Has the fishery contributed to a major shift in the distribution of South African sardine?

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Coetzee, J. C., van der Lingen, C. D., Hutchings, L., and Fairweather, T. P. 2008. Has the fishery contributed to a major shift in the distribution of South African sardine? – ICES Journal of Marine Science, 65: 1676–1688.

A major shift in the distribution of South African sardine (*Sardinops sagax*) has resulted in a significant spatial mismatch in fishing effort vs. fish abundance in recent years. The sardine fishery started on the west coast during the 1940s, and processing capacity there increased rapidly. This trend together with increases in annual landings continued up to the early 1960s, but then the fishery collapsed as a consequence of overfishing. The population then recovered steadily during the 1980s and 1990s, coincident with, but perhaps not entirely attributable to, the inception of conservative management practices, to support catches similar to pre-collapse levels. Since 2001, however, most of the sardine population has been situated on South Africa's south coast, far from processing facilities. Fishing effort has increased concomitantly on that coast, particularly during the past three years, reflecting the continued decline in the abundance of sardine on the west coast. Three hypotheses explaining the change in the distribution of sardine have been proposed: (i) intensely localized (i.e. west coast) fishing pressure depleted that part (or functionally distinct unit) of the population; (ii) the shift was environmentally induced; and (iii) successful spawning and recruit survival on the south coast contributed disproportionately more towards the bulk of recruitment, and progeny spawned there now dominate the population and exhibit natal homing. The first of these hypotheses is evaluated, and management implications of the shift discussed.

Keywords: biological indicators, distribution, environment, fishing effort, management, sardine, spatial dynamics.

Received 28 March 2008; accepted 4 August 2008.

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Introduction

The sardine (*Sardinops sagax*) is a major component of a valuable commercial, pelagic, purse-seine fishery that has been in operation since the 1940s off South Africa's west coast (Figure 1; Crawford, 1980; Crawford *et al*., 1987). Intensive exploitation during the first years of the fishery led to rapidly increasing annual catches through the 1950s, peaking at around 400 000 t in 1962. This high level of exploitation was unsustainable and preceded a massive decline in catches and the eventual collapse of the fishery by the late 1960s. Catches of sardine remained low during most of the 1970s, averaging ~80 000 t annually, then decreased even further during the 1980s to some 40 000 t annually. However, following the initiation in 1983 of a fishery-independent programme of acoustic surveys to estimate pelagic fish abundance (Hampton, 1987, 1992; Barange *et al*., 1999), a stock-rebuilding strategy, which included the setting and enforcement of an annual total allowable catch (TAC) based on the results of the surveys, was implemented during the mid-1980s. Subsequent recovery of the sardine stock to levels similar to those estimated before exploitation has been attributed in part to this conservative management policy (Cochrane *et al*., 1998). Catches of sardine averaged >200 000 t between 2001 and 2005 following a period of exceptional recruitment from 2001 to 2003. A prolonged period of poor recruitment since 2004 has led, however, to a rapid decline in sardine biomass and reduced catches since 2005.

The distribution and migrations of South African sardine at different life stages is not well understood, but has been assumed to be similar to that of anchovy, for which patterns have been well established (Crawford, 1980; Crawford *et al*., 1980; Shelton, 1986; Hampton, 1987; Hutchings *et al*., 1998). Therefore, the spatial dynamics of sardine are assumed to be influenced by the same environmental and oceanographic drivers that influence the spatial dynamics of anchovy.

The range of the South African sardine extends from southern Namibia, where the existence of an intense perennial upwelling cell off Lüderitz forms a thermal barrier to exchange with the Namibian sardine population (Lett *et al*. 2007), to Richard's Bay on South Africa's northeast coast (Beckley and van der Lingen, 1999). Most of the adult biomass has been confined to the southern west coast and Agulhas Bank, as far east as Port Alfred (Figure 1), during much of the period for which there are acoustic-survey results. However, whereas adult sardine have been concentrated mainly on the western Agulhas Bank (WAB) during their major spawning season in spring and late summer (Crawford, 1980; Crawford *et al*., 1980; Shelton, 1986; Armstrong *et al*., 1987, 1991; Hampton, 1992; van der Lingen and Huggett, 2003), shifts between predominantly west coast spawning and predominantly south coast spawning have been frequent in the past (van der Lingen *et al*., 2001, 2006). This ability to spawn in both areas is because sardine are relatively unspecific in

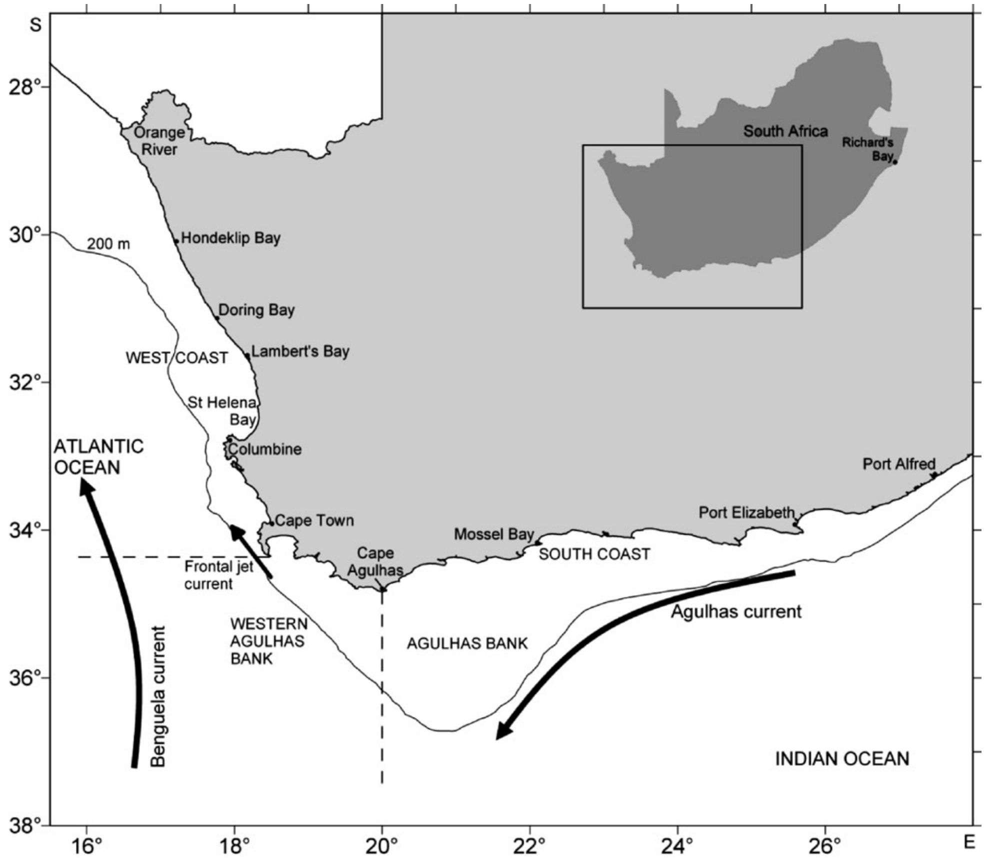

Figure 1. Map of South Africa showing the location of places mentioned in the text, the continental shelf (the 200-m isobath is shown) and the Agulhas and Benguela Currents. The west coast system is defined as extending from Cape Agulhas west and north, and the Agulhas Bank system as the area east of Cape Agulhas.

the selection of their spawning habitat (van der Lingen *et al*., 2001; Twatwa *et al*., 2005).

Ichthyoplankton is transported west and north towards the west coast nursery ground by a jet current (Figure 1) associated with a strong thermal front between cold upwelled water and warmer oceanic water flowing north along the shelf edge of the Cape coast (Shelton and Hutchings, 1982; Nelson and Hutchings, 1987; Fowler and Boyd, 1998; Miller *et al*., 2006). There is then a return migration of juveniles south along the west coast during late summer/early autumn, with recruitment to the adult population on the Agulhas Bank during autumn and winter (Hutchings, 1992; Hutchings *et al*., 1998, 2002; Barange *et al*., 1999).

Although a significant number of sardine recruits have been observed at times on the south coast during annual recruitment surveys conducted in winter (Barange *et al*., 1999; Beckley and van der Lingen, 1999), west coast recruitment remains dominant. A mechanism for south coast recruitment, which relies on local retention of eggs and larvae rather than transport to the west coast nursery ground, has recently been hypothesized (Lett *et al*., 2006; Miller *et al*., 2006), and it suggests that sardine may be able to optimize their reproductive strategy by spawning in either area, or sometimes in both (van der Lingen *et al*., 2001; Miller *et al*., 2006).

Adult sardine are generally targeted for canning, although some juveniles are caught as bycatch in the anchovy recruitment fishery on the west coast. During the early years of the fishery, most fishing effort was concentrated on the west coast (Crawford, 1980; Barange *et al*., 1999), where sardine were then abundant for most of the year, resulting in intensive development of infrastructure related to fish processing centred on the harbour at St Helena Bay (Figure 1). During the 1960s and 1970s, however, the fishing grounds for sardine expanded south and east as far as Cape Agulhas on the WAB (Crawford, 1980, 1981; Crawford *et al*., 1987). More recently, there has been an increase in fishing effort farther east (van der Lingen *et al*., 2005; Fairweather *et al*., 2006), particularly near Mossel Bay, following a shift in the distribution of sardine eastwards. The area west of Cape Agulhas, which incorporates the west coast, the southwest coast, and the WAB, contained the bulk of the sardine biomass during the 1980s and early 1990s (Barange *et al*., 1999). Although a gradual increase in the proportion of sardine biomass east of Cape Agulhas has been noted since 1995, most of the sardine were located on the WAB up to 1999, when for the first time since the acoustic surveys started, sardine biomass east of Cape Agulhas exceeded that to the west. This distribution pattern has persisted ever since and has had severe cost and logistical implications for the fishery and management of the stock, because of the mismatch between the locations of sardine schools and fish-processing facilities, as well as between fish abundance and fishing effort.

Several hypotheses have been suggested to explain the change in the distribution of sardine from the WAB to the central and eastern Agulhas Bank (van der Lingen *et al.*, 2005). These include local depletion of fish stocks on the west coast and WAB following higher levels of exploitation in the west than in the east, environmentally induced changes in the distribution of sardine spawners, and the fact that the successful south coast spawning and recruit survivorship contributed disproportionately more towards the recruitment, with progeny spawned in that region now dominating the population and exhibiting natal homing. The aim of this work is to evaluate the first of these hypotheses, which is related to fishing effort and local depletion, and to discuss the management implications of the sardine shift in distribution. Additionally, certain elements of the third hypothesis, which are linked to the first in terms of substock structure, and which may arise as a consequence of local depletion, are discussed.

Methods

Acoustic surveys and catch data

Two acoustic surveys have been conducted annually since 1984 to estimate the biomass and determine the distribution of small pelagic fish species off South Africa. The total biomass between Hondeklip Bay and Port Alfred is estimated in November each year, and recruitment is estimated in May between the Orange River and Cape Infanta, although recent surveys also extend to Port Alfred (Figure 1). Since 2000, survey effort towards the east has increased substantially during both surveys, as a result of a more easterly distribution of sardine and anchovy spawners. The surveys are conducted along a series of pre-stratified, randomly spaced, parallel transects, designed to obtain unbiased estimates of stock size and sampling variance (Jolly and Hampton, 1990; Barange *et al.*, 1999).

Trawl samples, conducted to determine fish size and species composition, were pooled per stratum to obtain size compositions of the entire populations surveyed. Individual trawl length distributions were weighted according to the acoustically estimated biomass near the trawl. Weighted size frequencies were computed for all strata, then summed to produce a species size frequency for the area west and east of Cape Agulhas. These length frequencies were transformed into numbers-at-age through the use of a von Bertalanffy growth curve calculated from a combination of November survey and commercial landings data (D. Durholtz, MCM, pers. comm.).

Data on the location, mass, and species composition of landed catches are collected by fisheries inspectors or monitors, or both, at designated landing points along the coast. Commercial catches are sampled at field stations next to the factories where most of the catch is landed for processing: data on species and size composition and biological characteristics have been collected routinely since 1953. Biological data collected include measurements of standard length, mass, sex, gonad mass, and macroscopic gonad maturity stage (Fairweather *et al.*, 2006). Individual landings are assigned a length frequency using the nearest (in space and time) sample length frequency, and catch length frequencies are raised according to their relative contribution to total catch to generate monthly and annual raised length frequency (RLF) tables. As for the survey data, RLF data were converted to numbers-at-age.

Spatial analysis of survey and catch data

Suggestions that sardine spawning is divided between two recruitment systems, with the west coast and WAB part of a west coast system and the remaining spawning areas part of an Agulhas Bank system (Lett *et al.*, 2006; Miller *et al.*, 2006), imply that a division of the continental shelf at Cape Agulhas to aid east–west comparisons is plausible (Figure 1). In this context, spatial statistics relating to survey distribution patterns, catch distributions, and biological indicators have been compared between the west coast and Agulhas Bank systems, respectively.

To evaluate the extent of mixing between the two areas, a spatial overlap index (SOI) between the west coast and Agulhas Bank systems at different levels of sardine biomass was computed in a rectangle stretching along the shelf ~120 nautical miles from 20 to 22°E (Cape Agulhas to Mossel Bay; Figure 1) and extending from the coast to the edge of the continental shelf. For each November survey, the proportion of positive elementary sampling distance units (~10 nautical miles long), where the density of sardine was greater than zero and which were within this area, was calculated and plotted against the total population size in November. The surface area occupied by the sardine population during each survey was computed by projecting the contoured density surface onto a plane, then calculating the positive area of the projection in square nautical miles.

Results

The total biomass of sardine increased gradually from <50 000 t in 1984 to some 2.5 million tonnes in 2000 (Figure 2), and although consecutive years of very good recruitment pushed the total biomass up to record levels above 4 million tonnes in 2002, a recent period of prolonged poor recruitment led to a decline in the adult biomass to <500 000 t in 2007.

Composite maps showing the distribution and relative abundance of sardine during periods of different biomass levels (low = 0–33.3 percentile; medium = 33.3–66.6 percentile; high = 66.6–100 percentile) are presented in Figure 3. The importance of the area west of Cape Agulhas, particularly the WAB but at times also farther up the west coast, as a preferred habitat during periods of low biomass is clear, with only low-density areas farther east (Figure 3a). At medium biomass levels, the WAB area remains the preferred area for sardine (Figure 3b), and the distribution there is expanded slightly north and south from that observed during periods of low biomass. The area occupied east of Cape Agulhas is also expanded significantly compared with that at low levels of biomass. At high biomass, the WAB remains important, but the area east of Cape Agulhas now supports most of the sardine biomass (Figure 3c).

A consistent separation is also evident (Figure 3) between sardine found west and east of Cape Agulhas, with overlap in the area (Cape Agulhas to Mossel Bay) between the two parts of the population only at very high levels of biomass. This is confirmed by the SOI (Figure 4), which shows an increasing presence of sardine in the overlap area between Cape Agulhas and Mossel Bay at higher levels of biomass. The increase in the total area occupied by sardine at higher biomass is also confirmed when calculating the area occupied by sardine as a function of biomass (Figure 5). Whereas the rate of increase was higher at low biomass (<1 million tonnes) than at high biomass, more variability in the area occupied at high biomass was evident than at low biomass. Further investigation into the changes in area occupied by the western and eastern parts of the population in relation to the biomass east and west of Agulhas revealed that the relationship between area and biomass was mostly driven by a rapid expansion of the area occupied by the eastern part of the population

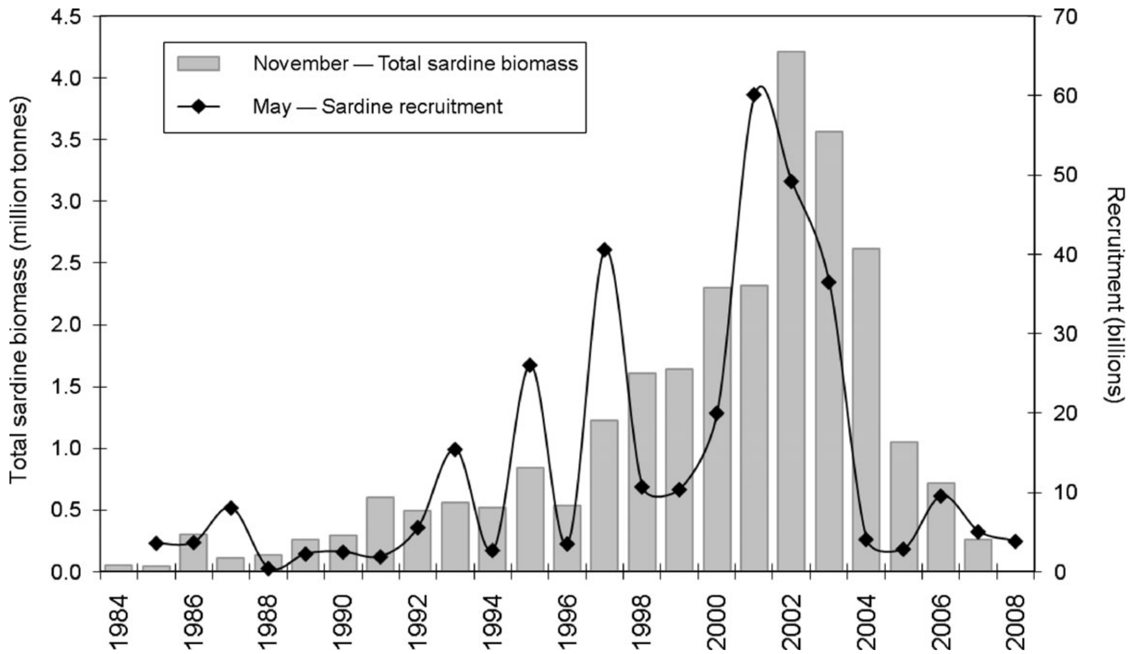

Figure 2. Annual acoustic estimates of total sardine biomass measured in November and sardine recruitment measured in the preceding May since 1984.

(Figure 6). Expansion of the area occupied by sardine in the western area was much slower in comparison, and the relationship between area occupied and biomass not as strong as for the area east of Cape Agulhas. ($r^2 = 0.48$ and 0.83, respectively).

Comparing the biomass east and west of Cape Agulhas (Figure 7), it is evident that the contribution of the biomass west of Cape Agulhas to total biomass was larger than that of the biomass east of Cape Agulhas before 1998. In 1999, a large increase in the biomass east of Cape Agulhas relative to that west of Cape Agulhas caused a shift in the relative distribution of sardine to the central and eastern Agulhas Bank. Further increases in the biomass of sardine east of Cape Agulhas after 1999 were mainly the result of the influx of a large number of 1-year-old sardine in 2001 and 2002, emanating from very successful west coast recruitment then.

The distribution of fishing effort over the same period as the survey data reveals that as the biomass of sardine and hence the TAC increased, larger catches were taken mostly from the area west of Cape Agulhas (Figure 8). The quantity of sardine caught east of Cape Agulhas only increased from 2001, although remaining small compared with landings made to the west of Cape Agulhas until 2005, when for the first time since the start of the fishery, catches east of Cape Agulhas exceeded those made west of it. The relative exploitation level, i.e. the annual total catch as a proportion of biomass from the November survey in the previous year, east and west of Cape Agulhas shows a striking difference between the two areas (Figure 9). Although the overall exploitation rate for the total population averaged ~11% of the biomass during the period 1987–2007, the exploitation level west of Cape Agulhas increased substantially, particularly after 1999, and reached 44% in 2006. The exploitation level has only recently increased east of Cape Agulhas.

Investigation of the age structure of the western and eastern part of the population from November data for the period 1998–2007 shows that the sardine west of Cape Agulhas (Figure 10) are represented mainly by two age classes, namely the fish that recruited to the population during the year and those that recruited during the previous year. Very few older fish are present there. Also evident is that the increase in biomass in the west was mainly influenced by the very strong recruitment from 2001 to 2003, resulting in a large number of 1- and 2-year-old fish there in 2002 and 2003. The relatively strong cohorts of 1- and 2-year-old sardine in November 2003, however, had practically disappeared by November 2004. Subsequent poor recruitment since 2004 has halted the increase in biomass west of Cape Agulhas, and the number of fish remaining there has decreased substantially. The age structure of fish east of Cape Agulhas during November surveys is generally broader than that found west of it and is often dominated by older fish. Also evident from this age structure is the increase in the number of older fish, in particular, as the biomass east of Cape Agulhas increased.

Annual plots of the age structure of sardine from commercial catches landed throughout the year west of Cape Agulhas (Figure 11) show generally large numbers of 0-year-old fish that were taken as bycatch in the anchovy-directed fishery. Most of the fish taken by the sardine-directed fishery from 1998 to 2007 were older (2+ years), mature fish, implying a greater level of exploitation on the spawning component of the population west of Cape Agulhas. The age structure of commercial catches taken east of the Cape confirms the broader age structure seen in the survey data in the area, and also emphasizes the disproportional exploitation rate on mature fish from the two regions.

The origin of the relatively large numbers of 0- and 1-year-old fish east of Cape Agulhas in November surveys each year is unclear, given that recruitment of sardine measured in May each year has been largely associated with the area west of Cape Agulhas (Figure 12). This may be indicative of winter spawning in the

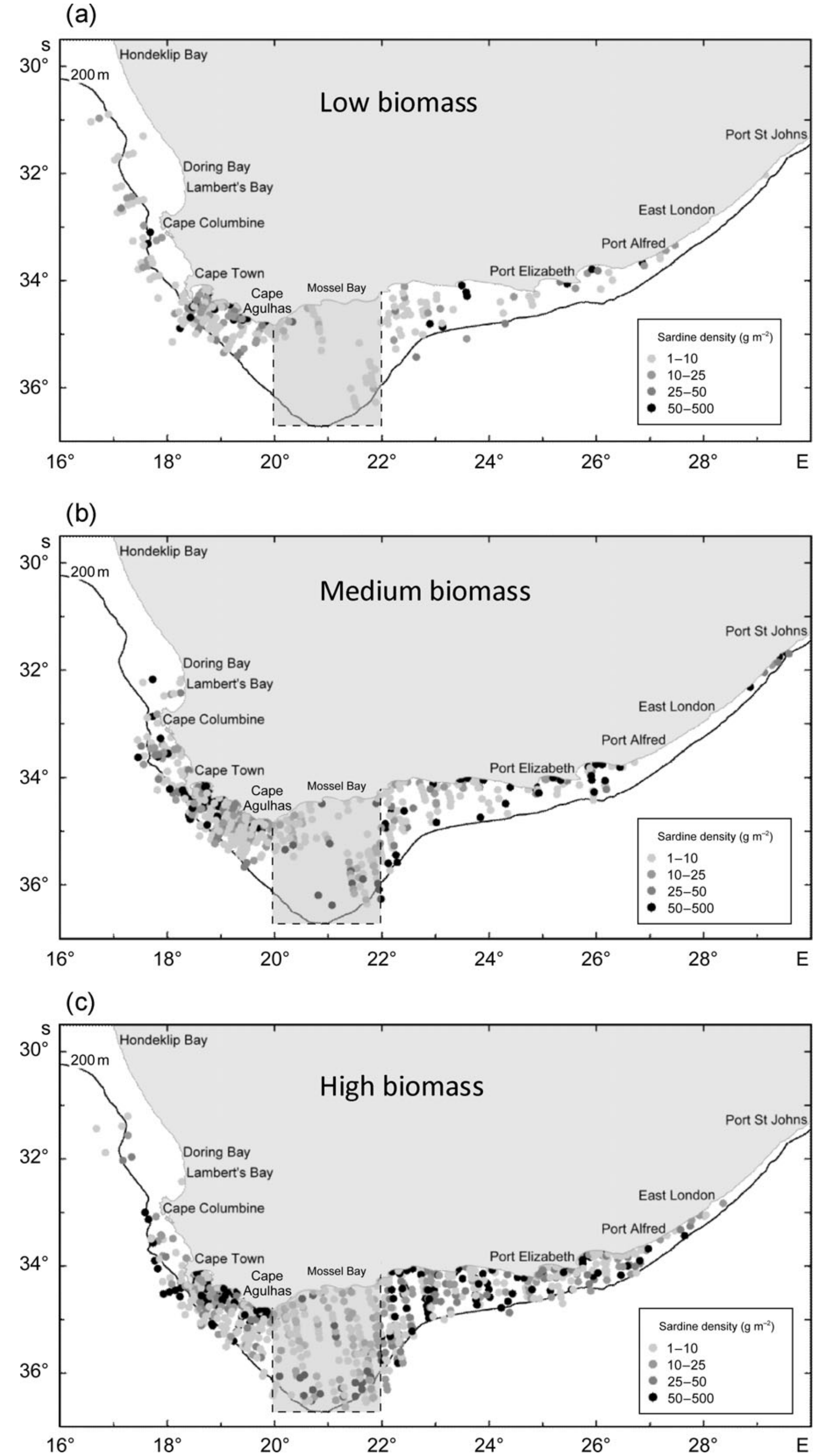

Figure 3. Composite density maps derived from November survey data for periods of (a) low, (b) medium, and (c) high sardine biomass. The grey block indicates the transition zone between the west coast system and the Agulhas Bank system for which an SOI was computed.

area east of Cape Agulhas along with local retention of recruits, which are detected for the first time during the subsequent November survey. Autumn (May/June) spawning by sardine has been observed in recent years, with a consistently located, high-density patch of eggs being found in association with the shelf edge south of Mossel Bay (MCM, unpublished data).

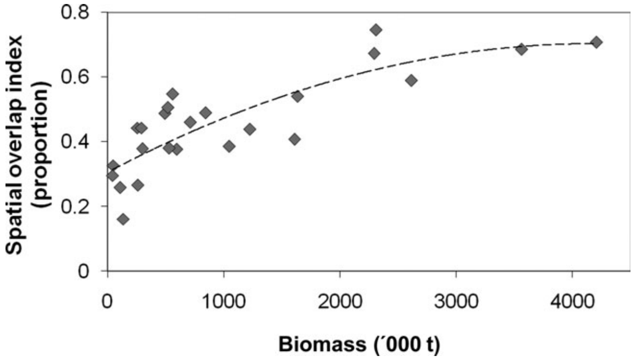

Figure 4. SOI computed from November survey data for the area between Cape Agulhas and Mossel Bay as a function of sardine total acoustic biomass measured in November for the period 1984–2007.

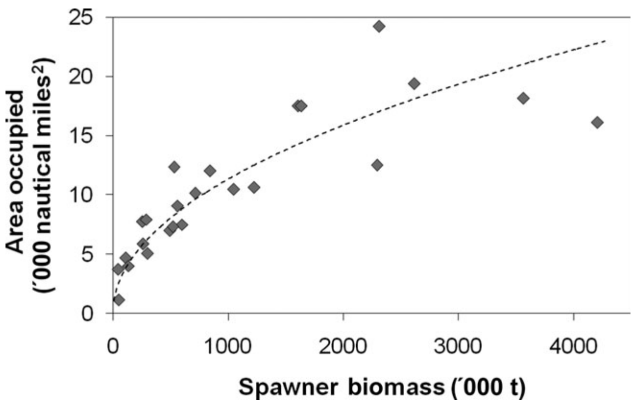

Figure 5. Total area occupied by sardine as a function of biomass from November survey data.

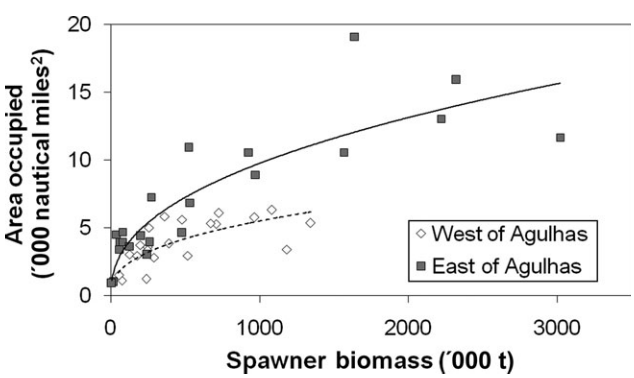

Figure 6. Comparison of the area occupied by sardine in relation to biomass east and west of Cape Agulhas during November surveys.

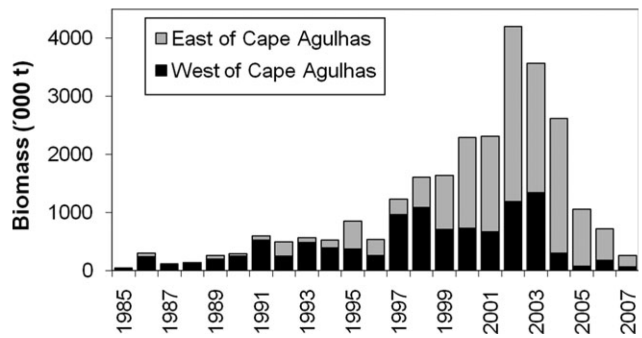

Figure 7. Acoustic biomass of sardine measured east and west of Cape Agulhas during November surveys.

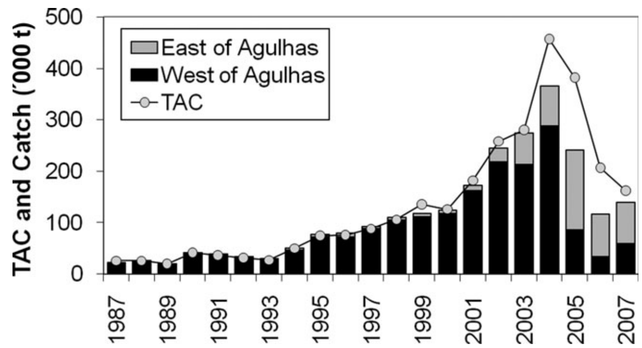

Figure 8. Annual TAC for sardine, and the catches taken commercially east and west of Cape Agulhas.

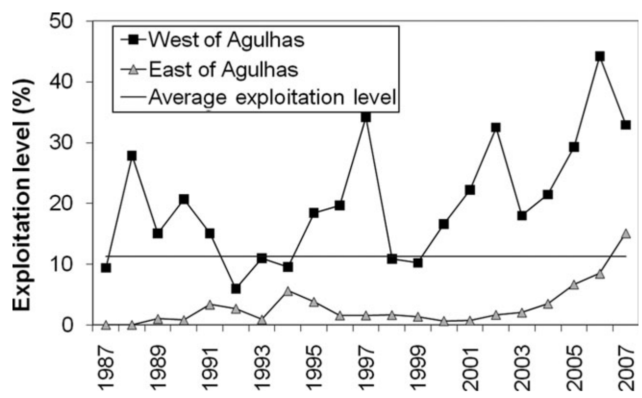

Figure 9. Exploitation level (annual catch and biomass in November of the previous year) east and west of Cape Agulhas.

Discussion

Both the age-structured production model used to assess the sardine stock (Barange *et al.*, in press) and the operational management procedure (OMP) used to manage the sardine fishery off the coast of South Africa currently assume a single population of sardine and do not consider spatial aspects of the distribution, or fishing effort (De Oliveira and Butterworth, 2004). As a consequence, the disproportionate expansion of the population at high levels of biomass has resulted in a spatial mismatch between fishing effort and fish biomass, with a higher-than-average relative level of exploitation, particularly on spawning adults, west of Cape Agulhas. Therefore, the pelagic fishing industry is facing huge logistic and cost burdens as a result of having to transport a substantial portion of the landed sardine catch by road from Mossel Bay on the south coast to the processing factories on the west coast, and the change in sardine distribution has also resulted in the fishery being unable to reach its TAC in recent years (Figure 8). This failure to achieve the TAC may, however, have been beneficial for the resource in view of the recent severe declines in abundance, at a rate more rapid and to levels far below those for which the OMP was designed.

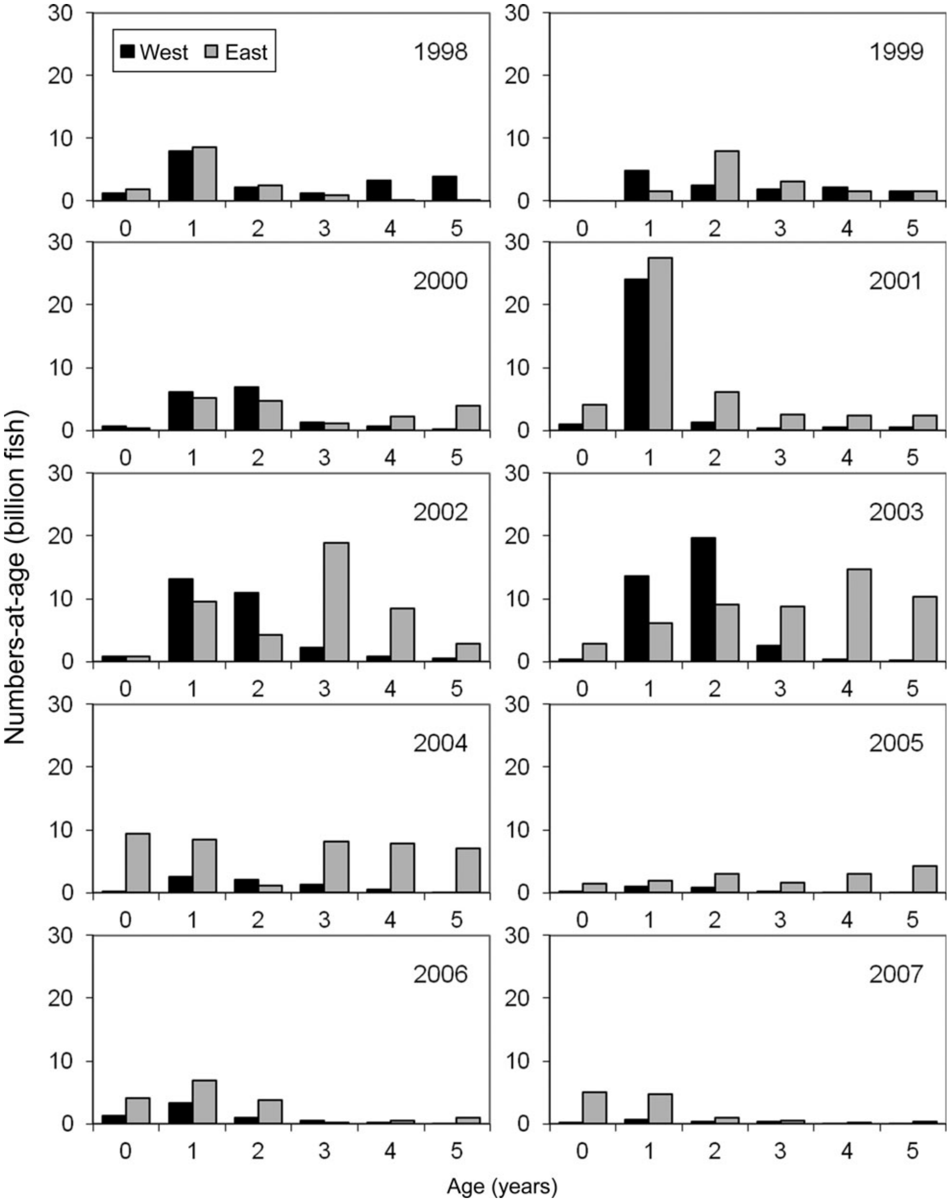

Figure 10. Age structure of sardine derived from November surveys for the areas west and east of Cape Agulhas.

Although no compelling explanation has yet been put forward for the cause of the eastward shift, incorporation of a spatial parameter into the OMP to take into account the possible existence of two separate, adult sardine spawning assemblages (i.e. a west and an east unit) should be considered. Based on a similar investigation into the existence of functionally distinct adult assemblages for the sardine stock off Southwestern Australia, Gaughan *et al.* (2002) caution against the setting of management rules for the whole population only and suggest that consideration be given to spatial aspects of the population. In the light of a possible revision of the OMP, the data used here were further analysed with the intention of highlighting spatial differences in the distribution of sardine in relation to fishing effort, and to provide insights into the possible causes and effects of the perceived shift in distribution of sardine.

Given the complexity of the situation and the many factors that may have contributed to an eastward shift in the sardine population, as well as possible consequences arising from it, a schematic summary that illustrates most of the mechanisms/hypotheses alluded to in the following discussion is provided in Figure 13.

Evidence of an increase in the area occupied by sardine as a function of increasing biomass accords with the well-documented expansion and contraction of the range occupied by small pelagic fish populations as their abundance increases or decreases (MacCall, 1990, in press). Although Barange *et al.* (1999) did not observe this trend in an earlier analysis, their speculation that the range of abundance and spatial coverage then was not extensive enough has now been confirmed. Since their work, a fourfold increase in the biomass of sardine has been accompanied by a threefold increase in the area occupied by the species. Importantly, the main change in the extent of spatial coverage has been due to the increase in size of the eastern part of the stock, which at times of low biomass was very small.

The SOI also suggests that the mid-shelf to offshore region in the area between Cape Agulhas and Mossel Bay is not a preferred

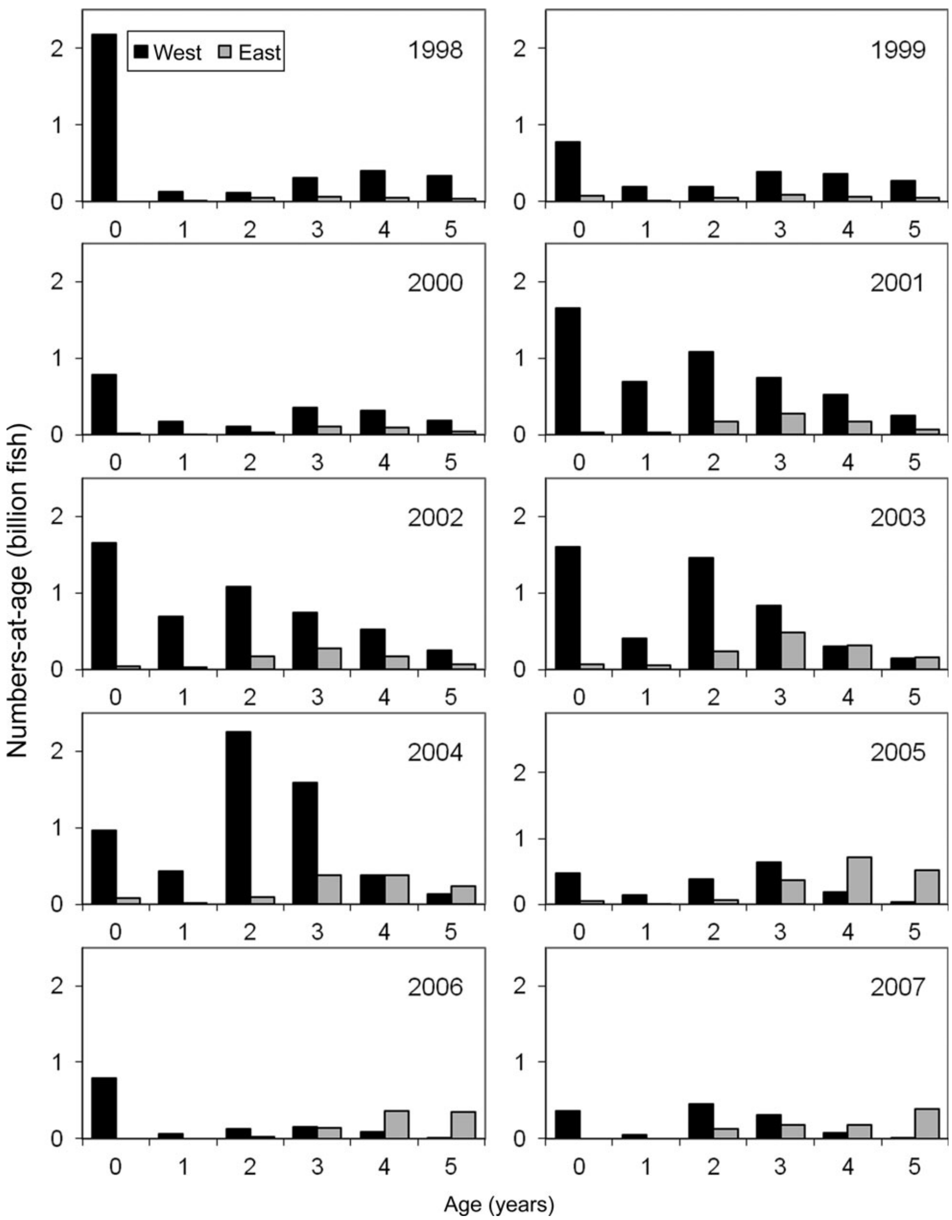

Figure 11. Age structure (numbers-at-age, billions) of sardine derived from commercial catches for the areas west and east of Cape Agulhas.

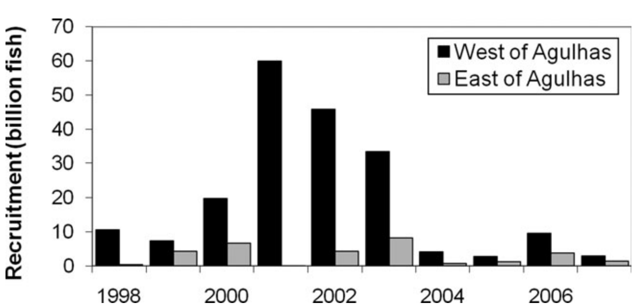

Figure 12. Recruitment in terms of numbers measured during May since 1998 for the area west and east of Cape Agulhas.

habitat for sardine and is only utilized at high levels of biomass. The scarcity of sardine in that area may therefore be related to optimal foraging, with the paucity of fish being related to a scarcity of food. Brown (1992) clearly showed that the central Agulhas Bank has lower average chlorophyll *a* concentrations in the upper 30 m than the western and eastern Agulhas Bank. Incidentally, Hutchings *et al*. (1995) found that the biomass of copepods is highest on the west coast and eastern Agulhas Bank, although copepod biomass on the central Agulhas Bank was inexplicably higher than on the WAB.

The large increase in biomass of the sardine stock east of Cape Agulhas is possibly associated with several factors, including low relative exploitation rate, increased reproductive output relative to the western part of the population, arising from the substantially greater reproductive output of large compared with small sardine (Le Clus, 1989), and the potential effects of higher temperature on growth rates and hence the survival of early life-history stages along with successful local recruitment on the east coast. The large number of 1-year-old fish in this area in November

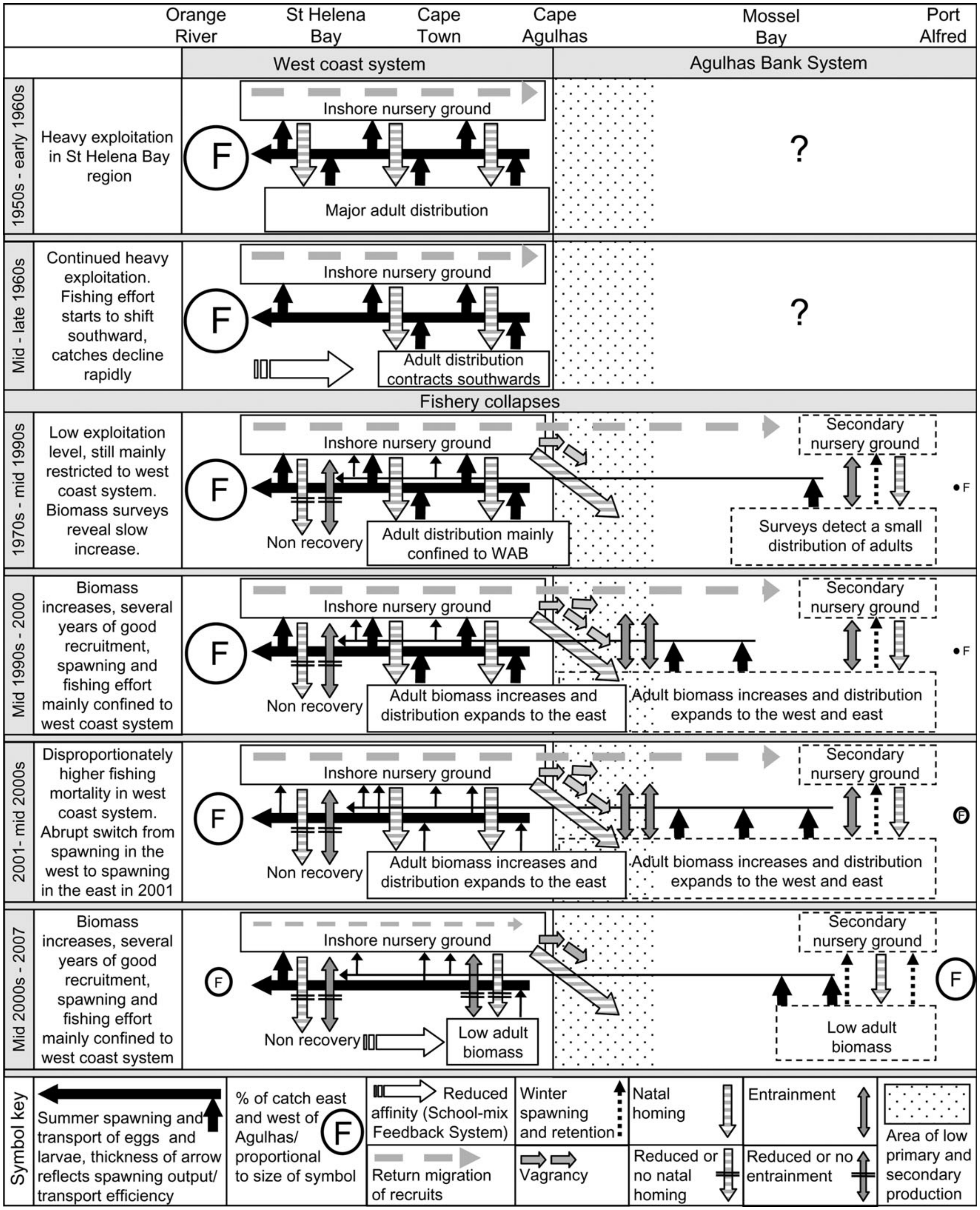

Figure 13. A schematic representation of the population life cycle of sardine during various periods since the inception of the fishery. The major areas of adult and spawning distributions, the mechanisms for transport and recruitment, and simplistic suggestions of how the various factors and hypotheses may have resulted in, or evolved as a consequence of, an eastward shift of the population, are shown. The question marks signify a general paucity of data, and lack of understanding, in the earlier years for the area east of Cape Agulhas.

2001 following record levels of west coast recruitment in May 2001 may suggest successful entrainment by adults of west coast recruit vagrants (Cury, 1994). Increased levels of vagrancy may have been facilitated through the association of strays with those recruits returning to their natal homing sites east of Cape Agulhas. This large influx of biomass in 2001, together with the presence of an increasing number of large sardine east of Cape Agulhas, particularly since 1999, may have led to the abrupt shift in the main sardine-spawning location (van der Lingen *et al*., 2006) from west to east of Cape Agulhas in 2001. This shift has been sustained since 2001 and may suggest a larger contribution to east coast recruitment attributable to the retention of spawned products in the area, particularly during winter, rather than a reliance on the transport of eggs and larvae to the west coast during the summer spawning season. This in turn may have led to a large number of recruits either being retained east of Cape Agulhas in certain years or to the return of fish to the area in which they were spawned east of Cape Agulhas (i.e. natal homing; Cury, 1994).

Diminished relative biomass west of Cape Agulhas is probably a consequence of higher-than-average levels of exploitation on older sardine in that area. The increase in fishing pressure on sardine in the west coast system not only removed a substantial part of the spawning population, but also could have led to a decreasing affinity of sardine for the area west of Cape Agulhas (school-mix feedback; Bakun 2001). Moreover, fewer recruits may be entrained there as a direct result of a reduced juvenile/adult encounter rate (see below).

Based on our analyses, it appears most likely that the perceived eastward shift in the South African sardine population was the consequence of an increase in the size of the eastern part of the population and the associated expansion in the area occupied by that portion of the stock. Additionally, higher-than-average exploitation on the western part of the stock, particularly the few remaining adults, seems to have exacerbated the situation. Spatially explicit management strategies whereby the population is either managed as two separate spawning units with independent or combined recruitment mechanisms, or whereby fishing effort and size selectivity of catches is managed in relation to available biomass, could well be considered.

It is not known, however, whether a reduction in fishing effort west of Cape Agulhas will lead to an increase in biomass there, because much of the life-history strategy of sardine is still poorly understood. For example, the reason for the non-recovery of a successful spawning unit on the west coast after the initial collapse of the sardine population in the 1960s is not clear and may be related to factors other than the fishery, such as disturbances to the life cycle of part of the population. The entrainment hypothesis states that maintenance of the life cycle depends on the establishment and sustainability of spawning migrations by repeat spawners that pass on the knowledge of migration patterns to their offspring (McQuinn, 1997; Corten, 2002; Petitgas *et al*., 2006). Data from the fishery suggest that the highly productive west coast was the preferred habitat of adult sardine from the start of the fishery in the 1940s up to the time of the collapse in the mid-1960s. Yet very few adult sardine were found on the west coast following the recovery of the population. This would have decreased the chances of adult/juvenile contact and subsequent juvenile entrainment on the west coast. If this mechanism, and possibly also others such as the school-mix feedback, is important in establishing and maintaining spawning units, the need to test by

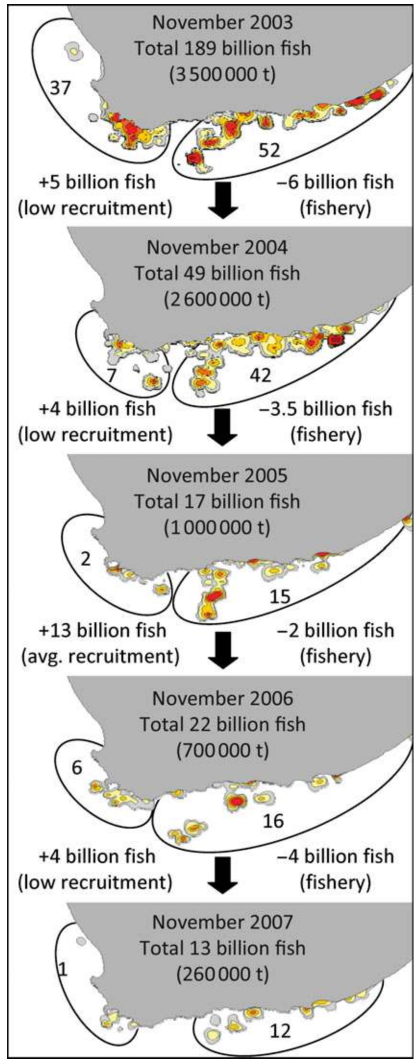

Figure 14. A schematic diagram showing the distribution and relative density of sardine observed during November surveys since 2003. Also shown is the total population size in terms of numbers and biomass, and the recruitment strength and fishing effort in the subsequent year. Ellipses and the numbers contained within them indicate the number of sardine (in billions) found west and east of Cape Agulhas during the November survey.

simulation the effect of fishing effort on adult sardine west of Cape Agulhas is greater.

The sharp decline in the biomass of the western part of the population since 2004 and of the eastern part since 2005 has been driven by a prolonged period of low recruitment since 2004 and unexplained increased adult mortality that was not accounted for by the fishery (Figure 14). The distribution of sardine eggs in November during this period has been restricted, almost exclusively, to the area east of Cape Agulhas (MCM, unpublished data). Although a mechanism exists whereby eggs and larvae from south coast and east coast spawning may be retained on the south coast (Lett *et al*., 2006; Miller *et al*., 2006), transport models show reduced transport success from the south coast to the west coast nursery grounds compared with transport success of spawning products released farther west (Miller *et al*., 2006). This indicates that spawning on the south coast ultimately contributes fewer larvae and juveniles to the west coast nursery area, which is still the main recruitment area for sardine. If strong recruitment depends on an adequate spawner biomass during summer in the area west of Cape Agulhas, where transport is optimal, it becomes even more important to protect the remaining adult fish there.

Although our analysis suggests that differential growth and exploitation of substocks is a plausible explanation for the sardine's eastward shift, we have no other evidence to demonstrate such stock differentiation. There is, however, some support from our data to suggest that the local sardine population may actually consist of two separate spawning units, one on either side of Cape Agulhas, occupying the mid-shelf and offshore. These spawning assemblages are not necessarily genetically distinct and likely overlap at times of high biomass when the distributions of both units expand. Based on the location of the catches made by the fishing industry (Crawford, 1981), a third unit comprising older, larger spawners may have existed on the west coast, north of Cape Columbine, before the start of the acoustic time-series. Alternatively, this west coast spawning unit may have been merely an extension of the spawning unit west of Cape Agulhas at times of high biomass during the period 1940–1960.

In addition, a possibility that the shift was environmentally induced cannot be discarded, because environmentally mediated changes in the distributions of small pelagic fish in other systems have been reported (MacCall, in press). An eastward shift in the distribution of southern Benguela anchovy (*Engraulis encrasicolus*) spawners over the Agulhas Bank has recently been linked with environmental change (Roy *et al*., 2007), although in that instance both the environmental change and the change in fish distribution were abrupt (i.e. interannual), rather than over a decade or so.

Decade-scale changes in the centre of distribution and the location of the bulk of the biomass associated with changes in population size have been observed for Pacific sardine *S. sagax* in the California Current system (Rodríguez-Sánchez *et al*., 2002). These were linked to decade-scale SST regime shifts in the North Pacific. Similarly, decade-scale changes in the distribution of anchovy (*E. encrasicolus*) and sardine (*Sardina pilchardus*) in the North Atlantic have been documented by Beare *et al*. (2004), and linked to natural climate variability and global warming (Alheit *et al*., 2007). Hence, distribution shifts or expansions of range as biomass has increased of at least some small pelagic fish have been plausibly linked to changes in the environment. Although the evidence for this mechanism for the South African sardine has not been found, such an environmentally mediated shift cannot be excluded, and further work is needed to assess whether or not this was the case.

The oceanography of the southern Benguela is, however, highly dynamic and complex (Shillington *et al*., 2006), and the Benguela tends to display greater variability than other eastern boundary upwelling systems (Reason *et al*., 2006), which may limit our ability to separate underlying environmental signals from mere noise. As a consequence, long-term trends in the southern Benguela are difficult to distinguish from decade-scale variability and strong interannual signals, but there are suggestions that the southerly winds have increased over the past 100 years, and particularly since 1950 (Taunton-Clark and Shannon, 1988). Oxygen levels close to the bottom in shelf waters of the west coast have also declined over the period 1983–2004 (Monteiro and van der Plas, 2006), but the records for phytoplankton are not sufficiently long to determine trends (Demarcq *et al*., 2007).

Values of chlorophyll *a* are generally higher on the west than the south coast, but no trends are apparent between 1997 and 2004. Long-term trends in zooplankton indicate a large increase on the west coast in St Helena Bay between 1950 and 1995, followed by a smaller decrease as pelagic fish recruit numbers and biomass rose markedly between 1995 and 2004 (Verheye *et al*., 1998). Mesozooplankton concentrations are approximately the same on both the west and south coasts, whereas macrozooplankton is about one-fifth less on the south coast (Hutchings *et al*., 1991). Given the lower phytoplankton concentrations, zooplankton productivity is likely to be lower on the south coast, so the expansion of sardine east from the west coast does not appear to be related to optimal foraging. There is, however, more zooplankton on the eastern Agulhas Bank, and it is more productive than the WAB (Peterson *et al*., 1992), so expansion across the Agulhas Bank may be a partial response to increased food availability east of Cape Agulhas, although this appears to carry a penalty in terms of transport success back to the west coast nursery grounds.

The eastward shift in sardine distribution has had significant ramifications for the general ecosystem and in particular for the distribution and relative abundance of seabirds that rely heavily on sardine for prey, such as Cape gannets (*Morus capensis*) and African penguins (*Spheniscus demersus*). For west and south coast colonies of gannets, the proportion of sardine in the diet was significantly related to an index of sardine west–east distribution derived from commercial catch data (Crawford *et al*., 2008). Similarly, the numbers of African penguins in the northernmost colonies, at Lambert's Bay, Malgas and Marcus islands on South Africa's west coast, decreased as the sardine shift commenced (Underhill *et al*., 2006), and penguins attempted to mitigate the effect of the sardine's eastward shift by themselves moving to the east and establishing a new colony on South Africa's south coast (Crawford *et al*., 2008). These impacts on the seabird predators of sardine highlight the critical effects of the eastward shift of the sardine on the ecosystem as a whole, in addition to its effects on the fishery They underscore, in effect, the need for improved understanding of the cause or causes of the shift, and in particular whether it is reversible, with its implications of the need for management measures to mitigate the consequences.

Acknowledgements

Members of the offshore surveys group of MCM are acknowledged for their help in the collection and analysis of the data. Field-station staff and Jan van der Westhuizen, in particular, are thanked for collecting and extracting the commercial landings data. Improvements to an early version of the manuscript as a result of suggestions made by Alec MacCall and Daniel Gaughan are also kindly acknowledged.

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doi:10.1093/icesjms/fsn184