New insights in the spatial dynamics of sardinella stocks off Mauritania (North-West Africa) based on logbook data analysis

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tables

Abstract

Sardinella spp. are the main species fished in Mauritanian waters. Logbook data (1991–2009) were used to standardise CPUE. This clearly revealed that the abundance of sardinella peaked in the warm season (July–September) which is the main, if not the only significant spawning season for round sardinella.

This study does not directly confirm or falsify the common belief that the adults migrate from the Senegalese EEZ up to north of the 21°N latitude, but it presents a variety of new hypotheses. If a single transboundary stock exists, part of its individuals, or a sub-stock, is probably more sedentary and remains in the permanent upwelling area located in northern Mauritania and southern Morocco.

Between years, changes in abundance index are dominated by a decrease from 1996 to 2006, depending on the months taken into account, and especially whether or not the warm (spawning) season is considered. For a given month, the spatial distribution of sardinella shows limited differences between years. In the southernmost latitudes of the Mauritanian EEZ the seasonal pattern, which is dominated by high catch rates during the warm season, is much stronger after the year 2001, and then tended to increase year after year.

Changes in species distribution and abundance during the twenty-year study period are difficult to relate to environmental dynamics. However, an inversion of the upwelling trend was observed in 2001, matching a change in the seasonality of sardinella catches, although the causality between the two phenomena could not be established. The increase in the abundance index of sardinella in the last five years, particularly during most of the core fishing season (July–September) might be due to favourable oceanographic conditions (higher upwelling index) and/or changes in the fishing strategies or efficiency. Before annual indices of abundance can be used in the future, it will be necessary to better understand possible changes in catchability during the warm/spawning season.

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1. Introduction

Eastern boundary upwelling ecosystems (EBUE) are among the most productive marine areas due to the high flow of nutrients coming from bottom waters and to the intense winds favourable to Ekman transport (Mackas et al., 2006). The high levels of primary production encountered in EBUEs favour higher trophic levels, due in particular to the high abundance of forage fish such as sardine and sardine-like species (e.g. genus Sardinops, Sardinella and Ethmalosa), anchovy, small carangids and small scombrids. As a result, EBUEs provide one fifth of the marine fish global catch and contribute significantly to securing food and livelihood strategies in many developing countries (Fréon et al., 2009). Among the four EBUEs, namely the Benguela, the California, the Canary and the Humboldt Current systems, the Canary Current is second to the Humboldt Current as far as fish catches are concerned. In the three North West African (NWA) countries – Morocco, Mauritania and Senegal – national or, in the case of Mauritania foreign distant fleets from Western and Eastern Europe, make the most catches. Despite its above-mentioned importance and unlike other EBUEs, not much is known about the Canary Current EBUE, particularly along the NWA coast. This hampers management efforts on national and regional scales (Fréon et al., 2009). The recent global increase in fishing pressure on small pelagic stocks (including the development of fishmeal-oriented extraction) as observed in the last two...
decades, may be endangering the sustainability of the exploitation (Tacon and Metian, 2009; Naylor et al., 2009; IMROP, 2010; FAO, 2011).

Sardinella (Sardinella aurita and Sardinella maderensis) play an important role in NWA fisheries and marine ecosystems (Fréon et al., 1982; Ould Taleb Sidi, 2005; Fréon et al., 2009; Braham, 2010; FAO, 2011). In the period from 1990 to 2009, catches of sardinella in the NWA area accounted for 26% (450,000 tonnes per year) of the total catch of small pelagic, with 28% of S. maderensis and 72% of S. aurita, commonly called round sardinella (FAO, 2011). This latter percentage increased during the last 4 years and now stands at 80% (FAO, 2013). Until the late 1990s, distant, large-vessel fleets working under various access regimes in Mauritania accounted for most of the catches. Most vessels did not land their catches in Mauritanian harbours. The artisanal fishery using canoes equipped with purse seines has become established in Mauritania during the last two decades with an increase in landings from 15,000 tonnes in 1994 to over 114,000 tonnes in 2009 (IMROP, 2010). Meanwhile, a European fleet of modern trawlers began fishing in the Mauritanian Exclusive Economic Zone (EEZ) in 1996, first under private agreements and under a EU fisheries agreement since 2002.

Although regular international assessments have highlighted the risks of overfishing (FAO, 2013), the NWA area fish stocks have not benefitted from intense and regular scientific programmes and the various bases of stock assessments (stocks structures and migration, spawning and recruitment periods and areas) must be consolidated. Scientific surveys at sea remain limited in time and space. Until 2006 the R/V Dr Fridtjof Nansen carried out acoustic surveys in November each year, covering the entire NWA area (IMROP, 2010). Since then, an echo-integration survey has been carried out annually in the Mauritanian EEZ. It is usually being done at the end of the year (Braham et al., 2012). Fisheries statistics recorded in the logbooks have been the most important source of spatio-temporal information since 1990. They have not, however, been subject to any in-depth analysis. One of the reasons is probably that commercial catch rates must be standardised for use as an index of relative/apparent abundance (Hilborn and Walters, 1992; Maunder and Punt, 2004). The main objective of the present paper is thus to extract meaningful and up-to-date knowledge on sardinella biology from standardised catch rates.

A long series of publications (e.g. Robson, 1966; Gavaris, 1980; Laurec and Fonteneau, 1979) discusses the question of the standardisation of catch rates to account for vessel effects (fishing power), spatial effects (fish distribution together with fishing effort allocation) and temporal effects (stock dynamics combined with technical and knowledge improvements of fishermen). In essence, all these techniques relate to linear models, the differences being in the structure of the data (qualitative versus quantitative, distribution free versus parametric, spatio-temporal versus spatial and temporal with additional interactions). The present paper is a contribution to the estimation and the analysis of fishing power and abundance index.

The Mauritanian EEZ is strongly influenced by a recurrent, though variable, upwelling. The variability of the abundance index obtained from our model output for the period between 1990 and 2009 is compared with the dynamics of the coastal ocean (upwelling, surface temperature and chlorophyll index). Even though they are not well known, the ecology of sardinella and in particular their migration and their reproduction strategies, are important clues for the analysis of fishery statistics. The results and therefore the data can equally provide new insights into the dynamics of stocks. Model outputs are used to develop new insights in the life history traits of sardinella in the Mauritanian area.

2. Material and method

2.1. Material

Logbook data are available from 1991 to 2009 for pelagic vessels fishing sardinella in the Mauritanian EEZ. All vessels fishing in the Mauritanian EEZ are obliged to write daily logbook entries reporting daily catches by species or group of species (kg), daily fishing effort (number of operations), the ship administrative code and the statistical square where fishing operations took place. Boats that
Table 1
Main characteristics of the Dutch and the Russian-type fleets.

<table>
<thead>
<tr>
<th>Vessel type</th>
<th>Capacity (tonne/day)</th>
<th>Width (m)</th>
<th>Length (m)</th>
<th>Power (CV)</th>
<th>Crew</th>
<th>Cumulated number 1991–2009</th>
<th>Average number per year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Russian-type trawlers</td>
<td>50–100</td>
<td>14–15</td>
<td>30–90</td>
<td>1000–8000</td>
<td>50–82</td>
<td>250</td>
<td>50</td>
</tr>
<tr>
<td>Dutch-type trawlers</td>
<td>250–300</td>
<td>15–18</td>
<td>100–120</td>
<td>6000–16,000</td>
<td>40–60</td>
<td>18</td>
<td>10</td>
</tr>
</tbody>
</table>

only fished in the EEZ occasionally, i.e. vessels that did not provide data on at least 25 days and at least two years, were not considered. The Mauritian EEZ is gridded into 60 squares of 30 × 30 (Fig. 1), of which only 32 were frequented by the different pelagic fleets.

The number of vessels operating in the large-scale fishery in a single year fluctuates around 50. They fly the flags of different countries (IMROP, 2010). This fleet may be divided into Russian-type trawlers and Dutch-type trawlers, both using four-panel, mid-water trawls. Russian-type trawlers primarily target horse mackerels (mostly Trachurus trachurus and T. tetroce) and chub mackerel (Scomber japonicus). They normally catch sardinella as by-catch. Dutch-type vessels started fishing off Mauritania in 1996. Contrary to Russian-type trawlers, they target sardinella directly and are larger in terms of length and tonnage (Table 1). Fishing in coastal fishing areas (the grounds shallower than 10–80 m according to latitude; Fig. 1) is prohibited and, since 2005, a Vessel Monitoring System (VMS) has been in place to monitor all foreign vessels.

For the purpose of this study, oceanic conditions were obtained from three sources.

Data from the US National Oceanographic Data Center and GHRST (http://pathfinder.nodc.noaa.gov) obtained by the AVHRR Pathfinder Version 5.2 (PFV5.2) were used to monitor sea surface temperature (SST). The PFV5.2 data are an updated version of the Pathfinder Version 5.0 and 5.1 collection, described in Casey et al. (2010). The spatial resolution was 4 km. SSTs are used to build an adequate upwelling index (Demarcq et al., 2003) based on the thermal difference between the coast and an optimally defined offshore reference (Demarcq and Faure, 2000). As a proxy to primary production, a spatially integrated index of chlorophyll a based on eight-day averages (Demarcq et al., 2003) was used. It was computed from MODIS (Moderate Resolution Imaging Spectroradiometer) data on board of the Aqua platform, from July 2002 onwards (http://oceancolor.gsfc.nasa.gov/).

2.2. Methods

Robson (1966) introduced the idea that catch per unit of effort can be modelled as the result of an abundance index multiplied by the fishing power of the individual vessels, combined with a residual variability. This is usually turned into an additive relationship by logarithmic transformation, which makes it possible to use linear regression techniques to estimate the unknown parameters. Such a two-factor model provides abundance indices per stratum, which are equivalent to standardised average CPUEs. Linear models and their extension into GLM (Generalised Linear Models) (McCullagh and Nelder, 1989) are widely used. They make it possible to consider several explanatory variables either categorical or continuous but more interestingly, their interactions.

Statistical tools, such as estimation variances of the estimates (or so-called information criteria) can provide assistance for choosing a specific model within GLM, be it a two-factor or a three-factor model. Such tools unfortunately rely on key assumptions regarding the residuals (normal distribution, homoscedasticity, statistical independence between residuals). When such assumptions are violated, simple least square fitting is not optimal, but, more importantly, statistical tests become irrelevant (the percentage of explained variance remains, however, a useful empirical goodness of fit criteria). Back transformation of log abundance indices into plain abundance indices in order to avoid biases also relies on assumptions on the distribution of the residuals (e.g. Laurent correction (Laurent, 1963) for log-normal data). Since we were primarily interested in relative fluctuations of abundance, results were given in logarithmic scales without back-transformation.

Several GLMs were considered based on the following considerations:

- Should fishing power be modelled by the vessel ID (N = 85 modalities, 85 vessels having been taken into account) or by some key characteristics of the vessels, i.e. gross tonnage, length, main engine horse power and flag, categorised in 3 or 4 levels each, in order to take into account possible non-linear and non-monotonic relationships?
- Should the spatio-temporal effects simply be described by an abundance index per stratum, or modelled as the sum of (i) a spatial effect (ii) temporal effects and (iii) their interactions?

The sensitivity and robustness of the selected model were analysed through several scenarios:

- Changes in the sizes of the individual spatio-temporal strata (groups of squares instead of elementary squares and/or fortnights instead of months).
- Elimination of the vessels associated to the highest mean square residuals.
- Selection of vessels according to targeted species.

Given the number of parameters to estimate, the sensitivity analysis was performed with a Fortran code based on the peculiarities of the set of equations associated to minimising mean square residuals (Laurec and Perodou, 1987) and a simple conjugate gradient algorithm. The final model was then also run under R.

3. Results

3.1. Choice of the model

Based on the explained variance, using vessel codes instead of vessel characteristics is better. The percentage of explained variance associated to this component of the model is 70% larger (Table 2a and 2b). Even if the number of parameters is higher when using individual vessels, it does not seem to us that this can explain such a high discrepancy in the explained variances. This suggests that the available parameters do not make it possible to explain individual vessels’ fishing power efficiently enough.

The choice of the spatio-temporal explanatory variables is more complex. The key choice opposes a model based on a single variable coding for spatio-temporal strata (N = 7299), i.e. squares-month-year voxels (Table 2c), and a model using a set of three variables: one coding for the spatial areas (i.e. the statistical pixel, N = 32), one for the months (N = 12) and one for the years (N = 19) (Table 2b). All mutual interactions (N = 1220), that is first level interactions only, were also included (accepting three-level interactions would refer us back to the first model). The percentage of explained variance...
Table 2
Fitting quality of different linear models.

<table>
<thead>
<tr>
<th>Model</th>
<th>log_{10}(CPUE)</th>
<th>Df</th>
<th>Sum Sq</th>
<th>R^2 (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. Model representing the vessels effect through the use of three of their technical characteristics and their flag as factors, and the spatio-temporal effects (month, year, square) as individual factor and first order interactions</td>
<td>TJB vessel</td>
<td>2</td>
<td>201</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>Vessel length</td>
<td>2</td>
<td>443</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Power vessel [kW]</td>
<td>2</td>
<td>1061</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>Flag vessel</td>
<td>4</td>
<td>723</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>Month</td>
<td>11</td>
<td>1242</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>18</td>
<td>1560</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>Square</td>
<td>31</td>
<td>196</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Year/Square</td>
<td>458</td>
<td>636</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>Month/Square</td>
<td>280</td>
<td>483</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>Month/Year</td>
<td>198</td>
<td>976</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>Total model</td>
<td>1006</td>
<td>7521</td>
<td>28</td>
</tr>
<tr>
<td>Residuals</td>
<td>64,526</td>
<td>18,916</td>
<td>72</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total sum of squares</td>
<td></td>
<td>26,437</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AIC</td>
<td></td>
<td>138,673</td>
<td></td>
</tr>
<tr>
<td>b. Model representing the vessels effect as a single factor (the individual vessels themselves) and the spatio-temporal effects (month, year, square) as individual factor and first order interactions</td>
<td>Vessel</td>
<td>84</td>
<td>4136</td>
<td>15.6</td>
</tr>
<tr>
<td></td>
<td>Month</td>
<td>11</td>
<td>1375</td>
<td>5.2</td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>18</td>
<td>1038</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>Square</td>
<td>31</td>
<td>159</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>Year/Square</td>
<td>458</td>
<td>553</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>Month/Square</td>
<td>280</td>
<td>434</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Month/Year</td>
<td>198</td>
<td>922</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>Total model</td>
<td>1080</td>
<td>8617</td>
<td>33</td>
</tr>
<tr>
<td>Residuals</td>
<td>64,454</td>
<td>17,820</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total sum of squares</td>
<td></td>
<td>26,437</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AIC</td>
<td></td>
<td>102,065</td>
<td></td>
</tr>
<tr>
<td>c. Model representing the vessels effect as a single factor (the individual vessels themselves) and the spatio-temporal effects (month, year, square) as second order interaction (Robinson, 1966)</td>
<td>Vessel</td>
<td>84</td>
<td>2686</td>
<td>10.15</td>
</tr>
<tr>
<td></td>
<td>(Year:Month:Squares)</td>
<td>3798</td>
<td>2794</td>
<td>10.01</td>
</tr>
<tr>
<td></td>
<td>Total model</td>
<td>3882</td>
<td>10,626</td>
<td>40.16</td>
</tr>
<tr>
<td>Residuals</td>
<td>61,421</td>
<td>15,832</td>
<td>59.84</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total sum of squares</td>
<td></td>
<td>26,458</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AIC</td>
<td></td>
<td>100,006</td>
<td></td>
</tr>
</tbody>
</table>

(40% instead of 33%) (Table 2) was better in the first model, which was then chosen and which writes:

\[
\log_{10}(CPUE_{ijkt}) = Vessel_i \cdot (Squares_j \cdot Year_k \cdot Month_t) + R_{ijkt}
\]

where \( CPUE_{ijkt} \) denotes catch per day of vessel \( i \) in the squares \( j \) for year \( k \) and month \( t \). \( R_{ijkt} \) represents the residuals. This model combines an individual vessel effect with a single third-level spatio-temporal interaction. This choice is also consistent with the model outputs (see below), which indicate that the square-month interactions are not homogenous over the studied period due to an important third-level interaction. A linear model with second-level interactions would have assumed that the square-month interaction had a constant expression over the entire period, which was too strong an assumption.

3.2. Residuals

Residuals associated to the model were subjected to a detailed analysis (see supplementary material). The histogram of the residuals does not reveal a major departure from a normal distribution. Residual variances exist (heteroscedasticity) between vessels and between strata. Strong seasonal patterns can, for instance, be observed within a square, which could result from changes over seasons of the heterogeneity within a square. There are, moreover, correlations between residuals, in particular between successive (in time) residuals associated to the same vessel. Residuals do not comply with the key assumptions and the statistical tools which require these assumptions have not been used.

3.3. Fishing power estimates/key elements of the spatial distributions

The estimated relative fishing power varies between 0.2 and 8.9 with a clear discrimination between the Dutch-type fleet, with higher than average efficiencies and the Russian-type fleet, with lower than average efficiencies (see supplementary material). The abundance index is the average daily catch of a standard vessel in an elementary square. The standard vessel is a virtual one, the logarithmic fishing power of which is set equal to zero, which corresponds to the fact that the arithmetic average of the logarithmic fishing powers of the real vessels of the analysed sample (most vessels described in Table 1) is also set to zero.

For each elementary time step (month) catches and estimated abundance were converted to percentages per elementary square in order to facilitate comparisons, the total abundance index for a time step just being the sum of standardised CPUEs per square, regardless of the total area or the exploited area in each square. Arithmetic means over time intervals were then calculated for each elementary square and for 1° N of latitude blocks (Fig. 1). Results show that 69% of the catches are made north of Cap Timirius (19B–20B) while there is an estimated 49% abundance in the same region. Fishing effort is particularly concentrated in some squares located in the northern area: 14% of the fishing effort is concentrated in only one square, for instance, i.e. 3% of the area visited by the pelagic fleet. Sensitivity analyses show a high stability of the above-mentioned results (see supplementary material).

3.4. Seasonality of the abundance indices – average seasonal patterns

The seasonal evolution of the estimated abundances cumulated by 1° N latitude blocks suggests a dome-shaped dynamic with high abundances from July to September (latitudes 19° N and 20° N) or July to October (latitudes 17° N and 18° N) (Fig. 2). The lowest values are observed between December and January. Around this general pattern, delays in the peaks of the abundance index are observed according to regions (square-month interaction). For instance, the abundance index is minimum in the northern region (19–21° N) at the beginning of October, while it peaks in the southern areas. Nonetheless, seasonal patterns are quite similar in blocks 17B, 18B, 19B and 20B. On the other hand, the southernmost area 16B reveals a different and somewhat chaotic pattern with sharp peaks and troughs (Fig. 2). In this area, however, data are very scarce during the warm season due to a very limited fishing effort (1% in 16B). Fig. 3 compares the average (from 2001 to 2009) of seasonal changes in the spatial distributions. Sardinella are widely distributed over most of the Mauritanian EEZ (above 17.5° N) all year round. Even if from November to March, standardised CPUEs are lower in the northern squares, there is never any discontinuity close to the northern limit. On the other hand, south of 17.5° N, fish abundance is likely to be too low to attract trawlers in August.
and September. The increase of the abundance index in June is not restricted to a specific set of squares (Fig. 3): there is no apparent north/south gradient in the May to June increase, but a possibly (slightly) higher index of abundance in the coastal squares. There is an overall decrease north of 18.5° N in September, while between 17.5° N and 18.5° N a new pattern emerges in October with richer coastal squares, without any apparent north/south gradient.

3.5. Changes over years of the seasonal patterns

Irrespective of the levels of abundance estimates in the different areas, the increase in the abundance index from May to August increases from approximately 5 to approximately 15 during the period 2002–2009, whereas this increase is not noticeable during the period 1991–2001, except for the block 20B where this index increases from 6 to 15 (Fig. 4). The average seasonal patterns show obvious differences between those two sets of years at almost all latitudes.

Fig. 5 quantifies the development of the abundance index for latitudes 18–20° N, from May to August by showing the ratio August to May of abundance indices aggregated for the whole period of observation (1991–2009). This graph makes it possible to assess the peak of abundance at the height of the warm season. This peak is not only higher on average after the year 2001, it also generally increases between 2002 and 2009 in northern latitudes. The Hovmöller diagram (Fig. 6) shows two periods of high abundance indices: from 1996 to 1997 and from 2007 to 2008. These interannual fluctuations are mainly due to the variation of abundance indices in the northern part of the Mauritanian EEZ, i.e. north of 18° N, during the first half of the year. As a result, beyond 2001 the annual abundance indices produce different graphs when calculated over all months, or only over the months of July–September (Fig. 6, lower part).

3.6. Environmental data

The upwelling intensity is high from November to June (Fig. 7a and c) and at its lowest from July to October, whereas the seasonal pattern of chlorophyll concentration varies according to latitudes (Fig. 7b and c). The latter displays the same seasonality as the upwelling index in the south (area 1) and progressively an opposite pattern with a summer maximum in the north (area 3). From 1982 to 2010 the average SST values increased irregularly during the warm season (August–October) from approximately 23 °C to 26 °C, with a moderate warming from 2001 onwards (Fig. 8). The interannual variation of the upwelling index displays a different and non-linear pattern marked by noticeable variations. Two periods of upwelling activity can be identified: a period of irregular decrease from 1982 to 2001, followed by a period of strong but non-linear upwelling increase until 2010, reaching the same level as in 1982 and 1983.

4. Discussion

4.1. Retained model and robustness of results

Although the model we used is dated and relies on a simple idea to standardise the CPUE from a heterogeneous fleet and to assess changes in the CPUE of sardine in the Mauritanian area, it proved useful and its performance was better than GLM without third-level interactions. Given the structure of the model, the number of parameters to be estimated was extremely large (N-parameters = 3884, N-residuals = 61,422).

The sensitivity analysis nevertheless demonstrates its robustness, i.e. the main patterns in the outputs (seasonal peak in August and minimum in November; concentration in the northern area and interannual variability) were systematically observed. The correlation between the abundance indices of the vessels targeting sardinella and those targeting horse mackerel were low (<50%), except in some instances such as the seasonal pattern in blocks 18B and 20B (see supplementary material). This difference between the effectiveness of vessels justifies the use of standardised catch rates instead of nominal catch rates, the standardisation factors being the estimated fishing power.

4.2. Fishing strategy of the different fleets

When compared with the Russian-type vessels, the higher fishing power estimates of the Dutch ones (see supplementary material) are consistent with their larger size and horsepower (Table 1), and with the respective fishing strategies of these two fleets. Dutch-type vessels target sardinella (65% of total catches)
4.3. Long-term variation of the abundance index

Monitoring changes in the abundance of pelagic species from commercial data was often difficult due to the high variability of these resources and their extremely aggregated geographical distribution (FAO, 1980; Fréon et al., 2005). An additional difficulty in this effort was that not enough fish length measurements were available for relating the abundance index variability to specific age/size classes. As noted earlier, the ratio of abundance indices from August to May was not high before 2001. Furthermore, the comparison between the abundance indices during the months of highest abundance (July–September) and all months still shows an opposite trend from 2001 onwards (Fig. 6). These observed changes make it difficult to reconstruct an abundance index for sardinella stocks. Nevertheless, a significant decrease in abundance can be observed between 1997 and 2001, and possibly afterwards, despite contradictory trends according to the group of months considered. It seems premature, however, to draw final conclusions about changes in the actual abundance of sardinella off Mauritania.
Changes in the years from 1993 to 2004 could well be due to a period of good recruitments followed by a period of poor recruitments.

Possible but not exclusive explanations for changes in the seasonal patterns following the year 2001 could be (1) the concomitant interannual increase in catchability (accessibility or vulnerability) during the spawning season in summer, (2) the increasing efficiency of the fishers who might have progressively learned how to take more and more advantage of the micro-distribution and behaviour of the spawning fish, (3) hydrological changes in the NWA area that could result in a change of abundance or catchability, (4) the stock was composed of fewer age groups in later years (Corten et al., 2012) and not necessary all age groups display the same seasonal pattern.

It is possible, at present, to analyse explanations 1 and 2 since the appropriate data are missing. However, the third hypothesis is analysed in detail in what follows. Although some environmental changes have been observed, their impact on abundance indices is not easy to interpret. Among these changes are noticeable anomalies in the November to July coastal upwelling index in 2001, followed by an inversion in the trend for this index as well as a positive trend in SST over the period from 1982 to 2009 (Fig. 8). Prior to 2001, the monthly catch of sardinella was distributed on average in a fairly uniform way within a year, with a moderate peak from June to September, particularly at 20°N. After 2001, the seasonal pattern of abundance index was characterized by very high concentrations from June to September in contrast to the rest of the year (Fig. 4). The hypothesis that the notable anomaly in 2001 acted as a trigger for a durable change in the seasonal pattern of abundance seems difficult to support. The possible link between this durable change and the inversion in the trend of the upwelling index after 2001 deserves further investigation. One could see an obvious functional relationship between the concomitant increase of the upwelling (Fig. 8) and abundance (Fig. 6) after 2001, but this is only true for the July–September abundance index, not for the 12-month index. Furthermore, there was no observable connection between upwelling and abundance prior to 2001.

It does not seem possible at present to speak in favour of one of the explanations for the observed changes of the seasonal patterns that were listed and discussed earlier. This illustrates yet again that great care is required when drawing conclusions on real abundance from commercial data (or from a combination of research survey data and commercial data). However, this would be of paramount importance if TAC-based management were to be put in place.

4.4. Seasonal variations of abundance index

The increase of the abundance index from May to July in blocks of major catches is steep (Figs. 1 and 2). Such seasonal changes are usually related either to (i) recruitment of young fish, (ii) fish individual growth, (iii) increase in fish catchability in relation to spawning, or (iv) to seasonal fish migration. Since the increase of the abundance index is abrupt here (twofold in two months on average, but more than tenfold in some years) and because most catches correspond to the adult age classes (Fig. 9), the effects of recruitment and individual growth, if any, are obviously not predominant. It is very likely that this increase either corresponds to a change in catchability or to a combination between the former and fish migration.

4.4.1. Increase in catchability in relation to spawning

The June/July to September period is mentioned in the literature as the most important spawning period for the main sardinella species, *S. aurita*, in Mauritanian (see supplementary material). There is little doubt that the high catch rates during this season could be due, at least partly, to the species’ spawning behaviour.

Changes in catchability can be a consequence of (i) a change in the horizontal or vertical distribution of the fish resulting in an increase of accessibility to the fleet, (ii) a concentration on geographically restricted spawning grounds, (iii) changes in micro distribution (e.g. denser clustering of the school, larger school size and/or changes in school behaviour), and (iv) modified reactions of the fish to the encounter of fishing gears, where these three latter points are related to a change in vulnerability (review in Fréon and Misund, 1999).

Sardinella are highly accessible to pelagic trawlers due to the large vertical opening of their large trawls and to the wide range of prospection of their large factory vessels. Accessibility changes could be due to inshore-offshore fish migration that would mean immigration from the prohibited coastal area to the fishing grounds. Changes in vulnerability in relation to spawning are well documented and more likely to occur in the studied fishery. On the other hand, the main spawning season (June/July to September) does not seem to be associated to a spatially restricted spawning area (Conand and Fagetti, 1971; Conand, 1975), which can be seen.
in Fig. 3. If catches are concentrated in a few squares during this period, this is likely to be the result of a concentration of fishing efforts in some squares (Fig. 1). Under the hypothesis that high catch rates of fish above first maturity size (Fig. 9) reflect the presence of spawning activity, the present analysis suggests that the main “apparent” spawning season takes place in a large part of the northern area from late June to September.

This is consistent with previous studies. By contrast, there is no indication of a separate offshore spawning peak from December to January as mentioned by Chavance et al. (1991). This is however not incompatible with a more coastal reproduction of younger fish as observed in Senegal by Boëly et al. (1982). Similarly, there is no direct indication that the spawning season starts sooner than June in the southern part of the Mauritanian EEZ although it does off Senegal (see supplementary material). More studies would, however, be required in order to better identify the involved species (S. aurita alone or both sardinelina species) and size ranges, especially in coastal areas.

The northern spawning season from July to September almost coincides with the season of low upwelling intensity (Fig. 7). It is striking that round sardine are close to their northern limit in northern Mauritania, and that their eggs and larvae thrive in the higher temperatures during the warm season. The presence of a retention area(s) in this season could prevent larval drift, while the available food would be plenty during the low upwelling intensity period. Because upwelling intensity is extremely high in Mauritania, this spawning strategy is consistent with the optimal-window-hypothesis (Curry and Roy, 1989). Indeed, this season is also associated to weaker winds and currents, minimising the drift of eggs and larvae towards offshore areas, thus creating favourable conditions for a retention area (Demarcq and Faure, 2000).

4.4.2. Fish seasonal immigration and migration schemes

There are hardly any studies on the migration of species in the NWA area. Elwertowski and Boëly (1971) and Boëly et al. (1982) studied the pattern of migration of round sardine in the NWA area. According to these authors, mainly the adults of the sardine stock are exploited. They migrate from Senegal to the south of Morocco from April to September. Starting at the end of September, sardine return to Senegal, thereby passing again through Mauritanian waters. Boëly et al. (1982) further indicate areas of recruitment in Mauritania and Senegal, which are affected by the migration cycle after the respective stocks have spent their first year in the local nursery where the first spawning occurred. Seasonal variation in primary production could be the driver of such long-range migration. The intensity of upwelling is a limiting factor to the abundance of chlorophyll in Senegal (Demarcq and Faure, 2000) but also in the southern part of Mauritania and, to a lesser degree in the central area, as suggested by Fig. 7. The northern area is less affected because of the quasi-permanent upwelling.

The fishing statistics of the distant fleet in Mauritania is consistent with the immigration from Senegal to Mauritania from April to September, although the arrival of the fish in southern Mauritania is not observed. This can be interpreted in two different ways, not exclusive from each other and both related to the narrowness of the Mauritanian continental shelf is in the south of the country. First, because the trawlers were not allowed to operate within a coastal band of 12 nm (later 13 nm), and 15 nm after our period of study the fish would not be accessible to the trawlers in the southern region, should they have an inshore distribution. Second, the narrow continental shelf is unlikely to be a suitable spawning ground. Therefore, adult round sardine are likely to cross this area quickly during their northern migration, which would result in a lower abundance and vulnerability. Large sardine-like
species like *S. aurita* and *Sardinops sagax* are known for their high swimming speed that makes them difficult to catch at a trawling speed lower than 4.5 knots. The medium–distance range of school speed observed for sardine (*S. sagax*)—a species whose morphology is similar to that of sardinella—in Japan and South Africa varies between 0.7 to 3.0 knots (Hara, 1987; Misund et al., 2003). We have no logbook data on the return migration from Morocco via northern Mauritania to Senegal, since no important concentrations are observed from October to November. This was also found by Chabanne and Elwertowski (1973) in historical data (1968–1972) and more recently by Corten et al. (2012), although these last authors also reported very coastal catches of sardinella by the artisanal fleet operating from Nouadhibou in October/November 2010 and 2011. This suggests that the return migration (if any) took place in very shallow waters, at least during these two years, and that the fish during this period were not accessible to the trawlers. In the present study a fast return migration (no spawning) and dispersion is also seen to explain the “low apparent abundance” described by Boély et al. (1982).

A first alternative to the migration pattern proposed by Boély et al. (1982) could explain the observed changes in catch rates in space and time within the Mauritanian EEZ. This scheme would imply a stock straddling north to the 21st parallel, which would not expand south beyond the 17th or 18th parallel, the southern limit moving north during the warm season (August/September). Under this scheme, one cannot exclude inflow from further north, which spreads rapidly in the Mauritanian EEZ during this season. There could be limited amplitude movements following the north/south axis, and possibly offshore/onshore migrations, but no large-scale north/south migration. Sardinella in the southern latitudes off Mauritania (16°N and marginally 17°N) would be related to migrations from a more southern stock straddling the limits of the Senegalese EEZ. This scheme is consistent with maps made from scientific acoustic surveys (Fig. 10), which unfortunately, however, do not cover all key periods. This could explain why length at maturity is higher (28–29 cm total length) in studies related to the Mauritanian EEZ than off Senegal and further south (Wague and M’Boudg, 2002).

Although this alternative hypothesis deserves more exploration, it also has weaknesses. It does not explain (1) the continuous presence of a single mode at 27 cm total body length mode (22 cm fork length) off Senegal during the last two quarters, which is incompatible with the accepted high growth rate of this species (22 cm during the first year); (2) the enormous deficit of the mode 30–31 cm (25–26 cm fork length) in Senegal. Using a model of growth and migration, Fréon (1988) demonstrated that the above-mentioned two anomalies could be easily explained by the conventional scheme of migration. Our more recent data (Fig. 9) confirms that the missing mode is present in Mauritania.

A second alternative migration scheme, that – in a sense – is reconciliatory to the two above schemes, was suggested by Fréon (1988) who mentioned that the observed presence of adult fish in northern Mauritania and southern Morocco all year round suggests the existence of a sedentary fraction of the stock in this area. This makes sense because the upwelling intensity and the productivity are always high in this region (Fig. 7), in contrast to the situation observed further south. Nonetheless, Fréon did not contemplate how this fraction is related to the rest of the stock and whether it is characterised by smaller-scale migration.

Data analysed in this paper do not allow a final conclusion on the migration scheme to be drawn because the information about fish smaller than 30 cm is limited and there are no clues about nursery areas. Logbook data only cover the Mauritanian EEZ, and migrations can be hidden by seasonal changes in catchability. Furthermore, abundance indices are only available for the strata where fishing took place. Sardinella can swim fast enough so that migrations can be hidden by spatio-temporal changes in catchability when using abundance indices. To conclude, more work is necessary before a final conclusion on the crucial issue of stock(s) structures and migrations can be drawn. At present it seems that the discussion about stock structures is worth reopening, and that this topic should be a priority for future research at the regional scale.

### 4.5. Perspective

Future research should focus on gathering evidences which could make it possible to select the proper hypothesis on migrations and stock structures. Like with most clupeids, sardinella are fragile and thus studies cannot easily benefit from tagging experiments. Despite fine spatial subdivisions in the statistical analysis, this work can be further refined with the use of VMS data in order to understand fishermen’s strategies and possibly refine some migration characteristics of sardinella. The disaggregation of day- and night-hauls data as well as sardinella two species identification should be requested in the logbook. Similar fishing activity data of the small-scale fishery, appropriately sampled and properly analysed should be made available, for the most important landing points along the Mauritanian coast. It should include sampling for length data that would provide crucial information on the migrations of the stock. Research surveys at sea should also target the migration/stock structures issue. For modelling purposes, single stock migratory patterns should be explored with a regional spatially disaggregated model. The way the corresponding parameters can be estimated should be carefully analysed. The influence of changes in catchability according to season, area and year should be studied, so that they are taken into account in the definition of effective annual fishing effort. For example, if catchability is multiplied by 3 during the spawning season, fishing effort during this season must be weighted, which would lead to overall annual effective time series very different from the basic time series of the annual nominal fishing effort. The conditions under which real time abundance indices and abundance forecasts can be modelled should be analysed, since this is a perquisite for management decisions. Such management schemes should take
into account that sardinella catches probably rely on several age groups as far as we can infer from the range of most body length distributions (Fig. 9), and that catches and catch rates follow relatively smooth multimodal curves.

To conclude, any research on sardinella in the area can only be efficient at the regional scale, involving at least Senegal and Morocco. The first step would be a wider analysis of all available logbook data in the region, on the basis of political agreements between these countries.

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Appendix A. Supplementary data
Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.02.020.

References


