



The selection of spawning location of sardine (*Sardinops sagax*) in the northern Benguela after changes in stock structure and environmental conditions

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ABSTRACT

Most reports on the distribution of spawning areas of sardine (*Sardinops sagax*) in the northern Benguela originate from the 1970s and 1980s. The northern Benguela system was in a high upwelling regime during those decades. Since the early 1990s upwelling favourable winds have decreased and a trend of increasing sea surface temperature (SST) has been observed. Changes in the structure of sardine stock in the northern Benguela have been observed and it has been suggested that a reduced biomass and changes in stock structure has led to decreased spawning in the favourable southern locations, thus preventing a recovery of the sardine stock. The present paper on the contrary shows that there has been a shift in spawning location from the less favourable northern areas in the early 1980s to spawning areas further south in the 2000s. Thus, the failure of the northern Benguela sardine stock to recover since its collapse in the late 1960s cannot be explained by spawning in less favourable areas. The shift in preferred spawning location to more southern areas since the 1980s was to be expected with a general warming of the northern Benguela system. Alternative explanations for the failure of the sardine stock to recover such as a reduction in average length as well as length at 50% maturity, leading to a reduction in reproductive out-

put, increased predation pressure, and increased low oxygen waters are proposed.

Key words: environment, northern Benguela ecosystem, sardine, spawning location, stock structure

INTRODUCTION

The northern Benguela upwelling system is one of four major eastern boundary upwelling systems in the world. Its dynamics have been extensively reviewed by several authors (Nelson and Hutchings, 1983; Shannon, 1985; Lutjeharms and Valentine, 1987; Fennel, 1999). The system is characterized by strong seasonal signals with higher water temperatures during austral summer and autumn (December to March) and lower temperatures during winter and spring (August to November) (Bartholomae and van der Plas, 2007), when upwelling favourable southwesterly winds are strongest.

Despite the clear seasonal cycles in the northern Benguela in wind, water temperature and dissolved oxygen concentrations, high inter-annual variability is observed (Bartholomae and van der Plas, 2007). Furthermore, there is evidence that long-term fluctuations in the system have occurred. Peard (2007) describes variability in the intensity of upwelling favourable winds at Lüderitz. The 1960s were characterized by weak upwelling favourable winds, the 1970s and 1980s were characterized by strong upwelling favourable winds, whereas since the 1990s the winds off Lüderitz have again been well below the long-term average, indicating a low upwelling regime. Satellite-derived data from the Angola-Benguela frontal region show a steady increase in sea surface temperatures since the early 1980s (Monteiro *et al.*, 2008). This increase as well as an increase in the time lag between seasonal warming at Cape Frio and the following upwelling peak at Lüderitz are likely to contribute to the intensification of seasonal hypoxia in the northern Benguela and hence a long-term decline in ecosystem function (Monteiro *et al.*, *op. cit.*).

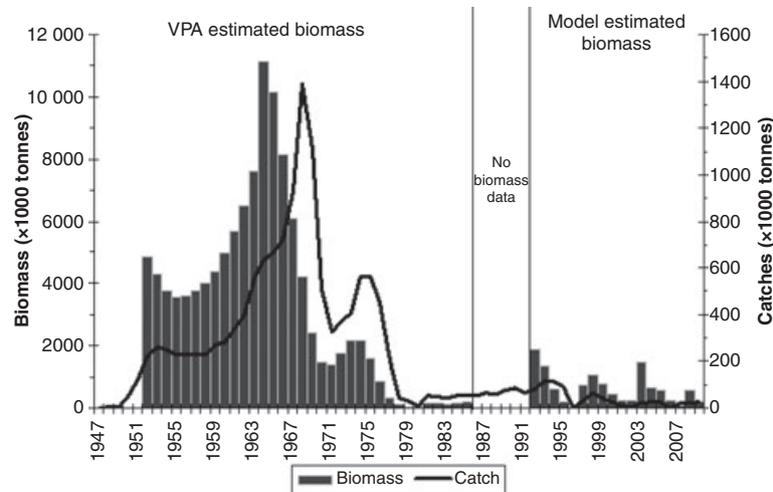
The sardine (*Sardinops sagax*) stock in the northern Benguela was estimated at around 11 million tons in

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Figure 1. Biomass and catches of sardine in northern Benguela from 1947 to 2008 (adapted from Kirchner *et al.*, 2009).



the mid-1960s (Thomas, 1986; le Clus *et al.*, 1988). There was a rapid decline by the late 1960s following intense fishing (Crawford *et al.*, 1987) and low recruitment (Thomas, 1986). By 1971 the stock was estimated to be over a million tons (Thomas, *op. cit.*; le Clus *et al.*, 1988) and has fluctuated at low levels since then (Fig. 1) (Kirchner *et al.*, 2009).

In the beginning of the 1990s the sardine stock increased slightly and by the end of 1991 it reached the highest recorded level since the 1970s. The stock gradually declined to a very low biomass subsequent to a low oxygen event in 1994 and a Benguela Niño in 1995 (Fig. 1). Since then the stock fluctuated at low levels, never exceeding a total biomass of 1 450 000 tons; three acoustic surveys estimated virtually zero sardine biomass (Kreiner and Boyer, 2001; Tjizoo *et al.*, 2006; Moroff, 2007). Along with the collapse of the stock, several changes in biological indicators such as a decrease in the number of age classes, as well as changes in length distribution and age at maturity were observed (Thomas, 1986; Fossen *et al.*, 2001).

The first reports of spawning of the sardine stocks in the northern Benguela came from Hart and Marshall (1951), who reported sardine spawning to occur mainly between 22°S and 26°S. A few years later Matthews (1964) confirmed these spawning distributions.

After the collapse of the sardine stock, two main spawning areas have been described in the northern Benguela, one off central Namibia, between 22°S and 25°S and another further north between 19°S and 21°S (O'Toole, 1974, 1977; King, 1977; Crawford *et al.*, 1987). The spawning season is described to be between August and April, with peaks in

September/October and March (O'Toole, 1977). Gonadosomatic information of the 1980s and 1990s (Kreiner *et al.*, 2001) as well as back-calculated birth date information of young fish (Hardmann-Mountford *et al.*, 2002) indicate that spawning is currently still peaking at the same time of the year.

Daskalov *et al.* (2003) investigated the relationship between sardine recruitment and environmental indices. Prior to the mid-1980s sardine recruitment was positively correlated with SST and negatively correlated with wind strength. These relationships reversed during the 1990s. Two hypotheses were formulated to explain these shifts: the first addressed a change in environmental regimes and the second suggested that these changes can be attributed to altered population structure and spawning behaviour, accepting that spawning in the Walvis Bay region has diminished after the sardine stock collapsed in the early 1970s, as suggested by Crawford *et al.* (1987).

Tjizoo (2008) has investigated spawning habitat selection of sardine with regard to temperature, salinity and oxygen during the 1980s and 2000s and could not find any significant differences in spawning habitat selection during those two time periods. He described sardine to spawn over a wide range of environmental conditions, without clear selection for certain conditions.

Variability in spawning areas of pelagic fish over time in other marine systems has been shown by different authors (Lynn, 2003; Stratoudakis *et al.*, 2003; Bellier *et al.*, 2007). In the Bay of Biscay, sardine egg distribution depends on the extent of the cold pool water mass (Bellier *et al.*, 2007), while Lynn (2003) has shown that off California zooplankton biomass as

well as temperature are important parameters in describing sardine spawning habitat. Off the coast of Portugal a reduction in the area of sardine egg distribution in the north has been observed, whereas in the south, the area of sardine egg distribution has increased (Stratoudakis *et al.*, 2003). They suggest that the change in spawning area is at least partly due to changes in the population structure of the sardine population (low number of young fish).

Most published data on the spatial distribution of early life stages of sardine in the northern Benguela originates from a time when the system was in a high upwelling regime and the stock was in a much healthier condition than during the 2000s. In this paper, biological parameters of sardine were compared for the past decades to investigate changes in stock structure. We further compared the preferred spawning areas of sardine between the early 1980s and the early 2000s in order to determine whether spatial changes in the spawning locations have occurred under different environmental regimes and altered stock structure.

MATERIALS AND METHODS

Sardine length-frequencies were compared using data from commercial landings. The recent length measurements were recorded as total length in centimetres (cm). Historical data was taken from Matthews (1960) and converted from caudal length to total length using the conversion formula from Kreiner *et al.* (2001). The two periods from 1952–1957 ('1950s') and 1997–2008 ('2000s') were compared. The Kolmogorov–Smirnov (KS) test was used to test whether length–frequency differences between the two periods were significant. This test is commonly used to compare two continuous distributions or to compare observed distribution with theoretical distribution. The test is important when comparing two distributions that could differ in their mean, variance, skewness or kurtosis. Distributions are compared based on their individual cumulative distribution function (CDF). The *t*-test was used for testing the null hypothesis of equal mean and equal variance (Daalgard, 2002).

Biological analyses were based on port samples (for details on sample collection see Kreiner *et al.*, 2001). Random samples from the commercial catches were collected for further biological analyses (total length, weight, sex, maturity, gonad weight, gutted weight and otolith collection). Total length was measured to the nearest mm below.

For length at 50% maturity (L_{50}) the biological information from commercial sampling was pooled for each of the periods of the 1980s (1984–1990), 1990s

(1991–1999) and 2000s (2000–mid-2009). Maturity was assessed by visual inspection of gonads.

The maturity ogives for the three periods (1984–1990, 1991–1999, 2000–2009) were compared using the logistic generalized linear model (GLM). Unlike the case with simple linear regression, GLMs possess two important attributes: first, they allow one to characterize the response distribution (in this case binomial); secondly, they define the corresponding link function that allows the different types of response variable to be modelled. The link function allows for a transformation of the response to a scale in which the relation to the explanatory variables is linear. In the case of the logistic GLM applied in this study, a logit link was used, taking the following form (Daalgard, 2002):

$$\text{logit } p = \log \left[\frac{p}{(1-p)} \right] \quad (1)$$

Logistic GLM models the log of the odds ratio as a function of the explanatory variables. Generally it takes the following form:

$$\ln(O_i) = \ln \left(\frac{P_i}{(1-P_i)} \right) = f(X_i) = \mu + \beta_1 * X_{1i} + \beta_2 * X_{2i} + \dots + \beta_p * X_{pi} \quad (2)$$

Fitted probability values are obtained as follows:

$$P_i = \frac{e^{f(x)}}{1 + e^{f(x)}} \quad (3)$$

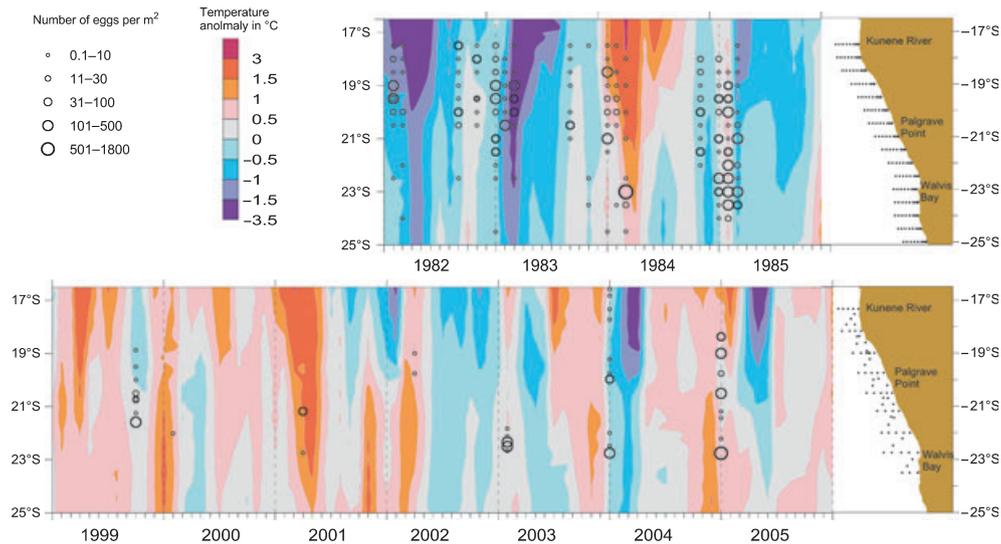
where O_i is the odds ratio, $\ln(O_i)$ the log of the odds ratio, P_i can be interpreted as the probability of sardine being mature, μ is the intercept term, β_1 is the regression parameter for predictor X_1 , and β_2 is the regression parameter for predictor X_2 .

Model selection was based on comparing the Akaike information criterion (AIC) value of models without year effect, models with main effect of length and year, and models with interaction of length and year. The model with interaction effect (model 3) had the minimum AIC values and hence was found to be the most parsimonious in terms of the AIC (Table 1).

Table 1. Results of the logistic GLM fitted to the maturity data.

Model No.	Model specification	Deviance	AIC
Model 1	$Y \sim \text{Length}$	1371.55	1564.06
Model 2	$Y \sim \text{Length} + \text{Year}$	523.169	719.679
Model 3	$Y \sim \text{Length} + \text{Year} + \text{Year} : \text{Length}$	260.653	461.163

Figure 2. Sardine egg distributions of the surveys overlaid on a Hovmüller plot of the temperature anomalies for the early 1980s and 2000s. Note that during the 1980s monthly surveys were conducted during the austral summer months, whereas during the 2000s only one survey per annum was conducted. On the right the typical cruise tracks of the surveys are shown as well as the important locations on the Namibian coastline.



Based on AIC, the best performing model was found to be the one with interaction effect, between length and year, where the slope and intercept of the maturity depend on the year.

To compare spawning areas between periods, the horizontal distribution of eggs was used. Sardine eggs were collected along the Namibian coast during regular SWAPELS (South West Africa Pelagic Surveys) cruises from 1982 to 1985. Ichthyoplankton was sampled with double oblique Bongo net tows with mesh sizes of 300 and 500 μm (for more details on the survey design of SWAPELS see Tjizoo, 2008). The typical sampling stations are shown in Fig. 2 (upper panel).

Annual ichthyoplankton surveys on board the Norwegian research vessel *Dr Fridtjof Nansen* were conducted from 1999 to 2005. The timing of these surveys depended on the target species and availability of the research vessel. One survey was conducted in September/October (1999) and two during February (2000 and 2003), April (2001 and 2002) and January (2004 and 2005). The spring survey in 1999 focussed on hake, whereas the surveys conducted in late austral summer focussed on horse mackerel, and the others on sardine and anchovy. Surveys generally covered the Namibian coast between 23°30'S and 17°15'S, some reaching into Angolan waters (2000, 2001, 2002 and 2004). However, the survey in 2003 only covered the area between 23°30'S and 20°00'S due to different survey objectives. The typical sampling stations of the surveys are shown in Fig. 2 (lower panel).

Eggs and larvae were sampled with a Multinet[®] (Hydrobios, Kiel, Germany) plankton net with a mesh size of 405 μm and an opening of 0.5 \times 0.5 m. A flowmeter was mounted in the opening of each of the five nets to record the filtered volume. A Scanmar depth recorder with acoustic transmission to the vessel was mounted on top of the Multinet. Sampling stations were positioned every 20 nautical miles and in the nearshore regions every 15 nautical miles.

Latitudinal egg distribution from all surveys was plotted and overlaid on a Hovmüller plot of temperature anomalies (Bartholomae and van der Plas, 2007) for the two time periods under study using SURFER 9[®] (Colorado, USA) (Fig. 2).

The preference of sardines spawning in certain parts of the coast was assessed using the single parameter quotient (SPQ) analysis on the egg distribution data. SPQ assesses the null hypothesis of even distribution of the response variable (in this case density of sardine eggs) across a gradient of a predictor of interest (in this case latitude and longitude). The quotients are calculated by taking the ratio of the percentage of the response variable in a given environmental bin (e.g. latitudinal and longitudinal bins) to the percentage of stations in that environmental bin. The version of the SPQ method used in this study differs from the traditional version in that upper and lower confidence intervals are calculated with the estimated quotient. This analysis was done using a modified version of the SHACHAR package developed by Bernal *et al.* (2007).

The confidence intervals were estimated by bootstrapping the original data 999 times. SPQ analysis was done including all months and repeated using only data collected during January, February and March. SPQ analysis is generally used to investigate the pattern of preference of spawning habitat by comparing the null hypothesis of even distribution of eggs with the observed egg distribution with respect to a covariate of interest (Twatwa *et al.*, 2005).

Single parameter quotient analysis was done for both time periods (early 1980s and 2000s) to identify preference for spawning location. In this analysis the original SPQ values are accompanied by the upper and lower confidence intervals obtained from bootstrapping. Observed SPQs above the upper 95% confidence interval line indicate a preference for that value. Taking the classification of Bernal *et al.* (2007), values lower than the upper 95% confidence interval and higher than the lower 95% confidence interval indicate tolerance values. SPQ values lower than the upper confidence interval indicate tolerance range and SPQ values lower than the lower confidence interval indicate avoidance. All analyses were conducted using R software (R Development Core Team, 2010).

RESULTS

Several changes in biological indicators have been observed since the stock collapsed. The mean length of sardine caught has decreased from 25.5 cm in the 1950s, when the biomass was estimated at 4 million

tonnes, to 21.25 cm in the 2000s (Fig. 3), when the biomass was <1 million tonnes. The KS test showed that this decrease is significant. As the KS test compares distributions in their mean, variance, skewness and kurtosis, a subsequent analysis was conducted to check whether the mean and variance of the two distributions were actually different; both were found to be significantly different between the two distributions. The total length distribution of the sardine caught by the pelagic fleet since 1997 was 15–26 cm, whereas in the 1950s it was 17–31 cm (Fig. 3).

Length at 50% maturity (L_{50}) continuously decreased over the last three decades. In the 1980s L_{50} was at 19.95 cm, in the 1990s it decreased to 19.16 cm, whereas in the 2000s it has been at an all time low of 16.46 cm (Fig. 4). Thus since 1984, L_{50} decreased by 3.49 cm. The maturity ogives of the three time periods were statistically different in terms of both slope and intercept.

Temperature anomalies show that from 1982 to 1985 the region was dominated by cold anomalies, the only exception being 1984, when a Benguela Niño was observed in the region (Shannon *et al.*, 1986). The spawning seasons from 1999 to 2005 were dominated by warm anomalies (Fig. 2) (Bartholomae and van der Plas, 2007).

Single parameter quotient analyses of both survey time series (early 1980s and 2000s) have shown that recently there has been a shift in the preferred latitude of spawning towards more southerly regions, as indicated by observed SPQs above the upper 95% confi-

Figure 3. Comparison of the percentage length frequency of sardine catches made between 1952–1957 and 1997–2008.

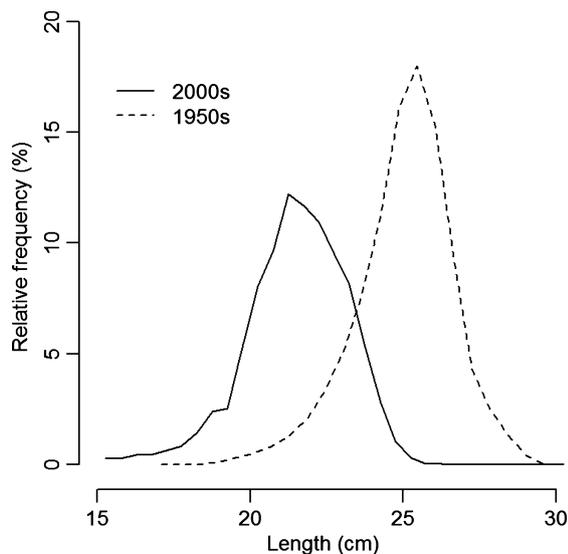


Figure 4. Length at 50% maturity (L_{50}) per decade since 1984 as sampled from commercial landings.

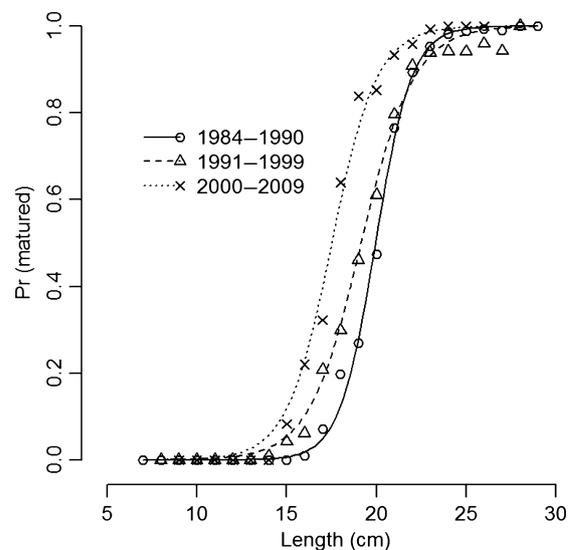


Figure 5. Preferred spawning location of sardine in terms of latitude for the 1980s (top panel) and 2000s (bottom panel). Solid lines are observed SPQ values, whereas the dashed lines are the upper 97.5% and lower 2.5% of the simulated SPQ, under the null hypothesis, containing the 95% confidence interval. The histograms show the distribution of sampling stations by latitude.

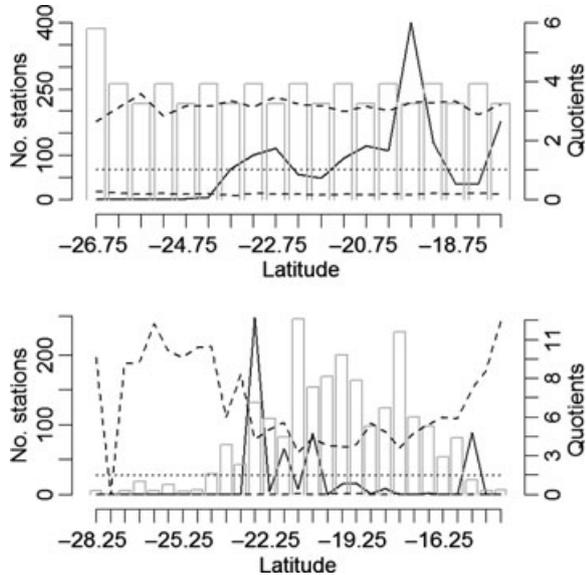
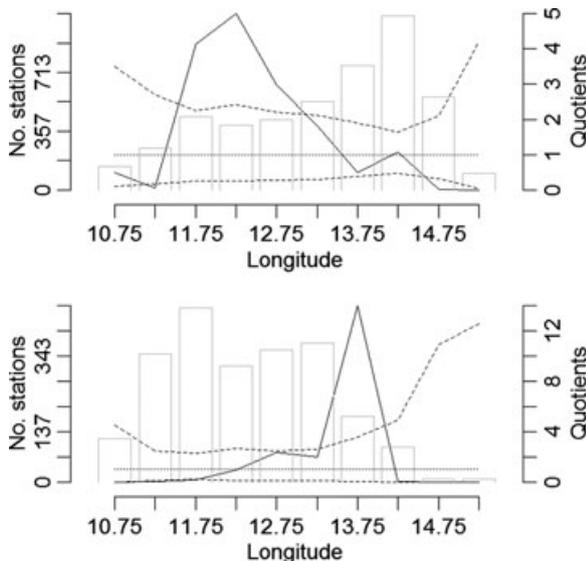


Figure 6. Preferred spawning location of sardine in terms of longitude for the 1980s (top panel) and 2000s (bottom panel). Solid lines are observed SPQ values, whereas the dashed lines are the upper 97.5% and lower 2.5% of the simulated SPQ, under the null hypothesis, containing the 95% confidence interval. The histograms show the distribution of sampling stations by longitude.



dence interval line (Fig. 5). In the 1980s, sardine preferred to spawn along the part of the coast around 19.5°S, whereas in the 2000s the preferred location is farther south, around 22.5°S. The shift in location with regard to longitude was from around 12°E to 13°45'E (Fig. 6). The SPQ analysis was done for all months of the year and repeated using only the months of January, February and March to check for the effect of difference in the sampling months. The result showed no difference in preferred spawning location with respect to latitude or longitude due to selection of sampling month.

DISCUSSION

The present analyses of stock status indicators from the last 25 yrs show that the sardine stock is currently under stress and that significant changes in size distribution and maturity ogive have occurred. Sardine larger than 26 cm total length are virtually absent in the current stock. In the past, larger sardine were mainly females (Matthews, 1964). The decrease in length in comparison with the 1950s leads to a lower fecundity of the sardine stock, as large sardine spawn more and larger eggs, which have a better chance of survival (le Clus, 1989). In later years, the sardine stock was largely composed of zero and 1-yr-old fish with some 2-yr-olds; the mean length of the population being about 21 cm (Fig. 3). Between 1952 and 1967 (before the 1968 collapse) <3% comprised zero and 1-yr-old fish. The mean length of the population was 25.5 cm and sardine reached the age of up to 11 yrs (Thomas, 1986).

A decline in length and age at maturity has been reported for several species to be a sign of stress on the stock, often observed after a collapse in biomass (Trippel, 1995; Watanabe and Yatsu, 2006; Olsen *et al.*, 2004). Matthews (1964) described sardine in the northern Benguela in the late 1950s, well before the collapse of the stock, as becoming sexually mature for the first time between 20.8 and 21.4 cm total length (17.0 and 17.5 cm caudal length, respectively), and 50% were mature between 22.0 and 23.7 cm TL (18.0 and 19.4 cm caudal length, respectively). Maturity data from the mid-1970s (Wysokinski and Krakus, 1977) show that sardine started spawning around 19.5 cm for males and around 21 cm for females. Currently, we see an onset of spawning around 14–17 cm. The reduction in L_{50} from around 22.0 cm in the late 1950s to 16.46 cm in the 2000s translates to a reduction of about 25%.

It has been shown for herring that repeat spawners, i.e. older spawners, are more likely to produce stronger

year classes than first-time spawners (Oskarsson and Taggart, 2010). Berkeley *et al.* (2004) and Bobko and Berkeley (2004) have shown that larvae of the black rockfish (*Sebastes melanops*) produced by larger females have higher survival rates than those produced by younger females. They suggest that this is because older females have more metabolic reserves and can invest more energy into reproduction. According to le Clus (1989) the reproductive potential of large sardine females (26.2–27.3 cm), as indicated by the total number of spawnings per year, is at least five times that of medium-small females (22.6–23.7 cm), three times that of medium females (23.8–24.9 cm) and twice that of medium-large females (25.0–26.1 cm). In other words, the total number of spawnings increases by 50–70% with each 1-cm increase in length. Davies (1956) showed that the number of eggs produced per female and the size of the eggs also increases with the size of the fish, indicating that larger females have higher reproductive output.

The length distribution of sardine caught by the pelagic fleet in the last decade ranges from about 15 to 26 cm. Comparing the recent length distributions to the length classes le Clus (1989) analyzed for her studies, it is obvious that the reproductive potential of the Namibian sardine stock is greatly reduced due to the low number of large fish in the population. In fact, the largest size class that le Clus (1989) analyzed does not exist in the population at this stage and even the medium-large females are only found in very low numbers. As the spawning stock currently consists virtually of only smaller females, the total number of spawnings as well as the number and quality of eggs per spawning are greatly reduced. Not only does this mean that fewer eggs are produced but, probably more important, the chances of a spawning during a period of favourable oceanographic conditions is also reduced. The reproductive potential of the sardine stock is therefore currently greatly reduced.

The SPQ analysis showed that during the 2000s the preferred latitudes for spawning were around 22°30'S, the area just north of Walvis Bay, which has previously been described as the most suitable area for pelagic spawning in the northern Benguela according to Bakun's triad hypothesis (Bakun, 1996). Here the coastline follows a slightly concave orientation and the shelf is fairly wide (Boyd *et al.*, 1987), which creates a relatively sheltered area conducive to near-surface thermal stratification (le Clus, 1990). During the early 1980s, the preferred spawning locations of sardine were around 19°30'S, where the shelf is narrower and conditions are much more variable due to the close proximity to the Angola–Benguela frontal

zone and the strong upwelling cell off Cape Frio (19°S) (Kirchner *et al.*, 2009). The shift in spawning location with regard to longitude from around 12° to 13°45'E can be explained by the slight northwest orientation of the Namibian coast.

The hypothesis put forward by Crawford *et al.* (1987) that the Walvis Bay area has diminished in importance as a spawning area after the stock collapse in the 1970s has since been quoted and described by several authors (Cole, 1997; Boyer and Hampton, 2001; Daskalov *et al.*, 2003; Bakun and Weeks, 2006; Alheit *et al.*, 2009). However, le Clus (1990) found that during the 1980s, well after the collapse of the sardine stock, sardine were found to spawn along the same latitudinal range as during the 1960s. Only during cool years did sardine spawn mainly in the northern areas (le Clus, 1990). Our results confirm that the central Namibian coast is still an important spawning area during at least some periods of the spawning season (January–March), despite the very low abundance and altered stock structure of the sardine spawning stock in Namibian waters. A shift in spawning away from the favourable Walvis Bay area is therefore not the reason for the reversal of the environment–fish relationship, as hypothesized by Daskalov *et al.* (2003), or the failure of the sardine stock to recover. le Clus (1991) observed spawning of sardine and anchovy in the areas off Walvis Bay during warmer years in the 1980s, whereas during cooler years, spawning of both species was confined to areas north of 22°S. Although no major environmental anomalies were observed during the recent study period, Bartholomae and van der Plas (2007) show that there has been a higher frequency of warm water events during the late 1990s to early 2000s compared with the 1980s. With positive SST anomalies observed in the northern Benguela system in the 2000s and a general warming of the system (Monteiro *et al.*, 2008), it would thus be expected that sardine eggs would be found predominantly off the central Namibian coast during more recent years. Selection of spawning location for the northern Benguela sardine seems to be driven by environmental conditions rather than biomass or stock structure. These findings are in contrast to MacCall's basin model (MacCall, 1990), which suggests that spawning habitat selection varies as a function of adult population size and population demographic structure.

Kreiner *et al.* (2009) have shown that sardine larvae are sensitive to dissolved oxygen concentration in the water column and avoid regions where dissolved oxygen concentrations are <2–3 ml L⁻¹. A more frequent and stronger build-up of poorly oxygenated waters and production of hydrogen sulphide due to

under-utilization of phytoplankton as a result of the low sardine biomass in the northern Benguela system has been suggested (Boyer *et al.*, 2001; Bakun and Weeks, 2004). Monteiro *et al.* (2008) describe the intensification of seasonal hypoxia. As the spawning area off central Namibia coincides with the region where the most severe hypoxic conditions develop, an increase in hypoxic conditions might negatively affect recruitment and hence play a role in the failure of the sardine stock to recover.

The recovery of the sardine stock might be hampered further by changes in the ecosystem functioning observed in the northern Benguela. Due to the low biomass of sardine, predation pressure has increased and may prevent the stock from recovering (Fossen *et al.*, 2001), in line with the predator pit hypothesis proposed by Bakun and Weeks (2006).

Several authors (Bakun and Weeks, 2006; van der Lingen *et al.*, 2006; Lynam *et al.*, 2006; Utne-Palm *et al.*, 2010) have suggested that the ecological niche opened up by the collapse of the sardine stock in the northern Benguela system has been taken over by other species such as jellies, gobies, mesopelagic fish and horse mackerel, hampering the recovery of the sardine stock. Conclusive evidence for the latter hypotheses, however, has not been provided.

We suggest that a reduced reproductive output due to changes in the stock structure as well as altered environmental conditions at the spawning locations, rather than the selection of spawning locations away from the favourable southern areas are the likely reasons for the failure of the sardine stock to recover in the northern Benguela. Changes in ecosystem functioning might also play a role. More research is required to investigate these possibilities.

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