



Studies of the Ecology of the Benguela Current Upwelling System: The TRAFFIC Approach

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Abstract

Under the umbrella of SPACES (Science Partnerships for the Adaptation to Complex Earth System Processes in Southern Africa), several marine projects have been conducted to study the coastal upwelling area off southwestern Africa, the Benguela Upwelling System (BUS). The BUS is economically important for the bordering countries due to its large fish stocks. We present results from the projects GENUS and TRAFFIC, which focused on the biogeochemistry and biology of this marine area. The physical drivers, the nutrient distributions, and the different ecosystem components were studied on numerous expeditions using different methods. The important aspects of the ecosystem, such as key species and food web complexity were studied for a later evaluation of trophic transfer efficiency and to forecast possible changes in this highly productive marine area. This chapter provides a literature review and analyses of own data of the main biological trophic components in the Benguela Upwelling System gathered during two cruises in February/March 2019 and October 2021.

11.1 Introduction

The Benguela Upwelling System (BUS) is one of four major Eastern Boundary Upwelling Systems (the others are the California, Canary and Humboldt Upwelling Systems) that are among the most productive marine ecosystems and account for up to 20% of global fish catches (Bonino et al. 2019). The BUS extends about 2000 km along the eastern margin of the South Atlantic between Cape Agulhas (35°S) and the Angola-Benguela Front at ~17°S (Sakko 1998). It is bounded by the Agulhas Current in the south and the confluence of the Benguela Current with the Angola Current at the Angola-Benguela Front in the north (Fig. 11.1), which are the two largest warm-water bodies in the area (Carter 2011). The BUS is divided by the intense upwelling cell off Lüderitz (26°–27°S) into a southern (sBUS) and a northern (nBUS) subsystem (Bakun 1996). Characteristic of the BUS, in relation to the other three eastern boundary upwelling systems, is the width and depth of the coastal shelf that often extends up to 250 km offshore (Bordbar et al. 2021), providing space for the establishment of both shelf break/oceanic fronts at the shelf edge through coastal jets at about 350 to 500 m depth (Ragoasha et al. 2019), and upwelling fronts closer to the coast (Mann and Lazier 1991), with subsequent effects

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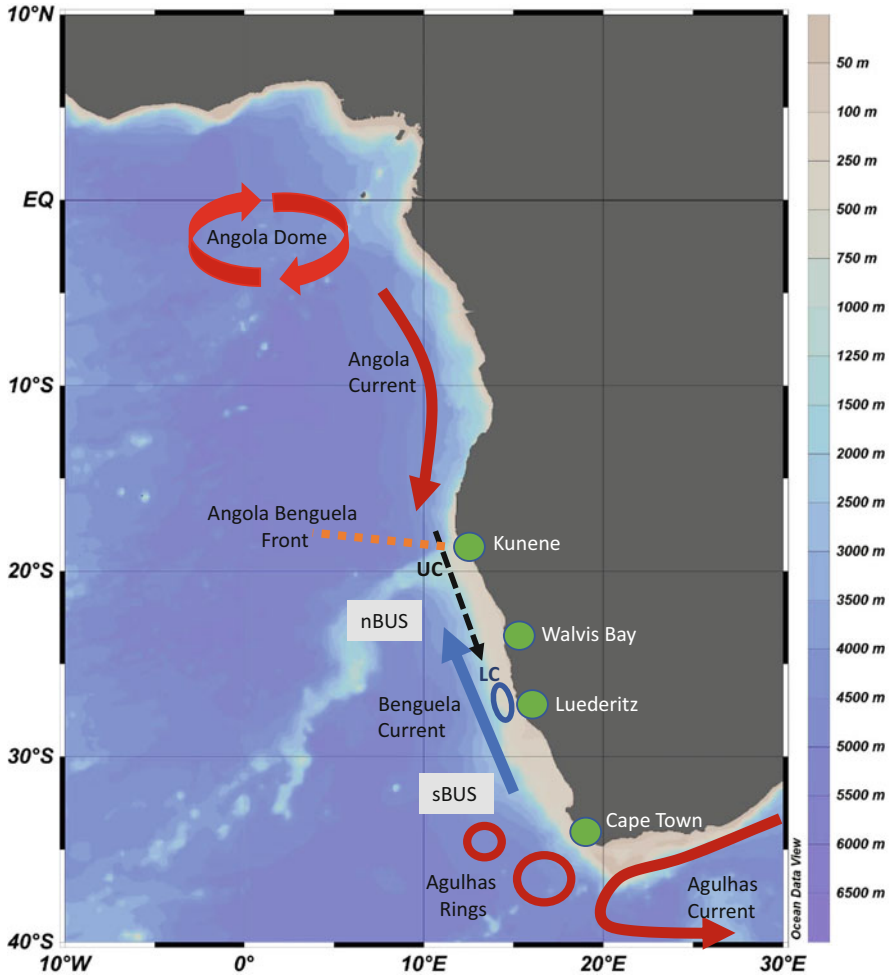


Fig. 11.1 Map of the Benguela Current Region, *LC* Luederitz Upwelling Cell, *UC* seasonally-varying poleward undercurrent, *nBUS* northern Benguela Upwelling System, *sBUS* Benguela Upwelling System

on nutrient supply (Flynn et al. 2020; Rixen et al. 2021) and possible larval trapping on the shelf (see Tiedemann and Brehmer 2017, for the Central East Atlantic).

Upwelling is the movement of surface water away from the coast and is caused by wind drag and Coriolis force. These water masses are replaced by cold and nutrient-rich water from deeper layers by coastal upwelling and Ekman transport (Ekman 1905). A second type of upwelling is the offshore upwelling facilitated through Ekman pumping (Rykanzewski and Checkley 2008; Bordbar et al. 2021). Whereas Ekman transport is dependent on a constant wind field, Ekman pumping responds to gradients in wind strength. This so-called wind stress curl is more

intense in the sBUS than in the nBUS (Fennel and Lass 2007; Bordbar et al. 2021) and important offshore upwelling is indicated for the Cape Columbine/Cape Town and the Lüderitz regions up to Walvis Bay. Wind stress curl-driven upwelling is further responsible for the surfacing of the poleward undercurrent originating in the nBUS, where coastally trapped Kelvin waves may modulate the intensity of the Angola Current. With increased wind stress curl, offshore upwelling uplifts undercurrent water masses to the surface creating highly variable surface currents and intensified upwelling. Important so-called upwelling cells (Shannon 1985) are located at Cape Frio (19°S), Walvis Bay (23°S), Lüderitz (25–26°S), Namaqua (30°S), Cape Columbine (32°S), and Cape Town (34°S). These regionally distinct oceanographic conditions form the basis for separate ecoregions within the BUS. For more details, see Chap. 9.

Upwelling events vary seasonally and locally (Carter 2011). In austral summer (December to March), warm oligotrophic water from Angola (South Atlantic Central Water, SACW) is transported southward and therefore can dominate upwelled water masses in the nBUS at that time of the year (Hutchings et al. 2006). In contrast, Eastern South Atlantic Central Water (ESACW) is transported northward, constituting the upwelled water mass in the sBUS, and also in austral winter in the nBUS (Monteiro et al. 2008; Mohrholz et al. 2014). The ESACW is oxygen-rich, but carries comparatively less nutrients than the SACW further north. ESACW is comprised of a mixture of central waters from the Indian Ocean which enter the Cape Basin as intrusions from the Agulhas Current retroflexion region, with central waters transported across the South Atlantic from the Brazil-Malvinas Confluence, and mode waters which are formed just north of the sub-Antarctic Front in the Southern Ocean (Kersalé et al. 2018; Lamont et al. 2015). Maxima in phytoplankton biomass emerge in spring (September–October) and during late summer/early fall in nBUS, while south of South Africa, on the Agulhas Bank shelf, maxima occur in fall (March–April) (Lamont et al. 2018). It is likely that excessive turbulence and substantial offshore advection in the Lüderitz cell, which is active year-round, is the reason for the phytoplankton minimum in this area (Hutchings et al. 2006, 2012; Lamont et al. 2018).

The high phytoplankton productivity in the BUS, however, is in surprising contrast to the relatively low productivity of the higher trophic levels as compared to the Humboldt Current System (Messié and Chavez 2015). Nutrients reaching the surface during upwelling are expected to be rapidly re-exported, given the substantial offshore transport of surface waters driven by upwelling-favorable winds, so that organisms of the higher trophic levels cannot effectively utilize the available production. The result of this inefficient retention of nutrients is, that, despite short trophic pathways, fisheries yields are relatively low. However, management effectiveness and industrial capitalization cannot be ruled out as a cause for the different rates in fisheries production.

From a human perspective, and regarding the opportunities of harvesting living marine resources, the productivity of an ecosystem's upper trophic levels is of particular interest. Many of the commercially targeted marine species are predatory fish at the upper end of the food chain. Inherently, upwelling systems are characterized

by exceptionally high productivity, the degree of which can be assessed as the ecosystem's trophic transfer efficiency (TTE), alternatively called energy transfer efficiency. In this chapter, we will provide literature and new data on the main biological trophic components in the Benguela Upwelling System. Two research cruises were conducted to cover seasonal variations. A summary of the results is in progress and will be provided elsewhere.

11.2 Previous Research and Hypotheses

The TRAFFIC (Trophic TRAnsfer eFFICIency in the Benguela Current) project is part of the SPACES II program and was conducted between 2018 and 2022. The members of the TRAFFIC consortium have had close collaborations with regional scientific organizations in southern Africa (NATMIRC*, BCC*, UNAM*, UCT*, and DFFE*) or with national projects (BIOTA Africa*, NAMIBGAS*, BENEFIT* (for abbreviations see end of chapter) for many years. These—mostly discipline-specific—precursory works have laid the scientific foundation for the predecessor SPACES I project GENUS (Geochemistry and Ecology of the Namibian Upwelling System). GENUS was a contribution to the international IMBER (Integrated Marine Biosphere Research) initiative of the IGBP (International Geosphere-Biosphere Programme) and was built on the established regional research collaborations BENEFIT (Benguela Environment Fisheries Interaction and Training, 1997–2007) and BCLME (Benguela Current Large Marine Ecosystem, since 2002). Many crucial data sources used as the knowledge base for TRAFFIC were developed in GENUS and other predecessor projects. In addition to providing valuable scientific results for understanding climate-induced changes in upwelling areas and the ecosystem services associated with them, TRAFFIC has deepened the collaboration with scientists in the partner countries Namibia and South Africa.

The GENUS project (see Ekau et al. 2018) has shown that, regarding the overall net flux of carbon dioxide, the northern Benguela subsystem releases CO₂ into the atmosphere, while the southern subsystem takes up CO₂ (Emeis et al. 2018). Previously, this difference was attributed solely to different oceanographic conditions. The nutrient- and CO₂-rich South Atlantic Central Water (SACW) is a main water supply to the northern Benguela, whereas the comparatively nutrient- and CO₂-poor Eastern South Atlantic Central Water (ESACW) forms the main upwelling water in the southern subsystem (Fig. 11.1). Consequently, upwelling in the nBUS promotes the emission of CO₂ to the atmosphere on the Namibian shelf and the export of carbon from the euphotic zone to the deep ocean, readable from the formation of the carbon-rich silt layers at the seabed. In contrast, upwelling in the sBUS leads to a net uptake of CO₂ and is accompanied by lower carbon sedimentation rates (Mollenhauer et al. 2004). Differences in fishery yields and results of biological studies show that in contrast to the relatively short food chain in the sBUS, which has been considered typical of upwelling systems, the food web is more complex in the nBUS. Because primary production is very similar in the northern and southern subsystems (Barlow et al. 2009), these relationships indicate

more efficient utilization within the food chain in the southern Benguela. The aim of the TRAFFIC project has been to unravel the biological processes leading to the differences in the TTE between the food webs of the two subsystems of the BUS.

TRAFFIC also relates studies of the food web to ongoing climate-related changes in the BUS. Recent findings from modeling studies have shown a poleward shift in subtropical high-pressure areas due to global climate change (Garcia-Reyes et al. 2015; Rykaczewski et al. 2015; Wang et al. 2015). As a result, the trade winds in the sBUS will likely intensify, whereas the wind speeds and upwelling intensities in the nBUS will likely weaken. Our investigation will unravel the effects of ongoing changes in physical forcing on the overall productivity and the food web structure of the Benguela Current subsystems.

Historically, it has been assumed that around 90% of material and energy is lost by metabolic activity from one trophic level to the next higher trophic level and that only 10% reaches the next level (Lindeman 1942). This value, however, can be very variable. Eddy et al. (2020) compiled data from several studies based on Ecopath with Ecosim models and calculated that the TTE ranges from 0.3% to 52.0% between trophic levels 2–3 and 3–4 with means of 12.0% in polar/subarctic-boreal regions, 9.6% in temperate regions, 8.6% in tropical/subtropical regions, and 8.0% in upwelling regions. In a warmer world, i.e., under climate change, the TTE may decrease due to higher metabolic losses. Freshwater plankton in artificial ponds that have been exposed for seven years to 4 °C warming relative to ambient conditions showed a decrease of TTE by up to 56% (Barneche et al. 2021). Projections by du Pontavice et al. (2020) also assume a decrease of TTE until 2100 under the RCP 8.5 global warming scenario, which would be associated with an increase of about 4.8 °C in global mean temperatures.

Different physical conditions affect primary production (PP) and subsequent consumers, thereby determining the efficiency with which the produced biomass is carried through the food web. Low-latitude stratified ecosystems are dominated by small phytoplankton and carbon is routed through many trophic levels (TLs) before reaching pelagic fish. The overall TTE (the transfer of energy from primary to secondary producers and higher trophic levels) is furthermore driven by the complexity of the food web (see also Armengol et al. 2019). The mean number of TLs between primary producers and fish is around 6 in oceanic, 4 in coastal, but only 2.5 in upwelling regions (Ryther 1969; Eddy et al. 2020). A short food chain generally results in a high trophic transfer efficiency, for example when large chain-forming diatoms are consumed directly by sardines, without an intermediate level of zooplankton consumers (Moloney et al. 1991; van der Lingen et al. 2006a). The timing of the development of the different components in the food web, i.e., the temporal match and mismatch of TLs (Cushing 1990), is crucial for an efficient overall TTE. However, alternative dead-end scenarios for carbon transport may exist when stochastic blooms of salps consume the entire primary production and carbon does not reach higher TLs but sinks into deeper water layers at an increased rate (Martin et al. 2017). Consequently, zooplankton composition as well as the food web structure determine the amount of carbon and energy reaching upper trophic levels such as fish, seabirds, and marine mammals, and ultimately fisheries.

From this point of view, ecosystems dominated by the zooplanktivorous (krill-dominated diet) but partly piscivorous horse mackerel (Pillar and Barange 1998; Kadila et al. 2020) will be less productive in comparison to those dominated by anchovy and/or sardines that feed on smaller (copepods) zooplankton but also phytoplankton (van der Lingen et al. 2006a). Results of the GENUS project revealed that trophic interactions and the community structure of trophic levels are not as simple and straight-forward as previously thought with Schukat et al. (2014) showing that trophic roles of calanoid copepods in the nBUS were far more complex than merely linking phytoplankton to pelagic fish.

Recent work has suggested that so-called “dead end” species (e.g., jellyfish and salps that feed on primary and/or secondary producers/consumers and were previously considered to be rarely consumed by predators) can be trophically important (Hays et al. 2018; Gibbons et al. 2021). Specifically, they can outcompete planktivorous fishes by forming intensive blooms when conditions are favorable and increase the export of organic matter to deeper layers by producing fast-sinking fecal pellets and mass mortality events. This reduces the energy available for higher trophic levels and the recycling of nutrients within the epipelagic realm.

The TRAFFIC project set out to closely investigate and compare the nBUS and the sBUS ecosystems in relation to the underlying oceanographic and biogeochemical processes. Based on the concept of three alternative structures of the food chain (Fig. 11.2) and on recent climate models that suggest an intensification of winds and upwelling in the sBUS, in contrast to a weakening of the upwelling intensity in the nBUS (Garcia-Reyes et al. 2015; Rykaczewski et al. 2015; Wang et al. 2015), TRAFFIC investigated how current conditions influence productivity, carbon export and food chain structure in the two subsystems, and hence their trophic transfer efficiency and potential to support top predators and fisheries.

11.3 Major Biological Components of the Benguela Upwelling System

For the comparison of the TTE of the northern and southern BUS it is not only crucial to get a picture of the community structure and food web complexity, but it is also necessary to identify the starting conditions such as the efficiency of primary production and to follow the energy from the base of the food web to top predator level. For this purpose, two research cruises in the TRAFFIC project have been undertaken: a first one with RV METEOR in austral summer (M153, February/March 2019) and a second one with RV SONNE at the end of austral winter (SO285, September/October 2021). During these cruises, samples were collected with different gears in order to measure physical drivers, and to quantify biomass, standing stocks and plankton and fish composition of the two ecosystems. Additionally, experiments were set up onboard the ships to measure vital rates such as primary production, respiration, growth, metabolism and grazing of various planktonic organisms.

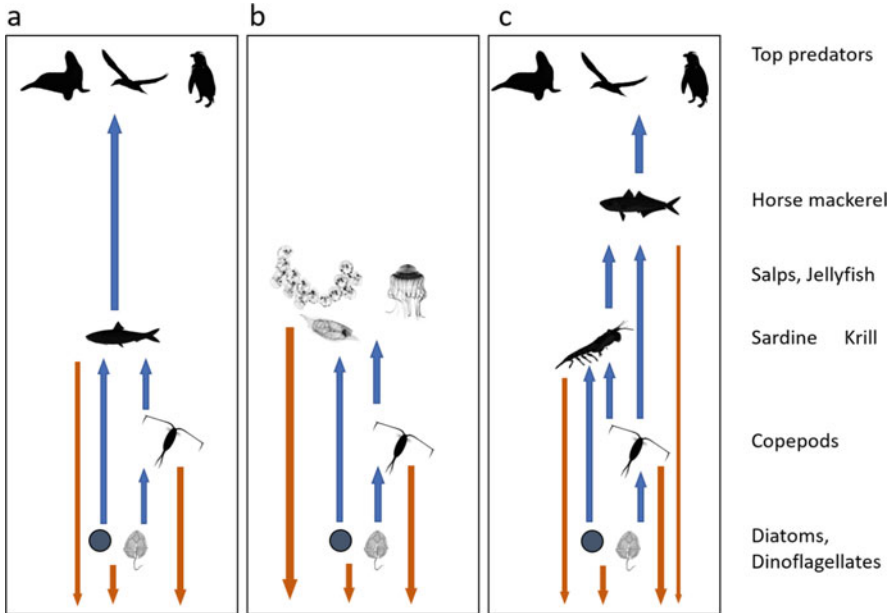


Fig. 11.2 Three alternative simplified food web structures which may establish in the Benguela Upwelling System and lead to different trophic transfer efficiencies: (a) Typical short food chain of an Eastern Boundary Upwelling System; highly efficient transfer of carbon to upper trophic layers (common in sBUS); (b) food chain structure during mass occurrences of gelatinous zooplankton (salps and jellyfish), decoupling from higher trophic levels (occasionally in nBUS and sBUS); (c) long food chain with less efficient overall trophic transfer, common in nBUS. Blue arrows: upward transport of energy and matter through the food chain; brown arrows: export flux of energy and matter

11.3.1 Abiotic Parameters and Chlorophyll Measurements

A high-speed remotely operated towed vehicle (ROTV, TRIAXUS) was used during cruise M153 in 2019 (see also Rixen et al. 2021) to measure temperature, salinity, oxygen content, nitrate, chlorophyll *a* (Chl *a*) and other pigments, turbidity, photosynthetic active radiation (PAR) and hydroacoustics on several transects in the nBUS and sBUS (Fig. 11.3). Zooplankton was analyzed using a mounted Video Plankton Recorder (Möller et al. 2012). The vehicle was towed at a speed of 8 knots with a horizontal offset out of the vessel's wake, undulating vertically between 5 and 180 m, depending on the water depth.

Vertical profiles of conductivity, temperature, pressure, oxygen, fluorescence, turbidity and photosynthetically active radiance (PAR) were obtained using a CTD in-situ (Fig. 11.4, left). These data were compared with satellite images of temperature and chlorophyll at the surface (Fig. 11.4, right) to provide background information for future evaluations.



Fig. 11.3 TRIAXUS on deck of RV METEOR

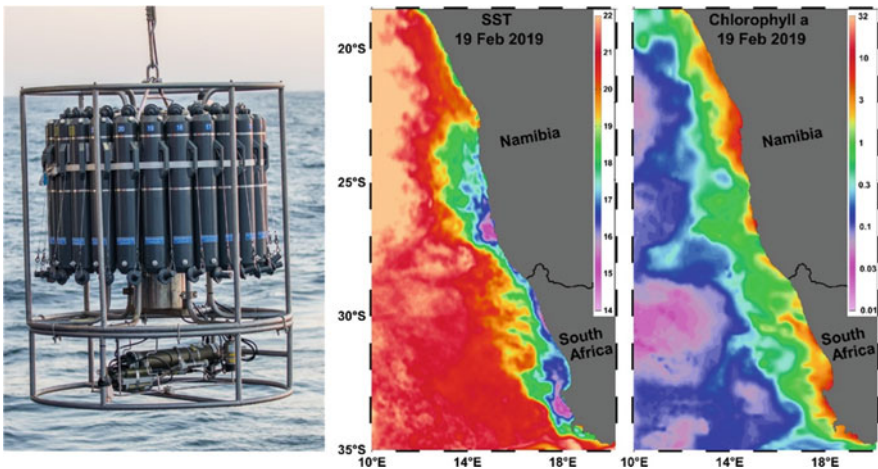


Fig. 11.4 Left: CTD with rosette; Right: Satellite data of sea surface temperature (SST) and Chl *a* during the expedition M153 in February 2019

11.3.2 Phytoplankton and Microzooplankton

The base of the food web, i.e., the primary producers and the microzooplankton were investigated to determine the quality and quantity of food available for higher trophic levels. For this purpose, water was taken from different depths using a Niskin bottle rosette attached to the CTD and filtered to determine the Chl *a*

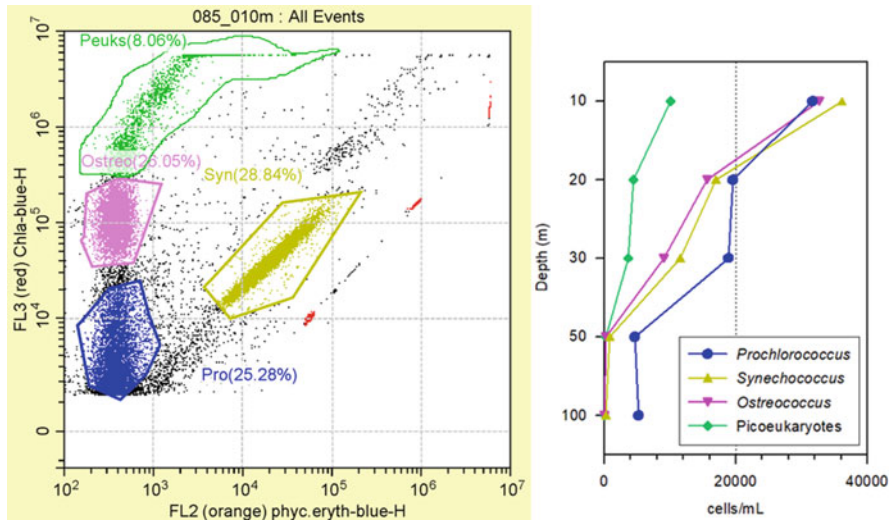


Fig. 11.5 Left: Bivariate plot of red fluorescence (FL3) vs. orange fluorescence (FL2) for acquired flow cytometry at 10 m depth, station 85 (30°S, 16°30'E). Preliminary gating was performed marking picoeukaryotes in green, *Ostreococcus* in pink, *Synechococcus* in yellow and *Prochlorococcus* in blue. Right: From flow cytometry converted abundance profile in the upper layer (10–100 m) of the main picophytoplankton groups at station 85

content by spectrometry and the pigment composition by HPLC (High-Performance Liquid Chromatography). The results will be intercompared with remotely sensed data. A fluoroprobe was used in addition to the water samples to analyze different phytoplankton groups (green-algae, blue-green algae, diatoms, and cryptophyta) *in situ*.

In order to assess the contribution and the community composition of picophytoplankton (0.2–2 μm) water samples were analyzed onboard using a flow cytometer (CytoFLEX, Beckman Coulter) for counting and identifying the main groups like *Prochlorococcus*, *Synechococcus*, and *Ostreococcus* as well as picoeukaryotes (Fig. 11.5).

Further water samples were taken to study nanophytoplankton composition by cross polarized light microscopy, as well as microphytoplankton composition by inverse microscopy in the home laboratories and to assess the photosynthetic fitness of the phytoplankton onboard the ship using the Fast Repetition Rate Fluorometry (FRRF, Fasttracka II, Chelsea Technology, UK). FRRF is a noninvasive method to measure the activity of primary producers using Chl *a* fluorescence (Oxborough et al. 2012). Small plankton were caught with an Apstein net (20 μm mesh size) to study the trophic positions and nutritional quality of phyto- and microplankton applying stable isotope and fatty acid analyses. The taxonomical composition was determined using fluid imaging (FlowCam). The FlowCam takes pictures of the organisms found in a sample (Fig. 11.6), which can be analyzed subsequently by

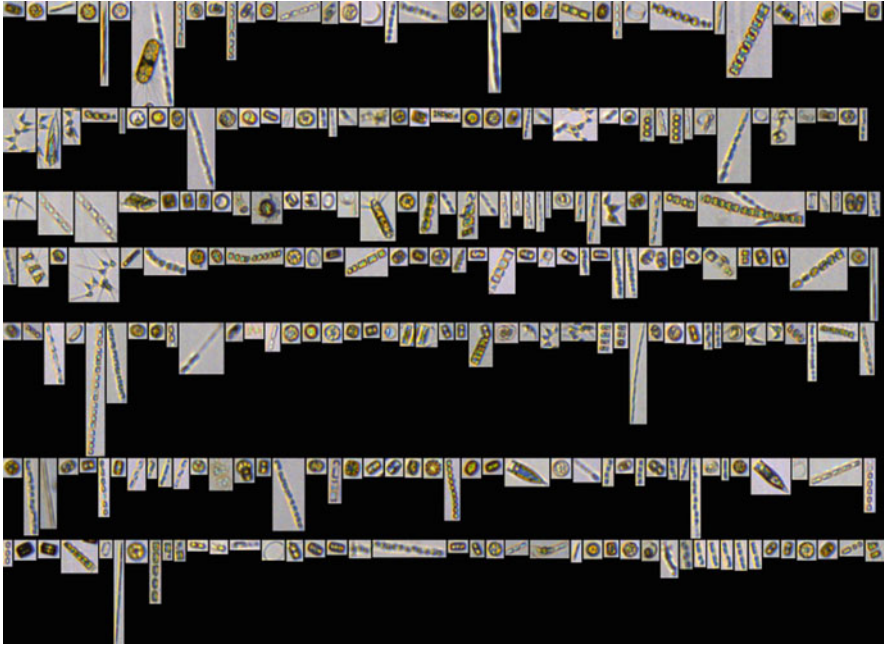


Fig. 11.6 FlowCam images from a diatom bloom in the sBUS during cruise SO285

a deep learning program which has been trained using plankton samples from the Benguela ecosystem.

Marine life does not react immediately following upwelling events but rather with certain time lags. Initially, abundance and productivity are low in recently upwelled and highly turbulent waters (Ayon et al. 2008; Ekau et al. 2018), because upwelling water originates from the central water layer below the thermocline, where the phytoplankton stock is low. Furthermore, strong turbulence inhibits phytoplankton growth by transporting the organisms out of the range of photosynthetic active radiance. Production peaks in moderate upwelling and in quiescent phases after upwelling events (Grote et al. 2007; Bode et al. 2014), forming an optimal environmental window (Cury and Roy 1989). 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.

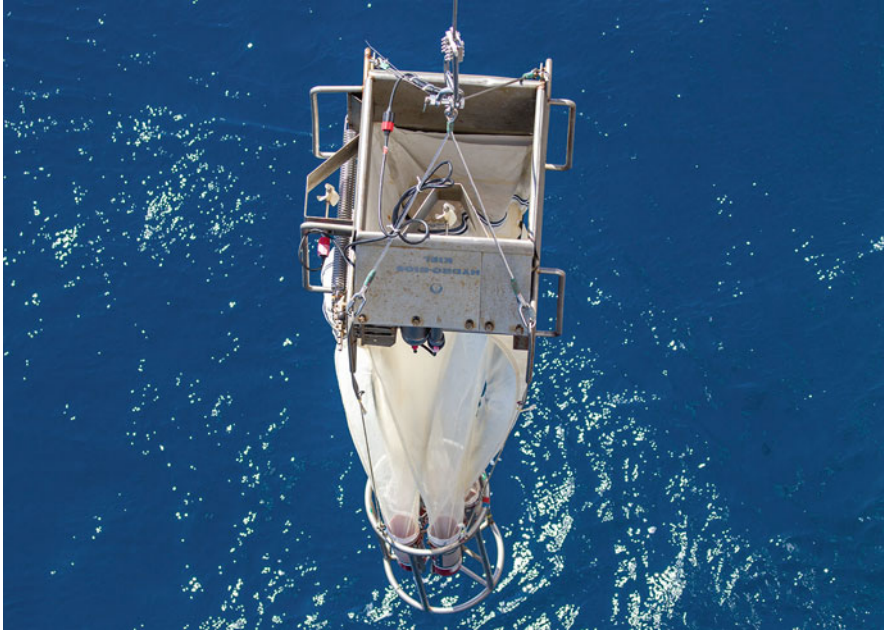


Fig. 11.7 Multinet Midi used to sample microzooplankton

Primary production and respiration rates were measured by incubation of water from the most productive layer (Deep Chlorophyll Maximum) at in-situ temperatures under different light conditions in a plankton-wheel.

In marine ecosystems, generally 60% to 70% of primary production is consumed by microzooplankton and 10% to 40% by mesozooplankton (Calbet 2001; Calbet and Landry 2004), with microzooplankton also being an important dietary component of mesozooplankton (Bollens and Landry 2000; Calbet and Saiz 2005). Phytoplankton growth rates and microzooplankton grazing were studied using the dilution method after Landry (1993). Landry (1993) postulated higher algae growth in water with less microzooplankton predators and undisturbed growth in the highest dilution. The experiment concomitantly gives information about the grazing activity of the microplankton.

Microzooplankton for taxonomic and stable isotopic analyses were collected with a HydroBios Midi (mouth area 0.25 m²) Multinet (multiple opening/closing net) system equipped with five nets (55 μm mesh size) in discrete depth intervals (Fig. 11.7). Vertical hauls were conducted with hauling speed of 0.2 m/s from 100 m depth up to the surface.

Microzooplankton (< 200 μm, sampled with 55 μm meshed nets) of the nBUS is often dominated by mixotrophic and heterotrophic dinoflagellates, tintinnids and small copepods (Bohata 2016). Figure 11.8 shows some of the microzooplankton organisms sampled during cruise M153.

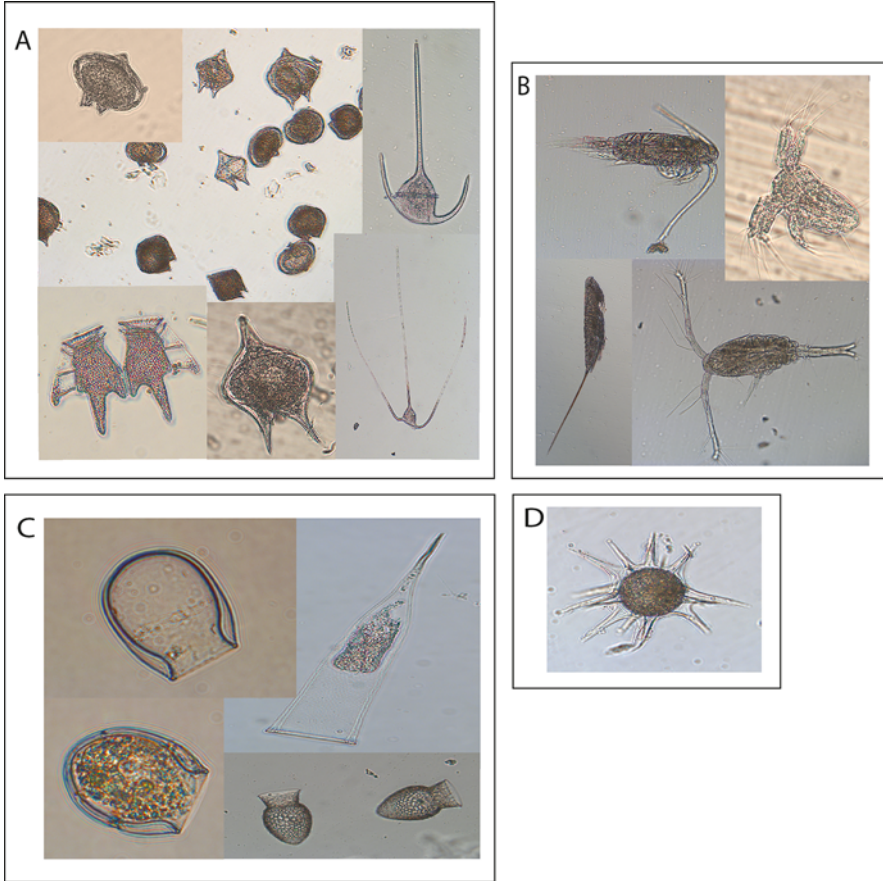


Fig. 11.8 Four important microplankton groups: (a) Mixo- und heterotrophic Dinoflagellata, (b) small Copepoda and nauplia, (c) Tintinnida, (d) Radiolaria

The microplankton distribution patterns revealed a shelf—offshore zonation and clear temperature associations (Fig. 11.9). Heterotrophic dinoflagellates such as *Protooperidinium* and *Noctiluca scintillans* prevailed in $<15^{\circ}\text{C}$ cold, recently upwelled water on the shelf, whereas subsequent succession stages in $15\text{--}20^{\circ}\text{C}$ warm surface water on the shelf were dominated by small copepods such as *Oncaea*, *Oithona* and *Microsetella*. *Protooperidinium*, Tintinnidae and the mixotrophic dinoflagellate *Ceratium* were abundant in decreasing order in $>20^{\circ}\text{C}$ warm surface water at the shelf break. Tintinnidae contributed $>37\%$ to microzooplankton at the medium-warm shelf break, followed by *Oncaea*, *Microsetella* and *Protooperidinium*. The cold water and shelf break areas were dominated by *Oncaea*, followed by *Protooperidinium* and *Ceratium*. The warm offshore region was dominated by Tintinnidae comprising $>30\%$ of total abundance. Mixotrophic (*Ceratium*) and heterotrophic (*Protooperidinium*) dinoflagellates were also very abundant here,

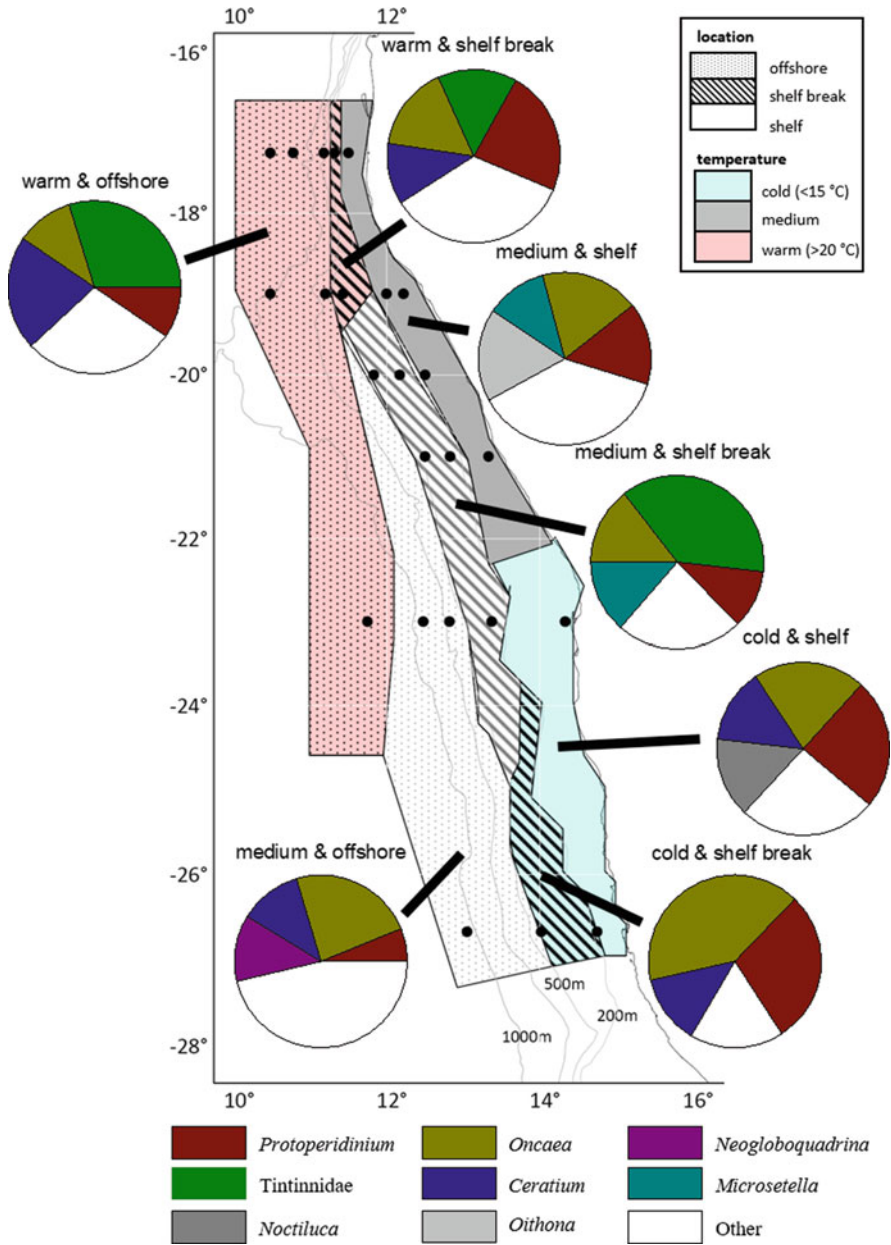


Fig. 11.9 Dominant microplankton taxa in different habitat zones of the northern Benguela Upwelling System during September/October 2011 (modified after Ekau et al. 2018)

collectively making up >30% of total abundance. The medium-warm offshore area was characterized by high abundances of *Oncaea* (> 23%) and the Foraminifera *Neogloboquadrina* (>14%) (see also Bohata 2016).

11.3.3 Mesozooplankton

Mesozooplankton plays a key role in the energy transfer from primary production and microzooplankton to higher trophic levels. Due to their short generation times and direct coupling to physical drivers, zooplankton reacts sensitively to climatic change and can be used as indicators of environmental change (Hays et al. 2005). Cyclopoid and calanoid copepods usually dominate the mesozooplankton communities (on average 70%–85%) in the nBUS and sBUS, playing a key role in sustaining marine fish stocks as a principal food source for larvae, juveniles and adults and sometimes all three stages (Hansen et al. 2005; Bode et al. 2014; Verheye et al. 2016). Furthermore, Bivalvia larvae can be sporadically dominant at near-shore regions, while Appendicularia (*Oikopleura*), Thaliacea (Doliolida, Salpida), Amphipoda and Euphausiacea can contribute substantially to abundance and/or biomass further offshore. Along the continental slope in the nBUS, the krill species *Euphausia hanseni* plays an important role in the active carbon flux from the productive shelf to the adjacent open ocean and into the deep sea because of its pronounced diel vertical migration (Werner and Buchholz 2013).

Mesozooplankton sampling consisted of vertical hauls with a multiple opening/closing net (HydroBios Multinet Midi, five nets, 0.25 m² mouth opening, 200 µm mesh size) at 0.5 m/s hauling speed. Samples were taken from discrete depth layers down to ~10 m above sea floor (minimum bottom depth 55 m at inshore stations, maximum sampling depth 1500 m offshore). Additional material of larger and more mobile species (krill, decapods) were collected from double oblique hauls of a Multinet Maxi (0.5 m² opening area, five nets of 300 µm mesh size; HydroBios). All samples were presorted onboard and potential key zooplankton and other species of the food web were deep-frozen at –80 °C for trophic biomarker analyses (stable isotopes and fatty acids). Key copepod species (Fig. 11.10) were selected from the net samples for in-situ experiments to measure respiration, egg production and fecal pellet production.

During periods of active upwelling, the BUS zooplankton communities on the shelf are dominated by the biomass-rich herbivorous-omnivorous copepod *Calanoides natalis* (ex *C. carinatus*; Bode et al. 2014) and small calanoid (esp. *Acartia*, *Clausocalanus*, *Ctenocalanus*, *Paracalanus*, *Calocalanus* spp.) and cyclopoid (esp. *Oithona* spp.) copepods (Verheye et al. 2016; Bode-Dalby et al. 2022). With increasing bottom depth closer to the continental slope, *Centropages brachiatus* and *Metridia lucens* occur at higher abundances. Further offshore, the copepod community is more diverse, due to mixing of cold- and warm-water species as well as deeper-dwelling diel vertical migrants such as *Pleuromamma* spp. When upwelling ceases and warmer water masses intrude/expand onto the shelf, the shelf community is replaced by medium-sized copepod species such as *Nannocalanus*



Fig. 11.10 Copepods and amphipods in the Benguela Upwelling System. Top row: *Pareucalanus sewelli*, *Pleuromamma quadrangulata*, *Candacia* sp.; second row: *Euchaeta* sp., *Gaetanus pileatus*, *Euchirella similis* female with two egg sacs; bottom row: *Vibilia armata*, *Phronima* sp.

minor (Schukat et al. 2013, 2014; Bode et al. 2014). A striking difference between the northern and southern Benguela copepod community is the absence of *Calanus agulhensis* in the nBUS, as it is apparently advected offshore and away from the nBUS by the strong and permanent Lüderitz upwelling cell. So far, *C. agulhensis* has not been recorded in the nBUS. *C. agulhensis* is the most abundant calanoid copepod on the Agulhas Bank, a major spawning ground for sardines and anchovies in the sBUS (Peterson et al. 1992; Huggett and Richardson 2000; Richardson et al. 2003). Later/older copepodid stages and adults of *C. agulhensis* are advected to the South African west coast, where its abundance is associated with warmer offshore waters (Huggett and Richardson 2000; Huggett et al. 2007).

Phytoplankton growth after an upwelling event is followed by increasing copepod abundance about 20–23 days after initial upwelling (Postel et al. 1995; Hutchings et al. 2006). In contrast to the sBUS, the seasonal signal in the nBUS is often diffuse with high interannual variability. Upwelling events, as well as

zooplankton abundances, can be strongly pulsed with huge local and interannual variability and multiple interacting factors. Long-term data series derived from the Namibian monitoring program emphasize the complex interannual variability in the nBUS, where years with intense upwelling in spring can be followed by strong warm-water intrusions of tropical Angola Current water masses in late summer (Bode et al. 2014; Martin et al. 2015). Such years with strong seasonal temperature gradients were characterized by high copepod abundances suggesting a strong link between zooplankton distribution and physical forcing (Bode et al. 2014).

In the sBUS, zooplankton abundance was positively correlated to upwelling intensity (Verheye et al. 1998), although seasonal cycles of mesozooplankton differ depending on the subregion (Verheye et al. 2016). For instance, around St. Helena Bay (32–33°S), mesozooplankton populations usually peak during late summer and show a distinct decline in autumn. On the western Agulhas Bank (35°S), on the other hand, maximum mesozooplankton abundance usually occurs during late autumn and spring. Differences in mesozooplankton abundances and community structure are not only caused by bottom-up mechanisms such as upwelling intensities and phytoplankton availability, but also by the distribution patterns of different planktivorous fish (“small pelagics”) and their life-history stages along the southwestern African coast (Verheye et al. 1998; Hutchings et al. 2006; van der Lingen et al. 2006b). Furthermore, stochastic mass occurrences (“blooms”) of gelatinous zooplankton such as salps or jellyfish can eliminate other plankton and reset the succession of the entire pelagic community (Martin et al. 2017).

Besides predator-prey interactions and food web structure, the availability of dissolved oxygen and the vertical extent of the oxygen minimum zone (OMZ) strongly determines the distribution of zooplankton in the BUS, especially in the nBUS (Auel and Verheye 2007; Ekau et al. 2010). Such OMZs occur regularly on the Namibian shelf in the nBUS (Schmidt and Eggert 2016) and around St. Helena Bay in the sBUS (Pitcher et al. 2014), yet, at different extents. The specific conditions on the Namibian shelf are favorable for benthic sulfur bacteria, which may form thick mats and, during occasional anoxic conditions, cause hydrogen sulfide eruptions (Schmidt and Eggert 2016). Many zooplankton species can cope with the upwelling-driven, highly pulsed productivity regime, strong advective processes and the regionally pronounced OMZs. The dominant copepod *C. natalis* is well adapted to the highly dynamic upwelling regime with its reproductive strategy, lipid accumulation, ontogenetic vertical migration, and dormant phase (diapause) of C5 copepodids at depth (Auel et al. 2005; Verheye et al. 2005; Auel and Verheye 2007; Schukat et al. 2013, 2014; Bode et al. 2015). Females of *C. natalis* and other species such as *M. lucens* or *C. agulhensis* maintain their populations in the productive shelf region through diel vertical migration (DVM) between surface currents and subsurface counter-currents (Timonin 1997; Huggett and Richardson 2000; Loick et al. 2005). Species that can retreat into OMZs for at least part of the day have various advantages, e.g., finding refuge from predators (Loick et al. 2005). The extent of DVM can also be adapted to upwelling intensities and food availability: *C. natalis* and *C. agulhensis* showed very pronounced DVM during periods of increased advection and high Chlorophyll *a* concentrations,

whereas DVM was reduced during quiescence of upwelling and low phytoplankton concentrations (Verheye and Field 1992; Huggett and Richardson 2000).

Since the 1950s, long-term changes of zooplankton abundance and biomass have been observed in the entire BUS (Verheye and Richardson 1998; Verheye 2000; Huggett et al. 2009; Hutchings et al. 2009; Verheye et al. 2016). Around Walvis Bay (23°S), copepod abundances increased six-fold from the 1980s to the early 2000s, followed by a decline after 2005 (Hutchings et al. 2009). In contrast to the nBUS, the sBUS has been studied more regularly in terms of zooplankton abundance and community structure making long-term assessments more reliable (reviewed by Verheye et al. 2016). A 100-fold increase in total copepod abundance (cyclopoids and calanoids) was reported for the sBUS between 1950 and 1995 (Verheye et al. 1998). Between 1988 and 2003 copepod biomass and production along the entire sBUS coast were around one order of magnitude higher than in the late 1970s (Huggett et al. 2009). This long-term increase in copepod abundance was accompanied by increasing wind stress and upwelling intensities (Shannon et al. 1992; Verheye 2000), and it also coincided with the onset of commercial fishing since the 1950s (Verheye et al. 2016). Since the mid-1990s, copepod abundance decreased again slightly; thus, the decline in copepod abundance started one decade earlier than in the nBUS (Verheye et al. 2016).

In both subsystems, there has also been a size shift in the mesozooplankton communities from larger to smaller species during the last decades (Verheye and Richardson 1998; Verheye et al. 2016). In the 1950s, euphausiids (esp. *Euphausia lucens* and *Nyctiphanes capensis*) and large to medium-sized copepods such as *C. natalis*, *R. nasutus*, and *C. brachiatus* prevailed in the species composition of St. Helena Bay. From the late 1980s onward, smaller copepod species such as “small calanoids” (mostly Clausocalanidae and Paracalanidae) and the cyclopoid *Oithona* spp. became clearly dominant (Hutchings et al. 2012; Verheye et al. 2016). The shift from larger to smaller species can be an indicator of ocean warming, whereas a cooling trend by up to 0.5 °C per decade has been evident from the 1980s onward due to intensification of upwelling in this region (Rouault et al. 2010; Verheye et al. 2016). Both oceanographic and biological processes (bottom-up control) together with predation effects (top-down control), particularly size-selective feeding of sardines and anchovies, seemed to cause these changes in the zooplankton communities (Verheye et al. 1998; Verheye and Richardson 1998; Hutchings et al. 2012). The decline of larger copepods in the St. Helena Bay region since the mid-1990s coincided with a marked increase in biomass of small pelagic fish such as anchovy, which potentially prey on these copepods (Hutchings et al. 2012; Verheye et al. 2016). In the nBUS, no clear predator-prey relationships between zooplankton and fish have been identified to date. After the decline of anchovies in the mid-1990s no increase of larger copepods was detected (Verheye et al. 2016). Hence, the relative importance of bottom-up vs. top-down effects remains uncertain, but it is clear that such changes in zooplankton have fundamental effects on biogeochemical processes, food web structure and thus ecosystem functioning and services.

Due to considerable interannual variability and different patterns in various sub-regions of the BUS, trends in one region and season cannot be extrapolated to other regions in the BUS, emphasizing the need for high spatial, seasonal, and taxonomic coverage of continuous monitoring programs (Huggett et al. 2009; Kirkman et al. 2016; Verheye et al. 2016). Thus far, the discontinuous and heterogeneous nature and the relatively poor data of the BUS compared to time series from other systems do not allow far-reaching conclusions about the synchronicity of fluctuations of zooplankton biomass and abundance at spatial scales similar to those found for fish species (Batchelder et al. 2012). This emphasizes the need for appropriate and concrete actions proposed by the Benguela Current Commission to advance sustainable development of the BUS goods and services (Verheye et al. 2016). Characterizing zooplankton communities by functional types and not only focusing on large species will help improving predictive biogeochemical and ecosystem models. The community structure of the small calanoid copepods in the BUS has not been well distinguished so far (Bode-Dalby et al. 2022). There are contradictory and uncertain mentions of *Microcalanus* (= *Clausocalanus*?) and *Pseudocalanus* (= *Ctenocalanus*?) spp. (Verheye et al. 2016); thus, it is not known how diversity of small copepods and their functional role has changed over the last decades.

11.3.4 Macrozooplankton and Micronekton

To investigate the trophic transfer efficiency in midwater ecosystem components, biomass size spectra comprising all major taxa encountered, i.e., fish, crustacean and gelatinous plankton (see Fock and Czudaj 2019) were analyzed, as well as diurnal feeding patterns and food composition of key fish species in combination with stable isotope ratios for selected fish species, medusa and crustacean plankton and other micronekton.

The vertical distributions of macrozooplankton and micronekton were analyzed using depth-stratified net catches (Multinet-maxi, Multinet-midi, Rectangular Midwater Trawl RMT, Figs. 11.7, 11.11) as well as horizontal surface sampling (Neuston catamaran). These were used to assess abundance, biomass, and species composition, and also to gain information about the behavior of fish larvae in relation to hydrography on meso-spatial scales and at high vertical resolution. Fishes were captured mostly at night in double oblique hauls down to 500 m depth.

In order to be able to construct normalized biomass size spectra (NBSS), samples were analyzed using digital imaging tools such as the ZooScan (Fig. 11.12). Similar to the FlowCam method for phytoplankton and microzooplankton, organisms like krill, chaetognaths, and fish larvae were scanned and measured digitally. Thus, size and volume could be calculated in addition to taxonomic classification and abundance. The age, RNA/DNA ratios, fatty acid composition and C/N isotope content of commercially important fish larvae (mostly *Trachurus capensis*, *Sardinops sagax*, and *Engraulis encrasicolus*) were analyzed to indicate their fitness and condition.

Fig. 11.11 Mesopelagic fishes, large crustaceans and gelatinous plankton were collected using a Rectangular Midwater Trawl (RMT 8)



A Kongsberg EK80 hydroacoustic system was used on the first cruise (M153) to detect fish and biomass aggregations of smaller nekton. A configuration using a frequency of 38 kHz and a long pulse duration of 1.024 ms allowed the detection of biomass down to 750 m depth (Fig. 11.13). Smaller particles could be detected using a 200 kHz transducer, but only to a depth of about 150 m. By continuous activation of the echosounder, the hydroacoustic systems were able to document the vertical distribution of biomass, diel vertical migration and behavioral changes of the spatial distributions of organisms like zooplankton and fish. In this way, the mesopelagic zone could be monitored continuously, which led to the first documentation of deep-scattering layers (DSL) in the Benguela ecosystem between 300 m and 600 m depth. The intense diel vertical migration between the DSL and the

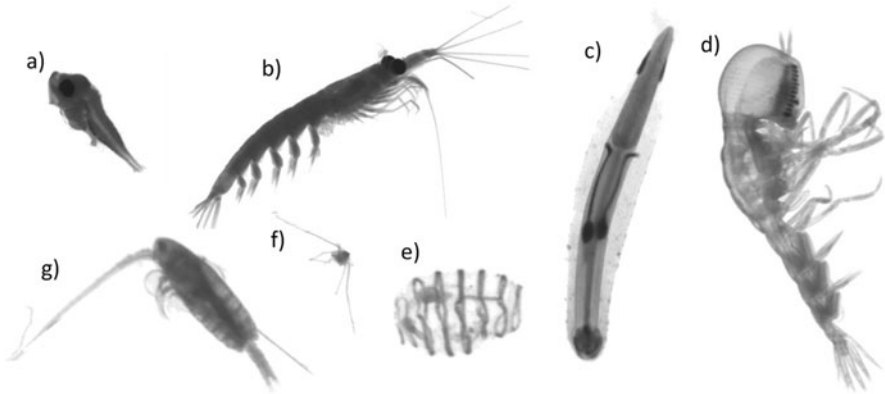


Fig. 11.12 Zooscan pictures of (a) *Trachurus capensis* larvae, (b) Euphausiacea, (c) Chaetognatha, (d) Amphipoda: *Paraphronima* sp., (e) Salpidae, (f) Pluteus larvae, (g) Copepoda

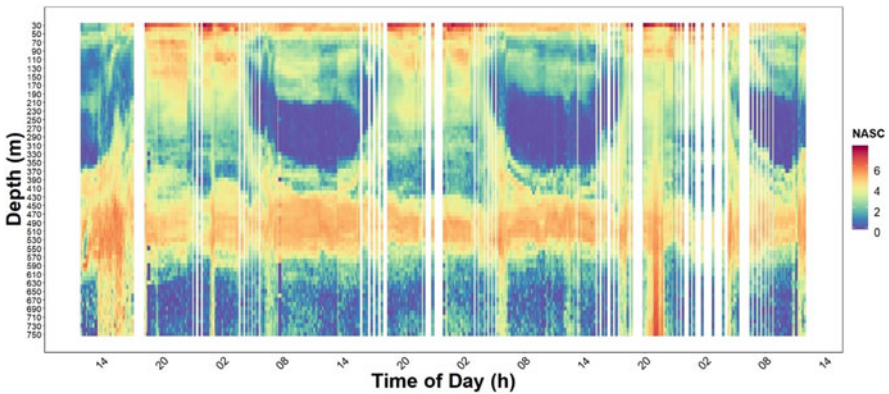


Fig. 11.13 Diel vertical migration from the Deep-Scattering Layer over a 72 h cycle at Station 18, sBUS, recorded by the EK80 during M153. Nautical Area Scattering Coefficient (NASC, as $\log \text{m}^2 \text{nm}^{-2}$) was calculated over 10 m depth bins and 10 min intervals and serves as a proxy for biomass

surface layers, dominated by certain euphausiids and mesopelagic fishes, shows the strong connection between the deep sea and the productive euphotic zone (see Fig. 11.13). During the cruise SO285, a more powerful hydroacoustic system was used. This EK60 configuration with four frequencies (18, 38, 120 and 200 kHz) allows for the distinction between acoustic response curves, or echoes, of different taxonomic groups and can help to distinguish between acoustic biomass of jellyfish, krill and different species of fishes. To further identify the origin of the acoustic biomass, rectangular midwater trawls were carried out in specific layers of high biomass. These reference hauls can then be compared to the acoustic signals of these layers to associate biomass with certain species or groups.

The Benguela Upwelling System is unique in its mesopelagic fish diversity, as it is influenced by the warm Angola and Agulhas Currents to the north and south, respectively, as well as the cold Benguela Current to the west (Duncombe-Rae 2004; Lett et al. 2007; Hutchings et al. 2009), leading to a mix of tropical, subtropical, and temperate species of mesopelagic fish (Duncan et al. 2022). Sutton et al. (2017) described the Benguela as a unique global biogeographical region for its mesopelagic fauna, where pseudo-oceanic species dominate due to the close distance of the frontal region to the shelf break (Hulley 1981; Hulley and Lutjeharms 1989), i.e., the myctophids *Lampanyctodes hectoris* and *Symbolophorus boops*, and the sternoptychid *Maurolicus walvisensis*. This ecoregion also exhibits the highest cephalopod diversity in the Atlantic (Rosa et al. 2008; Sutton et al. 2017). Influences of tropical and cold-water mesopelagic fish species can be seen within each of its two subsystems (Duncan et al. 2022). Few studies (Hulley 1981, 1992; Rubiés 1985; Hulley and Prosch 1987; Hulley and Lutjeharms 1989; Armstrong and Prosch 1991) have investigated the mesopelagic fish community in the Benguela. The most recent of these (Staby and Krakstad 2008) documented 18 families from five orders of mesopelagic fish using data collected during research surveys off Angola, Namibia and South Africa over the period 1985–2005. This study reported that the Myctophidae (*Diaphus* spp. off Angola and *Lampanyctodes hectoris* and *Symbolophorus boops* off Namibia and South Africa) prevailed and occurred most frequently in research trawls particularly over the shelf and slope, followed by the Sternoptychidae (predominantly *Maurolicus walvisensis*; also in shelf and slope waters), and then the Phosichthyidae (*Phosichthys argenteus*) that were typically found further offshore.

Lampanyctodes hectoris and *Maurolicus walvisensis* appear to be the most abundant mesopelagic fishes in the region (Hulley and Prosch 1987; Staby and Krakstad 2008). Acoustic surveys for the period 2006–2018 conducted in the sBUS (Coetzee et al. 2009, 2018) indicate a combined mean biomass of 1.25 million tons of three mesopelagic species (*L. hectoris*, *M. walvisensis* and *S. boops*), on average split between *M. walvisensis* and the myctophids 2:1. Dense aggregations were mostly found between 31°S and 35°S. As compared to mesopelagic biomass estimates for the Humboldt Current System, a biomass of 2–11 million tons for one single species (*Vinciguerria lucetia*) was estimated beyond the shelf break along the whole coast off Peru (see Cornejo and Koppelman 2006). Similar to the biomass of small pelagics, the biomass of mesopelagic fish appears to be low in relation to system primary production.

Most studies have focused on *L. hectoris* and *M. walvisensis* (Hulley 1981; 1992; Rubiés 1985; Hulley and Prosch 1987; Hulley and Lutjeharms 1989), and also on mesopelagic fish larvae (Olivar 1987; Olivar and Beckley 1994; Ekau and Verheye 2005). However, comparative studies of mesopelagic fish communities between these two dynamic upwelling systems as well as biological and ecological studies are lacking, especially including species of mesopelagic families such as Gonostomatidae, Stomiidae, Phosichthyidae, Bathylagidae, and Melamphaidae, among others (Staby and Krakstad 2008).

Data collected during the TRAFFIC research surveys show that the overall abundance of mesopelagic fish did not differ between the northern (north of Walvis Bay) and southern Benguela subsystems, but species accumulation curves indicate that the nBUS has a higher mesopelagic fish richness (Duncan et al. 2022). However, there is high heterogeneity within each subsystem, which demonstrates the need for increased sampling of these organisms at appropriate spatial scales. Species counts revealed 88 mesopelagic species for the TRAFFIC campaign so far, as compared to 131 species listed in the South African *Africana* data base and 98 listed in the BENEFIT project (Staby and Krakstad 2008). Seven mesopelagic fish communities have been identified on the shelf and slope of the Benguela system. These include one shelf group in each of the nBUS and sBUS, as well as several offshore groups (Fig. 11.14). The shelf group in the sBUS has low diversity and is dominated by *Maurolicus walvisensis*, which is a shelf/slope-associated species (Hulley and Prosch 1987; Prosch 1991) and corroborates the findings of Coetzee et al. (2009). In contrast, the shelf of the nBUS had very low abundance of mesopelagic fishes and is dominated by gobies and jellyfishes (Roux et al. 2013; unpublished data). The only species that defined the shelf ecosystem assemblage in the nBUS was the myctophid

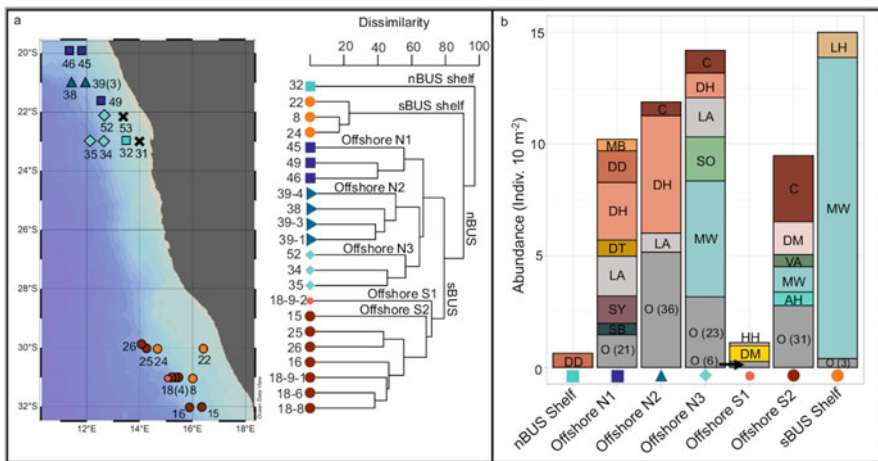


Fig. 11.14 Modified figure from Duncan et al. (2022) showing (a) Station map (left) with clusters of mesopelagic fish communities based on hierarchical cluster analysis (right) using the average linkage method for Bray-Curtis dissimilarity matrix for Hellinger-transformed abundance data. Panel (b) reflects the abundance of dominant species in each cluster, corrected by the number of stations representative of each cluster. Those species listed contribute at least 5% to the fraction of mesopelagic fishes and those contributing less have been combined to the category “other” with the total number of species contributing to “other” in parenthesis. Abbreviations stand for DD *Diaphus dumerilii*, DH *Diaphus hudsoni*, DM *Diaphus meadi*, DT *Diaphus taaningi*, HH *Hygophum hanseni*, LH *Lampanyctodes hectoris*, LA *Lampanyctus australis*, SY *Symbolophorus barnardi*, SO *Symbolophorus boops* (all Myctophidae), MB *Melanolagus bericoides* (Bathylagidae), SB *Stomias boa* (Stomiidae), C *Cyclothone* spp. (Gonostomatidae), AH *Argyropelecus hemigymnus*, MW *Maurolicus walvisensis* (both Sternoptychidae), VA *Vinciguerria attenuata* (Phosichthyidae), and O other unspecified fishes

Diaphus dumerilii. This species has a tropical distribution with populations along the equatorial Atlantic, both off the coast of Brazil and in the eastern Atlantic (Hulley 1981; Czudaj et al. 2021). Offshore stations in the sBUS were dominated by gonostomatid *Cyclothone* spp. as well as the myctophid *Diaphus meadi*, with the exception of one community, which was dominated by the myctophid *Hygophum hanseni*, one of the most abundant myctophids circumglobally, in the area of the Subtropical Convergence (Hulley 1981 and references cited therein). In the nBUS, offshore stations consist of three communities, two of which are dominated by the myctophid *Diaphus hudsoni*, and one where *M. walvisensis* prevails.

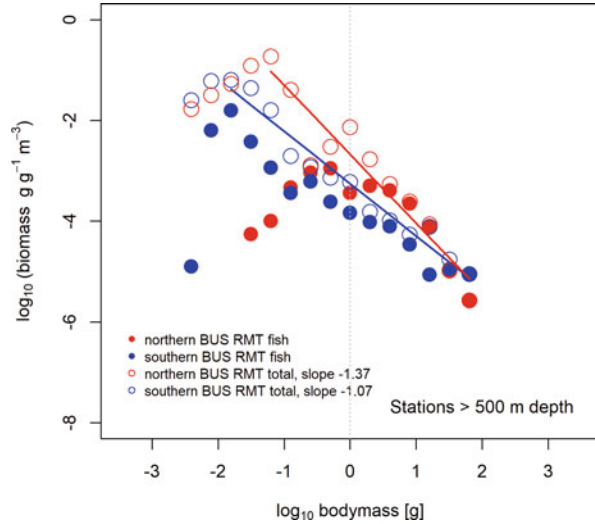
Environmental factors that drive mesopelagic fish species composition in the Benguela are water masses, surface chlorophyll *a* and oxygen concentrations. As the nBUS is more influenced by SACW and the Angola Current, species that are classified as having tropical patterns can be found, such as *Diaphus dumerilii* and *Diaphus taaningi* (Hulley 1981), while the sBUS has a higher abundance of fishes with temperate and convergence patterns (Hulley 1981), such as *D. meadi*. Hulley (1992) also found that the fishing depth and temperature influenced the downslope distribution of species. As tropical ecosystems tend to have a higher diversity of organisms than temperate regions, this is also reflected in the order Stomiiformes, for which 15 species were identified in the sBUS, while species were identified in the nBUS (Duncan et al. 2022). Overall, the subsystems found in the Benguela Upwelling System show mesopelagic fish diversity, that is highly influenced by differences in water masses, oxygen concentrations and currents. However, data on seasonality of mesopelagic fish communities are still lacking and there is a need for further investigation in order to fully assess the diversity and abundance of mesopelagic fishes in the Benguela Current.

Normalized biomass size spectra (Fig. 11.15) for the micronekton and macrozooplankton offshore components beyond the shelf break front, both indicate an exchange across the shelf break front, given the differences in slopes in particular for the nBUS as well as the influence of the shelf break Benguela jet, transporting anchovy larvae downstream spawned in the Agulhas Bank region. The latter is supported by the significant fish group normalized biomass with a body mass below 0.1 g wet mass (WM) in the sBUS, which mostly comprises anchovy larvae, *E. encrasicolus*. In turn, in the nBUS, euphausiids are dominating in this biomass range, mainly *Euphausia hanseni*, which are dependent on the upwelling regime. Given that TTE model parameters are the same for the two closely related subsystems, TTE is lower for the nBUS, i.e., the NBSS slope is steeper (-1.37) as compared to the sBUS (-1.07 , Fig. 11.15).

11.3.5 Higher Trophic Levels

The Benguela ecosystem hosts the species spectrum typical of upwelling systems and supports multiple species in higher trophic levels, including crustaceans, cephalopods, fishes, marine mammals and seabirds. A total of 133 fish species from 40 families are listed for the Benguela Current LME (www.Seararoundus.com).

Fig. 11.15 Normalized biomass size spectra for the northern and southern Benguela subsystems offshore micronekton and macrozooplankton from RMT8 samples obtained during the M153 late summer cruise, March 2019. “Total” refers to total community biomass, i.e. fish plus macroplankton



Some of these species (e.g., small pelagic fishes) can attain high biomass levels, and several are commercially important as fisheries resources including the Cape hakes (*Merluccius capensis* and *M. paradoxus*), Cape and Cunene horse mackerels (*Trachurus capensis* and *T. trecae*), and small pelagics (sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus* and round herring *Etrumeus whiteheadi*). Substantially smaller catches of crustaceans such as rock lobster (*Jasus lalandi*) and deep-water crab (*Chaceon* sp.) are also commercially important (van der Lingen et al. 2006b; Kirkman et al. 2016; Kainge et al. 2020). Additionally, high biomasses of as yet not commercially targeted mesopelagic fishes, gobies and jellyfish occur in the Benguela, the latter two in the nBUS in particular (Lynam et al. 2006; Roux et al. 2013; Kirkman et al. 2016; Salvanes et al. 2018). The southern part of the Benguela—from Luederitz to Cape Agulhas—provides nursery grounds for most of that subsystem’s ecologically and economically important fish species (Kirkman et al. 2016), including both hake species, the small pelagics, and horse mackerel.

11.3.6 Commercial Fishery

Important fisheries (in terms of economic value) in the Benguela are those for Cape hakes (most valuable) and horse mackerels (largest volume) in the nBUS, and Cape hakes (most valuable) and small pelagics (largest volume) in the sBUS (Kainge et al. 2020). The fishing gear, product utilization and markets, average catches, and management strategies of these fisheries are summarized in Table 11.1, and catch time-series shown in Fig. 11.16.

Historically, sardine dominated landings from 1950 to the late-1960s in both subsystems, with peak catches of >1 million tons in the nBUS and close to ½

Table 11.1 The fishing gear, species, product utilization, average annual catches (rounded to the nearest 100 tons; 2000–2016; \pm std. dev.), management strategies, and present stock status (Kainge et al. (2020) for Namibia and DEFF (2020) for South Africa) for the fisheries targeting small pelagics, horse mackerel and Cape hakes off Namibia (the nBUS) and South Africa (the sBUS and Agulhas Bank system). Also shown is the average annual catch by the three fisheries combined, and the % contribution by the marine fisheries sector to Namibia's and South Africa's GDP. OMP Operational Management Procedure, PUCI Precautionary Upper Catch Limit, TAC Total Allowable Catch

	nBUS	sBUS
Fishery		
Small pelagics (purse-seine; by-catch in midwater trawl fishery)	<ul style="list-style-type: none"> • <i>Sardinops sagax</i>, <i>Engraulis encrasicolus</i>, <i>Etrumeus whiteheadi</i> • Sardine frozen and canned for human consumption (export and local); anchovy and round herring reduced to fish meal and fish oil (export) • Average catch = 22,300 \pm 12,200 • Management = assessment and annual TAC (only for sardine) • Present status = sardine heavily depleted; fishery closed (under moratorium) from 2018 onward; 	<ul style="list-style-type: none"> • <i>Sardinops sagax</i>, <i>Engraulis encrasicolus</i>, <i>Etrumeus whiteheadi</i> • Sardine frozen and canned for human consumption and pet food (local); anchovy and round herring reduced to fish meal and fish oil (export) • Avg. catch: 431,900 \pm 110,900 • Management = OMP used to set annual TACs for anchovy and sardine; PUCI for round herring • Present status = sardine depleted; anchovy optimal; round herring abundant
Horse mackerel (midwater trawl and demersal trawl; juveniles taken by the small pelagic fishery)	<ul style="list-style-type: none"> • <i>Trachurus capensis</i> (dominant), <i>T. trecae</i> • Frozen for human consumption (local and export) • Avg. catch: 279,800 \pm 55,000 • Management = assessment and annual TAC • Present status = biologically sustainable 	<ul style="list-style-type: none"> • <i>Trachurus capensis</i> • Frozen for human consumption (local and export) • Avg. catch: 29,800 \pm 8300 • Management = annual TAC and effort limitation • Present status = optimal
Cape hakes (demersal trawl; long-line)	<ul style="list-style-type: none"> • <i>Merluccius capensis</i>, <i>M. paradoxus</i> • Fresh and frozen for human consumption (mostly export to EU markets) • Avg. catch: 144,100 \pm 18,000 • Management = assessment and annual TAC • Present status = overfished 	<ul style="list-style-type: none"> • <i>Merluccius capensis</i>, <i>M. paradoxus</i> (dominant) • Fresh and frozen for human consumption (local and export) • Avg. catch: 138,500 \pm 13,700 • Management = OMP used to set annual TAC (both species combined) • Present status = <i>M. capensis</i> abundant; <i>M. paradoxus</i> optimal
Combined average catch 2000–2016	446,200 \pm 69,800	600,200 \pm 120,300
Fisheries GDP contribution	3.6%	<1.0%

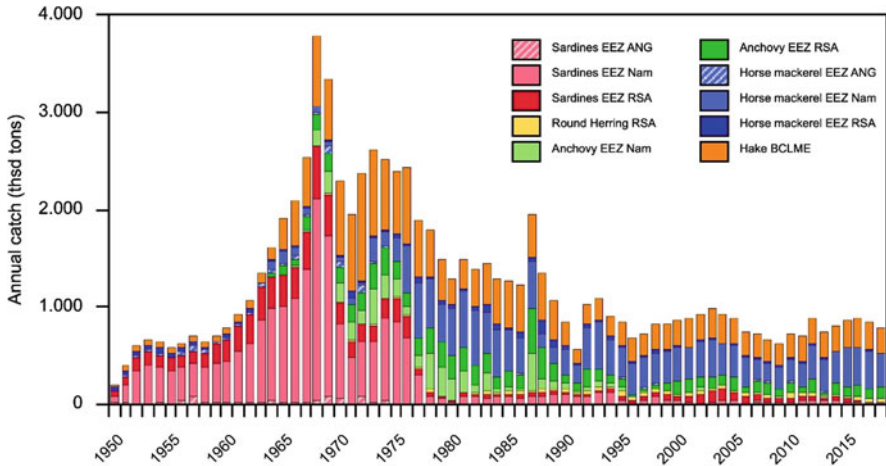


Fig. 11.16 Time series of catches of sardine, round herring, anchovy, horse mackerel and Cape hakes in the EEZs of Angola, Namibia and South Africa (RSA), 1950–2019. Catches for Cape hakes and horse mackerels off Namibia updated from Kainge et al. (2020) and for small pelagics from FAO (Namibian catches were included in South African catches from 1950 to 1989 and only specifically recorded post-independence (1990). Earlier catches are estimated by subtracting the South African catches (see below) from FAO catches. Catches for Cape hakes, horse mackerels and small pelagics off South Africa updated from DFFE (2020) and from FAO

million in the sBUS (Fig. 11.16), but catches of this species then declined rapidly off both Namibia and South Africa due to overfishing (van der Lingen et al. 2006b; Augustyn et al. 2018). Anchovy replaced sardine in South African catches for the next three decades, and sardine catches increased briefly before declining again to recent depleted levels (DEFF 2020) arising from prolonged poor recruitment and increased fishing mortality (Augustyn et al. 2018). However, despite changes in species dominance, and including a small contribution made by round herring, catches by the South African small pelagic fishery have been relatively stable (Fig. 11.16).

The Namibian sardine fishery has essentially been replaced by the fishery for horse mackerels (*Trachurus capensis* and *T. trecae*), with catches of the latter increasing rapidly from the early 1970s to a peak of almost 660,000 t in 1983. Since then this has been Namibia's major fishery in terms of volume despite a drop from peak catches to around 300,000 t annually since the mid-1990s (excluding 1997 when a catch of only 125,000 t was taken). Substantially smaller (by almost an order of magnitude) quantities of horse mackerel (*T. capensis* only) are caught off South Africa, mostly from the Agulhas Bank off the south coast. The Namibian fishery for hake started in the early 1960s with catches increasing rapidly to 820,000 t in 1972 owing to poor control and increased fishing by foreign vessels (Kainge et al. 2020). Improved control has resulted in sharply reduced catches, which then increased again during the 1980s before declining sharply again in the early 1990s (Fig. 11.16). Since the turn of the century however, catches have been relatively

stable and fluctuated between 100,000 and 200,000 t. South Africa's hake fishery was initiated in 1917 and increased steadily to a peak of 300,000 t in 1972, before declining and then leveling out between 100,000 and 150,000 t annually since the late-1970s.

Overall, catches by these major sectors have shown different trajectories in the two subsystems. In the nBUS, catches initially increased rapidly but then decreased rapidly, with the highest combined catch (just over 2 million t) occurring in 1969. Combined annual catches in the nBUS since 2000 have been low (around 20% of the maximum attained) but steady. In the sBUS, catches in each sector increased more slowly and declines were less or did not occur because of species replacements (i.e., anchovy for sardine), and the highest combined catch occurred in 1988. Combined annual catches in the sBUS since 2000 have averaged 70% of maximum catch, albeit with more variability (42%–93%) than in the nBUS.

11.4 Conclusion

Like every upwelling system, the Benguela system reacts to changes in physical forcing and is expected to be responsive to present and future climate changes, as it is extremely sensitive to global, regional, and local fluctuations in atmospheric circulation patterns (Bakun 1990; Bakun et al. 2010; Demarcq 2009). Various coastal upwelling systems have undergone dramatic changes (called ecosystem regime shifts) in their ecosystem structure and fishery productivity in the past (Alheit and Bakun 2010; Cury and Shannon 2004; Finney et al. 2010). These changes are not thought to have been triggered exclusively by human actions, but also by global or regional physical drivers (Overland et al. 2010; Rykaczewski and Checkley 2008). Although some models differ in their implications to projected climate change (Wang et al. 2010), most calculations and assessments that address the consequences of potential climate change in coastal upwelling areas postulate an intensification of physical forcing (wind) that results in stronger, more persistent, or more widespread upwelling, particularly in the poleward regions of these systems (Bakun 1990; Bakun et al. 2010).

We summarized TRAFFIC results together with data from the literature and previous projects in a synoptic presentation to shed light on trophic transfer efficiencies in the nBUS and sBUS. First results indicate that trophic transfer efficiency can be modified by metabolic processes and behavior of the animals, for instance in terms of predator-prey interactions. Schukat et al. (2021) compared life history traits of dominant calanoid copepods in the Humboldt Current System (HCS) with those in the nBUS to infer effects of behavior on trophic transfer efficiency. The authors concluded that higher transfer efficiency within the HCS was correlated with the lack of ontogenetic vertical migration of *Calanus chilensis*, making it easily accessible to epipelagic predators during all life stages. In contrast, in the nBUS, the large copepod *Calanoides natalis* tends to perform vertical migration through the oxygen minimum zone, taking it out of reach for hypoxia-sensitive predators and hence preventing efficient transfer toward higher trophic levels (Schukat et al.

2021). To establish a holistic view of the carbon transfer processes information from other ecological components have to be added. For example, the role of bacteria and DOC fluxes is still not understood. DOC export is estimated to account for around 20% of the global passive export production (Roshan and DeVries 2017). Model estimates of DeVries and Weber (2017) indicate that large plankton produce primarily labile DOC, which is rapidly remineralized within several days, whereas small plankton produce more non-labile DOC that persists for years and contributes to carbon export and sequestration. Investigations on small-sized plankton are in progress. At the other side of the size spectrum, higher trophic levels other than fish seabirds and marine mammals should be given more attention to fully assess trophic transfer efficiency.

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Glossary of Organizations and Projects

[The below list is limited to those organizations and projects cited in this chapter, and is not intended to represent a comprehensive overview of all marine initiatives in southern Africa]

Organizations

NATMIRC	National Marine information and Research Center, Swakopmund, Namibia
BCC	Benguela Current Convention, Swakopmund, Namibia
UNAM	University of Namibia, Windhoek and Henties Bay, Namibia
UCT	University of Cape Town, Cape Town, South Africa
DFFE	Department of Forestry, Fisheries and the Environment, Cape Town, South Africa

Projects

BIOTA Africa	BIODiversity Monitoring Transect Analysis in Africa. The German Federal Ministry of Education and Research (BMBF) was open to fund the initiative, meanwhile
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	several African countries and partner institutions added funding
NAMIBGAS	funded by BMBF
BENEFIT	Benguela Environment Fisheries Interaction and Training Programme, funded by a number of local, regional and international research and development sources
GENUS (2009–2015)	Geochemistry and Ecology in the Namibian Upwelling System, funded by BMBF
TRAFFIC (2019–2022)	Trophic Transfer Efficiency in the Benguela Current, funded by BMBF

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