of the model:

$$Ma = \frac{1}{1 + e^{-b(TL_t - L_{50\%})}} \times 100 \quad (4)$$

Ethmalosa fimbriata is an indeterminate batch spawner (Albaret & Gerlotto, 1976); therefore, measuring the number of hydrated oocytes produced in a single spawning batch is the only practical method for determining fecundity (Hunter, Lo, & Leong, 1985). Absolute batch fecundity (ABF) was assessed gravimetrically using the hydrated-oocyte method for indeterminate spawners (Döring et al., 2017). To predict the ABF of a female of a given length, a sigmoid function was fitted through the obtained data on fecundity, where “*a*” is the growth rate, “*b*” is the inflection point, “*TL*” is the total length and *c* is the asymptote (Equation 5):

$$ABF = \frac{C}{(1 + e^{-a \times (TL - b)})} \quad (5)$$

For each length class, spawning frequency was deduced from the inverse of the female spawning fraction (percentage of females with hydrated oocytes) (Pavlov et al., 2009). The number of spawning batches per month was calculated by dividing the days of the spawning month by the number of days that *E. fimbriata* of a given length spawned that month. In accordance with findings on the closely related clupeid species *S. aurita* in the shelf waters of Senegal (Baldé et al., 2019), the obtained biological parameters were considered interannually invariable throughout the sampling period.

Population fecundity (PFy) is defined as the total number of eggs released by all females of the spawning stock during the entire spawning season (Pavlov et al., 2009). We assumed that *E. fimbriata*’s spawning season lasts from January to June in the Senegalese shelf waters (Charles-Dominique, 1982). Accordingly, monthly population fecundity (PFm) was estimated by combining the following terms: (a) length at first maturity; (b) number of females per length class (c) number of spawning batches per length class; and (d) length-dependent ABF.

Often, it is not possible to express PF in absolute units because the absolute abundance of individuals in the spawning stock cannot be determined precisely. To account for the fact that fecundity could only be assessed in females, and that the relative abundance of fish is expressed as a percentage, the following formula was applied (Equation 6):

$$PF = \frac{k \sum_{TL_{1\%}}^{TL_{\max}} pn}{100} \quad (6)$$

Where *k* is the number of spawned egg batches per length class, *n* is the fecundity of a female of a certain length class, *p* is the relative abundance (%) of females in this length class, $TL_{1\%}$ is the length (cm) at first sexual maturity and TL_{\max} is the maximum length (cm) of females in the population.

TABLE 1 Akaike information criterion (AIC) results for choosing the best model

| Model | df | AIC |
|--|----------|-----------|
| $g(X(y)) = s_1(\text{CUI}_i) + s_2(\text{SST}_i) + s_3(\text{Chl.a}_i) + s_4(\text{Length}_i)$, Population fecundity _i | 24.45440 | 17,446.86 |
| $g(X(y)) = s_1(\text{CUI}_i) + s_2(\text{SST}_i) + s_3(\text{Length}_i)$, Population fecundity _i | 35.31283 | 17,426.87 |

Abbreviations: df, degree of freedom. SST, Sea surface temperature (in °C); CUI, Coastal Upwelling Index (in $\text{m}^3 \text{s}^{-1} \text{m}^{-1}$); Chl.a, Chlorophyll-*a* concentration (in mg/m^3).

Based on results of Scheffers and Conand (1976), *E. fimbriata* was assumed to reach maturity at a minimum size of 15 cm TL. Thus, PF was only calculated for individuals in size classes ≥ 15 cm.

2.5 | Statistical analyses

Population fecundity was assessed at annual and interannual temporal scales to test whether environmental parameters or fish size influenced the probability of a given fish being a member of the spawning population. The general additive model (GAM) (Diankha et al., 2018; Hastie & Tibshirani, 1986) was used to investigate the potential range of each environmental variable and determine the contribution of the climatic variables on population fecundity. Note that this model does not require any prior assumptions about any potential functional link between variable and monthly population fecundity. The explanatory variables selected for the model were SST, Chl-a, CUI and length frequencies. Multi-collinearity of explanatory variables was tested using the variance inflation factor (VIF) on SST, CUI, Chl-a and length frequencies (Length) (Crane & Surles, 2002; Tiedemann & Brehmer, 2017). Our model selection strategy was to begin with the full model and then check how it can be simplified (Augustin, Trenkel, Wood, & Lorange, 2013; Guisan, Edwards, & Hastie, 2002). We used multiple step regression to test the influence of these independent variables on PFm. The best-fit simple regressions (linear and nonlinear) were adjusted to all PFm, all potential explanatory variables (length, environmental parameters) to allow for a simple assessment of significant relationships. The variance inflation factors (VIFs) were calculated for all environmental variables to detect possible high dimensional collinearities (Diankha et al., 2018; Tiedemann & Brehmer, 2017; Zuur, Ieno, & Elphick, 2010). A VIF < 2 for all tested explanatory variables was considered adequate (Zuur et al., 2010). Abundance and recruitment were estimated by season to focus on species biology and the seasonal influence on fecundity (Charles-Dominique, 1982). Thus, seasonality was the time unit used to evaluate the effect of environmental variables. The models were adjusted using a backward selection, starting with the full models and removing the explanatory variables with insignificant partial effects. The Akaike information criterion (AIC) was used to select the best-fit model (lowest AIC) (Zuur et al., 2010). AIC showed that the best model was one that did not include Chl-a (Table 1). The final GAM model applied was formulated as:

$$g(X(y)) = s_1(\text{CUI}_i) + s_2(\text{SST}_i) + s_3(\text{Length}_i)$$
, Population fecundity_i (7)

g is the link function which is a parametric function allowing for the extension of the Gaussian distribution to the exponential family. $X(y)$ is the expected value of the response variable; variable y follows a

specified law of the exponential family, that is to say, summarized by a single formula and having common properties (the best known being the normal distribution) (Zuur et al., 2010). The implementation of this model requires the estimation of the smooth nonlinear functions $s_i(\beta_i) = 1, \dots, p$, for each explanatory variable β_i . We also used the smooth function “s”, estimated from the data. This function is used to define smooth terms in the GAM model formulas. The function does not evaluate a smooth (spline), but exists only to help configure a model using spline-based smoothing (Wood & Wood, 2017).

The polynomial model allowed us to produce a curve to find the OEW (SST and CUI) of the population fecundity of *E. fimbriata* from 2004 to 2012. Annual and seasonal population fecundity of *E. fimbriata* was analysed using a one-way analysis of variance (ANOVA), followed by a post hoc Kruskal-Wallis test. All statistical analyses were performed using the “stats”, “pgirmess”, “fmsb” and “mgcv” packages (McDonald, 2009; Nakazawa & Nakazawa, 2017; Sokal & Rohlf, 1969; Wood & Wood, 2017) in RStudio 1.1.463 (Team, 2015), with a significance level of $\alpha < 0.05$. Mean values are reported with standard deviations (SDs) or standard errors (SEs).

3 | RESULTS

3.1 | Environmental parameters

Coastal SST was low from January to April (minimum in February; 20.4°C) and high from May to December (maximum in October; 29.2°C). The seasonal cycle of SST contrasted the CUI and Chl-a cycles (Figure 3a). For instance, Chl-a and CUI showed a downward trend, with a peak from January to April, followed by a decline during the remainder of the year (minimum in August) (Figure 3a). All investigated environmental parameters exhibited high interannual variability. Both SST and Chl-a varied interannually from 2004 to 2012 (Figure 3b). SST increased in 2005, 2008 and 2010. The minimum Chl-a for this period occurred in 2005, which corresponded to the maximum SST for the same period. The coastal upwelling index increased slightly from 2007 to 2009.

3.2 | Biological reference points

The allometric parameters calculated for the length-weight relationship of *E. fimbriata* were $a = 0.0011$ and $b = 3.3199$. The female sex ratio increased in parallel to fish size; fish with >28 cm TL were almost all mature females (Figure 4). However, females were slightly underrepresented in mean (\pm SD) sex ratios ($36 \pm 8\%$). The logistic functions provided $L_{50\%}$ estimates (\pm SE) of 21.5 ± 0.2 cm. Analysis

of ovaries containing hydrated oocytes showed monthly spawning fractions of 10% to 20% in the larger size classes (23–28 cm). The absolute batch fecundity of female *E. fimbriata* as function of size was, consequently, estimated with the following formula:

$$ABF = 19365 / \left(1 + e^{-0.9305 \times (TL - 24.10)} \right) \quad (8)$$

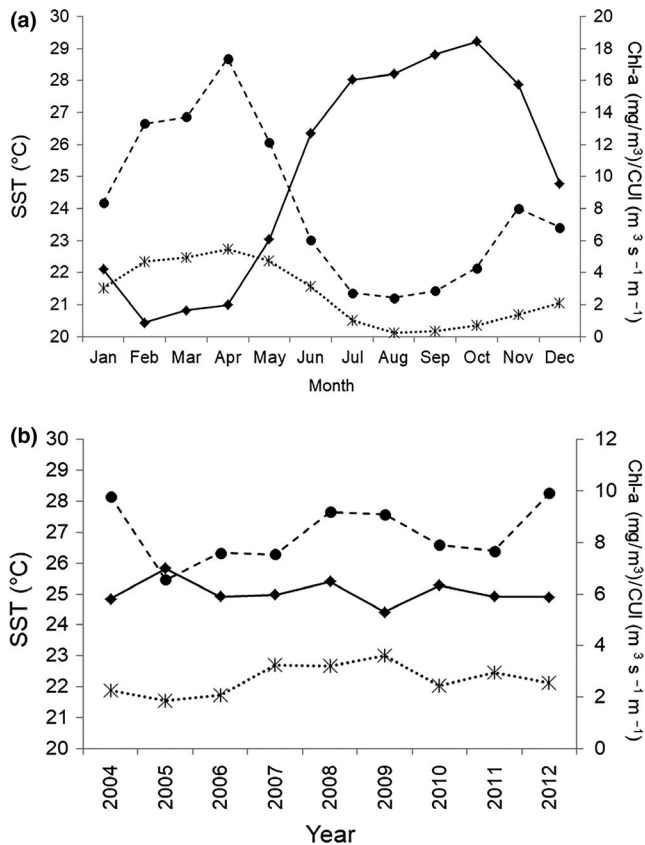


FIGURE 3 Normalized seasonal components of environmental change along the “Petite Cote” of Senegal from 2004 to 2012: (a) monthly and (b) annual data. Coastal sea surface temperature (SST in °C: solid line with diamond), Chlorophyll-a (Chl-a in mg/m^3 : dashed line with circles) and the Coastal Upwelling Index (CUI in $\text{m}^3 \text{s}^{-1} \text{m}^{-1}$: dotted line with asterisk)

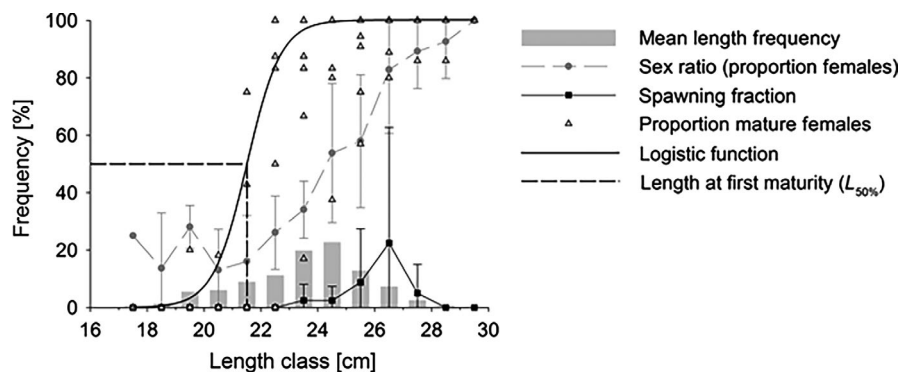


FIGURE 4 Frequency–length data for sampled *Ethmalosa fimbriata* landed at Joal (Senegal) from March to October 2014. Error bars depict ± 1 SD. The grey columns represent the mean length frequency; dashed lines with circles in grey represent the sex ratio (proportion females); the solid lines with a black square represent the spawning fraction; the triangles represent the proportion mature females; the full lines in black represent the logistic function; and dotted lines represent the length at first maturity

3.3 | Monthly and annual variability in population fecundity

Monthly analysis of the population fecundity (PFm) of *E. fimbriata* showed an increasing trend from January to June, with some variation (ANOVA; $F = 0.484$, $df = 1$, $p = 0.487$; Figure 5a).

Annual variation of PFy was high (ANOVA: $F = 7.858$, $df = 1$, $p = 0.005$), with peaks occurring in 2004, 2007, 2010 and 2012 (Figure 5b), indicating good fecundity years of the species for the PCS. PFy in 2004 was significantly higher than in 2005 and 2006 (Kruskal–Wallis test; $\chi^2 = 19.38$, $df = 8$, p -value = 0.013).

3.4 | Effect of fish length on population fecundity

The relationship between fish length and log total fecundity per size class in *E. fimbriata* (for the period 2004–2012) was best described by second-order polynomial functions (parabolic curve). A maximum total fecundity per size class was observed at body lengths of 25 and 26 cm. Length depending on total fecundity varied among years, as shown in the shift of the parabolic curves fitted to the data on a yearly basis (Table 2; Figure 6). The results of the GAM (total and partial deviances) are summarized in Table 2; the total explanation reaches 91% of the variation in *E. fimbriata* PFm during the study period. Length accounts for 47% of the total variability and is the most determinant factor while the environmental parameters represent 44%.

3.5 | Effects of environmental parameters on population fecundity

Population fecundity of *E. fimbriata* varied in response to local environmental conditions. The GAM results showed a significant correlation between SST and PFm (Table 2) and between CUI and PFm (Table 2). CUI represents 38% of the total variability and is the most important environmental factor.

During the study period (2004–2012), PFm reached a maximum at SSTs of around 25°C (Figure 7a) and at a CUI of around $2.5 \text{ m}^3 \text{ s}^{-1} \text{ m}^{-1}$ (Figure 7b).

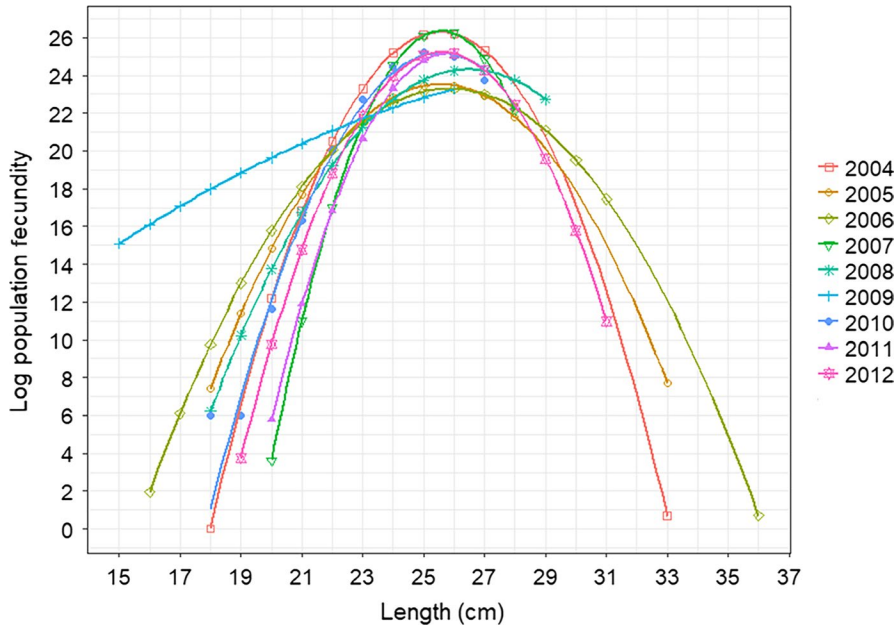


FIGURE 5 Predicted population fecundity of *Ethmalosa fimbriata* as a function of female length for the 2004–2012 study period [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

This study presents evidence of a close relationship between environmental parameters and population fecundity in *E. fimbriata* in the upwelling area of southern Senegal. A comparison was made with data from length–frequency distributions, batch fecundities and maturity stage estimates for *E. fimbriata* derived from land-based surveys. There were a number of uncertainties associated with this approach: for example, fish samples were provided by commercial fisheries (sometimes inaccurate transcription of weights and sizes of individuals); due to difficult circumstances during collection in the field (species catchability and availability of liquid nitrogen), only macroscopic maturity staging of gonads could be applied; and sample sizes were comparably small due to rarity of fully mature females. Considering the impossible task of eliminating all uncertainties, we regarded the deduction a maturity ogive and projections of population fecundity from landing site sampling data via VPA as feasible (Bromley, 2003). The presented and processed data are sufficiently reliable for the use in assessing population fecundity in generally data-poor fisheries. We were able to show that egg production in the examined population is highly dependent on upwelling strength and water temperature.

According to Hixon, Johnson, and Sogard (2014), fecundity generally increases with female age, simply as a function of body size. *E. fimbriata* females of intermediate sizes (24–28 cm) contributed significantly more eggs to the population's fecundity compared

to smaller (<23 cm) and larger (>29 cm) females. Nevertheless, increased investment could be manifested in a variety of ways (e.g. egg quality rather than quantity; Döring, Hauss, & Haslob, 2018). Younger females with reduced energy reserves might consequently change their allocation patterns and produce eggs of lower quality (i.e. hatching success) while maintaining a certain level of fecundity (Hixon et al., 2014). Egg size and quality follow a parabolic trend with the age or size of females, increasing as fish reach intermediate ages/sizes and then decreasing when females reach maximum sizes (Kamler, 2005). Still, egg quality in *E. fimbriata*'s Senegalese neritic population was shown to be independent of female size and spawning month (Döring & Ekau, 2018; Döring et al., 2019). We consequently assumed that hatching success remained constant in females of all sizes during the study period.

Abiotic factors (e.g. temperature, upwelling intensity, nutrient availability for planktonic food organisms) induce specific changes in the fecundity of a population (Checkley, Alheit, Oozeki, & Roy, 2009). Our results indicate that *E. fimbriata* preferred a certain water temperature range for spawning (around 25°C). Charles-Dominique and Albaret (2003) suggested that *E. fimbriata* avoids colder upwelling waters (16–17°C) and Döring et al. (2017) reported the spawning of individuals sampled at the PCS in waters with temperatures between 18 and 23°C. Albaret and Gerlotto (1976) reported a maximum spawning temperature of 30.2°C in the waters of the Ivory Coast. Thus, the species exhibits plasticity to adapt to the appropriate

| GAM variable | edf | Ref.df | F | Explained deviance (%) | Total explained deviance (%) | p-value |
|--------------|-------|--------|--------|------------------------|------------------------------|---------|
| S (Length) | 8.215 | 8.797 | 20.200 | 47 | 91 | <.001 |
| s (CUI) | 8.113 | 8.688 | 4.164 | 38 | | <.001 |
| s (SST) | 6.126 | 7.122 | 2.596 | 11 | | <.05 |

Note: edf, estimated degrees of freedom; Ref.df, estimated residual degrees of freedom; F, degrees of freedom matrix.

TABLE 2 Results of generalized additive models (GAM) adapted to the seasonality of the population Fecundity of *Ethmalosa fimbriata* with environmental parameters [SST (Sea surface temperature in °C), CUI (Coastal Upwelling Index in $m^3 s^{-1} m^{-1}$)] and fish length frequencies (in cm)

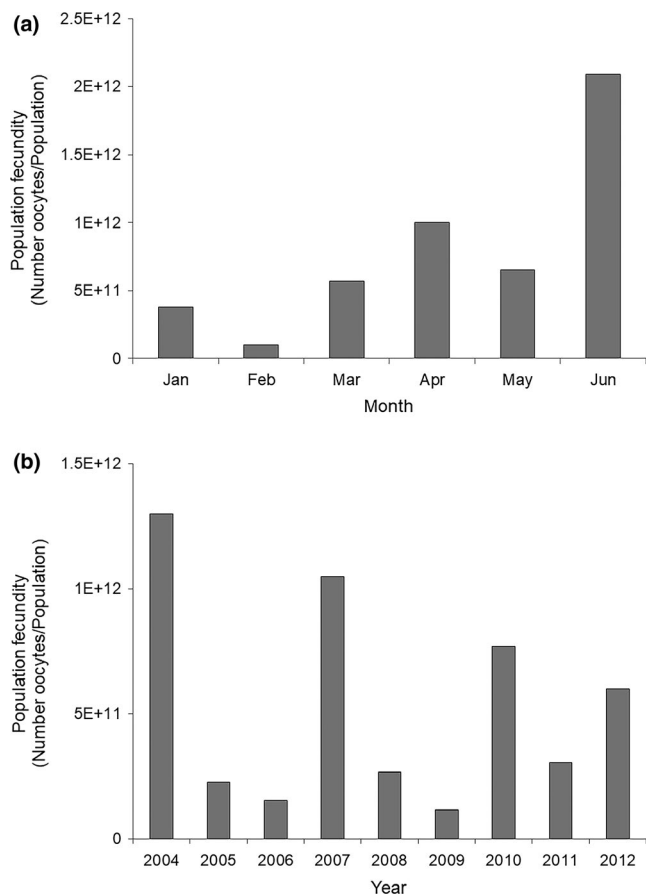


FIGURE 6 Variation in population fecundity of *Ethmalosa fimbriata* (2004–2012): (a) monthly and (b) annually

spawning temperature depending on the environment (eurytherm). Furthermore, water temperature is associated with a number of other factors (e.g. phytoplanktonic food availability) affecting reproduction.

Indeed, the fecundity of individual fish varies both temporally and spatially in relation to parental fitness (e.g. weight, condition), food availability (e.g. abundance and quality) and environmental (e.g. temperature and salinity) and evolutionary stressors (e.g. stock biomass and density, fishing pressure) (McBride et al., 2015). Our results showed that peaks in PFm correspond to periods of high intensities of CUI. According to Charles-Dominique and Albaret (2003), *E. fimbriata* encounters better environmental conditions during upwelling events (i.e. a substantial food supply). Indeed, the PCS is characterized by high phytoplankton biomass (Carr & Kearns, 2003; Lathuilière et al., 2008) and high chlorophyll content during upwelling events (Carr & Kearns, 2003), which are conditions optimal for providing a suitable nursery (Tiedemann & Brehmer, 2017). Tiedemann and Brehmer (2017) suggested that the retention of ichthyoplankton over the shelf was related to food availability and is important for the reproduction of many pelagic species during the planktonic stages. Thus, to cope with the dynamic conditions of upwelling systems, small pelagic populations have developed specialized spawning tactics (Cury & Roy, 1989; Roy et al., 1989), such as seasonal cycles or spawning under desirable environmental conditions (Baldé, 2019).

According to Hjort (1914), environmental factors determine recruitment success. Hence, adult fish use environmental cues to

synchronize spawning and hatching of eggs, with a peak in primary production. According to Fréon, Cury, Shannon, and Roy (2005), physical factors (e.g. oxygen, SST, CUI) directly influence the mortality of eggs and larvae. This phenomenon supports the concept for the evolutionary selection of an opportunistic reproductive tactic in a species, consisting of high fecundity associated with a prolonged spawning period over a large area (Fréon et al., 2005). This tactic allows for the continuous “testing” of favourable environmental conditions by these species. Indeed, Diankha et al. (2018) found a positive correlation between the recruitment of *S. aurita* and *S. maderensis* and variation in CUI in Senegal. This finding is consistent with the hypothesis of Lluch-Belda, Lluch-Cota, Hernandez-Vazquez, Salinas-Zavala, and Schwartzlose (1991), whereby continuous environmental changes (e.g. food availability and temperature) over a prolonged period of warming might allow a species to expand its spawning area and increase egg production, leading to an increase in stock size. According to Cushing (1975), the spawning tactic is the result of a compromise between several antagonistic environmental factors which may result in higher investment of energy in reproductions. According to Lasker (1975), the concentration of food regulates fish recruitment. Thus, timing and abundance of planktonic food regulate fish recruitment (Diankha et al., 2018). This obviously explains the observed dome-shaped relationship between the PF of *E. fimbriata* and CUI, and corresponds well with the hypothesis of Cury and Roy (1989). Indeed, Cury and Roy (1989) suggest that the relationship between recruitment and food availability is dome-shaped. For instance, if the upwelling is too strong, increased turbulence prevents the first feeding of the larvae, whereas a weak upwelling limits primary production and, thus, food availability.

The complexity of environmental conditions in an upwelling area aggravates modelling and forecasting population fecundity dynamics for species like *E. fimbriata*. With our approach, we could show how population fecundity is related to annual environmental variability. Due to the large interannual variability of environmental conditions, for example, currents, temperature, prey abundance of the PCS, the “right place and right time” for reproduction might vary across years. The plasticity allows *E. fimbriata* to exploit favourable environmental conditions successfully on occasion, which leads to some years with intense spawning when all environmental and biological parameters are optimal. Finally, this work underlines the difficulty for fisheries managers to deal with population variability, as it is associated with the nonlinear development of recruitment success. An interesting perspectives should consider inter- and intraspecific relationships, such as the importance of cannibalism on early life stages in the recruitment success of *E. fimbriata* and more widely small pelagic in West Africa.

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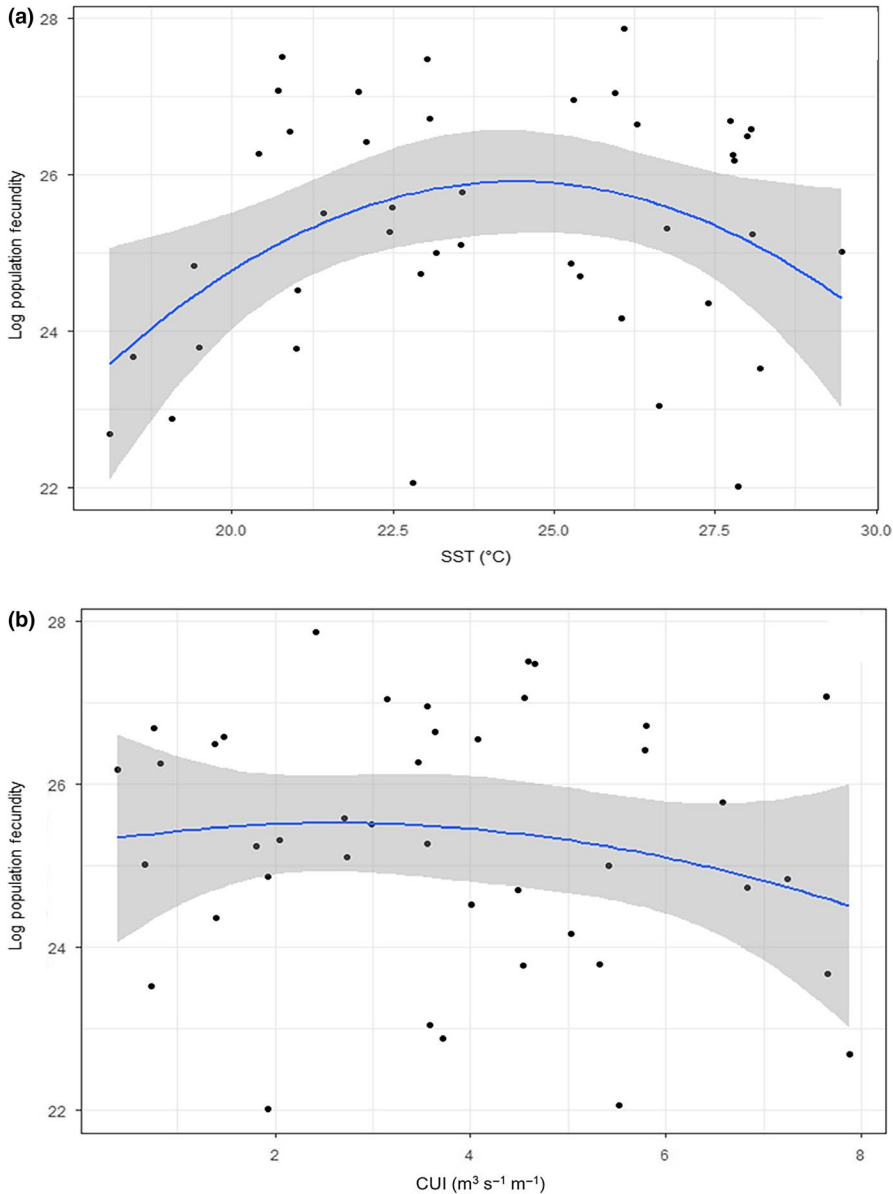


FIGURE 7 Population fecundity (PF) (Number of oocyte/Population) of *Ethmalosa fimbriata* throughout the study period (2004–2012) as a function of environmental conditions: (a) Sea surface temperature (SST in °C) and (b) Coastal Upwelling Index (CUI in $\text{m}^3 \text{s}^{-1} \text{m}^{-1}$). The solid lines (blue) represent the best-fit estimates; the grey shaded regions represent the confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

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CONFLICT OF INTEREST

The authors have declared that there was no conflict of interest.

AUTHOR CONTRIBUTIONS

Bocar Sabaly Baldé, Julian Döring and Werner Ekau conceptualized the study. Bocar Sabaly Baldé and Julian Döring designed the methodology; involved in data curation, formal analysis and project

administration; visualized the study; provided the resources and software for the study; and wrote the original draft. Werner Ekau and Patrice Brehmer involved in funding acquisition. Werner Ekau, Malick Diouf and Patrice Brehmer involved in supervision and validation. Bocar Sabaly Baldé, Julian Döring, Werner Ekau and Patrice Brehmer wrote, reviewed and edited the manuscript. The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript.

ETHICAL STATEMENT

No specific authorization was required for any of the activities undertaken during this work at any of the sites visited. The study was conducted in the waters of the Senegalese State. The activities carried out were in collaboration with the Local Fishing Committee (CLP in French) and the fishermen on site. Threatened or protected species have not been involved in any part of the field studies. Fish

samples were collected randomly from commercial catches of professional fishermen. No approval was required from the Institutional Animal Care and Use Committee, and no field licence was required during any part of the experiment.

DATA AVAILABILITY STATEMENT

Biological data on reproduction of *Ethmalosa fimbriata* as recorded in Senegal (Atlantic coast and Sine Saloum estuary) can be found on PANGAEA at <https://doi.org/10.1594/PANGAEA.880051>. Further biological, fisheries landing and environmental data that support the findings of this study are available on request from the corresponding author.

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