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## The Benguela Current: An ecosystem of four components

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## ABSTRACT

The Benguela system is one of the four major eastern boundary upwelling systems of the world. It is unusual as there are two stratified subtropical or warm temperate boundary regions, on either side of the major wind-driven upwelling region (19–34°S), which itself is subdivided at 26°S by the powerful Luderitz upwelling cell. Important biological components cross the boundary areas at different stages to complete the life-history cycle. While the “Bakun triad” of factors responsible for the development of large pelagic fish populations (enrichment, concentration and retention) provide an important unifying principle for understanding the compromise implicit in adaptation to upwelling systems, the role of predation has been neglected, as has the fish yield relative to photosynthesis. The role global climate change will have in the Benguela in terms of shifting boundaries or weakening or intensifying gradients is being explored. The interannual and decadal signals are so strong in the region that long term trends are difficult to distinguish. Intensive resource utilisation and the collapse of several fish stocks occurred in the Benguela region during the 1960s and 1970s, with different recovery trajectories in the north and the south. The Angolan subsystem can be described as a subtropical transition zone between the wind-driven upwelling system and the Equatorial Atlantic, with gentle upwelling-favourable winds, well-defined seasons, intermediate productivity and moderate, declining fisheries. It is separated from the Namibian subsystem by the Angola-Benguela front.

The northern Benguela shelf is a typical coastal upwelling system with equatorward winds, cool water, high plankton biomass and moderate to high fish biomass, which is currently in a depleted state. A shift from sardines to horse mackerel occurred during the period 1970–1990, while hake have never fully recovered from intensive fishing pressure up to 1990. Widespread oxygen-depleted waters and sulphur eruptions result from local and remote forcing, restricting the habitat available for pelagic and demersal fish species.

The Luderitz–Orange River Cone is an intensive perennial upwelling cell where strong winds, high turbulence and strong offshore transport constitute a partial barrier to epipelagic fish species. Upwelling source water alters in salinity and oxygen, across this boundary zone. A decline in upwelling-favourable winds occurred between 1990 and 2005.

The southern Benguela region is characterised by a pulsed, seasonal, wind-driven upwelling at discrete centres and warm Agulhas water offshore. High primary productivity forms a belt of enrichment along the coast, constrained by a front. Low-oxygen water, which only occurs close inshore, may adversely affect some resources. The west coast is primarily a nursery ground for several fish species which spawn on the Agulhas Bank and are transported by alongshore jet currents to the west coast.

The Agulhas Bank forms the southern boundary of the Benguela system and it displays characteristics of both an upwelling and a temperate shallow shelf system, with seasonal stratification and mixing, coastal, shelf-edge and dynamic upwelling, moderate productivity and a well oxygenated shelf. A large

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biomass of fish occupies the Bank during the summer season, with some evidence for tight coupling between trophic levels. A cool ridge of upwelled water, with links to coastal upwelling and to the Agulhas Current, appears to play an important but poorly understood role affecting the distribution and productivity of pelagic fish. A boom in sardine and anchovy populations was accompanied by an eastward shift, followed by 5 years of poor recruitment by sardine but successful recruitment of anchovy, indicating changes in the early life-history patterns of these two species.

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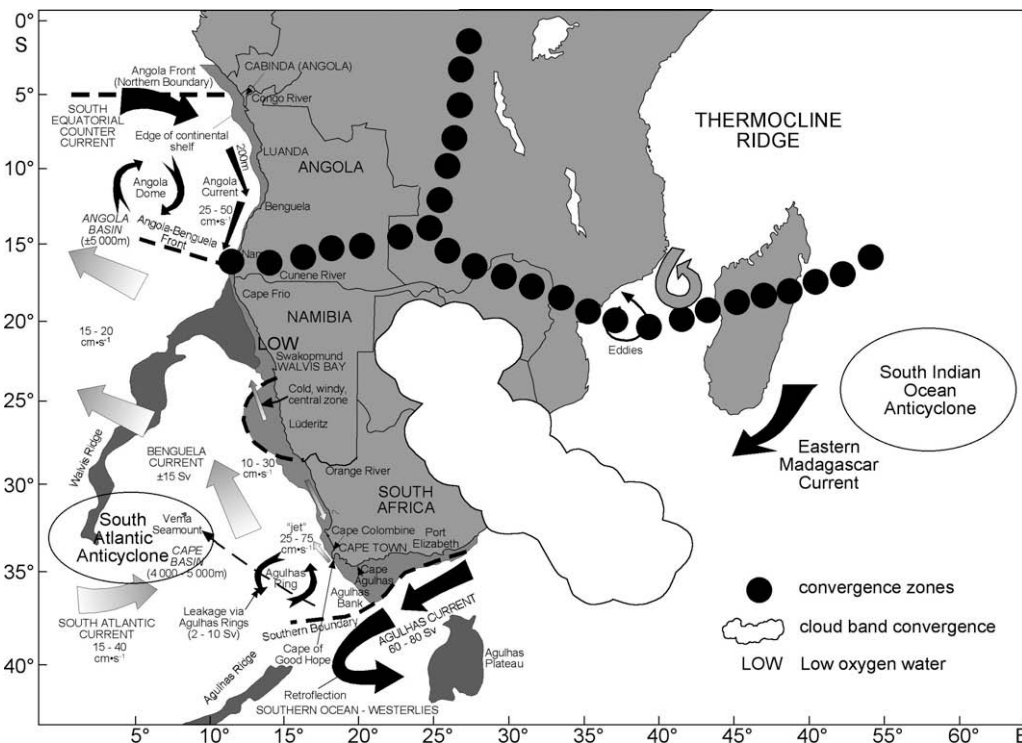
## 1. Introduction

The Benguela region has been subject to a number of disciplinary reviews (Andrews and Hutchings, 1980; Nelson and Hutchings, 1983; Shannon, 1985; Chapman and Shannon, 1985; Shannon and Pillar, 1986; Crawford et al., 1987; Shannon and Nelson, 1996; Hill et al., 1998; Field and Shillington, 2004; Mackas et al., 2006; Shannon et al., 2006; Shillington et al., 2006; van der Lingen et al., 2006). Two substantial multidisciplinary programs, the Benguela Fisheries and Environment Interactions and Training (BENEFIT) program, funded largely through the Norwegian Agency for Development and Co-operation (NORAD) and German Agency for Technical Cooperation (GTZ) and the Benguela Current Large Marine Ecosystems (BCLME) program, funded through the Global Environment Facility (GEF), recently terminated and provided a large stimulus for a coherent study of the entire Benguela region from 5°S, 12°E off Cabinda in Angola to the Nelson Mandela Metropole (Port Elizabeth) on the south coast of South Africa at 34°S, 26°E. While much focus has been on the continental shelf areas and the associated fishery and mineral resources, there has been a growing awareness of the large basin scale ocean and atmospheric forcing of the Benguela region, which comprises a number of fronts or boundary regions. This overview attempts to provide a concise multidisciplinary description of the major features of the Benguela system within the constraints of length. Interested readers are referred to Shannon et al. (2006) for more details.

## 2. Large scale features

Fig. 1 (modified from Shannon (2006)), indicates the major features affecting the ocean and atmosphere in the Benguela, compared to the review of Eastern Boundary regions by Mackas et al. (2006), who of necessity had to treat the upwelling systems as single entities. The South Atlantic and South Indian Ocean anticyclones shift seasonally and interactions with the continental low and associated cloud band convergence and the complex inter-tropical convergence zone create upwelling-favourable winds along the west coast and a warm, poleward-flowing western boundary current on the east coast, which retroflects south of the continent. Warm water of the Atlantic and central Indian Oceans influences the boundary conditions and rainfall patterns and, uniquely, provides warm equatorial water to both the northern and southern boundaries of the Benguela. South of the continent, which ends at 35°S, the free passage of cyclones in the westerly wind belt and the close proximity of the Southern Ocean allow strong signals to propagate into the Benguela region.

Major modes of variance in the South Atlantic are described by Reason et al. (2006) and Colberg and Reason (2007), using rotated Empirical Orthogonal Functions (EOF's) of the upper mixed layer temperatures from the ORCA2 model. (Fig. 2). The first mode is in the equatorial Atlantic and links the strength of trade winds and the occurrence of Benguela Nino's (Shannon et al., 1986) at roughly decadal scales, the second is located approximately over the South



**Fig. 1.** Large scale oceanic and atmospheric features impacting on the Benguela ecosystem (modified from Shannon, 2006). The anticyclone high pressure systems, the inter-tropical convergent zones over land and the west wind belt in the form of eastward moving cyclones determine the dynamic boundaries of the Benguela upwelling region. Warm tropical water is advected southwards in the Angola and Agulhas Currents to form intense mixing areas on the northern and southern boundaries of the Benguela.

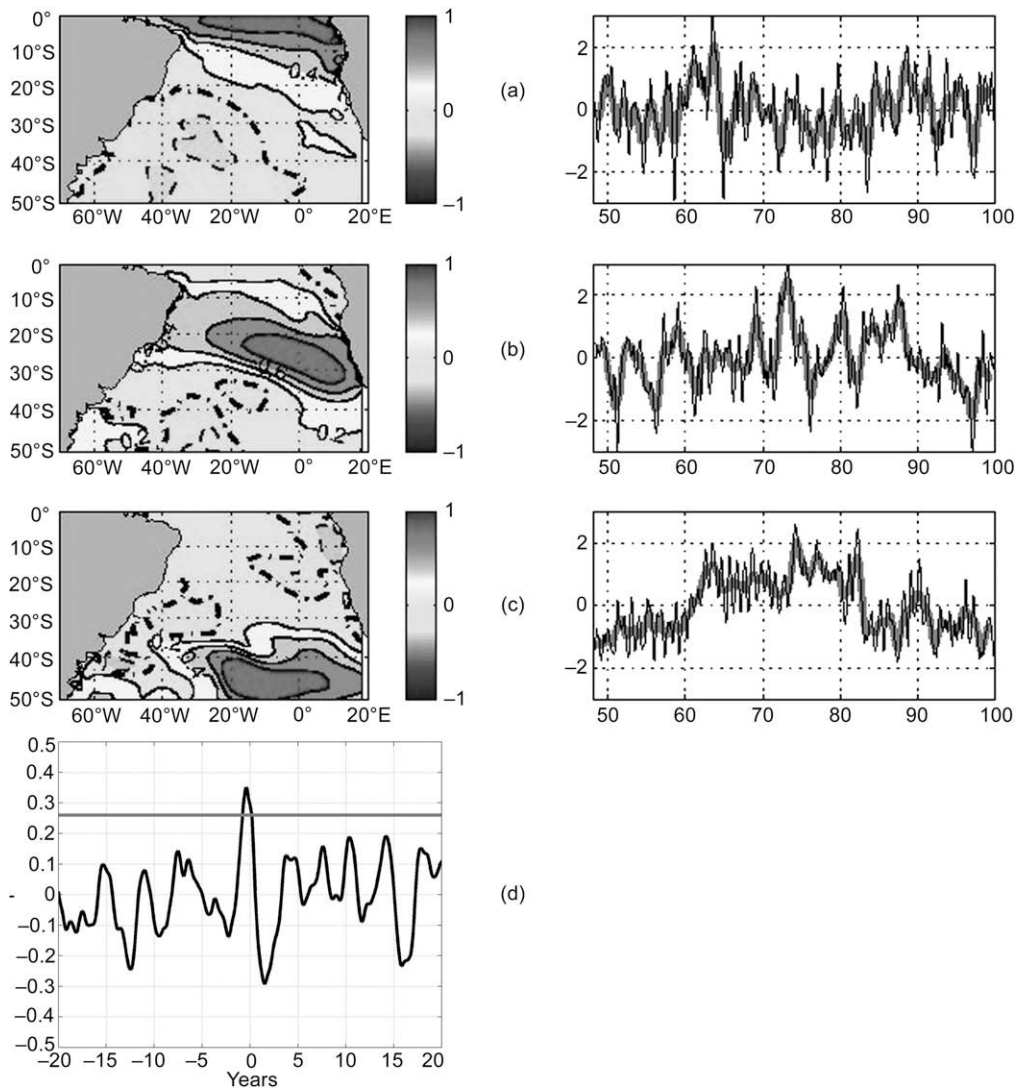
Atlantic anticyclone and is strongly linked to ENSO events and the third is in the midlatitudes with strong interdecadal patterns. The other major influence in the southern regions is the Southern Annular Mode, as indicated by the difference in pressure between 40°S and 65°S, which influences the intensity and pathways of the westerly winds. No clear decadal-scale oscillations comparable to the North Atlantic Oscillation or the Pacific Decadal Oscillation are apparent in the South Atlantic or South Indian Oceans. Strong dipole effects in both oceans also exert some influence on atmospheric forcing over the Benguela (Reason et al., 2006).

The major oceanographic features of the Benguela system, from north to south, are:

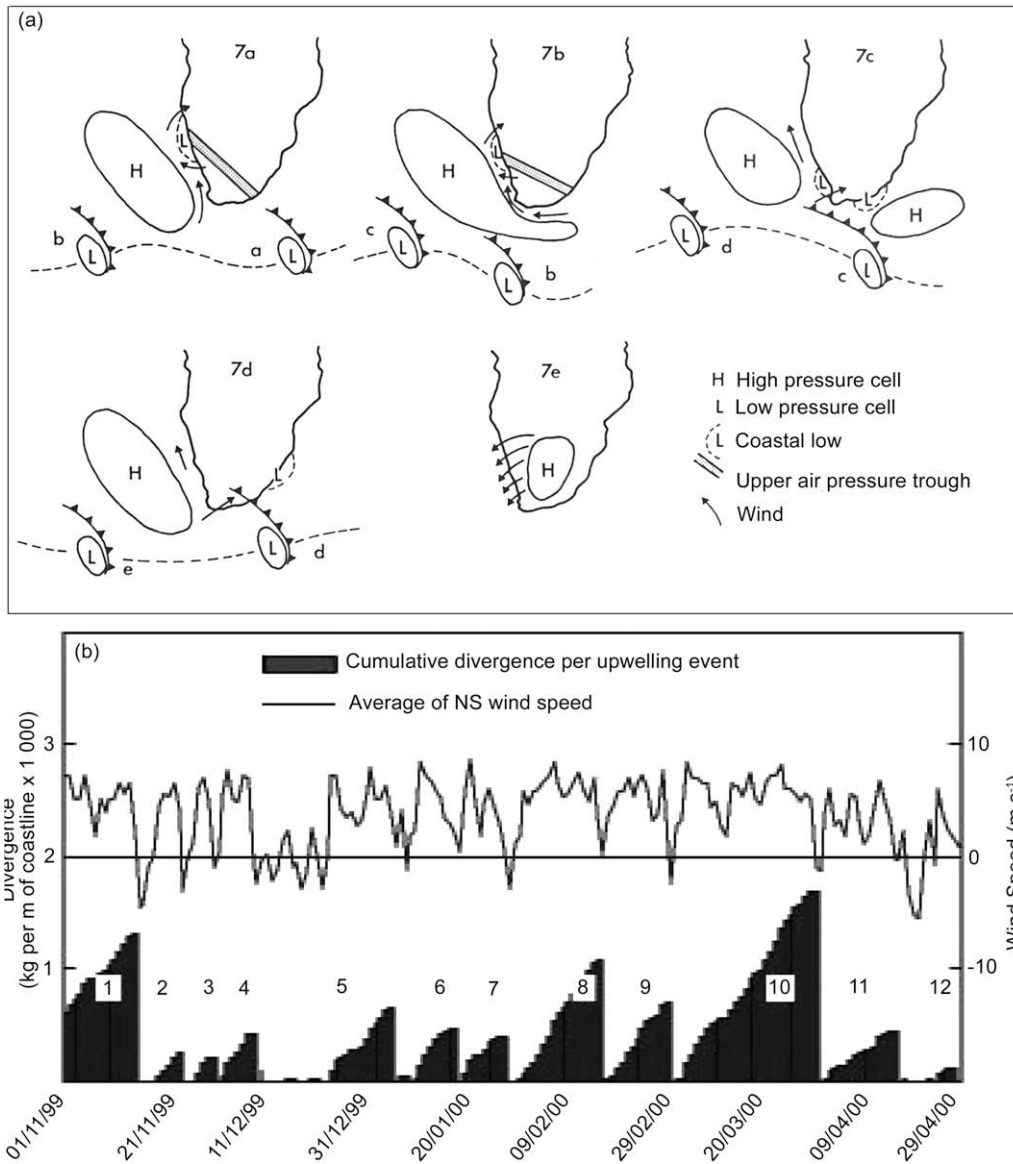
- a northern boundary near the Congo River plume that separates the tropical Gulf of Guinea from the subtropical Angola system;
- the Angola Current, which flows southward along the narrow shelf of Angola as an extension of the south equatorial counter-current, that forms the northern boundary of the wind-driven upwelling system at the conspicuous, very dynamic but relatively shallow Angola-Benguela front at ~17°S;
- the coastline orientation is roughly N–S between Cape Frio and Cape Agulhas, but curves to the north-east from 16°S to 12°S, before bending westward again at Benguela in Angola. Three

major embayments occur at Lobito (12°S), Walvis Bay (23°S) and St Helena Bay (32°S). The orientation changes radically at 34°S between Cape Point and Cape Agulhas from N–S to E–W;

- the major wind-driven Benguela upwelling zone is located between Cape Agulhas and Cape Frio;
- the very powerful upwelling at Lüderitz (26°S) with strong winds, high offshore advection and strong turbulent mixing serves to partially separate the northern and southern Benguela regions, with further subtropical boundary regions in Angola and on the Agulhas Bank;
- a combination of shelf width and coastal topography creates a number of discrete upwelling centres. These, combined with the passage of low pressure systems south of the continent and the formation of a coastally trapped low pressure cell in the lower atmosphere and its southward movement against the escarpment, produce strongly pulsed three-dimensional upwelling (Fig. 3a and b) at 3–10 day intervals (Nelson and Hutchings, 1983), particularly in the southern Benguela. This is crucial for driving short-term variability in plankton development and fish recruitment;
- cool productive water occurs in a narrow band from Cape Agulhas to Cape Frio, broadening at the Angola-Benguela front;



**Fig. 2.** (a–c) The first three rotated EOFs of the South Atlantic upper ocean temperatures. (a) Mode 1 is a generalised Atlantic/Benguela Niño. (b) Mode 2 is related to ENSO. (c) Mode 3 is a midlatitude interdecadal mode. (d) Lagged correlation between EOF2 and Niño 3.4 SST, showing the strongest correlations when the Niño 3.4 index leads about one season. (From Colberg and Reason 2007).



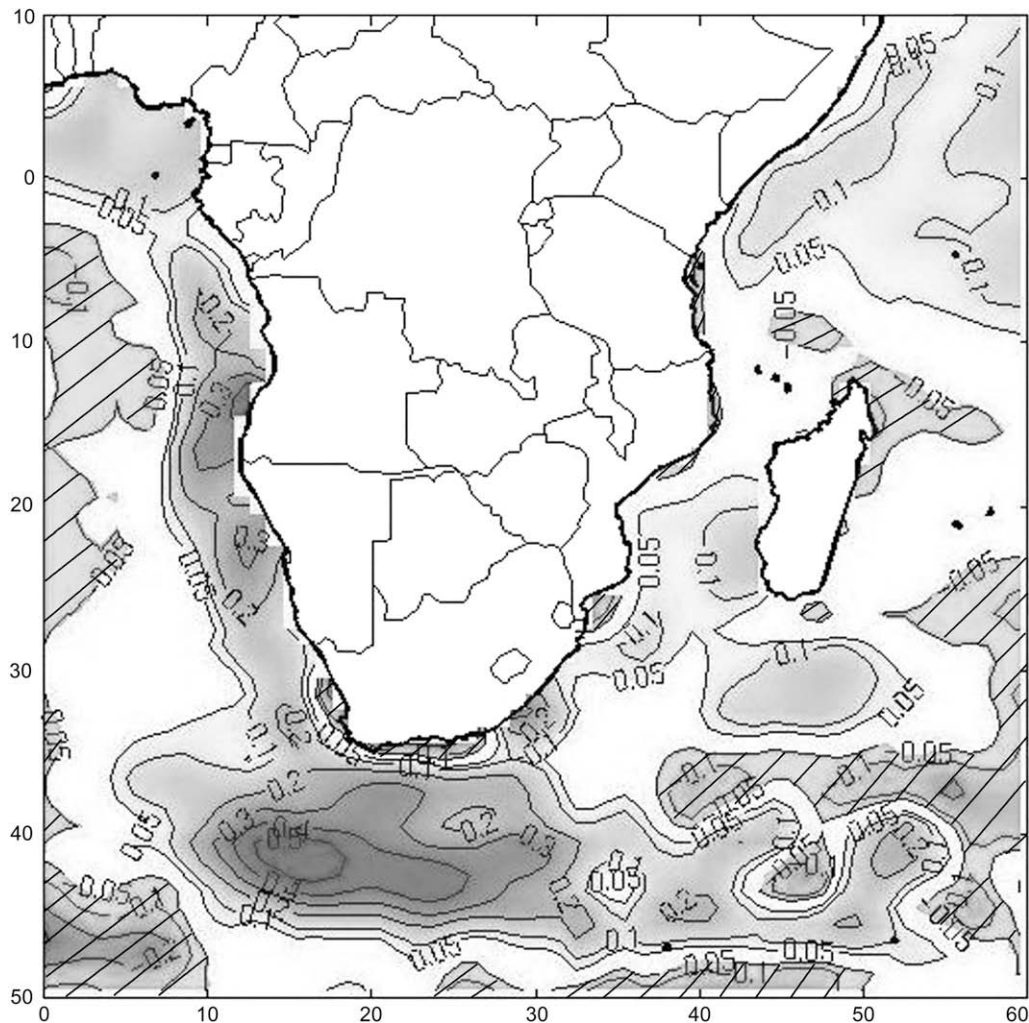
**Fig. 3.** (a) The free passage of cyclones south of the continent (from Nelson and Hutchings, 1983) and the formation of a trapped coastal low promote pulsed upwelling (b) in the central and southern Benguela region (from Roy et al., 2001), crucial for driving short-term variability in upwelling, plankton development and fish recruitment.

- on the eastern Agulhas Bank cool productive water surfaces where the Agulhas Current diverges from the coast at 26°E and on the central Bank (22°E) where the cool ridge is manifest as a shallow doming of isotherms;
- at the southern boundary, the Agulhas Current flows along the shelf break of the broad Agulhas Bank towards the west and while most of the 60–80 Sv current flow retroflects back into the south Indian Ocean, some warm saline water flows northwards into the South Atlantic in jets, filaments and large eddies (Agulhas Rings), some of which impact on the shelf ecosystem and
- offshore the broad South Atlantic gyre forms an ill-defined outer boundary of the Benguela upwelling system where Atlantic surface water, sun-warmed upwelled water and water of Agulhas Current and Agulhas Bank origin mix in complex eddies and filaments.

A noticeable feature of the Benguela has been the strong warming trend (Fig. 4, from Rouault, 2007) at the northern and southern

boundaries, while a cooling trend is detected close inshore in the southern Benguela.

Southerly winds peak in three particular locations in the Benguela (Fig. 5a), at Cape Point (34°S), Lüderitz (26°S) and Cape Frio (17°S), with reduced winds in between and a major decline in wind strength, and change in direction from southerly to south-westerly (onshore), in Angola. This illustration using QUICKSCAT data differs from Fig. 2.6 in Mackas et al. (2006), where Ekman transport is derived from inshore–offshore surface pressure gradients. It is only in Peru that low-level alongshore winds continue to blow nearly up to the equator, presumably isolated from the convergent zone over the Amazon basin by the Andes. Phytoplankton biomass (Fig. 5b) is most abundant downstream of these wind maxima peaks, with perennial, high concentrations on the central northern Namibian shelf (17–23°S), especially near Walvis Bay (23°S) and off the Nam-aqua shelf (29–33°S), particularly St Helena Bay (32°S). Despite perennial upwelling off Cape Frio (17°S), the phytoplankton signal is masked by the intrusion of chlorophylla-poor waters from Angola each austral summer (December–March). Cool, phytoplankton



**Fig. 4.** Sea surface temperature trends in °C per decade since the start of the satellite era (1982–2005) using Reynolds SST (from Rouault, 2007), showing warming in the boundary regions of the Benguela but cooling inshore in the southern Benguela.

rich water extends northward into Angola during late winter (July–September). There is a tendency for phytoplankton and winds to peak in late winter–spring in the northern Benguela and in summer and autumn in the southern Benguela, so that they show opposite seasonal signals. At Lüderitz, the strong winds, narrow shelf and excessive turbulence prevent the formation of dense phytoplankton concentrations in the area between 26 and 29°S.

### 3. Mesoscale features within zones

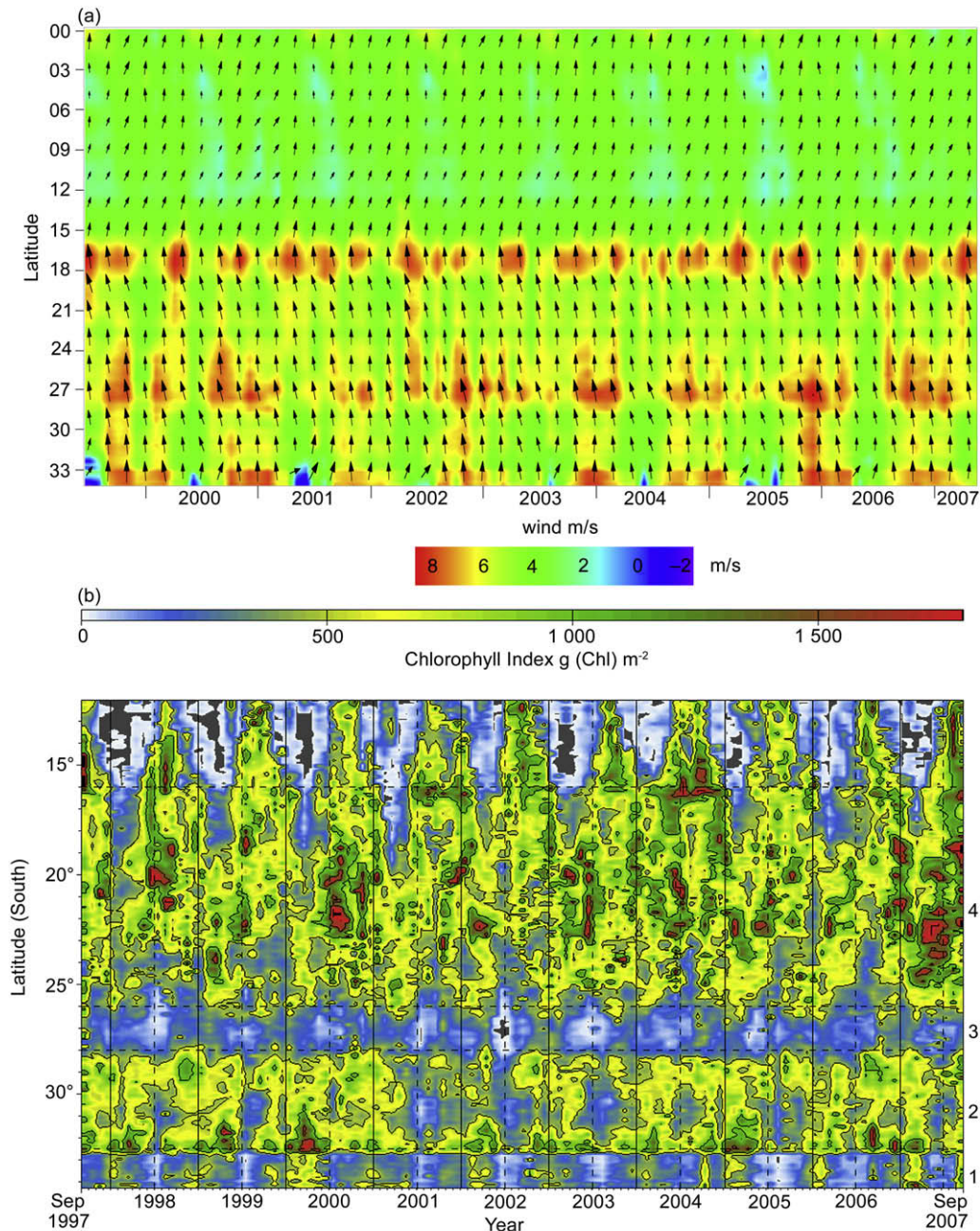
#### 3.1. The Angolan subtropical zone

Pronounced seasonal changes occur off the Angolan coast, with a warm season in December–March, with strongly stratified waters overlaying cooler productive waters below the thermocline, while the cool season, characterised by the elevated thermocline, extends from July to September (Ostrowski et al., 2009). The events are similar to those observed in the Gulf of Guinea (e.g. Houghton, 1976) and only in the extreme south is wind-driven upwelling prevalent for a few months of the year in August–September. Sea surface height anomalies, both positive and negative, propagate southwards in the form of coastally-trapped Kelvin waves into central Angola (Schouten et al., 2005), indicating that the seasonal cycle is remotely forced from the Equatorial Atlantic, rather than caused by wind-driven events (Fig. 6).

#### 3.2. The northern Benguela

The important features affecting this area include the Angola Current, the Angola-Benguela front, the low-oxygen water (LOW) and the upwelling cells at Cape Frio and at Lüderitz (Fig. 1). The Angola-Benguela front can be defined in terms of thermal gradients and shows seasonal and interannual changes in its location. Latitudinal anomalies in the frontal position are shown in Bartholomae and van der Plas (2007) with northward (cold) anomalies in 1982/1983, 1986/1987, 1992/1993 and 1997/1998, which coincide with strong ENSO events in the Pacific and reflect the northward movement of the South Atlantic high in those periods. Southward (warm) anomalies are less frequent, with major events that occurred in 1963, 1984 and 1995 appearing to be related to the zonal wind stress in the equatorial Atlantic (Florenchie et al., 2003). Less pronounced but more common warm events occurred during the 1995–2003 period, while cool events are less frequent, in line with the general warming in the northern Benguela (Rouault, 2007).

Winds at Lüderitz (Peard, NATMIRC, Namibia, unpublished data) show strong decadal variability, with southerly winds peaking in 1970–1973, 1976–1989 and 1997/1998, while lower winds occurred in 1961–1969 and again from 1990 to 2006. These coincide with SST anomalies in the northern Benguela region, which also show pronounced decadal cycles (Fig. 7). However, the infrequent intense warm anomalies, such as occurred in 1984 and



**Fig. 5.** (a) Wind patterns from Quikscat, showing high winds at 17°S, 26°S, and 34°S and sharply declining winds north of 16°S and (b) patterns of surface phytoplankton abundance showing high phytoplankton concentrations occurring downstream from strong upwelling centres, and the low phytoplankton concentration in the zone just south of Lüderitz (26°S). Updated from Demarcq et al. (2007).

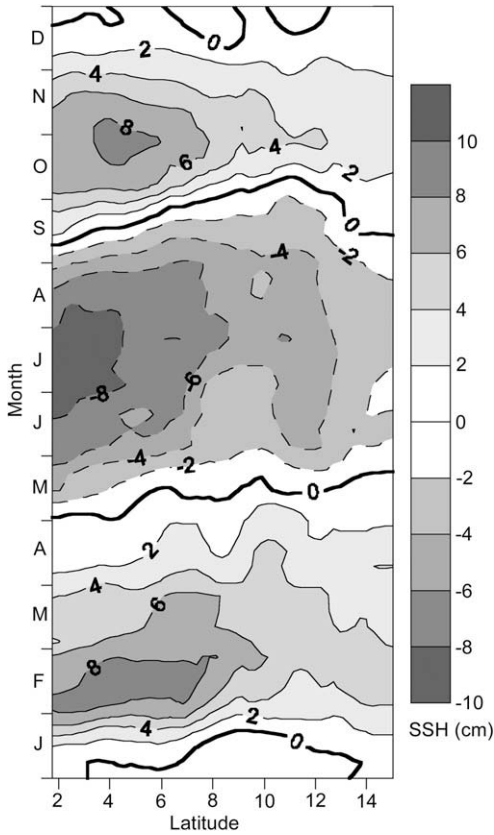
1995, can only be detected in the vicinity of Walvis Bay (23°S) with in-depth data from ships or moored instruments (e.g. see Fig. 4 in Bartholomae and van der Plas, 2007).

Low-oxygen water (LOW) on the northern Namibia shelf (Fig. 1) results from a complex interplay of several processes, including (i) the southerly influx of oxygen-depleted water from the Angola dome area; (ii) uplift onto the shelf at Cape Frio; (iii) local decay processes on the shelf; (iv) the influx of relatively oxygenated central water from the Cape Basin via upwelling at Lüderitz; and (v) stratification of the shelf waters (Fig. 8, Monteiro and van der Plas, 2006). The strength of the intrusion and the phase difference between upwelling at Cape Frio and at Lüderitz results in more or less intense LOW on the shelf with an overall trend of better oxygenation (i.e. a more habitable proportion) over the past 8 years, with

less water of <0.5 ml/l and more water of >2.5 ml/l on the monitoring transect to 120 km at 23°S off Walvis Bay (Fig. 9a). Phytoplankton concentrations on the transect declined sharply after 2005, while mesozooplankton (Fig. 13a) responded by decreasing and the relative abundance of two important species, *Calanoides carinatus* and *Metridia lucens* altered significantly, with *C. carinatus* declining.

### 3.3. The Lüderitz upwelling area

This area (Fig. 1) is characterised by strong winds, high turbulence, much offshore advection and low phytoplankton levels. It forms a partial barrier to a number of pelagic fish species, with populations to the north and south responding differently to heavy

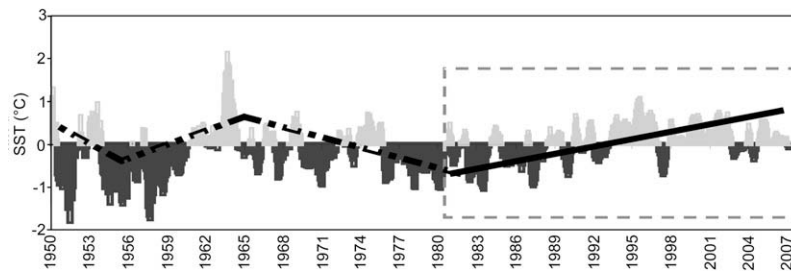


**Fig. 6.** The propagation of sea surface height anomalies southwards through Angola, indicating the influence of internal waves from the equatorial Atlantic on events in Angola, rather than upwelling wind stress, which declines and orientates onshore as latitude decreases. Only off Peru, where the Andes separate low level winds from the inter-tropical convergence zone in the Amazon basin, do alongshore winds persist to low latitudes.

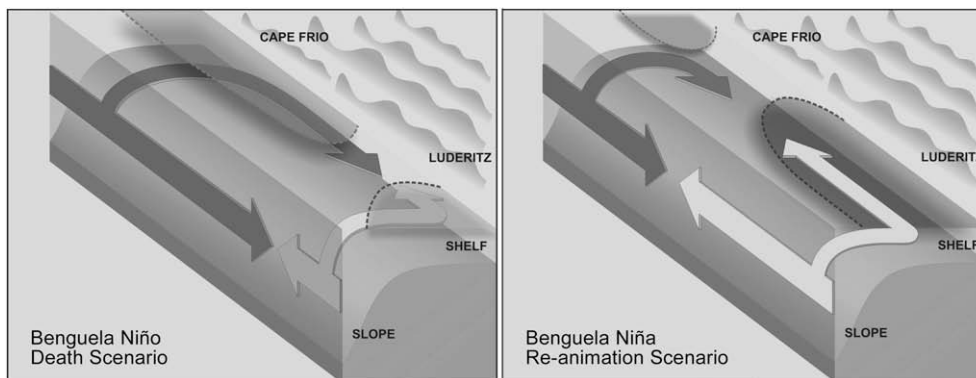
exploitation and subsequent management actions (see below under five: Living resources). Wind patterns at Lüderitz (26°S), Cape Columbine near St Helena Bay (33°S) and Cape Point (34°S), (Fig. 10) all display the same interannual and decadal scale variability but with some lags between them, mostly in response to shifts in the position of the South Atlantic anticyclone. Mesopelagic and demersal fish assemblages and mobile predators do not perceive the area as a barrier and only a few copepod and diatom species differ north and south of Lüderitz. There is a change in upwelling source water to a less saline and more oxygenated source from the Cape basin south of Lüderitz, but the major barrier mechanism appears to be the surface layer along the narrow shelf region (Lett et al., 2007), which mostly separates pelagic fish populations into northern and southern components.

### 3.4. The southern Benguela and Agulhas Bank

Hypoxic water is also prevalent but variable in a narrow inshore strip over the southern Benguela shelf region (Fig. 9b and c), but is linked solely to decay processes of phytoplankton enriched from the coastal upwelling and does not often reach the extreme depletion levels in the northern Benguela (Monteiro and van der Plas, 2006). While LOW is not as pronounced as further north, periodic mass mortalities of shellfish and rock lobsters have occurred with more frequency and intensity in the southern than the northern Benguela, usually in conjunction with the decay of dense phytoplankton blooms in the vicinity of St Helena Bay (Pitcher and Weeks, 2006). While oxygen concentrations vary seasonally and inter-annually, there is a long-term decline in oxygen concentrations in sub-thermocline waters of about 1 ml/l (35%) since 1961 (Fig. 9b, which is also reflected in the shorter-term records from the St Helena Bay Monitoring Line (Fig. 9c), in contrast to recent records for the northern Benguela (Fig. 9a). This decline in oxygenated waters appears to have deleterious effects on rock lobster: it has led to a shift in rock lobsters south-



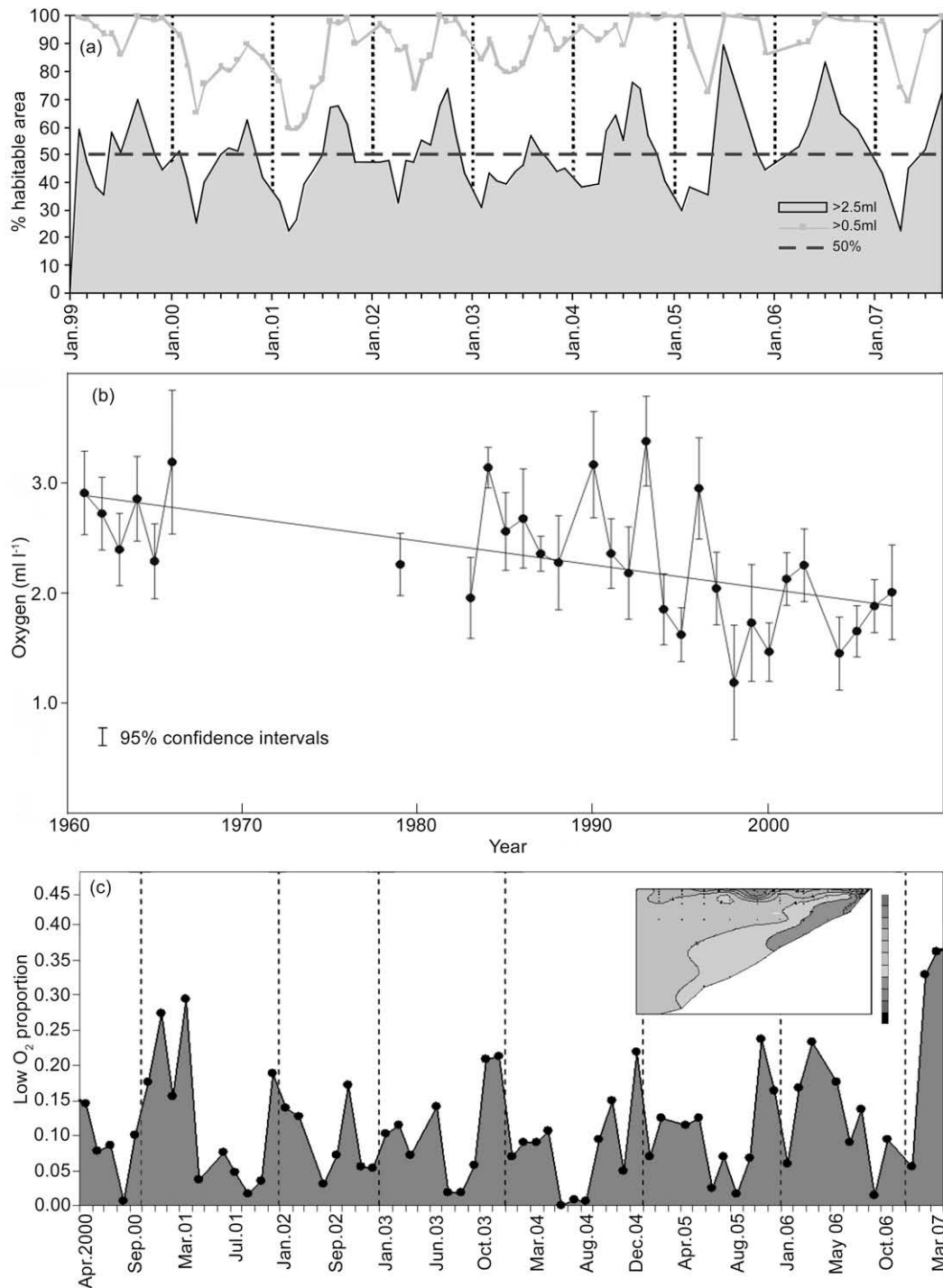
**Fig. 7.** SST anomalies for 22–24°S, from COADS and satellite, showing marked decadal variability that is closely linked to wind patterns (see Fig. 10).



**Fig. 8.** A schematic of the factors influencing the development of low-oxygen water on the Namibian shelf, with interplay between influx from the Angola basin, upwelling at Cape Frio, which lifts low-oxygen water onto the shelf and at Lüderitz, which lifts high oxygen water onto the shelf. Organic loading from the upwelling process and shelf stratification also play important roles in determining the intensity and location of extreme events such as sulphur and methane eruptions (from Monteiro and van der Plas, 2006).

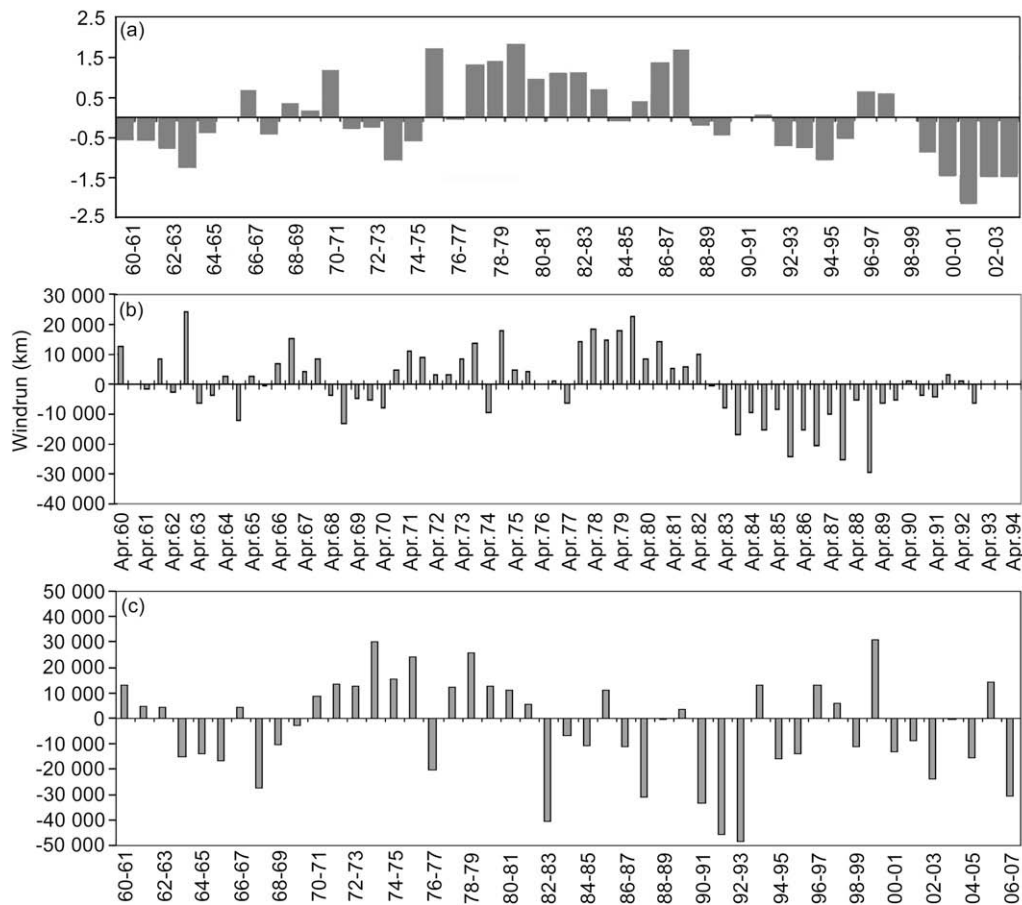
wards and eastwards (Cockcroft et al., 2008) and the frequency of walkouts has increased in the four decades from 1960 to 2000 (Fig. 11a–d). The decline in walkouts in the 2000s (Fig. 11d) may reflect the depleted state of lobsters in this vulnerable area. These have led to severe economic and social problems on the arid west coast, where alternative livelihood prospects are limited, while artisanal fishers in the southern region have benefited. Future trends remain uncertain.

Phytoplankton concentrations from ship and satellite observations are high and variable along the South African west coast (Figs. 5b and 12), with a seasonal signal apparent only in smoothed data, peaking in late summer and autumn. No obvious trend is evident in the relatively short time series, although there is a slight upward trend in upwelling-favourable winds, nutrients and potential production over the period 1980–2007 (J. Currie (unpublished) and M. Gibberd, UCT pers comm.).



**Fig. 9.** (a) Variability in the low oxygen indices >0.5 ml/l (threshold for hake) and >2.5 ml/l (threshold for pelagic fish) along the 23°S transect, indicating a slight increasing trend in the habitable area, 1999–2007. (b) Changes in mean oxygen concentrations (ml/l) in the sub-thermocline layer in St Helena bay (32°S), 1957–2007, indicating a significant decrease ( $p < 0.01$ ) in oxygen concentrations of approximately 1 ml/l (35%) over time and (c) Changes in the proportion of a standard section where  $O_2 < 2$  ml/l on the St Helena Bay Monitoring Line (SHBML) transect, 32°S, 2000–2007. Both (b) and (c) indicate a declining oxygen trend in the southern Benguela, in contrast to the northern Benguela, which shows a recent upward trend but no long term change.





**Fig. 10.** Wind anomalies at (a) Lüderitz (26°S), (b) Cape Columbine (32°S) and (c) Cape Point (34°S), showing interannual and decadal variability but similar trends.

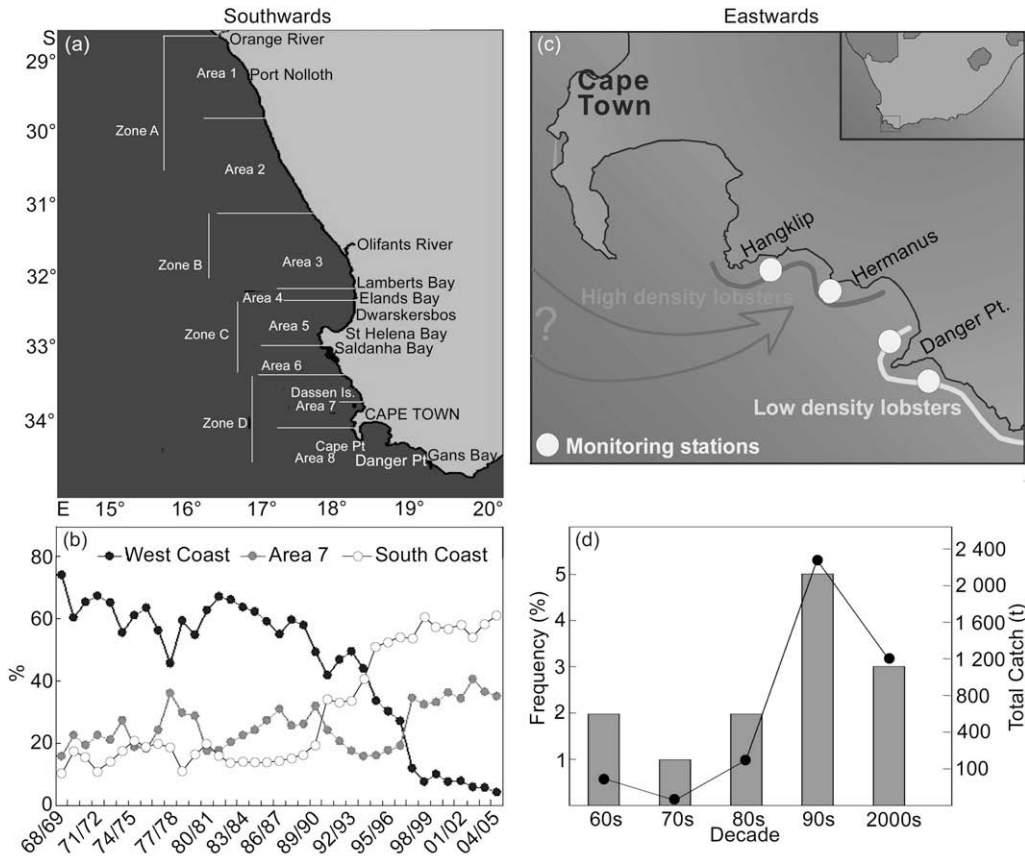
Mesozooplankton (Fig. 13b) displayed a distinct seasonal signal with a summer maximum for the period 2000–2003, when pelagic fish were very abundant on the west coast and this seasonal signal has declined in recent years. However a well defined 100-fold increase in zooplankton abundance occurred between 1950 and 1995, followed by a 10-fold decline in recent years as pelagic fish increased (Fig. 13c, Verheye et al., 1998). This increase in the southern Benguela is mirrored by a similar increase in the northern Benguela between 1970 and 2007 (Fig. 13d). Sardine and anchovy eggs and larvae on the SARP (Sardine–Anchovy Recruitment Program) line sampled off the Cape Peninsula (34°S, Fig. 14) reflect changes in the population status of the two major species, with sardine dominating through the 1990–2000, then a period of simultaneous high biomass until 2002, whereafter sardines declined sharply, resulting in a recent period of anchovy dominance. These changes in abundance were accompanied by an eastward shift, past Cape Agulhas (20°E), of both sardines (Coetzee et al., 2008) and anchovy (Roy et al., 2007) during summer months. The recruitment of anchovy, which spawn in midsummer, appears less deleteriously affected by the eastward shift than sardine, with bimodal spawning peaks on either side of the midsummer anchovy peak and which have experienced five consecutive years of poor recruitment since 2004.

#### 4. Modelling in the Benguela

The adaptation of the ROMS (Regional Ocean Modelling System, Penven et al., 2001), and other numerical models (Shillington et al., 2006) to the Benguela region has brought enormous benefits in

insight and understanding, allowing hypotheses of mechanisms driving shelf processes to be proposed and tested. While some aspects require further refinement, (e.g. there is too much coastal upwelling as well as Agulhas input in the southern Benguela region relative to observations), the models have allowed insightful manipulations, such as investigating the effect of Madagascar on regional flows and the role that the Agulhas Current plays in water column stratification on the Agulhas Bank (N. Chang, UCT, pers. comm.) and the west coast. Other aspects of interest include the equilibrium flow characteristics of the Benguela in the upper 1000 m, with the southern Benguela flowing equatorwards but the northern Benguela flowing polewards, with convergent offshore flow and a cyclonic eddy in the vicinity of the Lüderitz boundary region (Fig. 15). This convergent flow from two very productive regions may fuel exceptional mesopelagic fish abundance in the vicinity of the Lüderitz upwelling cell.

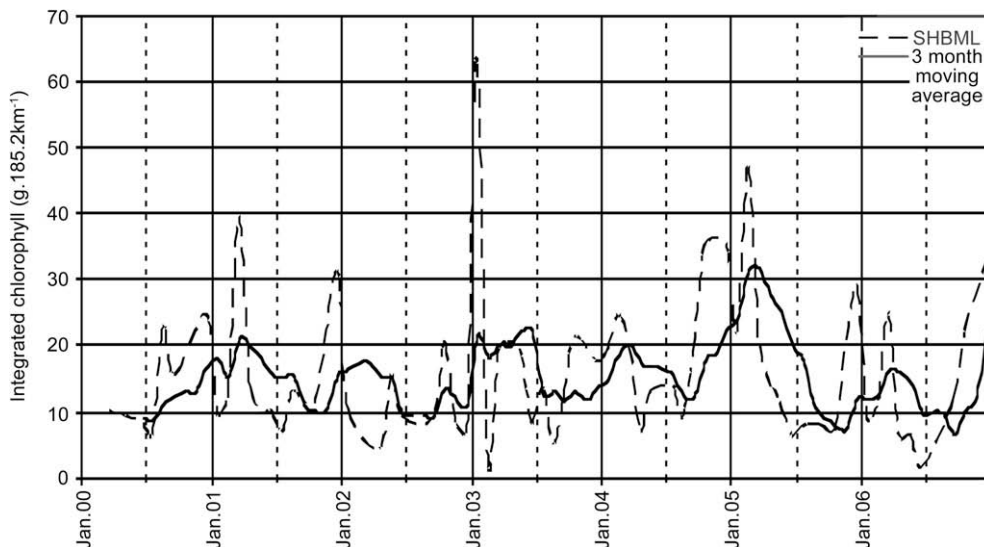
The use of Individual Based Models (IBMs) has allowed much progress in understanding the early life-history dynamics of pelagic fish from the Agulhas Bank to the west coast nursery areas in terms of season and location, from the release of eggs to the retention of juveniles in nursery areas (Fig. 16, Mullon et al., 2002, 2003; Huggett et al., 2003; Parada et al., 2003, 2008; Miller et al., 2006). The model outputs reflect observations, although older, larger fish appear to spawn in theoretically suboptimal habitats in terms of transport success on the central and eastern Agulhas Bank, while few eggs and larvae appear to survive until recruitment in the southern and eastern Agulhas Bank, even if retained in seemingly optimal habitats. Some features, such as predation of eggs and early larvae by up to 12 million tons of adult pelagic fish present on the Agulhas Bank during the summer months, need further



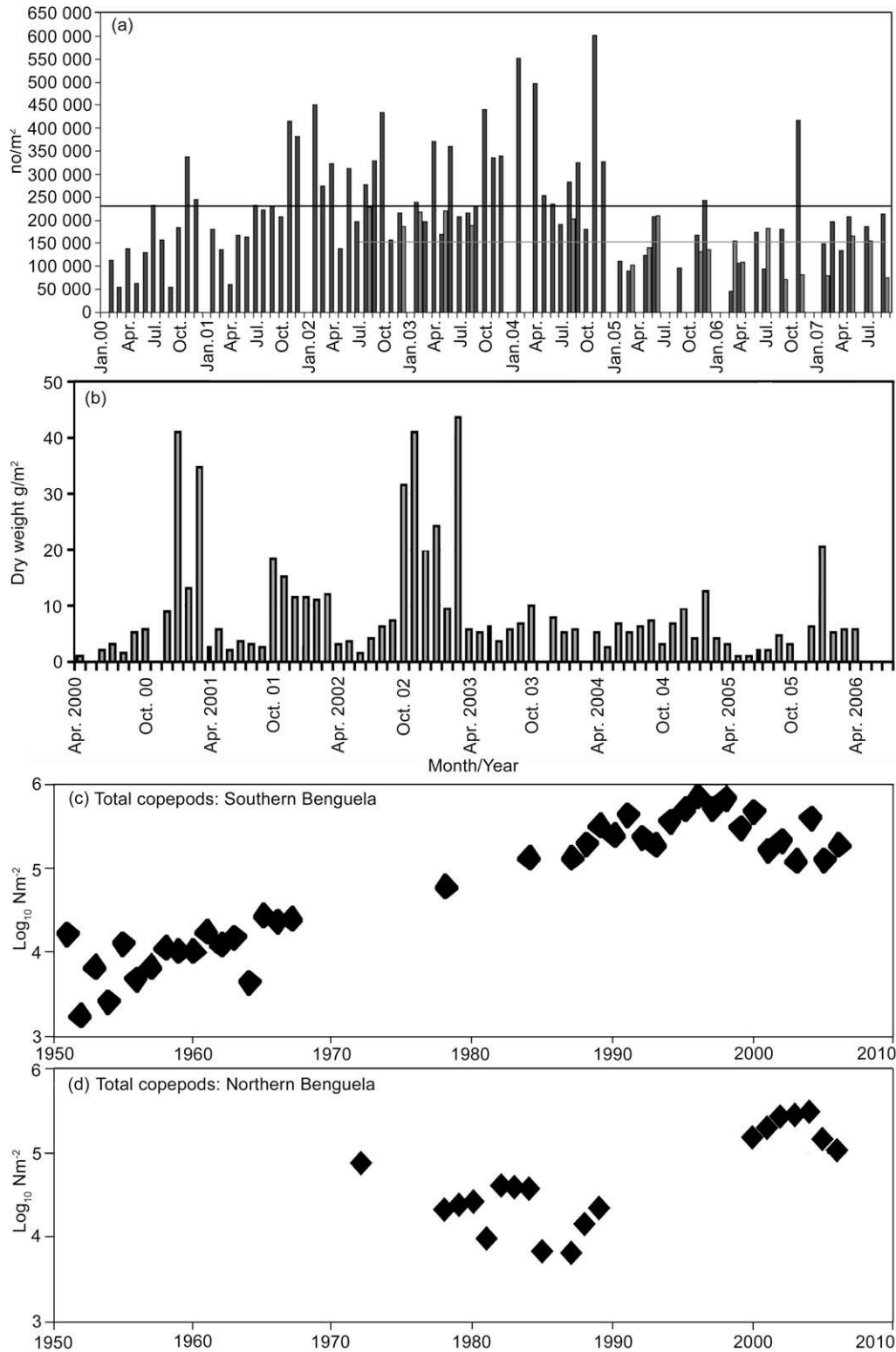
**Fig. 11.** (a) Rock lobster fishing zones and areas. (b) proportion of the catches from the west coast (Areas 1–6), Area 7 and the south coast (Area 8), showing southwards and (c) eastwards trends in the distribution of rock lobsters as far as Danger Point and (d) the number of walkouts per decade on the west coast (from Cockcroft et al., 2008). The decline in walkouts in the 2000s may be a result of depleted stocks in the vulnerable area.

attention as high predation probably explains the lack of recruits there compared with the west coast. Bakun’s triad hypothesis (Bakun, 1996) should perhaps be expanded to include predation to help explain why fish spawn and recruit where they do in the southern Benguela.

Pelagic fish migrate southwards onto the stratified Agulhas Bank to spawn when there is peak upwelling and maximum light levels in summer. This may explain the poor link between primary production and fish productivity, with diversion of carbon on the west coast to other pathways, such as the sediments, mesopelagic



**Fig. 12.** Monthly integrated chlorophyll in the upper mixed layer along the SHBML (32°S), 2000–2008, with a 3-month running mean, indicating a seasonal cycle, little overall trend but very high values attributable to dinoflagellate blooms in late summer/autumn (Pitcher and Weeks, 2006).



**Fig. 13.** (a) Copepod abundance (nos m<sup>-2</sup>) along the Walvis Bay transect at 23°S, and along 20°S, 2000–2007. (b) zooplankton dry weight (g m<sup>-2</sup>) along the SHBML transect at 32°S, 2000–2007, showing a strong then weak seasonal pattern. (c) Changes in the total copepod abundance (log<sub>10</sub> nos m<sup>-2</sup>) in the St Helena Bay region (32°S), 1950–2007. (From Verheye et al., 1998) and (d) changes in the total copepod abundance (log<sub>10</sub> nos m<sup>-2</sup>) in the Walvis Bay region (23°S), 1970–2007, showing 10–100-fold increase in copepods in both the northern and southern Benguela.

fish or offshore to the ocean interior. In winter, when the recruiting cohort reaches maximum biomass, the upwelling and light levels are at their lowest and the fish are feeding on plankton populations accumulated over the summer–autumn period. In addition, the

southward movement to the Agulhas Bank, against a food gradient, may be energetically costly and could account for the low pelagic fish productivity relative to primary productivity in the southern Benguela, as reported by Carr, 2002.

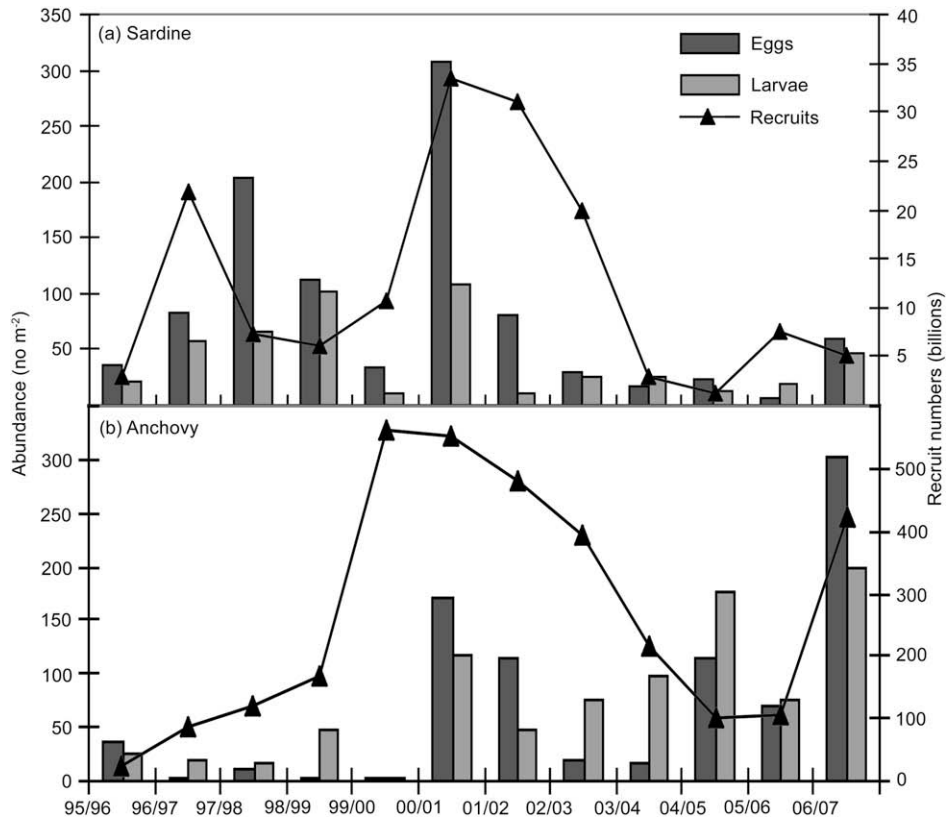


Fig. 14. Changes in anchovy and sardine eggs and larvae ( $\text{nos m}^{-2}$ ) on the SARP line ( $34^{\circ}\text{S}$ ), 1995–2007, together with acoustic estimates of recruitment numbers (billions) surveyed in May–June each year, clearly indicating the shift from sardine to anchovy dominance, with an overlap period in 2000–2003 MCM, Cape Town, unpublished data).

The major nursery grounds for pelagic spawners, as well as a wide variety of demersal and predatory fish, appear to be the shelf areas off northern-central Namibia, the west coast of South Africa, the Agulhas Bank and in the small but significant Natal Bight on the east coast (Fig. 17, Hutchings et al., 2002). Spawning occurs in the southern part of the west coast and on the Agulhas Bank, with transport in the strong shelf-edge jet which carries eggs and larvae alongshore rather than offshore, followed by an inshore movement of pre-recruits to feed in nursery grounds on the west coast of the southern Benguela. This contrasts with the offshore drift of eggs and larvae and inshore movement of recruits off central/northern Namibia. The Angola-Benguela front/mixing area may appear to be a potentially important spawning and nursery ground, but a narrow shelf and a very limited area of good retention (Largier and Boyd, 2001) with much offshore loss limit its importance to a few months in December–March each year, when warm water from Angola pushes southwards towards the nursery grounds on the central Namibia shelf. Little is currently known of Angolan spawning and nursery areas for major resources, except that sardinellas are suspected to spawn off the equatorial boundary in the vicinity of the Congo River outflow at  $5^{\circ}\text{S}$ .

5. Fish resources

Fig. 18, updated from van der Lingen et al. (2006), shows distinct differences in the catches and population status of a number of pelagic and demersal forage and predatory fish populations in the southern and northern Benguela.

Sardine were dominant in the northern Benguela from 1950 to 1975, then collapsed in the mid-1970s. Heavy purse-seine fishing was encouraged on anchovies in an attempt to limit competition

with sardines, but anchovies also declined to low numbers and sardines did not recover, leading to a steep decline in pelagic catches

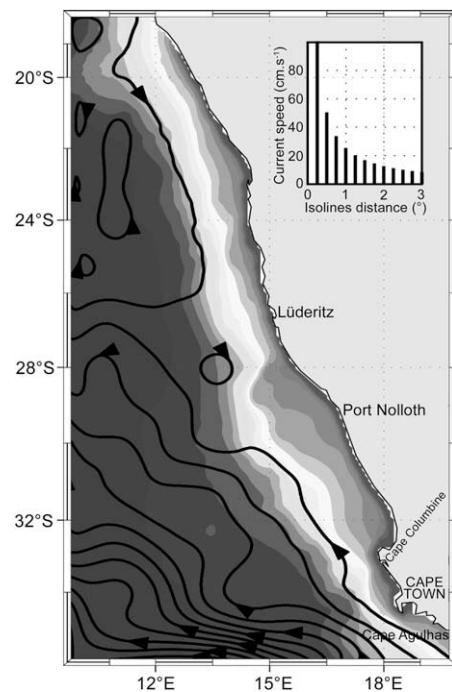
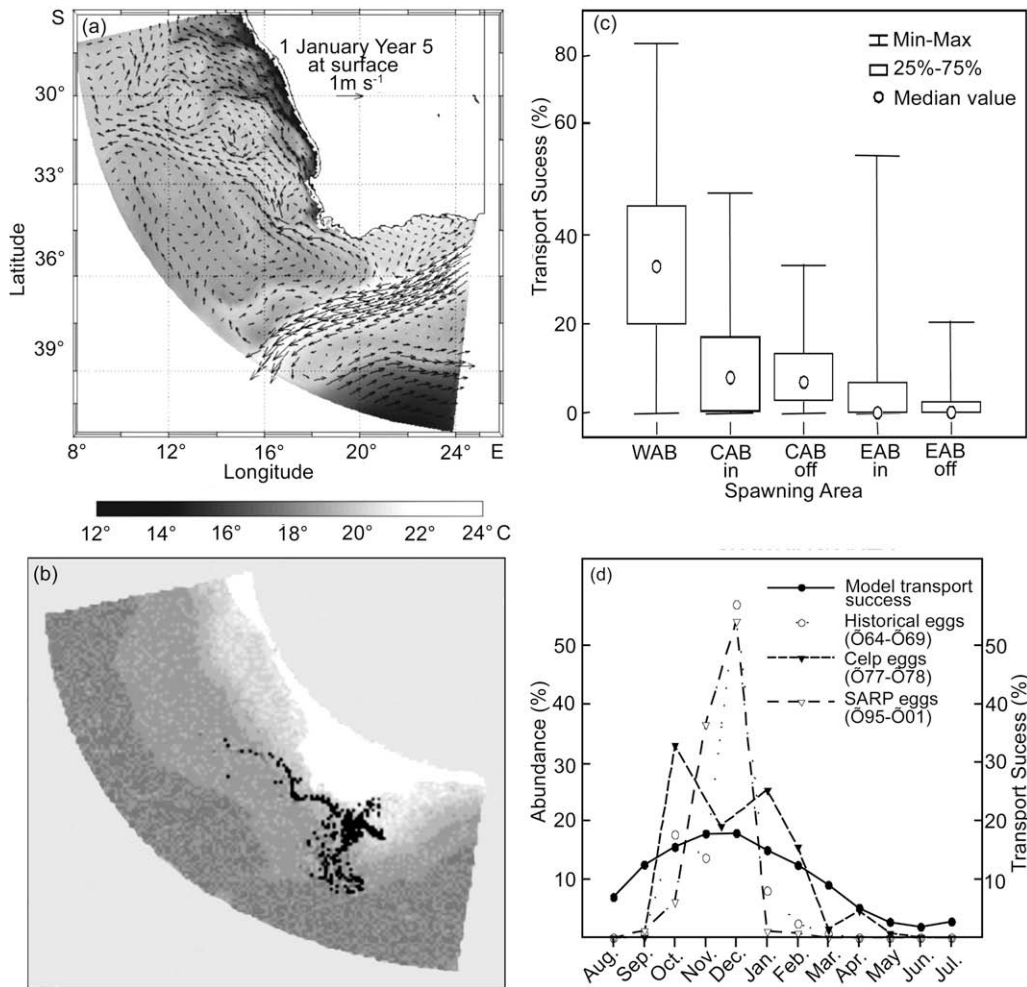


Fig. 15. Stream functions for the 0–1000 dbar layer from ROMS, showing northward flow in the southern Benguela and southward flow in the northern Benguela, with offshore convergent flow and a cyclonic eddy off Lüderitz. This convergent flow from two very productive regions may fuel exceptional mesopelagic fish abundance in the vicinity of the Lüderitz upwelling cell.



**Fig. 16.** Results from coupled circulation and IBM models evaluate the early life-history of pelagic fish and the success of transport from the Agulhas Bank to the west coast nursery grounds. (a) stream functions of surface currents and SST; (b) example of the distribution of eggs and larvae after 100 days; (c) transport success indicating optimal transport from the spawning grounds on the western Agulhas Bank (WAB) to the west coast nursery area and (d) modelled transport success and observed anchovy egg abundances (from van der Lingen and Huggett, 2003).

from a reported 1.3 million tons to less than 100,000 tons through the 1980s and early 1990s.

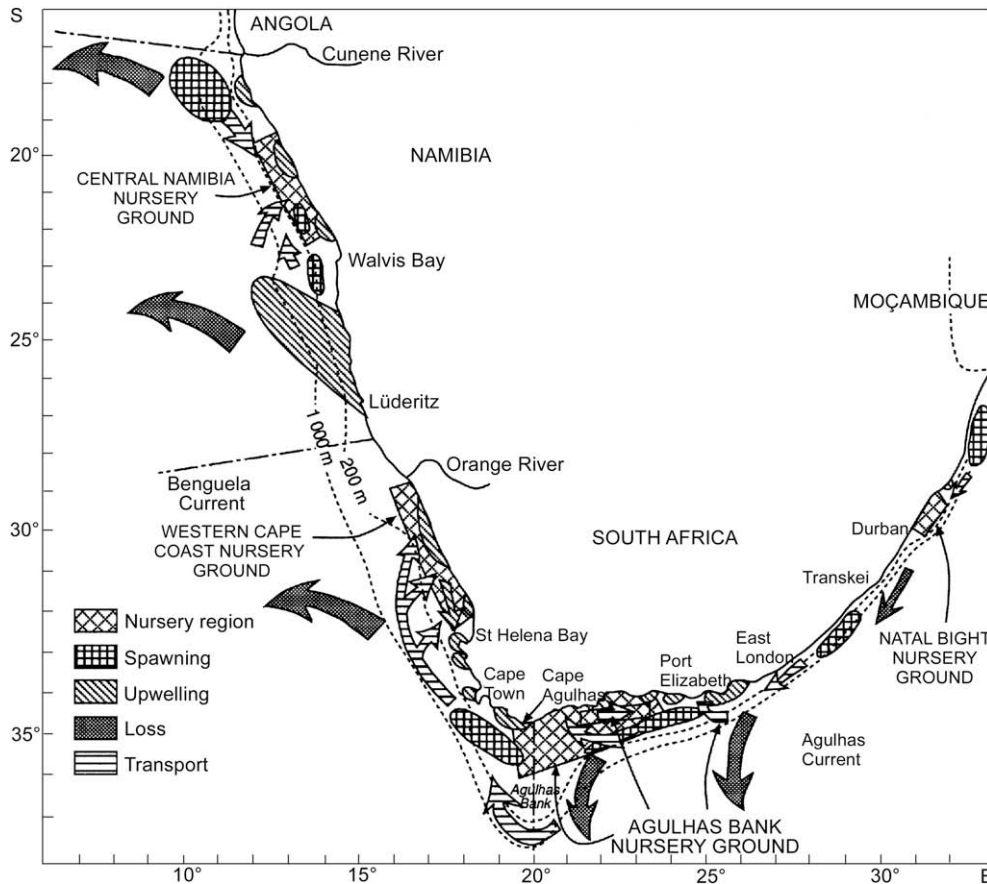
There was some sign of recovery in the early 1990s, but a combination of an extreme low oxygen event in 1994 (Monteiro and van der Plas, 2006) and a warm water intrusion in 1995, plus fishing pressure on a series of poor recruit years, led to further drastic declines in the biomass and the catches (Boyer et al., 2001; Boyer and Hampton, 2001). Recently sardines are at such a low biomass that only a “socio-economic” quota is given to sustain the minimum of employment and infrastructure for canning sardines at two factories in Walvis Bay.

In the southern Benguela, after a sharp peak in purse-seine sardine catches in the period 1958–1962, sardine declined to low biomass (and catches) for a prolonged period, as anchovy replaced sardine. From 1982/1983, sardine biomass and catches increased steadily until the early 2000s, when both sardine and anchovy peaked as a result of exceptional recruitment in the summers of 1999/2000–2002/2003 (Roy et al., 2001, MCM unpublished data). Sardine acoustic estimates subsequently declined sharply from over 4 million tons in 2002–260,000 tons in 2007 following 5 successive years of poor recruitment (Coetzee et al., 2008). Catches also declined proportionately following an operational management plan, which sets modest TAC limits for directed and bycatch sardine of roughly 12–14% of the total biomass estimated from the

acoustic surveys. The sardines and anchovy both moved eastwards in recent years (van der Lingen et al., 2006), resulting in economic hardships for the pelagic industry, as most vessels and processing facilities are based on the west coast of South Africa and high costs of transit to and from the fishing grounds and even trucking of fish to west coast canning factories from the south coast were incurred. Anchovy catches fluctuated around 300,000–500,000 tons between 1970 and 1995, dependent on recruitment variations, but declined through the 1990s until the exceptional recruitment in 2000. Despite an eastward shift in the adult distribution apparently mediated by SST gradients (Roy et al., 2007), anchovy recruitment on the west coast has remained high, and the anchovy population is currently in a healthy state, in contrast to sardine.

In the northern Benguela, horse mackerel (*Trachurus trachurus capensis*) were targeted by midwater trawling in the 1980s and 1990s and, although of relatively low value, dominated the fish landings in Namibia and catches have declined in recent years. In the southern Benguela, a small fishery, governed by a precautionary catch limit, occurs by pelagic, demersal and midwater fleets.

Cape hakes (*Merluccius capensis* and *Merluccius paradoxus*) targeted by bottom trawls, show a general decline due to heavy international fishing pressure, then slow recovery from low levels after declaration of the EEZ in South Africa in 1977 and in Namibia in 1990. Both species are distributed across the boundary between



**Fig. 17.** Spawning, transport and nursery grounds for pelagic fish in the southern African region (from Hutchings et al., 2002). Pelagic fish use strong convergent flow on the western Agulhas Bank and the jet currents outside the upwelling cells to transport eggs and larvae from the Agulhas Bank spawning grounds to the west coast nursery grounds, while in the northern Benguela there is more inshore-offshore movement. The strong upwelling cells are avoided.

Namibia and South Africa and biological and preliminary genetic evidence is contradictory as to the transboundary separation of stocks.

Snoek (*Thyrssites atun*) is an important fish predator in both the northern and southern Benguela, with very large but erratic catches of up to 78,000 tons being caught in Namibia by international midwater fleets in the period 1975–1991. The declared landings for handlined snoek for the southern Benguela are thought to be underestimated by up to 60%. This relatively fast growing top predator shows no overall trend but high interannual variability.

Rock lobster (*Jasus lalandii*) show a general decline throughout the Benguela, due to heavy sustained fishing pressure on such a slow growing species. A change from shallow water hoopnets to traps allowed access to deeper-dwelling offshore stocks, but this did not halt the decline to very low levels of abundance. Both low oxygen trends and wave action are additional important factors affecting catchability and the main catches of rock lobster have been displaced to the south.

## 6. Top predators

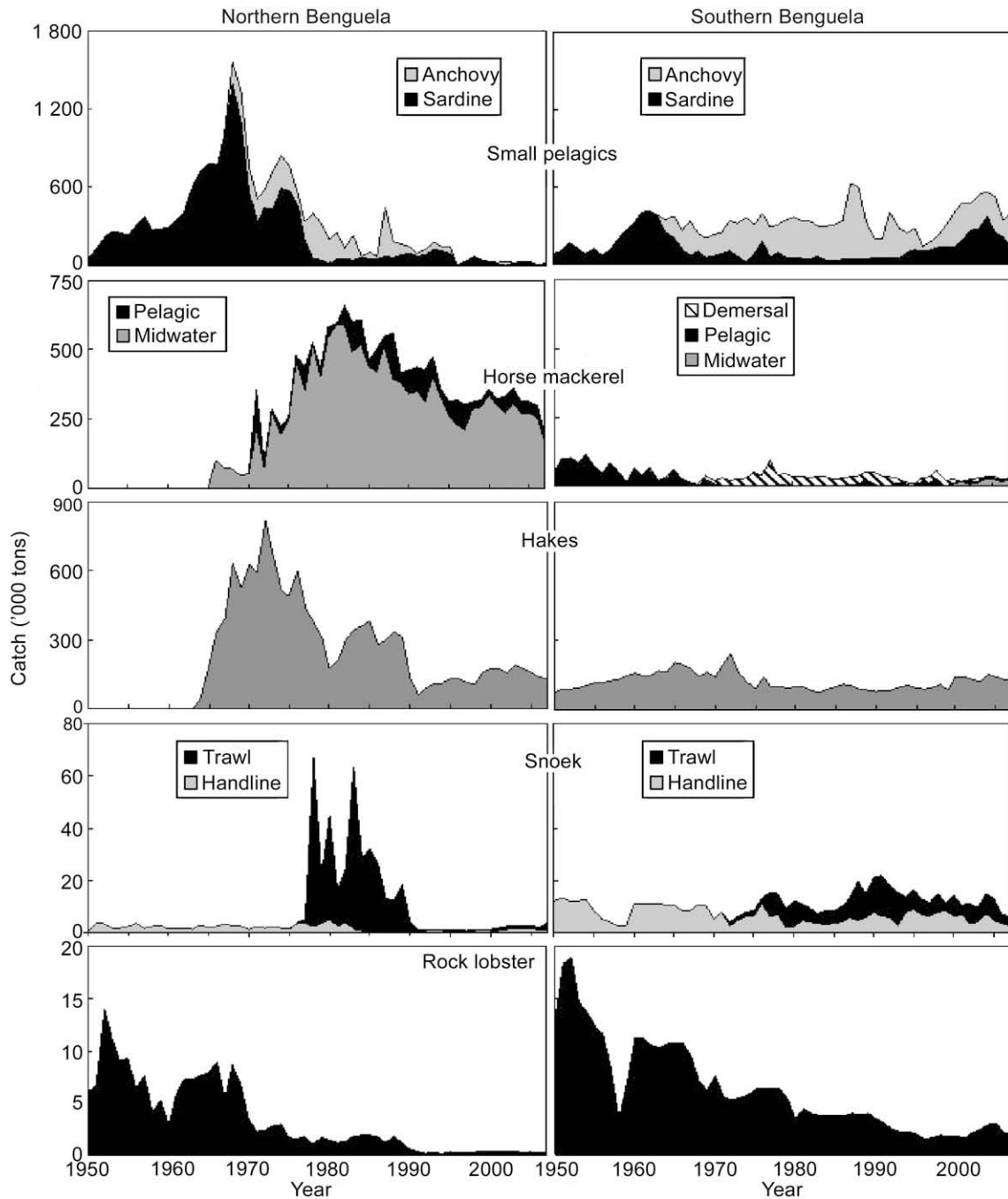
Seals (*Arctocephalus pusillus pusillus*) are generalist predators and seal populations, low in 1900 after heavy sealing pressure during the previous century, increased in both the northern and southern Benguela. Data from 1972 to 1993, based on estimates of pup numbers, indicates an increasing trend, followed by high variability which masks any current trend (Fig. 19). Large declines in the number of pups occurred through the period 1993–1996 and 1998–2002, with swift subsequent recoveries, in the northern

Benguela. Seals appeared to move north and south of their main colonies near Lüderitz and are even increasing in numbers in southern Angola (Kirkman et al., 2007). Seals can easily shift diet between sardine, hake, gobies or mesopelagics and appear to adapt successfully to the large changes in the ecosystem of Namibia. In the southern Benguela, seals increased rapidly until 1993 and then stabilized (Fig. 19). There are few suitable islands and little scope for mainland colonies on the densely populated south coast of South Africa, so no obvious movement of seals followed the shift in pelagic fish eastwards.

Cape gannets (*Morus capensis*) are relatively mobile, and show a decline in the northern Benguela and a corresponding increase in the southern Benguela (Fig. 19), particularly on the eastern Agulhas Bank (Crawford et al., 2008).

Penguins (*Spheniscus demersus*) are less mobile, and show a steep decline in the northern Benguela to very low numbers, while there is a decline in the southern Benguela from 1950 to 1990, a short increase and recently another steep decline as pelagic fish shifted eastwards.

In summary, the northern Benguela has seen a dramatic change in forage fish abundance (Fig. 20), with sardines and anchovies declining and being replaced by gobies, horse mackerel and perhaps jellyfish. Horse mackerel feed predominantly on large calanoid copepods and euphausiids and could potentially occupy a planktivorous trophic level a little higher than sardines, with a concurrently smaller population biomass and still maintain trophic balance. Only anecdotal evidence exists for the jellyfish increases, as plankton nets have been persistently badly clogged throughout the past five decades and no consistent time series exists of quan-



**Fig. 18.** Changes in catches of major fish resources in the northern and southern Benguela. (updated from van der Lingen et al., 2006). Catches are closely linked to biomass trends.

titative acoustic, visual surface or towed net estimates. If jellyfish had increased by orders of magnitude, as has been suggested by some authors, e.g. Bakun and Weeks (2006), the observed zooplankton increase (Fig. 13d) is unlikely, unless sardines are much more efficient predators than jellies. Despite a much reduced population, sardines still spawn sporadically throughout their former range and there is no evidence that the marked environmental and fishing pressures have resulted either in a northerly movement to Angolan waters or a southerly movement to the southern Benguela. Few sardines have been observed at intermediate localities along the west coast between Walvis Bay (23°S) and St Helena Bay (32°S) during the decline of the Namibian sardine and the increase of the South African sardine. Seabirds have declined, while

seals have adapted and maintained high population levels, despite erratic pup production (Kirkman et al., 2007).

In the southern Benguela by contrast, the pelagic yield has been maintained at remarkably constant levels, although sardine were replaced by anchovy in the 1960s and again in the 2000s, after two brief bursts of abundance. There has also been a marked eastward shift in pelagic resources during the past decade (Fig. 21). Predators appear to be more constant, with the less mobile penguins declining proportionately more than gannets, whereas the adaptable seals have either increased or stabilised. Areas of no fishing disturbance have been created around certain penguin colonies in an attempt to halt any further decline (Crawford et al., 2008). These differences in major resources reinforce the environmental

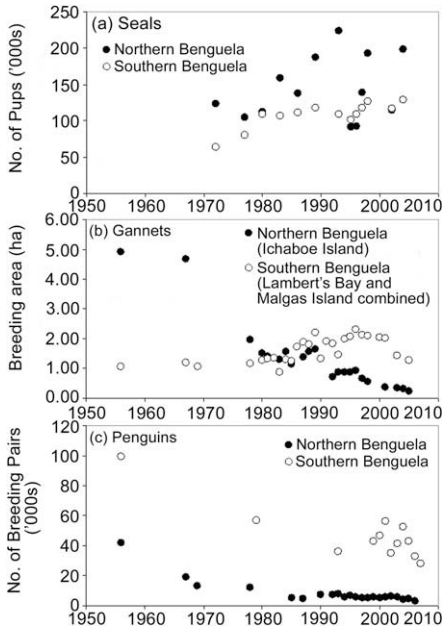


Fig. 19. Changes in top predators in the Benguela, updated from van der Lingen et al. (2006).

distinction between northern and southern parts of the Benguela system, with the northern part subject to tropical environmental variability and the southern part influenced by the Agulhas Current and the Southern Ocean, with atmospheric forcing the predominant mechanism for inducing variability.

**7. Major uncertainties in the Benguela system**

Despite great advances in our knowledge and understanding of the Benguela, much uncertainty remains in understanding this complex ecosystem. In particular, recruitment variability and natural mortality remain enigmatic and no amount of statistical treatment has yet unravelled the mechanisms underlying variability of resources in the Benguela. GLOBEC-type studies of the mechanisms and underlying processes are needed to improve our understanding of the complexities of our system between the physical driving forces and the production of fishery resources. The following are a preliminary list of current uncertainties, problems and questions:

- The large scale ocean–atmosphere connections between the S. Atlantic, SW Indian and Southern Oceans and the Benguela shelf ecosystem.
- The predictability of intense warm events in the northern Benguela.

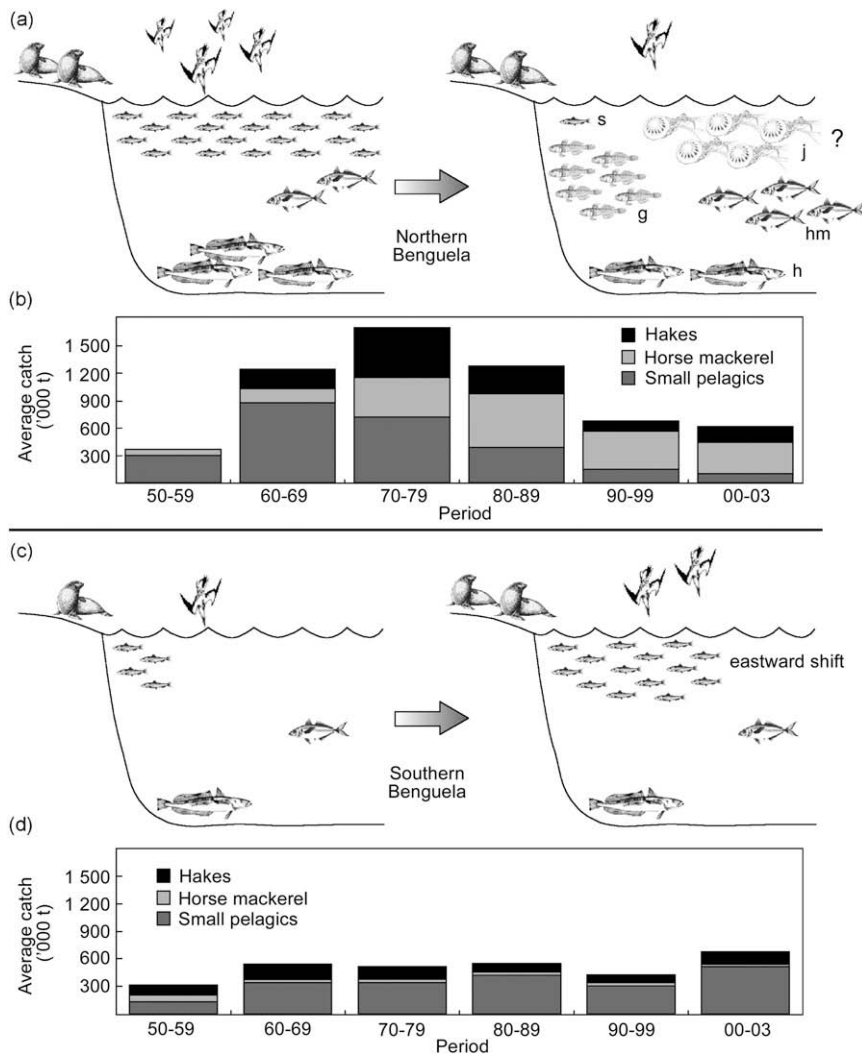
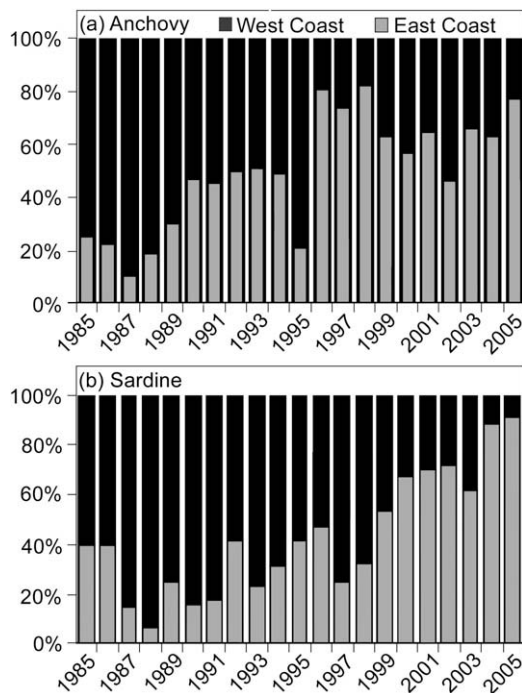


Fig. 20. Changes in the pelagic community in the northern and southern Benguela. See text for details.(modified from van der Lingen et al., 2006). s = sardines, j = jellyfish, g = gobies, hm = horse mackerel, h = hake. See text for details.





**Fig. 21.** Shifts in pelagic fish distribution (% of total biomass) from west of Cape Agulhas (20°E) to east of Cape Agulhas. From Coetzee et al., 2008.

- The intensity and duration of future low oxygen events.
- The nature of the Lüderitz barrier to epipelagic and mesopelagic/demersal species.
- Will boundary zones shift or will gradients intensify or weaken with the global warming trend?
- Will changing boundary zones affect the productivity and distribution of resources, or are the observed changes linked to decadal cycles?
- Is the reduced fish productivity of the northern Benguela ecosystem due to increased warm water, a lack of sardines, increased jellyfish or increased horse mackerel?
- What is the abundance and role of mesopelagic fish in the Benguela?
- Does the cost of migration decrease pelagic fish productivity in the southern Benguela, or is recruitment variability and transport success paramount in determining population levels?
- Why do pelagic fish not spawn on the west coast of South Africa, where enrichment, retention and concentration are optimal?
- The eastward shift of pelagic fish: why did anchovy recruit well and sardines recruit badly?
- Is the Benguela producing carbon-rich detritus instead of fish?
- The transboundary status of deep-water hake (*M. paradoxus*).
- Mechanisms underlying the southward and eastward shift of rock lobsters in South Africa.
- The implications of increased Agulhas flow for resources on the Agulhas Bank.
- Why phytoplankton production, low oxygen, zooplankton and pelagic fish appear to be uncoupled in the Benguela.
- Does predation on the Agulhas Bank prevent good recruitment there and partly explain the mismatch of primary production and fish production?

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