Progress in Oceanography 164 (2018) 12–27

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

# Complex small pelagic fish population patterns arising from individual behavioral responses to their environment

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ARTICLE INFO

*Keywords:*
Small pelagic fish
*Sardinella aurita*
Fish migration
Eastern boundary upwelling system
Individual based biophysical models
Dynamic energy budget

ABSTRACT

Small pelagic fish (SPF) species are heavily exploited in eastern boundary upwelling systems (EBUS) as their transformation products are increasingly used in the world's food chain. Management relies on regular monitoring, but there is a lack of robust theories for the emergence of the populations' traits and their evolution in highly variable environments. This work aims to address existing knowledge gaps by combining physical and biogeochemical modelling with an individual life-cycle based model applied to round sardinella (*Sardinella aurita*) off northwest Africa, a key species for regional food security. Our approach focused on the processes responsible for seasonal migrations, spatio-temporal size-structure, and interannual biomass fluctuations. Emergence of preferred habitat resulted from interactions between natal homing behavior and environmental variability that impacts early life stages. Exploration of the environment by the fishes was determined by swimming capabilities, mesoscale to regional habitat structure, and horizontal currents. Fish spatio-temporal abundance variability emerged from a complex combination of distinct life-history traits. An alongshore gradient in fish size distributions is reported and validated by *in situ* measurements. New insights into population structure are provided, within an area where the species is abundant year-round (Mauritania) and with latitudinal migrations of variable (300–1200 km) amplitude. Interannual biomass fluctuations were linked to modulations of fish recruitment over the Sahara Bank driven by variability in alongshore current intensity. The identified processes constitute an analytical framework that can be implemented in other EBUS and used to explore impacts of regional climate change on SPF.

## 1. Introduction

### 1.1. Small pelagic fish in upwelling systems

Small pelagic fish (SPF) dominate the marine species biomass in eastern boundary upwelling systems (EBUS) , and largely contribute to the energy transfer toward upper trophic levels (Cury et al., 2000). The population variables of these species, such as abundance, size distribution and spatial distribution, evolve rapidly in response to environmental and/or fishing pressure (*e.g.*, Bakun, 1996; Schwartzlose

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https://doi.org/10.1016/j.pocean.2018.03.011
Received 30 June 2017; Received in revised form 13 December 2017; Accepted 15 March 2018
Available online 16 March 2018
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et al., 1999). SPF populations in EBUS display a wide spatial distribution and are often exploited by several fisheries operating in the economic exclusive zones (EEZs) of the countries bordering these large marine ecosystems. Documented examples include shared SPF fisheries in the California Current System (CCS, shared between Canada, USA and Mexico; Lo et al., 2011; Javor et al., 2011) as well as in the Canary Upwelling System (CUS, shared between Morocco, Mauritania, Senegal, Gambia and Guinea Bissau; Boëly et al., 1982), and the Benguela Current System (BCS, shared between Angola, Namibia and South Africa; Cochrane et al., 2009).

Reaching agreements between countries exploiting the same renewable resources is a prerequisite for a good, equitable management in waters under national jurisdiction, *e.g.*, to avoid fish stock over-exploitation (Corten et al., 2012; Pitcher et al., 2002; Campbell and Hanich, 2015; Essington et al., 2015; Nguyen et al., 2018). International institutions in charge of building the fishing agreements need robust, accurate and coherent descriptions of SPF migration schemes, and more generally of the effect of environmental variability on abundance and distribution dynamics, which remains difficult to reach, even with state-of-the-art observational capabilities. Thus, a common theoretical framework for drivers of SPF migrations would be desirable in particular in the EBUS regions. Such a framework would be particularly useful in a global change context, which may disturb the existing ecosystem equilibria (Miller and Munro, 2004; Rykaczewski and Checkley, 2008).

The scope of the present study is to contribute to this research by developing a modelling approach to study the drivers of round sardinella (*Sardinella aurita*) population migration along northwest Africa. In particular, we aim to characterise the effect of environmental variability on population connectivity between EEZs and the fish abundance interannual variability.

### 1.2. The round sardinella in the Canary current

The Canary Upwelling System (CUS), one of the four major EBUS (Fréon et al., 2009), is situated along the northwest African coast. Because of the different seasonality of the upwelling favorable winds along the coast, important environmental contrasts exist between several sub-areas of the southern CUS (Arìstegui et al., 2009). Upwelling is permanent in its central part off Mauritania (~20°N), is of more variable intensity off Morocco (21–33°N) with a peak in summer, and is restricted to winter and spring off Senegal and Gambia (12°20′–16°N), sometimes extending as far south as Guinea Bissau (~11°N) (Benazzouz et al., 2014). The southern CUS circulation is relatively complex. Over the continental shelf, currents are southward when upwelling winds are present. Farther offshore, under the influence of the Mauritania Current, the surface flow is frequently northward, albeit with some seasonal (Stramma and Schott, 1999) as well as mesoscale/intraseasonal variability (*e.g.*, Alpers et al., 2013; Barth et al., 2005; Capet et al., 2017).

Industrial fishing foreign fleets and local, mainly Senegalese, artisanal fisheries exploit round sardinella in the northwest African EEZ, critical for the local economies and food security in west Africa (Boëly et al., 1982; Zeeberg et al., 2008; Failler, 2014). In the context of rapidly evolving fisheries in this area together with uncertain impacts of climate changes (Barton et al., 2013), there is an urgent need to better understand the link between environmental variability and sardinella population response to support fishery management at sub-regional scales (Corten et al., 2017).

Round sardinella is a SPF species that dominates the biomass in the southern part of the CUS ecosystem, undertaking large migrations over the continental shelf of the northwest African EBUS. The round sardinella seasonal migrations were first described by Boëly et al. (1982), based on data from the industrial fisheries operating between southern Morocco and Guinea Bissau from 1968 to 1972, suggesting a north-south seasonal oscillation of the area with maximum abundance of large round sardinellas from 11 to 25°N. Boëly et al. (1982) theorised that the majority of the population may follow this migratory scheme (Fig. 1), although they recognised that some fish may have a different migration behavior (*i.e.*, shift in timing and/or limited range of migration). Since then, some observations have been reported that challenge this scheme, *e.g.*, spatio-temporal patterns of catch rates within the Mauritanian EEZ, year-round stability of the body-length distribution, and high coastal densities in autumn in Mauritania (Braham et al., 2014; Corten et al., 2012, 2017). Thus, the question we address is: how variable is the actual migration of round sardinella among individuals, and what are the different migration schemes that may co-occur.

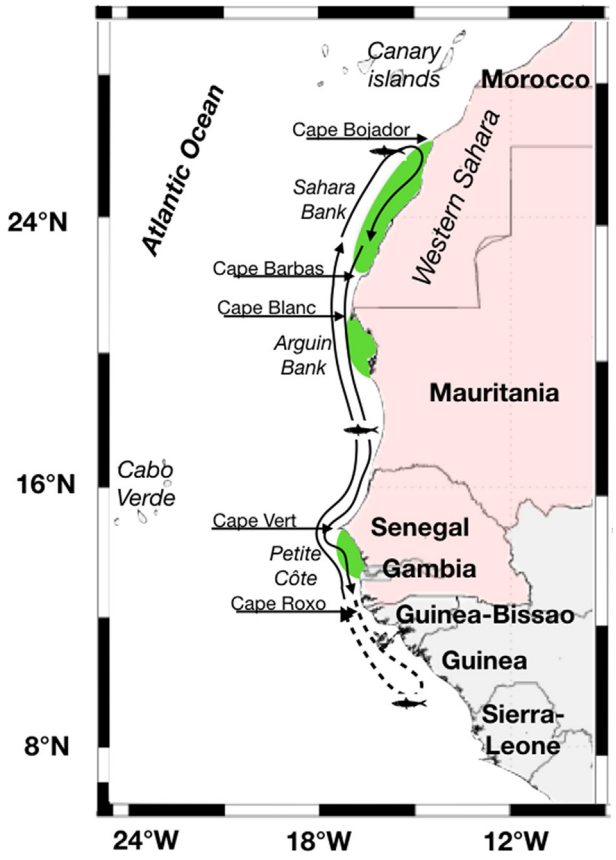


**Fig. 1.** Historical migration scheme for *S. aurita* in the sub-region (Corten et al., 2012; adapted from Boely and Chabanne, 1978). The green shading shows the main nursery areas (Sahara Bank, Arguin Bank, and Petite Côte). The arrows show the trajectory of the large individuals suggested by fishery data analysis. The southern part of the trajectory (dotted) is not well documented and there is uncertainty on the southern limit of the migration. The countries where round sardinella constitute a large part of the fisheries catch are colored in pink. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 1.3. Modelling strategy

Our approach consisted in coupling the full life-cycle of a single species, the round sardinella, with a quantitative representation of the environment in northwest Africa. The main working hypothesis was that the variability of environmental conditions (currents, temperature and associated primary/secondary production) drive the migrations of round sardinella off northwest Africa. We used a spatially explicit individual based biophysical model in which the round sardinella population variables emerge from individual growth, behavior and environmental forcing. This model, referred to as "Evol-Deb", was developed from Ichthyop (Lett et al., 2008) and Evol (Brochier et al., 2009), and links processes at different scales: physical and

biogeochemical regional dynamics, larval dispersion, fish dynamic energy budget (DEB) and swimming behavior. Environmental parameters were extracted from a coupled hydrodynamic/biogeochemical ROMS-PISCES model that produced a realistic 3-D mesoscale, seasonal and interannual variability simulation of the upwelling system (Auger et al., 2015, 2016; Mbaye et al., 2015). Details of the configuration studied here are given in Section 2 while a model description following the ODD protocol is offered in the Supplementary Material.

The model is evaluated at macroscales, *i.e.*, averaging over all super-individuals. We analyse the processes leading to the emergence of the round sardinella's seasonal abundance and its year-to-year variability. The environmental constraints were the ocean circulation that impact larval fish transport and adult fish movement, as well as variables that determine fish habitat quality (*e.g.*, temperature, phyto- and zooplankton biomass). We evaluate how these environmental constraints modulate abundance variability according to individuals' capacity of exploration (which increased with age/size) and the fishes' perception of their habitat's quality (based on temperature preference and food availability).

## 2. Methods

We developed a biophysical, individual based model for round sardinella off northwest Africa. The hydrodynamic environment was simulated by a regional model ("ROMS" Regional Oceanic Modelling System) configuration covering the area 10°–40°N and 5°–30°W, with an ~8 km resolution and 32 vertical sigma-levels in our area of interest (Auger et al., 2015, 2016). The biogeochemical compartments were simulated using the PISCES model (Pelagic Interactions Scheme for Carbon and Ecosystem Studies) coupled with ROMS. Based on the main nutrients (nitrate, phosphate, silicate and iron), PISCES simulates phyto- and zooplankton communities dispersed by ROMS currents. The model's functional types include pico-/nanophytoplankton and diatoms, ciliates and copepods, and small and large detritus pools collecting dead cells to be remineralized by bacteria (Aumont et al., 2015). These coupled models allowed simulation of the seasonal and interannual variability of the environment from 1980 to 2009 (Auger et al., 2015, 2016).

Virtual individuals represent groups of fish that were spawned at the same time and place and remain together during their life; hereafter, referred to as super individuals (SI). The SI can also be seen as "micro-cohorts", a level of granularity of the population sufficient to reproduce the main seasonal migration patterns (Le Fur and Simon, 2009). The SI were affected by *ad hoc* larval, juvenile, and adult fish swimming behavior, *i.e.* respectively diurnal vertical migrations and increasing horizontal swimming capacities. Individual physiology was described folowing round sardinella knowledge (e. g. Fontana, 1969; Chesheva, 2006; Gaamour et al., 2003, Pawson and Giama, 1985; see Supplementary Method) , using a Dynamic Energy Budget (DEB) model (Kooijman, 2010) dependent on local temperature and food availability. This type of approach is being increasingly used to study larval dispersion (*e.g.*, Werner et al., 2001; Brochier et al., 2011; García-García et al., 2016), fish migrations (*e.g.*, Le Fur and Simon, 2009; Okunishi et al., 2012; Politikos et al., 2015), and even for end-to-end modelling (Maury, 2010; Rose et al., 2015; Fiechter et al., 2015; Sánchez-Garrido et al., 2018). This model, named EvolDEB, allows us to address the issue of adult-mediated stock connectivity between areas corresponding to Senegal (12–16.5°N, *i.e.*, including Gambia), Mauritania (16.5–21°N), and southern Morocco (hereafter referred to as Sahara Bank; 21–27°N). Horizontal fish movement was determined by a kinesis algorithm (Watkins and Rose, 2013) dependent on a Habitat Quality Index (HQI). The HQI accounted for food availability and temperature preference. Larvae were assumed to perform diurnal vertical migrations (DVM) from the surface to 50 m as in Mbaye et al. (2015). Juvenile and adult fish in the vertical were assumed to follow a normal distribution centered at 30 m depth during the day and at 20 m during the night, according to the average behavior observed in Senegal (Brehmer et al., 2007; Brehmer 2004).

Natural mortality was size-dependent, with an exponential dependency to account for the reduced predation exerted on larger individuals (Okunishi et al., 2012). A fishing mortality of 1.4 per year was applied daily for SI representing fish larger than 12 cm, the minimal size in the fishery landings data in Senegal (Thiaw et al., 2017). When the number of fish represented by a SI dropped under 1000 the SI was removed from the simulation, which resulted in maximum longevity of the SI of ~4.5 years. Other sources of mortality – starving and exit from the domain – were applied directly at the SI scale. Starving occurs when the individuals' weight drops below 40% of the theoretical weight following the classical Von-Bertalanffy growth statistical model for round sardinella (Fréon, 1988; also see the methods applied in Rose et al., 2015). A comprehensive description of the model following the ODD protocol (Overview, Design concepts, Details; see Grimm et al., 2005, 2010) is provided in the Supplementary Material.

### 2.1. Available data

We followed a multi-scale validation method as recommended in the Pattern Oriented Modelling approach (Grimm et al., 2005). The main characteristics of the observed spatio-temporal dynamics of the round sardinella population were compared with those produced by the model, and the underlying processes responsible for these patterns were investigated. Specifically, we analyzed the seasonal and interannual variability of fish abundance in Senegal and Mauritania, and the spatio-temporal dynamics of fish length-spectra. The corresponding data, listed in Table 1, are described hereafter.

Seasonal variation in abundance was obtained through the CPUE (Catch Per Unit of Effort) index from local fisheries monitoring in Senegal (Thiaw et al., 2017) and Mauritania (Braham et al., 2014). In Senegal, the CPUE was based on Senegalese industrial fishery, authorized to operate beyond 6 and 7 nautical miles offshore respectively north and south of Dakar. In contrast, in Mauritania, the CPUE was based on international industrial fisheries authorized to operate only beyond 12 nautical miles offshore. A seasonal abundance index was not available for the northern limit of the population (southern Morocco).

Observations of round sardinella body-length distribution from southern Morocco to Senegal were collected from a variety of sources, including artisanal and industrial fisheries, scientific sampling (Boëly, 1980; Corten et al., 2012; Fréon, 1988; Braham et al., 2014; Thiaw et al., 2017), and *R/V Dr. Fridtjof Nansen* monitoring from 1996 to 2006, whose data were shared with marine research institutes in Morocco (INRH), Mauritania (IMROP) and Senegal (CRODT). The data suggest a robust spatial north-south pattern, with fish being larger in the northern part of the study area. Unresolved patterns from previous studies in Senegal and Mauritania include the stability of the body-length frequency distribution throughout the year in Mauritania, and during a six-month period in Senegal (Fréon, 1988).

Interannual time series of abundance are based on estimations of round sardinella mean biomass from acoustic observations conducted on-board the *R/V Nansen Dr Fridtjof* (Nansen Cruise reports I-III, 1995–2006, NORAD/FAO Project GCP/INT/730/NOR) and national research vessels (*R/V Itaf Deme* in Senegal, *R/V Al Awam* in Mauritania and *R/V Al Amir Moulay Abdallah* in Morocco), as well as on CPUE (Braham et al., 2014) between 1992 and 2009.

Spatio-temporal resolution of research vessel observations (about one cruise per year) and uncertainties associated with fisheries landings data led us to complement these sources with qualitative ecological knowledge from Senegalese fishermen having accumulated decades of intimate experience of fish population manifestations. Relevant information was collected through five individual interviews in Mbour and one focus group with seven fishermen in Kayar. All fishermen specialized in round sardinella fishery and are recognised experts in their community. Fishermen from the individual interviews performed

**Table 1**
Recapitulative table of the field data used for comparison with model emerging patterns.

| Type of data | Resolution | Period | References |
|---|---|---|---|
| Sardinella[a] Standardised CPUE in Mauritania from industrial pelagic vessels fishing sardinella | Mauritanian EEZ except from coast to 12 nm (nautic miles) offshore<br>Seasonal: monthly mean<br>Inter-annual: Yearly mean | 1991–2009 | Braham et al. (2014) |
| Round sardinella CPUE (kg per fishing day) from Senegalese industrial fisheries | Senegalese EEZ except from coast to 6 and 7 nm offshore resp. north and south of Dakar<br>Seasonal: monthly mean<br>Inter-annual: Yearly mean | 1966–2011 | Thiaw et al. (2017) |
| Round sardinella body-length distribution (fork-length in cm) observed during the annual stock assessment surveys | Data pooled by latitudinal range: 12–17°N, 17–21°N, 21–31°N<br>One cruise per year | 1992–2004 | Reports on surveys with the R/V Dr. Fridtjof Nansen Institute of Marine Research (IMR, Norway) http://brage.bibsys.no/xmlui/handle/11250/106981<br>Data were compiled from the UN Fish and Agriculture Organisation (FAO) database (present work) |
| Fishermen Knowledge of the behavioural response of round Sardinella to their environment | Senegal: Kayar, Mbour (landing site)<br>Regional: from Guinea to Southern Morocco<br>Cross-shore from coast until ~100 km off-shore<br>Individual fish school migration behavior<br>Year round observations | ~1950–2015 | Dedicated semi-directional interviews with recognised expert artisanal fishermen (n = 5) performed in 2014–2015 by the authors. |

CPUE: Catch Per Unit Effort. EEZ: Exclusive Economic Zone.
[a] No distinction was made between both sardinella species occurring in the ecosystem considered in our study but the average ratio during the period was 72% of *Sardinella aurita* and 28% of *S. maderensis*.

regional migrations during their fishing activities and had fishing experience covering the whole Senegal area. By contrast, fishermen from the focus group in Kayar were sedentary and modulated their fishing behavior according to the local changes in fish abundance. Such local ecological knowledge was used whenever possible to qualify the model behavior.

### 2.2. Forcing processes and parameters

The environmental forcing parameters were: (1) the temperature integrated over the surface mixed layer (which is in practice indistinguishable from SST), (2) the food proxy (defined as the sum of the biomass in the four PISCES plankton compartments, see Supplementary Material), and (3) the currents in the mixed layer, whose seasonal cycle had an effect on regional fish migration, with mesoscale variability that structures the habitat and modulates egg and larval retention rates over the continental shelf. The temperature and the food proxy were combined to define the Habitat Quality Index (HQI) of the environment experienced by each SI.

The individuals' model parameters were: (1) the swimming speed that impacts exploration capabilities through the movement algorithm (Kinesis); (2) the growth rate, computed by the Dynamic Energy Budget (DEB) model from temperature and food levels at each time step; (3) the half-saturation parameter of the food functional response; and (4) the preferred temperature.

In this paper, we analysed model sensitivities to the preferred temperature definition and to the fish swimming speed value. The preferred temperature was considered as an individual characteristic determined either by the natal environment (*i.e.*, the parental temperature preference; Burt et al., 2011) or as a species characteristic determined from observations of the average preferred temperature (21 °C; Fréon, 1988). Both hypotheses were tested. It is worth stressing that the natal homing rule implemented here is quite flexible. First, it considered a single environmental parameter, temperature, which displays wide seasonal range, in particular in the southern part of the domain (Fig. S14). Second, the HQI considered a normal distribution centered on the preferred temperature. The width of this distribution may be seen as the tolerance of the fish around its natal temperature, and was set as an increasing function of fish size, *i.e.*, larger fish may seek food in a wider range of temperature (Supplementary Material, Fig. S15).

The swimming speed was expressed in body-lengths per second ($BL\,s^{-1}$), assuming a linear relationship between body length and swimming capacity. The actual individuals' swimming speed was determined at each time step (1 h), as described by the kinesis algorithm according to changes perceived in habitat quality. It ranges between zero (passive) and a maximum instantaneous value. The frequency distribution of the swimming speed depends on the dynamics of the habitats (*e.g.*, more frequent high swimming velocity in a rapidly changing habitat), but on average, in the model, at a given time step only 50% of the individuals swim faster than half the maximum instantaneous swimming speed. Two different maximum instantaneous swimming speed values were tested for, 3 and $6\,BL\,s^{-1}$. Although no swimming speed observations were reported from laboratory experiments for round sardinella, there are values for a similar species (*Sardinops sagax*) (Beamish, 1984). These found that the maximum sustained swimming speed for a 10 cm fish is $0.32\,m\,s^{-1}$ with endurance time of one hour ($\sim 3\,BL\,s^{-1}$). Another field study for round sardinella in Angola report average migration velocity of $4.15\,BL\,s^{-1}$ with individual average school speed ranging from 1 to $8\,BL\,s^{-1}$ (Misund et al., 2005).

### 2.3. Simulations

Each simulation lasted for 30 years, from 1980 to 2009, with the initial seeding procedure taking place in 1980. The 1980–1989 period was considered as a spin-up period, with the analyses performed over the 1990–2009 period.

#### 2.3.1. Initialisation

During the first year, the initial seeding procedure involved the release of 3650 super-individuals (egg stage), uniformly distributed in time (10 per day) and randomly distributed over the continental shelves (0–200 m isobath) from 12°N to 30°N. We verified that this procedure ensured the stability of the results despite the stochastic swimming algorithm; each simulation was repeated three times with insignificant differences between them. All simulations included at least a 10-year spin-up period (1980–1989) to let patterns emerge and an 19-year analysis period (1990–2008) for which we have ample data in Senegal (Thiaw et al., 2017), Mauritania (Braham et al., 2014), and Morocco

(FAO, 2015). Furthermore, the sensitivity tests selected (see below) were repeated with three different forcing sets for the spin-up period: (1) 7 years of climatological forcings, (2) 7 years of a random list of hydrodynamic years between 1980 and 2009, (3) directly with the 1980–2009 forcing, with the initial seeding in 1980.

#### 2.3.2. Sensitivity tests

A large number of preliminary runs were performed, in particular to test different movement algorithms and target habitat definition. In the end, some of the tests revealed good or deteriorating correspondence with the observations. Two main parameters that impacted the level of model/data agreement were selected to perform a set of sensitivity runs. These parameters were the fish swimming speed ("slow" or "fast", which impacts the movement algorithm efficiency; see Section 1.7.2 in supplementary information for a broader presentation of sensitivities to the swimming algorithm), and six different combinations of food and/or temperature cues for the HQI. Preferred temperature was alternatively set to (1) the natal temperature (Burt et al., 2011), (2) an optimal temperature taken from the literature (21 °C, Fréon, 1988), or (3) not taken into account so that HQI only varied with food availability. The last case considered was a constant HQI = 1 over the continental shelf and HQI = 0.8 in deeper area, with a continuous gradient following bathymetry. For each HQI definition, we also performed a test in which the advection of post-larval individuals by the flow was removed (*i.e.*, movement was entirely due to swimming behavior), to assess the role of the currents in the population distribution. Overall, 18 simulations are presented in Table 2 (also see Appendix 1 for a representative figures), and are used to identify the processes implicated in the model sardinella population dynamics (Section 3.3). From the sensitivity tests, the simulation that globally best fit the available observations was identified, and was used to build an interpretation of the model's insight to stock connectivity and inter-annual variability in Section 3. A 19$^{th}$ simulation was carried out using only climatological forcings obtained by averaging the 1980–2009 ROMS-PISCES model outputs. This simulation was used to produce several initial conditions for the interannual runs. Because this climatological solution has very low intrinsic interannual variability, it allowed us to demonstrate the forced nature of the interannual signals in our primary set of simulations.

#### 2.3.3. Computation of observables

The fish biomass available for fisheries along the coast, and its length distribution, was computed as the sum of the SI's biomass located over the continental shelf (bathymetry < 200 m) at a given time. The model record outputs every 5 days, as a snapshot of all recruited SI's geographical position (longitude, latitude), DEB state variables (E, R, V) and "worth" (*i.e.*, number of individuals represented, following Rose et al., 2015's terminology). Body weight and length were computed from DEB state variables. Biomass of SI was defined as their worth times their body weight. It was considered that (lower) offshore biomass was not targeted by the fisheries because of its higher dispersion. For interannual time series, the annual biomass was calculated as the mean of the biomass at each record. Model analyses focused on the variability of the predicted biomass, rather than its absolute value, which linearly depends on the population closure parameter of the model, *i.e.*, the maximum number of new recruited SIs per day (limited computation time required a cap on the total number of simulated SIs).

**Table 2**
Set of simulations for the sensitivity analysis, combining 6 definitions for the target habitat quality index (HQI) (in columns), 2 different swimming velocities and one experiment in which the current advection was removed for the post-larval stages (in rows). Vmax = maximum swimming speed, in body-lengths per second (BL/s); No Advection = ignoring the effect of current advection on fish movement for post-larval stage; G = growth cue used in the Habitat Quality Index (HQI, Watkins and Rose, 2013), including a Gaussian distribution maximum at the natal temperature (Tnat), at 21 °C (Topp) alone or combined with the food functional response (f).

| | Vmax = 3 $BLs^{-1}$ | Vmax = 6 $BLs^{-1}$ | NO ADVECTION Vmax = 3 $BLs^{-1}$ |
|---|---|---|---|
| G = Tnat × f | Sim #1 | Sim #2 | Sim #3 |
| G = Topp × f | Sim #4 | Sim #5 | Sim #6 |
| G = f | Sim #7 | Sim #8 | Sim #9 |
| G = Tnat | Sim #10 | Sim #11 | Sim #12 |
| G = Topp | Sim #13 | Sim #14 | Sim #15 |

## 3. Results

Although with some differences, in most simulations the modeled sardinella population shared important qualitative similarities with the real one in the southern CUS waters. Most importantly, the model behavior self-organised around a few robust spatio-temporal spawning, growth and migration patterns that consistently emerged over the course of the simulation's spin-up.

The 'best fit' simulation was subjectively selected based on overall simulation performance at reproducing the available round sardinella observations of seasonal variability in local abundance and cross-shore distribution, as well as interannual variability of abundance. This directly or indirectly allowed us to test the realism of the emerging patterns.

The selected baseline simulation (sim #2) corresponds to model choices such that the habitat quality relied on a combination of natal temperature, food availability, avoidance of offshore predation, and with a hypothesis of "fast" swimming capacity (see Section 2). In the following sections, we successively present the patterns emerging from the baseline simulation that can be directly evaluated using observations (Section 3.1) and the patterns for which no observations are available to assess model realism (Section 3.2). Although the latter should be considered with caution they provide insightful information on the *modelled* relationships between sardinella and its environment. One additional step in this direction is made in Section 3.3 where the processes implicated in the emerging population patterns are identified through sensitivity tests and specific model diagnostics.

### 3.1. Evaluation of emerging fish population patterns against observations

#### 3.1.1. Seasonal abundance, spawning patterns, cross-shore distribution and their relation to migration

In Senegal, CPUE showed marked seasonality, with a coefficient of variation (hereafter, "CV", the ratio of the standard deviation to the mean) of 0.6, primarily peaking from March to June, with a secondary peak in November–December. The simulation also displayed marked seasonality (but lower than the data, CV = 0.4), and the cycle was correlated with the field observations (Pearson's linear correlation coefficient R = 0.3, p < 0.05; Fig. 2c). In Mauritania, maximum CPUE was detected from July to October, with smoother seasonality than in Senegal (CV = 0.3). The simulated biomass was consistently higher in Mauritania compared to Senegal in the simulation, supporting observations (cf. *Nansen* reports http://brage.bibsys.no/xmlui/handle/11250/106981). The simulation also displayed weak seasonality (CV = 0.25), but was not correlated with the data (R = 0.1; p = 0.5; Fig. 2b). The spatio-temporal spawning pattern predicted by the simulation closely followed the distribution of abundance, indicating that DEB constraints on spawning were generally not active.

The seasonal migration pattern predicted by the model also compared well with the ecological knowledge of Senegalese fishermen. Fishermen link the atmospheric conditions with fish seasonal abundance and distribution in Senegal, and use different types of wooden boats (pirogues) to target round sardinella according to its cross-shore distribution. They call "*Noor*" the dry and cold, season when the upwelling winds are strong, typically from January to April or May.

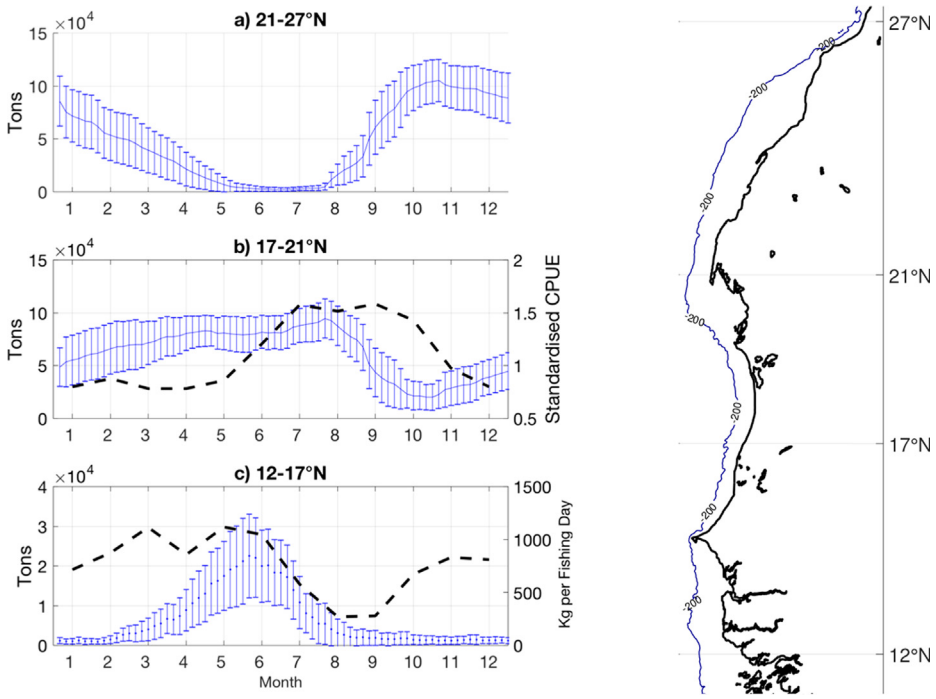


**Fig. 2.** Seasonal variability of round sardinella adult biomass from the model (Simulation #2, solid blue lines) and from fishery data (dashed lines). (a) Southern Morocco (no data available); (b) Mauritania (data: standardised Catch per unit effort (CPUE, IMROP, Braham et al., 2014); (c) Senegal and Gambia (data: CPUE (kg per fishing day), CRODT, Thiaw et al., 2017). The bars about the solid line indicated the range of variability of the model simulations. Note that the fishing efforts in Senegal and Mauritania refer to different types of fisheries (industrial and artisanal) so that the absolute values cannot be compared. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

During this period, the fishermen in the south of Senegal ("*Petite Côte*", 14°50′–13°40′) use large and heavy pirogues, allowing fishing trips up to 100 km offshore to find large abundances of round sardinella. When the upwelling winds' intensity drops, there is a ~2-month period before the first rains fall. This transition season is called "*Cooroon*," and is known to be the best fishing season for this species, because of calm seas and because the fish shift shoreward. The subsequent rainy season, called the "*Nawet*," occurs from July to October. During this season, fishermen use smaller and lighter boats to target small abundance of nearshore fish schools.

The start of the upwelling season is called the "*Lolli*", and is characterized by the end of the rains and the return of weak upwelling winds. Fishermen still catch round sardinella close to shore, but in higher abundance than during the rainy season, which leads to the second CPUE peak of the year. The cross-shore distribution of round sardinella predicted by the model off Senegal is particularly consistent with the fishermen perception and practice. Indeed, the model predicted that most of the fish biomass (80%) distribution fluctuates seasonally in an area between the shore and ~30 km offshore during upwelling relaxation (months 7–12) and from the shore to ~70 km when the upwelling is at its maximum intensity (Fig. 9a-d). The seasonal variability of industrial fishing operation distance to coast in Mauritania is also in line with this pattern (Fig. 6a in Zeeberg et al., 2008).

### 3.1.2. Fish size distribution patterns

The size spectrum reproduced for simulation #2 was computed for each season in the three sub-areas (Fig. 5). Hereafter, fish length-classes are referred as juveniles (fork length [FL] < 18 cm), young (FL 18–25 cm), and adults (FL > 25 cm). In Senegal, the simulated spectra are in line with field observations which show that all size classes tend to be found from January to June while younger individuals are mainly found during from July to December (Fréon, 1988). In Mauritania, the simulated spectra are also in line with industrial fisheries data from (Braham et al., 2014; Corten et al., 2012), and artisanal fisheries landings (Corten et al., 2017), which showed the continuous presence of all size classes, with adults being dominant year-round. Note that the model predicted a dominant mode of juvenile in autumn, which may be inaccessible to fisheries. Finally, the simulated spectra in autumn display a shift from smaller individuals being dominant in the south to biggest individuals in the north, a pattern that was also found in the compilation of the Nansen observations (11 cruises from 1992 to 2004, in November).

### 3.1.3. Interannual variability in Senegal and Mauritania

The model produced interannual variability of the biomass that, we demonstrate, resulted from interannual variability of the physical and biogeochemical environment. Indeed, the interannual CVs obtained with simulation #2 for Senegal and Mauritania were respectively 0.33 and 0.94. These are much higher values than the ones obtained with climatological forcing (CVs of 0.08 and 0.15) when the only source of interannual variability arises from the stochastic component of the movement algorithm and initial conditions and recruitment stochasticity (see supplementary method Section 1.4.7). The fact that environmental fluctuations strongly drive the interannual variability is also illustrated by the small standard deviation between simulation repetitions with different initial conditions (Fig. 3).

Comparing the CVs between model and data show that the simulated biomass time series displayed similar CVs in Mauritania (data CV = 0.34, model CV = 0.33), but higher CVs than in Senegal (data CV = 0.65, model CV = 0.94). The correlation coefficients between model and data are positive, but not significant (R = 0.45; P = 0.05 in Mauritania and R = 0.16; P = 0.5 for Senegal).

The model biomass peaks in southern Morocco in 1996, in Mauritania in 1997, and in Senegal in 1998. By contrast, the fishery based data (CPUE) with which we compare model outputs in Fig. 3 display a maximum in 1996–1997, and in 1993 in Senegal. However, when comparing with other data published by Zeeberg et al. (2008), the maximum CPUE of the EU fishery occurred in 1997–1998 (over the 1996–2005 period). Overall, the 1996–1998 period shows high biomass both in the model and in the data.

## 3.2. Other emerging population patterns

In the previous section we show good correspondence between several key aspects of the model behavior and available data for round sardinella. To complement this, additional model features which cannot be compared to observations are now presented.

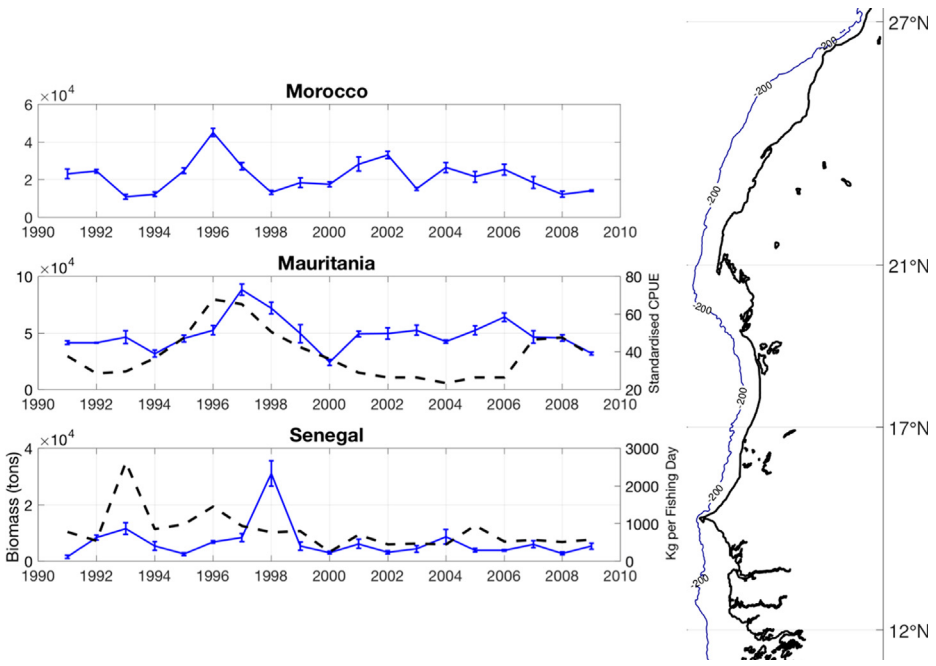


**Fig. 3.** Interannual fluctuations of round sardinella biomass emerging from the model (solid blue line) and comparison with field data (black dashed line). The model biomass series is computed as the yearly average biomass of fish > 12 cm located over the continental shelf of each country. The model time series presented is obtained from the mean of three repeated Simulation #2 runs with different initial conditions (see Table 1); the error bars correspond to the standard deviation between these three simulations. Model outputs are compared with (b) CPUE calculated by Braham et al. (2014) in Mauritania (IMROP), and (c) CPUE in Senegal (CRODT). No CPUE data were available for the Morocco area. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 3.2.1. Interannual and seasonal abundance in Morocco

Over the Sahara Bank, the simulation predicted a maximum of abundance in 1996 and 2002 (Fig. 3a). The large presence of round sardinella in the northern part of the domain emerges only with the natal temperature homing hypothesis and with a "fast" swimming behavior (Simulations #2 and #11, Table 2). A threshold for the swimming speed parameter was localised at four body-lengths per second, the minimal value for having a large seasonal presence of round sardinella in this area. Simulation #2 produced a marked seasonal cycle (CV = 0.56), with high biomass from August to December, and much lower biomass in June (Fig. 2a). The interannual variability of the seasonal cycle was also high (mean monthly CV = 0.66; *i.e.*, the mean of the CV computed for each month from 1990 to 2009).

### 3.2.2. Variability of the fishes' origin in each area

In the model, most of the population reproduces in Mauritania, with the fish hatching in this region representing, on average, about two-thirds of fish biomass in southern Morocco and in Senegal (Fig. 4). This result is in agreement with the fact that the population is genetically homogeneous in northwest Africa (Chiki et al., 1997). However, the relative contributions of each nursery area display interannual variability, especially for the Mauritanian and Sahara Bank areas. In the model, the interannual variability of the success of the Sahara Bank nursery area drives most of the interannual variability in total biomass (Fig. S16).

Tracking individual trajectories allowed us to assess adult-mediated connectivity between the different fishing grounds of the northwestern African countries. Depending on the year, about 10–30% of adult virtual fish performed the migration scheme described by Boëly et al. (1982), *i.e.*, from the south of the Cap-Vert peninsula (14°N) to the north of Cap Blanc (21°N). No fish remained in one EEZ throughout their life, but 15–50% remained north of 17°N year-round (depending on the year). Conversely, in the model almost no individuals (< 2%) remained south of 17°N year-round. The individuals performing the largest migrations (up to ~1200 km) were centered between 18°N and 21°N. However most of the individuals displayed smaller migration amplitudes ranging from 600 to 800 km, with mean distributions ranging between 17°N and 22°N (Fig. 1).

## 3.3. Underlying processes

The previously described patterns emerged from the interplay between environmental variability and fish responses to the environment. The underlying processes cannot be fully disentangled because feedbacks exist between them, in particular those generated by natal homing. In the following sections we strive nonetheless to isolate the effect of environmental variability, fish responses and their interactions, on the resulting fish biomass distribution and interannual variability.

### 3.3.1. Environmental variability and natal homing: a continuous adaptation of the preferred thermal habitat

In EvolDEB, the success of reproduction depended on a combination of spawning intensity, retention rate and food availability, resulting in three main areas/periods of recruitment: the Sahara Bank from August to October, the Arguin Bank almost continuously with a minimum in November, and southern Senegal (< 14°N) from March to July (Fig. 6a). With the temperature natal homing assumption, this led to the distribution of preferred temperature shown in Fig. 7b and corresponded to an average natal temperature ranging from 17 °C (Sahara Bank) to 26 °C (southern Senegal) (Fig. 6b). This preferred temperature range has major consequences on the distribution of biomass and its temporal variability. This is evidenced in the sensitivity analyses by comparing natal homing simulations #1, 2, 3, 10, 11, 12 with the constant preferred temperature simulations #4, 5, 6, 13, 14, 15. It resulted from an interplay between environmental variability of sea temperature and food availability which also influenced HQI.

In all test simulations, the bulk of the population (> 60% of the biomass) was recruited off Mauritania. This pattern was robust among the sensitivity tests performed on both swimming capabilities and temperature range preferences. Indeed, permanent upwelling off Mauritania ensured elevated and stable food availability. Temperature was not especially stable but the range of seasonal variability (~19–23 °C) was within acceptable limits so that HQI remained good year-round (Fig. S8).

In Senegal, during the upwelling relaxation (summer and early fall) the HQI was limited offshore by food availability. The HQI was also strongly influenced by high temperatures (up to 28–30 °C) which led to poor HQI, hence a need for migration away from the area.

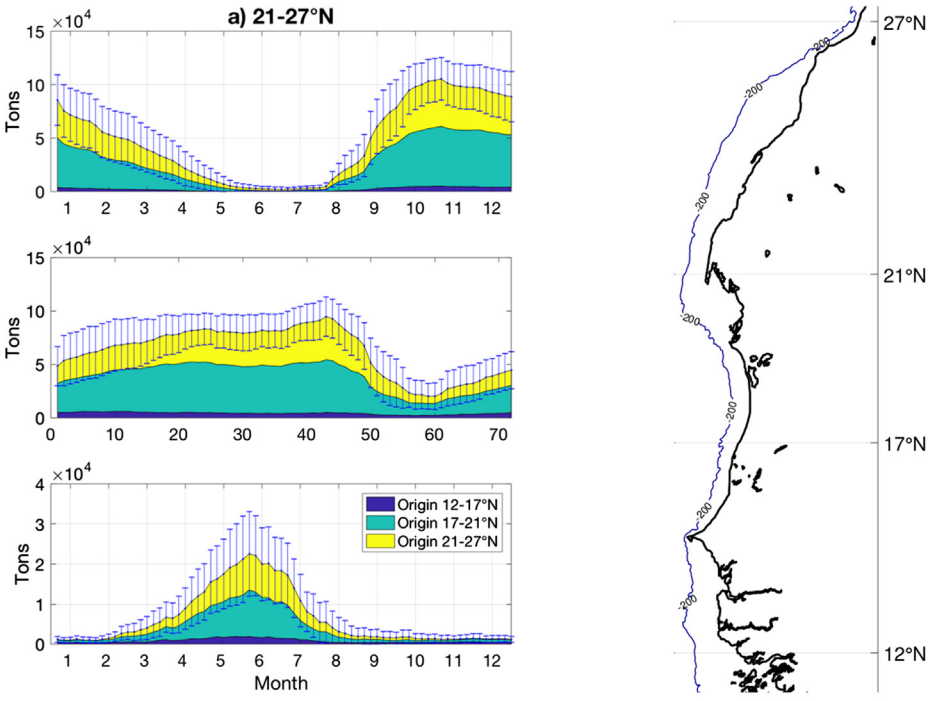


**Fig. 4.** Seasonal composition of round sardinella biomass reconstructed from model Simulation 2 as a function of fish origin (Table 1): Senegal and Gambia in blue (12–17°N), Mauritania in green (17–21°N) and Western Sahara in yellow (21–27°N). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

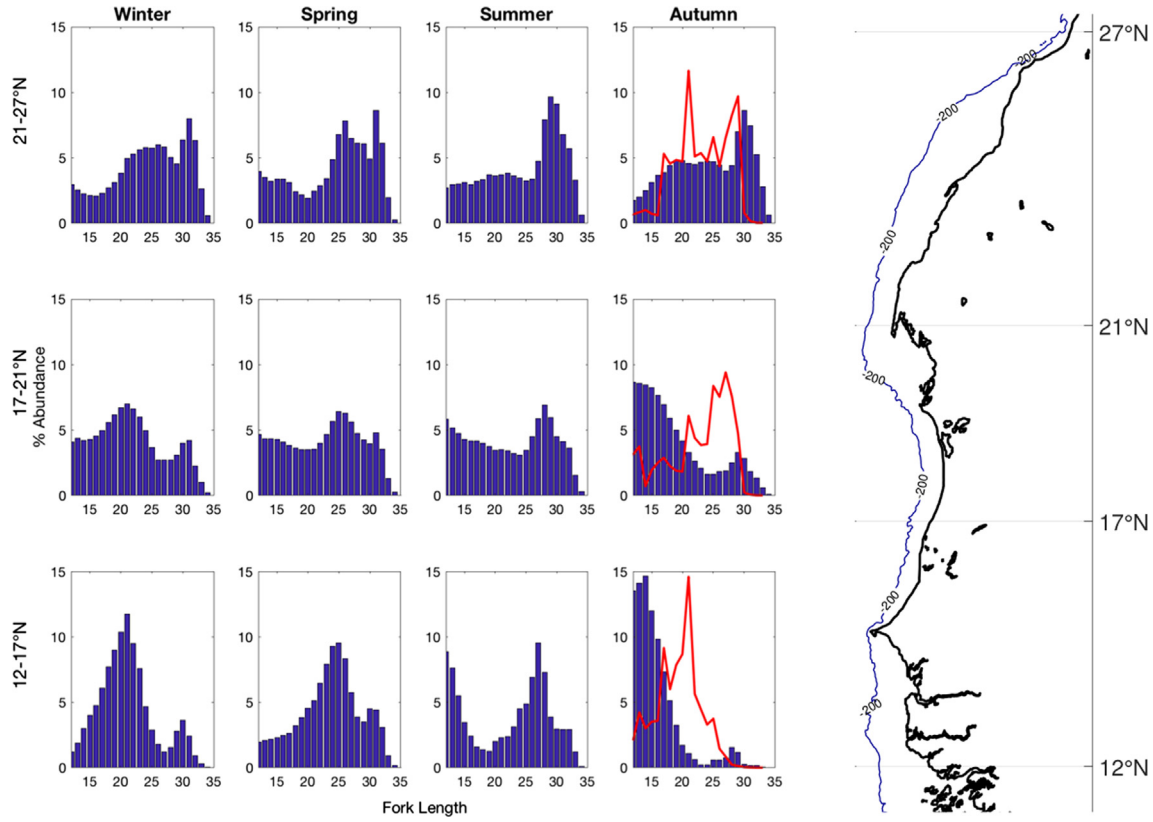


**Fig. 5.** Simulated fish length frequency by 1 cm class (fork length, cm) averaged over the period 1996–2004, by season and by area: Western Sahara (21–27°N), Mauritania (17–21°N) and Senegal-Gambia (12–17°N). For each area/season, the length frequency was based on the length of the fish represented by the super-individuals (SIs) weighted by the number of fish they represented (*i.e.*, their worth). Seasonal variabilities are in line with fisheries data in Mauritania and Senegal (see text for details), while the increasing average size of round Sardinella from south to north is in line with average observations by the 1996–2004 Nansen scientific survey (the red lines in the autumn, see text for references). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

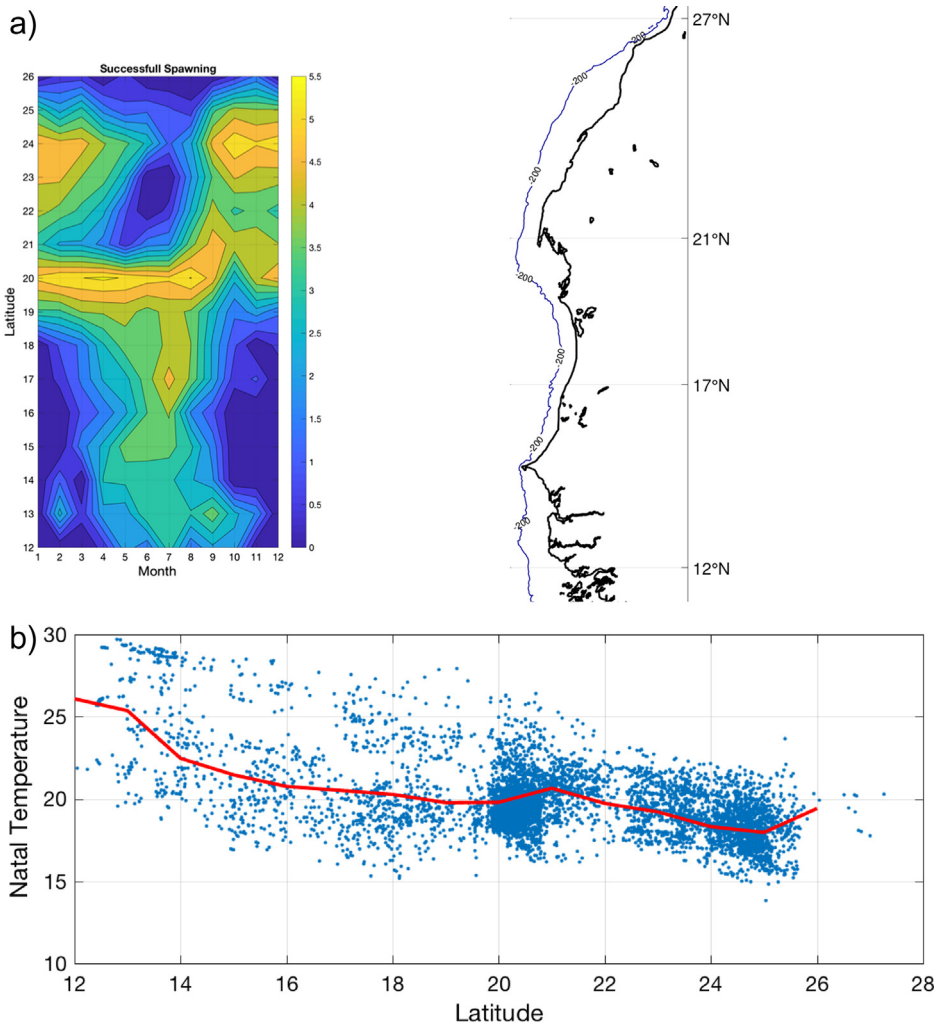


**Fig. 6.** (a) Spatio-temporal pattern of successful reproduction. The color bar corresponds to the number of recruited super-individuals (logarithmic scale). (b) Mean and standard deviation of sea surface temperature when successful reproduction occurs, according to latitude. Depending on the latitude, the successful reproduction mainly occurs during the first semester (south of 18°N), the second semester (north of 21°N) or year-round (from 18°N to 21°N), which explains the largest variability found at 19°N. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Southern Morocco has overall stable temperatures and relatively high food availability resulting in high HQI all year round (see Fig. S8 for a 21 °C preferred temperature, and Fig. 6b for the 22 °C preferred temperature, characteristic of the area) despite some subtleties discussed below. However, few SIs were recruited over the shelf with natal homing temperatures that matched the year-round ~17–21 °C range typical of the Sahara Bank (Fig. 6b). We relate this to the hydrodynamic constraints discussed below, in Section 3.3.2. The temperature at the coast frequently fell below 18 °C in the core of the upwelling (~25°N) and further south from December to July (Fig. S8). This is below the average natal homing habitat selection (~19 °C, Fig. 6b). Thus, during such periods, the HQI was reduced in the nearshore area because of low temperatures, thereby shifting the fish offshore to the continental slope with warmer temperatures and unlimited food (Fig. 7a and c). Thus, the offshore area was more suitable for SIs spawned in Mauritania, provided they were able to migrate northward despite the hydrodynamic constraints (see Section 3.3.2).

### *3.3.2. Effect of swimming capabilities, horizontal currents and mesoscale structures on the exploration of the potential habitat*

In the previous section we identified one nearshore area, the Sahara Bank, that offered high and permanent food availability but did not emerge as focal for sardinella, *i.e.*, it did not sustain a permanent part of the population. We have also previously noted marked latitudinal differences in size-distribution patterns. We now relate these features to the hydrodynamics and fish swimming ability.

The potential habitat is defined here as the areas where the HQI is high. If the environment were stable, the horizontal movement algorithm (kinesis) would rapidly result in a distribution of the fish that would be optimal with respect to their habitat preferences (Watkins and Rose, 2013), which is illustrated by sensitivity runs where advection was removed (see Table 2, simulations #3 and #12). In a turbulent environment with mesoscale variability, fish movements are perturbed by current advection, and the habitat structure varies over a wide range of scales. The habitat structure is particularly irregular over the Sahara Bank (Fig. 7c). In the model, the horizontal movement algorithm implies that only bigger fish, with higher swimming velocities, could stay in these structures. The smaller individuals had the tendency to be advected southward by the mean currents, while the larger individuals better succeeded in maintaining elevated HQI (Fig. 7b). Another indication of the major influence played by model swimming speed of the fish is the difference in northern distribution limit between experiments under slow or fast swimming scenarios (see Methods; Section 2) which are respectively 21°N and 24°N.

Results for the “no advection” experiments (Table 2) differed in many ways from the baseline experiment (Fig. 8). The body-length distribution in Senegal and in Morocco presented different features than in the case with advection, which highlights the role of the oceanic

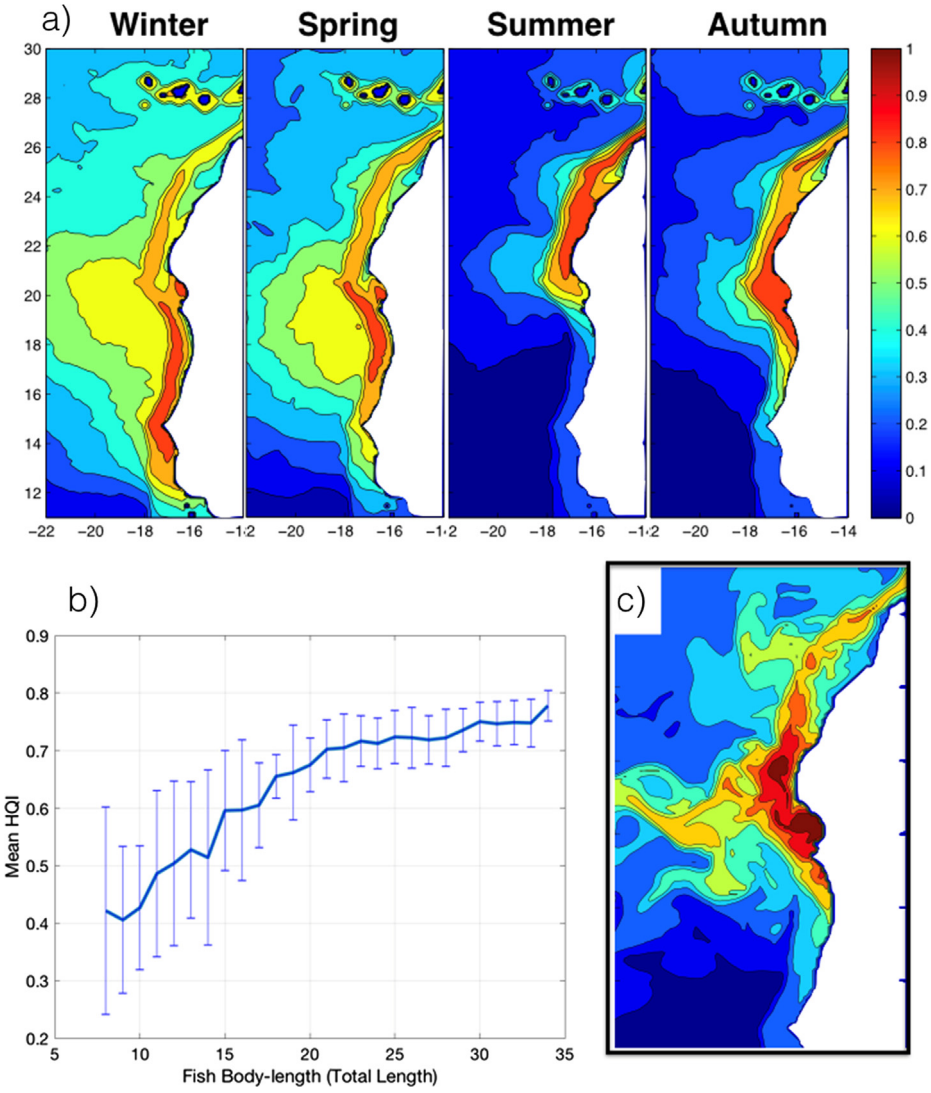


**Fig. 7.** Mean distribution of Habitat Quality Index for each season ($T_{pref}$ = 21 °C) (a), relationship between fish length and their ability to target high HQI (b), and a snapshot of the HQI distribution in August showing the patchy nature of HQI (c). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

currents on the spatial structure of the simulated length distribution. In addition, maximum fish biomass was located in the Sahara Bank between 22 and 24°N from October to March, while relatively low fish biomass was distributed in the area south of 16°N. This confirms that the Sahara Bank is an area that offers optimal HQI but is difficult to reach for round sardinella, particularly for juveniles.

An important consequence of the difference in southward current intensity between the north and the center of Mauritania (C. Blanc ~ 0.15–0.3 m $s^{-1}$ and C. Timiris ~ 0–0.2 m $s^{-1}$, see Fig. S9), was the formation of fish aggregations in the transition region during the second half of the year. During this period, the fish transported southward from the Sahara Bank by the intense southward current converged toward the fish swimming north, owing to the warming of Senegalese waters. The presence of juvenile fish around 20°N despite the intense southward current at this latitude is due to the Arguin Bank. This bank leads to high coastal retention of eggs and larvae (as demonstrated in Mbaye et al., 2015), and shelters juveniles that aggregate in this area in the model.

In Senegal, reducing model fish swimming speeds resulted in an increase of the adult biomass. In our reference experiment, fish moved north against the southward current when upwelling decreased, looking for food and/or colder temperatures. In the model, the size at which this northward migration can succeed depended on current intensity and choices made for swimming efficiency as a function of body-length.

### 3.3.3. *Emergence of interannual variability*

Explaining fish biomass interannual variability is not straightforward. Indeed, its relationship to fish environment variability is subtle as we will show for the most evident signal of biomass increase found between 1995 and 1998. In simulation #2, this fluctuation of fish abundance was generated by the variability in fish reproduction over the Sahara Bank (see Section 3.2.2; also Fig. S16). The variability of environmental parameters in this area (sea surface temperature, current and food availability, Fig. S10) was not directly correlated to the fluctuations in fish abundance. However, according to the processes affecting fish spatial distribution described before, the biomass increase between 1995 and 1998 can be related to a 4-year anomaly of the intense southward coastal current that flows along the Sahara Bank and northern Mauritania (Fig. S10), from 1994 to 1997. The weakening of this current caused an increase of the recruitment (visible in Mauritanian from 1994, Fig. S16), and facilitated the northward migration toward the Sahara Bank. From 1995 to 1997 the round sardinella reproduction over the Sahara Bank was amplified by the natal homing process, making this area the main nursery of the population. After

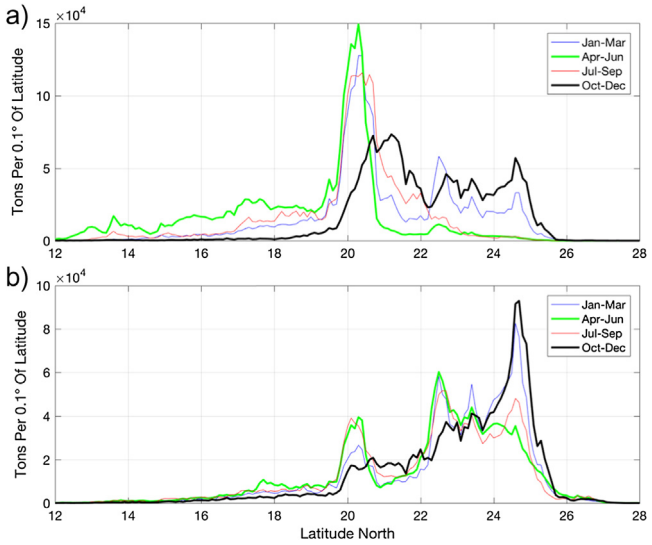


**Fig. 8.** (a) Mean latitudinal distribution of the population per season (blue = quarter 1, green = quarter 2, red = quarter 3, black = quarter top) obtained from model Simulation #2 (see Table 1), (b) a simulation with same parameters as Simulation #2 but in which the individuals' advection term was removed, *i.e.*, the only fish movement is due to swimming behavior. For each 0.1° of latitude, the biomass present on the continental shelf was sum. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1997, the southward flow intensified, limiting the migration and recruitment over the Sahara Bank. A great part of fish recruited on the Sahara Bank then shifted southward, and the Arguin Bank became the main nursery area, as before 1995 (Fig. S16).

The increase of the upwelling winds strengthens the average current intensity of the Sahara Bank during the main spawning period, which in turn reduces the egg and larval retention rates. This is amplified by the fact that during strong upwelling, the spawning habitat may shift to the continental slope because temperatures near the coast become too cold. This results in a larger contribution of the Sahara Bank nursery area to the recruitment in periods of moderate upwelling.

Interannual variability was also very sensitive to the swimming speed parameter. Indeed, sensitivity tests showed that the maximum fish swimming speed (3 or 6 $BL\,s^{-1}$) modulated the average northern limit of the population to between ~21°N (for 3 $BL\,s^{-1}$) and ~24°N (6 $BL\,s^{-1}$), further showing that in the model, the southward current that flows over the Sahara Bank limit the northward extent of the round sardinella population (which was also confirmed by the "no advection" experiments). We conclude that the Sahara Bank acts as a barrier that limits the northward migration of round sardinella; the latitude of this limit changes according to interannual fluctuations of the upwelling winds and impacts the regional fish abundance.

## 4. Discussion

Key parameters and model assumptions for the emergence of round sardinella population patterns with important qualitative similarities to the observed ones in northwest Africa were identified (Fig. 9a-d; see sensitivity tests, Section 2.3). From the model analyses, three major population level patterns emerge having deep consequences for understanding the NW African round sardinella population connectivity between EEZ and year-to-year variability. The three main contributions to the understanding of the round sardinella dynamics in NW Africa are: (1) the definition of an emergent "focal area" off Mauritania where the species is abundant year-round (Fig. 9e), in line with (2) a finer description of migratory routes diversity and superposition, that extend the scheme proposed by Boëly et al. (1982), and (3) the model pointing to the key role of the Sahara Bank (off southern Morocco), as an intermittent nursery area that drives the overall round sardinella abundance year-to-year variability off NW Africa (Fig. 9f). Also, the processes driving seasonal migrations may be at least partly generic for SPF. These findings are discussed next.

### 4.1. Emergent patterns for round sardinella

First, a "focal area" emerged for the NW Africa round sardinella population: the Mauritania EEZ (latitude range 17–21°N) where, on average, the model predicted the higher biomass. The reduced seasonal and interannual biomass variability in this area, and the importance of recruitment in the 17–21°N range, responsible for ~1/3–2/3 of the total sub-regional biomass (respectively in periods of high/low biomass; Fig. 9e) indicates the central role played by the Mauritanian coastal waters in the model. The Arguin Bank nursery area contributes to most of the reproduction success predicted in Mauritania, while a secondary nursery area appeared at ~17°N (Fig. 6a). These two nurseries were previously reported from satellite (Demarcq and Faure, 2000) and field observations (Boëly et al., 1982; Conand and Fagetti, 1971; Connand et al., 1977). However, there is still a lack of field observations to confirm the major role of the Arguin Bank as SPF nursery (Guénette et al., 2014), which should be in turn protected from human/fisheries threats. Indeed, despite its MPA status (Guénette et al., 2014), the Arguin Bank is facing increasing anthropogenic pressure, undergoing increased fishing (Corten et al., 2017), illegal fishing activity (Babacar Ba, Sub Regional Fisheries Commission, pers. comm.), and disturbances through infrastructure construction and exploitation of hydrocarbon resources. Our study suggests that a reduction of the Arguin Bank nursery efficiency may in turn affect the sub-regional round sardinella population.

Second, the model produces a wide range of migratory routes, determined by natal temperature, fish age and body-length, with a common crossing area in Mauritania (Fig. 9e), which we refer to as a focal area. The diversity of migratory routes, together with the determinant role of the fish body-length in the migration routes in the strong current areas, is consistent with the year-round stability of the body-length distribution observed in Mauritania (Fig. 5; Corten et al., 2017). The north-south fish length population structure predicted by the model was also found in the observations (Fig. 5). The increasing range of migrations according to fish body-length has been observed and modeled for other SPF species (*e.g.*, Nøttestad et al., 1999; Lo et al., 2011).

Braham et al. (2014) proposed the existence of two separate stocks with distinct migratory schemes in Mauritania (but point to the lack of data for validation). Here we extend this hypothesis to a large number of subpopulations with distinct migratory schemes, but that are not separated since they are mixed during the common part of their migration routes, especially in the focal area, and they spawn throughout their migration and thus contribute to each-other's recruitment. Thus, based on these results, the round sardinella off NW Africa cannot be seen as a metapopulation since local populations dynamics are not determined by local birth and death (Grimm et al., 2003), and thus constitute a single sub-regional "stock", *i.e.*, from south Morocco to south Senegal, and probably Guinea (although the model did not cover this area).

Third, the model produces a new hypothesis for the environmental driver responsible for the round sardinella abundance inter-annual variability off NW Africa. Indeed, in the model, low-frequency variability of amplitude comparable to that observed in fish stock assessment time series was produced by environmental variability alone (as opposed to requiring added fishing pressure representation), as expected in overefished areas (Mcowen et al., 2015). The environmental conditions modulated the contribution of the Sahara Bank nursery and feeding ground (off southern Morocco). Moreover, the variable importance of the recruitment in this area to the sub-regional mixed

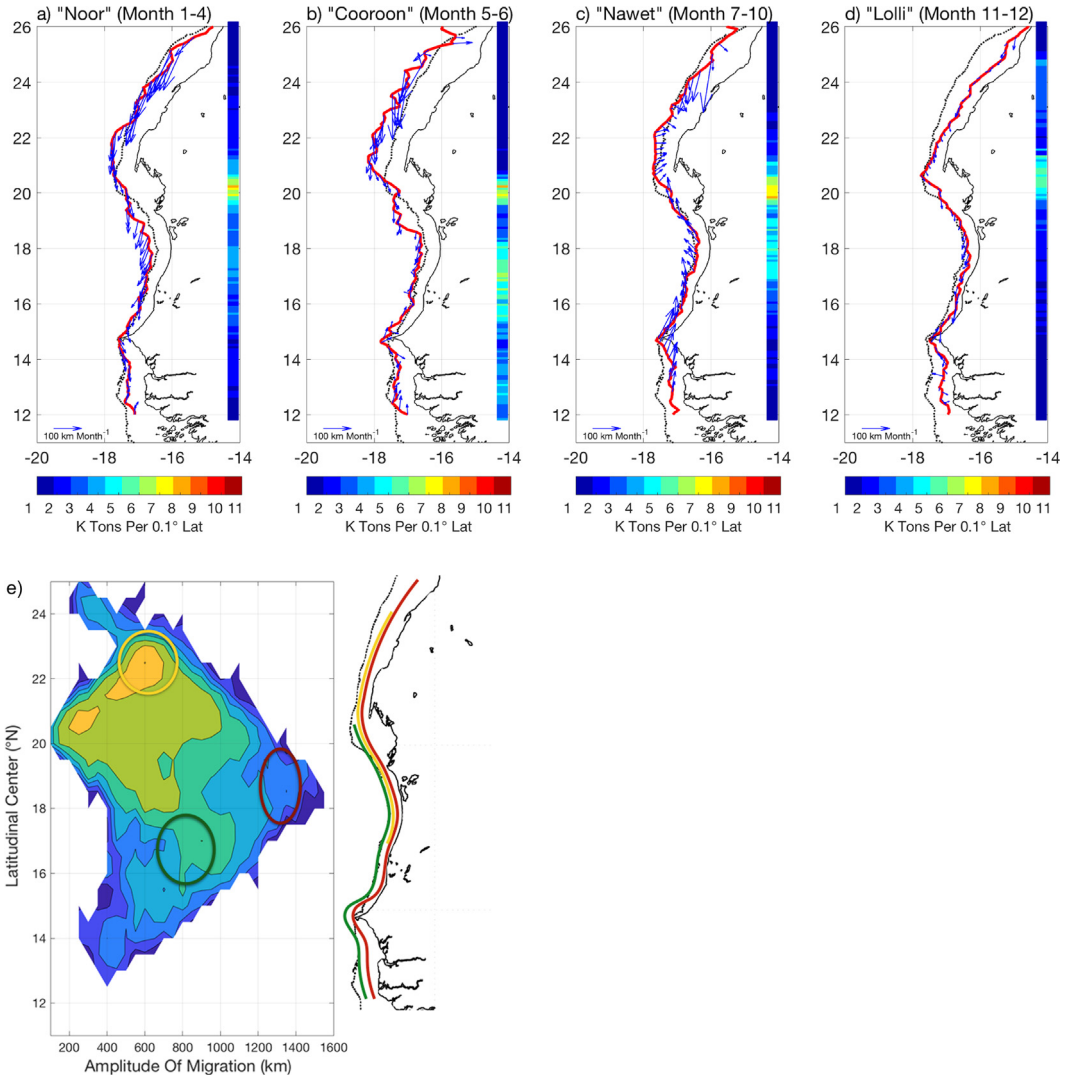


**Fig. 9.** Round sardinella populations traits emerging from model simulations. (a-d) Seasonal variability in spatial distribution, corresponding to the Senegalese fishing seasons; arrows show average movements (direction and intensity). The terms Noor, Cooroon, Nawet and Lolli are Senegalese terms referring to the fishing seasons and are explained in the text of the paper. The vertical color bar indicates fish biomass density (1000 Tons per 0.1° latitude). The thick red line highlights the limit of the offshore extent (80% of the biomass being inshore of that limit), and the black dashed line is the 200 m isobath. (e) Distribution of migration routes (for individuals older than 12-months at the end of the year). The color scale indicates the number of individuals (color scale not shown, increasing from blue to yellow). The circled areas' migratory routes are shown on the adjacent map. (Simulation #2, *cf.* Supplementary Table 3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

population was the source of the low-frequency fluctuations of the total abundance. In the model, higher recruitment in Sahara Bank occurred during periods of relatively low wind intensity during the upwelling season, as observed in Senegal (Diankha et al., 2018), and corresponded to periods of high sub-regional abundance (Fig. 9f). Although we cannot test the temporal changes in the contribution of the Sahara Bank nursery to the total population against observations, strong interannual variability in round sardinella abundance has been noted previously off southern Morocco (Binet, 1988). Two other observations support the hypothesis. First, the near-shore southward migration predicted by the model in autumn from the Sahara Bank to Mauritania is in line with high coastal densities observed in Mauritania at this season (Corten et al., 2017). Second, the northern limit of the population that emerges at ~27°N in the model is consistent with a recent study based on round sardinella otolith analysis that shows that sardinella from northern Morocco could be isolated from the Senegalese-Mauritanian population (Bacha et al., 2016). Unfortunately, no relevant abundance index can be calculated from the fishery data in his area. Indeed, the available data came from the Russian and Ukrainian commercial fisheries that reported landings maximum in 1990, in 1997–2000 and 2006–2008 (FAO/COPACE stock evaluation groups in which several authors of the present work are involved). This fishery mainly targeted mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus* spp.) taking other species (sardinella and sardine) as bycatch. However, during periods of low abundance of target species, the fishery adopts an opportunistic strategy and primarily targeted sardinella and sardine. Thus, CPUE index could not be calculated for this fishery.

### 4.2. Model sensitivities and limitations

The fish displacement algorithm used here, *i.e.*, extended kinesis, has been shown to yield realistic simulations of SPF migration in a changing environment (Okunishi et al., 2012) without artificially imposing long-range fish displacements, as is frequently done in spatially-explicit individual-based model of fish populations (*e.g.*, Huse, 2001; Rose et al., 2015). Note that we found swimming speed to be a key parameter that modulates the exploration capacity of the super-individuals (here related to fish schools). Actually, the values of the

swimming speed parameter cannot be compared to *in-situ* observations because it was used as a proxy for exploration ability against current advection, while in reality the vertical behavior of the fish (not resolved here) might play a major role in regulating its advection by surface currents (Werner et al., 1993). Thus, the "fast" swimming speed value may reflect the need to account for unresolved processes and behaviors, *e.g.*, the existence of submesoscale circulation variability, the possibility to swim at depth to avoid strong surface currents (as reported in Schmidt, 1972), or "tower shaped school" structures close to the bottom (Petitgas and Levenez, 1996). Future modelling and observations should focus on the vertical behavior to improve this point. Given the sensitivity of model solutions to imposed behaviours, understanding emerging behaviours in response to complex environments and their gradients requires additional study (*e.g.*, see Berdahl et al., 2013).

The balance between fishes' ability to explore their environment and the intensity of the horizontal currents underscores the importance of the hydrodynamics simulations' accuracy. In the present model, the nearshore currents provided by the ROMS simulation largely drive the spatial distribution of the population, thus "sorting" the individuals following their swimming capacities, *i.e.*, body length. This mechanism supports the analysis of Braham et al. (2014), who demonstrated that the continuous presence of young fish observed in Senegal during the second semester was not compatible with high round sardinella growth rates if no migration was taken into account.

Note also that the larval dispersal phase relies entirely on hydrodynamics, hence the critical importance of producing realistic circulations in the nearshore nursery areas. Some model deficiencies may be compensated by swimming capacities adjustments, *e.g.*, in our case increasing the swimming speed parameter to allow adults access the Sahara Bank nursery area, thus compensating a possible over-estimate of southward current flow of the hydrodynamic simulation. These adjustments may implicitly account for the unrepresented vertical processes above mentioned (*cf.* Section 2.2), but also for unresolved subgridscale physics (transport by submesoscale, internal waves, retention in estuaries) and other detailed behaviors, *e.g.*, unresolved swimming behavior adaptation to the structure of the current system, or distance to shore, as observed by the fishermen (Abdoulaye Diop, head of "*Comité National des Pêcheurs du Sénégal*" Kayar, pers. comm.). A higher resolution of the hydrodynamic model would also increase the simulated retention and recruitment in shallow area as the southern coast of Senegal ("Petite côte", see Fig. 1) and thus its contribution to the regional round sardinella population (Ndoye et al., 2017). In the same way, juvenile catch reports in the Sahara Bank area may be explained by the existence of a strong coastal retention area between Dakhla and Cape Barbas (Auger et al., 2015) that our model has insufficient horizontal resolution to reproduce.

The southern boundary of the spatial grid we used (10°N) probably also prevents the emergence of a significant subpopulation centered in southern Senegal, while observations tend to suggest one (*e.g.*, Mbaye et al., 2015; Boëly et al., 1982; Corten et al., 2012). Indeed, such a subpopulation would have temperature preferences (set by natal homing) that would require southward migration beyond the model boundaries during the coldest part of the year. Future model development will include the extension of the domain southward, which might allow a southern subpopulation to emerge.

The impact of the combination of temperature and/or food cues for definition of habitat in the sensitivity tests highlights the major effect of the natal homing trait, *e.g.* the natal temperature being the preferred temperature, for the round sardinella population reproducing in southern Morocco. Indeed, natal homing was an essential model assumption for round sardinella reproduction in this area, which then largely contribute to the total population recruitment ($\gtrsim$30% in average, see Appendix 1). With temperature natal homing, the recruitment variability over the Sahara Bank largely increases the interannual variability of abundance. In particular, it strongly contributes to the emerging 1996–1998 "high biomass" period (Fig. 3), in line with the data presented here and other literature data (Zeeberg et al., 2008). In effect, the natal-temperature homing assumption results in a wide distribution of preferred temperature among individuals (Fig. 6b), which favours a more complete use of the habitat at the population level. Such a mechanism was previously suggested to explain abrupt changes in anchovy abundance in the Benguela Current System through a shift in the spawning area (Roy et al., 2007).

A simplification of the model worth mentioning, is the fixed development time of eggs and yolk-sac larvae. The dependence of these early life stages on ambient temperature can be a fundamental factor explaining the variability of the adult population. In absence of existing data, laboratory experiments must be conducted to parametrise the DEB model to simulate realistic egg and yolk-sac larvae stage duration variability (Kooijman et al., 2011). Taking into account these parameters might impact the relative contribution of the nurseries obtained in the present version of the model.

### 4.3. Applicability to other species and EBUS regions

West African sardinella is a well-suited population to test the model. The documented long-range seasonal migrations associated with periodic upwelling conditions offered clear and strong abundance signals for the model to simulate. The socio-economic context and need for better fisheries management also provided a strong motivation for this work. Having said that, the model may, with relatively minor adaptations, provide insights into SPF populations variables for other ocean regions. We briefly discuss its application to SPF populations in upwelling systems below.

Like round sardinella in the Canary upwelling system, California sardines (*Sardinops sagax*) perform long range migrations broadly consistent with expected habitat seasonality (Félix-Uraga et al., 2004; Zwolinski et al., 2011; Demer et al., 2012), and several subpopulations seem to exist (Javor et al., 2011). Exploring emergent patterns in EvolDEB for this system would be useful, including for comparing the identified subpopulations. An essential distinction between the two systems is that sardines in California occupy the offshore area, including during early life stages. There are many environmental reasons why this may be the case: intense meso/submesoscale currents responsible for strong cross-shore exchanges; mesoscale eddies that offer suitable offshore habitats and nurseries; narrow shelves that are unsuited for coastal retention. Also, the temperature variability in the Pacific Northwest modulates the northern limit of the sardine population (Emmett et al., 2005). This may play a role in the low frequency variability of regional population abundance in the California Current System (CCS) as does the variability of reproduction success over the Sahara Bank in the Canary upwelling system.

Sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*) dominate the SPF community in the Benguela Current System (BCS). In the southern Benguela, a clear separation between spawning and feeding grounds is observed, and the alternative search for spawning and feeding habitats seems to drive the seasonal migrations (Mullon et al., 2002; Hutchings, 1992). This strategy contrasts with the continuous spawning of the round sardinella during their migration trip in the Canary upwelling system, pattern also observed for Namibian sardines on the west coast of the Benguela (Miller et al., 2006). The Lüderitz upwelling cell may act as an environmental barrier to ichthyoplankton transport (Lett et al., 2007) that would separate the Namibian sardine population from the southern population (*e.g.*, Newman, 1970). In the northern Benguela, concurrent with the decline in biomass in the late 1960s, the sardine stock kept the same spawning latitudinal ranges as before (le Clus, 1990; Kreiner et al., 2011) but underwent major changes in stock structure (mean total length, length at first maturity; Jarre et al., 2015). Applying our model to these time series would allow us to assess whether these changes could emerge from environmental forcing alone. In the southern Benguela, catches of SPF show low frequency variability over the last decades and suggest species alternations

between sardine and anchovy, a hypothesis that could also be tested with separate single species modelling approaches.

The Humboldt Current System (HCS) is an interesting case because despite its very large extent (5–38°S), no seasonal latitudinal migrations of the main small pelagic fish species, anchovies (*Engraulis ringens*) are reported. The anchovies undergo mainly cross-shore displacements, following the offshore distribution of the food (Bertrand et al., 2004). Indeed, the upwelling intensity fluctuates seasonally but the phyto- and zooplankton production remains sufficient to avoid food limitation for anchovies in coastal areas. Thus, food is locally available year-round, even during El Niño events (Bertrand et al., 2004). Regarding sea surface temperature, the seasonal variation locally ranges within 3–6 °C (17–23 °C at 8°S and 13–16 °C at 35°S) which may be compatible with the individual range of temperature tolerance, as in Mauritania. On average, over the continental shelf the surface current is oriented northward year-round in the Humboldt current system (Echevin et al., 2008). This surface current is relatively weak except in the area off Paracas (14°S) in Peru. The anchovies are found in the surface current most of the time because the southward (poleward) undercurrent, is very poor in oxygen (Chaigneau et al., 2013). This might tend to accumulate fish in the northern Peru by preventing the southward migration of the juveniles and favouring the northward transport of the individuals present south of Paracas, with no other driver for a return migration (*i.e.*, no mean habitat quality gradient southward). This could partly explain the very high production of small pelagic fish in the northern Humboldt current system as related to the observed primary production (Chavez et al., 2008) and could be tested using Evol-DeB.

### 4.4. Conclusion and perspectives

We deem the modelling approach proposed herein to be useful insofar as the study of small pelagic fish connectivity within a given ecosystem, *e.g.*, between spawning areas or fishing areas, mediated by both adult movement and larval dispersal. Furthermore, the model can suggest new hypotheses to explain patterns of change in abundance, for example by highlighting the role of a particular nursery area. Model-generated hypotheses, when confirmed by observations, may be used for directly supporting specific management decisions. For example, the major role of the Sahara Bank nursery (southern Morocco) for the NW Africa round sardinella population suggested by the model argues to associate Morocco with the Sub-Regional Fishery Commission (SRFC) to consider joint work on round sardinella fishery management.

At the local (national) scale, the cross-shore seasonal variability of abundance predicted by the model may be of critical interest for policy makers who have to define the offshore extension of the area where industrial fishing is restricted to limit overlaps with small scale fisheries. At the sub-regional scale, our model could be used to assess the effect of fishing agreements scenarios on the sub-regional stock. The present approach can help understand the way environmental and fishing forcings interact. Thus, it becomes possible to address the challenge of producing *ad hoc* recommendations to regulate exploitation of the sub-regional shared fish stocks, and to project changes in fish distribution triggered by global warming and changing environmental conditions.

In that sense, regional downscaling of the main IPCC scenarios could be used to force EvolDEB, as it was done in the HCS with the Ichthyop larval dispersal model (e.g. Brochier et al. 2013). Recent studies suggest that global warming may cause a poleward shift of the subtropical anticyclones, combined with a general slowdown of the atmospheric circulation (IPCC AR5, Stocker et al., 2013; García-Reyes et al., 2015; Sydeman et al., 2014). The impacts of these changes on EBUS remain uncertain, with substantial regional and seasonal differences among models. EvolDEB can be used to explore the effect of these contrasting hydrodynamic and productivity scenarios on SPF spatial distribution, migration patterns and abundance, and to evaluate potential impacts in these ecosystems, so far, the most productives of the world.

## Acknowledgements

We acknowledge support from the AWA project “Ecosystem Approach to the management of fisheries and the marine environment in West African waters” funded by the BMBF and IRD (grant agreement 01DG12073E). We are also grateful for support from PREFACE, funded by the European Commission’s Seventh Framework Programme (2007–2013) – Cooperation (ENV.2013.6.1-1: Climate-related ocean processes and combined impacts of multiple stressors on the marine environment); under Grant Agreement number 603521. Additional support for the second author was provided by the Instituto Milenio de Oceanografia funded by the Iniciativa Cientifica Milenio (ICM-Chile). Adama Mbaye (CRODT) conducted the focus groups with expert active fishers. We are grateful to Pierre Fréon for his constructive comments on an earlier version of the manuscript. We also thank the colleagues from ISRA/CRODT, IMROP, INRH, UCAD/IFAN and IRD for feedback and interesting discussions during the onset of this work. Many thanks to Noel Keenlyside (Univ. of Bergen, Norway) for interesting discussions on the effect of climate change in EBUS. Paolo Domenici (CNR, Italy) provided useful discussion and references for round sardinella swimming capabilities. Finally, we thank two reviewers, one anonymous the other Kenneth Rose for their constructive comments.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2018.03.011.

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