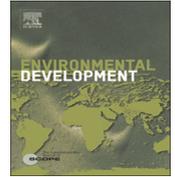




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Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME)

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ABSTRACT

Environmental drivers that have been observed to cause changes in phytoplankton biomass and production include surface warming, increased wind stress and upwelling, extension of low oxygen zones, changes in nutrient distributions, and increased stratification. While there have been documented variations in phytoplankton biomass and primary production at seasonal and interannual time scales in the BCLME, there appears to be no strong evidence of decade-scale changes or the expected ecosystem-wide increase/decrease in production in response to projected increases/decreases in upwelling-favourable winds. During the past six decades there have been substantial, long-term changes in abundance, biomass, production and species and size composition of neritic zooplankton communities in both the northern and southern Benguela subsystems. Copepods have increased since the 1950s in both subsystems, until a turning point around the mid-1990s in the south and a decade later in the north, after which they have been declining. Both subsystems also experienced a shift from large to smaller species dominating. These major changes reflect patterns of spatial, temporal and size-based heterogeneity in the BCLME and are thought to be mediated locally and differentially through bottom-up and top-down forcing mechanisms. While the relative importance of these control mechanisms remains uncertain, changes in the plankton as observed in the BCLME have fundamental effects on biogeochemical processes, food web structure and ecosystem functioning, as well as on the ecosystem services supported by the plankton. Because plankton are ideal indicators of ecosystem change, continued transboundary monitoring of their communities in the BCLME is warranted in the long term, e.g. using cost-effective technologies such as satellite imagery of ocean colour and the deployment of Continuous Plankton Recorders from ships-of-opportunity.

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1. Introduction

The Benguela Current Large Marine Ecosystem (BCLME) is one of the world's four major Eastern Boundary Upwelling Systems (EBUSs) and is situated in the SE Atlantic east of the 0° meridian, between 14°S and 37°S (Fig. 1). It spans the coasts

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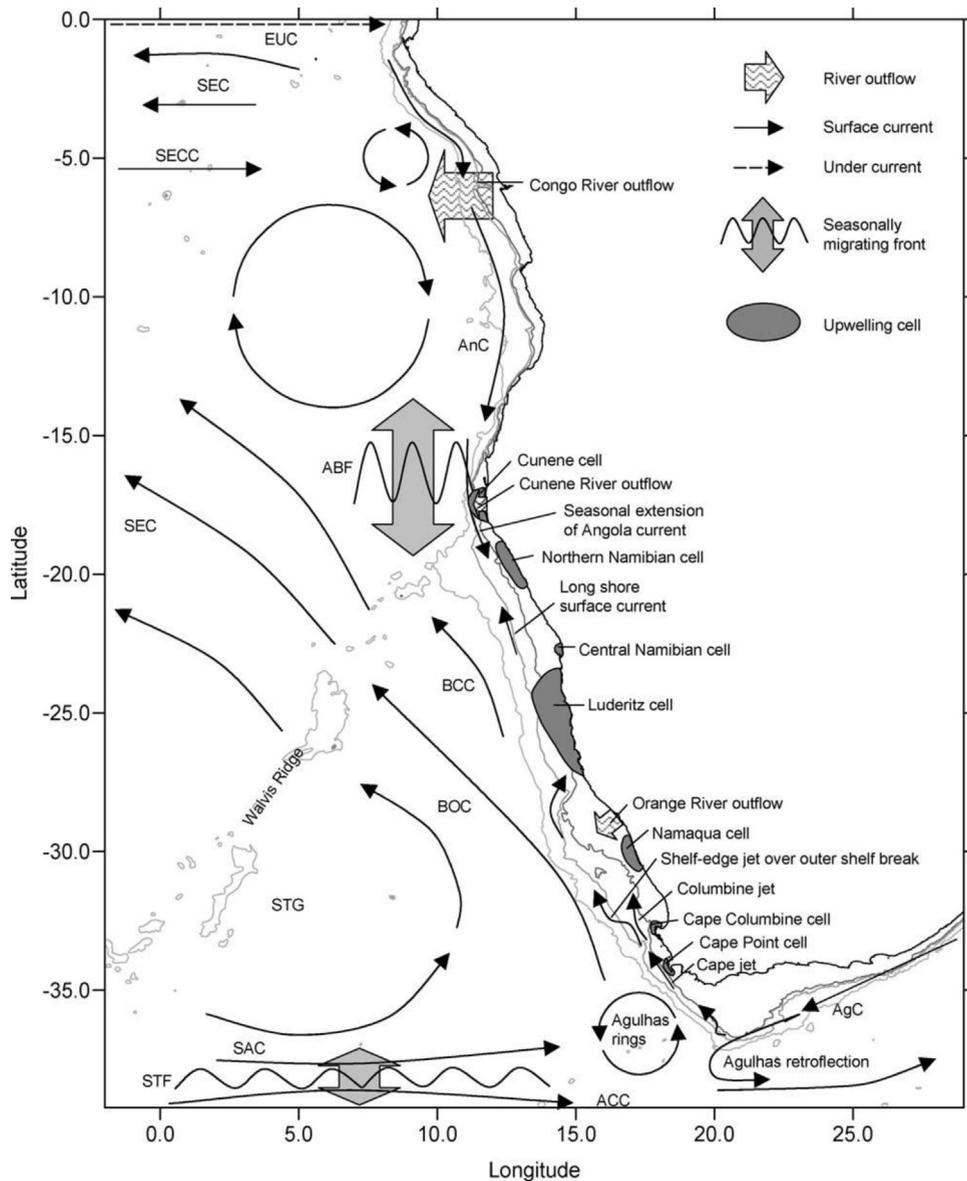


Fig. 1. The BCLME and major oceanographic features of the Southeast Atlantic: surface and near-surface currents, frontal zones, upwelling cells, major areas of freshwater input and bathymetry. EUC: Equatorial Under Current; SEC: South Equatorial Current; SECC: South Equatorial Counter Current; AnC: Angola Current; BOC: Benguela Oceanic Current; BCC: Benguela Coastal Current; SAC: South Atlantic Current; AgC: Agulhas Current; ABF: Angola-Benguela Front; STF: Subtropical Front; STG: Subtropical Gyre; ACC: Antarctic Circumpolar Current. Reprinted from [Hardman-Mountford et al. \(2003\)](#), with permission from Elsevier.

of Angola, Namibia and South Africa, characterized by a coastal belt of cold, phytoplankton-rich water. Wind-driven, coastal upwelling of nutrients fuels high productivity and supports large fisheries. As in other EBUSs, extensive fluctuations in pelagic fish yields and regime shifts of fish populations have been experienced in the BCLME ([Lluch-Belda et al., 1989, 1992](#); [Schwartzlose et al., 1999](#); [Blamey et al., 2015](#)), reflecting substantial, decade-scale food web changes over the past 5–6 decades. These changes are also manifested in long-term variations in abundance, distribution and community structure of plankton (see [Perry et al., 2004](#) and [Pepin et al., 2012](#), and references therein) on which these fish, at one or another stage in their life history, rely for their successful growth and recruitment.

There are seven particularly active, wind-driven upwelling sites within the Benguela upwelling region ([Fig. 1](#)), of which the Lüderitz cell in the central Benguela (25–26°S) is the most powerful in terms of wind, offshore advection (Ekman transport) and turbulent mixing (see [Shannon, 1985](#); [Shannon and Nelson, 1996](#); [Hutchings et al., 2009b](#) for comprehensive reviews of the physical features of the BCLME). As a result, this upwelling cell forms a partial environmental barrier ([Duncombe Rae, 2005](#)) to epipelagic biota ([Lett et al., 2007](#)) including certain plankton species ([Gibbons and Hutchings,](#)

1996) and separates the northern from the southern Benguela sub-system. In contrast to the Lüderitz cell, where upwelling is perennial, coastal upwelling elsewhere in the ecosystem is highly pulsed and seasonal. The northern Benguela is a typical coastal upwelling system driven by equatorward, south-easterly winds favourable for the upwelling of cool, nutrient-rich water from the deep onto the shelf, fuelling high phytoplankton production, with large plankton biomass supporting moderate-to-high fish stocks (Hutchings et al., 2009b). In contrast, wind-driven upwelling at discrete upwelling centres in the southern Benguela is strongly pulsed and shows greater seasonal differences, with a narrow band of high plankton productivity in the southern part, restricted to the narrow coastal zone by warm Agulhas water offshore forming a front. North of Cape Columbine, the southern Benguela is characterised by a wider shelf, with elevated biomass and production extending further offshore (Demarcq et al., 2007; Hutchings et al., 2009b).

The seaward boundary of the BCLME is at the highly dynamic interface of the northward flowing Benguela Current and the South Equatorial Current (Fig. 1). Unlike the other EBUSs, the cool Benguela upwelling regime is bounded in the north and south by warm, tropical or subtropical regimes. In the north, the confluence of the warm Angola and cold Benguela currents forms the Angola–Benguela Frontal Zone (ABFZ) at 12–18°S (Veitch et al., 2006), whereas in the south, the Agulhas Current Retroflexion Zone (ACRZ) between 36 and 37°S forms the southern boundary (Veitch et al., 2009). These zones are characterised by extensive mixing and variability, which strongly influence the dynamics of the system, particularly on the Agulhas Bank to the south of South Africa, which is a major spawning area supporting recruitment of many species to the west coast nursery grounds (Hutchings et al., 2009b).

In addition to commercial fishing and marine aquaculture, the BCLME provides ecosystem goods and services from offshore oil and gas production, coastal and marine diamond mining, coastal tourism, and shipping. Collectively, these are estimated to be worth between US\$ 54.3 billion (www.thegef.org) and US\$ 269 billion (www.benguelacc.org), making the BCLME one of the richest ecosystems in the world. In order to promote integrated management, sustainable development and protection of the BCLME environment and its resources using an ecosystem approach to ocean governance, Angola, Namibia and South Africa established a multi-sectoral *interim* Commission in 2007 focusing, *inter alia*, on the management of shared fish stocks, environmental monitoring and early warning, biodiversity and ecosystem health, socio-economics and governance. On March 18th 2013, the three countries signed the Benguela Current Convention and launched the Benguela Current Commission (BCC), a permanent inter-governmental organisation (www.benguelacc.org). The convention promotes a coordinated regional ecosystem approach to the long-term conservation, protection, rehabilitation, enhancement and sustainable use of the BCLME, to provide economic, environmental and social benefits. One of the broad thematic areas of the BCC's Science Programme is oceanographic and coastal monitoring, including plankton.

2. Plankton studies in the BCLME

Plankton productivity forms the base of LME food webs and determines energy flow to higher trophic levels such as fish, shellfish, seabirds and marine mammals. It is one of the five modules used in the LME approach to the assessment and management of marine resources and their environments as a “strategy for measuring the changing states of an ecosystem and for taking remedial actions toward recovery and sustainability of degraded resources and environments” (Sherman and Hempel, 2009, p. 5). In the BCLME, plankton collections were initially made during the 18th and 19th centuries by naturalists (Shannon and Pillar, 1986), with perhaps the greatest marine expedition of discovery being the voyage of the HMS *Challenger* around the world under the leadership of Sir John Murray in 1872–1876 (Fraser, 1962).

Large-scale, quantitative monitoring of phytoplankton in the BCLME started early in the 20th century during the *Meteor* expeditions in 1925–1927 (see Shannon and Pillar, 1986). These early studies, for instance, identified the waters around Walvis Bay in the northern Benguela to rank among the most productive globally. Already then, the BCLME proved to be generally a diatom-dominated system, which was subsequently confirmed by many other studies in both sub-systems. In addition, there were contrasts in the spatial distribution of the phytoplankton between the northern and southern Benguela sub-systems, with diatoms being the dominant group in the neritic zone in both sub-systems, while dinoflagellates were relatively more important offshore in the northern Benguela than in the southern Benguela (Shannon and Pillar, 1986).

Zooplankton research in the BCLME has, as in the other EBUSs, lagged far behind that of phytoplankton. The development in the early 1950s of a pelagic fishery in St Helena Bay on the west coast of South Africa, where fishing efforts were then concentrated, was a first turning point in oceanographic research emphasis from essentially qualitative, taxonomic studies to semi-quantitative, large-scale monitoring surveys of zooplankton (see Shannon and Pillar, 1986 for a comprehensive review of earlier studies in the BCLME, and Hutchings et al., 2012 for an overview focusing on the St Helena Bay area, in the southern Benguela).

In their review, Shannon and Pillar (1986) synthesise knowledge about the phyto- and zooplankton communities of the Benguela ecosystem, thereby emphasising processes such as plankton production and dynamics, both in the northern and southern Benguela sub-systems. Subsequent reviews and syntheses focused in detail on different components of the plankton and on specific aspects of plankton research and monitoring in the BCLME. They include works by Brown et al. (1991), Brown (1992), Gibbons et al. (1992), Hutchings et al. (1991, 1995, 1998), Painting et al. (1992), Pillar et al. (1992), Pitcher et al. (1992), Timonin et al. (1992), van der Lingen and Huggett (2003), Verheye et al. (1992), and more recently by Hutchings et al. (2006, 2009b) and Pitcher and Weeks (2006), as well as relevant sections in Lamont (2011), Hutchings et al. (2009a, 2012) and Jarre et al. (2015).

The objectives of this paper are to consolidate historical and contemporary data – published and unpublished – of phyto- and zooplankton abundance, biomass, community structure and production in order to update existing and present new time-series of these essential biological ocean variables, in the two Benguela sub-systems. In addition, given the ever rising costs associated with research and monitoring – particularly of plankton – on board research vessels, we advocate more cost-effective ways to continue large-scale, transboundary plankton surveys in the BCLME in the long term, providing indices of long-term change in plankton communities and ecosystem functioning as a whole, which will assist sustained ecosystem-based management.

3. Phytoplankton biomass and primary production

Similar diatom assemblages (incl. the common *Chaetoceros*, *Nitzschia*, *Thalassiosira* and *Rhizosolenia*) are found in both the northern and southern sub-systems, while small flagellates are prevalent in warmer, less saline waters offshore (e.g. Barlow et al., 2005, 2006). Exceptions to this general pattern include the abundant diatoms *Delphineis karstenii*, restricted to the north, and *Skeletonema costatum*, particularly abundant in the south, while the large *Coscinodiscus* spp. are common in areas of high turbulence (Hampton, 2012). In St Helena Bay, the most productive and by far best studied area on the west coast of South Africa, phytoplankton assemblages observed during the late 1980s–early 1990s were very similar to those identified four decades earlier, although smaller species such as flagellates and small diatoms were observed more frequently in the recent collections, likely due to the use of more advanced taxonomic knowledge and microscope technology (Hutchings et al., 2012).

Pitcher et al. (1998) have demonstrated the importance of a range of dinoflagellate species, which usually comprise the bulk of harmful algal blooms (HABs) in upwelling systems (Pitcher and Pillar, 2010). On the West Coast, harmful algae usually form persistent and widespread blooms during late summer when waters are stratified (Pitcher and Boyd, 1996; Probyn et al., 2000; Pitcher et al., 1998). HABs negatively impact the ecosystem by introducing toxins that are detrimental to marine and human life (Botes et al., 2003). Settling organic matter, which follows bloom decay, has a high respiratory demand, and as such high biomass blooms are often associated with rapid oxygen consumption that can lead to hypoxia and anoxia (Pitcher et al., 2008; Pitcher and Weeks, 2006; Pitcher and Cockcroft, 1998). In some rare and extreme cases, bloom decay may also lead to the production of hydrogen sulphide (Weeks et al., 2002, 2004; Matthews and Pitcher, 1996). In the southern Benguela, the occurrence of hypoxic water has been linked to the decay of dense phytoplankton blooms (Monteiro and van der Plas, 2006; Pitcher and Probyn, 2011) and has periodically resulted in mass mortalities of rock lobster and shellfish (Cockcroft, 2001; Pitcher and Weeks, 2006). It is in the nearshore regions, where the orientation of the coastline and the bottom topography strongly influence water column stratification and retention, that these impacts are most significant (Pitcher and Pillar, 2010). The persistence of a deep pool of hypoxic water located in the central region of St Helena Bay throughout the year, with substantial shoreward and offshore expansion due to the accumulation of decaying organic matter during the upwelling season, has been demonstrated by Lamont et al. (2015). Toward the end of the upwelling season, severe and rapid declines in nearshore oxygen of up to 6 ml L^{-1} over 2–5 days have been observed (Pitcher et al., 2014).

Past attempts to estimate phytoplankton and bacterioplankton biomass and production in the BCLME include various *in situ* studies, such as those by Barlow (1982a, b, c), Barlow et al. (2009), Brown (1984), Brown and Field (1985, 1986), Brown and Hutchings (1987a,b), Brown et al. (1991), Cushing (1971), Estrada and Marrasé (1987), Lamont et al. (2014), Lucas et al. (1987), Mitchell-Innes and Walker (1991), Mitchell-Innes et al. (2000), Painting et al. (1989), Shannon and Field (1985), Shannon and Pillar (1986), Verheye-Dua and Lucas (1988), Waldron and Probyn (1992), and Wasmund et al. (2005). However, compared with other EBUSs, these investigations have been relatively infrequent and limited in area, and more data are available for the southern than the northern Benguela. In recent years, estimates of phytoplankton biomass and production have become dominated by the use of remotely-sensed ocean colour and modelled output, rather than *in situ* measurements (Demarcq et al., 2003, 2007; Demarcq, 2009; Koné et al., 2005; Weeks et al., 2006).

In upwelling regions, maximum chlorophyll concentrations are usually both spatially and temporally coincident with the seasonal maximum in upwelling and are observed downstream of upwelling cells, while the centres of upwelling cells are associated with lower concentrations (Demarcq et al., 2003, 2007; Thomas et al., 2001, 2003; Weeks et al., 2006). Phytoplankton biomass is highly variable in the BCLME, with the highest abundances usually found in the nearshore regions (20–80 km from the coast), although elevated chlorophyll *a* has been observed to extend over 100 km offshore following periods of intense upwelling (Brown et al., 1991; Weeks et al., 2006). Phytoplankton blooms typically last for about a week, developing over three days and declining over the following four days (Brown and Hutchings, 1987a, b). Chlorophyll *a* concentrations $< 1 \text{ mg m}^{-3}$ are usually associated with recently upwelled water ($< 10 \text{ }^\circ\text{C}$), while in maturing upwelled water ($10\text{--}12 \text{ }^\circ\text{C}$) they range from $1\text{--}20 \text{ mg m}^{-3}$, and higher values ($1\text{--}30 \text{ mg m}^{-3}$) are found in aged upwelled water ($12\text{--}16 \text{ }^\circ\text{C}$) (Barlow 1982a, b, c).

Most of the primary production in the BCLME occurs over the shelf, and the area over which production occurs, increases and decreases along the coastline in accordance with the width of the shelf (Koné et al., 2005; Pitcher et al., 1992; Weeks et al., 2006). Estimates of primary production in the BCLME have been made using a variety of techniques, including both *in situ* and on-board bottle incubations, assumptions using Redfield ratios, as well as natural fluorescence measurements and Photosynthesis-Irradiance experiments; in what follows, primary production estimates were standardized to a common

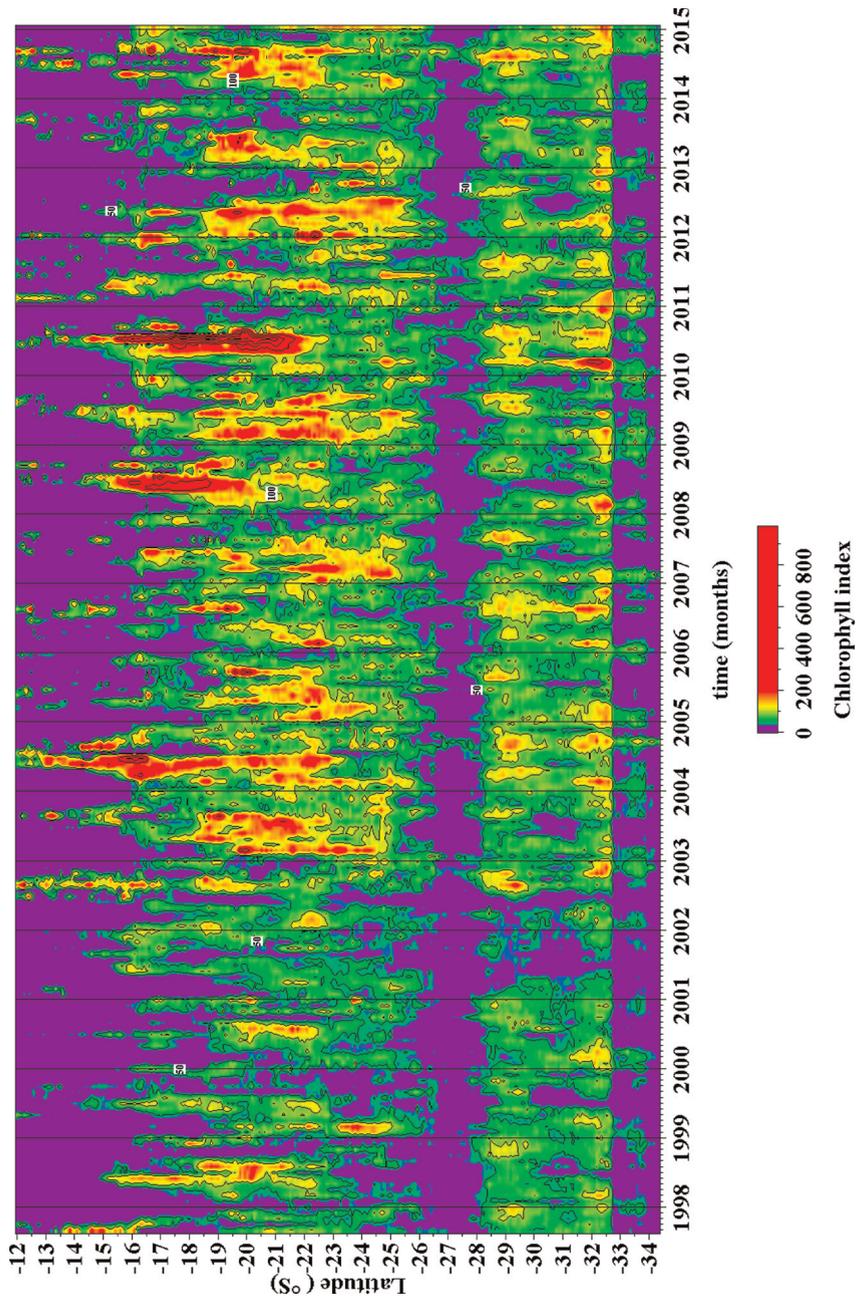


Fig. 2. A space-time plot of the chlorophyll index for the BCLME west coast (12–34°S) from September 1997 to January 2015. The solid vertical lines indicate January of each year – updated from Jarre et al. (2015).

unit of $\text{g C m}^{-2} \text{d}^{-1}$ to allow comparison. Brown et al. (1991) estimated the total primary production in the northern and southern Benguela to be $1.2 \text{ g C m}^{-2} \text{d}^{-1}$ and $2 \text{ g C m}^{-2} \text{d}^{-1}$, respectively. Shannon and Field (1985) estimated the rate of total production (new and regenerated combined) to be $2.8 \text{ g C m}^{-2} \text{d}^{-1}$, while Waldron and Probyn (1992) estimated annual new production in the Benguela (northern and southern) to be $0.649 \text{ g C m}^{-2} \text{d}^{-1}$ during 1987. During winter 1999 and summer 2002, Barlow et al. (2009) reported rates of $0.14\text{--}2.26 \text{ g C m}^{-2} \text{d}^{-1}$ and $0.39\text{--}8.83 \text{ g C m}^{-2} \text{d}^{-1}$, throughout the BCLME, respectively. In the southern Benguela during mid-spring 2006, integrated production rates varied between 0.71 and $6.98 \text{ g C m}^{-2} \text{d}^{-1}$, while lower rates were observed during May, ranging from 0.7 to $3.37 \text{ g C m}^{-2} \text{d}^{-1}$ (Lamont et al., 2014). In the northern Benguela, estimates range between 0.4 and $1.1 \text{ g C m}^{-2} \text{d}^{-1}$ in spring, and $0.5\text{--}3.6 \text{ g C m}^{-2} \text{d}^{-1}$ in autumn (Estrada and Marrasé, 1987). In the vicinity of the Cape Frio upwelling cell and the Angola-Benguela Front off northern Namibia, Wasmund et al. (2005) observed rates of $0.52\text{--}4.1 \text{ g C m}^{-2} \text{d}^{-1}$.

Nearshore estimates showed that average primary production around the Cape Peninsula varies from $4.05 \text{ g C m}^{-2} \text{d}^{-1}$ in summer to $2.23 \text{ g C m}^{-2} \text{d}^{-1}$ in winter (Brown, 1984). Other investigations off the Cape Peninsula measured $1.02 \text{ g C m}^{-2} \text{d}^{-1}$ in newly upwelled water, while in mature upwelled water rates were $1.48\text{--}10.07 \text{ g C m}^{-2} \text{d}^{-1}$ (Brown and Field, 1985, 1986). In St Helena Bay, a 27-day anchor station time-series study showed production between $0.99 \text{ g C m}^{-2} \text{d}^{-1}$ and $7.85 \text{ g C m}^{-2} \text{d}^{-1}$ (Mitchell-Innes and Walker, 1991), while Mitchell-Innes et al. (2000) observed rates of $2.4\text{--}5.6 \text{ g C m}^{-2} \text{d}^{-1}$ off Lambert's Bay. During red tide blooms, which occur frequently in this region during late summer, production can be as high as $12 \text{ g C m}^{-2} \text{d}^{-1}$ (e.g. during a bloom dominated by *Ceratium furca* and *C. dens*; Mitchell-Innes et al., 2000).

While a close relationship is to be expected between primary production and upwelling of nutrient-rich water over short time scales, it is generally assumed that long-term shifts in upwelling-favourable winds will lead to changes in upwelling and, consequently, to changes in phytoplankton production and biomass on similar scales (Hampton, 2012). However, patterns observed from *in situ* and satellite data provide no clear indications to suggest that such a straight-forward link between primary production and upwelling variability occurs in the Benguela, but there is evidence of substantial inter-annual and decade-scale changes in both phytoplankton production and upwelling at a number of times and locations in both the northern and southern Benguela sub-systems.

Most LMEs have shown warming trends (Belkin, 2009), which have been correlated to large spatial changes in phytoplankton distributions and a reduction of global primary production since the early 1980s (Behrenfeld et al., 2006). While a significant warming in the southern boundary region of the BCLME has been observed, a strong cooling trend has been identified in the inshore region of the southern Benguela (Rouault et al., 2009, 2010).

Off northern Angola, warming has been observed to have resulted in less contrasts between summer and winter temperatures, while off southern Angola, warming has been observed throughout the year (Jarre et al., 2015). Likewise, off Namibia, decreases in upwelling-favourable winds and warming have been noted during all seasons (Hutchings et al., 2009b; Jarre et al., 2015). Upwelling-favourable winds off South Africa have exhibited interannual and decade-scale variations (Jarre et al., 2015), and regime shifts have been identified from sea surface temperature, upwelling and other ecosystem indices (Blamey et al., 2012; Howard et al., 2007; Shannon et al., 2010). In contrast, temperatures in the upper layers of St Helena Bay between 1950 and 2005 showed no evidence of a long-term trend, but clear decade-scale variations were evident (Hutchings et al., 2012).

Verheye (2000) documented an increase in mean surface chlorophyll concentration measured *in situ* in St Helena Bay during the 1990s, coincident with marked increases in the concentration of nutrients (phosphate, nitrate, silicate). de Villiers (1998) found that marked interannual variations in CZCS (Coastal Zone Colour Scanner) satellite-derived chlorophyll concentration on the South African west coast (off Cape Columbine and Cape Peninsula) during 1979–1986 corresponded with variations in sea surface temperature rather than with seasonal variations in upwelling-favourable winds. Demarcq et al.

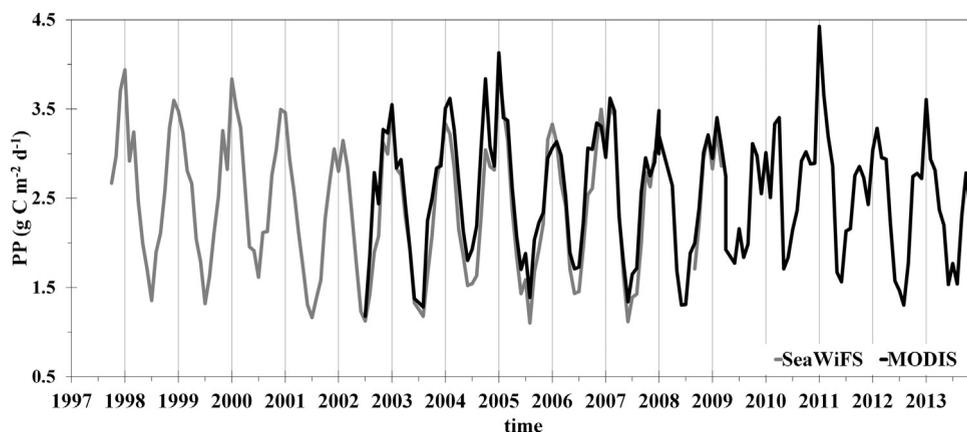


Fig. 3. Monthly means of primary production (PP, $\text{g C m}^{-2} \text{d}^{-1}$), averaged over a 200 km-wide area along the southern Benguela coast – updated from Lamont (2011).

(2007) used a chlorophyll index to describe the spatial and temporal variability in phytoplankton biomass in the BCLME over a period of eight years, and noted that the seasonal signal was the dominant variation, with clear interannual changes, and that no clear long-term signal was evident. Similar interannual variations have been described by Weeks et al. (2006). A more recent study illustrated that the productivity of most EBUSs has shown an increasing trend from 1998 to 2007 whereas a decreasing trend has been noted in the offshore regions (Demarcq, 2009).

Following the method of Demarcq et al. (2007), an index of chlorophyll concentration along the west coast of southern Africa was computed by integrating monthly averages of surface chlorophyll *a* concentration, obtained from satellite sensors, in a zonal direction from the coast to the 1 mg Chl m⁻³ offshore level. SeaWiFS data were used from September 1997 to June 2002, and MODIS Aqua data thereafter. The most prominent features of the West Coast chlorophyll index (Fig. 2) between 1997 and 2010 have been summarised in Jarre et al. (2015). The addition of a further four years of data (Fig. 2 and DEA, 2015) confirms and supports the strong seasonal, interannual and multi-annual variations described by Jarre et al. (2015). In accordance with the findings of Brown et al. (1991) and Shannon and Field (1985), the chlorophyll index and the productive area in the northern Benguela are greater than in the southern Benguela, and have remained so throughout the time-series (Fig. 2). While no decade-scale regime shifts have been detected in these data (Jarre et al., 2015), there appears to have been a shift toward increased seasonality in biomass, with greater differences between summer and winter index values. This is particularly evident in the northern Benguela over the last four years, but not so in the southern Benguela (Fig. 2).

Satellite-derived estimates of primary production within a 200 km-wide area along the southern Benguela coast (Fig. 3), determined using the Vertically Generalised Production Model (VGPM, Behrenfeld and Falkowski, 1997), illustrate strong seasonal and interannual variability. In addition, there is marked multi-annual variability in the amplitude of seasonality as well as in the minimum and maximum production values (Lamont, 2011). Annual mean production values range between 2.19 and 2.83 g C m⁻² d⁻¹ from 1998 to 2013 (Fig. 3), with no substantial differences between SeaWiFS and MODIS Aqua data, and there is no significant long-term trend (Jarre et al., 2015; Lamont, 2011).

While the spatial patterns of biomass and production identified from satellite data have been corroborated with *in situ* observations from numerous investigations (e.g. Barlow et al., 2009; Lamont et al., 2014; Mitchell-Innes et al., 2000), this is not the case for many of the temporal variations. In some instances, satellite and *in situ* data time-series show contradictory temporal variations and trends. Some of the discrepancies, as well as possible reasons for their existence, have been discussed in detail by Jarre et al. (2015). However, with the already limited and ever-decreasing availability of *in situ* data, it is unlikely that many of these satellite-derived temporal patterns will ever be adequately corroborated and validated.

In conclusion, different signals and patterns of variability have been identified in time-series of both phytoplankton biomass (or chlorophyll *a*) and primary production, which vary depending on the datasets used. This not only highlights the persistence of gaps in our understanding of the driving forces and mechanisms that underlie variability in phytoplankton communities in the BCLME (Jarre et al., 2015), but also emphasises the need for continued *in situ* monitoring at the spatial and temporal scales relevant to phytoplankton dynamics at the level of individual groups and populations, as well as at the level of sub-systems and LMEs.

4. Zooplankton abundance, biomass, community structure and secondary production

Past estimates of zooplankton biomass, abundance and production in different sectors of the BCLME during various periods and at different times of the year have been summarised by Verheye (1991), Hutchings et al. (1991, 1995), Verheye et al. (1992), Richardson et al. (2001), and Huggett et al. (2009). Relatively good estimates of zooplankton (especially copepod) abundance, biomass and production exist for the southern Benguela. There is a clear seasonal cycle associated with the upwelling cycle, and there is also substantial short-term variability, which is driven by the pulsed nature of upwelling, the dynamics of phytoplankton blooms in response to that, and the species-specific life-history characteristics of the zooplankton (Hampton, 2012). In contrast, comparatively few such estimates are currently available in the northern Benguela and less is known about its zooplankton dynamics, including production (Richardson et al., 2001). Abundance peaks seem to correspond with periods of maximum phytoplankton abundance during November–December, in the main upwelling season, and during March–May when upwelling is moderate and stratification weak, and there is a tendency for zooplankton to be more abundant offshore of the coastal phytoplankton-rich belt (Hampton, 2012).

In what follows, the focus is on changes of zooplankton communities, primarily copepods because of their abundance, in both Benguela sub-systems in the long term. The information presented here is based on multi-decadal time-series that have been reconstructed using historical data, both published and unpublished, as well as retrospective analysis of sample archives from a variety of historical monitoring programmes.

4.1. Southern Benguela

Changes in zooplankton communities on the west coast of South Africa have been monitored since the late 1940s, coincident with the development of the pelagic fishery there (Hutchings et al., 2012). In St Helena Bay (32–33°S) the zooplankton during the 1950s was dominated by large copepod species (predominantly *Calanoides carinatus* s.l. – see Viñas et al., 2015) and euphausiids; small copepod species (*Paracalanus*, *Ctenocalanus* (= *Pseudocalanus*?) and *Clausocalanus*

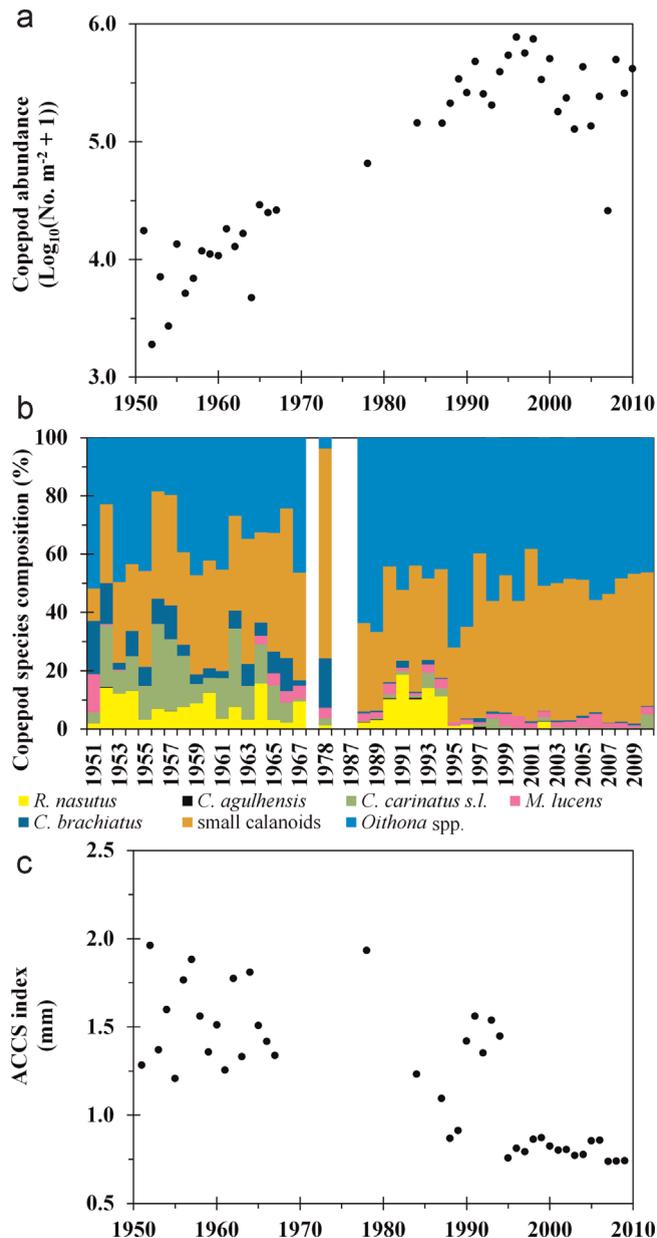


Fig. 4. St Helena Bay, southern Benguela: 1951–2010 time-series of year-to-year changes in (a) total copepod abundance (log-transformed) – updated from Verheye et al. (1998) and Verheye and Kreiner (2009), (b) percentage copepod species composition, and (c) average copepod community size (ACCS) index.

(=*Microcalanus*?)), which are currently highly abundant in St Helena Bay, were then not as important. Of the 18 species of euphausiid recorded in the southern Benguela (see Shannon and Pillar, 1986), *Euphausia lucens* was by far the dominant species in St Helena Bay, followed by *Nyctiphanes capensis*. A decrease in relative abundance of the latter species was noted between the 1950s and 1980s, remaining scarce through the 2000s, whereas the former species is at present still the most prevalent (Hutchings et al., 2012).

A pilot retrospective analysis of a subset of the historical west coast zooplankton sample archive that had accumulated since 1951 was initiated under the umbrella of the Benguela Ecology Programme (BEP) during 1982–2006 (Moloney et al., 2004). Zooplankton samples collected in St Helena Bay between 1951 and 1996, specifically during austral autumn (April–June), when peak recruitment of anchovy and sardine occurs, were analysed in terms of abundance, species and size composition of the copepod community following a standard, quantitative protocol (see Verheye et al., 1998). Likewise, samples collected during subsequent annual fisheries surveys in the area until 2010 were analysed, extending the initial 1951–1996 time-series until 2010 (see Hutchings et al., 2006; Hutchings et al., 2009b and Fig. 4). The St Helena Bay zooplankton time-series thus covers six decades of data, with a large hiatus in the dataset during the 1970s and early 1980s,

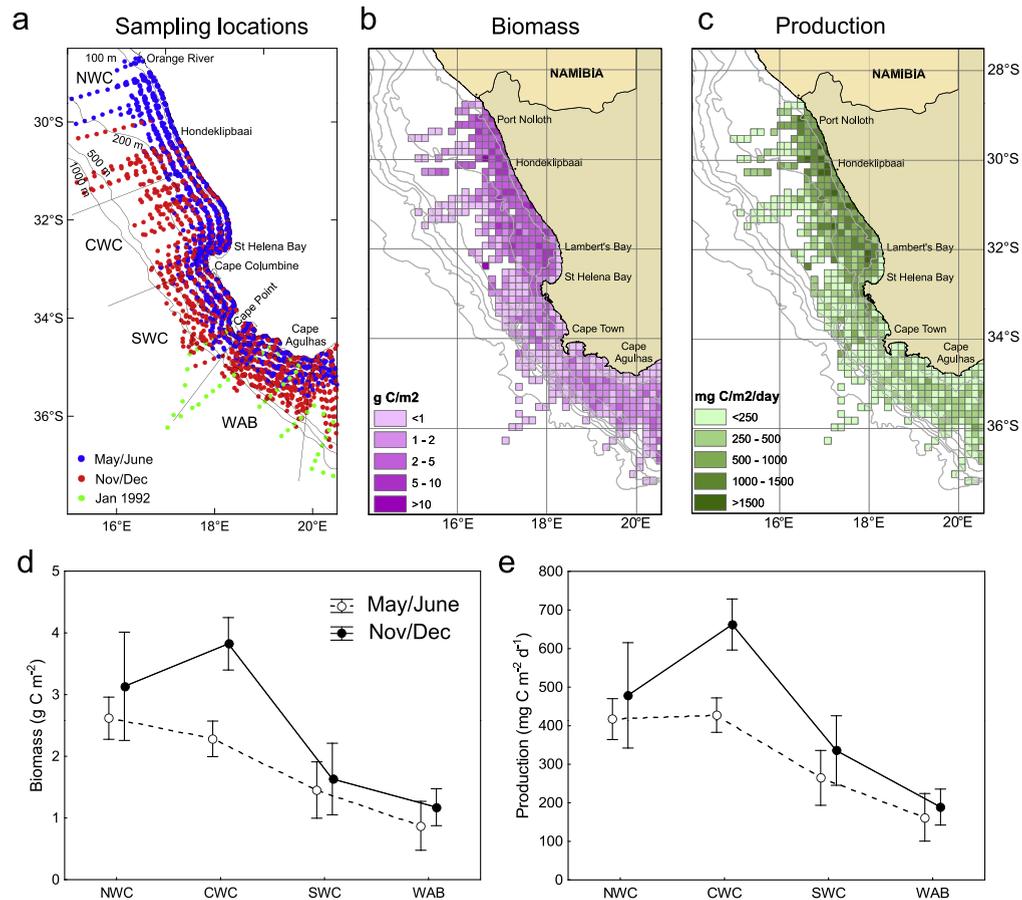


Fig. 5. (a) Map of the southern Benguela showing location of stations where zooplankton was collected during late autumn/early winter (May/June) and late spring/early summer (November/December) pelagic acoustic surveys between 1988 and 2003, as well as during an additional cruise in January 1992; maps of (b) mean copepod biomass (g C m^{-2}) and (c) mean daily copepod production ($\text{mg C m}^{-2} \text{d}^{-1}$) throughout the southern Benguela derived from the above surveys; plots of (d) mean copepod biomass (g C m^{-2}) and (e) mean daily copepod production ($\text{mg C m}^{-2} \text{d}^{-1}$) over the continental shelf ($\leq 200 \text{ m}$) during May/June and November/December for four areas in the southern Benguela, for the years 1988 to 2003. Reprinted from Huggett et al. (2009), with permission from Elsevier. The areas, from north to south, are the North West Coast (NWC) from the Orange River to 31°S , the Central West Coast (CWC) from 31°S to Cape Columbine, the South West Coast (SWC) from Cape Columbine to Cape Point, and the Western Agulhas Bank (WAB) from Cape Point to Cape Agulhas.

while there has also been no autumn sampling since 2010.

There is clear evidence of an initial, multi-decadal trend of increasing abundances of copepods (Fig. 4a) and other zooplankton taxa (see Verheye et al., 1998) since the 1950s, reversing around the mid-1990s and declining thereafter, with possibly another turning point around the mid-2000s. Similar patterns of alternating increases and decreases in abundance were also observed in the dominant species, albeit to varying extents dependent on body size (Verheye et al., 1998; Verheye and Richardson, 1998). As a result, there was a marked shift from large- to small-species dominance over the time-series period (Fig. 4b). Medium to large copepods such as *Centropages brachiatus*, *C. carinatus* s.l. and *Rhincalanus nasutus*, which form the preferred prey species of anchovy (James, 1987), were more prominent during the 1950s–1960s than later, whereas smaller copepods such as *Oithona* spp. and small calanoid species, preferred by sardine (van der Lingen, 2002), as well as *Metridia lucens*, became more prominent from the late 1980s onward compared with the 1950s and 1960s.

These changes over time in copepod abundance and species composition can be tracked using a size-based index, average copepod community size (ACCS). Copepods are robust and have a finite growth so that adults have a narrow, species-specific size range, making the ACCS an ideal indicator of community composition (Batten et al., 2015). The approach of using this index is based on the hypothesis that warm-water zooplankton communities are usually dominated by species of a smaller size than their cold-water counterparts, so that a shift over time to a smaller average community size in an ecosystem is indicative of ecosystem warming, whereas a shift to a larger average size indicates cooling. The ACCS is based on adult females and calculated according to Beaugrand et al. (2003) as

$$\bar{S} = \frac{\sum_{i=1}^N (L_i \times X_i)}{\sum_{i=1}^N X_i}$$

where for each sample, the body length L (in mm) of each copepod species i (represented by adult females) is multiplied by its abundance X_i , summed over all species (N), and divided by the total abundance.

The ACCS index for St Helena Bay (Fig. 4c) shows a shift from high values of 1.2–2.0 mm during the 1950s and 1960s, representing a community generally dominated by large species, to lower values of < 1.0 mm during the mid-1990s and 2000s, when smaller species were more prevalent. The exceptionally elevated ACCS index values during the early 1990s coincided with a prolonged El Niño episode (Prof. C. Reason, Univ. of Cape Town, pers. comm.), when increased numbers of both *R. nasutus* and *Calanus agulhensis*, a typical Agulhas Bank species, persisted in St Helena Bay for some years. While this shift from larger to smaller species in St Helena Bay is indicative of ocean warming, there is evidence to suggest a cooling trend (by up to 0.5 °C per decade) in the southern Benguela from the 1980s onward due to an intensification of upwelling (Rouault et al., 2010).

Verheye et al. (1998) and Verheye and Richardson (1998) speculated that the observed changes in the zooplankton were caused by upward-propagating effects of oceanographic and biological processes (bottom-up control) in concert with downward-cascading effects of predation, particularly by anchovy and sardine, which abound in St Helena Bay preferentially feeding size-selectively on different plankton size categories. For instance, the 10-fold decline in copepods, especially of the larger calanoid species, in St Helena Bay since the mid-1990s coincided with a marked increase in pelagic fish biomass (Jarre et al., 2015), suggesting that increased predation pressure was the primary forcing mechanism controlling zooplankton populations in this fish-recruitment area.

Moreover, in support of the bottom-up hypothesis, Verheye (2000) provided evidence of parallel decade-scale changes across multiple lower trophic levels, which he attributed to a long-term increase in wind stress. In addition, the long-term increase in copepod abundance following the onset of commercial fishing since the early 1950s, along with changes in the species and size structure of the copepod community between periods of sardine and anchovy dominance, were thought as evidence for a measure of concomitant top-down control (Verheye, 2000). Further evidence of top-down control of particularly the larger copepod species by anchovy was subsequently provided by Hutchings et al. (2006). They found negative correlations between the abundance of large copepods and anchovy recruits on the West Coast in autumn and spawners on the South Coast in summer. Although the relative importance of these 'bottom-up' and 'top-down' feedback mechanisms remains largely unknown (Verheye and Richardson, 1998; Cury et al., 2000), Hutchings et al. (2012, p. 578) concluded that "the absence of any long-term trend in the biogeochemistry in St Helena Bay suggests that top-down processes have been the major drivers of the observed changes in the pelagic ecosystem over the past 60 years".

On a larger spatial scale, Huggett et al. (2009) documented longshore, seasonal (late-autumn/early-winter vs late-spring/early-summer), interannual and long-term changes in copepod biomass and production along the entire coast of the southern Benguela, from the Orange River to Cape Agulhas, during routine surveys between 1988 and 2003 (Fig. 5a). Compared to the late 1970s (from Pillar, 1986), their biomass estimates were an order of magnitude higher, which confirms the above-discussed long-term trend of increasing copepods observed in autumn in St Helena Bay. Mean copepod biomass and daily production were significantly higher in the region north of Cape Columbine (North and Central West Coast) compared to the region between Cape Columbine and Cape Agulhas (South West Coast and Western Agulhas Bank, Fig. 5b and c). In addition, both copepod metrics were higher in late spring/early summer compared to late autumn/early winter, but only significantly so in the area downstream from the Cape Columbine upwelling cell (Central West Coast, Fig. 5d and e). Predation by pelagic fish, which recruit in this region in autumn, may compound this seasonal disparity.

The size composition of the copepod community was also shown to vary spatially and seasonally, with different patterns observed for each of four size classes (Huggett et al., 2009). There was considerable interannual variability in biomass and production over the 16-year time-series, with different interannual patterns evident for each sub-region, as well as for the two seasons during which the study was undertaken, indicating the danger of extrapolating trends from one location or season to another within this variable system.

4.2. Northern Benguela

Zooplankton in the northern Benguela has been sampled semi-routinely at variable spatial and temporal scales since the late 1950s, with most studies focusing on the area off Walvis Bay (23°S), an important pelagic fish nursery ground and the traditional hub of pelagic fishing in Namibia (Kreiner and Yemane, 2013). While no clear seasonal fluctuations in zooplankton were discernable in a study during the early 1960s, there were two annual peaks in the area of highest productivity (November–December and March–June; Unterüberbacher, 1964). Hansen et al. (2005) subsequently identified an autumn low and an early summer (November–December) high in the abundance of copepods during 2000. Based on sporadic accounts of the species composition of calanoid copepods in the region published over the past five decades, they also suggested long-term changes in copepod community structure (see their Table 2).

An extensive ichthyoplankton sample collection had been built up during the routine SWAPELS (South West African Pelagic Eggs and Larvae Surveys) Programme between 1972 and 1989 (see Shannon and Pillar, 1986), but retrospective analysis of the zooplankton component of this historical sample archive was undertaken much later. Following a pilot study under the auspices of the Benguela Fisheries and Environment Interactions and Training (BENEFIT: 1997–2007) Programme (Anon., 1997), sample analysis was fast-tracked during the Benguela Current Large Marine Ecosystem (BCLME: 2002–2007) Programme (Anon., 1999). Both programmes involved post-graduate students (see Verheye, 2007) and were respectively funded jointly through the Norwegian Agency for Development and Cooperation (NORAD) and German Agency for

Technical Cooperation (GTZ) as well as through the Global Environment Facility (GEF).

As in St Helena Bay in the southern Benguela, the focus of sample analysis was on the copepods and only samples collected off Walvis Bay are considered here. This allowed reconstruction of a multi-decadal time-series, by merging data from the SWAPELS collection (1978–1989) and data from Namibia's ongoing Monthly Oceanographic Monitoring programme since 2000 along a cross-shelf transect off Walvis Bay at 23°S (Kreiner and Yemane, 2013; see Bode et al., 2014 for monitoring results on a transect at 20°S since 2005). The Walvis Bay dataset was further augmented by monthly observations of total zooplankton biomass (expressed as biovolume) for 1959 from Kollmer (1963) and copepod species abundance data for 1997 from an unpublished manuscript (Rippe and Tjédor, 1999). Although different samplers and sampling strategies were used during these sampling programmes (see Tsotsobe, 2005 for details), methodological differences were accounted for according to Verheye et al. (1998), which allowed combining the datasets to reconstruct a single, yet discontinuous, copepod time-series.

For numerical and taxonomic sample analyses, standard protocols published in the literature for the southern Benguela (see Verheye et al., 1998; Huggett et al., 2009) were generally followed to species and developmental stage level whenever possible. Copepod species abundances (No. m^{-2}) integrated over the sampling depth (max. 200 m) were log-transformed ($\text{Log}_{10}(\text{No. m}^{-2} + 1)$). For total zooplankton biomass, values of settled volume (SV) of the entire sample (ml m^{-2}) were converted to wet weight (g Wet Wt m^{-2}) assuming that $1 \text{ ml SV} = 1 \text{ g Wet Wt}$. Copepod biomass per sample was calculated by multiplying abundance of each taxon (No. m^{-2}) by their respective individual body mass ($\mu\text{g Dry Weight}$), using information from Richardson et al. (2001) and Huggett et al. (2009), then summed for all species and converted to carbon

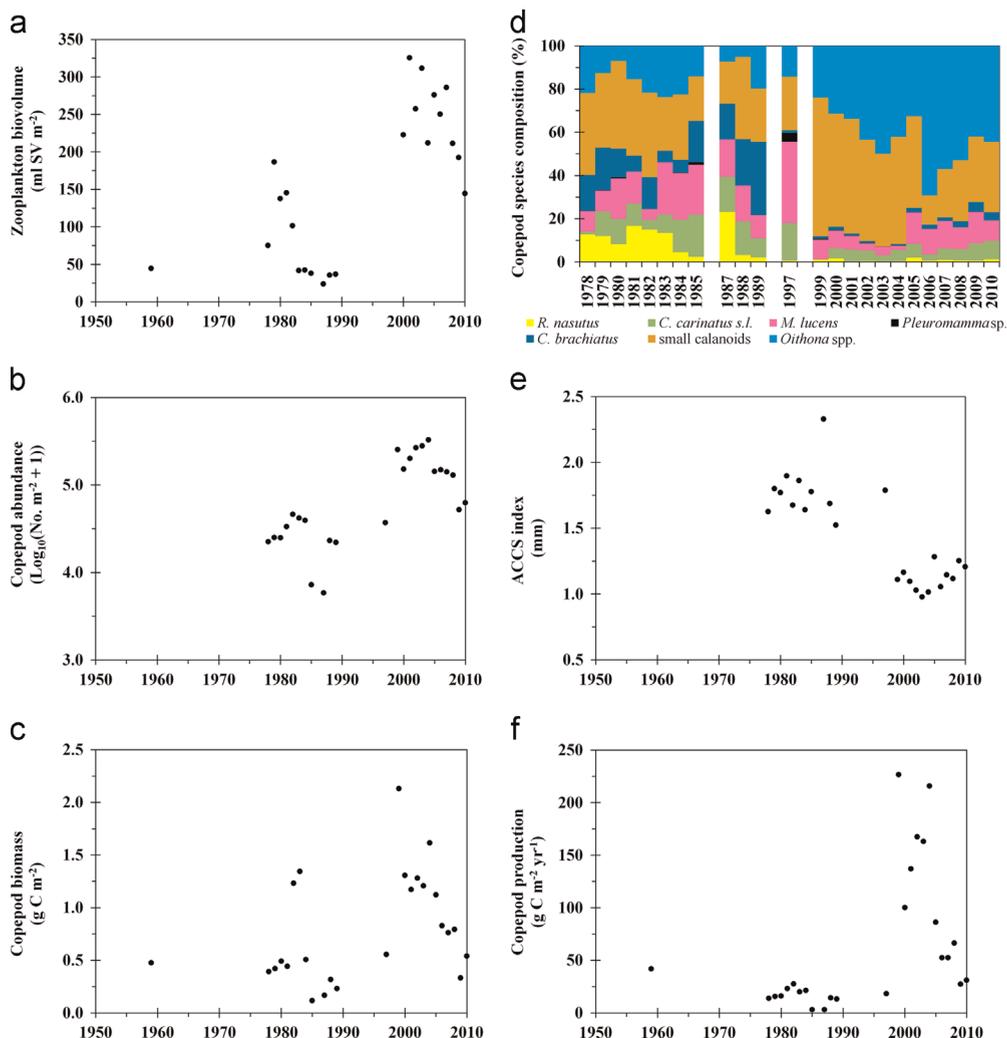


Fig. 6. Walvis Bay, northern Benguela: 1959–2010 time-series of year-to-year changes in (a) total zooplankton biomass (data for 1999 were excluded due to contamination of samples by gelatinous zooplankton) – updated from Verheye (2007), (b) total copepod abundance (log-transformed) – updated from Verheye and Kreiner (2009), (c) copepod biomass, (d) percentage copepod species composition (adults only) – updated from Verheye and Kreiner (2009), (e) average copepod community size (ACCS) index, and (f) annual copepod production. Data for 1959 in (c) and (f) were calculated using linear regression analysis between copepod biomass and zooplankton biovolume, and between copepod production and copepod biomass, respectively.

Table 1

Time-series averages (and ranges) of zooplankton biomass and copepod abundance, biomass and annual production for the late 1950s (1959), late 1970s–1980s and late 1990s–2000s in the northern Benguela, off Walvis Bay.

| Zooplankton metric | 1959 | Late 1970s–1980s | Late 1990s–2000s | 1959–2010 |
|--|-------------|----------------------|------------------------|-----------------------|
| Zooplankton biomass (g Wet Wt m ⁻²) | 44.5 (–) | 78.6 (23.9–186.6) | 244.6 (144.6–325.6) | 161.6 (23.9–325.6) |
| Copepod abundance (x10 ³ indiv. m ⁻²) | – | 26.4 (5.9–46.2) | 168.5 (36.9–327.6) | 103.4 (5.9–327.6) |
| Copepod biomass (g C m ⁻²) | 0.48 (–) | 0.52 (0.12–1.34) | 1.05 (0.33–2.13) | 0.81 (0.12–2.13) |
| Copepod production (g C m ⁻² yr ⁻¹) | 42.0 (–) | 15.6 (3.1–27.7) | 103.5 (18.4–226.6) | 63.2 (3.1–226.6) |

assuming a carbon:dry weight ratio of 40% for crustaceans (Lovegrove, 1966; Parsons et al., 1977). Copepod mean biomass per annum was derived by averaging summed species biomasses per sample for all samples collected in a given year, irrespective of time of year or distance offshore. Calanoid copepod production per sample was calculated by multiplying northern Benguela species- and stage-specific dry body mass (*BM*) values (from Richardson et al., 2001) by their respective size-specific daily growth rate (*g*) obtained from a non-linear model $g = 0.866 \times 10^{-0.075 BM}$ ($r^2 = 0.81$) fitted by Richardson et al. (2001) to empirical growth rate – body mass data for the northern Benguela over broad ranges of temperature and food conditions, and converted to carbon as described above. Production rates of cyclopoids (*Oithona* spp.) were estimated according to Huggett et al. (2009). Copepod mean annual production was derived by averaging summed species productions per sample for all samples collected in a given year, irrespective of time of year (month) or distance offshore. Time-series of the above metrics are shown in Fig. 6a–f while decade-specific ranges and means are summarised in Table 1. Copepod biomass and production data for 1959 were obtained from linear regression analysis between copepod biomass and zooplankton biovolume, and between copepod production and copepod biomass, respectively.

There has been a long-term increase in total zooplankton biomass from < 50 g Wet Wt m⁻² in the late 1950s to > 300 g Wet Wt m⁻² in the early 2000s, declining to < 150 g Wet Wt m⁻² in the late 2000s (Fig. 6a). Copepods showed a 10-fold increase in abundance and biomass from the late 1970s, until an all-time high around the early to mid-2000s (i.e. one decade later than in the southern Benguela), when the trend reversed, and biomass and abundance levels have since been declining (Fig. 6b, c). Interestingly, there was a sharp drop in both copepod metrics following the Benguela Niño event of 1984.

Concomitant with these abundance and biomass fluctuations, there was a shift in copepod community structure, from a large-species dominance in the 1970s–1980s (Fig. 6d), when biomass was low, to smaller species dominating the community during the 2000s, when biomass was higher. Most strikingly is the comparative prominence (up to 23% of total abundance) of the largest calanoid copepod, *R. nasutus*, during the 1980s followed by its quasi-disappearance from the samples during the 2000s. Likewise, large to medium species *C. carinatus* s.l., *M. lucens* and *C. brachiatus* were also much more prevalent during the 1980s (collectively 25–60%) than the early 2000s (< 10%), although an increase in dominance is evident from 2005 onward. Conversely, the smallest of species recorded, the cyclopoid *Oithona* spp., increased in dominance from < 25% of total copepod abundance during the 1980s to 30–70% during the early 2000s, then decreased again. Likewise, the small calanoid copepod species increased in relative abundance from 20–40% in the 1980s to 40–65% in the early 2000s, then declined to 15–30% in the late 2000s. These long-term changes in copepod community structure are clearly illustrated in the ACCS index time-series (Fig. 6e), with high index values of 1.5–2.3 mm during the 1970s–1980s, dropping to 1.0–1.3 mm during the 2000s.

Annual copepod production calculated over the past four decades was, on average, 63.2 g C m⁻² yr⁻¹ (Table 1). This is of the same magnitude as Cushing's (1971) pre-1970 estimates of 52 g C m⁻² yr⁻¹ (north of Walvis Bay) and 69 g C m⁻² yr⁻¹ (south of Walvis Bay) assuming perennial production. Given the observed changes in abundance, biomass and community structure, with species-specific body size being a most important determinant of individual growth rate, annual copepod production levels varied extensively both interannually and interdecadally (see Table 1). Initially, during the late 1970s and 1980s copepod production was very low (3–28 g C m⁻² yr⁻¹), but rose rapidly from 1997 until the mid-2000s to levels of 100–> 200 g C m⁻² yr⁻¹ (Fig. 6f), well above the empirical value of 39 g C m⁻² yr⁻¹ obtained by Richardson et al. (2001) for the northern Benguela during autumn 1997 and winter 1999. Production subsequently dropped steeply during the second half of the 2000s, to around 1980s levels of < 50 g C m⁻² yr⁻¹ by the end of the time-series (Fig. 6f).

Such changes in zooplankton communities are likely to have fundamental effects on biogeochemical processes, food web structure and ecosystem functioning of the BCLME. According to Hampton (2012), compared to the southern Benguela, there is no clear predator–prey relationship between pelagic fish and zooplankton in the northern Benguela, and although top-down control of zooplankton populations may well have occurred there until the collapse of pelagic fish stocks in the 1970s, its impact may subsequently have been insignificant given the persistently low planktivorous pelagic fish stocks off Namibia in the past few decades. Although the effective disappearance of anchovy from Namibian waters in the mid-1990s (Boyer

and Hampton, 2001) may expectedly have reduced predation pressure on copepod populations (Hampton, 2012), in particular the larger species, their preferred prey, these did not increase since then (Fig. 6c and f). Instead, major environmental perturbations, such as Benguela Niños (Shannon et al., 1986), are likely to have had more impact on zooplankton communities, e.g. after the 1984 event, when copepod abundance and biomass dropped steeply and only recovered 3–4 years later (Fig. 6b and c).

While it is apparent that total copepod abundances in the northern and southern Benguela increased over the past 5–6 decades, there is no evidence of synchrony in either duration or phasing of the low-frequency (inter-decadal) fluctuations observed in the two subsystems, despite relatively close proximity of their respective sampling sites. Likewise, while cumulative chlorophyll *a* indices for the northern and southern Benguela (Jarre et al., 2015) suggest an increase in surface chlorophyll *a* in the northern but not the southern Benguela, the most striking feature is the lack of synchrony between variations in the two sub-systems. Whether zooplankton show coherent temporal synchrony or teleconnectivity across very large spatial scales as well as between ocean basins (Perry et al., 2004), as seen in small pelagic fish in widely separated EBUSs (Kawasaki et al., 1991; Schwartzlose et al., 1999; Cury et al., 2000; Alheit and Bakun, 2010), was one of the motivations for the formation of SCOR Working Group 125 on *Global Comparison of Zooplankton Time Series* (Mackas et al., 2012). Based on an analysis of zooplankton biomass or abundance time-series data from > 100 sites world-wide, Batchelder et al. (2012) found moderate-to-strong positive correlation among neighbouring time-series locations, and a significant temporal synchrony at spatial scales up to 1000–3000 km. Unfortunately, because of the discontinuous nature and relatively poor data overlap of the two Benguela time-series, they could not be considered in their analyses.

5. Future basin-scale, long-term monitoring of plankton in the BCLME

While the caveats of using satellite-derived data for the continual monitoring and assessment of phytoplankton biomass and production are well known and globally accepted (Behrenfeld et al., 2006; Demarcq et al., 2007; Lamont, 2011; Weeks et al., 2006), remotely-sensed ocean colour measurements have been, and are likely to remain, the only cost- and time-effective means of obtaining *quasi*-synoptic observations over large spatial scales. Numerous investigations have shown the utility of satellite data in improving our understanding of phytoplankton biomass and production patterns at global, regional, and local scales, but the discrepancies in temporal variations and trends observed from satellite *vs in situ* data emphasises the necessity for continued and systematic collection of *in situ* data at multiple spatial and temporal scales. Likewise, the limited capability of satellite observations to provide adequate representations of sub-surface patterns and changes further stresses the requirement of water-column measurements, throughout the upper mixed layer and euphotic zone, in particular.

Unlike satellites or costly local-scale research cruises, the Continuous Plankton Recorder (CPR) collects phytoplankton and zooplankton abundance and community structure data over large temporal and spatial scales. The CPR is a robust, tried and tested, cost-effective plankton sampling device deployed at high speeds (> 20 knots) from commercial ships-of-opportunity on their normal trading routes. Designed by Sir Alister Hardy (1896–1985) to sample Antarctic krill on the *Discovery* cruises of 1925–27, CPRs have after only minor modification been deployed since 1931 in the North Sea and subsequently in many other parts of the world's oceans, including the BCLME (since late 2011), to map changes in abundance, distribution and species composition of plankton assemblages (Reid et al., 2010). Despite several biases associated with CPR sampling and data (see Richardson et al., 2006), results from CPR surveys are globally used by marine scientists, research institutes and governments in environmental change studies to address marine environmental management issues such as sustainable fisheries, biodiversity loss, pollution, eutrophication, HABs, the introduction of alien species, invasive species, ocean acidification, and global climate change. While samples from CPR tows in the BCLME are currently being analysed, preliminary results (e.g. the occurrence of several species of the genus *Dinophysis* responsible for diarrhetic shellfish poisoning; fish eggs and larvae; and micro-plastics) already indicate the potential of using CPR data as an essential contribution to ecosystem-based management of the BCLME. In addition, the recent detection in CPR samples from the BCLME of the bacterium *Vibrio cholerae* (hosted by crustacean zooplankton), the causative agent of epidemic cholera, highlights the usefulness and value of CPR surveys in studies of the origin and proliferation of the disease in endemic areas for cholera such as the BCLME (Vezzulli et al., 2015).

Whereas microscope analysis of species composition, dry mass measurements and bottle incubations have formed the mainstay of zooplankton biomass and secondary production measurements over the past 50–60 years in the BCLME, a number of new techniques and technologies have emerged that could improve upon, or supplement, our existing methodology. Multi-frequency acoustic samplers (e.g. Holliday et al., 1989; Lebourges-Dhaussy et al., 2009) and optical samplers (e.g. Vanderploeg and Roman, 2006; Vandromme et al., 2014) are now available commercially or institutionally for moored or *in situ* applications, and bench-top instruments such as the FlowCAM (Sieracki et al., 1998) and ZooScan (Grosjean et al., 2004; Gorsky et al., 2010) offer semi-automated image analysis, including enumeration and biometric analysis, of nano- to microplankton, and mesozooplankton, respectively. The chitobiase assay (Oosterhuis et al., 2000; Sastri and Roff, 2000) is a promising biochemical tool for assessing *in situ* crustacean secondary production, and DNA barcoding (Hebert et al., 2003) is increasingly being used to identify zooplankton (e.g. Bucklin et al., 2010).

6. General conclusion

While upwelling-favourable winds have generally increased in summer in the northern and southern Benguela sub-systems over the past few decades, there is – contrary to expectation – a lack of evidence of an ecosystem-wide, long-term increase in primary production in response to changed wind fields, calling into question a direct link between the wind field and phytoplankton production on a large scale in the BCLME. Neritic copepods have, however, increased in abundance by at least one order of magnitude since the 1950s–1960s in both sub-systems over the same period, with turning points reached asynchronously, around the mid-1990s in the southern Benguela and the mid-2000s in the northern Benguela, when abundances in both declined again. There was also a concomitant gradual shift in prevalence from large to smaller species in both sub-systems, which typically would suggest ocean warming in the BCLME as a whole. While this seems to be in agreement with observed widespread surface warming in the northern Benguela and at the BCLME frontal boundaries in the north and south, it is in contrast to the general cooling of coastal waters observed in the southern Benguela. At the same time, there has been a marked increase in planktivorous pelagic fish populations (sardine and anchovy), notably in the southern Benguela. Whether the observed changes in the zooplankton are mainly due to bottom-up (primary production) or top-down (predation) effects, or both, and in the latter case, what the relative importance of these forcing mechanisms is, remains unclear.

While it is tempting to conclude that the observed changes in the plankton in the entire BCLME can be seen as a response to a common long-term change in ocean climate, such a conclusion is premature based on current evidence for the following reasons (Hampton, 2012): the effects of the different pelagic fishing histories in the two sub-systems are confounding; regional differences in the relative importance of bottom-up and top-down plankton forcing mechanisms may exist; and independent evidence of a common long-term environmental change over the time period considered here is lacking. Therefore, continued monitoring of the oceanography, chlorophyll, phytoplankton cell size, primary production and the zooplankton food base for supporting the fisheries resources of the BCLME as well as the socio-economic and food security benefits to the people of Angola, Namibia and South Africa is of paramount importance. Essential basic technology such as satellites providing synoptic sea surface ocean colour, and regular ecosystem-wide CPR surveys mapping near-surface phyto- and zooplankton assemblages should be augmented by systematic deployments of simple plankton nets of appropriate mesh size (Koslow and Couture, 2013) and optical instrumentation in key areas of the BCLME to monitor a wider selection of the ichthyoplankton and zooplankton communities. Such quantitative monitoring and assessment are necessary to support appropriate actions by the BCC to advance sustainable development of BCLME goods and services.

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References

- Alheit, J., Bakun, A., 2010. Population synchronies within and between ocean basins: apparent teleconnections and implications as to physical-biological linkage mechanisms. *J. Mar. Syst.* 79, 267–285.
- Anon, 1997. BENEFIT Science Plan. BENEFIT Secretariat, Windhoek, Namibia, 90pp.
- Anon, 1999. Benguela Current Large Marine Ecosystem Programme: Transboundary Diagnostic Analysis UNDP/GEF/UNOPS, 51pp.
- Barlow, R.G., 1982a. Phytoplankton ecology in the southern Benguela current. I. Biogeochemical composition. *J. Exp. Mar. Biol. Ecol.* 63, 209–227.
- Barlow, R.G., 1982b. Phytoplankton ecology in the southern Benguela current. II. Carbon assimilation patterns. *J. Exp. Mar. Biol. Ecol.* 63, 229–237.
- Barlow, R.G., 1982c. Phytoplankton ecology in the southern Benguela current. III. Dynamics of a bloom. *J. Exp. Mar. Biol. Ecol.* 63, 239–248.
- Barlow, R., Sessions, H., Balarin, M., Weeks, S., Whittle, C., Hutchings, L., 2005. Seasonal variation in phytoplankton in the southern Benguela: pigment indices and ocean colour. *Afr. J. Mar. Sci.* 27, 275–287.
- Barlow, R., Louw, D., Balarin, M., Alheit, J., 2006. Pigment signatures of phytoplankton composition in the northern Benguela ecosystem during spring. *Afr. J. Mar. Sci.* 28, 479–491.
- Barlow, R.G., Lamont, T., Mitchell-Innes, B., Lucas, M., Thomalla, S., 2009. Primary production in the Benguela ecosystem, 1999–2002. *Afr. J. Mar. Sci.* 31, 97–101.
- Batchelder, H.P., Mackas, D.L., O'Brien, T.D., 2012. Spatial-temporal scales of synchrony in marine zooplankton biomass and abundance patterns: a worldwide comparison. In: Pepin, P., Mackas, D. and H. Verheye (Eds.), *Global Comparisons of Zooplankton Time Series*. Prog. Oceanogr. 97–100, 15–30.
- Batten, S.D., Chiba, S., Edwards, M., Hall, J., Hosie, G., Melrose, C., Muxagata, E., Richardson, A.J., Verheye, H.M., Helaouet, P., Rochester, W., Stevens, D., 2015. The Status of Zooplankton Populations. In: UNEP 2015 and IOC-UNESCO, *The Open Ocean: Status and Trends vol. 5*. United Nations Environment Programme, Nairobi, Kenya.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664.
- Behrenfeld, M.J., Falkowski, P.G., 1997. A consumer's guide to phytoplankton primary productivity models. *Limnol. Oceanogr.* 42, 1479–1491.

- Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444, 752–755.
- Belkin, I.M., 2009. Rapid warming of Large Marine Ecosystems. *Prog. Oceanogr.* 81, 207–213.
- Blamey, L.K., Howard, J.A.E., Agenbag, J., Jarre, A., 2012. Regime-shifts in the southern Benguela shelf and inshore region. *Prog. Oceanogr.* 106, 80–95.
- Blamey, L.K., Shannon, L.J., Bolton, J.J., Crawford, R.J.M., Dufois, F., Evers-King, H., Griffiths, C.L., Hutchings, L., Jarre, A., Rouault, M., Watermeyer, K.E., Winker, H., 2015. Ecosystem change in the southern Benguela and the underlying processes. *J. Mar. Syst.* 144, 9–29.
- Bode, M., Kreiner, A., van der Plas, A.K., Louw, D.C., Horaeb, R., Auel, H., Hagen, W., 2014. Spatio-temporal variability of copepod abundance along the 20°S monitoring transect in the northern Benguela upwelling system from 2005 to 2011. *PLoS ONE* 9 (5), e97738, <http://dx.doi.org/10.1371/journal.pone.0097738>.
- Botes, L., Sym, S.D., Pitcher, G.C., 2003. *Karenia cristata* sp. nov. and *Karenia bicuneiformis* sp. nov. (Gymnodiniales, Dinophyceae): two new *Karenia* species from the South African coast. *Phycologia* 42, 563–571.
- Boyer, D.C., Hampton, I., 2001. An overview of the living marine resources of Namibia. *S. Afr. J. Mar. Sci.* 23, 5–35.
- Brown, P.C., 1984. Primary productivity at two contrasting nearshore sites in the southern Benguela upwelling region. *S. Afr. J. Mar. Sci.* 2, 205–215.
- Brown, P.C., 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the euphotic zone in the southern Benguela/Agulhas ecosystem. In: Payne, A.I.L., K.H. Brink, K.H. Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. *S. Afr. J. Mar. Sci.* 12, 515–525.
- Brown, P.C., Field, J.G., 1985. Diel variation in production rates of natural phytoplankton populations in the southern Benguela upwelling system. *Bot. Mar.* 28, 201–208.
- Brown, P.C., Field, J.G., 1986. Factors limiting phytoplankton production in a nearshore upwelling area. *J. Plankton Res.* 8, 55–68.
- Brown, P.C., Hutchings, L., 1987a. The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 1. Drogue movements, hydrography and bloom development. In: Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.), *The Benguela and Comparable Ecosystems*. *S. Afr. J. Mar. Sci.* 5, 357–391.
- Brown, P.C., Hutchings, L., 1987b. The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 2. Nutrient relationships. In: Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.), *The Benguela and Comparable Ecosystems*. *S. Afr. J. Mar. Sci.* 5, 393–409.
- Brown, P.C., Painting, S.J., Cochrane, K., 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *S. Afr. J. Mar. Sci.* 11, 537–564.
- Bucklin, A., Ortman, B.D., Jennings, R.M., Nigro, L.M., Sweetman, C.J., Copley, N.J., Sutton, T., Wiebe, P.H., 2010. A “Rosetta Stone” for metazoan zooplankton: DNA barcode analysis of species diversity of the Sargasso Sea (Northwest Atlantic Ocean). *Deep-Sea Res. II* 57, 2234–2247.
- Cockcroft, A.C., 2001. *Jasus lalandii* ‘walkouts’ or mass strandings in South Africa during the 1990s: an overview. *Mar. Freshw. Res.* 52, 1085–1093.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre-Teichmann, A., Quinones, R., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci., Symp. Ed.* 57 (3), 603–618.
- Cushing, D.H., 1971. Upwelling and the production of fish. *Adv. Mar. Biol.* 9, 255–334.
- DEA (Department of Environmental Affairs), 2015. State of the Oceans and Coasts Around South Africa Report 2014. Verheye, H., Crawford, R. (Eds.), Department of Environmental Affairs, Oceans and Coasts, Report no. 13, March 2015, Cape Town, 40 pp.
- Demarcq, H., 2009. Trends in primary production, sea surface temperature and wind in upwelling systems (1998–2007). *Prog. Oceanogr.* 83, 376–385.
- Demarcq, H., Barlow, R.G., Hutchings, L., 2007. Application of a chlorophyll index derived from satellite data to investigate the variability of phytoplankton in the Benguela ecosystem. *Afr. J. Mar. Sci.* 29, 271–282.
- Demarcq, H., Barlow, R.G., Shillington, F.A., 2003. Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as observed by satellite imagery. *Afr. J. Mar. Sci.* 25, 363–372.
- de Villiers, S., 1998. Seasonal and interannual variability in phytoplankton biomass on the southern African continental shelf: evidence from satellite-derived pigment concentrations. *S. Afr. J. Mar. Sci.* 19, 169–180.
- Duncombe Rae, C.M., 2005. A demonstration of the hydrographic partition of the Benguela upwelling ecosystem at 26°40'S. *Afr. J. Mar. Sci.* 27, 617–628.
- Estrada, M., Marrasé, C., 1987. Phytoplankton biomass and productivity off the Namibian coast. In: Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.), *The Benguela and Comparable Ecosystems*. *S. Afr. J. Mar. Sci.* 5, 347–356.
- Fraser, J., 1962. *Nature Adrift. The Story of Marine Plankton*, 178. G.T. Foulis & Co, London.
- Gibbons, M.J., Hutchings, L., 1996. Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *S. Afr. J. Mar. Sci.* 92, 63–76.
- Gibbons, M.J., Stuart, V., Verheye, H.M., 1992. Trophic ecology of carnivorous zooplankton in the Benguela. In: Payne, A.I.L., K.H. Brink, K.H. Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. *S. Afr. J. Mar. Sci.* 12, 421–437.
- Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemman, L., Romagnan, J.-B., Cawood, A., Pesant, S., García-Comas, C., Prejger, F., 2010. Digital zooplankton image analysis using the ZooScan integrated system. *J. Plankton Res.* 32 (3), 285–303.
- Grosjean, P., Picheral, M., Warembourg, C., Gorsky, G., 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOOscan digital imaging system. *ICES J. Mar. Sci.* 61, 518–525, <http://dx.doi.org/10.1016/j.icesjms.2004.03.012>.
- Hampton, I., 2012. Biophysical features and trends in the Benguela Current Large Marine Ecosystem (rapporteurs). In: *Proceedings of the FAO/Benguela Current Commission Workshop on Climate Change Implications for Fisheries of the Benguela Current Region: Making the Best of Change*. FAO Fisheries and Aquaculture Proceedings. vol. 27, pp. 79–125.
- Hansen, F.C., Cloete, R.R., Verheye, H.M., 2005. Seasonal and spatial variability of dominant copepods along a transect off Walvis Bay (23°S), Namibia. *Afr. J. Mar. Sci.* 27 (1), 55–63.
- Hardman-Mountford, N.J., Richardson, A.J., Agenbag, J.J., Hagen, E., Nykjaer, L., Shillington, F.A., Villacastin, C., 2003. Ocean climate of the South East Atlantic observed from satellite data and wind models. *Prog. Oceanogr.* 59, 181–221.
- Hebert, P.D.N., Ratnasingham, S., deWaard, J.R., 2003. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proc. R. Soc. Lond. B (Suppl.)* DOI 10.1098/rsbl.2003.0025.
- Holliday, D.V., Pieper, R.E., Kleppel, G.S., 1989. Determination of zooplankton size and distribution with multifrequency acoustic technology. *Journal du Conseil International pour l'Exploration de la Mer* 46, 52–61.
- Howard, J., Jarre, A., Clarke, A., Moloney, C.L., 2007. Application of the sequential t-test algorithm for analyzing regime shifts to the southern Benguela ecosystem. *Afr. J. Mar. Sci.* 29, 437–451.
- Huggett, J., Verheye, H., Escribano, R., Fairweather, T., 2009. Copepod biomass, size composition and production in the Southern Benguela: spatio-temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Prog. Oceanogr.* 83, 197–207.
- Hutchings, L., Pillar, S.C., Verheye, H.M., 1991. Estimates of standing stock, production and consumption of meso- and macro-zooplankton in the Benguela ecosystem. *S. Afr. J. Mar. Sci.* 11, 499–512.
- Hutchings, L., Verheye, H.M., Huggett, J.A., Demarcq, H., Cloete, R., Barlow, R.G., Louw, D., da Silva, A., 2006. Variability of Plankton with Reference to Fish Variability in the Benguela Current Large Marine Ecosystem – An overview. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., Woods, J. (Eds.), . 14. Elsevier, Amsterdam, pp. 111–146.
- Hutchings, L., Verheye, H.M., Mitchell-Innes, B.A., Peterson, W.T., Huggett, J.A., Painting, S.J., 1995. Copepod production in the southern Benguela system. *ICES J. Mar. Sci.* 52, 439–455.
- Hutchings, L., Barange, M., Bloomer, S.F., Boyd, A.J., Crawford, R.J.M., Huggett, J.A., Kerstan, M., Korrübel, J.L., De Oliveira, J.A.A., Painting, S.J., Richardson, A.J., Shannon, L.J., Schüle, F.H., van der Lingen, C.D., Verheye, H.M., 1998. Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. *S. Afr. J. Mar. Sci.* 19, 211–225.
- Hutchings, L., Roberts, M.R., Verheye, H.M., 2009a. Marine environmental monitoring programmes in South Africa: a review. *S. Afr. J. Sci.* 105, 94–102.
- Hutchings, L., van der Lingen, C.D., Shannon, L.J., Crawford, R.J.M., Verheye, H.M.S., Bartholomae, C.H., van der Plas, A.K., Louw, D., Kreiner, A., Ostrowski, M.,

- Fidel, Q., Barlow, R.G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J.C., Monteiro, P.M.S., 2009b. The Benguela Current: an ecosystem of four components. *Prog. Oceanogr.* 83, 15–32.
- Hutchings, L., Jarre, A., Lamont, T., van den Berg, M., Kirkman, S.P., 2012. St Helena Bay (southern Benguela) then and now: muted climate signals, large human impact. *Afr. J. Mar. Sci.* 34 (4), 559–583.
- James, A.G., 1987. Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In: Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.), *The Benguela and Comparable Ecosystems*. S. Afr. J. Mar. Sci. 5, 673–692.
- Jarre, A., Hutchings, L., Kirkman, S.P., Kreiner, A., Tchikalanga, P., Kainge, P., Uanivi, U., van der Plas, A., Blamey, L.K., Coetzee, J., Lamont, T., Samaai, T., Verheye, H.M., Yemane, D.G., Axelsen, B.E., Ostrowski, M., Stenevik, E.K., Loeng, H., 2015. Synthesis: climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fish. Oceanogr.* 24 (Suppl. 1), S122–S149.
- Kawasaki, T., Tanaka, S., Toba, Y., Taniguchi, A. (Eds.), 1991. Long-term variability of pelagic fish populations and their environment. In: *Proceedings of the International Symposium, Sendai, Japan 14–18 November 1989*. Pergamon Press, Exeter, UK, 402pp.
- Kollmer, W.E., 1963. The pilchard of South West Africa (*Sardinops ocellata*). Notes on zooplankton and phytoplankton collections made off Walvis Bay. *Invest. Rep. Mar. Res. Lab. S. West Afr.* 8, 78.
- Koné, V., Machu, E., Penven, P., Anderson, V., Garçon, V., Fréon, P., Demarcq, H., 2005. Modelling the primary and secondary productions of the southern Benguela upwelling system: A comparative study through two biogeochemical models. *Glob. Biogeochem. Cycles* 19 (4), <http://dx.doi.org/10.1029/2004GB002427>. GB4021.
- Koslow, J.A., Couture, J., 2013. Follow the fish. A global, long-term programme of ecological monitoring is needed to track ocean health. *Nature* 502, 163–164.
- Kreiner, A., Yemane, D., 2013. Spatial and temporal variability of copepod communities along a monitoring transect in the Northern Benguela from 2000 to 2010 in relation to environmental parameters Annual Research Meeting: “From monitoring to Science”, Ministry for Fisheries and Marine Resources, Swakopmund, pp. 262–276.
- Lamont, T., 2011. Bio-optical Investigation of Phytoplankton Production in the Southern Benguela Ecosystem. Ph.D. Thesis. University of Cape Town 129pp.
- Lamont, T., Barlow, R.G., Kyewalyanga, M.S., 2014. Physical drivers of phytoplankton production in the southern Benguela upwelling system. *Deep-Sea Res. I* 90, 1–16.
- Lamont, T., Hutchings, L., van den Berg, M.A., Goschen, W.S., Barlow, R.G., 2015. Hydrographic variability in the St. Helena Bay region of the southern Benguela ecosystem. *J. Geophys. Res.* Oceans 120, 2920–2944. <http://dx.doi.org/10.1002/2014JC010619>.
- Lebourges-Dhaussy, A., Coetzee, J., Hutchings, L., Roudat, G., Nieuwenhuys, C., 2009. Zooplankton spatial distribution along the South African coast studied by multifrequency acoustics, and its relationships with environmental parameters and anchovy distribution. *ICES J. Mar. Sci.* 66, 1055–1062.
- Lett, C., Veitch, J., van der Lingen, C., Hutchings, L., 2007. Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.* 347, 247–259.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith, P.E., 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* 8, 195–205.
- Lluch-Belda, D., Schwartzlose, R.A., Serra, R., Parrish, R.H., Kawasaki, T., Hedgecock, D., Crawford, R.J.M., 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.* 1 (4), 339–347.
- Lovegrove, T., 1966. The determination of the dry weight of plankton and the effect of various factors on the value obtained. In: Barnes, H. (Ed.), *Some Contemporary Studies in Marine Science*, George Allen and Unwin, London, pp. 429–467.
- Lucas, M.I., Probyn, T.A., Painting, S.J., 1987. An experimental study of dinoflagellate bacterivory: further evidence for the importance and complexity of microplanktonic interactions. In: Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.), *The Benguela and Comparable Ecosystems*. S. Afr. J. Mar. Sci. 5, 791–810.
- Mackas, D.L., Pepin, P., Verheye, H., 2012. Interannual variability of marine zooplankton and their environments: within- and between region comparisons. In: Pepin P., Mackas D. and H. Verheye (Eds.), *Global Comparisons of Zooplankton Time Series*. *Prog. Oceanogr.* 97–100, 1–14.
- Matthews, S.G., Pitcher, G.C., 1996. Worst recorded marine mortality on the South African coast. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*, Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 89–92.
- Mitchell-Innes, B.A., Pitcher, G.C., Probyn, T.A., 2000. Productivity of dinoflagellate blooms on the west coast of South Africa, as measured by natural fluorescence. *S. Afr. J. Mar. Sci.* 22, 273–284.
- Mitchell-Innes, B.A., Walker, D.R., 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system. *Phytoplankton production and biomass in relation to species changes*. *Prog. Oceanogr.* 28, 65–89.
- Moloney, C.L., van der Lingen, C.D., Hutchings, L., Field, J.G., 2004. Contributions of the Benguela Ecology Programme to pelagic fisheries management in South Africa. *Afr. J. Mar. Sci.* 26, 37–51.
- Monteiro, P.M.S., van der Plas, A.K., 2006. Low oxygen water (LOW) variability in the Benguela ecosystem: key processes and forcing scales relevant to forecasting. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., Woods, J. (Eds.), *Benguela: Predicting a Large Marine Ecosystem*. *Large Marine Ecosystems* 14, Elsevier, Amsterdam, pp. 71–90.
- Oosterhuis, S., Baars, M.A., Klein Breteler, W.C.M., 2000. Release of the enzyme chitinase by the copepod *Temora longicornis*: characteristics and potential tool for estimating crustacean biomass production in the sea. *Mar. Ecol. Prog. Ser.* 196, 195–206.
- Painting, S.J., Lucas, M.I., Muir, D.G., 1989. Fluctuations in heterotrophic bacterial community structure, activity and production in response to development and decay of phytoplankton in a microcosm. *Mar. Ecol. Prog. Ser.* 53, 129–141.
- Painting, S.J., Moloney, C.L., Probyn, T.A., Tibbles, B., 1992. Microheterotrophic pathways in the southern Benguela upwelling regions. In: Payne, A.I.L., K.H. Brink, K.H. Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. S. Afr. J. Mar. Sci. 12, 527–543.
- Parsons, T.R., Takahashi, M., Hargrave, B., 1977. *Biological Oceanographic Processes*, second ed Pergamon, Oxford, 489.
- Pepin, P., Mackas, D., Verheye, H. (Eds.), 2012. *Global Comparison of Zooplankton Time Series*. *Progress in Oceanography*, 97–100, 1–186.
- Perry, R.I., Batchelder, H.P., Mackas, D.L., Chiba, S., Durbin, E., Greve, W., Verheye, H.M., 2004. Identifying global synchronies in marine zooplankton populations: issues and opportunities. *ICES J. Mar. Sci.* 61, 445–456.
- Pillar, S.C., 1986. Temporal and spatial variations in copepod and euphausiid biomass off the southern and south-western coasts of South Africa in 1977/78. *S. Afr. J. Mar. Sci.* 4, 219–229.
- Pillar, S.C., Stuart, V., Barange, M., Gibbons, M.J., 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. In: Payne, A.I.L., K.H. Brink, K.H. Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. S. Afr. J. Mar. Sci. 12, 393–409.
- Pitcher, G.C., Bernard, S., Ntuli, J., 2008. Contrasting bays and red tides in the southern Benguela upwelling system. *Oceanography* 21, 82–91.
- Pitcher, G.C., Boyd, A.J., 1996. Cross-shelf and alongshore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*, Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 243–246.
- Pitcher, G.C., Boyd, A.J., Horstman, D.A., Mitchell-Innes, B.A., 1998. Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Mar. Ecol. Prog. Ser.* 172, 253–264.
- Pitcher, G.C., Brown, P.C., Mitchell-Innes, B.A., 1992. Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. In: Payne, A.I.L., K.H. Brink, K.H. Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. S. Afr. J. Mar. Sci. 12, 439–456.
- Pitcher, G.C., Cockcroft, A.C., 1998. Low oxygen, rock lobster strandings and PSP. In: Wyatt, T. (Ed.), *Harmful Algae News* No. 17, Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 1–3.
- Pitcher, G.C., Pillar, S., 2010. Harmful algal blooms in eastern boundary upwelling systems. *Prog. Oceanogr.* 85, 1–4.
- Pitcher, G.C., Probyn, T., 2011. Anoxia in the southern Benguela during the autumn of 2009 and its linkage to a bloom of the dinoflagellate *Ceratium balechii*. *Harmful Algae* 11, 23–32.

- Pitcher, G.C., Weeks, S., 2006. The variability and potential for prediction of harmful algal blooms in the southern Benguela Current. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C.L., Woods, J. (Eds.), *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14, 14. Elsevier, Amsterdam, pp. 125–146.
- Pitcher, G.C., Probyn, T.A., du Randt, A., Lucas, A.J., Bernard, S., Evers-King, H., Lamont, T., Hutchings, L., 2014. Dynamics of oxygen depletion in the nearshore of a coastal embayment of the southern Benguela upwelling system. *J. Geophys. Res. Oceans* 119, 2183–2200, <http://dx.doi.org/10.1002/2013JC009443>.
- Probyn, T.A., Pitcher, G.C., Monteiro, P.M.S., Boyd, A.J., Nelson, G., 2000. Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. *S. Afr. J. Mar. Sci.* 22, 285–297.
- Reid, P.C., Batten, S., Burkhill, P., Carlotti, F., Chiba, S., Conversi, A., Dickson, R., Dooley, H., Edwards, M., Flinkman, J., Goes, J., Greene, C.H., Hare, J., Hays, G., Head, E., Hood, R., Hosie, G., Hunt, B., John, T., Jonas, T., Jossie, J., Kirby, R., Kitchener, J., Kobayashi, D., Lakkis, S., Llope, M., MacDiarmid, A., McQuatters-Gollop, A., Malone, T., Matondkar, P., Richardson, A., Robinson, K., Stenseth, N.C., Sugisaki, H., Stevens, D., Verheye, H.M., Vezzulli, L., 2010. A global Continuous Plankton Recorder programme. In: Hall, J., Harrison, D.E., Stammer, D. (Eds.), *Proceedings of Ocean Obs'09: Sustained Ocean Observations and Information for Society* (vol. 2), Venice, Italy, 21–25 September 2009, 306. , ESA Publication WPP.
- Richardson, A.J., Verheye, H.M., Herbert, V., Rogers, C., Arendse, L.M., 2001. Egg production, somatic growth and productivity of copepods in the Benguela Current system and Angola-Benguela Front. *S. Afr. J. Sci.* 97, 251–257.
- Richardson, A.J., Walne, A.W., John, A.W.G., Jonas, T.D., Lindley, J.A., Sims, D.W., Stevens, D., Witt, M., 2006. Using continuous plankton recorder data. *Prog. Oceanogr.* 68, 27–74.
- Rippe, L., Téjedor, M.F., 1999. Mesozooplankton community structure and standing stock off Central Namibia during early upwelling season (unpublished manuscript).
- Rouault, M., Penven, P., Pohl, B., 2009. Warming of the Agulhas Current since the 1980s. *Geophys. Res. Lett.* 36, L12602, <http://dx.doi.org/10.1029/2009GL037987>.
- Rouault, M., Pohl, B., Penven, P., 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *Afr. J. Mar. Sci.* 32, 237–246.
- Sastri, A.R., Roff, J.C., 2000. Rate of chitobiase degradation as a measure of development rate in planktonic Crustacea. *Can. J. Fish. Aquat. Sci.* 57, 1965–1968.
- Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., Nevarez-Martinez, M.O., Parrish, H., Roy, C., Serra, R., Shust, K.V., Ward, M.N., Zuzunaga, J.Z., 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* 21, 289–347.
- Shannon, L.J., Jarre, A., Petersen, S., 2010. Developing a science base for an ecosystem approach to fisheries in the Benguela. *Prog. Oceanogr.* 87, 289–303.
- Shannon, L.V., 1985. The Benguela ecosystem Part I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Annu. Rev.* 23, 105–182.
- Shannon, L.V., Boyd, A.J., Brundrit, G.B., Taunton-Clark, J., 1986. On the existence of an El-Niño type phenomenon in the Benguela system. *J. Mar. Syst.* 44 (3), 495–520.
- Shannon, L.V., Field, J.G., 1985. Are fish stocks food-limited in the southern Benguela pelagic ecosystem? *Mar. Ecol. Prog. Ser.* 22, 7–19.
- Shannon, L.V., Nelson, G., 1996. The Benguela: Large scale features and processes and system variability. In: Wefer, G., Berger, H., Siedler, G., Webb, D.J. (Eds.), *The South Atlantic: Present and Past Circulation*, Springer-Verlag, Berlin, pp. 163–210.
- Shannon, L.V., Pillar, S.C., 1986. The Benguela ecosystem Part III. Plankton. *Oceanogr. Mar. Biol. Annu. Rev.* 24, 65–170.
- Sherman, K., Hempel, G. (Eds.), 2009. The UNEP Large Marine Ecosystem Report: a perspective on changing conditions in LMEs of the world's Regional Seas. UNEP Regional Seas Report and Studies no. 182. United Nations Environment Programme, Nairobi, Kenya.
- Sieracki, C.K., Sieracki, M.E., Yentsch, C.S., 1998. An imaging-in-flow system for automated analysis of marine microplankton. *Mar. Ecol. Prog. Ser.* 168, 285–296.
- Thomas, A.C., Carr, M.-E., Strub, P.T., 2001. Chlorophyll variability in Eastern Boundary Currents. *Geophys. Res. Lett.* 28, 3421–3424.
- Thomas, A.C., Strub, P.T., Carr, M.-E., Weatherbee, R., 2003. Comparison of chlorophyll variability between the four major eastern boundary currents. *Int. J. Remote Sens.* 24, 1–5.
- Timonin, A.G., Arashkevich, E.G., Drits, A.V., Semenova, T.N., 1992. Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod *Calanoides carinatus*. In: Payne, A.L.L., K.H. Brink, K.H., Mann and R. Hilborn (Eds.), *Benguela Trophic Functioning*. *S. Afr. J. Mar. Sci.* 12, 545–560.
- Tsotsobe, S.V., 2005. Temporal and spatial variability in copepod abundance, distribution and community structure off Walvis Bay in the northern Benguela Current, 1979–1981. M.Sc. Thesis. 113. University of Cape Town.
- Unterüberbacher, H.K., 1964. The Pilchard of South West Africa (*Sardinops ocellata*). Zooplankton studies in the waters off Walvis Bay with special reference to the copepod. Investigational Report of the Marine Research Laboratory South West Africa, 11, 42 pp.
- van der Lingen, C.D., 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *S. Afr. J. Mar. Sci.* 24, 301–316.
- van der Lingen, C.D., Huggett, J.A., 2003. The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In: Browman, H.I., Skiftesvik, A.B. (Eds.), *The Big Fish Bang*. In: *Proceedings of the 26th Annual Larval Fish Conference*. Institute of Marine Research, Norway, pp. 303–343.
- Vanderploeg, H.A., Roman, M.R., 2006. Introduction to special section on analysis of zooplankton distributions using the Optical Plankton Counter. *J. Geophys. Res.* 111, C05S01, <http://dx.doi.org/10.1029/2006JC003598>.
- Vandromme, P., Nogueira, E., Huret, M., Lopez-Urrutia, Á., González-Nuevo González, G., Sourisseau, M., Petitgas, P., 2014. Springtime zooplankton size structure over the continental shelf of the Bay of Biscay. *Ocean Sci.* 10, 821–835, <http://dx.doi.org/10.5194/os-10-821-2014>.
- Veitch, J., Florenchie, P., Shillington, F.A., 2006. Seasonal and interannual fluctuations of the Angola-Benguela Frontal Zone (ABFZ) using 4.5 km resolution satellite imagery from 1982–1999. *Int. J. Remote Sens.* 27, 987–998.
- Veitch, J., Penven, P., Shillington, F., 2009. The Benguela: a laboratory for comparative modelling studies. *Prog. Oceanogr.* 83, 296–302.
- Verheye, H.M., 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Abundance, distribution and estimated production of mesozooplankton with special reference to *Calanoides carinatus* (Krøyer, 1849). *Prog. Oceanogr.* 28, 91–119.
- Verheye, H.M., 2000. Decadal-scale trends across several marine trophic levels in the southern Benguela upwelling system off South Africa. *Ambio* 29 (1), 30–34.
- Verheye, H.M., Hutchings, L., Huggett, J.A., Painting, S.J., 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. In: Payne, A.L.L., Brink, K.H., Mann, K.H., Hilborn, R. (Eds.), *Benguela Trophic Functioning*. *S. Afr. J. Mar. Sci.* 12, 561–584.
- Verheye, H.M., Richardson, A.J., 1998. Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951–1996): bottom-up or top-down control? In: Colijn, F., Tillmann, U. and T. Smayda (Eds.), *The temporal variability of plankton and their physico-chemical environment*. *ICES J. Mar. Sci.* 55, 803–807.
- Verheye, H.M., 2007. Retrospective analysis of plankton community structure in the Benguela Current Large Marine Ecosystem (BCLME), to provide an index of long-term changes in the ecosystem. Final report BCLME. Project EV/PROVARE/02/05. 73pp.
- Verheye, H., Kreiner, A., 2009. Retrospective analysis of zooplankton community structure in the Benguela Current Large Marine Ecosystem. In: Hampton, I., Barange, M., Sweijid, N. (Eds.), *Benguela Environment Fisheries Interaction and Training Programme (BENEFIT) Research Projects*. GLOBEC Report 25, ii, 100–103.
- Verheye, H.M., Richardson, A.J., Hutchings, L., Marska, G., Gianakouras, D., 1998. Long-term trends in the abundance and community structure of coastal zooplankton in the southern Benguela system, 1951–present. In: Pillar, S.C., Moloney, C.L., Payne, A.L.L., Shillington, F.A. (Eds.), *Benguela Dynamics: impacts of variability on shelf-sea environments and their living resources*. *S. Afr. J. Mar. Sci.* 19, 317–322.
- Verheye-Dua, F., Lucas, M.I., 1988. Southern Benguela frontal region: I. Hydrology, phytoplankton and bacterioplankton. *Mar. Ecol. Prog. Ser.*, 47; 271–280.
- Vezzulli, L., Staunder, M., Grande, C., Pezzati, E., Verheye, H.M., Owens, N.J.P., Pruzzo, C., 2015. *gfpA* as a novel qPCR target for the species-specific detection of *Vibrio cholerae* O1, O139, Non-O1/Non-O139 in environmental, stool, and historical Continuous Plankton Recorder samples. *PLoS ONE* 10 (4), e0123983, <http://dx.doi.org/10.1371/journal.pone.0123983>.
- Víñas, M.D., Blanco-Bercial, L., Bucklin, A., Verheye, H., Bersano, J.G.F., Ceballos, S., 2015. Phylogeography of the copepod *Calanoides carinatus* s.l. (Krøyer)

- reveals cryptic species and delimits *C. carinatus* s.s. distribution in SW Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.* 468, 97–104.
- Waldron, H.N., Probyn, T.A., 1992. Nitrate supply and potential new production in the Benguela upwelling system. In: Payne, A.L.L., Brink, K.H., Mann, K.H., Hilborn, R. (Eds.), *Benguela Trophic Functioning*. *S. Afr. J. Mar. Sci.* 12, 29–39.
- Wasmund, N., Lass, H.-U., Nausch, G., 2005. Distribution of nutrients, chlorophyll and phytoplankton primary production in relation to hydrographic structures bordering the Benguela-Angolan frontal region. *Afr. J. Mar. Sci.* 27, 177–190.
- Weeks, S.J., Barlow, R., Roy, C., Shillington, F.A., 2006. Remotely sensed variability of temperature and chlorophyll in the southern Benguela: upwelling frequency and phytoplankton response. *Afr. J. Mar. Sci.* 28, 493–509.
- Weeks, S.J., Currie, B., Bakun, A., 2002. Satellite imaging: massive emissions of toxic gas in the Atlantic. *Nature* 415, 493–494.
- Weeks, S.J., Currie, B., Bakun, A., Peard, K.R., 2004. Hydrogen sulphide eruptions in the Atlantic Ocean off southern Africa: implications of a new view based on SeaWiFS satellite imagery. *Deep-Sea Res. I* 51, 153–172.

Web references

- <http://www.benguelacc.org> (accessed 30.05.15).
- <https://www.thegef.org/gef/news/benguela-current-convention> (accessed 14.07.15).