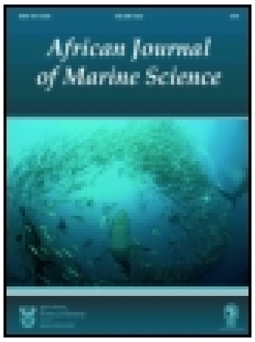

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Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela

C Roy[1]*, CD van der Lingen[2,3], JC Coetzee[2] and JRE Lutjeharms[4]

[1] Institut de Recherche pour le Développement (IRD), UR ECO-UP, Centre IRD de Bretagne, BP 70, 29280, Plouzané, France
[2] Marine and Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, South Africa
[3] Marine Biology Research Institute, Zoology Department, University of Cape Town, Private Bag, Rondebosch 7700, South Africa
[4] Department of Oceanography, University of Cape Town, Rondebosch 7700, South Africa
* Corresponding author, e-mail: claude.roy@ird.fr

Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela showed an eastward shift in their distribution on the Agulhas Bank that occurred abruptly in 1996 and has since persisted. We assessed whether this shift was environmentally mediated by examining sea surface temperature data from different regions of the Agulhas Bank, which showed that in 1996 the inner shelf of the Agulhas Bank to the east of Cape Agulhas abruptly became 0.5°C colder than in previous years and has since remained that way. In addition, signals, coherent with the 1996 shift recorded in sea surface temperatures, were also found in atmospheric surface pressure and zonal wind data for that region; interannual coastal SST variability is also shown to be correlated with zonal wind-stress forcing. As a result, increased wind-induced coastal upwelling east of Cape Agulhas is proposed as the main driver of the observed cooling in the coastal region. The synchrony between the environmental and biological signals suggests that the eastward shift in anchovy spawner distribution was environmentally mediated and arose from a change in environmental forcing that altered the relative favourability for spawning between regions to the west and east of Cape Agulhas. The results highlight how a relatively minor change in environmental conditions can lead to a drastic spatial reorganisation of the life history of one species in an ecosystem.

Keywords: Agulhas Bank, anchovy, Cape Agulhas, distributional shifts, *Engraulis encrasicolus*, environmental variability, southern Benguela

Introduction

Cape anchovy *Engraulis encrasicolus* is an economically important small pelagic fish found in South African waters, which, together with sardine *Sardinops sagax*, is the target of a medium-sized purse-seine fishery, with average annual catches of just under 400 000t over the past six decades (van der Lingen *et al*. 2006b). Anchovy is also ecologically important because it is a significant predator of plankton and is important prey for many piscivorous fish, bird and marine mammal species (Cury *et al*. 2000). On account of its importance, a substantial amount of research effort in the region has been directed at elucidating the life-history strategy of Cape anchovy and understanding environmental factors that impact its recruitment variability (Hutchings *et al*. 1998, Moloney *et al*. 2004).

Cape anchovy spawn over the Agulhas Bank during a prolonged summer spawning season and their eggs and early larvae are transported by a shelf-edge jet current from the Agulhas Bank spawning grounds to nursery grounds off the West Coast (Figure 1). As the juveniles grow, they move inshore and begin a return migration to the spawning grounds, reaching the Agulhas Bank as sexually mature fish at an age of around one year.

Interannual changes in the abundance and distribution patterns of Cape anchovy have been assessed bi-annually by means of acoustic surveys conducted since 1983 (Hampton 1992, Barange *et al*. 1999). Data collected during pelagic spawner biomass surveys conducted in spring/early summer indicate that anchovy spawners have shifted their distribution eastward over the past two decades, from being located primarily over the western Agulhas Bank (west of Cape Agulhas) during the early part of the time-series to over the central and eastern Agulhas Bank (east of Cape Agulhas; Figure 2). This shift in spawning distribution occurred abruptly in 1996 and has persisted since then, with around two-thirds (on average) of the anchovy spawner population found east of Cape Agulhas during subsequent surveys (Figure 2). The eastward shift in anchovy distribution occurred when the spawner stock was

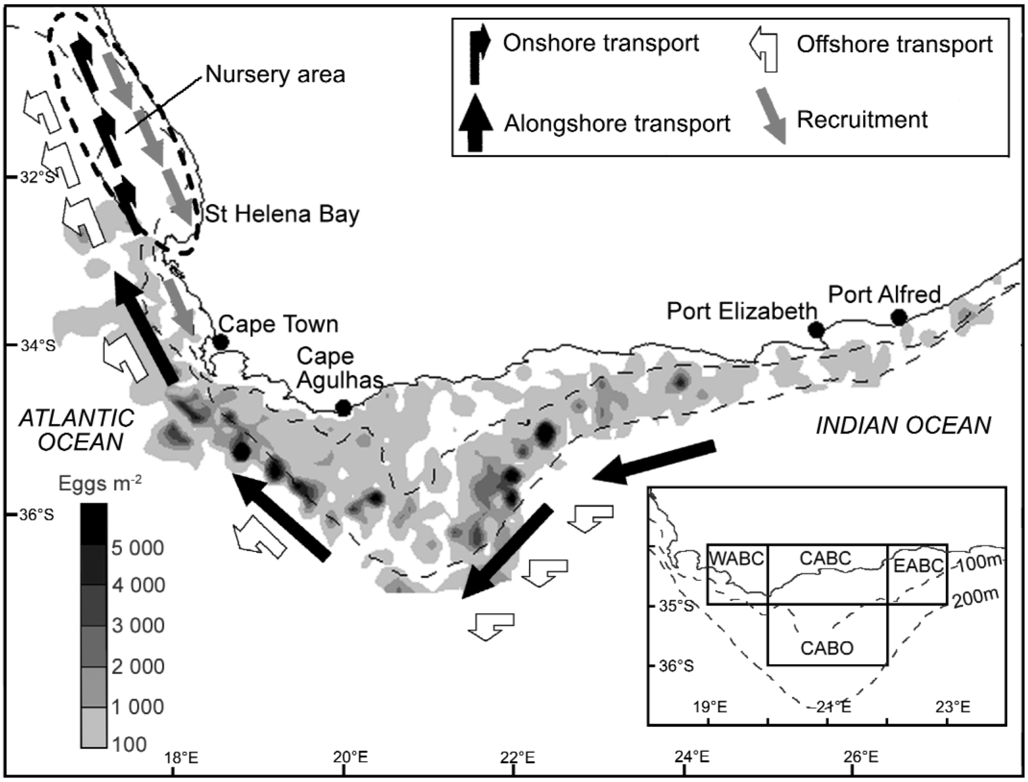

Figure 1: Map showing places mentioned in the text, the composite distribution of anchovy eggs from pelagic spawner biomass surveys conducted over the period 1984–2000 (from van der Lingen and Huggett 2003), the location of the anchovy nursery area, and transport and loss processes that impact on anchovy eggs and larvae. The 100m and 200m depth contours are shown, and the map at bottom right shows the location of the four subdomains (WABC, CABC, CABO and EABC) of the Agulhas Bank for which monthly SST time-series were constructed

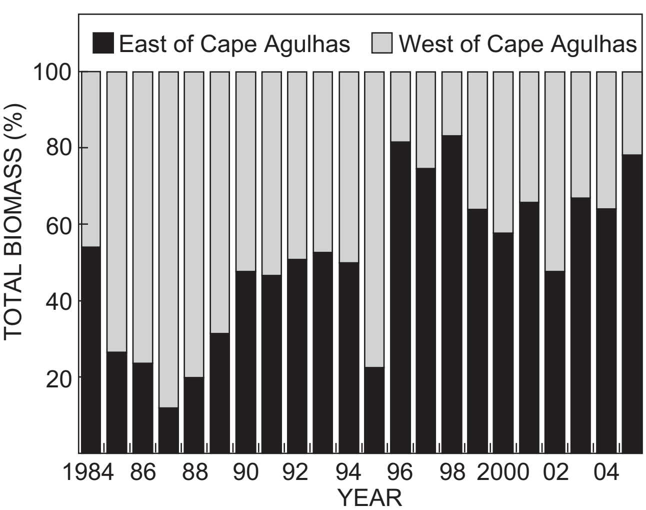

Figure 2: Percentage of the total anchovy spawner biomass located to the east and west of Cape Agulhas observed during pelagic spawner biomass surveys conducted annually in spring/early summer (late October to early December), 1984–2005

at its lowest recorded level (Barange *et al*. 1999, JCC unpublished data). The persistence of the eastward shift was hypothesised as arising from an 'extended natal homing' reproductive strategy (van der Lingen *et al*. 2002). Under that strategy, spawning individuals avoid new reproductive environments by attempting to replicate the environmental conditions in which they were spawned (Cury 1994). For Cape anchovy, this meant that newly spawned anchovy memorised environmental cues characteristic of the central and eastern Agulhas Bank through teleonomic and irreversible imprinting, and attempted to return there to spawn. The persistence of the eastward shift in the distribution of anchovy spawners supports the natal homing hypothesis (van der Lingen *et al*. 2002).

Here, we present an alternative hypothesis for the eastward shift in anchovy spawning location, which proposes that the shift was environmentally mediated, and arose from a change in environmental conditions that impacted the relative favourability of the spawning regions to the west and east of Cape Agulhas. We also briefly discuss the biological implications of the eastward shift in anchovy spawner distribution, and suggest further research to test our hypothesis.

Material and Methods

Environmental data

Monthly sea surface temperature (SST) time-series in four subdomains of the Agulhas Bank (Figure 1) were constructed using data from the optimally interpolated SST analysis (hereafter referred to as OISST) from the National Centers for Environmental Prediction (NCEP) Climate Prediction Center (Reynolds and Smith 1994, Reynolds *et al*. (2002). OISST is an operational SST product built using a blend of *in situ* (buoys and ship) and satellite-derived SST, and is available from November 1981 onwards at a global 1°-square resolution. The latitudinal extension of the first three subdomains (WABC, CABC and EABC) is from 34°S to 35°S in order to cover the coastal side of the Agulhas Bank: WABC is located on the western side of Cape Agulhas and extends from 19°E to 20°E, CABC covers the central part of the Bank east of Cape Agulhas from 20°E to 22°E, and EABC covers the eastern coastal side from 22°E to 23°E (Figure 1). The fourth subdomain (CABO) ranges from 35°S to 36°S and covers the central mid-shelf part of the Agulhas Bank from Cape Agulhas (20°E) to 22°E (Figure 1).

These three coastal and the mid-shelf SST time-series are used to investigate the temporal variability of SST over the Agulhas Bank, with a special emphasis on the identification of potential changes east of Cape Agulhas in the mid-1990s, when the shift in the distribution of anchovy spawners occurred.

In addition to the SST data, we also used monthly surface atmospheric pressure and monthly zonal wind speed data extracted from the NCEP/NCAR model reanalysis to investigate the broad-scale decadal pattern of variability of the atmosphere over the Agulhas Bank (Kalnay *et al*. 1996). Monthly data from the 22.5°E, 35°S grid point were downloaded from the web site of the IRI/LDEO Climate Data Library (http://iridl.ldeo.columbia.edu/), and these, as well as seasonal and annual averages derived from the monthly data, were used in the analysis.

Acoustic data

Acoustic surveys of small pelagic fish species in the southern Benguela were designed to estimate their abundance and map their distribution, and combine echo-integration techniques to estimate fish density with midwater trawling to determine species composition and size frequency distributions (Hampton 1987, 1992). Surveys comprise a series of pre-stratified, randomly spaced, parallel transects orientated perpendicularly to the coast, with strata pre-defined according to expected distribution patterns based on results from previous surveys. During spawner biomass surveys, transects extend across the continental shelf from close inshore to around the 200m isobath or as far offshore as pelagic fish are encountered. Acoustic backscatter (echo returns) are integrated over 10 nautical mile intervals along survey transects, with backscatter being apportioned to the different pelagic species using samples collected with the midwater trawl. The transformation of backscatter strength to fish density is achieved using species-specific target strength expressions for back-scattering cross-section per kilogram as a function of fish length (Barange *et al*. 1996). Distribution maps for each species are obtained via interpolation of the 10 nautical mile-integrated fish density data using standard Kriging routines. A full description of the methods used during the acoustic surveys is given by Barange *et al*. (1999).

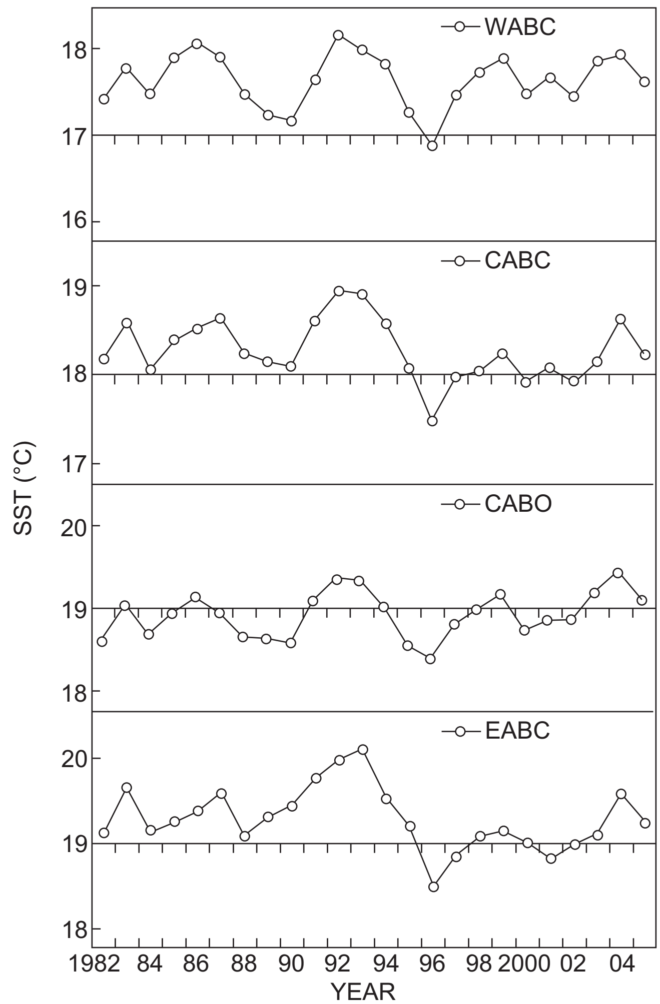

Figure 3: Annual SST time-series from 1982 to 2005 in four subdomains of the Agulhas Bank

Results

Shift in sea surface temperature over the Agulhas Bank

The monthly sea surface temperature (SST) time-series in the four subdomains show the expected seasonal alternation between the low winter temperature and high summer temperature (data not shown). The four time-series also exhibit a coherent pattern of interannual variability, such as anomalously high SSTs during the summers of 1992 and 1993, low SSTs during the summers of 1989 and 2001, and low SST during the winter of 1996. However, the CABC and EABC time-series show a unique decadal pattern with higher than normal winter SSTs persisting from the mid-1980s until the mid-1990s. This is followed by a persistent pattern consisting of lower winter SSTs from the mid-1990s onward. This decadal pattern is not apparent on the WABC and the CABO SST time-series. A plot of the annual SST means in the four subdomains gives a clear picture of the the mid-1990s shift (Figure 3). Whereas 1996 was the coldest year in each of the time-series from 1982 to 2005, the mid-1990s shift (with SST being 0.5°C cooler on average after 1996) appears to be restricted to the two coastal regions east of Cape Agulhas (EABC and CABC). Mean SST for the period 1982–1995 was significantly different (t-test) to mean SST for the period 1996–2005 on both the CABC and the EABC, but no difference was detected for the WABC and CABO regions (Table 1).

The CABC and EABC SST time-series indicate that the coastal region east of Cape Agulhas had a pattern of decadal variability distinct from that occurring on the mid-shelf region (CABO subdomain) and the coastal subdomain west of Cape Agulhas (WABC). An important consequence of this was a change over time of the cross-shelf SST gradient in the central and eastern part of the Agulhas Bank. This was best quantified by calculating the difference between the mid-shelf SST time-series (CABO) and the three coastal SST time-series (Figure 4), which shows that, starting in 1996, there was a sudden pronounced shift in the cross-shelf temperature gradient east of Cape Agulhas (Figure 4b, c). The difference between the 1986–1995 and 1996–2005 long-term average cross-shore SST gradient reaches about 0.5°C for the two subdomains located east of Cape Agulhas, with SSTs in both coastal regions becoming 0.5°C colder, on average, from 1996 onward. This translates into an enhanced (from 0.46°C to 0.89°C) cross-shelf gradient on the central part of the Bank from 1996 onward (Figure 4b), whereas farther east (EABC) the cooling of the coastal region results in a reduced (from –0.61°C to –0.08°C) cross-shelf difference starting in 1996 (Figure 4c). West of Cape Agulhas, there is almost no difference in the amplitude of the cross-shelf SST gradient between these pre- and post-1996 decadal periods (Figure 4a).

An abrupt and pronounced SST change raises the possibility that the change resulted from an artificial signal arising from the data-processing procedure. However, the contrasts between the decadal variability in the SST time-series (Figure 3), as well as in the cross-shelf SST differences (Figure 4a–c) to the east and west of Cape Agulhas, indicates that these observed decadal shifts were not an artefact of the OISST data processing. Hence, it is highly improbable that the OISST data-processing procedures would have flaws only east of 20°E.

There is a statistically significant relationship between the decadal and interannual variability of the cross-shore SST gradient over the central Agulhas Bank during the peak anchovy spawning season (October–December), and the percentage of the anchovy spawner biomass located east of Cape Agulhas in November (Figure 5). This quantitative result supports the hypothesis that the 1996 shift in the spawning location of Cape anchovy was environmentally mediated.

Other data

We also found evidence of a mid-1990s environmental shift on the Agulhas Bank in other independent time-series. Because observations that would permit the construction of reliable time-series extending over several decades are sparse for the Agulhas Bank region, we had to rely on the NCEP/NCAR model reanalysis that provides continuous atmospheric parameters from January 1949 onwards (Kalnay *et al.* 1996). The annual surface atmospheric pressure data over the Agulhas Bank grid point (35°S, 22.5°E) from the NCEP/NCAR reanalysis show a decadal pattern of variability similar to that observed in the cross-shelf SST gradient over the Central Agulhas Bank, with

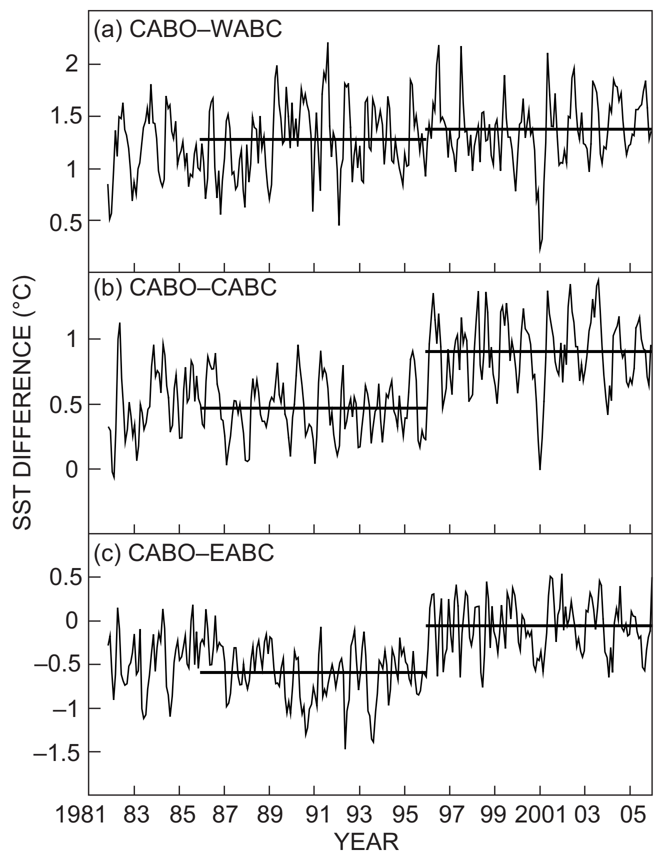

Figure 4: Monthly difference (solid lines) between the mid-shelf SST over the Agulhas Bank (CABO) and the three coastal subdomains (WABC, CABC and EABC) from November 1981 to December 2005. Decadal averages (1986–1995 and 1996–2005) are represented as dashed lines

Table 1: Results from t-test analyses (under the null hypothesis of no significant difference) comparing mean SSTs for the four subdomains of the Agulhas Bank between two periods (1982–1995 and 1996–2005). The mean (± standard error) SST for each period are given and the degrees of freedom (df), t-statistic and associated p value for each of the subdomains, are shown

Subdomain	Mean SST 1982–1995	Mean SST 1996–2005	df	t-statistic	p-value
WABC	17.66 ± 0.09	17.60 ± 0.10	22	0.4951	0.6254
CABC	18.42 ± 0.08	18.06 ± 0.09	22	2.9377	0.0076
CABO	18.90 ± 0.07	18.96 ± 0.09	22	–0.4864	0.6315
EABC	19.47 ± 0.09	19.03 ± 0.09	22	3.4415	0.0023

1996 appearing as an inflexion point (Figure 6a). In addition, the annual zonal wind speed extracted from the NCEP/NCAR reanalysis at the same grid point also shows a shift in the mid-1990s, with a decrease of about 0.6m s^{-1} in the magnitude of the zonal wind speed (Figure 6b). Although there is not a perfect synchrony between these two datasets because the wind speed time-series leads the pressure time-series by about two years, the mid-1990s appears as an inflexion point in the atmosphere dynamics over the Agulhas Bank. The NCEP/NCAR and OISST time-series are two independent datasets, and to observe the occurence of a shift in the mid-1990s in both of these increases our confidence in the reality of the 1996 decadal shift. Whether the change in the magnitude in the zonal wind speed is coherent with observed changes in the coastal SST time-series is discussed in the following section.

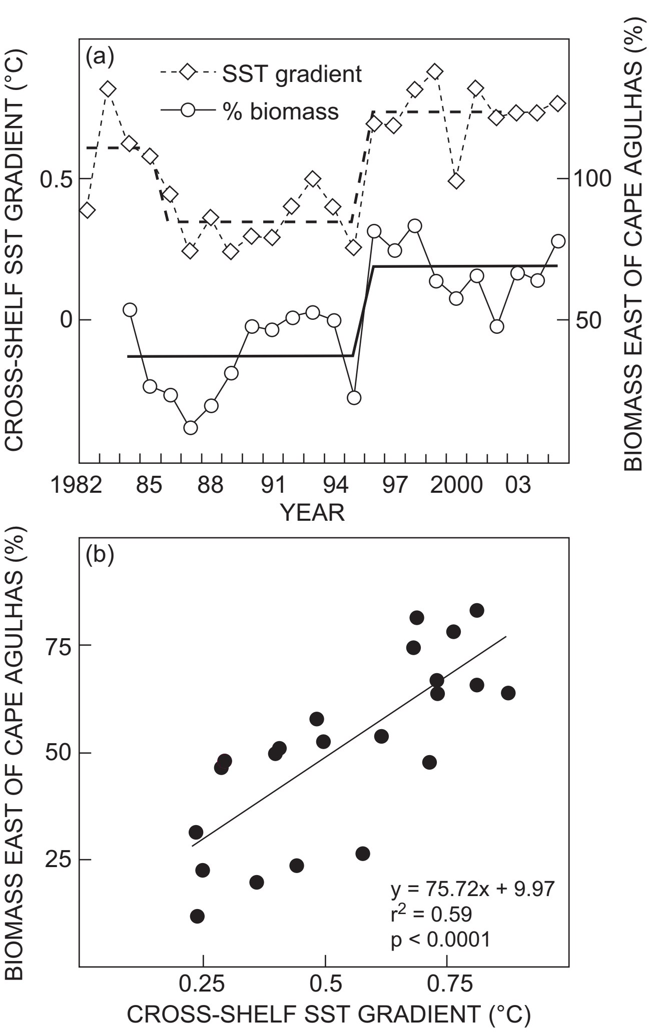

Figure 5: (a) Time-series of the cross-shelf SST gradient (CABO–CABC) over the central part of the Agulhas Bank during the anchovy peak spawning season (October–December) from 1982 to 2005, with the decadal averages superimposed (thick dashed line), and of the percentage of the anchovy spawner biomass that was located to the east of Cape Agulhas during spawner biomass surveys from 1984 to 2005, with the decadal averages superimposed (thick solid line); (b) scatterplot of the above-mentioned two variables with the corresponding fitted linear regression

Mechanisms to explain the coastal cooling

The known mechanisms that determine SSTs on the Agulhas Bank are complex and site-specific. First, the seasonal insolation normal to the subtropics has a marked impact on temporal temperature changes for all three regions. However, the surface temperatures over this part of the continental shelf are also affected by other non-seasonal sources.

On the eastern edge of the Agulhas Bank, the Agulhas Current is the dominant circulation feature. Shear-edge features on its landward border produce surface plumes of warm water (Lutjeharms *et al.* 1989) that may penetrate right to the coast on occasion (e.g. Goschen and Schumann 1994). The impact of this intermittent influx of warm water on surface temperatures has not been quantified. On its western edge, the Agulhas Bank is similarly influenced by offshoots of the Agulhas Current in the form of warm surface filaments (Lutjeharms and Cooper 1996), flow generated by passing Agulhas rings (Lutjeharms *et al.* 2007) and by a cyclonic lee eddy driven by the Agulhas Current (Penven *et al.* 2001a). Along its northern edge — the southern coastline of South Africa — occasional coastal upwelling (Schumann

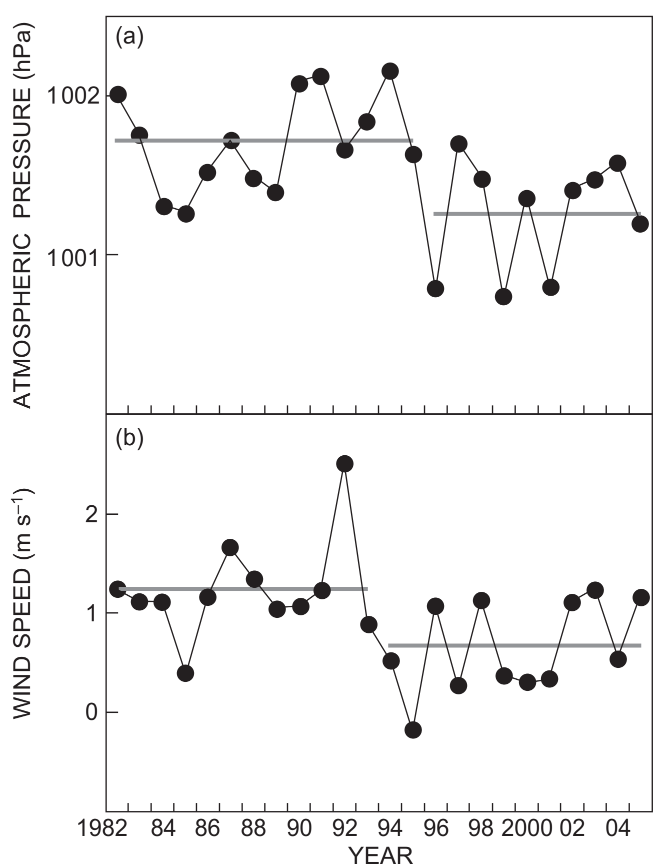

Figure 6: (a) Mean annual atmospheric surface pressure and (b) mean annual zonal wind speed over the Agulhas Bank at the 35°S, 22.5°E grid point, from 1982 to 2005 (source NCEP/NCAR), with decadal averages (thick grey lines) superimposed

et al. 1982) creates pockets of cold water along the coastline (Beckley 1983) under the appropriate wind conditions. Filaments of cold suface water may penetrate across large parts of the Agulhas Bank. Depending on wind direction, the contiguous upwelling of the southern Benguela upwelling regime may start at Cape Point on the far western side of the Agulhas Bank, or at Cape Agulhas, closer to the centre of the Bank. With a more easterly component of the wind, a larger coastal strip of the surface waters of the Agulhas Bank will therefore be relatively cold. The subsurface circulation over the Bank will also at times affect the surface temperatures (Lutjeharms *et al.* 1996).

The seasonal solar heating at the sea surface is mirrored in an unusual way by cooling from the bottom over the greater part of the Agulhas Bank (Lutjeharms *et al.* 1996). It has been asumed that this cooling is due to the influx of cold water that is upwelled at the shelf edge by the Agulhas Current (JREL unpublished data). This upwelling has not been observed anywhere along the eastern shelf edge of the Agulhas Bank except at the far eastern part (Lutjeharms *et al.* 2000). It has therefore been inferred that cold water is upwelled near Port Alfred, and then flows westward to intrude across the greater part of the bottom of the eastern Agulhas Bank. What effect does this have on the temperature of surface waters? The upwelled waters at Port Alfred may reach the surface, and this cold surface water can be seen as filaments moving along the shoreward side of the Agulhas Current (Walker 1986). In the austral autumn, or after particularly severe storms, this cold bottom water may also be mixed to the surface (Walker 1986) over other parts of the shelf.

Which of these mechanisms could have been responsible for the surface cooling observed in the CABC subdomain (Figure 4)? There is a slight average warming of the sea surface in the CABO, but this is not statistically significant (Table 1) and only makes a minor contribution to the increased temperature difference between these two subdomains after 1996. Two possible mechanisms for surface cooling are likely: enhanced upwelling at the coast (*vide* Schumann *et al.* 1982) and enhanced intrusions of cold surface water from the Port Alfred upwelling cell. The usual trajectory of the latter would not enter the CABC subdomain, so this mechanism seems improbable.

Despite limitations arising from its coarse spatial and temporal resolution, the zonal wind speed data from the NCEP/NCAR reanalysis offers an opportunity for testing whether the interannual SST variability along the coast of the Agulhas Bank to the east of Cape Agulhas can be related to wind fluctuations. Along this east–west orientated coast, located in the southern hemisphere, coastal upwelling results from the surface forcing of a westward zonal wind component (i.e. alongshore). The climatology derived from the NCEP/NCAR zonal wind data at the 35°S, 22.5°E grid point shows that, on average, the zonal wind component is orientated toward the west (and therefore upwelling-favourable) from November to April (Figure 7a). Testing of the link between the interannual zonal wind fluctuations and the Agulhas Bank coastal SST response is done by calculating the regression between the averaged November–April OISST data from 1982 to 2005 in the CABC and EABC areas and the averaged November–April zonal pseudo wind stress derived from the zonal wind data at the grid point during the same time period (Figure 7b and c). The results presented in Figure 7b and 7c show that, during the period when the NCAR/NCEP and OISST data-series overlap (1982–2006), interannual zonal wind fluctuations are able to explain a statistically significant ($p < 0.01$) part of the interannual variability of the coastal SST in the CABC and EABC areas. In both regions, enhanced westward

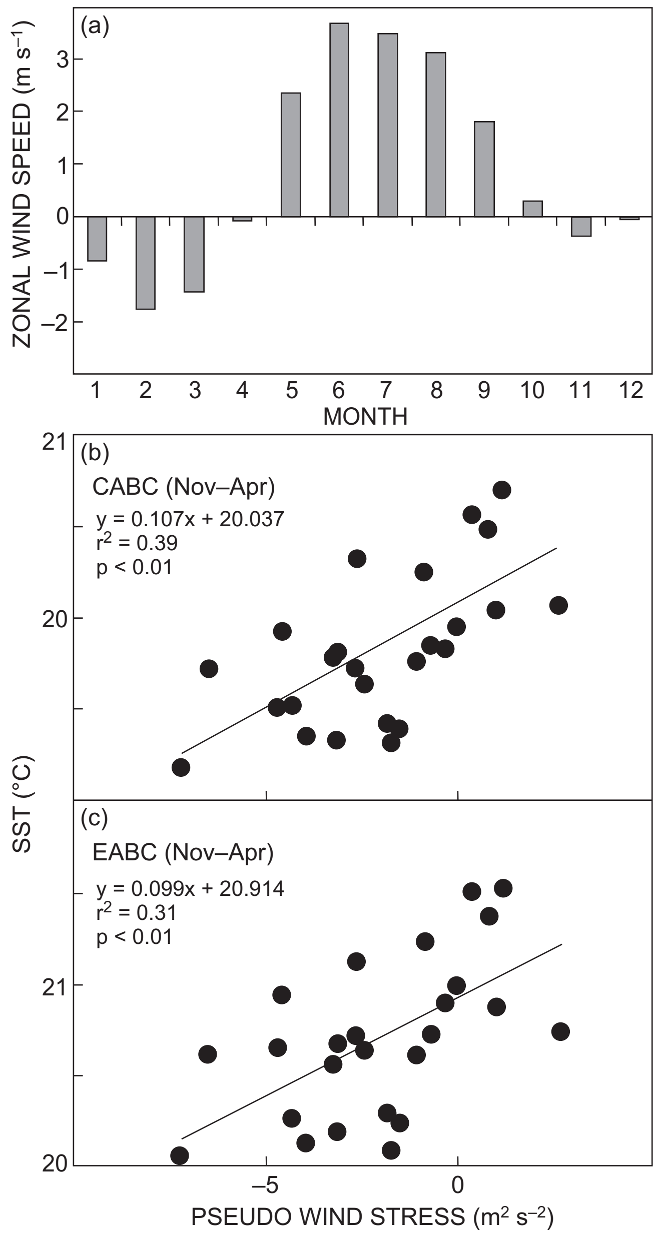

Figure 7: (a) Monthly climatology (1949–2006) of the zonal wind component from the NCEP/NCAR reanalysis at the 35°S, 22.5°E grid point; linear regression between the mean November–April pseudo wind stress at the grid point and the mean November–April SST for (b) the CABC area and (c) the EABC area, from 1982 to 2006. Negative pseudo wind-stress values correspond to a westward orientation (upwelling favourable) of the zonal wind forcing

pseudo wind stress (negative values) corresponds to lower SST along the coast (Figure 7b, c). This result supports the hypothesis that the mechanism responsible for the surface cooling in the coastal regions of the Agulhas Bank east of 20°E is enhanced coastal upwelling.

Further testing was conducted using AVHRR SST data. Satellite-derived coastal temperatures do show that the winter of 1996 was one of the coldest on record, but monthly sea surface temperatures from thermal infrared sensors in this cloudy region were insufficient to indicate clearly that there was a greater intensity of coastal upwelling since 1996.

We therefore conclude that intensification of coastal upwelling east of Cape Agulhas is a likely mechanism for the mid-1990s shift in the coastal SST and in the average SST gradients over the Agulhas Bank. However, further testing is needed to resolve some of the uncertainties that remain. Such testing could involve high-resolution modelling studies using coupled ocean-atmosphere models, as well as an in depth analysis of the hydrodological data that have been collected in the region during seasonal surveys conducted by Marine and Coastal Management.

Discussion

We identified a shift in SSTs on the Agulhas Bank that occurred in 1996. The shift appeared as a sudden cooling of the surface water in the coastal region relative to the central mid-shelf part of the Bank, and is limited to the coastal domain east of Cape Agulhas, with the western part of the Agulhas Bank being unaffected. The observed shift in cross-shelf SST gradient occurred at the same time as anchovy shifted their spawning, and the statistically significant ($p < 0.01$) correlation between the two supports the hypothesis that the shift in anchovy distribution was environmentally mediated. We also observed that the pattern of decadal variability in the cross-shelf SST gradient is similar to the pattern shown by surface atmospheric pressure near Cape Agulhas, which also shifted in 1996. Further evidence for the 1996 shift comes from results of a modelling experiment conducted by Lett *et al*. (2006). Using outputs from an hydrodynamic model of the southern Benguela (Penven *et al.* 2001b, Blanke *et al.* 2002) forced with realistic wind fields derived from the ERS 1 and 2 satellite scatterometers from 1992 to 1999, Lett *et al.* (2006) designed a set of Lagrangian experiments to quantify the seasonal pattern of retention over the Agulhas Bank. Unpublished results from those experiments provide evidence of a shift in the intensity of retention on the Agulhas Bank, with a 20% increase in retention to the east of Cape Agulhas in 1996 that lasted until the end of the modelled period in 1999 (C Lett, IRD, pers. comm.). Thus, four independent time-series (anchovy distribution, cross-shelf SST gradient, surface atmospheric pressure and the derived measure of retention) all indicate a shift in environmental/biological conditions on the Agulhas Bank in 1996. A fifth independent time-series (zonal wind speed) also shows a shift that occurred in the mid-1990s, although this change occurred in 1994, two years before the other shifts.

In addition to the eastward shift in anchovy spawner distribution, the mid-1990s also saw a change in the trajectory of zooplankton abundance off South Africa's west coast. Zooplankton abundance during winter in St Helena Bay (see Figure 1) increased 100-fold since the 1950s (Verheye *et al*. 1998), but this long-term trend was reversed in the mid-1990s with declining abundances particularly evident for large calanoid copepods, as reported by Hutchings *et al*. (2006). Those authors document an inverse relationship between anchovy recruit biomass and the abundance of large calanoid copepods, and attributed the copepod decline to increased recruit biomass. However, the mid-1990s were not years of exceptional anchovy recruitment (those occurred during the early 2000s; van der Lingen *et al*. 2006b) and it may be that the inflexion point in copepod abundance was driven by a wider-scale change in the southern Benguela upwelling ecosystem, another signal of which was the events on the Agulhas Bank described in this paper.

The oceanographic data show that the shift in environmental conditions was restricted to the coastal region of the Agulhas Bank east of Cape Agulhas. Because it was limited to the coastal domain, it is unlikely that the shift was driven by the Agulhas Current, which flows along the shelf break of the Agulhas Bank. Our analysis shows that coastal SST fluctuations east of Cape Agulhas are tightly linked to interannual alongshore wind variability. As a consequence, enhanced coastal upwelling east of Cape Agulhas appears to be the most likely process to account for the observed enhanced sea surface cooling from 1996 onward. We hypothesise that the shift in anchovy spawner distribution arose from a change in environmental conditions that impacted on the relative favourability for spawning of regions to the west and east of Cape Agulhas. This hyphothesis is illustrated in Figure 8, which shows the observed distribution of anchovy spawners in 1988, a year of reduced cross-shelf SST gradient, and in 1998, a year of increased cross-shelf SST gradient. Also shown is the distribution of anchovy during 1983, a year for which detailed data are unfortunately not available (hence precluding the calculation of the relative distribution of biomass) but one for which an anchovy distribution map was generated (Hampton 1987). The 1983 data clearly show that most of the anchovy biomass observed during the November 1983 pelagic spawner biomass survey was distributed east of Cape Agulhas. The 1983 data also showed a high cross-shelf SST gradient over the CAB that was similar in magnitude to the values observed from 1996 onwards.

As well as inducing a relative cooling of the coastal regions on the eastern side of Cape Agulhas, enhanced wind-induced coastal upwelling could also enhance the feeding conditions for spawning anchovy relative to western parts of the Bank. The spawning success of small pelagic fish depends on both their stored energy reserves and their ambient feeding environment (Hunter and Leong 1981, Koops *et al.* 2004). The hypothesised improved ambient food environment east of Cape Agulhas, in 1996 and thereafter, appears a plausible driver of the eastward shift in the distribution of anchovy spawners. Total copepod biomass is higher on the CAB and EAB compared with the western Agulhas Bank (Hutchings *et al*. 1995, Hutchings and Field 1997), and this is particularly true for *Calanus agulhensis* (Huggett and Richardson 2000), the dominant large copepod

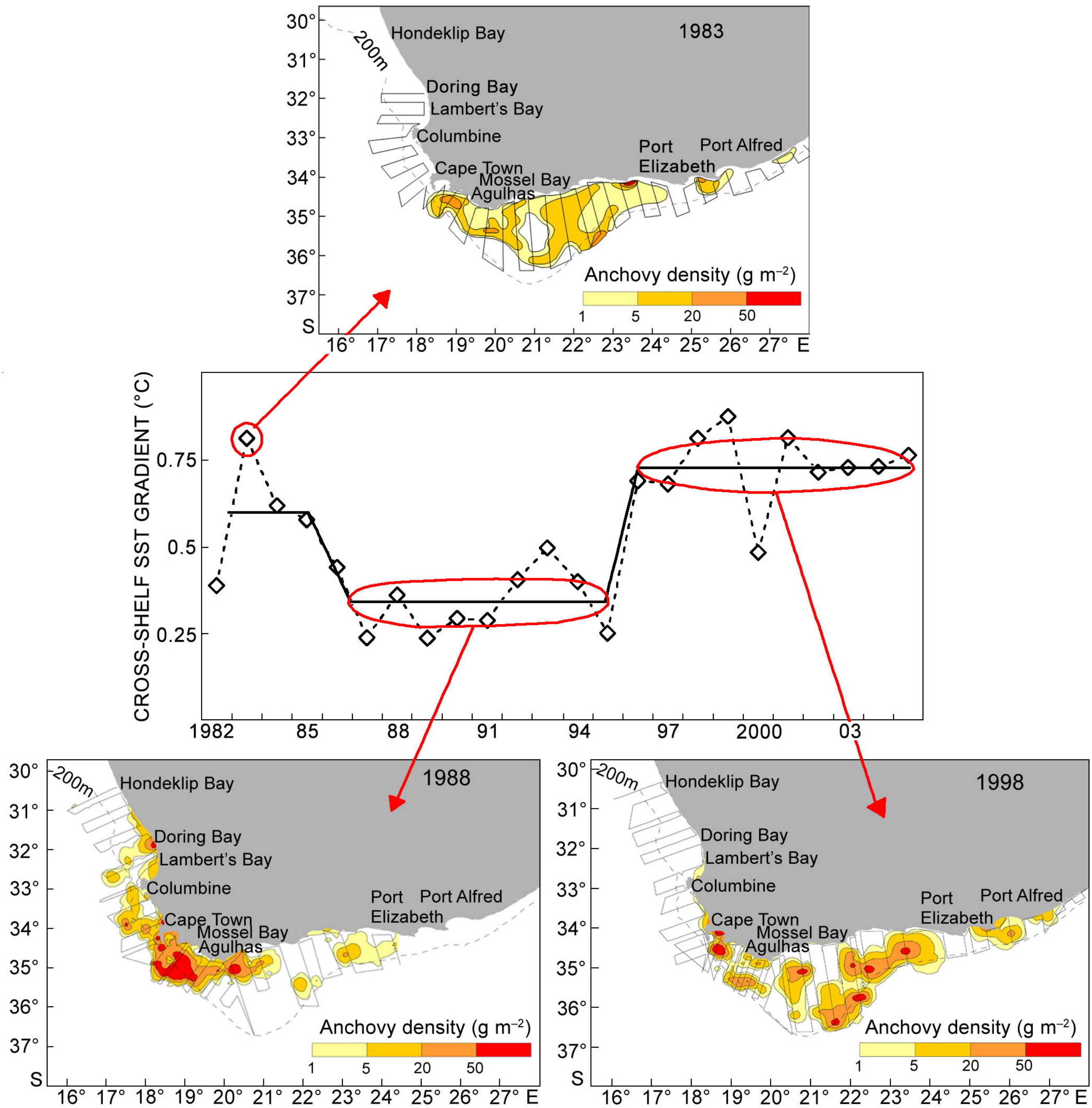

Figure 8: Schematic drawing of the environmentally mediated anchovy shift hypothesis, showing the annual mean cross-shelf SST gradient over the central Agulhas Bank from October to December for the period 1982–2005 (graph), and decadal trend and anchovy distribution maps for 1983 (redrawn after Hampton 1987), 1988 and 1998. Survey transects are superimposed on the distribution maps

on the Agulhas Bank and an important prey item for anchovy. However, the relative copepod biomass levels west and east of Cape Agulhas before and after 1996 remain undetermined.

That the ambient food environment east of Cape Agulhas is better than west of it for pelagic fish is supported by data on the lipid content of anchovy collected during spawner biomass surveys. Those studies suggest that anchovy east of Cape Agulhas have a higher lipid content than do their counterparts to the west of Cape Agulhas (van der Lingen *et al*. 2002, CDvdL unpublished data). Whereas that result is preliminary, the same spatial pattern is seen for sardine *Sardinops sagax*; those east of Cape Agulhas are in significantly better condition than those to the west (van der Lingen *et al.* 2006a). Fish in good condition produce better quality eggs than those in poor condition (e.g. Morimoto

1996 for Japanese sardine *Sardinops sagax*), and female condition has been positively linked to egg survival and hatching success (e.g. Laine and Rajasilta 1999 for Baltic herring *Clupea harengus membras*). Hence, food availability may affect recruitment by influencing spawning success and egg and larval survival (Bell and Sargent 1996, Marshall *et al.* 1999), and we hypothesise that anchovy spawners responded to an increased food availability by shifting their distribution eastwards. Environmentally driven changes in food availability have been suggested as responsible for variations in reproductive traits of Atlanto-Iberian sardine *Sardina pilchardus* (Silva *et al.* 2006), although biological characteristics examined in that study were length-at-maturity and duration of the spawning season, and not the distribution of spawners as was done here.

The present results suggest that we should perhaps revise the existing paradigm that regards the transport of eggs and larvae from the western Agulhas Bank to the West Coast upwelling region as a key process for anchovy recruitment in the southern Benguela (Hutchings *et al.* 1998, Roy *et al*. 2001). Anchovy recruitment remains a predominantly West Coast phenomenon despite the eastward shift in the distribution of spawners (Coetzee *et al.* 2006), so, the transport of eggs and larvae from the eastern spawning area to the West Coast nursery grounds must still occur. However, individual-based models developed to improve understanding of the factors impacting on recruitment variability of anchovy (Mullon *et al.* 2003) and sardine (Miller *et al.* 2006) in the southern Benguela have suggested that eggs spawned to the east of Cape Agulhas have a substantially reduced probability of being successfully transported to the West Coast nursery grounds compared with those spawned on the WAB, and have a higher probability of being retained in the region where they were spawned. Nonetheless, sufficient eggs from anchovy spawning on the CAB and EAB must be transported to the West Coast given observed recruitment patterns. It seems likely that anchovy larvae spawned on the central and eastern Agulhas Bank arrive on the West Coast at a larger size than those spawned on the western Agulhas Bank, given the longer transport path from east of Cape Agulhas to the West Coast, which may act to increase the relative contribution to recruitment made by spawning east of Cape Agulhas compared with that made by fish spawning to the west. However, the circulation path connecting the east and west parts of the Bank and the mechanisms that control its variability remain to be identified.

The hypothesis of an environmentally mediated shift in the distribution of anchovy spawners, and Cury's (1994) natal homing hypothesis previously posed to explain the anchovy spawner eastward shift, are not necessarily exclusive, because the latter may have acted to reinforce the shift in distribution arising from an altered environment in 1996. In that year, the anchovy spawner population was at its lowest level over the past 22 years, and it seems reasonable that a small population, the bulk of which was located to the east of Cape Agulhas (see Figure 7 of Barange *et al*. 1999), would be the most likely configuration for the natal homing hypothesis to occur, should such homing exist in anchovy.

Finally, our hypothesis of an environmentally mediated shift in the distribution of anchovy spawners emphasises the importance of the Agulhas Bank in the dynamics of the southern Benguela ecosystem, particularly given the occurrence of anchovy recruitment on the West Coast. Therefore, we need to better understand the major factors forcing the oceanography of the Bank (including wind, the Agulhas Current, etc.), whether these forcing factors have changed in time, and how to position the shift in terms of the regional climate context. The results here also provide some indication of how small pelagic fish may respond to climate variability, which could be used in the future to build scenarios of the impact of climate change on fish habitats in different areas. Additional work, outside the scope of this paper, to test our hypothesis of a strengthening of coastal upwelling along the east coast of the Agulhas Bank in 1996 and thereafter, could involve detailed analysis of high-resolution, satellite-derived SST and chlorophyll *a* images, as well as high-resolution, hydrodynamic modelling using regional models (e.g. Penven *et al.* 2006).

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