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Climate modulates the effects of *Sardinella aurita* fisheries off Northwest Africa

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Abstract

The fluctuating abundance of round sardinella (*Sardinella aurita*) in Mauritanian waters over the past ca. 20 years can be related to environmental dynamics off Northwest Africa. Trends in the fishery are evaluated using FAO data, acoustic surveys, and catch statistics from the EU fleet (1996–2006). Remote sensing data demonstrate rising annual sea surface temperatures, up to 3 °C higher than the long-term average in 2002–2003, following a shift in ocean climate in 1995. Fish abundance and repeated expansion of the sardinella population in the past 10 years are attributed to favorable oceanographic conditions and increased recruitment success. Sardinella thrives with intense upwelling and high primary production during spring, and retention of waters over the shelf during summer and autumn. The stock of *S. aurita* over the Northwest African shelf oscillates with the cold–warm states of the habitat. Favorable hydrographic conditions and extended habitat has resulted in unprecedented rise of sardinella abundance in the late 1990s, which was counterbalanced by the impact of fisheries. A backshift to a cold-state ecosystem, with extensive regional upwelling and decreased sardinella habitat, would topple that balance.

Keywords: Pelagic; Sardinella; Remote sensing; Oceanography; Northwest Africa

1. Introduction

1.1. Research question and context

In the Eastern Central Atlantic (Fig. 1), the dynamics of an eastern boundary current interacting with trade wind-driven upwelling control a marine ecosystem with exceptionally high primary and secondary productivity (Cury and Roy, 1989; Binet, 1997; Demarcq and Faure, 2000). This productivity sustains a large variety of pelagic species, including commercial fish species sardinella (*Sardinella aurita* and *Sardinella maderensis*), horse mackerel (*Trachurus trachurus*, *Trachurus trecae* and *Caranx rhonchus*), mackerel (*Scomber japonicus*) and sardine (*Sardina pilchardus*). The pelagic stocks off West Africa have been exploited since the 1960s by long-distance fleets from Eastern Europe (Boely and Fréon, 1979). With the collapse of central economies in Eastern Europe after 1990, these state-supported fleets declined, and their role was taken over by private companies in Eastern and Western Europe. From 1996, a fleet of modern trawlers from the European Union began working in the Mauritanian Exclusive Economic Zone (EEZ = 200 nm).

An EU fisheries agreement with Mauritania has been effective since 2002 and is worth €80 million in subsidies annually. From 2006, €11 million of this amount is allocated for implementation of national fisheries management, to stimulate sustainable exploitation of the fish stocks. This reflects EU policies to better match and integrate its policies on fisheries, development cooperation and protection of biodiversity. The framework of international law for treaties protecting marine biodiversity is the UN Convention on the Law of the Sea (http://www.un.org/Depts/los). With the FAO Code of Con-

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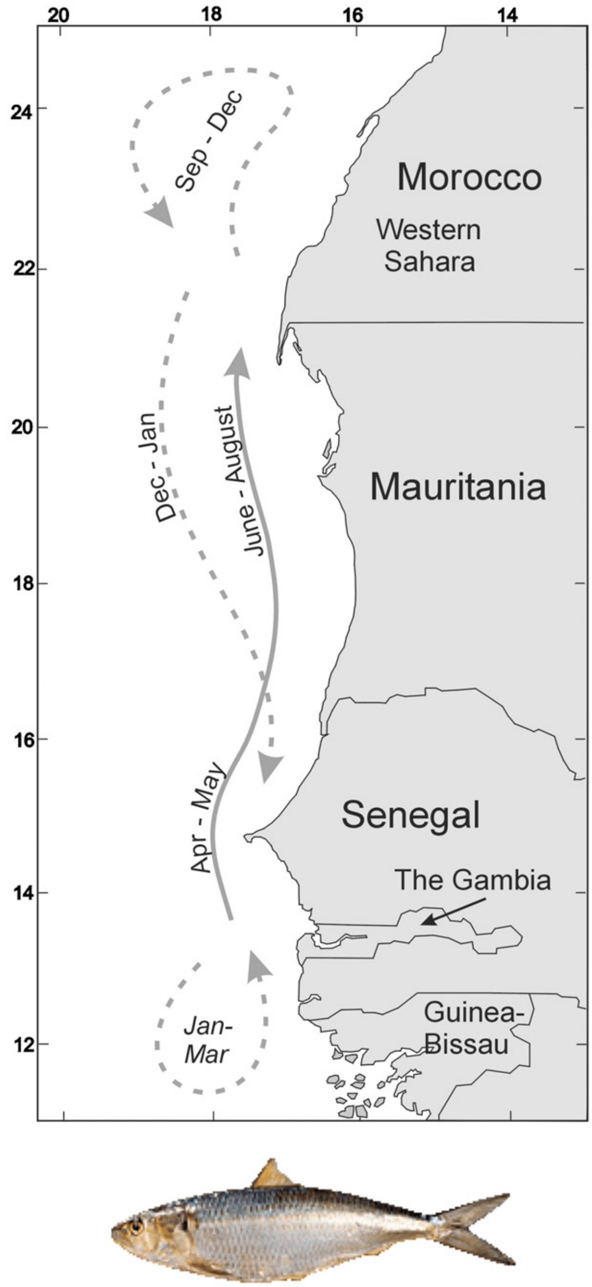

Fig. 1. Migration pattern of *Sardinella aurita* in West Africa, reflecting the characteristics of regional oceanography and seasonality. For the position of this box see Fig. 10.

duct for Responsible Fisheries (1995: http://www.fao.org/fi) this defines the rights and general duties of a coastal state on the use of its marine living resources. Much however depends on the capacity and willingness of the nation to monitor the fisheries, and on the science that may result in the adaptation of appropriate measures and regulations.

While fisheries management in more developed countries is based on extensive programmes of data collection and analysis, detailed information on Northwest African stocks is patchy and incomplete. The activities of the European vessels in the Mauritanian EEZ were monitored between 1998 and 2006 through a Mauritanian/Dutch research project that studied the relation between fish catches, hydrography, and megafauna bycatch (Zeeberg et al., 2006). EU vessels concentrated mainly on round sardinella (*S. aurita*), the most abundant species at the time of the arrival of the fleet (ter Hofstede and Dickey-Collas, 2006). After some years of high catches, sardinella abundance started to decline and the fishery became oriented towards other species such as horse mackerel and sardine. Declining sardinella abundance (Fig. 2) was attributed primarily to overfishing (FAO, 2006a). However, due to the variable dynamics of the upwelling system it is likely that *S. aurita* distribution over the region is also affected by hydrographic conditions. Low catches in the early 1990s coincided with intense upwelling and generally cold regional conditions, but it is unclear to what extent ocean climate may have influenced the fishery.

Here we combine catch data from the EU fleet with the results from acoustic surveys collected during the Norwegian research program with R/V Fridtjof Nansen off West Africa. The Nansen data are available through the FAO and are also used in regional fisheries management working groups (e.g. FAO, 2006a,b). To explain variability in *S. aurita* catches and survey data, we use observational evidence collected on board the EU trawlers, and compare with ocean dynamics that may have influenced sardinella ecology and the success of these fisheries over the past two decades.

1.2. The fishery and ecology of *S. aurita* in West Africa

S. aurita occurs in the vicinity of several West African upwelling systems (Schmidt, 1972; Cury, 1991; Vakily and Pauly, 1995; Quaatey and Maravelias, 1999; Binet et al., 2001). A single population or a number of subpopulations constituting one metapopulation is assumed to occupy waters over the Northwest African shelf (Fig. 1), between Senegal, Mauritania and Morocco (Garcia, 1982). To the south of Senegal, *S. aurita* is also found in some quantities, but the connection of these fish to the more northern populations is unknown. Catch statistics for *S. aurita* have been grouped in Fig. 2 for Senegal + Gambia, and for Mauritania + Morocco. The fishery in Senegal and The Gambia is conducted exclusively by artisanal fishermen, operating from canoes (piroques). In Mauritania and Morocco, the main fishery is conducted by large pelagic trawlers.

The total regional catch of *S. aurita* (Morocco, Mauritania, Senegal and The Gambia) increased from 280,000 tonnes in

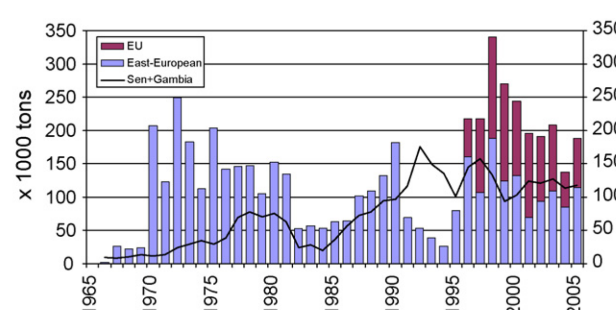

Fig. 2. Total catches *S. aurita* in Morocco + Mauritania (bars) and Senegal + Gambia (line). Data from FAO (2006a).

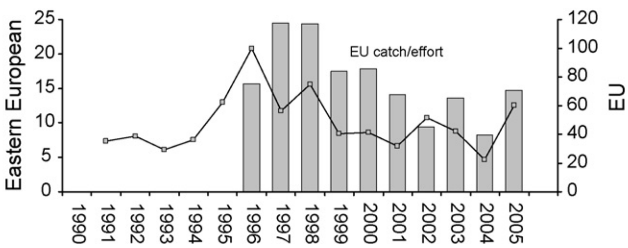

Fig. 3. Annual total sardinella catches of the Eastern European (line: Russia, Ukraine, and others) and EU industrial trawler fleets standardised per numbers of fishing days (corrected for horse power). Data from FAO (2006a).

1990 to 470,000 tonnes in 1998 (FAO, 2006b). In that year, the EU fleet accounted for 23% of the regional catch of this species with a total annual catch reaching 110,000 tonnes (Figs. 2 and 3). The artisanal fishery accounted for about 50,000 tonnes in southern Mauritania and 15,000 tonnes in northern Mauritania. These captures are taken in the 12-mile zone from which the industrial fishery is excluded. *S. aurita* is often caught together with the related species *Sardinella maderensis*. This species is shorebound and less migratory than *S. aurita*. The percentage of *S. maderensis* decreases in the catches during summer, when *S. aurita* abundance increases. On average it comprises only 7% of the total sardinella catch (ter Hofstede and Dickey-Collas, 2006).

The commonly accepted migration pattern for *S. aurita* in northwest Africa (Fig. 1) shows fish moving between Senegal and Morocco (Boely and Fréon, 1979; Garcia, 1982). Sardinella passes Mauritania both on their way north and on their way south. During the northbound migration, the fish stay for several months in Mauritania and are then targeted by the pelagic trawlers. Around August/September catches in Mauritania decline, presumably because the fish continue their migration towards Morocco. The return migration from Morocco to Senegal is less understood. Catches in Mauritanian waters during November–February are very low, indicating that the fish on their southbound migration are out of reach for the trawlers. *S. aurita* has been observed to migrate offshore over deep water (300–1500 m) at depths of 100–300 m, occasionally ascending to surface layers (Schmidt, 1972; Binet et al., 2001). However, there are also reports of adult sardinella migrating close inshore during winter. Artisanal fishermen in St. Louis, Senegal refer to fish arriving in December and January as “4 m sardinella”. This name obviously does not refer to the length of the fish, but to the water depth in which they are found (B. Samb, personal communication).

The migration and abundance of *S. aurita* in most parts of the world is controlled by water temperature and other hydrographic parameters. In the Gulf of Guinea the abundance of *S. aurita* has fluctuated strongly between 1963 and 1992 in response to annual changes in the extent of the upwelling habitat (Binet and Servain, 1993; Binet, 1997; Binet et al., 2001; Koranteng and McGlade, 2001). Long-term variations in small pelagic fish stocks are attributed to recruitment success as a result of oceanographic conditions during the juvenile stage (e.g. Cury and Roy, 1989; Cury et al., 2000; Huggett et al., 2003). Over the northwest African shelf, high primary production, low turbulence, and a favorable circulation in summer provide an “optimum environmental window” for both spawning and foraging (Cury and Roy, 1989; Demarcq and Faure, 2000). This window appears to shift over the region, evoking sardinella migrations.

1.3. Regional oceanography

The oceanography over the Mauritanian shelf (water depths <200 m) represents a dynamic balance between flow from the north and flow from the south, largely controlled by atmospheric variability (cf. Mittelstaedt, 1991; Hagen, 2001). Records of sea-level pressure (SLP) from Nouadhibou and Nouakchott document a maximum SLP in spring (January–April), consistent with the seasonal strengthening of the Azores High and associated N-NE winds. The trade winds thus intensify south of 20°N in spring and north of 26°N during summer. Between 20–26°N (Cape Blanc to Cape Bojador) a strong alongshore wind blows all year round. As a result the offshore Ekman transport and associated upwelling are permanent between 20–26°N, and seasonal during winter and summer south of 20° and north of 26°N, respectively.

During the upwelling season, the influx of nutrients creates high primary productivity in the photic zone. When the winds weaken in May/June and upwelling lessens, the surface waters become stratified and unproductive. In this period, a front of Tropical Surface Water (TSW) propagates north until an ocean boundary establishes around 20°N (Arfi, 1987; Barton, 1998; Hagen, 2001). This stable, convergent front between permanent upwelling waters and advected TSW serves as a feeding area for a large variety of pelagic species, including many megafauna species (Zeeberg et al., 2006). The advection of TSW is probably generated through a downwelling process associated with remotely forced coastally trapped Kelvin waves (Schouten et al., 2005). A sea level rise associated with these waves depresses the thermocline and invokes a poleward, surface-intensified geostrophic current transporting TSW (Stramma and Schott, 1999).

The Senegalese EEZ, where the sardinella resides during winter (January–April), is dominated by several cyclonic (cold-cored) gyres, including the Guinee Dome at 10°N, 20°W, driven by the North Equatorial Counter Current (Tomczak and Godfrey, 1994, p. 237). Because the cyclonic rotation induces upwelling (doming of the thermocline), these features are more productive than the surrounding waters. In Ghana, field sampling has shown that these eddies serve as retention cells for eggs and larvae (Binet, 1997).

2. Materials and methods

2.1. Fisheries data

To understand changes in sardinella abundance and distribution in Mauritanian waters, we compare fisheries and survey data with ocean dynamics observed by satellites. The fisheries data includes both observational data and catch-effort records, i.e. catch positions and logbook data provided by EU freezer trawlers between 1996 and 2006. These 125–145 m-long trawlers, with a total engine power of 9000–18,000 hp, are equipped with modern fish finding instruments that enable them to locate fish schools within a radius of 3 km around the vessel. When searching for fish schools, the vessels tend to work together and can screen the entire Mauritanian fishing zone within a few days. We therefore assume that in general the fleet will find sardinella concentrations whenever they occur within Mauritanian waters.

The catch rate of the vessels will depend not only on fish abundance but also on schooling behavior. In the early part of the season (April–May) the fish move fast, at speeds up to 7 knots, and even the most powerful vessels are unable to catch them. In this situation, fish abundance apparent on the sonar screen is not reflected by catch results. Conversely, at other times of the year when the fish are easier to catch, the vessels may locate schools and take good catches, while the overall abundance of the stock is low. Because of these uncertainties, the use of catch rates as an index of fish abundance can be disputed. For a lack of better data, however, catch per day, in combination with observational data provided by fishermen and fishery observers, does provide a first-order approximation of the presence and relative abundance of the fish. For this purpose we use this measure, although we are fully aware of its restrictions.

Latitudinal and longitudinal shifts in the fishery have been assessed through calculation of a centre of gravity (CG) of the catches for each month. This CG is the average position of the catches during 1 month, weighted by the size of the individual catches. The longitudinal shift of the fishery is defined as the distance between the CG and the 12 nm fishing limit (trawlers are not allowed to fish within 12 miles off the coast). The distance between the CG and the Moroccan border at 20°46′N provided a measure of latitudinal shifts.

2.2. Acoustic data

Acoustic surveys by the Norwegian research vessel "Dr. Fridtjof Nansen" provide quantitative abundance estimates. This vessel has conducted regular surveys over the West African shelf since 1995. Standard equipment used during these surveys is a EK-500 *Simrad Scientific Sounder* used in combination with the BI (Bergen Integrator) software. Identification of echo traces is done by fishing either a pelagic trawl or a bottom trawl. Results are reported annually to the FAO Working Group on Small Pelagic Fish in West Africa (FAO, 2006a). The surveys are normally conducted in November and give a snapshot picture of the regional distribution of the fish at this particular time of year. At the time of the survey, most *S. aurita* have migrated from Mauritania into Morocco. The results of the acoustic surveys in Mauritania, therefore, differ considerably from the results of the fishery in this area; the latter taking place in summer when the bulk of the stock is found in Mauritanian waters.

2.3. Remote sensing and oceanographic data

To identify characteristic patterns in the ocean climate we combine remotely sensed data on the ocean surface (sea surface temperature, ocean color and surface geostrophic currents based on sea surface height) and compare these with the literature on regional oceanography off northwest Africa. The observer program on board the EU trawlers included daily monitoring of ocean conditions through remote sensing, using commercial packages (OrbImage *Orbmap*) and sea surface temperature (SST) charts acquired by NOAA satellites (NOAA-12, 14–17) and received by the University of Las Palmas de Gran Canaria (ULPGC). The Advanced Very High Resolution Radiometer (AVHRR) on the NOAA satellites measures SST in the first millimeters of the surface layer and correlates >0.9 with ship measurements (engine cooling water intake) and buoy data. This is consistent with assessments of a thermally well-mixed upper water column, with a wind-mixed layer of ca. 10 m and thermocline at ca. 50 m in summer and 70 m in winter (Barton, 1987, 1998; Ould-Dedah and Wiseman, 1999). The satellite images have a 1 km resolution and are taken to reflect mesoscale surface temperature patterns (Van Camp et al., 1991; Nykjær and Van Camp, 1994). Temperature is used as indicator for water masses, to distinguish between upwelled, mixed water and stratified, unproductive water. Geostrophic surface flow demonstrating advection was projected over the SST images from altimetric data provided by radar satellites. Surface geostropic currents can be retrieved through the Global Ocean Observation System (GOOS) (http://www.aoml.noaa.gov/phod/dataphod/work/trinanes/INTERFACE).

In addition to the high-resolution SST imagery, monthly averaged, 9-km gridded SST-data from the Jet Propulsion Laboratory were used to extract a time series of monthly SST and to produce anomaly data for each month from January 1985 to January 2005 (Vazquez et al., 1998). The data have a 0.088° pixel resolution in a cylindrical equidistant projection (Standard Mapped Image). Best descending (night) imagery was selected to eliminate the effects of surface heating over calm, unmixed water. These monthly composites provided SST time series data for the Senegalese and Mauritanian spawning grounds. Phytoplankton density (chlorophyll α) was obtained from ocean color satellite images provided by the SeaWiFS satellite. Due to atmospheric disturbance by dust and clouds, plankton images are only incidentally available.

3. Results

3.1. Seasonal and inter-annual variations in fish distribution and abundance

The catch rate of sardinella in the EU fishery demonstrates a consistent decline over the period 1998–2005 (Figs. 3 and 4). Catch per day in 2005 was less than half the level it held in the first years of the fishery. As a result of declining sardinella catches, the fishery reoriented towards other species, notably cold-water species sardine and horse mackerel. The percentage contribution of sardinella to the total catch has declined after 1999 from 90% to a low around 40% in 2004.

Although some quantities of *S. aurita* are taken in the Mauritanian EEZ in each month of the year, there is a clear seasonal pattern in the fishery. On average, EU catches gradually increase from January to May (Fig. 5a). This is followed by a peak season

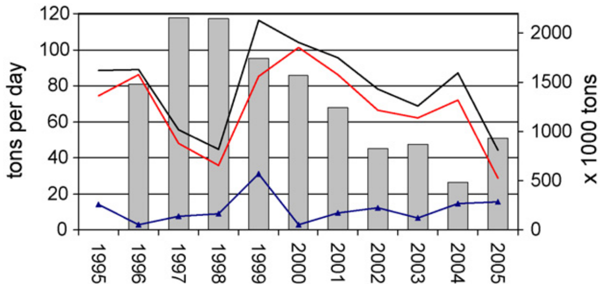

Fig. 4. Annual catch per day of sardinella in the EU fishery (bars) in Mauritania compared with R/V Fridtjof Nansen biomass estimates (*Sardinella aurita*). Stock numbers have been grouped for Morocco and Mauritania (top line); for Mauritania (middle), and Senegal (bottom w/markers). See also Fig. 7.

in June–August, when the bulk of the population has arrived from Senegal. From September to December, catches in Mauritania decline, probably reflecting migration of the fish towards Moroccan waters when upwelling in Mauritania ceases. The timing of the fishery has narrowed and from 1998 is concentrated in the summer months (June–August: Fig. 5b). Catches have declined in autumn. From 2003 there has also been a sharp reduction of catches in the early part of the season (January–April).

A shift of the fishery towards the coast in the second half of the year is evident from the eastward displacement of the center of gravity of the monthly catches (Fig. 6A). As upwelling-favoring winds decrease and water temperature rises, the water in the offshore areas becomes stratified. Chlorophyll imagery demonstrates that in this situation, productivity and food availability is restricted to shallow coastal waters (depth <50 m) where upwelling still continues. During the fishing season, the center of gravity also shifts northward, reflecting the overall northward migration of the population. Over the period of observations there is a general northward displacement of the annual center of gravity (Fig. 6B).

3.2. Acoustic observations

The acoustic data from R/V "Dr. Fridtjof Nansen" for the combined stock in Northwest Africa show a period of high abundance during the years 1999–2001, followed by a gradual decline (Fig. 4). The high stock level is preceded by a sharp dip in the years 1997–1998. However, these were years when the EU fleet in Mauritania took its highest catch rates and fishing skippers reported an abundance of sardinella schools. We

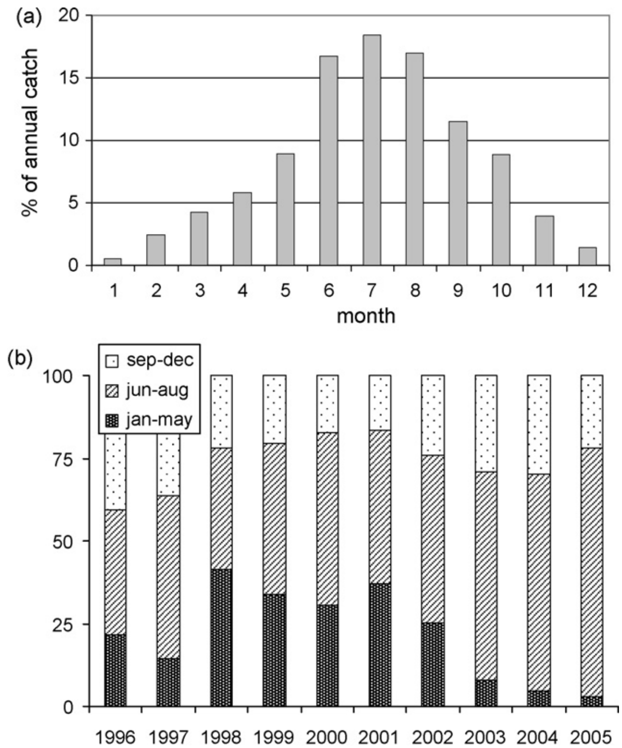

Fig. 5. (a and b) Seasonal distribution of sardinella catches by the EU fleet in Mauritania. (a) Average for 1996–2005. (b) *Sardinella* catch per season: disappearing catches in spring reflect intense upwelling and adjusted fishery.

therefore assume that the acoustic surveys in November 1997 and 1998 have missed part of the stock. Both data sets, however, indicate that *S. aurita* reached a peak abundance in Northwest Africa in 1999–2001, and that the abundance declined in later years.

Acoustic data also demonstrate the distribution of the stock over the various national zones. Surveys found an increased abundance of *S. aurita* in the Moroccan zone in 2000 and later years (Fig. 7). Apparently, the northward migration of the fish was more pronounced during this period than in the preceding years. It should be noted that these graphs represent the distribution of the stock in November, i.e. the time of the year when the stock has reached its northernmost distribution. Sardinella biomass reduction in Mauritania from 1.8 to 0.3 million tonnes between 1995 and 2002 (Figs. 4 and 7), and simultaneous increases in Morocco and Senegal suggests decreased residence time of the stock in Mauritanian waters. The acoustic surveys in

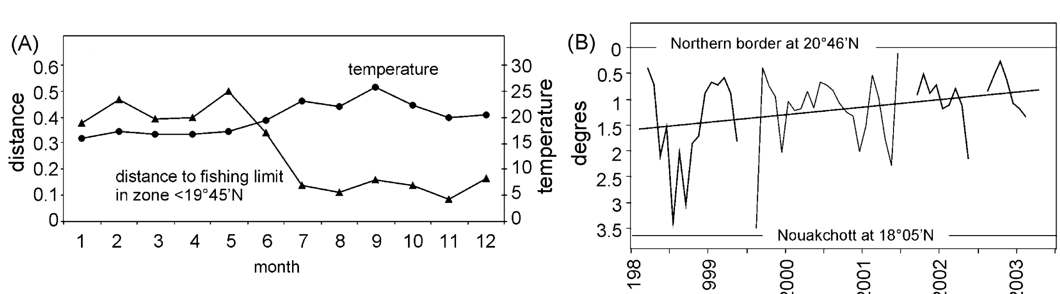

Fig. 6. (A and B) Shift of the fishery's Centre of Gravity: E-W (A) and N-S (B) between 1998 and 2004. In the second part of the year the fishery concentrates in shallow waters (water depth 40–50 m) over the shelf.

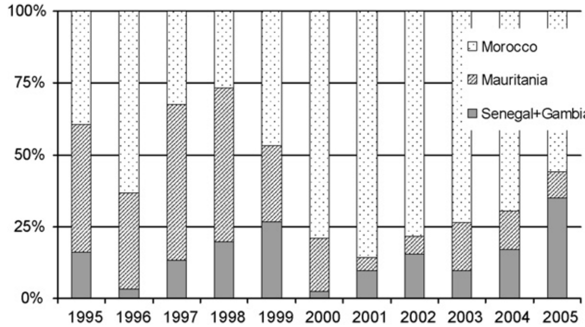

Fig. 7. Acoustic biomass *S. aurita* by country: contribution by each country to regional total (percentages). There is a marked shift towards Morocco in warm years 2000–2004.

November do record a remaining amount of *S. aurita* in Senegal, after the main body of the stock has migrated north. These are mainly juveniles that do not yet participate in the migration towards Mauritania and Morocco.

3.3. Oceanographic observations

Oceanographic changes, as observed in the SST and altimetry (surface flow) images, may influence the timing and speed of sardinella migration and the success of recruitment. SST and ocean color (chlorophyll) images reveal a semi-permanent meander detaching from the shelf at ∼16°N in spring and ∼17°N in summer–winter (Fig. 9A and B). The meander probably reflects the advection of Tropical Surface Water interacting with coastally trapped Kelvin waves and/or deviation of poleward flow through form drag of the continental shelf (Hill and Hickley, 1998, p. 41; Schouten et al., 2005). The feature appears to sustain several anticyclonic eddies centered around 18.30°N and especially prominent and stable in summer. The remote sensing data in July 2002 demonstrated the development of a large anticyclonic (warm-cored) eddy (Fig. 9C). The cell developed over a period of about 10 days and dissipated during weeks thereafter. The eddies, hence, may prolong the residence time of water masses over the Mauritanian shelf up to 1 month.

The 1985–2005 SST time series (Fig. 8a) demonstrates a shift from a period of below average temperatures in 1985–1995 to above average temperatures in 1996–2005. This upswing in SST off Northwest Africa since 1995, with summer SST up to 3 °C higher than the 1985–2006 average, is associated with changes in the regional pressure field. The close relationship between wind strength and direction and upwelling/SST off Mauritania was well established by earlier authors (e.g. Arfi, 1987; Mittelstaedt, 1991; Binet, 1997). Both the cold anomalies of 1993–1994 (−2.8 °C) and warm anomaly of 1995 (+2.8 °C) are connected with increased/decreased upwelling-favorable winds (Fig. 8b). The above-average temperatures of the past decade (1996–2005) were apparent mainly during summer and autumn (July–January). The spring periods (February–June), in contrast, were relatively cold (Fig. 8a).

Because the upwelling is wind-driven, temporal variability of the ocean climate at inter-annual scales reflects the seesaw of atmospheric pressure over the eastern tropical Atlantic, as documented by the North Atlantic Oscillation index (e.g. Jones et al., 1997). On sub-decadal and decadal time scales, climate extremes appear to be generated by El Niño-like warm events

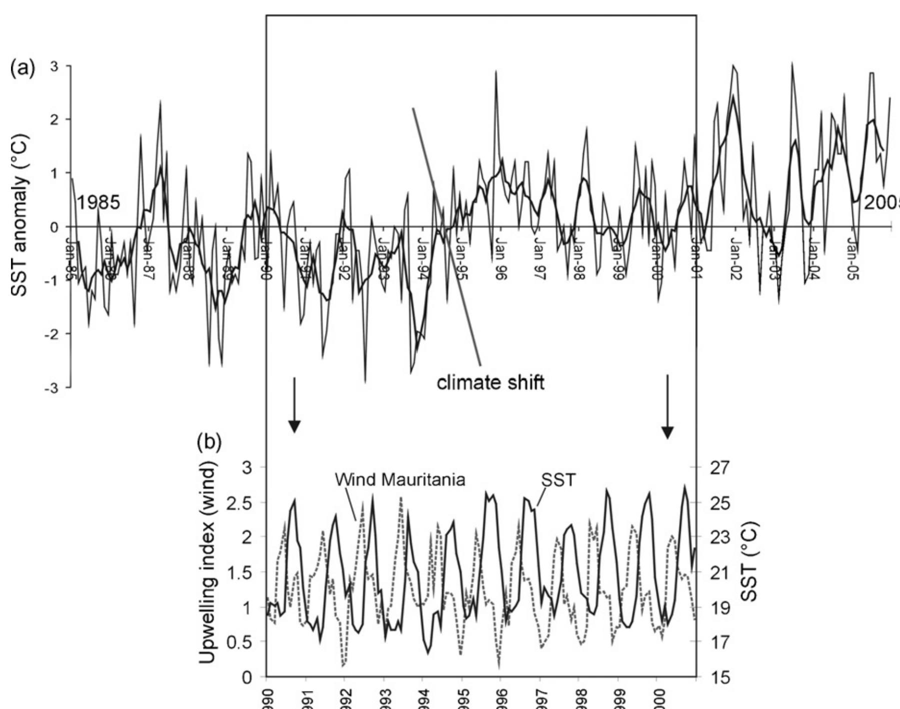

Fig. 8. (a) Smoothed (5-month moving average) SST anomalies for 19.5°N. (b) Box highlights SSTs in combination with the upwelling index (broken line) based on wind data from Nouadhibou Airport, Mauritania. Over the 1995–1996 climate shift, low winds and low upwelling generated immediate regional warming. The spatial extent of these temperature events is shown in Fig. 10.

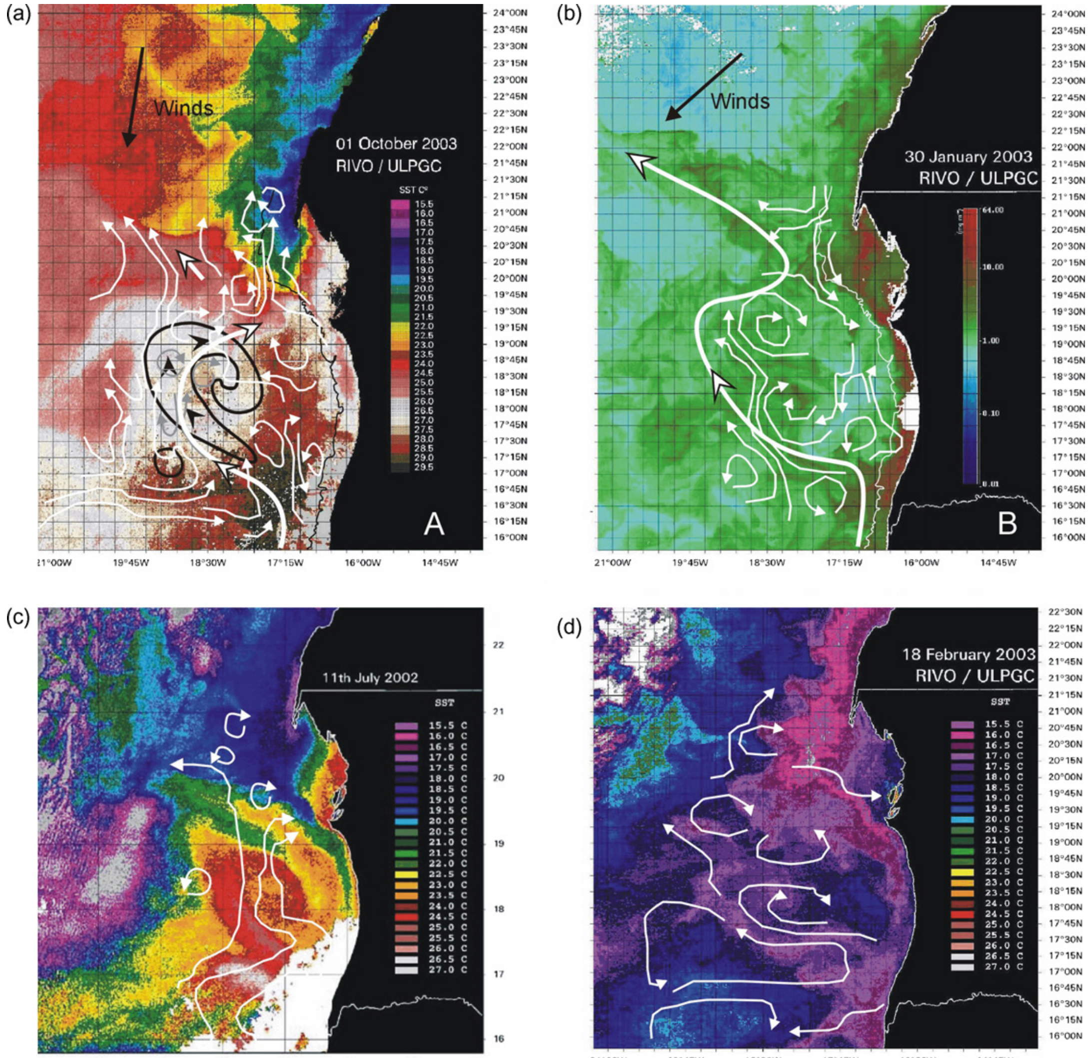

Fig. 9. SST charts (range 15–30 °C) of the Mauritanian upwelling and (B) an ocean color chart showing phytoplankton density (range 0.01–64 mg/m^3). (A) 1 October 2003, (B) 30 January 2003, (C) 11 July 2002, and (D) 18 February 2003. White arrows represent geostrophic surface currents derived from satellite altimetry. The anticyclonic eddy in C (black structure in A) is a warm-cored, semi-permanent feature, possibly generated by poleward flow along the shelf (white meander in A and B). The 200 m isobath (black in A; white in B) indicates the continental shelf margin.

(Binet et al., 2001; Hagen, 2001). The Atlantic Ocean component of an El Niño-event is a downwelling Kelvin wave that propagates along the equator from South America to Africa in 4 months, increasing thermocline depth and geostrophic currents (e.g. Binet et al., 2001). The 1997 El Niño (Pacific) coincided with anomalous warmth (+2.1 °C) off Africa in February–March 1998 (Figs. 8 and 10) and apparent strengthening of the northward currents between Senegal and Mauritania.

4. Discussion

4.1. Environmental controls on the seasonal migration of S. aurita

The strong seasonality of sardinella abundance apparent from catch data (Fig. 4) is connected with the upwelling-dominated SST cycle. Our observations suggest that round sardinella off Northwest Africa seek the temperature fronts and high primary productivity associated with upwelling. The fish appear to avoid entering the upwelling areas, possibly due to low oxygen content of these waters (as a result of oxidation processes: Barton, 1998; Tomczak and Godfrey, 1994) and/or cold temperature (15–21 °C). Sardinella filters planktonic organisms from the water column, often targeting specific zooplankton, including juveniles of their own species. This is a distinct difference from sardine (*S. pilchardus*), which forages on phytoplankton and seeks the centre of upwelling regions for spawning (Boyer et al., 2001; Ettahiri et al., 2003). Sardinella migration appears to be primarily driven by foraging needs and spawning preferences.

Over the Mauritanian shelf, temperatures are below 21 °C during winter (January–March: Fig. 9). Although primary production is at a maximum in these months, wind mixing is high, and “upwelling filaments” (Nykjær and Van Camp, 1994; Barton, 1998) transport waters away from the coast to the unproductive ocean (cf. Rodrigues et al., 1999; Demarcq and Faure, 2000; Bécognée et al., 2006). These conditions are unfavorable for *S. aurita* because the growth of the fish is limited by temperature and spawning will be less successful (cf. Cole and McGlade, 1998). At this time of the year, most *S. aurita* are found in Senegalese waters where the temperature remains above 21 °C. The productivity of the Senegalese waters is high during winter, as a result of river run-off after the rainy season, localized upwelling, and cyclonic eddies retaining productive waters.

Around May, the hydrographic conditions off Senegal become less favorable, with SST rising towards ca. 25 °C, stratification of surface water, and decreasing food availability. The buildup of vertical stratification appears to prompt *S. aurita* migration. When the strength of the trade winds decreases in April/May, tropical water advects north with strong surface geostrophic currents as demonstrated by sea surface height imagery (http://www.aoml.noaa.gov/phod/dataphod/work/trinanes/INTERFACE). The bulk of the sardinella population then moves north along this “highway” towards Mauritania, seeking a more suitable foraging and spawning habitat in the northern extremity of the distribution area.

During May–July, the fish profit from high productivity in the Mauritanian zone by feeding and spawning at the same time. Spawning conditions are optimal during this period. The semipermanent eddies observed in the satellite imagery enhance survival of fish larvae by increasing residence time of waters across the Mauritanian shelf by up to 1 month. This permits the development of a copepod generation, an important feed for sardinella larvae (Binet, 1997). In August/September, high water temperatures indicate stratification of surface waters and strongly reduced productivity, as demonstrated by ocean color images (Fig. 9B). Increased surface heating and reduced wind speeds limit upwelling to a narrow coastal strip, and the sardinella follow the retreating productivity zone towards the coast. When food production is further reduced, the fish leave Mauritania and migrate north into Moroccan waters. Here upwelling continues all year round, and food remains abundant in autumn. It is uncertain what factor triggers the return migration from Morocco to Senegal: lower temperatures, food shortage, or a biological clock connected with solar elevation and shifting circulation patterns. Because little is known about the behavior of the fish in Moroccan waters, this question remains to be answered.

4.2. Sardinella spawning strategy

There are substantial strategic differences in spawning cycle between *S. aurita* and more temperate clupeids such as Atlantic herring (*Clupea harengus*). Herring spawns only once a year at a specific time and place. The fish stop feeding several months before spawning, and they control their gonad development by staying in water masses of a certain temperature (Ottersen et al., 2005). This predetermined spawning guarantees optimum growth conditions for newly born larvae (Christensen et al., 1985), usually during a very short time interval. In the (sub)tropics, the environmental conditions that trigger spawning are less predictable, resulting in a strategy such as found in *S. aurita*, where fish spawn repeatedly as long as conditions remain favorable. To be able to do so, the fish must combine spawning with feeding. Maturity data collected by observers on board the EU trawlers between 2000 and 2003 show that both gonad weight and fat content reach maximum values during summer (ter Hofstede et al., 2007; cf. Bécognée et al., 2006).

In other tropical regions where *S. aurita* occurs, spawning is also geared to periods of high ocean productivity. In Ghana, fish spawn during upwelling periods when the mean SST falls below 25 °C (Quaatey and Maravelias, 1999). This is comparable with water temperatures of 19–23 °C observed for sardinella catches in Mauritania. Off Venezuela and Equatorial Africa, turbulence and river discharge (Orinoco and Congo rivers) determine optimum feeding conditions and thereby the spawning period (Freon et al., 1997; Binet et al., 2001). Sardinella spawning in the Northwest African upwelling region is linked with fairly saline and productive water of the oceanographic boundary in summer, because egg and larval concentrations are found in water of 18–21 °C at 35–37 psu (Ettahiri et al., 2003; Bécognée et al., 2006). Our observations indicate that the Northwest African sardinella spend the winter months in tropical water and in spring occupy the northern shelf region, likely expanding their habitat with advecting surface water.

4.3. A climatic interpretation of S. aurita abundance variability

The shift into warmer sea surface temperatures in 1995 appears to have shifted the optimal habitat for feeding and spawning for round sardinella northwards towards Mauritania and West Sahara (20–23°N). *S. aurita* is a warm water species that has its basis in the waters of Senegal and countries further south. It is only in summer that the main part of the population migrates north to feed and spawn off Mauritania and Morocco. Rising water temperature and extension of sardinella habitat has lead to an overall increase of the recruitment to the stock. This trend is clearly exhibited by an expansion of adult stock in 1997–1998 (Fig. 4) and increased catch from 1995.

S. aurita has a high growth rate, and fish recruit to the fishery already at an age of 1–2 years (Boely et al., 1982). Increased recruitment since 1995 will have led to the observed expansion of adult stock in 1997–1998. The abundance of *S. aurita* in Mauritania may thus be explained by a change in distribution area of the fish, a shift of spawning from Senegal to the north, and an increase in population size as a result of strong recruitment. A similar oscillation, with habitats and recruitment alternating between warm and cold states, has been described for the Angola-Namibia region (10–20°S), dominated by the Benguela Current (Binet et al., 2001).

Sardinella catches in the Mauritanian EEZ are low both during extremely cold periods and extremely warm periods. In cold periods, as in 1990–1995 (Fig. 8), sardinella abundance appears to be reduced in the northern region, either because the fish avoid cold waters and/or because recruitment success is negatively influenced by the prolonged upwelling process. Under these circumstances (strong spring-winds, ‘filament’ transport, and concomitant turbulence), the development of zooplankton food sources is limited, while survival of phytoplankton feed-

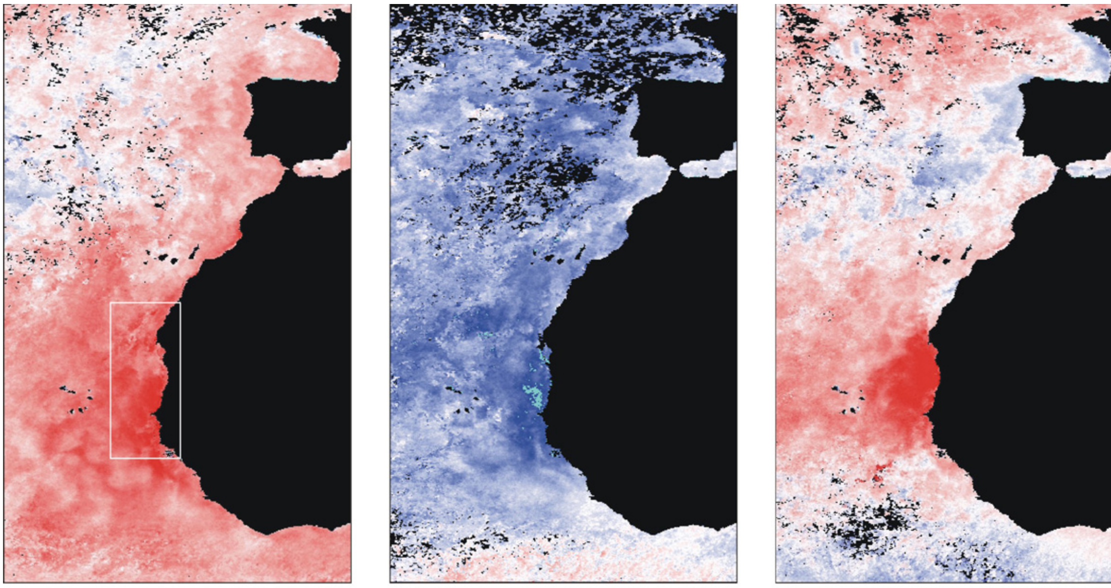

Fig. 10. Spatial extent of temperature anomalies in Fig. 8a for February 1998 (El Niño) and December 1993 and 2001.

ers such as sardines may be enhanced. Low sardinella catches during most of the 1980s and the early 1990s (Fig. 2) probably signify low abundance as a result of the cold ocean climate (Fig. 10).

Low catches in warm periods, as in 2002–2004 are attributed to decreased residence time of the fish in Mauritania and shortening of the fishing season. Over the transient period, 1996–2001, with cold, productive springs and favorable summers, sardinella was abundant, giving rise to the expansion of a multinational fishery. EU vessels arriving between 1996 and 1998 were attracted by the exceedingly high densities of sardinella in Mauritanian waters. This is consistent with the acoustic surveys, which demonstrate a considerable stock size increase in the mid-1990s to more than 2.5 million tonnes regionally (FAO, 1983, 1987, 1989, 1992; cf. Boyer et al., 2001).

The EU fleet had a significant impact on the *S. aurita* stock as demonstrated by the decline of the catch per day in this fishery over the period 1997–2005. The decline of the stock apparent from total catches (Fig. 2), catch rates (Fig. 3), and acoustic estimates (Fig. 4), indicates that sardinella is presently overexploited (FAO, 2006a). The close association of sardinella abundance with the ocean climate, and significant changes of ocean dynamics in the past decade, warrants strict management measures, because the effects of climate may aggravate the effects of fisheries and *vice versa*.

5. Conclusions

- Seasonal migration of *S. aurita* between Senegal, Mauritania and Morocco is attuned to the seasonality of the Northwest African upwelling. With localized upwellings and cyclonic eddies retaining productive waters, the oceanographic situation at Senegal during winter is similar to the situation on the Mauritanian shelf in summer. Therefore, the fish are found in tropical water in Senegal in winter. With the extension of tropical surface water in spring and summer, the fish extend their habitat north into Mauritania.
- The ocean climate off northwest Africa experienced a shift to a warmer regime since 1995, with maximum sea surface temperature (SST) anomalies observed during summer-autumn 2002–2003 (+3 °C higher than the long-term average). The shift in ocean climate is associated with changes in the regional pressure field and low winds during a change to low monthly indices of the North Atlantic Oscillation.
- As a result of the 1995 climate shift, the Mauritanian waters became more suitable as feeding and spawning area, and overall recruitment to the stock increased. Shortening of the upwelling season and steady increase of sea water temperatures in summer and autumn, however, have caused the fish to shorten their stay in Mauritanian waters. In the past 5 years, this has resulted in a shortening of the fishing season and reduction of catches in Mauritania during the last months of the years.
- The stock of *S. aurita* over the Northwest African shelf oscillates with the cold-warm states of the habitat. Favorable hydrographic conditions and extended habitat have resulted in a strong rise of sardinella abundance in the late 1990s, which was counterbalanced by the impact of fisheries. Stock decline apparent from total catches, catch rates, and acoustic estimates, indicates that sardinella is presently overexploited. A backshift to a cold-state ecology would topple the balance.

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