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# Synthesis: climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela

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## ABSTRACT

The NansClim project (2010–2013) represented a regional collaboration to assess the effects of climate on Benguela dynamics. Based on *in situ* (since the 1960s in Namibia and South Africa and 1985 in Angola) and satellite (since the 1980s) observations, the project focussed on four subsystems, namely the Angola subtropical, northern Benguela upwelling, southern Benguela upwelling and Agulhas Bank. This contribution summarizes the findings for selected key

questions, ranging from changes in the physico-chemical habitats, plankton, pelagic and demersal fish communities, to cross-cutting evaluation at subsystem and regional scales. The results underline the overriding importance to of considering the combined effects of climate and fishing as drivers of the dynamics of the ecosystem components. Each subsystem currently continues to function largely as a separate entity as described in earlier reviews. However, some changes have been observed across several subsystems, e.g., a coherent shift from one relatively stable period to another occurred in the northern and southern Benguela in the mid-1990s. Future climate change could weaken the boundaries between the four subsystems. The findings underline the need for continued regional research collaboration and regional surveys focussed at ecosystem, rather than resource, assessment. Our conclusions include implications for ecosystem-based fisheries management, and recommendations for future regional research.

**Key words:** Benguela Current Large Marine Ecosystem, long-term ecosystem-scale change, climate variability, ecosystem approach to fisheries management

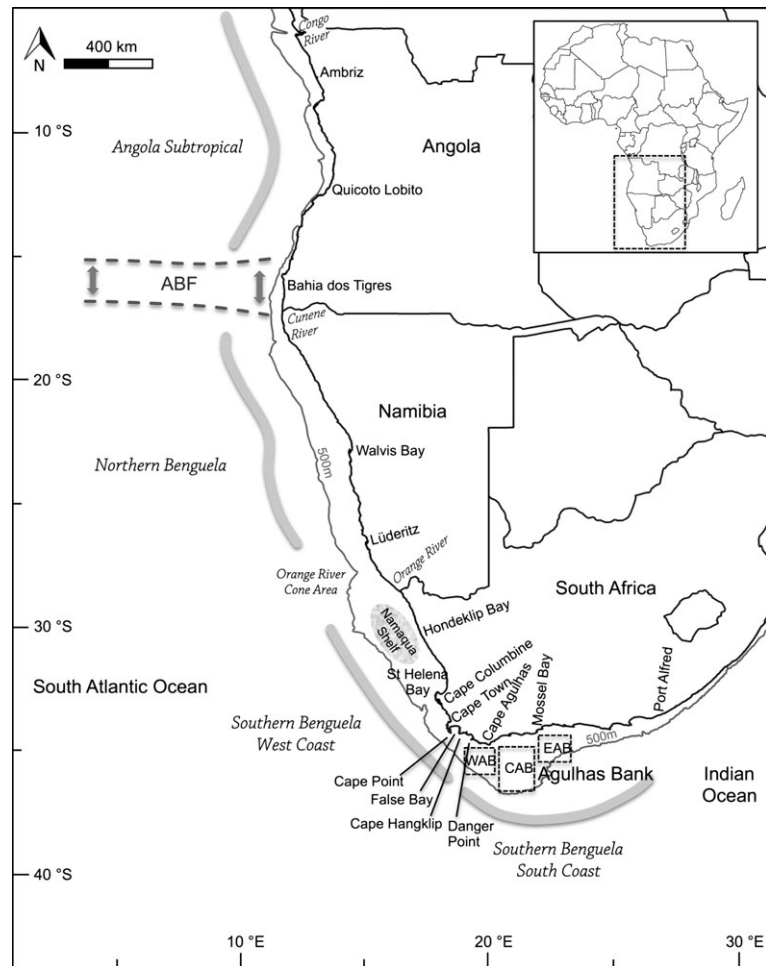
## INTRODUCTION

The Benguela Current Large Marine Ecosystem (BCLME), one of the four large marine eastern boundary current systems dominated by coastal upwelling, is a very productive region sustaining important fisheries for the three coastal countries, Angola, Namibia and South Africa. The high variability in the region, which is comprised of four alongshore subsystems (Fig. 1), has been documented widely (see e.g., Hutchings *et al.*, 2009 for a review). The latitudinal boundaries of the two northernmost of these subsystems, the Angolan subtropical subsystem, and the northern Benguela upwelling, coincide roughly with political boundaries between Angola, Namibia and South Africa. The two southern subsystems, the southern Benguela upwelling and the Agulhas Bank, are located off the South Africa west and south coasts, respectively. The Benguela Current Commission (BCC; www.benguelacc.org) has been established as an

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**Figure 1.** The Benguela Large Marine Ecosystem, focus area of NansClim. Note location of the four subsystems. (ABF, Angola-Benguela Frontal Zone; WAB, CAB, EAB, Western, Central and Eastern Agulhas Bank).

intergovernmental regional organization to harmonize research and provide advice for the management of human activities in the BCLME. The region has set out to implement an Ecosystem Approach to Fisheries (*sensu* FAO, 2003), and issues have been identified and prioritized through Ecological Risk Assessments (ERAs) and ERA reviews for all major fisheries in the region (Nel *et al.*, 2007; Petersen *et al.*, 2010).

In support of the ‘ability to achieve’ dimension of an ecosystem approach, and in the light of climate change anticipated in the region, the NansClim project ([www.nansclim.org](http://www.nansclim.org)) was established with funding from the Norwegian government through the Norwegian Agency for Development Cooperation, NORAD. Its main objective was to identify and describe possible trends and variability in ocean climate and corresponding changes in marine biodiversity and fisheries in the BCLME. Information was available from the Nansen Programme supplemented by extensive national sampling programmes. The approach was to select and collate data from the

Nansen database with regional datasets, and to proceed in three task groups, the first investigating climate variability and climate change in the ocean, and the second and third investigating the responses of pelagic and demersal communities, respectively. The research in the three task teams was guided by five key objectives: (i) to identify ecosystem changes as a consequence of changes in the drivers, fishing and climate; (ii) to document changes in the distribution and abundance of species and communities; (iii) to identify potentially useful species as indicators of change; (iv) to identify sensitive areas or hot-spots of change; and (v) to document changes in productivity.

On a global scale, environmental drivers of change include warming of the surface ocean, increased wind stress, more extensive low-oxygen zones, increased surface stratification and changes in nutrient distributions (Moloney *et al.*, 2013). Such changes would be superimposed on heavy fishing pressure throughout the Benguela since the 1960s. With the southernmost

extension of the continent at 35°S and warm water boundaries present all around the Benguela, this ecosystem cannot extend polewards, presenting special difficulties for temperate-water biota in the face of climate changes.

This synthesis aims to utilize the findings of the NansClim project and other progress achieved to address the five NansClim objectives and some of the uncertainties listed in the Hutchings *et al.* (2009) review of the BCLME. Specifically, we focus on the following questions:

- Are trends in environmental drivers apparent during the observation period?
- What external drivers of ecosystem dynamics other than climate need to be considered?
- Do plankton provide clear signals of long-term variability and change in the system?
- What changes have occurred in the distribution, age structure or spawning of fish populations?
- Can fish species be used as indicators of systematic changes in sea temperature in the BCLME?
- Are there biodiversity hotspots in the BCLME which are susceptible to climate change?
- What are the relative roles of environment and fishing in driving ecosystem changes, species dominance alternations and trends in fish yields?
- What are the implications for ecosystem-based management of human activities in the BCLME?

The following sections of this contribution address these questions typically by subregion and then attempt to draw out cross-linkages and region-wide patterns. It must be noted that, in line with the objectives of the NansClim project, we relied exclusively on the observational data, and did not utilize results of community or ecosystem modelling studies in the region. Shortcomings in this approach are highlighted in the concluding section, which also contains recommendations for further research.

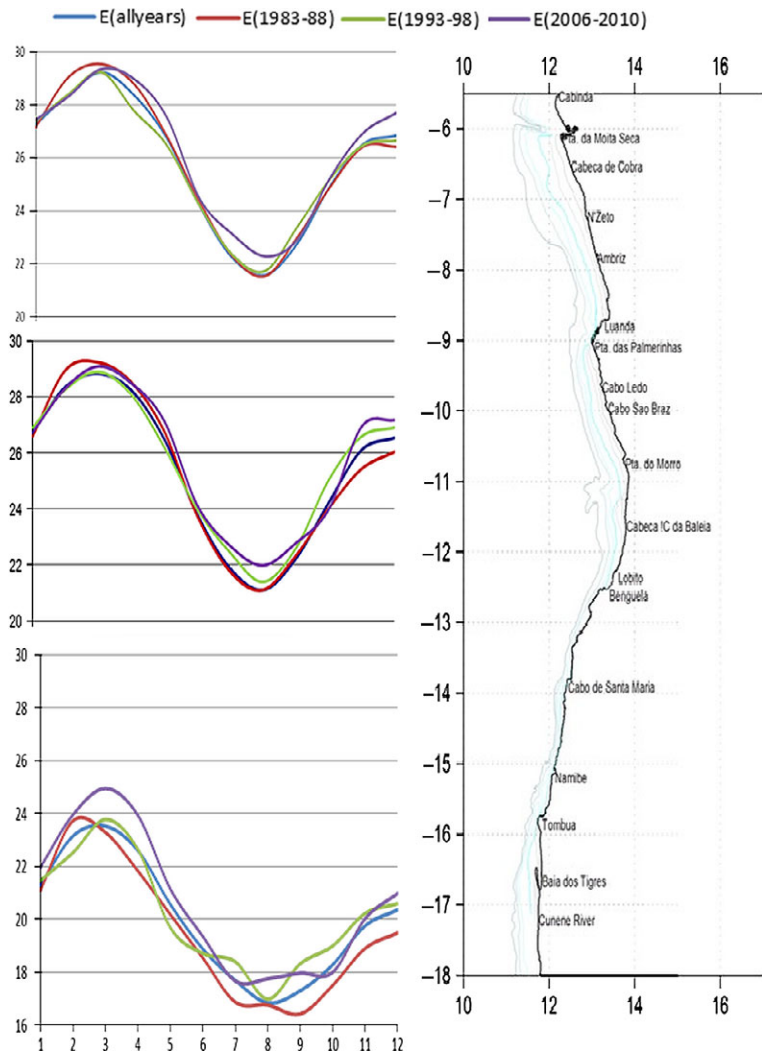
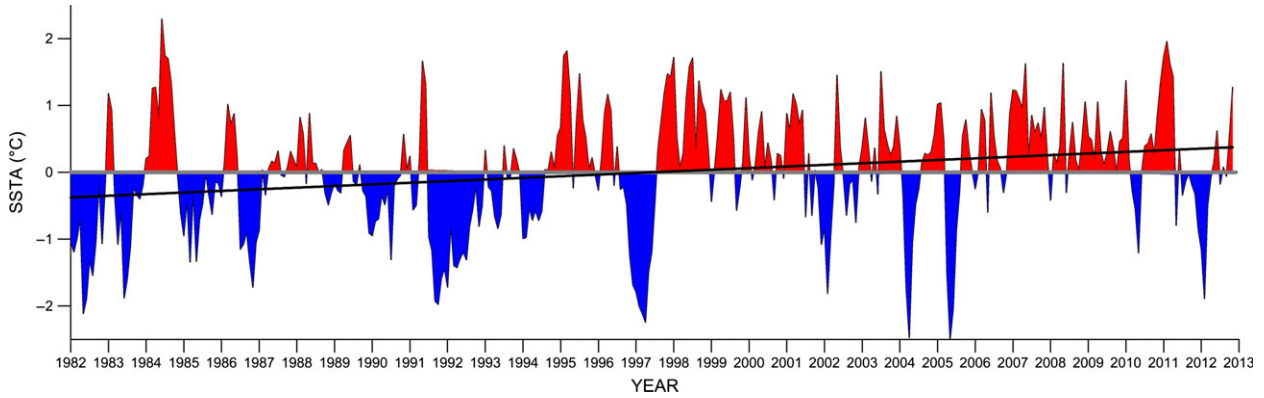
### ARE TRENDS IN ENVIRONMENTAL DRIVERS APPARENT DURING THE OBSERVATION PERIOD?

Large (basin-) scale features which affect the physical environment of the BCLME during the summer include the tropical waters of the South Atlantic and the Indian Oceans (via atmospheric teleconnections), the location of the intertropical convergence zone (ITCZ), the location and intensity of the South Atlantic and South Indian Ocean High Pressure Systems, and variability in the Agulhas Current (see Hutchings *et al.*, 2009). Important sources of variability include the tropical Atlantic, the ENSO

signal, the Indian Ocean Dipole Zonal Mode and anomalies in sea surface temperature (SST) in the Indian Ocean (Reason *et al.*, 2006a,b). These together modulate the intensity and location of frontal regions separating the subsystems within the Benguela and the upwelling intensity (and thereby SSTs) in the shelf zone of the three countries. In winter, the latitudinal variations of the westerly wind belt south of the continent and interactions between the ITCZ and the Hadley Cells between the Tropics and Subtropics affect the intensity and position of the Anticyclones, and the variability of westerly winds in the extreme south of the Benguela (Reason *et al.*, 2006b). Broad-scale wind patterns are driven by the pressure gradient between the oceanic high pressure systems and the low pressure over the continent, modulated by the passage of eastward moving cyclones in the westerly wind belt at 30–40°S (Nelson and Hutchings, 1983), which can affect patterns as far north as 25°S. The wind patterns at specific locations (as mentioned below) therefore apply to broad areas of the shelf. Hutchings *et al.* (2009) synthesized oceanographic data from 1950 to 2007. Subsequently, with the inclusion of further years of data, a number of initiatives including NansClim studies (e.g., Blamey *et al.*, 2012; Hutchings *et al.*, 2012; Jarre *et al.*, 2014) have improved our understanding of changes in the oceanographic drivers in the BCLME, together with the inclusion of another 4–5 yrs of data.

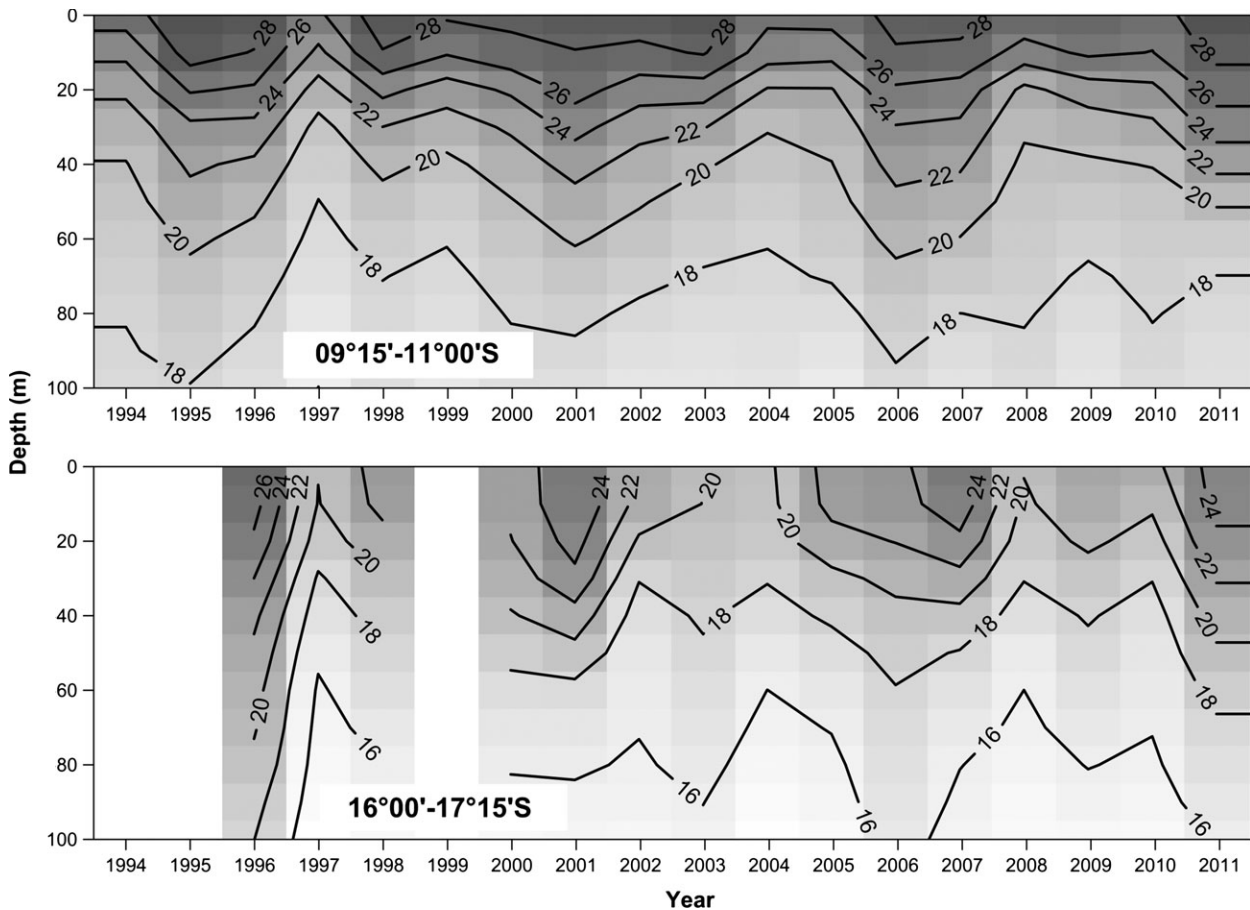
Off Angola, where the SST exhibits a distinct annual cycle of warm and cool seasons (Hirst and Hastenrath, 1983), the ocean surface shows a warming trend from the 1980s to the 2000s, interspersed with pronounced warm and cool events (Fig. 2) with increased warming towards the south (Fig. 3), according to satellite-derived data. According to the methodology of Blamey *et al.* (2012), detection of regime shifts (defined as an abrupt change in relation to the duration of a regime, from one characteristic behaviour to another; Mantua and Hare, 2002) at a decadal scale indicates two robust shifts in the SST anomaly (see Fig. 2), namely a large positive shift in 1994, which partly reverted in 2011 (details of the analysis not shown). The warming has modified SST seasonality, which off northern Angola has shifted towards a lower temperature contrast between summer and winter, and generally warmer SSTs during winter. In southern Angola, warming has occurred throughout the year (Fig. 3). Five warm events occurred between 1995 (strong Benguela Niño) and 2011; these were notable in the upper 50 m of the water column (Fig. 4). The most intense cold event occurred in

**Figure 2.** Satellite-derived evolution of the sea surface temperature anomaly off Angola during 1982–2013, combined from the two 4-km resolution data products, Pathfinder version 5.1 (1982–2009) and Modis Aqua (2002–2013). Data were extracted from the coast to approximately 100 km offshore and averaged over 9°S to 16°S. The trend line indicates an average warming of 0.23°C per decade.



**Figure 3.** Seasonality of sea surface temperature (SST) off three areas along the Angolan coast: Ambiz (07.49–08.00°S, 12.0–14.0°E), Quicoto-Lobito (12.0–12.40°S, 12.0–14.0°E), Bahia dos Tigres (16.30–16.48°S, 10–12°E). Data were derived from Pathfinder satellite observations during 1983–2010. ‘All years’ pertains to an average over this period. ‘E’ in the graph legend denotes ‘period’.

**Figure 4.** Temperature during late austral summer (February–March), 1994–2011, in the top 100 m of the water column off central Angola (top) and in the Angola-Benguela Frontal zone (bottom), based on the data collected on RV Dr. Fridtjof Nansen. Each time-point is an average of all CTD casts deployed in the respective region, and only includes stations with bottom depths of more than 100 m. Shading represents data density. The white areas denote years without data coverage.



1997, with other cold events in 2004, 2008 and 2010. These cold events are mostly evident in the southern zone (Fig. 4). There are no links to northward winds, with much of the variability in upwelling being linked to internal waves of tropical origin (Ostrowski, 2007, and references therein).

An analysis of Pathfinder (version 5.2) data for 1982–2010 indicates a positive linear trend off Namibia in all seasons (Dr F. Dufois, CSIRO, pers. comm.), corroborating Hutchings *et al.* (2009) finding of an increase between 1980 and 2007, after a period of stability between 1938 and 1978 (C.H. Bartholomae and A.K. van der Plas, NatMirc, pers. comm.). A decline in upwelling-favourable winds at Lüderitz (Fig. 1) since 1960 (Peard, 2007; Hutchings *et al.*, 2009) has persisted in recent years (Bartholomae, pers. comm.). Strong southward intrusions of warm water that pushed the Angola-Benguela front southwards, known as Benguela Niños, occurred in 1963, 1984, and 1995.

In 2001, moderate warming occurred in the midst of a general warming period (1997–2010) (Bartholomae and van der Plas, 2007), resulting in less well-defined extreme warm events.

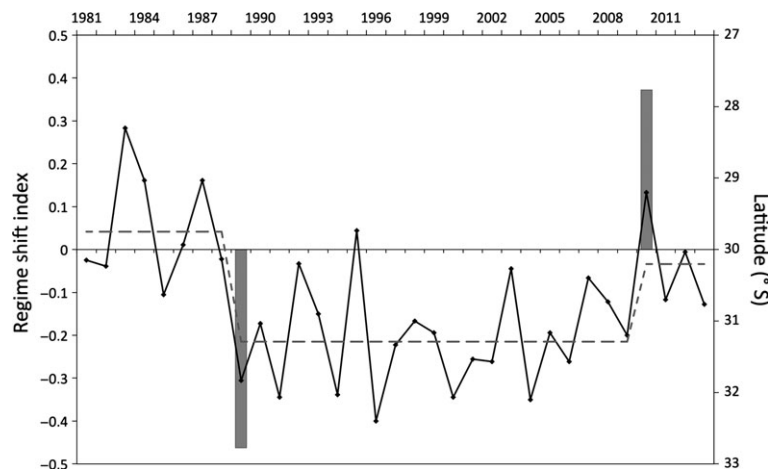
Whereas dissolved oxygen off Namibia shows marked seasonal and interannual variability with no clear trend (Bartholomae and van der Plas, 2007; Hutchings *et al.*, 2009), Stramma *et al.* (2008) indicated an expanding area of low oxygen water ( $<60 \mu\text{mol kg}^{-1}$ – $1.35 \text{ mL L}^{-1}$ ) in the Angolan dome area. According to the model of Monteiro and van der Plas (2006, c.f. Hutchings *et al.*, 2009), this serves to advect low oxygen water southwards in the poleward undercurrent. Low oxygen also forms locally through decay of organic matter on the shelf (van der Plas *et al.*, 2007). Time series of hydrogen sulphide ( $\text{H}_2\text{S}$ ) eruptions are fragmented (Brüchert *et al.*, 2009; Lavik *et al.*, 2009; Ohde and Mohrholz, 2011), and it cannot at present be said whether the frequency of these

events has been increasing. However, events have been recorded as far back as the early 20th century (Gilchrist, 1916; Copenhagen, 1953). Extreme low oxygen water is necessary to allow sulphide eruptions to occur (van der Plas *et al.*, 2007), in addition, methane (CH<sub>4</sub>) eruptions may entrain hydrogen sulphide into the water column. One would hypothesize that with increased stratification and higher concentrations of phytoplankton (see below), there should be increased low oxygen in the near-bottom zone but so far there is no obvious trend.

Off the South African west coast, upwelling-favourable winds display decadal-scale variability with peaks in the early 1970s and the late 1990s/early 2000s, and low winds in the late 1960s, 1980s and mid-2000s. Environmental regime shifts off the west coast have been documented for the late 1950s, 1971 and 1996/7 from SST series (Howard *et al.*, 2007; Shannon *et al.*, 2010a) and upwelling indices derived from geostrophic winds (Blamey *et al.*, 2012). Intra-annual variability of upwelling increased in the first half of the 1990s (Blamey *et al.*, 2012). Interestingly, the position of the South Atlantic High in terms of mean latitude shifted in 1989/90, moving about 1.5 degrees south (Fig. 5). This corresponds to the shift in winds off Lüderitz, and may explain the differences in the SST and upwelling time series off Hondeklip Bay versus Cape Columbine as documented by Howard *et al.* (2007) and Blamey *et al.* (2012). Data from the Reynolds reanalysis data set used in Howard *et al.* (2007) show that the inshore-offshore thermal gradient at 32°S increased

slightly between 1910 and 2005 (c. 0.2°C) as a result of warming offshore or cooling inshore. However, temperatures in the upper mixed layer inshore in St Helena Bay during 1950–2005 show only decadal-scale variability, with no evidence of a long-term trend (Hutchings *et al.*, 2012), so offshore warming is likely to contribute to the increasing thermal gradient. Oxygen depletion off the St Helena – Namaqua Shelf (see Fig. 1), which is largely driven by the decay of phytoplankton after upwelling, shows high seasonal and interannual variability (Jarre *et al.*, 2014a). It is limited to a narrow coastal strip extending to the 150-m isobath, with maximum seasonal depletion in late summer–autumn (February–May). Maximum depletion on a decadal time scale is linked to intermediate levels of upwelling, using the cumulative upwelling divergence calculated from National Centers for Environmental Prediction (NCEP) winds for the period September to January. The wind time series since 1949 indicates severe oxygen depletion in the first half of the 1950s and the 1990s, and improved oxygen conditions during the 1960s and 1970s and perhaps in the 2000s (Jarre *et al.*, 2014). Oxygen depletion on this part of the shelf has been less severe since the early 2000s. There does not seem to be any significant unidirectional trend from this time series. Intense localized oxygen depletion occurs within the confines of St Helena Bay and leads to mass mortalities in inshore benthic communities, but these events are driven by very local harmful algal blooms (e.g., Pitcher and Probyn, 2011) and are different from the shelf-scale variability. There

**Figure 5.** Changes in the mean summer (Dec–Feb) latitudinal position of the South Atlantic High Pressure System between 1981 and 2013. 1°×1° monthly sea level data were obtained from <http://las.pfeg.noaa.gov/las/main.pl> for the area 5–35°S, 30°W–10°E. The resulting 40 × 30 array was then smoothed using a 3 × 3 moving average procedure and the highest pressure was determined along with the average latitude and longitude for the cells with that pressure. The mean summer (Dec–Feb) latitude was then calculated and analysed using STARS (see method details in Blamey *et al.*, 2012). Both the 1989 and 2010 shifts were considered to be robust.



appears to be frequent oxygen depletion in the Orange River cone (Fig. 1) (Jarre *et al.*, 2014a). Some of this water is advected south in the inshore counter-current (de Decker, 1970), where it can add to upwelling-related oxygen depletion from the Hondeklip Bay upwelling cell. These dynamics, however, are not well understood as a result of poor sampling coverage.

Along the South African south coast, analysis of upwelling indices (derived from geostrophic winds) at Cape Hangklip (south-west coast) and Cape Agulhas (south coast, central Agulhas Bank), over the period 1981–2010, indicate an increase in upwelling in the early to mid-1990s and a decrease in the early 2000s (Blamey *et al.*, 2012). In addition, increases in the intra-annual upwelling variability were documented in this area at the end of the 1980s and again in 2007 (Blamey *et al.*, 2012). Major drivers of the hydrology of the Agulhas Bank, in addition to the wind regime, include the Agulhas Current flowing along the shelf break and the seasonal overturn of the shelf waters. Satellite and modelling studies by Rouault *et al.* (2009) indicate a strengthening of the Agulhas Current flow over the past 25 yr, resulting in warmer offshore waters, whereas Rouault *et al.* (2010) used OISST temperatures to confirm the offshore warming and demonstrate cooling inshore, in line with the findings of Roy *et al.* (2007). An analysis of Pathfinder data (version 5.2) does not confirm these results, but instead indicates a consistent warming trend in all seasons, most pronounced in early summer (Nov–Jan), with an approximately 0.3°C increase per decade since the 1980s (Dr F. Dufois, CSIRO, pers. comm.). The variability of subsurface features, notably the dynamics of stratification and the Cool Ridge, remain poorly understood owing to data limitations (Largier and Swart, 1987; Roberts, 2005).

Summarizing, it is evident that much of the oceanography across the region has been changing since a turning point around 1990. The Angolan subtropical waters and the northern Benguela have been warming since the early 1990s. The southern Benguela off Namaqualand north of Hondeklip Bay has likewise warmed. The observed regional warming has been coincident with a southward shift of the centre of the South Atlantic High Pressure Cell in summer by 1.5 degrees latitude, to 31.5°S (just north of St Helena Bay). The intra-annual variability of coastal upwelling has increased off the South African west and south coasts since the early 1990s. In contrast to the warming in the north, there has been some increase in summer upwelling at Cape Columbine and south of it since the mid-1990s, which partly reverted in the early 2000s. Over the south coast, upwelling variability has

increased further since 2007, with less congruency between the signals of the different data sets for this coast than for the west coast. The discrepancies are a focus of ongoing research.

#### WHAT EXTERNAL DRIVERS OF ECOSYSTEM DYNAMICS OTHER THAN CLIMATE NEED TO BE CONSIDERED?

Descriptions of the fisheries in the four subsystems can be found in van der Lingen *et al.* (2006) and Hutchings *et al.* (2009). Heavy fishing pressure in the 1950s to early 1970s off South Africa and until 1990 off Namibia led to the collapse of sardine stocks and heavy depletion of hake stocks, followed by consolidation and diversification of the offshore industry (see, e.g., Paterson *et al.*, 2013; and Jarre *et al.*, 2013 for reviews for Namibia and South Africa). More conservative fisheries management followed the declaration of exclusive economic zones (EEZs) for South Africa in 1977 and for Namibia in 1990 (Angola declared an EEZ in 1974, but the civil war prevented adequate enforcement). This led to some recovery of the hake stocks and of South African sardine, but Namibian sardine have not recovered yet. Ecosystem effects of demersal fishing, acting in concert with changes in the abiotic environment, have been documented for Namibia (Mafwila, 2011) and South Africa (Atkinson *et al.*, 2011). Documented ecosystem effects of fishing for small pelagic fish, which include food shortages for dependent predators such as seabirds (Crawford *et al.*, 2007a,b, 2008b, 2011; Cury *et al.*, 2011), has prompted a study to determine whether such effects can be quantified through an experiment involving the closure to purse-seine fishing around certain African penguin *Spheniscus demersus* colonies in South Africa (DAFF, 2010). Accidental mortalities of seabirds in the hake (demersal trawl and longline) fisheries are currently being mitigated in South Africa, and experimental mitigation has started in Namibia. The Cape fur seal population and populations of large whales have shown recovery after successful implementation of conservation measures, with commercial harvesting of seals only ongoing in Namibia (Best *et al.*, 2001; Kirkman *et al.*, 2007, 2012). The relevance of trawl feeding as a major food source for seals remains contested, although earlier papers have proposed that it was not a major factor in the observed seal population increase (David, 1987; Wickens *et al.*, 1992).

In embayments close to densely populated areas or major industrial structures, such as Luanda Bay, Walvis Bay, Saldanha Bay and Table Bay, there is localized



moderate-to-severe pollution. Oil exploitation constitutes an important part of the Angolan economy, and is taking place both inshore in the northern part of Angola, extending into deep (2000 m) waters. Significant contamination of hydrocarbons and extraction-related compounds such as barium lead, copper, chromium and zinc has been documented downstream from oil rigs at some locations, with local impact on the composition of benthic fauna. There were, however, no indications of significant large-scale contamination or disturbances of benthic fauna (Anon, 2009). The BCLME has few large rivers entering the coastal ecosystem. Their water levels fluctuate seasonally with only very occasional large floods. The levels of pollution emanating from these rivers is thought to be relatively minor.

Diamond mining is disturbing coastal marine habitats on the northern Namaqua shelf off South Africa, as well as the southern Namibian shelf up to depths of 130 m (Gründlingh *et al.*, 2006). The role of discharge plumes in deterioration of rock lobster habitat continues to be contested (Basson, 2010). Applications for mining of phosphates off Namibia and South Africa have been received by the relevant ministries and are currently being evaluated.

Currently, mineral and oil extraction influence a small fraction of the shelf area off Namibia and the South African west coast. In northern Angola and on the central Agulhas Bank, there are increased effects as a result of exclusion zones around rigs and prospecting zones. In summary, fishing activities are considered to be the main human impact on the shelf systems of the Benguela.

## DO PLANKTON PROVIDE CLEAR SIGNALS OF LONG-TERM VARIABILITY AND CHANGE IN THE SYSTEM?

### *Phytoplankton*

Spatial and temporal variation in phytoplankton biomass for the entire west coast off Angola, Namibia and South Africa are graphically presented in a Hovmöller space-time plot of satellite-derived monthly surface chlorophyll-*a* concentrations since 1997, integrated (over the pixels) between the coast and the level of  $1 \text{ mg m}^{-3}$  (Fig. 6). A reference point of chlorophyll concentration was selected instead of a fixed distance or depth, because the offshore boundary of an upwelling system is highly dynamic and convoluted. SeaWiFS data were used to compute this surface chlorophyll index from September 1997 until June 2002, and MODIS-Aquadata thereafter (updated from Demarcq *et al.*, 2007; DEA, 2013). Djavidnia *et al.* (2010)

concluded that the two sensors were comparable and observed changes would, therefore, be true reflections of near-surface chlorophyll-*a* concentrations. However, there is some indication that MODIS reflects somewhat higher values than SEAWIFS, although SEAWIFS did show an increase in 2002–2003 during the overlap period.

Inter-annual variability is pronounced off southern Angola, with elevated surface chlorophyll in 2002–2004, and in 2008–2011, especially during the cool season (Fig. 6). However, satellite data measured in the visible part of the spectrum should be interpreted with caution for Angola, as these data are only available 40% of the time owing to persistent cloud cover (Stammer *et al.*, 2003; Rouault *et al.*, 2007). *In situ* measurements indicate that much of the chlorophyll-*a* in the system displays a subsurface maximum, particularly in the warm season (RV Fritjof Nansen/IMR/INIP unpublished data). It is thus possible that satellite measurements of biomass do not fully capture chlorophyll concentrations off Angola.

The cumulative chlorophyll index (Fig. 7) suggests an increase in surface chlorophyll-*a* in the northern Benguela since 2003, which is not evident in the southern Benguela. However, the shipboard-derived estimate of integrated (0–30 m) phytoplankton biomass off Walvis Bay indicates a decrease during 2001–2006 (NatMIRC, unpublished data), implying that it is unlikely for surface estimates to be representative of the entire euphotic zone, even if the shipboard-derived phytoplankton series increased again from 2006–2010. Both satellite-derived series show distinct patterns of multiannual variability, which are sometimes in phase between these two subsystems but out of phase at other times (Fig. 7). Time series analysis using the Sequential *t*-test for the Analysis of Regime Shifts (STARS) did not detect decadal-scale regime shifts in these time series, unlike for the oceanographic variables (details of the analysis not shown). In the northern Benguela, the increase in surface chlorophyll-*a* according to the satellite-derived data is contrary to expectation considering the decrease in upwelling-favourable winds and increasing SST. However, it may be that the surface wind speed has been more optimal for near-surface phytoplankton recently than before 2003, in that the associated reduction in turbulence and mixing may have resulted in less deep mixing but a still adequate nutrient supply to a shallower mixed layer. This may have led to an increase in chlorophyll-*a* detected by satellite. Upwelling continues to be at a maximum in austral winter, leading to chlorophyll maxima around mid-year.

**Figure 6.** Sea surface chlorophyll-a index for the southern African (a) west coast (12–34°S) and (b) south coast (19–29°E), from September 1997 to December 2011. Data were derived from Seawifs/Modis satellite observations and are intergrated from the coast to the 1 mg m<sup>-3</sup> chlorophyll-a isopleth. Adapted from DEA, 2013, with permission. Numbers on the right hand side refer to zones in Fig. A1.

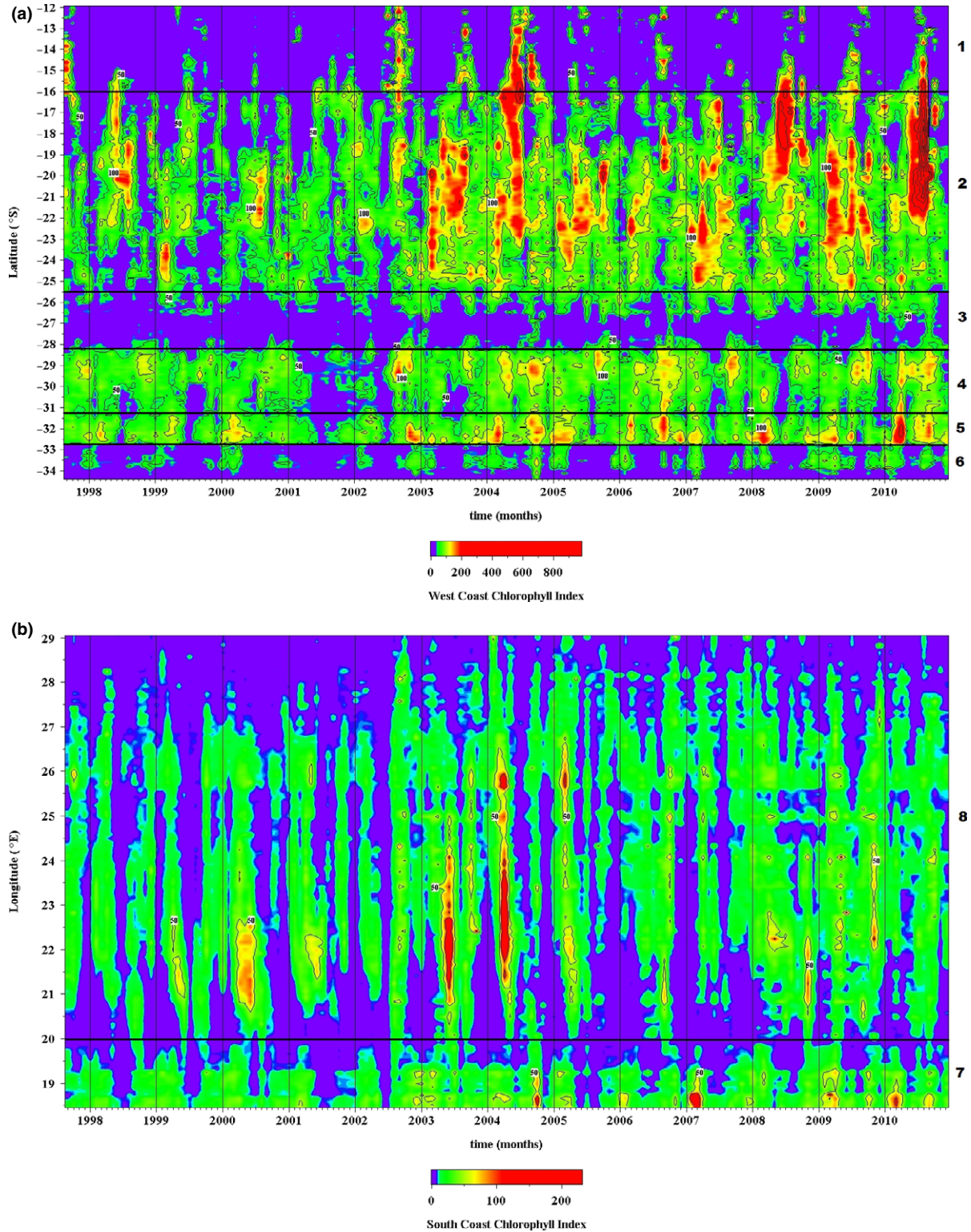
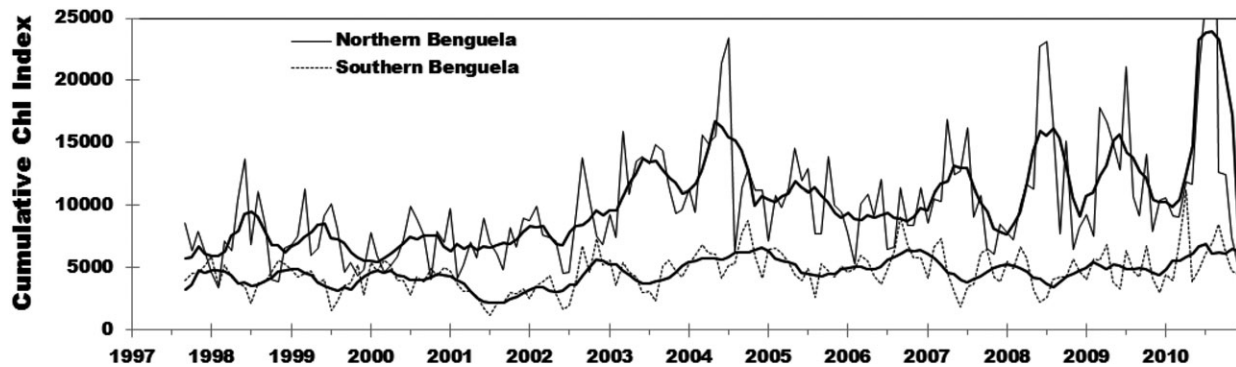


Figure 7. Sea surface chlorophyll-*a* index for the northern and southern Benguela (regions 2 and 4–8 in Fig. 6, respectively).



In the southern Benguela between 28 and 33°S, chlorophyll index values are usually elevated in association with the three major coastal upwelling cells (Namaqua, Cape Columbine and Cape Peninsula), but with a typical seasonality of summer maxima and winter minima, opposite to that in the northern Benguela (Fig. 7). The increase in chlorophyll-*a* in the 1990s observed *in situ* (Verheye, 2000) does not appear to have persisted, based on the satellite-derived surface chlorophyll observations (Fig. 7; Fig. A1). Primary production estimates from satellite-derived chlorophyll-*a* and SST (Lamont, 2011) show seasonal and interannual variability both at the bay and shelf scales, but likewise no trend. The satellite-derived estimates do, however, differ from production estimates based on nitrate deficit in St Helena Bay (Hutchings *et al.*, 2012), which would indicate an increase in primary production from the mid-1980s to 2007. Again, and as is the case for chlorophyll-*a*, there are different signals from different datasets, highlighting continued gaps in our understanding.

On the Agulhas Bank along the south coast of South Africa (35°S), the chlorophyll index values are consistently lower than along the West Coast (Fig. 6). Well-defined chlorophyll maxima are observed in March/April and October, and these maxima are normally most prominent between Mossel Bay and Port Alfred. Because of the importance of subsurface features (e.g., Carter *et al.*, 1987), chlorophyll concentration and primary production on the Agulhas Bank are likely underestimated from satellite imagery.

#### Zooplankton

Whereas zooplankton collections have been insufficient to provide a coherent time series for the Angolan subtropical subsystem, in the northern and southern Benguela the abundance of copepods (which form the largest proportion of mesozooplankton in terms of

biomass) shows an increasing trend by at least one order of magnitude, during the past two decades in the northern Benguela (year round) and the past six decades in the southern Benguela (in autumn) (Hutchings *et al.*, 2009; Verheye and Kreiner, 2009). While there is very little new information on abundance trends, changes in size and species composition were not reviewed by Hutchings *et al.* (2009). These are relevant to changes in ecosystem structure and function and are discussed here. These include recent NansClim findings of Hutchings *et al.* (2012) and Kreiner and Yemane (2013).

The most abundant calanoid copepod species in the northern Benguela have generally been the same since the 1960s, but their rank order has shown some variation during recent decades (Hansen *et al.*, 2005). *Calanoides carinatus*, a typical herbivorous upwelling species, was most abundant in all studies prior to 2000. Since then *Metridia lucens*, an omnivore, has become the most abundant calanoid copepod with *C. carinatus* ranked second (Hansen *et al.*, 2005), albeit with some interannual and seasonal variation in the ranking order (Kreiner and Yemane, 2013). *Rhincalanus nasutus*, the largest of the calanoid species, was also a prominent member (10–30%) of the community off Walvis Bay during the late 1970s to early 1980s, after which they all but disappeared from the samples. Coincidentally, the cyclopoid *Oithona* spp., among the smallest copepods of the community under study, increased in dominance from around 20–40% during the 1970s to as high as 90% of total copepod abundance during the 2000s (Verheye and Kreiner, 2009). In St Helena Bay in the southern Benguela, a marked shift in zooplankton community structure has been evident from autumn surveys. Whereas medium to large copepod species (*R. nasutus*, *C. carinatus* and *Centropages brachiatus*), the preferred prey of anchovy, dominated during the 1950s–1960s, smaller species (*Oithona* spp. and

small calanoid spp.) preferred by sardine became numerically more important since the mid-1990s, with *M. lucens* also becoming more prominent during the latter period compared with previously published data (Verheye *et al.*, 1998; Verheye and Richardson, 1998; Verheye, 2007; DEA, unpublished data).

The long-term, major changes in zooplankton abundance and community structure both in the northern and southern Benguela subsystems since the 1950s were thought to be attributable to increased primary production, combined with reduced predation pressure by pelagic fish owing to increased fishing and increased predation pressure by top predators (Verheye *et al.*, 1998; Verheye, 2000). However, there is uncertainty about the relative importance of these bottom-up and top-down forcing mechanisms.

Whereas the community shift from dominance by large to small species in both the northern and southern Benguela subsystems may be indicative of ocean warming, warming has been documented only for the northern Benguela, as no trend from inshore temperature observations were evident in the South African datasets (see Hutchings *et al.*, 2012 and also by the more recent seasonal satellite analyses). The decline in zooplankton since the mid-1990s in St Helena Bay coincided with a three-fold increase in the biomass of pelagic fish recruits during autumn since that time, suggesting that increased predation pressure was the primary forcing mechanism controlling zooplankton populations in this recruitment area. Seasonal and interannual variation in copepod biomass in St Helena Bay have been high during 2000–2011 with summer densities of the dominant species indicating a possible increase but no significant trend (Hutchings *et al.*, 2012). The difference in summer and autumn time series could be attributable to the lower abundance of planktivorous fish during summer when they are spawning over the Agulhas Bank, compared with their peak recruitment period in April–July (Barange *et al.*, 1999).

On a larger spatial scale (i.e., the remainder of the southern Benguela), zooplankton abundance and species composition have been measured annually from 1988 to 2011 during routine shelf-wide acoustic surveys of pelagic fish during late autumn (May/June, recruitment period) and late spring/early summer (October–December, upwelling season, main anchovy spawning season) (Huggett *et al.*, 2009). These confirmed the results observed in St Helena Bay: biomass was highest downstream of the major upwelling centres, concentrations were higher in summer than autumn and there was an increase from the 1970s to the 1988–2003 period.

To investigate interannual and spatial variability in zooplankton on the Agulhas Bank, between 1988 and 2012, mean copepod biomass was calculated using data from stations sampled across the shelf on transects off Danger Point on the western Agulhas Bank (WAB) and off Mossel Bay on the central Agulhas bank (CAB). In both areas, in spite of higher interannual variability on the WAB, there has been a marked decline in copepod biomass over the past two decades, in particular that of the large, dominant calanoid species *Calanus agulhensis* (Dr J. Huggett, unpublished data, in DEA, 2013). This decline has corresponded with a gradual shift towards a smaller copepod-dominated community. While the decline in zooplankton biomass is thought to be largely caused by predation by pelagic fish (anchovy, red-eye and sardine), the biomass of which has increased dramatically over the CAB since 1997, the shift to an increasing dominance of smaller copepods may reflect possible warming in the region (Belkin, 2009; F. Dufois, CSIRO, pers. comm.) and/or size-selective predation by pelagic fish.

In conclusion, total copepod abundance in the southern and northern Benguela is much higher now than in the 1950s and 1960s, although in both regions it seems like turning points have been reached and abundances have somewhat reduced again. A shift towards smaller copepods has occurred. It remains unclear whether the observed changes are mainly due to bottom-up or top-down effects, or a mix of both.

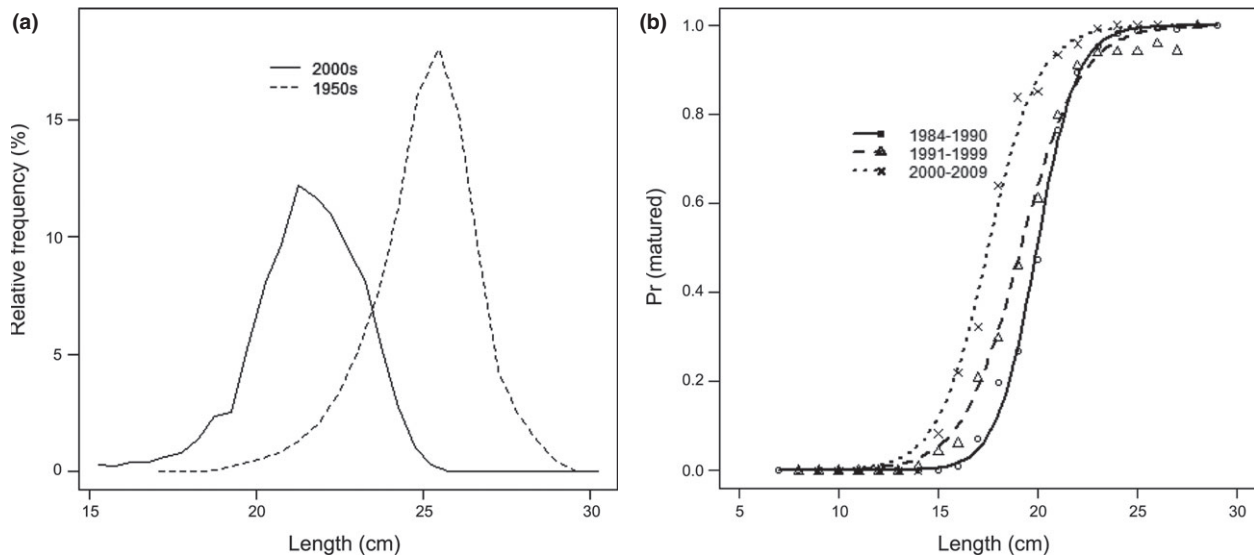
## WHAT CHANGES HAVE OCCURRED IN THE DISTRIBUTION, AGE STRUCTURE OR SPAWNING OF FISH POPULATIONS?

### *Small pelagic fish*

Whereas migrations of the two dominant clupeid species in Angola, *Sardinella aurita* and *Sardinella maderensis*, have been documented (Boley and Fréon, 1980), and the effects of seasonality and anomalous events on their catches have been described (Binet *et al.*, 2001; Ostrowski, 2007; Ostrowski *et al.*, 2009), no long-term changes in their distributions and range sizes have been documented so far.

The biomass of sardine in the northern Benguela estimated from Virtual Population Analysis showed a peak in the mid-1960s and a sharp decline in the late 1960s with no real signs of recovery since then (van der Lingen *et al.*, 2006; Kirchner *et al.*, 2009). Concurrent with the decline in biomass the sardine stock has undergone major changes in stock structure. The mean total length of sardine caught by the fishing industry has decreased by over 4 cm between the 1950s and 2000s (Fig. 8a). Length at 50% maturity

**Figure 8.** (a) Comparison of the percentage length frequency of sardine catches made between 1952–1957 and 1997–2008; (b) Length at 50% maturity ( $L_{50}$ ) per decade since 1984 as sampled from commercial landings – from Kreiner *et al.* (2011, with permission).



decreased by over 3 cm from the 1980s to the 2000s (Fig. 8b). In spite of these changes, sardine spawn within the same latitudinal ranges as before and the selection of spawning location seems to depend on environmental variability, with spawning taking place along the central Namibian coast during warmer years and along the northern Namibian coast during cooler conditions (le Clus, 1990; Kreiner *et al.*, 2011). A partial recovery of sardine biomass occurred in the early 1990s, but biomass declined again after low-oxygen and warm-water events in 1994 and 1995 (Boyer *et al.*, 2001).

The most obvious change in the southern Benguela over the past two decades has been a distributional shift of anchovy and sardine from the West Coast subsystem to the Agulhas Bank subsystem in the late 1990s/early 2000s. This shift is not believed to be as far reaching or as likely to be irreversible as the shift (i.e., the decline of epipelagic fish) in the northern Benguela (Cury and Shannon, 2004), but its causal factors are poorly understood, although it was likely that the shifts were at least partly environmentally driven. Adult anchovy shifted eastwards abruptly in 1996, in conjunction with an abrupt increase (by 0.5°C) in the inshore–offshore thermal gradient as a result of coastal cooling (Roy *et al.*, 2007). Whereas the eastward shift of anchovy resulted from an abrupt increase in the biomass of anchovy on the CAB, relative to that on the WAB, the biomass of anchovy on the WAB remained high after the shift and recruitment appeared unaffected. Overall, anchovy

recruitment and adult biomass have been higher after the shift than before.

In contrast, the biomass of sardine on the WAB declined quickly subsequent to the shift, possibly as a result of higher than normal fishing pressure on this portion of the population and predominantly south and east coast spawning which resulted in sustained poor recruitment (Coetzee *et al.*, 2008). Sardine show broader environmental tolerances in spawning than anchovy (Mhlongo *et al.*, 2014) and perhaps for this reason the eastward shift of sardine was more gradual than that of anchovy, with >50% of their biomass situated to the west of Cape Agulhas between 1985 and 1998, but >50% located to the east of Cape Agulhas between 1999 and 2007 (Coetzee *et al.*, 2008). In four out of the five most recent years (2008–2012), >50% of the biomass was distributed west of Cape Agulhas again; however, this was at very low biomass levels with the exception of 2011, when biomass was moderate and most of sardine were distributed east of Cape Agulhas. The shift in sardine distribution was matched by an eastward shift in the centre of gravity of sardine catches (Fairweather *et al.*, 2006). Mechanisms other than environmental changes are likely to have played a role in facilitating the eastward expansion of sardine, particularly in the early 2000s, when strong cohorts of juvenile sardine recruited further to the east (Coetzee *et al.*, 2008). Amongst these, entrainment of juvenile sardine on the Central Bank by adult sardine (ICES, 2007a), and their subsequent offshore movement to spawn, has been suggested as a possible enabling

mechanism, which includes an element of natal homing (Coetzee *et al.*, 2008). Another possibility is that sardine expanded eastward in response to the eastward expansion of anchovy, which would explain the gradual – rather than abrupt increase in the size of the sardine population located to the east of Cape Agulhas. In this case, juvenile sardine, which were less abundant than anchovy, would have schooled together with anchovy of a similar size to avoid predation (Bakun and Cury, 1999) and they would have become entrapped in anchovy schools that were migrating eastward.

#### Horse mackerel

Data from bottom trawls indicate that the distributional extent of horse mackerel (*Trachurus capensis*) in Namibia has decreased in the northern areas (17°30'S to 20°30'S) since 1990 and increased in the central area (20°30'S to 24°30'S) since 2009 (Salvanes *et al.*, 2014). This was concomitant with a gradual increase in biomass from about 800 000 tonnes to around 1.3 million tonnes between the mid-1990s and 2012 (Kirchner, 2012; after previously declining from about 3 million tonnes in the early 1960s). As was the case for the sardine stock the horse mackerel population in the northern Benguela has undergone changes in stock structure. Length at 50% maturity has decreased from 25.9 cm total length (TL) to 18.9 cm TL in the 2000s (Kirchner, 2012). Modal lengths (TL) of commercial catches changed from around 29 cm during the 1980s to around 23 cm averaged for 2003 to 2012 (Fig. 9). However, changes in modal length of commercial catches from 20 cm in 2007 to 25 cm during 2009 to 2012 indicate a recent improvement in stock structure (Kirchner, 2012). Eggs and larvae of horse mackerel during the early 2000s were found in similar latitudinal and environmental ranges as during the 1970s,

indicating that horse mackerel can spawn over a wide range of environmental conditions and are rather robust to environmental changes (Kreiner *et al.*, 2014).

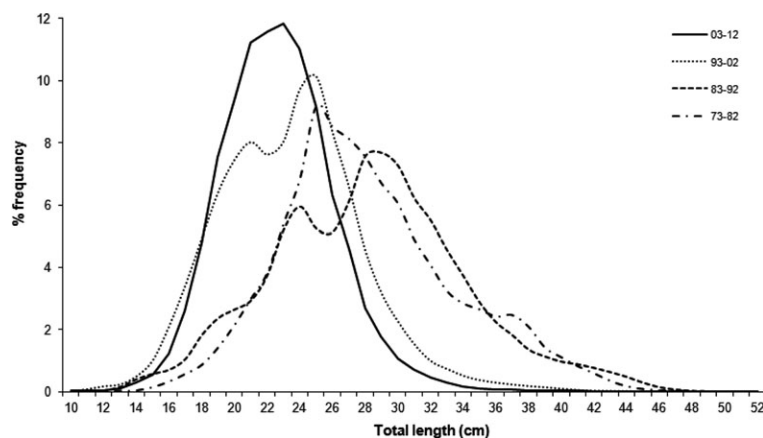
In South Africa catches of horse mackerel declined in St Helena Bay during the 1950s and by the end of that decade few adult horse mackerel were observed there. Adult horse mackerel are now found mostly over the Agulhas Bank and are caught by the mid-water trawl fishery and as bycatch of the hake-directed bottom-trawl fishery (Hutchings *et al.*, 2012).

#### Pelagic goby

The pelagic (bearded) goby (*Sufflogobius bibarbatus*) is extremely tolerant towards low oxygen conditions (Utne-Palm *et al.*, 2010) which allows it to seek refuge in the suboxic zone from potential predators (Salvanes *et al.*, 2014). Since 2000 the goby has extended its distributional range over a larger area of the northern (17.5°S–20.5°S), and to some degree also of the central (20.5°S–24.5°S) shelf areas of Namibia, in line with the general warming of the system (Salvanes *et al.*, 2014). Increased stratification should enhance low oxygen formation. However, as yet there is no conclusive evidence for an increase in extent of low oxygen bottom water in the northern Benguela (see section, 'Are trends in environmental drivers apparent during the observation period?'). The increase in gobies may be due to lessened competition from pelagic species (see Roux *et al.*, 2013).

#### Demersal fish

To assess distributional shifts of demersal species in terms of latitude or depth, four different indices of change based on the species distribution data were employed (Yemane *et al.*, 2014a). These included annual change in mean depth or mean latitude, and



**Figure 9.** Length frequency distribution of horse mackerel in mid-water trawl catches made during 1982–2012. Data for 1973–1989 were derived from Russian length frequency data from division 1.4 (ICSEAF Sampling Bulletins). Data for 1991–2012 stem from mid-water trawl data collected by fisheries observers.

annual change in depth range or latitudinal range. Given the differences between Angola, Namibia and South Africa, e.g., in terms of demersal survey design and trawl gear (Axelsen and Johnsen, 2014), the data series of the three countries were generally analysed separately. The species that showed changes in distribution are shown in Tables A1–A3. It was evident that observed changes in distribution, both in terms of magnitude and directionality, varied between the three countries. This variation was especially evident for changes in mean latitude: whereas the Angolan subsystem was characterized mainly by southwards shifts in mean latitude, in the other two countries approximately half of the identified shifts were to the south and the other half to the north. Changes in the other three indices were more consistent between the three countries, with increases in mean depth to greater depths, and increases in latitudinal range and depth range prevailing in all three countries. No strong relationship was discernible between the documented long-term bottom temperature and the distributional changes in the demersal communities, which seems to indicate that temperature changes on their own could not have accounted for the observed changes at the population or community levels of demersal fauna in the BCLME and other factors such as oxygen levels, other environmental variables and effects of fisheries would need to be considered.

However, there is also evidence that the northern and central spawning areas described for Cape Hake (*Merluccius capensis*) for the late 1960s–1980s have shifted southward since the 1990s (Wilhelm, 2012; Wilhelm *et al.*, 2014). This southward shift of gravity of the spawning aggregations in the 2000s was also supported by Wilhelm *et al.* (2013) showing that the proportion of seal scats sampled from van Reenen Bay in the south of Namibia (27 S) which contained young *M. capensis* increased since 2000. These shifts appear to be simultaneous with the relaxation of the wind stress in Lüderitz, possibly allowing for better transport and survival of the early life history stages and better temperature conditions for spawners and recruits in the south than during the 1980s.

#### CAN FISH SPECIES BE USED AS INDICATORS OF SYSTEMATIC CHANGES IN SEA TEMPERATURE IN THE BCLME?

The identification of a list of potential fish species that may be used as indicators of systematic changes in water temperature in the BCLME in summer was carried out in the demersal task group, based on the width of their observed temperature ranges, as determined

from analysis of bottom temperature measurements conducted in the vicinity of trawl stations during the summer surveys. The rationale for this approach was that species with narrower observed temperature ranges are likely to be more responsive to temperature shifts in summer and consequently might possibly be useful indicators thereof. The classification of taxa for each country according to their inferred sensitivity as indicators is available in Tables A1–A3. These Appendices also provide information on the exploitation status of species (targeted or bycatch).

The next step was to gauge the usefulness of the approach by retrospectively assessing the performance of potential indicator species in terms of changes in their abundance and distribution in relation to concurrent temperature shifts in summer, and comparing with species adjudged to be more eurythermal and therefore less suitable in this regard. In general, there were no clear patterns in the abundance trends of species identified as potentially useful indicators, over the study period. Species identified as eurythermal and species identified as stenothermal (P. Kainge, Nat-MIRC, unpubl. data) were both characterised by population regime shifts during the study period, as shown by Kirkman *et al.* (2014). Yemane *et al.* (2014a) observed changes in distribution of several species, both in terms of magnitude and directionality, which varied between three subsystems: mainly southwards in the Angolan Subtropical and both northwards and southwards in both Northern and Southern Benguela West Coast, and generally to greater depths in these three subsystems. According to the outcomes of three-way contingency table tests based on the results for each country (summarized in Table 1), there was no association between the shifts in distribution of taxa and their indicator status, even after accounting for the effect of their exploitation status (Mantel–Haenszel  $\chi^2 = 2.59$ , d.f. = 1,  $P$ -value = 0.1078; R Development Core Team, 2013). The fact that distributional shifts and regime shifts (see Tables A1–A3; Kirkman *et al.*, 2014) of populations were common to both stenothermal and eurythermal species seems to indicate that temperature changes on their own would not have accounted for the observed changes at the population or community levels of demersal fauna in the BCLME and other factors such as oxygen levels, other environmental variables and effects of fisheries will need to be considered. Given this and that the drivers of changes may vary throughout the region given differences in the environments and in the histories of fishing pressures between countries, using a suite of different types of indicators for detecting changes, may be advisable.

**Table 1.** The numbers of taxa from summer demersal trawl surveys in each country that were considered in analyses, summarized by indicator status and exploitation status, and showing the numbers of taxa that showed distributional shifts or regime shifts.

Country	Indicator status <sup>1</sup>	Exploitation status	Number of taxa	Number showing distributional shifts <sup>2</sup>	Number showing population shifts <sup>3</sup>
Angola	Sensitive	Targeted	4	4	0
		Bycatch	28	11	0
	Poor indicator	Targeted	5	5	0
		Bycatch	50	21	4
Namibia	Sensitive	Targeted	3	3	3
		Bycatch	18	12	4
	Poor indicator	Targeted	0	0	0
		Bycatch	33	15	4
South Africa	Sensitive	Targeted	1	1	0
		Bycatch	25	14	2
		Poor indicator	1	1	0
		Bycatch	27	13	3

<sup>1</sup>'Sensitive' includes taxa that were classified as 'highly sensitive' or 'moderately sensitive' indicators of summer temperature changes (see Tables A1–A3).

<sup>2</sup>Include taxa that showed a change in distribution according to at least one of the four indices of distributional change (see Tables A1–A3).

<sup>3</sup>Includes taxa that showed a regime shift according to at least one of the two methods to detect regime shifts at the population level (see Tables A1–A3).

Moreover, there are several potential limitations to the approach used for identifying indicator species. For example, for many species only part of their range was covered by the surveys therefore their observed temperature ranges may not be representative. Also the range of temperature conditions experienced by species throughout the year was not covered because only summer survey data were considered. Such limitations could have had implications for the effectiveness of the indicators in terms of their availability at the spatial and temporal scales at which an effect occurred, and their specificity and sensitivity to the effect. Therefore they could have influenced the lack of distinction between the responses (in terms of trends in abundance and distribution) of species adjudged to be stenothermal or eurythermal. This preliminary list of demersal indicator species for systematic changes in water temperature in the BCLME should therefore be seen as an initial step towards determining an adequate suite of indicators of distribution changes for the region.

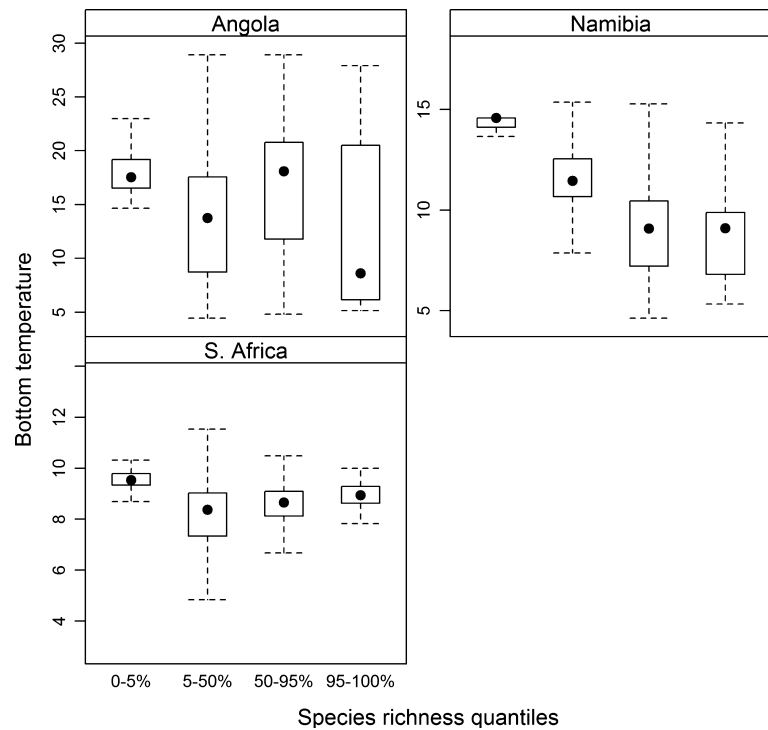
#### ARE THERE BIODIVERSITY HOTSPOTS IN THE BCLME WHICH ARE SUSCEPTIBLE TO CLIMATE CHANGE?

Diversity patterns of demersal fish fauna, as measured by three different indices of diversity (species richness  $S$ , Pielou's evenness index  $J'$ , and Shannon-Weiner index  $H'$ ), were found to be contrasting between

Angola, Namibia and South Africa, in terms of the form and strength of the relationship between the indices and different sets of predictors (Yemane *et al.*, 2014a,b). For example, whereas in Angola there was no distinctive pattern of diversity in terms of depth, depth was the most important determinant of diversity in Namibia and South Africa, where hotspots of  $S$  were mostly associated with greater depths and cooler bottom temperatures (Fig. 10; Kirkman *et al.*, 2013). The general latitudinal pattern of  $S$  conformed with that found in numerous other marine studies (e.g., Willig *et al.*, 2003; Mora and Robertson, 2005) in that it increased with decreasing latitude, and it was also broadly similar to the pattern of bottom temperature in the region (Yemane *et al.*, 2014a,b). Data on research trawls east of Cape Agulhas (20°E) were not considered in the analysis, but species richness is known to increase east of the Agulhas Bank (Yemane *et al.*, 2010).

In spite of changes in community structure and in species abundance and distributions that were documented during the study period (Kirkman *et al.*, 2014; Yemane *et al.*, 2014a,b), the presence of  $S$  hotspot areas were consistently predictable for much of the study area over the 20- to 30-yr study period, varying by country (Kirkman *et al.*, 2013). These included the shelf edge of northern Namibia and the shelf edge and outer shelf areas of southern Namibia and northern South Africa off the Orange River mouth. There were also localized areas of low  $S$  including in southern





**Figure 10.** Box-whisker plots of bottom temperature associated with different quantiles of species richness for Angola, Namibia and South Africa, according to GAM predictions (from Kirkman *et al.*, 2013). Closed circles represent the median values, the upper and lower hinges represent the upper and lower quartiles, respectively, and the whiskers represent 1.5 times the interquartile range.

Angola and inshore areas of Namibia and off the west coast of South Africa (Yemane *et al.*, 2014a,b). These localized areas of low diversity were generally associated with upwelling cells (Yemane *et al.*, 2014a,b). Increased biodiversity might be expected in such areas (although this has not yet been observed) with slackening of upwelling. However, any such changes are unlikely to have major ramifications for the overall biogeographical patterns of demersal biodiversity, whereby the highest diversity is generally associated with the shelf edge.

#### WHAT ARE THE RELATIVE ROLES OF ENVIRONMENT AND FISHING IN DRIVING ECOSYSTEM CHANGES, SPECIES DOMINANCE ALTERNATIONS AND TRENDS IN FISH YIELDS?

The previous section documents changes within specific habitats and communities in each of the subsystems of the Benguela. This section examines cross-cutting links in each of these subsystems, and considers the relative importance of environmental versus human drivers.

##### *Angola Subtropical*

Assuming that there is no artificial trend in the chlorophyll-*a* patterns estimated from satellite as a result of high cloud cover, the warming trend observed over the

past 20 yr does not appear to translate into any trend in chlorophyll-*a* (Fig. A1, Table A4). Warm events (e.g., in 2001) have been linked to biomass declines in horse mackerel *T. trecae*, which, together with the reduction in catches since 1997 led to the closure of the midwater trawl fishery in 2002 (Kirchner, 2012). In contrast, the reduction in sardinella catches in 1990 and again in 1997 were not linked to an environmental anomaly: instead these were most probably linked to changes in effort. It is currently unclear whether the increase in the proportion of *S. aurita* observed in research surveys off Angola since 2004 (Kirchner, 2012) can be linked to the ocean warming. This species expands further south than the more estuarine *S. maderensis*, but its occurrence in the Namibian pelagic resource surveys has not yet increased. The regime shift observed in the demersal community (Kirkman *et al.*, 2014) could have been induced by the warm event in 2001, taking into account time lags, or else by the cold event in 2004 in case of a shorter time lag. Alternatively, fishing pressure could have played a role in inducing the observed community regime shift, because it coincided with escalating catches of hakes (*M. polli* and/or *M. capensis*), and the highest reported catch of hake off Angola in that year.

##### *Northern Benguela*

From a long-term perspective, there are no clear responses in chlorophyll-*a* at the sea surface to changes

in oceanographic drivers such as wind, upwelling and SST (Table A5). The increase in zooplankton abundance contrasts with the warming trend [expectations from studies in the southern Benguela, e.g., Andrews and Hutchings (1980) and Travers-Trolet *et al.* (2014) suggest a decrease in abundance with warming], even although the dominance of smaller species would be expected. Importantly, there are complex interactions between jellyfish, gobies, horse mackerel and zooplankton which may mask the direct effects of oceanographic (bottom-up) drivers on zooplankton and its direct predators.

Excessive fishing pressure caused the collapse of Namibian sardine in the late 1960s/early 1970s, with total allowable catches (TACs) being set to levels higher than was scientifically recommended since the early 2000s, testifying to continued high fishing pressure on sardine in recent years. The partial recovery of sardine in the early 1990s was halted by the 1994/1995 marked low oxygen event and warm anomaly, which together constrained their pelagic habitat (Kreiner *et al.*, 2009, 2011). However, the general warming trend off Namibia since the 1990s is not necessarily detrimental to sardine, as shown by good recruitment in some years (1995/6, 2001/2 and 2009/10). These good recruitment events, however, are not reflected in the adult population. Possible explanations include higher fishing mortality of sardines than was reported, e.g., caused by bycatch in the mid-water trawl fishery.

Horse mackerel appear quite robust to environmental variability and changes in the upper mixed layer. Increased horse mackerel mid-water trawl catches in the 1970s occurred after the decline of sardine, with high fishing pressure and good catches continuing into the 1990s irrespective of the surface warming. During 1990–2005, horse mackerel TACs were not always filled, which may have been related to distributional shifts to the inshore, or structural changes such as Namibianization of the fishing fleet and/or marketing problems. Likewise, the extreme increase in horse mackerel catch per unit effort in 2008 does not appear to be linked to an environmental event, but could possibly be linked to the arrest of mid-waters trawlers for dumping in 2007.

An additional consequence of the replacement of sardines by horse mackerel and gobies is that predators such as hake are now consuming lower energy prey, and the eroded food base may contribute to limiting predator recovery (Ludynia *et al.*, 2010; Roux *et al.*, 2013). There is major coupling that takes place through the food web between the pelagic and demersal communities, in that many demersally caught species feed on zooplankton as juveniles and as adults

feed on small pelagics, mesopelagics and shrimp. In addition, the generation of particulate organic matter from the pelagic community may decrease the oxygen concentrations and hence contribute to habitat changes at the bottom at seasonal and interannual scales. In the demersal community, a regime shift may have occurred immediately after the 1995 Benguela Niño and the 1994 low-oxygen event, although the interpretation is confounded by gear changes in 1994–1996 (e.g., Mafwila, 2011; Axelsen and Johnsen, *this volume*; Kirkman *et al.*, *this volume*). The absence of any clear direct links between oceanography and fish (with the exception of sardine) from the results underline the overriding importance considering the combined effects of climate and fishing as drivers of dynamics in the northern Benguela subsystem.

#### *Southern Benguela*

Two ecosystem regime shifts have taken place in the southern Benguela. The first one, in the wake of the sardine collapse during the early-mid 1960s, was induced by fishing. The second one, the eastward shift during the mid-1990s to the early 2000s, is thought to be induced by environmental changes but aggravated by fishing (Howard *et al.*, 2007; Roy *et al.*, 2007; Coetzee *et al.*, 2008; Blamey *et al.*, 2012). In addition to conservative management of the small pelagics fishery, the recovery of sardine since the mid-1980s coincided with decreased upwelling and warming, as well as increased upwelling variability on the west coast during that time (Howard *et al.*, 2007; Blamey *et al.*, 2012). As discussed above, the observed decrease in zooplankton abundance in autumn on the west coast from the mid-1990s onward (Table A6) may be attributable to predation pressure by very abundant pelagic fish during that period. The cause(s) for the coinciding shift from large to small zooplankton species is not obvious, but this could be linked to preference of anchovy, which were very abundant at the time, for larger zooplankton, as opposed to sardine which were less abundant and prefer smaller zooplankton. Likewise, the decreased abundance of *C. agulhensis* on the Agulhas Bank has been linked to the increased abundance of small pelagics there since the mid-1990s (Dr J. Huggett, DEA: Oceans and Coasts, pers. comm.). Should ocean warming be confirmed in the region, it would be expected to contribute to the shift towards smaller species.

With respect to the demersal community, in the absence of major changes in demersal fishing effort, the shift observed in the early 1990s (Atkinson *et al.*, 2011, 2012; Kirkman *et al.* *this volume*) is attributed to environmental forcing, possibly acting in concert with

long-term effects of fishing, as suggested by Atkinson *et al.* (2011, 2012). In the southern Benguela, the pelagic-demersal coupling does not appear to have changed to the same extent as off Namibia. Hakes, as the dominant demersal predators, have switched their diet to mesopelagics in periods of reduced abundance of small epipelagic fish on the west coast (Payne *et al.*, 1987; Punt *et al.*, 1992). Mesopelagic fish populations (as well as crustaceans) have been poorly documented in the Benguela as a whole, in spite of their potentially important role in the system's resilience (through provision of alternative trophic pathways) under conditions of ocean climate change.

#### *Relative importance of environmental and human drivers*

Both South Africa and Namibia embarked on traditional fishery management strategies aimed at recovery of depleted pelagic and demersal stocks after heavy fishing pressure by local and international fleets (prior to the implementation of EEZs). However, the altered, less efficient food web structure in Namibia has had limited recovery under fishing pressure which, although reduced, has still been moderate to high. The current low stock size of sardine in particular, in combination with the restricted size/age range (Kreiner *et al.*, 2011), renders Namibia's sardine stock even more susceptible to environmental variability than it used to be before its collapse. Similarly in South Africa, a conservative management strategy that had allowed sardine to recover in the second half of the 1980s and early 1990s, was not appropriate in a regime characterized by reduced stock productivity and spatially disproportionate fishing after the eastward shift in distribution (Coetzee *et al.*, 2008; Jarre *et al.*, 2013). In this regard, the need for spatial management of the fishing effort is gaining support.

Changes in the stock structure of horse mackerel in the northern Benguela suggest that the population was under stress until the early 2000s. Since 2007, with reduced fishing pressure, biomass levels and biological indicators, especially modal length distributions show signs of recovery of the stock (Kirchner, 2012).

Fisheries in the Benguela have always had to contend with high seasonal and interannual variability in fish availability, and the structure of the fisheries have adapted to this, as evident from the increasing consolidation of effort and diversification of target species and products in the highly capitalised offshore industries (Jarre *et al.*, 2013; Paterson *et al.*, 2013). Major changes in the offshore fisheries include the shift to mid-water trawling for horse mackerel in the northern Benguela and Angola, and for horse mackerel in the southern Benguela with recent exploratory fishing for

mesopelagics. Inshore fisheries typically are adapting to variability by switching small-scale sectors, e.g., between rock lobster and linefish. However, this adaptation to short-term variability is insufficient with respect to ecosystem-scale, long-term regime shifts, which have been too infrequent for people to learn from experience. In South Africa, an ecosystem regime shift that was environmentally induced in the 1990s (Howard *et al.*, 2007; Blamey *et al.*, 2012) may have been exacerbated by fishing, thus preventing the recovery of sardine on the west coast (Coetzee *et al.*, 2008). With this, the economic basis for the canneries continued to be compromised and the losses of jobs that went along with factory closures and other consolidation contributed to increased poaching in the inshore fisheries sectors in South Africa, placing further pressure on the stocks (Jarre *et al.*, 2013).

With respect to demersal fish assemblages both in the northern and in the southern Benguela, our results, as discussed above, confirm the view of Atkinson *et al.* (2011) that the changes detected are probably a reflection of long-term direct (catch and bycatch mortality) as well as indirect (species replacements, trophic cascades and seabed modifications) effects of fishing in combination with environmental changes. Shannon *et al.* (2010b), using a suite of ecosystem indicators across demersal and pelagic communities, made the point that in spite of the documented effects of fishing, food web changes in upwelling systems in particular cannot be understood without careful consideration of environmental drivers. This is inevitable owing to the wasp-waist role of short-lived species in these upwelling food webs. In the BCLME, even although temperatures at depth have changed less than at the surface, the surface warming may intensify stratification and thereby reduce vertical exchange processes. In the northern Benguela especially, this could contribute to the development of further bottom hypoxia, although this has not yet been observed. Associated physiological stress may lead to changes in distribution and productivity of the fisheries resources base, and contribute to reducing its resilience to moderate or heavy fishing pressure.

In addition, the contrasting or conflicting drivers of turbulence and nutrient limitation may alter the optimal environmental window for early life history stages of pelagic and demersal fish (Cury and Roy, 1989). Fisheries-induced changes in the pelagic community (e.g., towards smaller/younger fish) have also been documented for both the northern and southern Benguela, further reducing resilience to environmental stress. In the northern Benguela, any movement southwards with declining upwelling and turbulence at

Lüderitz is tempered by closer proximity to the two main fishing ports. In the southern Benguela, the eastward shift has resulted in increased cost of fishing, but has created a larger distance between spawning areas and the most productive nursery grounds. The interactions between environment and fishing are complex and the relative role of these drivers may change as the ecosystems themselves alter.

It has been suggested that high abundances of jellyfish in the northern Benguela observed in recent years have led to changes in the ecological functioning of the ecosystem (Lynam *et al.*, 2006; Roux *et al.*, 2013). Lynam *et al.* (2006) estimated the total jellyfish (wet) biomass in the northern Benguela to be 12.2 million tonnes, about three times as high as the total biomass of fish (3.6 million tonnes) during the same survey. While there is no doubt that the biomass of pelagic fish is presently much lower than 50 yr ago, there is an ongoing debate regarding the abundance of jellyfish and their potential influence on the failure of the sardine stock to recover. Flynn *et al.* (2012) analysed fisheries-dependent and independent data as well as published and unpublished information in order to assess if there has been an increase in the abundance of jellyfish. They have provided circumstantial evidence that jellyfish abundance might have increased, but noted that quantitative evidence for this is lacking. Roux *et al.* (2013) argue that the overfishing of small pelagic fish in the northern Benguela has led to irreversible changes in the ecosystem (Cury and Shannon, 2004), which now favours pelagic goby and jellyfish. As jellyfish feed on eggs and larvae of pelagic species, high abundances of jellyfish may negatively affect the recruitment of sardine. However, it is unclear why copepod abundance in the northern Benguela remains high when there is an apparent 12 million tonnes of jellyfish in the subsystem, considering that jellyfish prey heavily on zooplankton.

In summary, links between observed changes in environmental factors and fish distributions and fishery yields appear complex in all subsystems of the BCLME. Considerable interannual and seasonal variability, as well as large changes in fishing effort, have co-occurred throughout the BCLME. The lack of consistent data for the Angolan subtropical system does not allow us to draw inferences on the relative role there of environment and fishing in the long term. Excessive fishing pressure has been an important driver of system-level changes in the 1960s and 1970s in the southern and northern Benguela subsystems, respectively. In the northern Benguela in particular, changes in the pelagic-demersal coupling have occurred. Environmental

regime shifts in the early and mid-1990s have contributed to community and system-level changes in the northern and southern Benguela. The absence of clear direct links between long-term environmental variability and/or change suggest that fishing continues to contribute to the observed changes. The interactions between environment, fishing and the food webs are complex and their relative role may change as the ecosystems themselves alter.

#### WHAT ARE THE IMPLICATIONS FOR ECOSYSTEM-BASED MANAGEMENT OF HUMAN ACTIVITIES IN THE BCLME?

There is ample empirical evidence of the effect of climate variability on the dynamics of marine ecosystems (e.g., Bakun, 2010; Barange *et al.*, 2010a; Wassman, 2011). Ecological responses to climate variation can be immediate or time-lagged, linear or non-linear, and may result from the amplification of climate effects as a result of fishing (e.g., Kaiser *et al.*, 2000; Bakun, 2010; Planque *et al.*, 2010). Marine life can be affected at different levels of biological organization, from genetics to ecosystems (Brierly and Kingsford, 2009; Brander, 2010; Moloney *et al.*, 2010). The BCLME exhibits several unique habitat features that create a challenging environment for marine biota (shallow continental shelves, deep waters, areas dominated by coastal upwelling and areas with low oxygen), providing a broad range of spatial and temporal scales that increase the possible pathways by which climate variability and change may affect ecological processes, either directly or indirectly (Moloney *et al.*, 2010; Ottersen *et al.*, 2010). Direct effects include physiological changes, whereas indirect effects include changes to the biotic (predators, prey, species interaction) and the abiotic environment (habitat type and structure) (Moloney *et al.*, 2010; Ottersen *et al.*, 2010). The above have potentially important implications for commercial fisheries (e.g., Barange *et al.*, 2010b; Perry *et al.*, 2010), therefore the responses of commercial species to future climate change is of great interest to scientists, governments and fishing communities.

Roux (2003) proposed four scenarios of possible change to the northern Benguela, elaborating on possible consequences to fisheries and mitigating actions. Although a slackening of the trade winds and warming of the sea surface since the 1990s has been observed (his Scenario 1), these have so far been muted by stability in oxygen concentrations and surface chlorophyll-*a* (his Scenario 4). The general warming trend and the decrease in upwelling winds in the northern Benguela could potentially lead to a weakening of the

gradients in the Angola-Benguela frontal zone, with implications for transboundary movements of populations. For example, sardinella could move into Namibian waters more frequently, or with warming, sardine on the central Namibian shelf might move southwards towards Lüderitz, as was observed in 1963 at the time of a Benguela Niño.

At Lüderitz the boundary zone in the epipelagic habitat is maintained by strong winds, turbulent mixing and offshore advection, resulting in low primary production. If upwelling winds decline further, increased permeability to marine resources can be expected. Events have been documented in the past where this was the case. In 1986, 300 000 tonnes of anchovy were caught off Namibia when anchovy moved north from South Africa (Boyer and Hampton, 2001). The recent eastward shift in the distribution of small pelagics in South Africa has reduced the chance that such an event could re-occur. However, in instances of intense spawning on the western Agulhas Bank and northwards transport by ocean currents of early life history stages and newly metamorphosed fish a weakened Lüderitz upwelling cell could make it possible for this situation to re-occur (Dr C. van der Lingen, DAFF: Fisheries, pers. comm). Increased temperatures such as observed at present are not thought to be limiting for the distribution of anchovy, but in combination with smaller zooplankton, this could cause the habitat to be less preferred. Although no trend in oxygen concentrations has been observed to date, decreased upwelling from very high rates to intermediate levels off Lüderitz is likely to lead to increased oxygen depletion, as source water in the Lüderitz upwelling cell is relatively well oxygenated (Duncombe-Rae, 2005). The increased oxygen depletion is expected to be deleterious to small pelagic fish such as sardine (e.g., Ekau and Verheye, 2005), whereas it may provide a competitive advantage for goby (Salvanes *et al.*, *this volume*).

The major changes in the demersal community included a southward shift of several species in the Angola Subtropical subsystem, both northward and southward shifts of species in the Northern Benguela and Southern Benguela West Coast subsystems, and increases in mean depth, depth range and latitudinal range of several species in all three countries. It is possible that the location of species-richness hotspots may track the prevailing directionality of species distribution shifts, however, the location of hotspots, mostly associated with the shelf edge, appeared consistent over the time series (Kirkman *et al.*, 2013). Nevertheless, sustained distributional shifts of the fish populations, in terms of depth or latitude, could have several

consequences, including ecological (via trophic interactions), economic (increased cost of having to fish at greater depths) or political (greater transboundary sharing of stocks) implications.

Potential changes in transboundary movements of populations will have implications for transboundary assessments and management, and consequently for the role of the BCC. This may be relevant, for example, to changes in the frequency of movement of sardinella, Cape horse mackerel and sardine between Namibian and Angolan waters. Changes in the distribution, abundance and diet of several marine top predators have been affected by the changes documented at lower trophic levels. For example, the eastward shift of small pelagic prey species between the southern Benguela and the Agulhas Bank in the late 1990s/2000s resulted not only in spatially disproportionate fishing effort, but also in mismatches between the distribution of predators (including threatened seabird species) and their pelagic prey west of Cape Agulhas (Crawford *et al.*, 2008a,b, 2011; Grémillet *et al.*, 2008). Addressing such problems require spatial management strategies, which are currently being discussed in South Africa (Smith *et al.*, 2013). In addition to large-scale spatial management of the fisheries, temporary closure of fisheries around colonies of seabirds to fishing, in order to enhance availability of forage fish to breeding animals, currently in its feasibility phase, may need to be formalized in the future (e.g., Weller *et al.*, 2014). Although these shifts fall within a national boundary, they are still shifts between two subsystems of the Benguela Large Marine Ecosystem and therefore relevant to transboundary assessment and management.

The challenges of continued resource utilization and biodiversity conservation can only be met by ongoing regional collaboration. Of relevance to transboundary cooperation and to spatially explicit management of marine biodiversity in the region is a recent proposal for a transboundary 'Ecologically or Biologically Sensitive Area' (EBSA) between South Africa and Namibia, which was motivated for on the basis of a transboundary demersal biodiversity hotspot in this area (Kirkman *et al.*, 2013).

However, the adoption of appropriate regime-specific and/or spatial management strategies requires still greater understanding of the impacts of long-term climate variability and change. This includes comprehensive environmental monitoring as well as understanding of indirect effects and feedback loops. International applications of regime-specific approaches include the Californian sardine and North Sea herring (Jacobson *et al.*, 2005; ICES, 2007b,c;

King *et al.*, 2011). In addition to lower yield as a result of changes in the food web, as documented for the northern Benguela, the loss of resilience of several commercially important stocks imply that yields are unlikely to return to historic heights. Conservative fisheries management is an essential requirement to maximize resilience to further warming and stratification.

## CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

The NansClim project provided the framework for a region-wide discussion on ecosystem dynamics, which previous projects that have looked at the individual subsystems did not provide. Its main accomplishments were integrating diverse data from three countries over 25 yr, using the RV Dr Fridtjof Nansen data time series as a basis and enhancing it with national observations, and attempting to link environmental changes to changes in pelagic and demersal biological communities. The latter was partly based on observed responses of the marine ecosystem to observed climate variability, from which the relative importance of environmental and human drivers were explored and consequences for ecosystem-based fisheries management were considered. This synthesis provides qualitative answers to questions raised regarding effects of climate variability and change. Additionally, we identify (below) a number of knowledge gaps, which if resolved will contribute to reducing the uncertainty associated with predicting ecosystem effects of climate change.

A better understanding of interactions between climate and the marine ecosystem is required before the high levels of uncertainty associated with predicted responses of climate change can be reduced. Current IPCC models do not as yet provide sufficient detail of the boundary regions of the BCLME. For example, neither the West African monsoon, nor the Agulhas Current are well captured in these models. Currently, general expectations include a warming of the oceans around southern Africa, a southward shift in the high pressure belts and increased stratification of the water column. However, observations over the past 60–100 yr, where available, do not support all of these expected manifestations of climate change in the Benguela region. In the coastal and shelf waters of the southern Benguela, the detection of long-term trends in ocean temperature is complicated by decadal-scale variability. While a warming trend has been apparent offshore of the South African coast, and in the Angolan subtropical and northern Benguela subsystems,

associated trends in productivity and oxygen concentrations have been contrary to expectations. Whereas lowered productivity is to be expected in the northern Benguela where warming, decreasing upwelling and increasing stratification have been observed, there appears rather to be an increase in near-surface chlorophyll in the northern region (even after correcting for a difference in satellite sensors). Given the increased stratification, one would expect an increased oxygen deficit. But this was also not apparent against the background of marked interannual and decadal-scale variability. Therefore the continued low biomass of sardines in the northern Benguela and the expansion of low-oxygen tolerant gobies lack coherence with the oceanographic drivers, pointing to continued gaps in our understanding.

In contrast, our understanding of regime shifts, particularly the shift that occurred during the mid-1990s which (likely) spanned all three countries, has been considerably enhanced. The results have also shown that fishing pressure, in spite of far more conservative fisheries management after the declaration of EEZs, has continued to play a role in determining the current situation, where some stressed pelagic and demersal populations lack resilience to future climate change. Therefore, more modest yields can be expected in the region. While the comprehensive monitoring programmes that were put in place in the 1980s and 1990s have provided the basis for an enhanced understanding of the system, an improved balance between environmental monitoring, fisheries resource surveys and biodiversity assessments needs to be established for future long-term observational programmes. There is also a need for improvements in the implementation of existing surveys, for example, use of acoustics during demersal surveys and conducting of environmental sampling at every biological/rawl station, or at least better alignment of CTD and trawl stations. It is clear that continued monitoring would benefit from effective regional co-ordination.

### *Major gaps in understanding: recommended priorities for future research*

Some of the knowledge gaps below are already being addressed by national, bilateral or international research projects/programmes that are ongoing in the region. In addition to the annual meeting of marine researchers in the region, which is already in place, there is a need for further, improved co-ordination and collaboration between government, academic and other research institutions. South Africa already maintains a well-functioning network of natural scientists conducting coastal and oceanic research, bridging

diverse research institutions, and which could be expanded to the southern African region. However, additional staffing would be required should such a network take an active role in co-ordination of integrated research efforts in the BCLME.

*Understanding of changes in large-scale environmental forcing and changes in boundary conditions.* Changes in the location and intensity of the high pressure systems, the ocean basin dipoles in the South Atlantic and Indian Oceans, and the wind stress across these basins have important implications for shelf-scale dynamics and the strength and location of the Agulhas Current. This, in turn, impacts biological communities on both the west coast and the south coast shelf regions as warm water penetrates into the South Atlantic in rings, filaments and minor eddies. Meaningful future climate scenarios can only be developed with a better understanding of the regional dynamics across these basin and shelf scales. There is a continued need to improve regional oceanographic models (as bounded by global/IPCC models).

In addition, changes in the boundary conditions may be important when addressing climate change in the Benguela. The large-scale drivers of change in winds and currents will affect the inshore, offshore and lateral boundaries of the relatively narrow but highly productive coastal and shelf areas where the major resources are located. Also, they may change the intensity or location of the frontal regions which help separate the four subregions of the Benguela. The tropical boundary off northern Angola at 4–5°S, the Angola/Benguela front at 16–17°S, the Lüderitz upwelling cell and the changes in the links between the South African west coast upwelling system and the Agulhas Bank are important for the life history strategies of marine resources. Understanding changes in the biophysical habitat and transport are crucial for anticipating future productivity of the living marine resources.

*Spawning and early life history traits of important fish species.* Since the mid-1980s only snapshots of egg and larvae distributions of the important fish species in Namibia and Angola have been collected. The results of these surveys helped in describing the spawning habitat selection of some species (e.g., sardine and horse mackerel in Namibia), however, no data on the seasonality of spawning is available for the past 30 yr. Also for Angola there is very limited information on the spawning location, season and early life history available for most species. Such information is urgently needed to further understanding of

recruitment and stock dynamics. In particular, the role of the Angola-Benguela Frontal (ABF) area in the early life history of pelagic species is poorly understood. Frontal areas usually present favourable feeding conditions for larvae owing to the concentration of food particles. Offshore displacement of water from the currents colliding and moving offshore will lead to offshore transport of larvae. In this area, high primary productivity also occurs further offshore, therefore food should not be a limiting factor for larvae, and the juveniles may be able to migrate back to the coastal regions. To date, few surveys have specifically investigated the *offshore* distribution limit of eggs and larvae in the ABF area. The ABF region might be an important area for spawning for pelagic species and any changes in this area could affect recruitment of pelagic species. Dedicated ichthyoplankton surveys in the area of the ABF will contribute to further understanding of the early life history of important species.

*Understanding the role of gobies, round herring, jellyfish and mesopelagics in the changing foodwebs of the Benguela.* Our understanding of the functioning of all four subsystems of the Benguela remains incomplete. Whereas historically, research has focused on the commercially important sardine and anchovy, key to the understanding of their dynamics under ecosystem change could lie in the lesser-known components, notably pelagic goby, round herring, jellyfish and mesopelagics. Environmental change and internal food web dynamics may play an important role in their relative abundance, by modifying habitats and species overlap. Process studies, surveys and ecosystem modelling will all be required to render a more complete understanding of the dynamics in the pelagic communities.

*Linking spatio-temporal pattern in biodiversity to environmental and human drivers.* The NansCLIM project found that the nature of changes in the demersal communities during the study period were extremely complex, with some changes conforming to expected responses of warming conditions and others not, and with little or no clear differences between the responses of targeted and non-targeted species, or between species with different temperature tolerances. The interpretation was that changes were attributable to environmental forcing, possibly acting in concert with long-term effects of fishing, but there is a need to further disentangle climate and fisheries as drivers of biodiversity. This can be done by assessing whether there is a link between the spatial distribution of biodiversity (as represented by diversity indices) and indices

of exploitation and the environment, using correlation-based methods [e.g., regression-type models including generalized linear model (GLMs), generalized additive models (GAMs) and regression tree analysis]. The aim would thus be to determine whether fishing or the environment contribute more to variability in biodiversity. This can be assessed from local to regional scales to determine whether the importance of different drivers change with spatial scale, i.e., a multi-scale assessment of the relative importance of different drivers on biodiversity patterns, using multivariate and geostatistical approaches.

*Modelling interactive effects of environmental and human drivers on ecosystem changes.* Environmental drivers, human pressures and internal system dynamics all play an important part in determining the state and dynamics of the Benguela subsystems. Their combined effects can only be analysed through process and ecosystem modelling. Modelling studies that are cross-cutting, with plausible future climate scenarios, need to be carefully designed and implemented at a regional scale. End-to-end modelling approaches are needed to integrate bottom-up and food-web processes and to evaluate the effects of human pressures on the marine ecosystem. Ecosystem models such as Ecopath with EcoSim (Shannon *et al.*, 2008, 2009), Osmose (Travers *et al.*, 2009) and Atlantis (Fulton *et al.*, 2011; Smith, 2013) have provided a promising start in the Benguela region. The learning curves from global research initiatives, such as GLOBEC (Hoffman *et al.*, 2010) or IMBER (IMBER, 2005), provide important guidance in this respect. Less complex, well-focused model of ecological interactions have proven useful for understanding dynamics in inshore and offshore habitats (e.g., Plagányi *et al.*, 2000; Blamey *et al.*, 2013; Smith and Jarre, 2011), and their comparative application across Benguela subsystems likewise holds considerable promise in reducing uncertainty in our understanding of the relative importance of external drivers and internal dynamics, and the prediction of likely effects of management strategies.

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## SUPPLEMENTARY INFORMATION

**Figure A1.** Cumulative sea surface chlorophyll-*a* index for eight zones in the BCLME. Zone 1: Angolan subtropical sub-system; Zone 2: northern Benguela; Zone 3: Lüderitz/Orange River Cone; Zone 4: Namaqua Shelf; Zone 5: St Helena Bay; Zone 6: Cape Columbine to Cape Point; Zone 7: Western Agulhas Bank; Zone 8: Eastern Agulhas Bank. Numbers on the right-hand side refer to zones in Fig 6. The figure updates information in Demarcq *et al.* (2007).

**Table A1.** Relevant characteristics of the demersal-trawl caught species considered in the analyses for Angola, and a summary of the results pertaining

to each species from NansClim demersal task group studies investigating their potential usefulness as indicators of sea temperature changes in summer (P. Kainge, NatMIRC, unpublished data), changes in distribution and range size (Yemane *et al.*, 2014a) and regime shifts (Kirkman *et al.*, 2014).

**Table A2.** Relevant characteristics of the demersal-trawl caught species considered in the analyses for Namibia, and a summary of the results pertaining to each species from NansClim demersal task group studies investigating their potential usefulness as indicators of sea temperature changes in summer (P. Kainge, NatMIRC, unpublished data), changes in distribution and range size (Yemane *et al.*, 2014a) and regime shifts (Kirkman *et al.* 2014).

**Table A3.** Relevant characteristics of the demersal-trawl caught species considered in the analyses for South Africa, and a summary of the results pertaining to each species from NansClim demersal task group studies investigating their potential usefulness as indicators of sea temperature changes in summer (P. Kainge, NatMIRC, unpublished data), changes in distribution and range size (Yemane *et al.* 2014a) and regime shifts (Kirkman *et al.*, 2014).

**Table A4.** Events pertaining to long-term variability and change in the Angolan Subtropical region.

**Table A5.** Events pertaining to long-term variability and change in the northern Benguela region.

**Table A6.** Events pertaining to long-term variability and change in the southern Benguela region.