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Pelagic key species and mechanisms driving energy flows in the northern Benguela upwelling ecosystem and their feedback into biogeochemical cycles



Werner Ekau^{a,*}, Holger Auel^b, Wilhelm Hagen^b, Rolf Koppelmann^c, Norbert Wasmund^f, Karolina Bohata^c, Fritz Buchholz^d, Simon Geist^{a,e}, Bettina Martin^c, Anna Schukat^b, Hans M. Verheye^{g,b}, Thorsten Werner^d

^a Leibniz Centre for Tropical Marine Research, Department of Ecology, Bremen, Germany

^b BreMarE - Bremen Marine Ecology, Marine Zoology, University of Bremen, Bremen, Germany

^c Institute of Hydrobiology and Fisheries Science, University of Hamburg, Germany

^d Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

^e Texas A&M University Corpus Christi, Department of Life Sciences, Corpus Christi, USA

^f Leibniz Institute for Baltic Sea Research, Warnemünde, Germany

^g Department of Environmental Affairs, Cape Town, South Africa

^h University of Cape Town, Marine Research Institute, Rondebosch, South Africa

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ABSTRACT

The northern Benguela Upwelling System (nBUS) has been facing increasing temperatures and decreasing dissolved oxygen (DO) levels over the last decades. This has implications for key processes and trophic interactions within the ecosystem including shifts in community composition, distribution ranges, and trophic levels, changes in energy flows and migration patterns with feedbacks to biogeochemical processes. Here we summarise the results gained from the GENUS project (Geochemistry and Ecology of the Namibian Upwelling System) focussing on the geochemical and ecological structures and processes dominating the pelagic component of the nBUS. Spatial and temporal distribution patterns of key species of zooplankton and fish larvae yielded biomass estimates (5 to 81 g Wet Mass m^{-2} (10 to 90% quantile) with a median of 19.5 g Wet Mass m^{-2} for the upper 200 m) and potential impacts on the vertical carbon flux. Vertical distribution ranges of key taxa were determined reflecting their specific abilities to tolerate hypoxia and, hence, their different adaptive mechanisms to cope with the Oxygen Minimum Zone (OMZ). The shoaling of the $2.5 \text{ mL O}_2 \text{ L}^{-1}$ -oxycline (0.24 m y^{-1}) constraints sensitive species and hampers daily and seasonal vertical migrations. It may also affect the ability of organisms to maintain themselves within nearshore habitats by hindering vertical migration into deeper onshore currents. Respiration rates of key species were determined with one standard method (optode respirometry), showing an average respiration rate of 54.6 mL $O_2 d^{-1}$ (g Dry Mass)⁻¹ for the bulk fraction of mesozooplankton, allowing also the estimate of DO consumption by mesozooplankton at different depth layers. Stable isotopic ratios (N, C) revealed trophic interactions and positions of zooplankton and fish. Our results reveal many players within a small range of trophic levels and a dominance of zooplankton taxa (copepods, euphausiids) in terms of biomass over small pelagic fish (sardine, anchovy), essential to consider for future higher-resolution ecosystem modelling.

1. Introduction

Eastern Boundary Upwelling Systems (EBUS) comprise < 2% of the ocean's surface, but support 7% of global marine primary production, and provide $\sim 20\%$ of global fish catches (Pauly and Christensen, 1995; Sydeman et al., 2014). The Benguela upwelling ecosystem shows

highest primary production rates among the four major EBUS, very similar to those of the Canary Current EBUS off Northwest Africa, but is among the lowest concerning fish production, about tenfold less than the Humboldt Current EBUS (Chavez et al., 2008). Bound between two warm water currents, the Angola Current in the north and the Agulhas Current in the south, the Benguela EBUS is divided into two very

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^{*} Corresponding author at: Leibniz Centre for Tropical Marine Research, Department of Ecology, Bremen, Germany. *E-mail address:* werner.ekau@leibniz-zmt.de (W. Ekau).

distinct subsystems by the strong Lüderitz upwelling cell: a northern part (northern Benguela Upwelling System - nBUS) influenced by South Atlantic Central Water (SACW), accompanied by an extensive Oxygen Minimum Zone (OMZ), and a southern part (sBUS) dominated by Eastern South Atlantic Central Water (ESACW). In the northern part, smaller upwelling cells are found off the Cunene River mouth (17°S), around Cape Frio (19°S), and off Walvis Bay (23°S). The dynamics of the Benguela Current (BC) EBUS have been described extensively (Shannon, 1985; Lutjeharms and Valentine, 1987; Fennel, 1999; Monteiro et al., 2008; Mohrholz et al., 2014).

All major coastal upwelling systems have shown some evidence of response to past climate change as demonstrated by empirical and modelling approaches (Emeis et al., 2009; Finney et al., 2010; Leduc et al., 2010; Bakun et al., 2015). They are expected to respond to future climate change, since they are uniquely sensitive to global, regional, and local changes in atmospheric circulation patterns and driving forces (Bakun, 1990; Bakun et al., 2010; Demarcq, 2009; Sydeman et al., 2014; García-Reyes et al., 2015; Wang et al., 2015). Several EBUS have experienced dramatic shifts in ecosystem structure and fisheries yield (so-called ecosystem regime shifts) in the past (Alheit and Bakun, 2010; Cury and Shannon, 2004; Finney et al., 2010; Kirkman et al., 2015). According to current thinking, these shifts in ecosystem structure were not exclusively caused by anthropogenic impacts, but may have also been expressions of global or regional shifts in physical drivers (Overland et al., 2010; Rykaczewski and Checkley, 2008). This view is supported by evidence of similarly radical regime shifts that occurred in the geological past (Finney et al., 2010). However, various physical EBUS models differ significantly in their projections of the response of the systems to climate change (Wang et al., 2010).

South Atlantic Central Water is a prominent water source in the northern Benguela from July to December when upwelling is strongest. Low oxygenated water originating from the Angola Dome region is upwelled at Cape Frio (18°S) during January to June when it usually dominates the central Namibian coast (Monteiro et al., 2006; Monteiro and van der Plas, 2006; Mohrholz et al., 2008). The Benguela EBUS, especially the northern part, has been facing increasing temperatures and decreasing dissolved oxygen (DO) concentrations over the last decades (Stramma et al., 2008). Vertical distributions of zoo- and ichthyoplankton (Ekau and Verheye, 2005; Auel and Ekau, 2009) are constrained by DO concentration, and migration patterns seem to be impacted by physical and biogeochemical factors. Hence, changes in community composition are related to temperature and DO content. As also indicated by findings from the Humboldt Current EBUS (Bertrand et al., 2010), the position of the oxycline is a major factor structuring and limiting the "habitable space" for pelagic organisms. Adaptive responses to these limitations affect the community level; species can either cope with low oxygen levels and pass through or migrate into the OMZ, or they are bound to abandon the area.

Based on a long-term cooperation with southern African partners since the early 1990s, the GENUS project (Geochemistry and Ecology of the Namibian Upwelling System) was an integrative research project funded by the German Federal Ministry for Education and Research (BMBF). GENUS quantified fluxes of energy and matter in the pelagic realm of this EBUS to clarify relationships between climate change, biogeochemical cycles, and ecosystem structure in the nBUS off the Namibian coast. The nBUS shows a high seasonal and interannual variability in atmospheric forcing, in properties of water masses on the shelf, and in oxygen supply and demand on the shelf. As a consequence, concentrations and ratios of nutrients in upwelling waters and their CO₂ content have steep gradients in space and time. GENUS provided comprehensive information on hydrographic features (Fennel et al., 2012; Mohrholz et al., 2008, 2014; Muller et al., 2013, 2014), energy and nutrient fluxes, as well as greenhouse gases (Emeis et al., 2018), phytoplankton and primary production (Hansen et al., 2014; Wasmund et al., 2014, 2016), distribution and physiology of zooplankton (Martin et al., 2015, 2017; Schukat et al., 2013a, 2013b, 2014; Teuber et al.,

2013; Werner et al., 2015) and ichthyoplankton (Grote et al., 2012; Geist et al., 2013, 2015). Changes in plankton communities have been observed, indicating horizontal and vertical shifts in distribution patterns. The results from physiological investigations provided information on respiration rates of key species and energy turnover.

In this paper, we aim at integrating and synthesising the results obtained from the biological components of the GENUS project with existing knowledge on the nBUS by addressing three major questions:

- 1. What are the distribution patterns of key zooplankton taxa in the nBUS and the likely effects of global change?
- 2. How does the expanding OMZ affect zooplankton and fish communities, and what is the feedback of changing pelagic communities on the development of the OMZ?
- 3. What are the contribution of vertical migration and feeding behaviour of zooplankton and fishes to the vertical carbon flux?

2. Methods

Results of the biological component of the GENUS project have thus far been presented in a large number of peer-reviewed publications listed on the GENUS website and in the final report (GENUS, 2018). For the present paper, results from many GENUS publications were synthesised, and additional non-published data from former cruises integrated. Detailed descriptions of methods applied are given in the respective publications. Here, we briefly present an overview of the research cruises carried out during GENUS and of those bilateral cruises realised before that are related to the topic, highlight certain methodological advances developed within the framework of GENUS, and focus on the methods used for the synthesis and integration of data for the present paper.

2.1. Research cruises

Cooperation started in 1999 with empirical investigations on the composition and abundance of plankton in the nBUS and was carried out during a number of cruises onboard German, South African, Namibian, Norwegian, and British research vessels. Cruises relevant for the biological/ecological work are listed in Table 1. GENUS started with pilot studies in 2008 and ended field work in 2014. These cruises provided insight into the structure and functioning of the pelagic ecosystem in the nBUS and its hydrographical and biogeochemical

Table 1

Expeditions within the cooperation relevant for biological/ecological work in the pelagic ecosystem before and during the GENUS-project. Standard gears used were CTDO, vertical and towed Multinet-midi (©Hydrobios) and MOCNESS on selected transects and cruises.

Year	Month	Ship	Cruise	Chief scientist	Region
1999	Jul	Africana	Afr155	Bailey	BC
2002	Jan/Feb	Africana	Afr166	Boyd	BC
2004	Feb	A.v.Humboldt	AHAB-4	Ekau	BC, ABFZ
2007	Jan/Feb	Dr. Frithjof	NanOxy	Kraksted/Ekau	BC, ABFZ
		Nansen			
2008	Mar	Maria S. Merian	07/2b	Mohrholz	BC
2008	Mar/Apr	Maria S. Merian	07/3	Ekau	BC, ABFZ
2009	Dec	Africana	Afr258	Verheye/Ekau	BC
2010	Sep/Oct	Discovery	356	Buchholz	BC
2011	Jan-Mar	Maria S. Merian	17/3	Lahajnar	BC, ABFZ
2011	Jul/Aug	Maria S. Merian	18/4	Schmidt	Angola, BC
2011	Sep/Oct	Maria S. Merian	19/1a-c	Visbeck/Ekau/	BC
				Zabel	
2013	Jan	Mirabilis	13-01	Louw	BC
2013	Sep	Meteor	100/1	Buchholz	BC
2013	Dec	Meteor	102	Ekau	BC, Agulhas
2013/14	Dec/Jan	Meteor	103/1	Lahajnar	BC, ABFZ
2014	Jan/Feb	Meteor	103/2	Mohrholz	BC

background. They also enabled physiological and ecological studies on board to assess the role of key species and their trophic interactions.

During these cruises, CTD probes with oxygen sensors were routinely deployed. The data were used to calculate mean oxycline depths for a latitudinal section from 18 to 24°S. WODC (World Ocean Data Center) data were used to calculate mean oxycline depths for years prior to 2001.

2.2. Multi-channel optode respirometry for respiration measurements with pelagic organisms

Measurements of respiration rate performed over a wide size range of organisms from small copepods to macrozooplankton (e.g. euphausiids, decapods), ichthyoplankton and juvenile fish were essential for GENUS's objectives to quantify carbon and energy flows through the marine food web of the nBUS (Bode et al., 2013; Geist et al., 2013; Schukat et al., 2013a, 2013b; Werner, 2013). Respiration rates were also used to characterise ecophysiological thresholds and potential adaptations to hypoxic conditions in the oxygen minimum layer (Teuber et al., 2013). Therefore, GENUS scientists optimised the application of multi-channel optode respirometry for respiration measurements with planktonic organisms on board. Applying the same technique and measurement principle adjusted to different (size) groups of organisms ensured comparability of results across taxonomic groups. Only optode respirometers from PreSens, Regensburg, Germany, were used, either one-, four- or ten-channel systems. Small plankton organisms were incubated in closed bottles for 12 to 24 h and the declining DO concentration was continuously monitored, whereas larger and more active specimens such as euphausiids were incubated for 3 to 6 h only. Juvenile fish were kept in flow-through cells with optode respirometry controlling the DO concentrations at the in- and outflows. Incubation experiments and respiration measurements were conducted on board in temperature-controlled laboratories in order to simulate in-situ temperatures. Controls without the respective animals were used in every set of experiments to correct for potential microbial oxygen consumption. The method proved to be efficient and was easy to operate onboard research vessels. It is applicable even for small or diapausing copepods with a drastically reduced metabolism.

2.3. Zooplankton biomass and estimates of community respiration

Different zooplankton size fractions were sampled with various devices and methods. For composition and abundance of smaller microzooplankton (20-100 µm), seawater was filtered from Niskin bottles or rosette water samplers using sieves of 20 and 100 µm mesh size. Larger microzooplankton (55-200 µm) was sampled with a multiple opening-closing net (Hydrobios© Multinet, type Midi) equipped with five 55 µm meshed nets (for details of microzooplankton sampling see Bohata (2016). Mesozooplankton was collected by vertical hauls with a Hydrobios© Multinet, type Midi equipped with five 200 µm meshed nets for stratified sampling. Single and double MOCNESS© tows (1 m² effective mouth opening, 300 µm mesh size) were used to catch mesoand macrozooplankton between the surface and 1000 m depth in 9 or 18, respectively, separate depth intervals (for details see Bohata and Koppelmann, 2013; Koppelmann et al., 2013, 2014; Martin et al., 2015, 2017). Ichthyoplankton catches were made using an obliquely towed Hydrobios© Multinet, type Midi with five 500 µm meshed nets between the surface and 200 m depth. All samples were preserved in 4% formaldehyde-seawater solution buffered with sodium-tetraborate and stored for subsequent analyses in the laboratory.

For the MOCNESS[©] catches we vertically integrated wet mass (WM) from the surface to the seafloor at shelf and shelf-break stations or down to 800–1000 m maximum sampling depth at oceanic stations, while for the obliquely towed Multinet-Midi[©] samples we integrated WM per m² in the upper 200 m (or bottom depth, respectively). The latter was the routinely used gear on the cruises from 1999 through to

2014, with 260 hauls during austral summer and 31 hauls in austral winter covering a wide geographical range from ca. 13 to 27°S. While smaller developmental stages of mesozooplankton may be underestimated, adults of key species are represented adequately and provide a good picture of the abundance and spatial distribution of these species. Mesozooplankton Wet Mass was converted to Dry Mass (DM) using an average conversion ratio of 10:1 (Hagen, 2000) to subsequently roughly estimate mesozooplankton community respiration at a certain water depth by multiplying biomass data with the average mass-specific respiration rate of a wide range of copepod species, determined by Schukat et al. (2013a, 2013b) in the Benguela EBUS:

Zoopl.O₂ consumption (mL O₂
$$d^{-1} m^{-3}$$
) = Zoopl. Dry Mass (g DM m^{-3})

Calculations and mapping were carried out with ODV software (Ocean Data View; Schlitzer, 2017).

2.4. $\delta^{15}N$ stable isotope analysis

In order to establish trophic levels for key components of the pelagic food web, δ^{15} N ratios were measured (Schukat et al., 2014), using atmospheric air (IAEA-N1) as reference. Isotopic ratios are expressed as δ^{15} N in ‰ according to Hobson et al. (2002). Analyses were performed by Agroisolab GmbH in Jülich, Germany, using a mass spectrometer (EA NA1500 Series 2, Carlo Erba Instruments) and helium as carrier gas. Small zooplankton was measured as entire animals, whereas subsamples (fraction of the whole grinded animal) were used for larger taxa. For fish species, homogenized parts of their muscles were measured. For Fig. 7 data have been compiled from Schukat et al. (2014) and from unpublished GENUS results (Geist, unpublished).

3. Results and discussion

3.1. Distribution patterns of mesozooplankton in the nBUS and the potential impact of global change

In the 1990s Bakun's hypothesis inspired a novel perception of the effects of global climate change on coastal upwelling systems. Bakun (1990) postulated that global warming would affect continental land masses stronger than adjacent oceans leading to more pronounced gradients in air pressure between the subtropical high pressure above the ocean and low-pressure systems over the subtropical regions of the continents. As a consequence, this would lead to an intensification of upwelling-favorable winds and hence increased coastal upwelling, possibly resulting in higher primary production and ultimately higher fisheries yield from coastal upwelling systems. However, time-series data on wind strength, sea surface temperature and ecological effects in coastal upwelling systems seem to tell a different story. In the nBUS, strong winds and strong upwelling intensity prevailed during the 1980s, whereas the first decade of the 21st century was relatively warm and showed comparatively low upwelling intensity (Kreiner et al., 2011; Jarre et al., 2015).

Meanwhile, Bakun's hypothesis has been modified by modelling studies, rather indicating a poleward shift of the subtropical high than an intensification throughout the entire region (García-Reyes et al., 2015; Rykaczewski et al., 2015; Wang et al., 2015). This poleward shift will lead to more pronounced air pressure gradients and stronger trade winds in the poleward parts of coastal upwelling systems (i.e. in the southern Benguela EBUS), whereas air pressure gradients and average wind speeds in the equatorward parts of upwelling systems will relax. Yet, it is still highly uncertain how these changes in physical forcings will affect the productivity of coastal upwelling systems and whether they will propagate through the food web impacting upper trophic levels (García-Reyes et al., 2015).

As detected in other regions (Ayón et al., 2008), plankton

abundance and production peak when moderate upwelling activities prevail (Grote et al., 2007; Bode et al., 2014), both on seasonal and spatial scales. In contrast, abundance and productivity are low in recently upwelled water, because upwelling water originates from the central water layer below the thermocline, where the phytoplankton stock is at a minimum. Excessive turbulence created by too strong upwelling inhibits productivity rather than stimulating it. The development of a diatom-dominated phytoplankton bloom in the nutrient-rich upwelling plume and a community succession from diatoms to flagellates requires time to respond to upwelling conditions. The increase of phytoplankton biomass by an order of magnitude takes approximately two weeks (Hansen et al., 2014).

A mixed population of dinoflagellates, coccolithophores and microflagellates was detected on cross-shelf transects off Walvis Bay in newly upwelled waters (< 13 days old) close to the coast. In contrast, diatoms dominated maturing waters (13–55 days old) 40 to 250 km off the coast, whereas dinoflagellates prevailed in waters older than 55 days after the upwelling event. Estimates of primary production in mesocosm experiments peaked at 70 to 100 mg C m⁻³ h⁻¹ (Wasmund et al., 2014, 2016). This agrees with ¹⁴C-based production rates of ca. 80 mg C m⁻³ h⁻¹ measured in a frontal region of the southern Benguela (Pitcher et al., 1998).

In marine ecosystems, generally 60–70% of primary production is consumed by microzooplankton and 10–40% by mesozooplankton (Calbet, 2001; Calbet and Landry, 2004), with microzooplankton being an important dietary component of mesozooplankton (Bollens and Landry, 2000; Calbet and Saiz, 2005). Microzooplankton (< 200 µm, sampled with 55 µm meshed nets) of the nBUS is generally dominated by mixotrophic and heterotrophic dinoflagellates, tintinnids and small copepods (Bohata, 2016). Their distribution patterns revealed a shelf offshore zonation and clear temperature associations (Fig. 1).

Heterotrophic dinoflagellates such as *Protoperidinium* and *Noctiluca scintillans* prevailed in < 15 °C cold, recently upwelled water on the shelf, whereas subsequent succession stages in 15–20 °C warm surface water on the shelf were dominated by small copepods such as *Oncaea*, *Oithona* and *Microsetella*. *Protoperidinium*, *Oncaea*, Tintinnidae and the mixotrophic dinoflagellate *Ceratium* were abundant in decreasing order in > 20 °C warm surface water at the shelf break.

Tintinnidae contributed > 37% to microzooplankton at the medium-warm shelf break, followed by *Oncaea*, *Microsetella* and *Protoperidinium*. The cold shelf break was dominated by *Oncaea*, followed by *Protoperidinium* and *Ceratium*. The warm offshore region was dominated by Tintinnidae comprising > 30% of total abundance. Mixotrophic (*Ceratium*) and heterotrophic (*Protoperidinium*) dinoflagellates were also very abundant here collectively making up > 30% of total abundance. The medium-warm offshore area was characterized by high abundances of *Oncaea* (> 23%) and the foraminifer *Neogloboquadrina* (> 14%) (Fig. 1).

High mesozooplankton biomass values during the study period compared to low values during the period 1978–1986 (Hutchings et al., 1991) confirm differences in the observed copepod abundances between the two time periods, as described by Verheye and Kreiner (2009) and Verheye et al. (2016). Based on MOCNESS catches on a transect off Walvis Bay (Martin et al., 2015), annual mean mesozooplankton biomass in the nBUS comprised ca. 23 g Wet Mass (WM) m⁻² on the shelf, 33 g WM m⁻² at the shelf break and above the continental slope, and 23 g WM m⁻² in the oceanic region.

Based on Multinet catches collected between 1999 and 2014, mesozooplankton abundance in the upper 200 m ranged from 5 to 81 g WM m⁻² (10 to 90% quantiles) with a median of 19.5 g WM m⁻². During the upwelling season in the North and South, maxima of up to 800 g WM m⁻² were determined off the Cunene River mouth (17°S) in austral winter, whereas maxima in austral summer were located off Walvis Bay at 23°S during the upwelling season (Fig. 2, central panel). Using averaged biomass values and grid cell sizes ranging from 6.3 to 46.1 km² in the ODV graphs, an assessment of the mesozooplankton standing stock for the area between $15^{\circ}40'$ and $24^{\circ}S$ resulted in 15×10^{6} t WM in summer and 24×10^{6} t WM in winter. High biomass concentrations were found in the surface layer (Fig. 2, left and central panels), represented here as g WM 100 m⁻³ at the 10 m isocline. Only smaller biomass fractions were detected at 100 m depth, and a slight southward shift of the hotspots occurred at greater depth. In the majority of the investigated area overall biomass concentration was low (< 50 g WM 100 m⁻³), except for some isolated spots and patches off Walvis Bay. Both day and night catches were analysed here.

According to Multinet and MOCNESS catches, mesozooplankton biomass was related to temperature. During summer cruises, concentrations above 100 g WM m^{-2} were found between 17 and 22 °C. whereas in winter such high concentrations occurred from 14 to 20 °C. Temperature can be regarded as a proxy for the age of the upwelling plume, indicating that zooplankton biomass maxima were not correlated to highest upwelling intensity. As a matter of fact, highest biomass values were detected during moderate upwelling (15-20 °C), whereas intense (<15°C) and calm (>20°C) upwelling resulted in lower zooplankton biomasses (Fig. 3). Higher biomass values > 55 g WM m⁻² were often caused by Thaliacea blooms, which contributed up to 63% to the numerical zooplankton abundance (Martin et al., 2017). These gelatinous organisms are efficient filter-feeders and remove phytoplankton particles. They produce large and fast-sinking fecal pellets and contribute significantly to the vertical carbon flux. When a bloom decays, a secondary flux event of dead and moribund thaliaceans occurs (Koppelmann, 1994).

The composition and abundance of smaller gelatinous (Cnidaria and Ctenophora) and semi-gelatinous (Pteropoda, Chaetognatha and Thaliacea) organisms were analysed by Bohata and Koppelmann (2013), Koppelmann et al. (2013, 2014) and Martin et al. (2017). A total of 40 taxa of Cnidaria (4 Scyphozoa and 36 Hydrozoa, including 18 Siphonophora), 1 taxon of Ctenophora, 20 taxa of Thecosomata (Pteropoda), 17 taxa of Chaetognatha and 7 taxa of Thaliacea (3 Doliolida and 4 Salpida) were identified. Usually, the lowest diversity of all these groups occurred on the shelf increasing towards the open ocean. Maximum abundances of the carnivorous groups (Cnidaria, Ctenophora and Chaetognatha) were encountered on the shelf, but Cnidaria were also abundant offshore. Pteropoda were most common at the slope stations, whereas high numbers of Thaliacea were sampled on the shelf and at the shelf break during bloom events. Stable isotope analyses confirmed the trophic level of these gelatinous plankton groups to range between 1.2 and 2.2 (Koppelmann et al., 2013). Pteropoda and Thaliacea compete with micro- and mesozooplankton for food, whereas Cnidaria and Chaetognatha show higher mean trophic levels of 2.2 and 3.2, respectively. They are strong competitors of fish larvae and other predators.

Copepods and euphausiids are an important food source for several fish species in the region (Macpherson and Roel, 1987). Euphausiids show a clear zonation pattern in the food web of the nBUS: *Euphausia hanseni* and *Nematoscelis megalops* occur in the same areas, but largely avoid interspecific competition by occupying different depth strata and exploiting different food size spectra (Werner and Buchholz, 2013), whereas *Nyctiphanes capensis* occurred in different areas. Krill biomass was three times higher in the northern part (\sim 3 g C m⁻²) of the nBUS (17–19°S) than in the southern part (21–23°S) (Werner et al., 2012). Apparently, abundance and biomass of these krill species were high and independent of the upwelling phase and rather stable over the years from 2011 to 2014, indicating an important role of these taxa in the food web.

Our data on mesozooplankton standing stocks suggest that there is sufficient food for early stages of fishes, at least during austral summer. This supports Brochier's hypothesis that tertiary production is decoupled from upwelling intensity in the Benguela (Brochier et al., 2011). It remains unclear, however, why this food supply seems to be insufficient to support a recovery of the sardine stocks.

The main spawning activities of commercially important fish species



Fig. 1. Microzooplankton taxa dominating the different habitat zones of the northern Benguela Upwelling System off the Namibian coast during September/October 2011. Relative abundances are based on individuals.

such as horse mackerel (*Trachurus capensis*), sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) occur during austral summer, when physiological conditions (nutritional status and growth) of the fish larvae are generally better than in winter. Hake (*Merluccius* spp.) and horse mackerel avoid regions with high upwelling intensity in favour of regions with moderate upwelling (Geist et al., 2015; Grote et al., 2007). Moreover, species-specific differences in physiological adaptations to changing environmental conditions influence the different fish stocks.

Larvae of horse mackerel and sardinellas (*Sardinella aurita*) generally increased in abundance over the last 10–15 years, but also shifted their distribution centre slightly southward over the years, due to the hydrographic changes, especially in 2011 (see Junker et al., 2017). Pelagic goby (*Sufflogobius bibarbatus*) seems to follow a different strategy. Highest abundances of their larvae were observed in September/October, whereas during austral summer abundances were low, although by means of an ROV (Remotely Operated Vehicle) many adult gobies



Fig. 2. Composite of mesozooplankton distribution 1999–2014 obtained from towed multinet hauls at 10 and 100 m depth. Left panels represent mesozooplankton concentrations during austral summer, central panels represent cruises from austral winter (g wet mass 100 m⁻³). The right panels give total zooplankton abundance as g WM m⁻² in summer and winter. Using average respiration rates for copepods (Schukat et al., 2013a, 2013b), O₂ consumption rates were calculated as mL O₂ d⁻¹ m⁻² (scale given in red using colour scheme of biomass distribution.

were observed near the seafloor under hypoxic conditions (Mertzen, 2013).

Overall, the classical view of a direct coupling between upwelling intensity and primary and secondary production via a short food chain between phytoplankton and fish is not supported by our results from the nBUS. Maximum secondary productivity occurs either temporally highest during moderate upwelling conditions (Cushing, 1996) or spatially with some distance from the centre of upwelling, confirming the optimal environmental window hypothesis of Cury and Roy (1989). Furthermore, our results revealed that more trophic levels than previously assumed are involved in the food web leading to a higher complexity (Schukat et al., 2013b, 2014), and hence a reduced transfer of material and energy from phytoplankton to fish. This may partly explain differences in fish production between different upwelling systems, e.g. the Humboldt System, despite similar rates in primary production (Chavez and Messié, 2009).

The decline of small pelagic fish stocks in the northern Namibian Upwelling System has been explained by overfishing and accompanied by an increase in jellyfish over the last decades (Boyer and Hampton, 2001; Flynn et al., 2012; Roux et al., 2013). These assumptions on increasing jellyfish biomass are largely based on data by Venter (1988) and especially Fearon et al. (1992). Their biomass assessments of gelatinous plankton reached maxima of 245 g WM m⁻² in nearshore

areas, corresponding to about 2.5 g DM m^{-2} and jellyfish can locally become highly significant. While the increase of jellyfish biomass is apparently not significant on a global scale (Condon et al., 2013), the high abundances of *Aequorea forskalea* and *Chrysaora fulgida* in the nBUS suggest locally strong competition with and predation on other zooplankton organisms including fish larvae. Such a competitive relationship could be especially detrimental to sardines. In recent years, sardine spawning was largely constrained to the region around Walvis Bay (Kreiner et al., 2011), which was also the hotspot of jellyfish occurrence between 1997 and 2006 (Flynn et al., 2012).

We hypothesize that long-term climate-induced changes with increasing temperature and wind speed/upwelling intensity could enhance the decoupling of primary production and upper trophic levels, suppress traditional fish species and favour a different faunal community (e.g. with more jellyfish) that is neither of commercial importance, nor of high energetic value for other top predators. The strengthening of the OMZ may accelerate this process, as outlined in the next section.

3.2. How does the expanding OMZ affect zooplankton and fish communities, and what is the feedback of changing pelagic communities on the development of the OMZ?

The development of the OMZ in the nBUS has been modelled by



Fig. 3. Mesozooplankton standing stocks (g wet mass m⁻²) for the upper 200 m for winter (left panel) and summer (right panel) stations in relationship to the temperature at 10 m depth. Temperatures < 15 °C are reflecting strong upwelling, whereas values from 15 to 20 °C reflect moderate upwelling and values > 20 °C indicate low upwelling intensities. Data derived from cruises listed in Table 1.



Fig. 4. Development of the OMZ (blue line) in the northern Benguela EBUS derived from WODC (1958–2001) and cruise data from 2002 to 2014. Yellow line shows the trend over the last decades with $z_{oxy2.5} = -530 + 0.238 * t$. Small picture inlay at left taken from Stramma et al. (2008). The red (sardine) and green (horse mackerel) lines show the catches of the two main small pelagic fish species in relation to the oxycline.

Stramma et al. (2008) and is also prominent in oxygen data derived from WODC (1958–2001) and cruise data from 1999 to 2014 (see Table 1; Fig. 4) for the latitudinal sector between 19 and 23°S. While bottle data from WODC are highly variable and not available for all years before 1980, recent data collected with CTDO are more reliable and show a trend of shoaling over the last 20 years. Comparing the position of the oxycline $(2.5 \text{ mL O}_2 \text{ L}^{-1})$ with catches of commercially important species shows some coincidence of shallow oxyclines in the period from 1977 to 1992 with high horse mackerel and low sardine catches. Combined with a strong correlation of larval abundance with DO concentration (Ekau and Verheye, 2005) it provides evidence for the impact of low oxygen on these stocks. Stramma et al. (2008) reported an overall decrease of O₂ in the OMZ of 0.17 μ mol O₂ kg⁻¹ y⁻¹. Using data from Fig. 4 we find a shoaling of the oxycline of 0.24 m y⁻¹. Nevertheless, the variability of the oxycline depth is high. In Fig. 5 we show the cross-shelf average of the oxycline for the area between 17 and 23°S for the summer cruises 2002 to 2014 with the shallowest position in 2008 and the deepest position in 2014.

The vertical distribution of copepods and fish larvae was investigated during the GENUS project (Ekau and Verheye, 2005; Auel and Ekau, 2009; Bode et al., 2014). A high seasonal variability and pronounced stratification could be observed, closely related to the W. Ekau et al.



Fig. 5. Variability of the oxycline depth in austral summer, averaged for the cross shelf section between 17 and 23°S according to bottom depth. Dotted lines show December values for 2009 and 2013; hatched lines represent winter values from 1999 and 2010. Overall average values of oxyclines for the summer cruises are indicated at the oxycline depth axis.

oxycline. Based on oxygen consumption and tolerance measurements as well as depth distributions of prevailing copepod and larval fish species, we could establish vertical distribution ranges for these species (Fig. 6). Besides showing some north-southward variation between 17 and 24°S over the years, species such as Calanoides natalis (ex C. carinatus), Centropages brachiatus, Metridia lucens, Nannocalanus minor, Pleuromamma borealis and Rhincalanus nasutus displayed species-specific vertical distribution ranges and vertical migration behaviour. Copepods of the families Eucalanidae and Metridinidae dominated within the OMZ (Auel and Verheye, 2007; Teuber et al., 2013). They showed physiological and behavioural adaptations to life at hypoxic conditions including lower metabolic rates, additional anaerobic activity and/or diel vertical migration (DVM), which allows them to restrict their presence in the OMZ to relatively short periods of the day (Auel and Verheye, 2007; Teuber et al., 2013). DVM species such as Pleuromamma spp. use anaerobic metabolic activity to overcome oxygen limitation during their passage through the OMZ. This temporary oxygen debt can be compensated during times spent in the well-oxygenated surface layer. By contrast, reduced metabolic activity and generally low oxygen demand allow Eucalanidae to reside within the OMZ for extended periods of time. Hence, for these species, the OMZ serves as a refuge from predation and competition by less hypoxia-tolerant species including small pelagic fish.

Oxygen consumption by mesozooplankton and its influence on the development and maintenance of the OMZ were estimated by converting mesozooplankton biomass to total community respiration by applying an average zooplankton respiration rate of 54.6 mL $O_2 d^{-1}$ (g DM)⁻¹ (Schukat et al., 2013a, 2013b) (Fig. 2). Total mesozooplankton ranged from 1 to $3 \text{ mL O}_2 \text{ d}^{-1} \text{ m}^{-2}$ respiration generally $(45-135 \,\mu mol \,O_2 \,d^{-1} \,m^{-2})$ and reached maxima of > 20mL $O_2 d^{-1} m^{-2}$ (900 µmol $O_2 d^{-1} m^{-2}$) associated with some upwelling cells. During winter, maxima in community respiration were found off the Cunene River mouth (17°S) within the Angola-Benguela Front, whereas during summer highest values occurred off Walvis Bay (23°S).

In euphausiids, clear differences were detected between dominant species (Fig. 6). While *Euphausia americana* was restricted to the upper, well-oxygenated water layer, *E. recurva* showed vertical migration into the OMZ, but avoided oxygen concentrations below $1 \text{ mL} \text{ O}_2 \text{ L}^{-1}$. *Nematoscelis megalops* was found within the OMZ, obviously using it as a refuge. In contrast, *E. hanseni* exhibited extensive daily vertical migrations, spending the night near the surface for feeding (Werner and Buchholz, 2013).

For fish larvae, a clear difference between species was observed related to hypoxia tolerance and the extent of the oxygenated surface layer, respectively (Fig. 6). No larvae of the dominant species were found below the oxycline (Ekau et al., 2001). Sardinops sagax is largely restricted to the upper 25 m, whereas the distribution of Trachurus capensis extends to about 50 m depth. Engraulis encrasicolus and Merluccius spp. show deeper ranges and Sufflogobius bibarbatus, the pelagic goby, is less sensitive towards lower oxygen levels and prevailed at depths with $< 2.5 \text{ mL O}_2 \text{ L}^{-1}$. In addition to these differences in vertical distribution, we found shifts in horizontal distribution patterns of the larvae of some of the above species mainly between 14 and 24°S from 2002 to 2014, exhibiting a general trend to move their distribution centres towards higher latitudes. We detected these patterns for two clupeid species, Sardinops sagax and Sardinella aurita as well as for Trachurus capensis (Ekau, unpublished; see Supplementary data). S. sagax larvae had their main distribution between 16 and 19°S from 2002 to 2007 and moved southward to 21 to 24°S with peak abundances in 2011, which corresponds to the findings of Kreiner et al. (2011), while S. aurita larvae shifted its distribution centre from southern Angola (~13-17°S) in 2004 to northern Namibia (~19-23°S) in 2011 and 2014. A similar shift could be observed for horse mackerel with increasing larval abundances over the years. Abundance of S. bibarbatus larvae was low during GENUS cruises (total catch of 540 larvae during summer cruises 2002–2008; 151 larvae in cruises 2009 to 2014). However, in the 1970s this gobiid species dominated the larval community (O'Toole, 1977). Although stomach analyses of top predators show an increasing contribution of adult gobiids to the diet of seals and seabirds, the slow growth rates of larval and adult pelagic gobies (Michalowski, 2011; Christiansen, 2013) as well as their lower lipid and energy contents (van der Bank et al., 2011) compared to clupeids are likely to limit their potential to replace sardines as a key species in the northern Benguela food web.

Zooplankton organisms in the nBUS have developed very different strategies to cope with the naturally occurring OMZ in the region. Adaptation to low DO concentrations and the utilization of hypoxic or even anoxic water bodies to avoid predation are found in several species from different phyla. Some fish species are used to enter the OMZ for feeding. All of these would need to return to the surface to replenish their blood with oxygen. Seasonal vertical migrations through the OMZ were only performed by oceanic species, copepods as well as euphausiids and mesopelagic fish. However, some species depend on highly oxygenated surface waters and cannot escape from this habitat. A shoaling of the upper oxycline of the OMZ will have severe consequences for all of these species due to contraction of their preferred habitat and/or an interruption of their life cycle dynamics by increasing the passage time through the OMZ (Ekau et al., 2010).



Fig. 6. Depth distribution ranges of prevailing copepod, euphausiid and fish larvae species related to OMZ (the purple colour indicates low oxygen water - OMZ). For fish larvae the relative vertical abundance is also provided as yellow line. The red line indicates the average depth of the 2.5 mL oxycline.

3.3. What are the contributions of vertically migrating zooplankton and fish species and their feeding behaviour to the vertical carbon flux?

Vertical migration of organisms and passive sinking of dead organic material and fecal pellets contribute to the biological pump (Schnetzer and Steinberg, 2002). Various euphausiids (*E. hanseni* and *E. recurva*), certain copepod species, and mesopelagic fish reside in deeper water layers in or below the OMZ during the day and perform pronounced diel migrations into the surface layer for feeding at night. Depending on gut passage time in different species, this provides a potential pathway for transport of large amounts of carbon to deeper layers. On the other hand, top predators such as fish and seals dive into the OMZ and feed on krill and fish, reversing the carbon flux back to the surface, from where part of the carbon uptake is again sinking to greater depths via fecal pellets. An important contribution to carbon export is due to gelatinous and semi-gelatinous plankton taxa (Cnidaria and Ctenophora; Koppelmann et al., 2014), Pteropoda (Koppelmann et al., 2013), Chaetognatha (Bohata and Koppelmann, 2013), and Thaliacea (Martin et al., 2017), as well as due to Decapoda (Schukat et al., 2013a, 2013b) via particulate (fecal pellets) or dissolved material. Salps and doliolids (Thaliacea) develop intensive "blooms" and are able to consume large portions of the primary production. Active vertical transport of carbon was assessed for decapods (mean of $4.4 \text{ mg C m}^{-2} \text{d}^{-1}$) and copepods (means between 1.1 and $5.1 \text{ mg Cm}^{-2} \text{d}^{-1}$) (Schukat et al., 2013a). Martin et al. (2017)calculated that approximately 700–1100 mg C m⁻² d⁻¹ in fecal pellets were exported during a salp bloom in the northern Namibian upwelling region, corresponding to 25-100% of the local primary production. Passive vertical export of organic matter was measured with sediment traps, deployed near Walvis Bay (23°S) at \sim 60 m and at 130 m water depth (Libuku, 2014). The data showed a seasonal pattern reaching a maximum of 790 mg C_{org} m⁻² d⁻¹ in October/November 2013.

Fishes are a poorly investigated group with respect to their role in vertical transport of carbon. Using acoustic data, Utne-Palm et al.

(2010) showed that pelagic goby (Sufflogobius bibarbatus) regularly ascend into surface layers during the night, presumably to feed and potentially to recover from their residence in hypoxic waters. Their biomass per trawling hour, mainly between 100 and 200 m water depth, was one order of magnitude ($\sim 20 \times$) lower compared to that of hake and horse mackerel (Salvanes et al., 2015). The role of gobiids in the Benguela ecosystem is still being debated (Roux et al., 2013) and the fragmented information on their population status makes it difficult to quantify their contribution to the vertical carbon transport. However, assuming biomass estimates in Namibian waters of 1 million t for horse mackerel and of 750,000 to 1 million t for hake for the last years (Kathena et al., 2016: Kirchner et al., 2010: Kirchner and Leiman, 2014), an estimate of 75,000 t for pelagic goby seems realistic. This is a huge amount of biomass performing daily vertical migration with high potential of contributing to the downward transport of carbon. Even more important could be mesopelagic fish, because of their higher, but unfortunately as yet unquantified abundance.

Horse mackerel may counter-act this process. The species is caught in bottom trawls at greater depths near the shelf edge, indicating their ability to enter hypoxic waters feeding, e.g. on krill, and to return into oxygenated surface waters (Boyer and Hampton, 2001). Hence, they transport organic material from greater depths back into surface waters. Horse mackerel larvae are very tolerant towards low oxygen concentrations and can cope with DO down to 10% saturation (Geist et al., 2013; Kreiner et al., 2015). Similar tolerance values are found for juvenile hake (Hamukuaya et al., 1998). Based on general assumptions of oxygen tolerance at different life-cycle stages (Pörtner and Farrell, 2008) it can be assumed that adult fish show an even greater tolerance and easily enter the OMZ for feeding. Horse mackerel perform vertical migrations in the southern Benguela system (Barange et al., 2005), but there they are not exposed to the same levels of hypoxia. In the nBUS, biomass of horse mackerel varied around 1 million tons during the period from 1990 until 2010, having decreased from about 2 million tons in the 1970s (Kirchner et al., 2010).

Collectively, horse mackerel and hakes in the nBUS represent a biomass of 1.75 million tons and both have the potential to enter the OMZ for feeding. Assuming a daily consumption rate of 4% of their body mass and at this point not taking into account digestion time, this would result in a daily uptake of biomass of ca. 70,000 tons, with large portions probably originating from below the thermo- and oxyclines. Calculated for a shelf area of 95,000 km² as a potential habitat, this gives a total consumption of biomass of $\sim\!0.75\,g\,WM\,m^{-2}\,d^{-1}$ (~0.04 g C m $^{-2}$ d $^{-1}$), equivalent to about 10% of the C_{org} sedimentation measured by Libuku (2014) in sediment traps. Whether this is a significant contribution to the carbon pump can only be estimated if digestion times and egestion rates are considered, but both these data are not yet available for the relevant species. Sardines, having dominated the system under "normal" EBUS conditions, would not contribute to this transport, as they feed predominantly on microzooplankton (plus phyto- and mesozooplankton) in the oxygenated surface layer (van der Lingen et al., 2006).

Different components of the pelagic community play important roles in the biogeochemical cycles of the nBUS. However, the current pelagic community composition in the nBUS strongly differs from the standard expectation for coastal upwelling systems. Stock size of small pelagic fish (sardine and anchovy) is rather low. This is also reflected in Fig. 7, which shows biomass estimates of various components of the pelagic community in the nBUS and their δ^{15} N ratio as proxy for trophic level. Instead of a typical short food chain with few members and a dominance of small pelagic fish, GENUS results revealed that many players occupy a small range of trophic levels (Fig. 7) and that in terms of biomass zooplankton taxa (copepods, euphausiids) dominate over small pelagic fish (sardine, anchovy). Actually, horse mackerel is now the dominant pelagic fish species in the nBUS, although it occupies a higher trophic level than sardine or anchovy.

transport of water masses is a major challenge for modelling of carbon budgets. However, the fragmented results obtained from the GENUS project in this respect, combined with some global calculations for the contribution of fish, show that the overall contribution of pelagic organisms to the biological pump through active or passive transport could be quite substantial.

Journal of Marine Systems 188 (2018) 49-62

4. Conclusions

1. What are the distribution patterns of mesozooplankton species in the northern Benguela EBUS and the potential impact of global change?

Changes in temperature and oxygen in the northern Benguela Upwelling System have been documented over the last decades. Empirical and experimental approaches demonstrated that these changes have a strong impact on the ecophysiology of organisms, their distribution, productivity and condition. The physiological mechanisms governing these responses to environmental changes, such as temperature increase and oxygen decrease, have been analysed in detail. For the nBUS, shifts in distribution of various taxa were observed over the last two decades (Bode et al., 2014; Ekau and Verheye, unpubl. data). This may also have significantly changed foodweb structure and energy pathways from low to higher trophic levels, and thus caused a change in the trophic level (TL) of some of the organisms. Copepod species occupy trophic levels essentially between 2.4 and 3.2, indicating a broad mix of herbivorous, omnivorous and carnivorous species (Table 2). Euphausiids rank somewhat higher at trophic levels of 2.6-3.9. Fish species show a wider range in their trophic positions (see horse mackerel T. capensis larvae and adults in Fig. 7), changing their food preferences with size and spanning orders of magnitude in terms of prev size during their life history (in case of *T. capensis* from TL 2.8 to 3.4). Investigations of larval condition of three key species (sardine, anchovy and horse mackerel) revealed no significant food restrictions for smaller larvae at current densities. Rather than direct dietary constraints, survival seems to depend more on their physiological capacities such as hypoxia and temperature tolerance, or their ability to perform vertical migrations. This makes early developmental stages of fish especially vulnerable to the environmental changes in the nBUS.

2. How does the expanding OMZ affect zooplankton and fish communities, and what is the feedback of changing pelagic communities on the development of the OMZ?

For the northern Benguela Current system, a major threat is the periodical intrusion of low-oxygen waters from the north that leads to an overall extension of the OMZ and a decline of dissolved oxygen within the OMZ (Rouault, 2012; Stramma et al., 2008). This results in an annual vertical oscillation of the oxycline, challenging species with limited vertical distribution ranges such as copepods, krill or fish larvae. Our investigations on vertical distribution and migration patterns in relation to hypoxia tolerance have shown that pelagic organisms were constrained in their ability to adapt to the changes. We were able to identify preferred depth ranges for various copepod, krill and fish species. Alternatively, some species showed an affinity to low oxygen levels in the OMZ and near the seafloor and as such may benefit from reduced competition and predation in these refugia. The oxygen tolerance limits determined for several species from different taxonomic groups clearly indicate their constraints in vertical migration (Ekau and Verheye, 2005; Auel and Verheye, 2007). A shoaling of the upper oxycline may thus inhibit the vertical migration and/or life cycles and impact retention mechanisms by hindering organisms to reach subsurface counter-currents for transport into suitable areas. Changing species compositions in the pelagic realm could be a consequence of such a development.

Coupling these trophic processes with along-shore or cross-shelf



Fig. 7. The δ^{15} N values reflecting the trophic level for key pelagic organisms in the northern Benguela Upwelling System produced and biomass relationships according to field data retrieved from GENUS activities. Size of squares reflects biomass of the components. Tc – *Trachurus capensis*, Ss – *Sardinops sagax*, Ee – *Engraulis encrasicolus*.

3. What are the contributions of vertically migrating zooplankton and fishes and their feeding behaviour to the vertical carbon flux?

Organic carbon produced by phytoplankton is transferred through the food web to higher trophic levels with an efficiency of 10-20% per trophic level (Pauly and Christensen, 1995). The remaining 80–90% is released as CO₂ or as dissolved or particulate organic carbon. Zooplankton and fishes contribute strongly to the carbon flux from the euphotic zone into deeper meso- and bathypelagic layers by both passive and active transport mechanisms. Dead and moribund organisms as well as fecal pellets and moults of crustaceans sink passively to greater depths and stochastic events like "blooms" of jellies and thaliaceans occasionally cause a major carbon export. A considerable amount of material, however, is transported actively by diel and ontogenetic vertical migrations. Key components of the pelagic system, such as calanoid copepods, euphausiids, decapods and myctophid fishes, ingest carbon near the surface and migrate regularly (daily) to deeper zones around 300–500 m, where carbon is released and

Table 2

Biomass of key plankton species as Wet Mass in mg m⁻² and converted to mg C m⁻². Trophic levels are based on stable isotope (∂^{15} N, ∂^{13} C) measurements. Data mostly unpublished.

Taxonomic Group	Biomass range	$mmm m^{-2}$ (mg WM m ⁻²)		Biomass (mg C m $^{-2}$)	Trophic Level
	0-50 m	50-100 m			
Microzooplankton	30-9000	0.1-5.0			-
Pteropods	0-1.7				1.7 ^a
Cnidarians, ctenophores	< 1-2.1				2.2 (1.9-2.7)
Chaetognaths	2.4-16.4				3.2 (3.0-3.4) ^c
Thaliaceans	< 0.1-10.2				$1.7 (1.2-2.2)^{d}$
Mesozooplankton ^e					2.0-3.5
Shelf			22977	1282	
Shelf edge			32655	1822	
Slope			32733	1827	
Oceanic			23101	1289	
Copepods			0-1000 m	0-1000 m	
Calanoides natalis (C5/F)	337 (0-1947)	84 (0-590)	2956 (140-10609)	458 (50-1645)	2.4-3.0
Rhincalanus nasutus (F)	4 (0-28)	36 (0-280)	352 (0-905)	49 (0-124)	3.2
Aetideopsis carinata (F)	4 (0-24)	4 (0-32)	1264 (0-7254)	160 (0-917)	2.4
Euphausiids (krill)			0-1000 m	0-1000 m	2.6-3.9
Euphausia hanseni	0-11459	0-6320	0-63966	860	2.6-3.1 ^e
Nematoscelis megalops	0-2168	0-795	0-32013	420	3.0-3.9 ^e
Nyctiphanes capensis	0-144440	0-50	0-144440	920	3.2-3.4 ^e
Euphausia americana	0-4213	0-367	0-4213		
Euphausia recurva	0-4814	0-49	0-5592		
Decapods			0-1000 m	0-1000 m	2.5-3.2
Pasiphaea semispinosa	14 (0-148)	94 (0-857)	390 (0-18297)	50 (0-997)	3.1
Oplophorus novaezeelandiae	0	56 (0-719)	939 (0-4529)	62 (0-287)	2.5
Sergia robusta	0	101 (0-1143)	1049 (0-6728)	64 (0-322)	3.2
Fish larvae			0-200 m	0-200 m	
Trachurus capensis larvae			238 (0-7493)	19.2 (0-606)	3.1-3.2 ^f
Sardinops sagax			18 (0-1826)	1.4 (0-140)	3.9-3.0 ^g
Engraulis encrasicolus			21 (0-3106)	1.7 (0-255)	2.7-2.8 ^g

^a relative to POM_{sus}, Koppelmann et al. (2013).

^b relative to POM_{sus}, Koppelmann et al. (2014).

^c only Walvis Bay shelf edge, relative to POM_{sus}, mod. after Bohata and Koppelmann (2013).

 d relative to POM_{sus}, Martin et al. (2017).

^e Werner (2013).

^f Geist et al. (2015).

^g Schukat et al. (2014).

transferred via respiration, egestion, moulting and mortality. During ontogenetic migration large amounts of calanoid copepods migrate to deeper zones between 500 and 1000 m to overcome adverse conditions for several months (Jónasdóttir et al., 2015). All these mechanisms, which are not fully understood yet, foster the transport to bathypelagic layers below 1000 m, where released carbon is sequestered and cannot exchange with the atmosphere over centennial time scales. In contrast, top predators such as fishes feed at deeper water layers and transport carbon into surface waters. Assessments presented here on the contribution of single biological groups to these fluxes give a first impression, however, we are far from providing a holistic view of the processes and their interactions on longer time scales.

Our results emphasize the pronounced variability of the pelagic component in the northern Benguela Upwelling System and the central role of mesozooplankton in the biogeochemical and energy cycles in the system. The complexity of vertical and horizontal distributions of various taxa and their interactions with hydrographical and biogeochemical processes and changes underline the importance to include mesozooplankton in modelling approaches to arrive at realistic results describing energy and biogeochemical fluxes in upwelling systems.

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