Microzooplankton of the northern Benguela Upwelling System

Dissertation
Zur Erlangung der Würde des Doktors der Naturwissenschaften
des Fachbereichs Biologie,
der Fakultät für Mathematik, Informatik und Naturwissenschaften,
der Universität Hamburg

vorgelegt von

Karolina Bohata

aus Prag

Hamburg
Dezember 2015

Datum der Disputation: 21.3.2016

Erstgutachter: Prof. Dr. Christian Möllmann
Zweitgutachter: Prof. Dr. Friedrich Buchholz

Content

1 Summary

The Benguela Upwelling System belongs to the major Eastern Boundary Upwelling Systems of the world's coastal regions, which are characterized by a high productivity and a high content of energy. Upwelling is an important physical process that has a significant impact on autotrophic and heterotrophic production, larval recruitment, and fisheries. Despite increasing knowledge about the importance of microzooplankton in different ecosystems, the community composition, dynamics and role of this faunal group within the food web are insufficiently understood in the Eastern Boundary Upwelling Systems.

One of the main objectives of this study was to characterize the composition and distribution of microzooplankton in the northern Benguela Upwelling System. A total of 193 net samples (55 µm mesh size) and 73 water samples were analysed for this thesis, detecting 81 microzooplankton taxa, belonging to 16 microzooplankton groups. The main contributors to the microzooplankton abundance were mixo- and heterotrophic dinoflagellates (17 taxa), naked ciliates (18 taxa), tintinnids (22 taxa), and copepods (5 taxa). The association of microzooplankton to temperature, salinity, chl *a* and spatial structures was analysed in order to understand the distribution of different microzooplankton taxa within this productive environment. The combination of environmental parameters, chl *a* and temperature explained about 54% of the variation in the distribution of total abundance, whereas the spatial variables (latitude/longitude) explained 49% of the variation. We detected spatial differences in the distribution of microzooplankton taxa between the northern and southern part of the area. Distinct spatial differences were obvious within the tintinnid group. The northern part of the area, influenced by intrusions of warm water from the Angola Dome, was dominated by warm-temperate species, such as *Rhabdonella* sp., *Epiplocylis acuminata* and *Climacocylis* sp., whereas the southern part, influenced by stronger upwelling intensity all year long, was dominated by the cosmopolitan species *Codonellopsis morchela* and *Codonella galea*. The distribution of tintinnids is probably influenced by different water masses entering the northern Benguela Upwelling System from the South (Eastern South Atlantic Central Water) and from the North (South Atlantic Central Water). Therefore we assumed that tintinnids could be used as indicators of different water masses. However, the distribution of microzooplankton species is relatively patchy due to complex biological and physical interactions.

The distribution and composition of microzooplankton changed in direction from the shelf towards the open ocean. Variations in phytoplankton community (abundance, composition and cell size) and chl *a* concentrations directly influence the composition and diversity of microzooplankton. High abundances of microzooplankton were associated with high chl *a* values. Naked ciliates and small dinoflagellates dominated the fresh upwelled water whereas high abundances of larger mixo- and heterotrophic dinoflagellates were found more offshore. Also the diversity of microzooplankton changed with increasing distance from the shore. On the shelf, the diversity was very low, whereas further offshore at the shelf break the diversity rapidly increased as a result of a more complex food web.

During a filament study, the association of microzooplankton to upwelling filaments was investigated. The microzooplankton community was partially associated with environmental parameters and conditions related to the upwelling filament. High abundances of microzooplankton were found at the southern front and the centre of a filament as a result of internal water circulation. However, the functioning of upwelling filaments is very complex and the changes of zooplankton community connected to the upwelling fronts depend on physiological parameters related to properties of the entering water masses, the water circulation within the filament and many biological parameters such as the composition of the original community at the beginning of the filament.

In addition, the relationship between water column processes like primary production, micro- and mesozooplankton composition and abundance as well as physical parameters like temperature, salinity, oxygen content, currents and shelf morphology were investigated to explain a distinct small-scale heterogeneity detected in the benthos. The main parameters forming the benthic community seem to be related to different patterns in primary production and particle fluxes, oxygen content and the width and steepness of the shelf.

In conclusion, this study provides important information about the key role of microzooplankton in the high productive northern Benguela Upwelling Ecosystem. This knowledge is essential to understand the biological dynamics in upwelling systems, the food web design and interactions between physical and biological components. Predicted changes in climate probably influence the lower trophic levels including the microzooplankton and alter biogeochemical cycles and feedback mechanisms in this ecosystem.

2 Zusammenfassung

Das Benguela Auftriebsgebiet ist eines der großen östlichen Küstenrand-Auftriebssysteme der Erde. Auftriebsgebiete sind gekennzeichnet durch ihre hohe Produktivität und ihren hohen Energiegehalt. Das Phenomen des Auftriebs ist ein wichtiger physikalischer Prozess, welcher die autotrophe und heterotrophe Produktion, larvale Rekrutierung und auch die Fischerei nachhaltig beeinflusst. Die Zusammensetzung, Dynamik und die Rolle des Mikrozooplanktons innerhalb des Nahrungsnetzes in Auftriebsgebieten ist noch nicht ausreichend untersucht und verstanden.

Ein Hauptziel dieser Arbeit stellt die Beschreibung der Zusammensetzung und Verteilung von Mikrozooplankton im nördlichem Benguela Auftriebesgebiets dar. Im Rahmen dieser Arbeit wurden 193 Netzproben mit einer Maschenweite von 55 µm, sowie 73 Wasserproben analysiert. Insgesamt wurden 81 Mikrozooplanktontaxa, welche 16 Mikrozooplanktongruppen zugeordnet werden konnten, in den Proben gefunden. Die gefundenen Hauptgruppen des Mikrozooplanktons sind mixo- und heterotrophe Dinoflagellaten (17 Taxa), unbeschalte Ciliaten (18 Taxa), Tintinniden (22 Taxa) und Copepoden (5 Taxa). Diese Arbeit leistet einen wichtigen Beitrag zum Verständinis der Verteilung bestimmter Mikrozooplanktonarten innerhalb dieses hochproduktiven Gebiets. Zudem erfasst diese Arbeit die Zusammenhänge zwischen der Mikrozooplanktongemeinschaft und verschiedenen Umweltparametern wie Temperatur, Salinität, Chl *a* Gehalt und räumlichen Strukturen (geographische Breite und Länge). Eine Kombination von Umweltvariablen (Chl *a* Gehalt und Temperatur) konnte 54% der Variabilität der Gesamtabundanzen erklären, während die räumlichen Variablen 49% der Variabilität erklären. Innerhalb der Gemeinschaft der Tintinniden konnten zudem räumliche Unterschiede festgestellt werden. Im nördlichen Teil des Untersuchungsgebiets, welcher von den einströmenden Wassermassen aus dem Angola Dome beeinflusst wird, wurden hauptsächlich warm-gemäßigte Arten wie beispielsweise *Rhabdonella* sp., *Epiplocylis acuminata* und *Climacocylis* sp., gefunden. Im südlichen Teil des Untersuchungsgebiets, welches durch eine permanente Auftriebszelle vor Lüderitz beeinflusst wird, wurden vor allem global vorkommende Arten, wie beispielsweise *Codonellopsis morchela* oder *Codonella galea*, gefunden. Die Verbreitung der Tintinniden-Arten wird höchstwahrscheinlich durch die unterschiedlichen Wassermassen im Norden (South Atlantic Central Water) und im Süden (Eastern South Atlantic Central Water) beeinflusst. Daher könnte diese

Mikrozooplanktongruppe als Indikator für die unterschiedlichen Wassermassen verwendet werden.

Eine Veränderung der Verteilung und Zusammensetzung von Mikrozooplankton von der Küste bis in den offenen Ozean konnte festgestellt werden. Variationen innerhalb des Phytoplanktons (Konzentration, Zusammensetzung und Zellgröße) und Chl *a* Gehalt haben einen direkten Einfluss auf die Zusammensetzung und Vielfalt des Mikrozooplanktons. Unbeschalte Ciliaten und kleine Dinoflagellaten wurden häufig in frischem Auftriebswasser gefunden. Weiter vom Schelf entfernt wurde die Gemeinschaft von großen mixo- und heterotrophen Dinoflagellaten dominiert. Zusätzlich ändert sich auch die Artenvielfalt mit zunehmende Entfernung von der Küste. Die niedrigste Artenvielfalt wurde auf dem Schelf entdeckt, während weiter in Richtung offene See die Anzahl der Arten fast drei mal so hoch war, was eine Folge der Veränderungen im Nahrungsnetz darstellt. Direkt auf dem Schelf ist das Nahrungsnetz relativ einfach und mit zunehmende Entfernung von dem Schelf wird deutlich komplexer.

Der Zusammenhang zwischen Auftriebsfilamenten und Mikrozooplankton wurde ebenfalls untersucht. In der Filamentstudie konnte festgestellt werden, dass die Mikrozooplanktongemeinschaft teilweise mit den Umweltparametern und Bedingungen des Filaments assoziiert ist. Sehr hohe Abundanzen wurden in der südlichen Front und im Zentrum des Filaments gefunden. Diese Mikrozooplanktonakkumulation wurde wahrscheinlich durch Wasserströmungen innerhalb des Filaments verursacht. Die Funktion von Auftriebsfilamenten ist jedoch sehr komplex und die Veränderungen innerhalb der Zooplanktongemeinschaft in Verbindung mit den Filamentfronten ist von physikalischen Parametern wie beispielsweise den einströmenden Wassermassen, der Wasserzirkulation im Filament und vielen anderen biologischen Parametern wie beispielsweise die Zusammensetzung der Zooplanktongemeinschaft am Anfang der Filamententwicklung abhängig.

Zusätzlich wurden die Zusammenhänge zwischen Prozessen in der Wassersäule wie der Primärproduktion, Mikro- und Mesozooplanktonzusammensetzung und deren Abundanzen ebenso wie die physikalischen Parameter Temperatur, Salzgehalt, Sauerstoffgehalt, Strömungen und Oberflächenstruktur des Schelfs untersucht, um kleinskalige Unterschiede innerhalb Benthosgemeinschaften zu erklären. Die Benthosgemeinschaft wird hauptsächlich durch unterschiedliche kleinskalige Strukturen in der Primärproduktion, den daraus folgenden unterschiedlichen

Partikelflüssen, dem Sauerstoffgehalt sowie Steilheit und Breite des Schelfs beeinflusst.

Diese Arbeit liefert wichtige Informationen über die Schlüsselrolle des Mikrozooplanktons in dem produktiven nördlichen Benguela Auftriebsgebiet. Die Erkenntnisse dieser Arbeit sind von großer Bedeutung, um biologische Abläufe in Auftriebsgebieten zu verstehen. Veränderungen im Ökosystem durch Klimawandel haben höchstwahrscheinlich auch einen Effekt auf die niedrigeren tropische Ebenen wie beispielsweise das Mikrozooplankton und können die biogeochemische Abläufe und Rückkopplungs-Mechanismen in dem Ökosystem nachhaltig verändern.

Chapter 3

General Introduction

3.1. The study area

The Benguela Upwelling System (BUS; Blamey et al. 2012) is one of the major Eastern Boundary Upwelling Systems (EBUS) of the world (Hutchings et al. 2009). Generally, upwelling systems are special features within the world's coastal regions due to their high productivity and high content of energy. Upwelling is an important physical process that has a significant impact on primary production, larval recruitment, and fisheries (Traganza 1987; Roughgarden 1991; Rau et al 2001). In the southern hemisphere, trade winds blow northwards along the coast and the surface ocean water is transported offshore by the Coriolis deflection (Abel & McConell 2010). The current direction of the surface layer is 45° and due to the Ekman transport, the direction of the net water transport is about 90° to the left of the wind direction. The water deficit near the coast is replaced by deep water with high concentrations of nutrients fostering the primary production in the euphotic zone and resulting in ample resources (Lalli & Parson 1993).

The BUS is situated off the west coast of Africa and spans from the Cape of Good Hope in the south along the coast of the South Africa and Namibia into Angola waters (figure 3-1; Shannon & O'Toole 2003). A high pressure system over the central South Atlantic Ocean induces south-eastern winds along the African coast, modified by seasonal low pressure cells above the continent and eastward moving cyclones to the south (Nelson & Hutchings 1983). This supports the upwelling-favourable south-easterly winds during the spring and summer seasons in the southern part of the BUS and during southern autumn and spring in the northern BUS. The central BUS from about 26°S to 28°S experiences almost perennial upwelling-favourable conditions (Summerhayes et al. 1995; Shannon & Nelson 1996).

The BUS can be divided into two sub-ecosystems: the northern BUS and the southern BUS. These two sub-ecosystems are split by the permanent upwelling cell off Lüderitz (24°00'S – 28°00'S). This region is one of the world's most intense and consistent upwelling regions (Bakun 1996). A high intensity of developing eddies and filaments are typical for this region. Sometimes even 'superfilaments' extending over 1000 km into the South Atlantic develop.

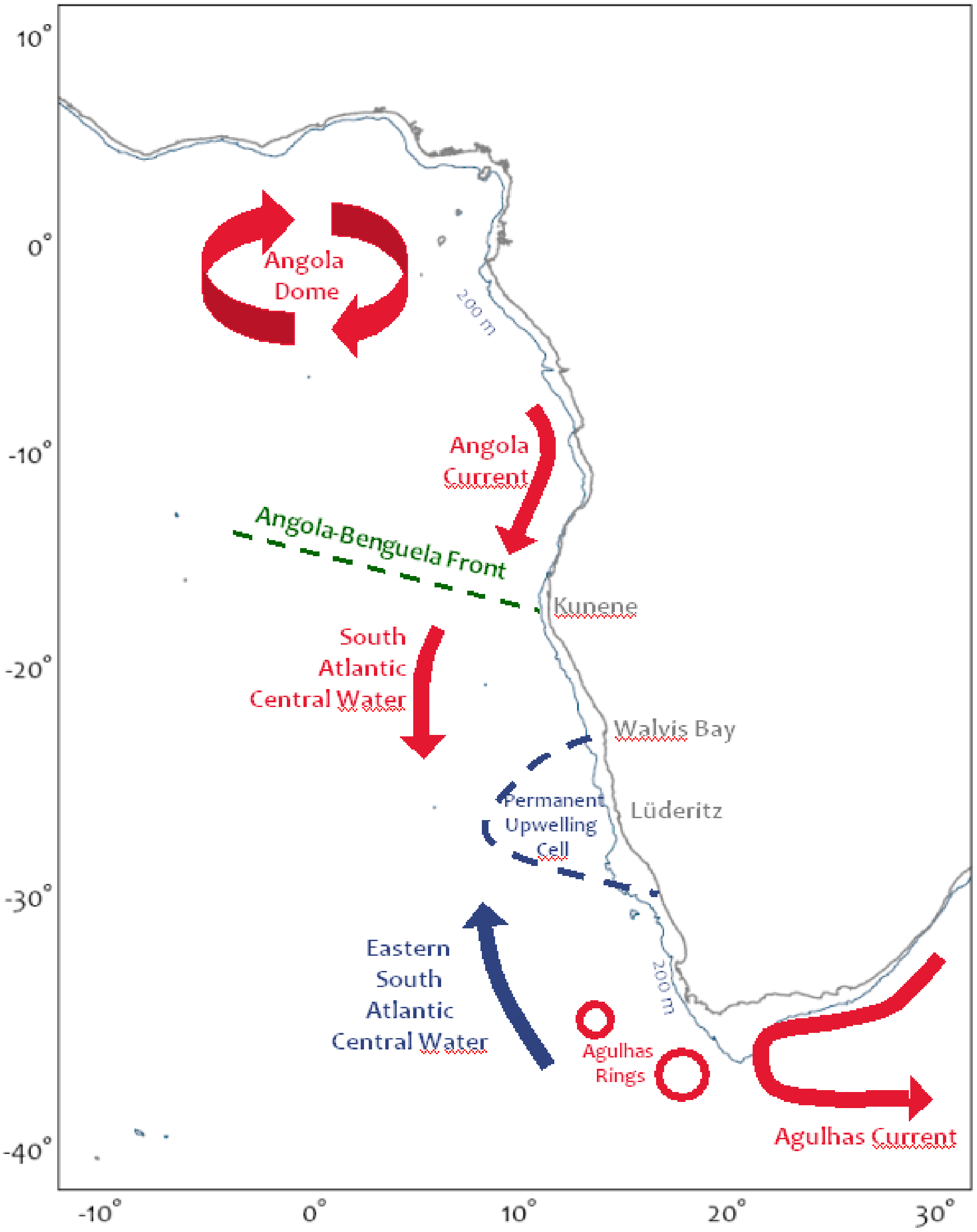


Figure 3-1: The Benguela Upwelling System. Red and green arrows indicate warm currents, blue arrows cold currents (modified after Shannon 2006).

Oceanographic processes from the South Atlantic and Indo-Pacific Oceans influence the southern region of the BUS; ring-formations from the Agulhas Current enter the Atlantic Ocean (Shannon & O'Toole 2003). The rings of the Agulhas Current and the South Atlantic Current create the high oxygenated Eastern South Atlantic Central Water (ESACW), which is transported from the Cape of Good Hope across the South African coast to the equator (Shannon & O'Toole 2003). The northern region of the BUS is affected by the Angola-Benguela front as a result of seasonal and inter-annual changes of the intensity of upwelling cells at Cape Frio (Clarke & Gorley 2006) and Lüderitz (Hutchings et al. 2009). The Angola-Benguela front is a convergence zone between the cool equatorward flowing Benguela Current and the warm, highly saline poleward flowing Angola current (Mohrholz 2001).

An important component of the circulations in all EBUS are upwelling filaments (Lutjeharms 1991, Escribano 2000). Upwelling filaments transport cold and nutrient rich waters from the coast to hundreds of kilometers offshore (Brink 1983) and have been described for Eastern Boundary Currents off southern Africa (Lutjeharms & Meeuwis, 1987; Muller et al. 2013), northwest Africa (Navarro-Pérez 1998; Marchesiello & Estrade 2009), California (Brink 1983; Mackas et al. 2006), Chile (Marín et al. 2001; Sobarzo & Figueroa 2001) and Portugal (Haynes et al. 1993; Cravo et al. 2010). These upwelling filaments are important hydrographic structures for the dynamics of EBUS and transport nutrients and plankton to the open ocean (Nelson & Hutchings 1983; Strub et al. 1991; Álvarez-Salgado et al. 2001; García-Muñoz et al. 2004; Mackas et al. 2006). On regional scales, upwelling filaments occasionally transport more volumes of water offshore than the Ekman transport (Barton et al. 1998; Muller et al. 2013). Filaments are able to transport a large fraction of coastal primary production even during low upwelling intensity. However, the dimension and nature of transported organic matter depends largely on the species composition and the related size structure of the plankton community.

3.2. Plankton of the Benguela Upwelling System

3.2.1. Phytoplankton dynamics

Maximum chl *a* concentrations are usually observed during the high intensity upwelling season (southern winter) and downstream of upwelling cells, whereas the center of the upwelling cells are associated with low chl *a* concentrations (Thomas et al. 2001; Demarq et al. 2003). During the high upwelling intensity period, the phytoplankton bloom spreads over 100 km offshore and last for about a week (Brown and Hutchings 1987a, b).

Usually small dinoflagellates, coccolithophores and microflagellates dominate fresh-upwelled, nutrient-rich water inshore, whereas larger diatoms are more abundant in the matured upwelled water with exhausted nutrient concentrations (Hart & Currie 1960; Pitcher et al. 1998; Hansen et al. 2014). Farther offshore, the abundance of larger diatoms decreases again and the phytoplankton community is dominated by small dinoflagellates (Hansen et al. 2014).

Generally, long-term shifts in upwelling-favourable winds will lead to changes in upwelling, and consequently to changes within the phytoplankton production and composition on similar scales (Verheye 2015). Thereby shifts toward increased seasonality in biomass with greater differences between the summer and winter index values have been noted (Verheye et al. 2015).

3.3.2. Microzooplankton

The community composition and the dynamics of microzooplankton are generally insufficiently understood in the EBUS. Microzooplankton consists of many groups of organisms like ciliates, hetero- and mixotrophic dinoflagellates, foraminiferas, pteropods, radiolarians, nauplius larvae, several copepodite stages and small copepods in the size range from 20 to 200 µm. Since the seminal work of Landry and Hasset (1982) who introduced the dilution method to estimate microzooplankton grazing rates on phytoplankton, and Azam *et al.* (1983), which described the ‘microbial loop’, microzooplankton attracted increasing attention as an important part of the food web. Microzooplankton may consume on average between 60 and 75% of the particulate primary production (Calbet & Landry 2004) while the mesozooplankton directly consume on average only 15% of particulate primary production in the surface ocean (Calbet 2001). Microzooplankton is also a significant food source for mesozooplankton, both in quantitative and qualitative aspects. They are preferred food for copepods due to their optimal cell size and biochemical composition (Kleppel et al. 1993; Castellani, 2005). Microzooplankton transfers minerals, vitamins, amino acids, fatty acids and sterols from lower trophic levels to mesozooplankton (Gifford & Dagg 1991). They may also produce new compounds, such as essential lipids (Klein-Breteler et al. 1999). The copepod grazing impact on ciliates is very variable (Dolan et al. 1991, Nielsen & Kiøboe 1994, Lonsdale et al. 2000). Copepods may extensively influence ciliate abundance or production in productive areas such as the EBUS characterized by high copepod biomass (Calbet & Saiz 2005).

The role of microzooplankton as a part of the food web depends on the trophic status and the ambient conditions of the ecosystem. For instance, small flagellates seem to be the main grazers on phytoplankton in oligotrophic areas, while mixo- and heterotrophic dinoflagellates are important grazers in high productive areas such as upwelling systems (Calbet 2008). Microzooplankton is further able to adapt to changing environmental conditions due to fast reproduction cycles and its variety of feeding mechanisms including omnivory, mixotrophy and bacterivory (Dolan & Pérez 2000).

It has been generally accepted that short food chains prevail in high productive upwelling areas; a high production of large phytoplankton cells is passed directly to mesozooplankton and to larger animals like fish. During the last two decades, however, research revealed that this simple view of the food chain in the upwelling region does not correspond to the reality. It is important to understand the driving mechanisms (bottom-up or top-down) in the food web to characterize the trophic interactions in the ecosystem. Until now, interactions between bottom-up and top-down control in the EBUS are poorly understood. Verheye and Richardson (1998) proposed several mechanisms, which probably influence long-term changes in the abundance of zooplankton in the BUS. From the bottom-up view, an increase in upwelling favorable wind stress and associated processes could cause an increase in zooplankton abundance. From the top-down view, an increase in zooplankton could be related to a long-term decrease in the abundance of pelagic fishes as a result of increasing fishing effort. These suggestions could be applied to smaller scale interactions between environmental parameters, primary producers, microzooplankton and mesozooplankton.

The trophic structure of the ecosystem is also determined by the diversity of the ecosystem. Increasing predator size spectra enhance the strength of top-down control on prey through diet niche partitioning (Ye et al. 2013). The diversity of microzooplankton is influenced by the size-class diversity of potential phytoplankton prey (Dolan et al. 2002). Small phytoplankton cells, mainly diatoms and dinoflagellates, are well adapted to fresh upwelled water high in nutrients, whereas larger cells and dinoflagellates adapted to stratified and nutrient poor waters are associated with matured offshore water (Hansen et al. 2014). Therefore the diversity of microzooplankton is supposed to be lower in fresh upwelled water near the coast and further offshore, and highest above the deeper shelf and at the shelf break. This assumption is in contrast to other studies, which reported about increasing diversity of other plankton groups in direction from the shelf to offshore (Miloslavić et al. 2012; Bohata & Koppelmann 2013; Koppelmann et al. 2014).

As mentioned above the physical environment is not only an affecting the trophic interactions in the ocean but also the temporal and spatial distribution, growth, and dominance of species. Flow patterns in the ocean, which influence the distribution of organisms on all spatial scales, are important drivers (Mann & Lazier 2005). The distribution of species in the ocean is also controlled by biological dynamics such as food availability or sexual encounters among individuals of relatively rare species (Franks 2005). These biological and physical drivers are responsible for the patchy distribution of the plankton, but are still not well understood.

3.3.3. Main groups of microzooplankton

The main contributors to the microzooplankton biomass are mixo- and heterotrophic dinoflagellates, ciliates and small copepods and their larvae (figure 3-2; Quevedo & Anadón 1999; Elangovan et al. 2012).

Mixo- and heterotrophic dinoflagellates

The importance of mixo- and heterotrophic dinoflagellates in marine pelagic systems have been recognized since Lessard and Swift (1985, 1986) showed that some dinoflagellates in marine plankton lack chloroplasts and consumed other plankton cells. The feeding plasticity may allow them to ingest prey ranging in size from ca. 1 µm (Strom 1991; Jeong 2005) to many times their body size (Hansen 1992). They are relatively non-selective feeders, and may be able to persist at low food abundances (Sherr & Sherr 2007). Three different types of feeding mechanisms occur among the mixo- and heterotrophic dinoflagellates: direct engulfment, pallium feeding and tube feeding (Gaines and Elbrächter 1987; Hansen & Calado 1999). Therefore, they can be as significant as mesozooplankton in consuming bloom-forming diatoms (Sherr & Sherr 2007). Some species are known to form cysts when the food concentration is low (Goodman 1987). Or simply reduce metabolic activity (Fenchel and Finlay 1983). These features make them to excellent survivors in different marine ecosystems.

Ciliates (Ciliophora)

During last two decades, ciliate microzooplankton have become acknowledged as playing an important role in most planktonic food webs (Pierce & Turner 1992). The planktonic ciliates are a morphologically diverse group. Most of the ciliates are naked (aloricate ciliates or naked ciliates), but several groups and species form a lorica (e.g. tintinnids; loricate ciliates). All loricate ciliates are heterotroph; the naked ciliates are further divided by nutritional function into autotrophic, mixotrophic and heterotrophic naked ciliates. (Petz 1999).

Life cycles of ciliates vary depending upon the adaptive strategy of the species. A typical life cycle of ciliates is asexual binary fission (Raikov 1996). When food is a limiting factor, the ciliates become sexually active and enter the conjugation phase of the cycle. If there is no available partner around, ciliates can undergo encystment i.e. formation of resting cyst (Petz 1999).

Naked ciliates are the main component of the ciliate community. They can be up to 50 times more abundant than tintinnid ciliates (Smetacek 1981; Pierce & Turner 1992). These aloricate ciliates occur in high concentrations and may consume significant quantities of the autotrophic and heterotrophic microbial production (Pomeroy 2007; Di Poi 2013). The naked ciliates are often dominated by oligotroch species belonging to the Strombidium group (Beers 1971; Tumantseva & Kopylov 1985).

Tintinnids, loricate ciliates, generally represent only a small fraction of the ciliate community (<10%) of total cell numbers or biomass (Dolan & Marrasé 1995; Dolan 2000). Although tintinnids play a minor role in carbon cycle processes or nutrient regeneration, they are ideal indicator organisms to determine changes in the structure of the microzooplankton community and therefore mirror changes in the ecosystem (Thompson et al. 1999). Changes in tintinnid composition can be detected relatively easy using lorica morphology.

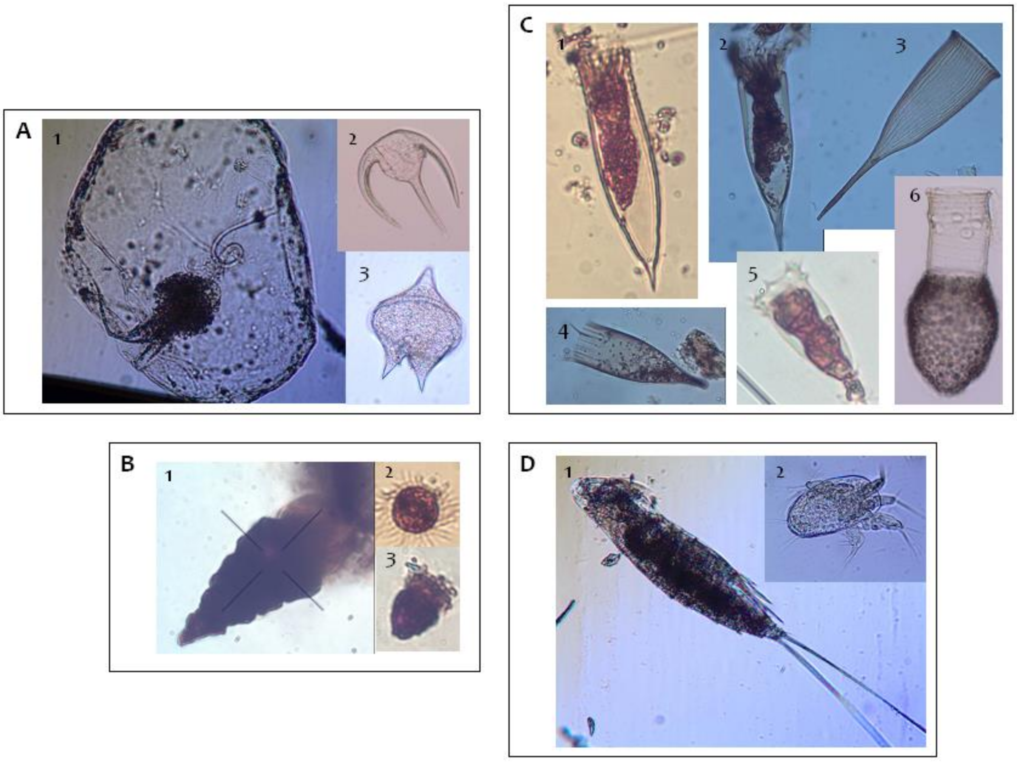


Figure 3-2: The three main groups of microzooplankton: mixo- and heterotrophic dinoflagellates (A), naked ciliates (B), tintinnids (C), copepods and nauplius larvae (D). *Noctiluca scintilans* (A1), *Ceratium* spp. (A2) and *Protoperidinium* spp. (A3), *Laboea strobila* (B1), *Strombidium* spp. (B2+B3), *Helicostomella* (C1), *Favella* (C2), *Rhabdonella spiralis* (C3), *Dadayiella* sp. (C4), *Acanthostomella conicoides* (C5), *Codonelopsis morchella* (C6), *Microsetella* sp. (D1), nauplius larvae (D2).

Generally, the abundances of ciliates decrease from coastal regions towards the open ocean (Alder 1999). High numbers often occur in bays and estuaries, but high densities may also be found in nutrient-rich water masses such as upwelling regions (Porter 1985; Laybourn-Parry 1992). The majority of ciliates is mainly found in the upper 40 m and decreases with depth (Beers & Steward 1969; Margalef 1973). The general distribution of naked ciliates reflects the phytoplankton distribution (Beers et al. 1980; Dolan & Marrasé 1995; Leakey et al. 1996).

Small copepods

Small planktonic copepods (<200 µm) are the most abundant metazoans on Earth (Turner 2004). Despite their high abundance and important position in the food web, there is still limited knowledge about these small copepods in comparison to the larger calanoid taxa. They play an important role as grazers of bacterioplankton and mixo- and heterotrophic protists and as a prey for larger organisms such as ichthyoplankton or other large pelagic carnivores (Turner 1984).

This group includes mainly cyclopoid copepods such as *Oithona* spp., *Oncaea* spp. and harpacticoid copepods such as *Microsetella* sp., but also adults and copepodites of calanoid copepods like *Paracalanus* sp., *Pseudocalanus* sp. or *Acartia* sp.; and nauplius larvae of almost all copepod species.

3.4. General Objectives

This thesis represents for the first time very detailed information about the microzooplankton of the Benguela Upwelling System. The aims of this thesis are to investigate distribution patterns, appearance and abundance of diverse microzooplankton species and to investigate the importance of microzooplankton within food web more complex then hitherto thought.

The main objectives underlying this thesis are:

- distribution patterns in dependence on environmental and biological drivers (*manuscript 1:* **Spatial patterns of microzooplankton in the northern Benguela Upwelling System**)

- influence of upwelling filaments on microzooplankton community (*manuscript 2:* **Microzooplankton communities: fluctuating fundamental components of upwelling filaments**)

- dynamics of microzooplankton community during short-time series (*manuscript 3:* **Microzooplankton patchiness: short-time series**)

- interactions between microzooplankton, mesozooplankton and the benthic community (*manuscript 4:* **Benthic structures in the Namibian Upwelling Region and the pelago-benthic coupling**)

3.5. References

Abel DC, McConnell RL (2010) Environmental oceanography: Topics and analysis, Vol. Jones and Barlett Publishers, Sudbury

Alder VA (1999) Tintinnoinea. In: Boltovskoy D (ed) South Atlantik Zooplankton. Backhuys Publishers, Leiden, p 1706

Álvarez-Salgado XA, Doval MD, Borges AV, Joint I, Frankignoulle M, Woodward EMS, Figueiras FG (2001) Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System. Progress in Oceanography 51:321-337

Azam F, Fenchel T, Field GJ, Gray JS, Mayer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10:257-263

Bakun A (1996) Patterns in the Ocean: Ocean Processes and Marine Population Dynamics., Vol. University of California Sea Grant, Centro de Investigaciones Biologicas de Noroeste, San Diego

Barton ED, Arístegui J, Tett P, Cantón M, García-Braun J, Hernández-León S, Nykjaer L, Almeida C, Almunia J, Ballesteros S, Basterretxea G, Escánez J, García-Weill L, Hernández-Guerra A, López-Laatzen F, Molina R, Montero MF, Navarro-Pérez E, Rodríguez JM, van Lenning K, Vélez H, Wild K (1998) The transition zone of the Canary Current upwelling region. Progress in Oceanography 41:455-504

Beers JR, Stewart GL (1969) Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Marine Biology 4:182-189

Beers JR, Stewart GL (1971) Microzooplankton in the plankton communities of the upper waters of the eastern tropical Pacific. Deep-Sea Res 18:861 - 883

Beers JR, Reid FMH, Stewart GL (1980) Microplankton of the North Pacific Central Gyre. Population structure and abundance, June 1973. Internationale Revue gesamten Hydrobiologie 60:607-638

Blamey LK, Howard JAE, Agenbag J, Jarre A (2012) Regime-shifts in the southern Benguela shelf and inshore region. Progress in Oceanography 106:80-95

Bohata K, Koppelmann R (2013) Chaetognatha of the Namibian Upwelling Region: Taxonomy, Distribution and Trophic Position. PLoS ONE 8:e53839

Brink KH (1983) The near-surface dynamics of coastal upwelling. Progress in Oceanography 12:223-257

Brown PC, Hutchings L (1987a) The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 1. Drogue movements, hydrography and bloom development. South African Journal of Marine Science 5:357-391

Brown PC, Hutchings L (1987b) The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 2. Nutrient relationships. South African Journal of Marine Science 5:393-409

Calbet A (2001) Mesozooplankton Grazing Effect on Primary Production: A Global Comparative Analysis in Marine Ecosystems. Limnology and Oceanography 46:1824-1830

Calbet A (2008) The trophic roles of microzooplankton in marine systems. ICES Journal of Marine Science 65:325-331

Calbet A, Saiz (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Calbet A, Landry MR (2004) Phytoplankton growth, Microzooplankton grazing, and carbon cycling in marine systems. Limnol Oceanog 40:51 - 57

Castellani C, Irigoien X, Harris RP, Lampitt RS (2005) Feeding and egg production of Oithona similis in the North Atlantic. Marine Ecology Progress Series 288:173-182

Clarke RK, Gorley RN (2006) Primer V6: User Manual - Tutorial, Vol. Plymouth Marine Laboratory, Plymouth

Cole J, McGlade J (1998) Clupeoid Population Variability, the Environment and Satellite Imagery in Coastal Upwelling Systems. Reviews in Fish Biology and Fisheries 8:445-471

Cravo A, Relvas P, Cardeira S, Rita F, Madureira M, Sánchez R (2010) An upwelling filament off southwest Iberia: Effect on the chlorophyll a and nutrient export. Continental Shelf Research 30:1601-1613

Demarcq H, Barlow RG, Shillington FA (2003) Climatology and Variability of Sea Surface Temperature and Surface Chlorophyll in the Benguela and Agulhas Ecosystems As Observed by Satellite Imagery. African Journal of Marine Science 25:363-372

Di Poi E, Blason C, Corinaldesi C, Danovaro R, Malisana E, Fonda-Umani S (2013) Structure and interactions within the pelagic microbial food web (from viruses to microplankton) across environmental gradients in the Mediterranean Sea. Global Biogeochemical Cycles 27:1034-1045

Dolan JR (1991) Microphagous ciliates in mesohaline Chesapeake Bay waters: Estimates of growth rates and consumption by copepods. Marine Biology 111:303-309

Dolan JR, Marrasé C (1995) Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993. Deep Sea Research Part I: Oceanographic Research Papers 42:1965-1987

Dolan JR, Pérez MT (2000) Costs, benefits and characteristics of mixotrophy in marine oligotrichs. Freshwater Biology 45:227-238

Dolan JR, Claustre H, Carlotti F, Plounevez S, Moutin T (2002) Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean. Deep Sea Research Part I: Oceanographic Research Papers 49:1217-1232

Elangovan SS, Kumar MA, Karthik R, Sankar RS, Jayabarathi R, Padmavati G (2012) Abundance, species composition of microzooplankton from the coastal waters of Port Blair, South Andaman Island. Aquatic Biosystems 8:20

Escribano R, Hidalgo P (2000) Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling. Journal of Marine Biological Association of the United Kingdom 80:283-290

Fenchel T, Finlay BJ (1983) Respiration rates in heterotrophic, free-living protozoa. Microbial Ecology 9:99-122

Franks PJS (2005) Plankton patchiness, turbulent transport and spatial spectra. Marine Ecology Progress Series 294:295-309

Gaines G, Elbrächter M (1987) Heterotrophic nutrition. In: Taylor FJR (ed) The biology of dinoflagellates. Blackwell Scientific Publications, Oxford, p 229-267

García-Muñoz M, Arístegui J, Montero MF, Barton ED (2004) Distribution and transport of organic matter along a filament-eddy system in the Canaries â€“ NW Africa coastal transition zone region. Progress in Oceanography 62:115-129

Gifford DJ, Dagg MJ (1988) Feeding of the estuarine copepod Acartia tonsa Dana: carnivory vs. herbivory in natural microplankton assemblages. Bulletion of Marine Science 43:458-468

Goodman DK (1987) Dinoflagellate cysts in ancient and modern sediments. In: Taylor FJR (ed) The Biology of Dinoflagellates. Blackwell Scientific Publications, Oxford, p 649-722

Hansen PJ (1992) Particle size selection, feeding rates and growth dynamics of marine heterotrophic dinoflagellates, with special emphasis on *Gyrodinium spirale*. Marine Biology 114:327-334

Hansen PJ, Calado AJ (1999) Phagotrophic Mechanisms and Prey Selection in Free-living Dinoflagellates1. Journal of Eukaryotic Microbiology 46:382-389

Hansen A, Ohde T, Wasmund N (2014) Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. Journal of Marine Systems 140, Part B:130-137

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Haynes R, Barton ED, Pilling I (1993) Development, persistence, and variability of upwelling filaments off the Atlantic coast of the Iberian Peninsula. Journal of Geophysical Reasearch 98:681-692

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress In Oceanography 83:15-32

Jeong HJ, Kim JS, Kim JH, Kim ST, Seong KA, Kim TH, Song JY, Kim SK (2005) Feeding and grazing impact of the newly described heterotrophic dinoflagellate *Stoeckeria algicida* on the harmful alga *Heterosigma akashiwo*. Marine Ecology Progress Series 295:69-78

Klein-Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. Marine Biology 135:191-198

Kleppel GS (1993) On the diets of calanoid copepods. Marine Ecology Progress Series 99:183-195

Koppelmann R, Jung SA, Lahajnar N (2014) Abundance and trophic position of gelatinous zooplankton in the Namibian Upwelling Region. In: Kehayias G (ed) Zooplankton: species diversity, distribution and seasonal dynamics. Nova Science Publishers, New York, pp. 177-207

Lalli CM, Parson TR (1993) Biological oceanography: An introduction., Vol. Pergamon, Oxford

Landry MR, Hassett RP (1982) Estimating the grazing impact of marine micro-zooplankton. Marine Biology 67:283-288

Laybourn-Parry J (1992) Protozoan Plankton Ecology. The Journal of Protozoology 39:740-741

Leakey RJG, Burkill PH, Sleigh MA (1996) Planktonic ciliates in the northwestern Indian Ocean: thenabundance and biomass in waters of contrasting productivity. Journal of Plankton Research 18:1063-1071

Lessard EJ, Swift E (1985) Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. Marine Biology 87:289-296

Lessard EJ, Swift E (1986) Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. Journal of Plankton Research 8:1209-1215

Lonsdale DJ, Caron DA, Dennett MR, Schaffner R (2000) Predation by Oithona spp. on protozooplankton in the Ross Sea, Antarctica. Deep Sea Research Part II: Topical Studies in Oceanography 47:3273-3283

Lutjeharms JRE, Meeuwis JM (1987) The extent and variability of South-East Atlantic upwelling. South African Journal of Marine Science 5:51-62

Lutjeharms JRE, Shillington FA, Duncombe Rae CM (1991) Observations of extreme upwelling filaments in the southeast atlantic ocean. Science 253:774-776

Mackas DL, Peterson WT, Ohman MD, Lavaniegos BE (2006) Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophysical Research Letters 33:L22S07

Mann KH, Lazier JRN (2005) Biology and Boundary Layers. In: Dynamics of Marine Ecosystems. Blackwell Publishing Ltd., p 512

Margalef R (1973) Distribución de los ciliados planctónicos en la región de afloramiento del noroeste de Africa. Resultados expediciones científicas del buque oceanográfico "Cornide de Saavedra":109-124

Marchesiello P, Estrade P (2009) Eddy activity and mixing in upwelling systems: a comparative study of Northwest Africa and California regions. International Journal of Earth Sciences 98:299-308

Marín VR, Escribano R, Delgado LE, Olivares G, Hidalgo P (2001) A numerical study of the upwelling circulation off central Chile. Continental Shelf Research 21:1317-1329

Miloslavić M, Lučić D, Njire J, Gangai B, Onofri I, Garić R, Žarić M, Miri Osmani F, Pestorić B, Nikleka E, Shumka S (2012) Zooplankton composition and distribution across coastal and offshore waters off Albania (Southern Adriatic) in late spring. Acta Adriatica 52:165-180

Mohrholz V, Schmidt M, Lutjeharms JRE (2001) The hydrography and dynamics of the Angola-Benguela Frontal Zone and environment in April 1999 : BENEFIT Marine Science. South African Journal of Science 97:p.199-208

Muller AA, Mohrholz V, Schmidt M (2013) The circulation dynamics associated with a northern Benguela upwelling filament during October 2010. Continental Shelf Research 63:59-68

Navarro-Pérez E (1998) The physical structure of an upwelling filament off the North-west African coast during august 1993. African Journal of Marine Science 19

Nelson G, Hutchings L (1983) The Benguela Upwelling Area. Progress in Oceanography 12:333-356

Nielsen TG, Kiøboe T (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. Limnology and Oceanography 39:508-519

Petz W (1999) Ciliophora. In: Boltovskoy D (ed) South Atlantic Zooplankton. Backhuys Publishers, Leiden, p 1706

Pierce RW, Turner JT (1992) Ecology of planktonic ciliates in marine food webs. Reviews in Aquatic Science 6:139-181

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Marine Ecology Progress Series 172:253-264

Pomeroy LR, Williams PJ, Azam F, Hobbie JE (2007) The Microbial Loop. Oceanography 20:28-33

Porter KG, Sherr EG, Sherr BF, Pace M, Saunders RW (1985) Protozoa in planktonic food webs. J Protozool 32:409 - 415

Quevedo M, Anadón R (2000) Spring microzooplankton composition, biomass and potential grazing in the central Cantabrian coast (southern Bay of Biscay). Oceanologica Acta 23:297-310

Raikov IB (1996) Nuclei of ciliates. In: Hausmann K, Bradbury PC (eds) Ciliates: Cells as Organisms. Gustav Fischer, Stuttgart, p: 221-242

Rau GH, Ralston S, Southon JR, Chavez FP (2001) Upwelling and the condition and diet of juvenile rockfish: A study using 14C, 13C, and 15N natural abundances. Limnology and Oceanography 46:1565-1570

Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. . Acta Oecologica 12:35-51

Shannon LV, Nelson G (1996) The Benguela: Large Scale Features and Processes and System Variability. In: The South Atlantic. Springer Berlin Heidelberg, p 163-210

Shannon LV, O'Toole M (2003) Sustainability of the Benguela: ex Africa semper aliquid novi. In: Hempel G, Sherman K (eds) Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research. Elsevier, p 423

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Marine Ecology Progress Series 352:187-197

Smetacek V (1981) The annual cycle of protozooplankton in the Kiel Bight. Marine Biology 63:1-11

Sobarzo M, Figueroa D (2001) The physical structure of a cold filament in a Chilean upwelling zone (Peninsula de Mejillones, Chile, 23°S). Deep Sea Research Part I: Oceanographic Research Papers 48:2699-2726

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the opwen Subarctic Pacific Ocean. Marine Ecology Progress Series 78:103-113

Strub PT, Korso PM, Huyer A (1991) The nature of the cold filaments in the California Current System. Journal of Geophysical Reasearch 96:743-768

Summerhayes CP, Kroon D, Rosell-Melé A, Jordan RW, Schrader HJ, Hearn R, Villanueva J, Grimalt JO, Eglinton G (1995) Variability in the Benguela Current upwelling system over the past 70,000 years. Progress in Oceanography 35:207-251

Thomas AC, Carr M-E, Strub PT (2001) Chlorophyll variability in eastern boundary currents. Geophysical Reasearch Letters 28:3421-3424

Thompson GA, Alder VA, Boltovskoy D, Brandini F (1999) Abundance and biogeography of tintinnids (Ciliophora) and associated microzooplankton in the Southwestern Atlantic Ocean. Journal of Plankton Research 21:1265-1298

Traganza ED, Redalije DG, Garwood RW (1987) Chemical flux, mixed layer entrainment and phytoplankton blooms at upwelling fronts in the California coastal zone. Continental Shelf Research 7:89-105

Tumantseva NI, Kopylov AI (1985) 985) Reproduction and production rates of planktonic infusoria in coastal waters of Peru. Oceanology 25:390-394

Turner JT (1984) The Feeding Ecology of Some Zooplankters That are Important Prey Items of Larval Fish Vol 7. NOAA/National Marine Fisheries Service

Verheye HM, Lamont T, Huggett JA, Kreiner A, Hampton I (2015) Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME). Environmental Development:ENVDEVD1500081

Verheye HM, Richardson AJ (1998) Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951-1996): bottom-up or top-down control? ICES Journal of Marine Science: Journal du Conseil 55:803-807

Ye L, Chang C-Y, García-Comas C, Gong G-C, Hsieh C-h (2013) Increasing zooplankton size diversity enhances the strength of top-down control on phytoplankton through diet niche partitioning. Journal of Animal Ecology 82:1052-1061

Chapter 4

Spatial patterns of microzooplankton in the northern Benguela Upwelling System

Bohata Karolina, Otto Saskia A., Koppelmann Rolf, Brust-Möbius Juliane*, Mertzen Matthias, Müller Anja

Institute for Hydrobiology and Fisheries Science, Center for Earth Systems Research and Sustainability, University of Hamburg, Hamburg, Germany

*Leibniz-Institute for Baltic Sea Research Warnemünde, Germany

Abstract

The main objectives of this study were to characterize the composition of microzooplankton and asses spatial community patterns in the northern Benguela Upwelling System between 17°15'S and 26°40'S. This study investigates the association of microzooplankton to environmental parameters such as temperature, salinity, chl *a* and spatial structures in order to understand the distribution of different microzooplankton taxa in this high productive environment. The distribtuion of total abundance of microzooplankton is related to broad spatial scales ($R^2 = 0.49$) and primary production (chl *a* content; $R^2 = 0.28$), whereas the diversity is more likely influenced by environmental conditions (temperature, $R^2 = 31\%$). The RDA analyses could explain 54% of the constrained variance of the taxonomic groups and showed a strong difference between the center region vs. the northern/southern regions. The center region was dominated by the Tintinnida group, whereas the microzooplankton in the southern and northern region mainly composed of mixo- and heterotrophic Dinoflagellata. The Tintinnida taxa distribution showed longitudinal and latitudinal shifts in composition. Tintinnida were dominated by the cosmopolitan species *Codonella galea* and *Codonellopsis morchella* in the South and by the warm-temperate species *Rhabdonella spiralis* in the North. The knowledge about the distribution patterns of organisms is nessesary to understand of the complexity of variable ecosystems such as upwelling systems.

4.1. Introduction

Microzooplankton are organisms between 20 and 200 µm and consists of many groups of organisms like ciliates, hetero- and mixotrophic Dinoflagellata, Foraminifera, Pteropoda, Radioloaria, Nauplius Larvae, several copepodite stages and small Copepoda. Microzooplankton may consume on average between 60 and 75% of the particulate primary production (Calbet & Landry 2004) while the mesozooplankton consumes in average only 15% of particulate primary production in the surface ocean directly (Calbet 2001). Microzooplankton is also a significant food source for mesozooplankton, both in quantitative and qualitative aspects. They are preferred food for copepods due to their optimal cell size and biochemical composition (Kleppel et al. 1993; Castellani 2005). Microzooplankton transfers minerals, vitamins, amino acids, fatty acids and sterols from lower trophic levels to mesozooplankton (Gifford & Dagg 1988).

Assemblages of zooplankton species reflect the relations between environmental conditions and organisms (Hughes 2000). Physical and chemical factors influence zooplankton distribution, especially the effect of temperature and salinity on zooplankton has been well studied. Temperature strongly influences the vital physiological rates of zooplankton such as respiration (Roddie et al. 1984) and excretion (Gaudy et al. 2000). Temperature may also influence the life history of zooplanktonic organisms such as Copepoda effecting the egg production (Halsband-Lenk et al. 2002), growth (Hirst & Kiørboe 2002; Leonardo et al. 2006) and mortality rates (Hirst & Kiørboe 2002). Salinity has an effect on the overall composition of the zooplankton and individual species at different stages of their life cycle (Anger 2003, Queiroga & Blanton 2004). Also mechanical conditions such as turbulence directly effect feeding behaviour of zooplankton (Yamazaki et al. 1991; Kiørboe & Saiz 1995; Saiz & Kiørboe 1995). Some zooplankton species, e.g. Tintinnida, are related to specific water properties (Sanders 1986, Dolan 2000) and may be used as indicators for different water masses (Kato & Taniguchi 1993).

Additionally, the environmental conditions affect the microzooplankton community indirectly through the food web. The phytoplankton composition is influenced by the strength of the upwelling intensity. Small phytoplankton cells, mainly small Diatomea (<10 µm) and small Flagellata (<10 µm), are well adapted to strong water mixing and high nutrient concentrations (Walker and Peterson 1991; Pitcher et al. 1998; Hansen et al. 2014). They are commonly associated with fresh upwelled water. Larger Diatomea (>50 µm) cells are typical for matured water with reduced nutrient concentrations (Walker and Peterson 1991; Hansen et al. 2014). In contrast, the offshore water masses, characterized by low nutrient concentrations and well-developed stratification, are an ideal environment for blooms of small Dinoflagellata (Hart and Currie 1960; Shannon and Pillar 1986, Hansen et al. 2014). These differences in the composition of the primary producers influence the microzooplankton community (Lynn and Montagnes 1991). The size of phytoplankton determines the microzooplankton composition since not all microzooplankton groups are able to prey on large Diatomea cells. Typically, Ciliata selectively feed on small prey with a predator-prey ratio of 10:1 (Jonsson 1986, Fenchel 1987), while heterotrophic Dinoflagellata are able to prey on organisms ranging in size from ca. 1 µm (Strom 1991; Jeong et al. 2005) to several times their body size (Lessard 1991; Hansen 1992; Horner et al. 2005; Saito et al. 2006, Sherr and Sherr 2007). Hence, this selectivity affects the structure of the phytoplankton community. Consumption of Diatomea by mixo- and heterotrophic Dinoflagellata and Ciliata discard empty silica frustules and produce small fecal pellets composed of frustules with associated carbon and, hence, influences biogeochemical cycles (Buck and Newton 1995; Strom and Strom 1996). Furthermore, the grazing of microzooplankton plays a role in recycling of inorganic nitrogen and phosphorus due to excretion of dissolved and particulate materials (Caron and Goldman 1990; Dolan 1997).

As described above, abiotic and biotic processes in the ocean influence the structures of zooplankton communities (Steele & Henderson 1994). If these environmental parameters are structured, their pattern is reflected in the zooplankton community. We differentiate between broad spatial scales and fine spatial scales. The broad spatial scales are structures, e.g. latitudinal and longitudinal distribution patterns, encompassing areas over 100 km (Folt & Burns 1999). These patterns are mostly structured by physical and chemical environmental conditions such as changes in temperature, salinity, oxygen content or nutrient concentrations. Fine spatial scales, whose sizes are in the order of distances between nearby stations mainly reflect patterns in zooplankton distribution related to species interactions and interactions between the organisms such as relationships within the food web (Pinel-Alloul 1995; Rovinsky et al. 1997).

Despite its ecological importance within the food web, very little is known about microzooplankton community dynamics in upwelling systems. For the Benguela Current region, which is one of the five major eastern boundary upwelling regions, studies documenting the complex microzooplankton community in this productive region are completely lacking.

In this study, we aim to characterize the composition of microzooplankton and assess spatial community patterns within this heterogeneous region. We speculate that the composition of the microzooplankton community is significantly influenced by environmental differences in this productive region.

Specifically, we address the following questions:

(1) Are there any differences in the microzooplankton diversity (i.e. total abundance and species richness) and composition between the northern part and the southern part of the northern BUS study region (i.e. at broad spatial scale)? Are there any spatial differences at finer scales? For the composition, we specifically focus on the major taxonomic groups as well as tintinnid species.

(2) What are the major environmental drivers for the observed spatial patterns at different scales?

4.2. Methods

4.2.1. Study area

The Benguela Upwelling System is driven by equator-ward wind stress along the entire west coast of southern Africa (Parrish et al. 1983; Shannon 1985). This large ecosystem can be divided into two sub-ecosystems, the southern and northern Benguela Upwelling System (BUS), which are separated by a permanent upwelling cell off Lüderitz at 27°S (Hart and Currie 1960; Shannon 1985; Shannon and Pillar 1986; Hutschings et al. 2009). The northern part of the northern BUS is influenced by seasonal intrusions of the warm, saline waters from the Angola Current (Shannon 1985; Shannon and Pillar 1986; Hutchings et al. 2009). The southern part of the northern BUS is affected by the Lüderitz upwelling cell, which is characterized by strong winds, high turbulences, intense offshore advection and low phytoplankton concentrations (Hutchighs et al. 2009). Generally, upwelling in the northern BUS occurs throughout the whole year with highest intensities during late winter and spring (Shannon and Pillar 1986).

4.2.2. Microzooplankton sampling and analysis

The abundance and biomass of microzooplankton was investigated during moderate upwelling conditions off the Namibian coast in January and February 2011 (southern summer) as a part of the GENUS-project on RV Maria S. Merian. The samples were collected at 24 stations along 6 transects by stratified hauls with a Multi-Closing-Net (Hydrobios) using a mesh size of 55 µm (table 4-1). The sampling intervals were 200-100-50-25-0 m depth for the shallow hauls and 1000-600-400-200-0 m depth for the deep hauls. All material was preserved in a 4% formaldehyde-seawater solution buffered with sodium-tetraborate for later analyses.

In home laboratory, samples were transferred into a sorting fluid composed of 94.5% fresh water, 5.0% propylene glycol and 0.5% propylene phenoxetol (according to Steedman 1976) for the analyses of taxonomic composition and distribution. The samples were fractionated using 55 µm and 300 µm sieves. Only the fraction below 300 µm has been further analyzed and identified to the species level or to the nearest taxonomic level that morphological characteristics allowed and counted. The abundance was expressed as ind. m^{-3}.

4.2.3. Environmental data

Salinity and temperature was measured with a CTD (Seabird 911+) at 51 stations along and between the transects.

MODIS Aqua chl *a* concentrations were extracted for each sampling site. Due to intense cloud coverage and frequent sunglint during time of sampling the availability of matching satellite data was limited. Therefore the monthly MODIS Aqua level-3 product of February 2011 was used for chlorophyll extraction. The level-3 chl *a* concentrations are based on the OCI (ocean color index) algorithm according to Hu et al. (2012).

4.2.4. Statistical analysis

Total abundance and species richness

We applied a trend-surface analysis to identify the presence and relative scale of spatial patterns of total abundance N and species richness S in the upper 50m (Borcard et al. 2011). Within a linear regression model framework we related both diversity indices to the centred X-Y coordinates of the sampling sites, which allows the identification of linear trends. In addition, we included second- and third-order polynomial terms of the coordinates in the model to test also for curvilinear structures, i.e. spatial structures at finer spatial scales in XY, X^2, Y^2, X^2Y, XY^2, X^3, Y^3 patterns.

We started with a full model including all 9 spatial variables and carried out a backward selection procedure based on Akaike's Information Criterion (Akaike 1974). The optimal model was validated and checked for assumptions (i.e., normality, homogeneity, and spatial independence) by applying diagnostics plots on the residuals. The effect of environmental conditions on total abundance N and species richness S was similarly assessed. Starting with a full model, both response variables were modelled as a linear function of temperature, salinity, bottom depth, and Chl *a* (ln-transformed). A backward model selection was performed using again the AIC as selection criterion.

Community composition

Spatial patterns in the composition of main taxa and tintinnid abundances were analysed by applying the polynomial trend-surface analysis on the community data within a redundancy analysis (RDA). The method was first proposed by Legendre (1990) and involves generating a spatial matrix using the centred geographic coordinates of the sampled area and their seven second- and third-order polynomials. Conceptually, RDA is a multivariate multiple linear regression followed by a PCA of the fitted values. Each species abundance variable **a**, which has been Hellinger-transformed before, is regressed on the explanatory spatial matrix **S** and the fitted values **â** stored into a matrix **Â**. A PCA is then computed on the **Â** matrix, which produces a vector of canonical eigenvalues and a matrix **U** of canonical eigenvectors.

In a first step, an RDA was performed using the community matrix and the full spatial matrix to calculate the adjusted R-square threshold for the selection of the best predicting spatial variables. A forward selection using the double-stopping criterion developed by Blanchet et al. (2008) was then performed to reduce the model to its significant components only. The statistical significance of the final RDA (global model) and the individual canonical axes was tested through permutations, with the null hypothesis of an absence of a linear relationship between Y and X. For the community matrix the Hellinger transformation was used *a priori* to overcome the problems that arise when Euclidean distances are applied to ecological community data (Legendre & Gallagher 2001).

More recent techniques that find increasing adoption are the RDA with principal coordinates of neighbour matrices (PCNM) as explanatory spatial matrix (Borcard & Legendre 2002; Borcard et al. 2004) and its wider family of methods called Moran’s eigenvector maps (MEM; Dray et al. 2006). These methods provide a more flexible and elegant way of constructing sets of linearly independent spatial variables to account for different scales of spatial dependence than the polynomial method. However, with irregular spatial sampling designs as in the presented study, i.e. short distances between stations from the same transect and partly great distances between stations of neighbouring transect, interpretation of fine scale pattern can be cumbersome. In this case, the rather coarse polynomial RDA can be more robust and, hence, was our method of choice.

Table 4-1: Stations data for 6 transects along the Namibian coast

station no.	transect name	date	daytime	coordinates	water depth [m]
233	26°40’S	02.02.11	day	26°41'S, 14°45'E	195
235	26°40’S	03.02.11	day	26°43'S, 14°01'E	460
236	26°40’S	03.02.11	day	26°40'S, 13°30'E	1092
241	23°00’S	06.02.11	day	22°59'S, 11°45'E	2963
242	23°00’S	06.02.11	day	23°00'S, 12°29'E	1650
243	23°00’S	07.02.11	day	23°04'S, 12°49'E	919
250	23°00’S	08.02.11	day	23°07'S, 13°22'E	336
264	23°00’S	09.02.11	day	22°59'S, 14°20'E	66
269	21°00’S	11.02.11	day	20°59'S, 13°20'E	95
271	21°00’S	12.02.11	night	20°59'S, 12°50'E	300
272	21°00’S	12.02.11	night	21°00'S, 12°30'E	433
274	20°00’S	12.02.11	night	20°00'S, 11°50'E	410
275	20°00’S	13.02.11	night	20°00'S, 12°10'E	278
276	20°00’S	13.02.11	day	20°00'S, 12°10'E	156
282	19°00’S	14.02.11	day	19°00'S, 12°13'E	109
285	19°00’S	14.02.11	day	18°59'S, 12°00'E	206
292	19°00’S	15.02.11	night	19°00'S, 11°26'E	411
295	19°00’S	16.02.11	day	19°05'S, 11°12'E	1200
298	19°00’S	17.02.11	day	19°00'S, 10°29'E	2054
305	17°15’S	19.02.11	day	17°15'S, 11°30'E	143
306	17°15’S	19.02.11	night	17°19'S, 11°19'E	427
307	17°15’S	20.02.11	day	17°16'S, 11°11'E	820
309	17°15’S	21.02.11	day	17°15'S, 10°47'E	3384
310	17°15’S	22.02.11	day	17°15'S, 10°29'E	3267

To evaluate whether the spatial patterns found for both, main taxa and Tintinnida composition, are related to environmental condition we used 2 different approaches. In a first approach, we simply regressed the fitted site scores of the significant canonical axes on the environmental data and assessed, which variable can best explain the individual axes. In a second approach, we combined the polynomial RDA with a variation partitioning (Borcard et al. 2011). This approach allows quantifying the various unique and combined fractions of variation explained by the several environmental and spatial sources. For instance, a linear trend (spatial gradient) can be considered as a source of variation like any other. The trend is likely to act on the response as well as the explanatory variables. The variation partitioning has the advantage to disentangle the fraction of variation explained purely by the gradient, the fraction explained by the environmental variable that shows also this gradient and the fraction explained by the variation of the same environmental variable that is independent of the gradient (i.e. at the local scale).

For this, 3 independent RDAs and forward selection procedures were performed before the variation partitioning: one with the environmental data, one with the centred X-Y coordinates (i.e. broad scale, gradient), and one with the second- and third-order polynomials of the X-Y coordinates (i.e. fine scale) as explanatory matrix.

All analysis was performed using the R language and environment, version 3.2.1 (R Core Team 2015) and the package 'vegan' (Oksanen et al. 2015).

4.3. Results

4.3.1. Environmental conditions

Typical southern summer conditions were observed during the cruise. The area was characterized by a temperature gradient from west to east with cooler water near the coast in the southern part of the area indicating coastal upwelling (figure 4-1A). The southern part of the area, between 22°S and 27°S, was influenced by more intensive upwelling with temperatures below 16°C and salinities below 35.2. The northern transects 17°30`S, the 19°00'S and partially 20°00'S were influenced by transitions of warm and more saline waters from the Angola current. The temperature and salinity reached values up to 24°C and 36.0, respectively, and tropical conditions.

High chl *a* concentrations of > 9.0 mg m^{-3} were detected close to the coast at the whole study area. Further offshore, the chl *a* concentrations were very low around 1 mg m^{-3} northwards from the 19°00'S transect. Southwards from the 20°00'S transect, the phytoplankton bloom spread further offshore with high chl *a* concentrations above 7.0 mg m^{-3}.

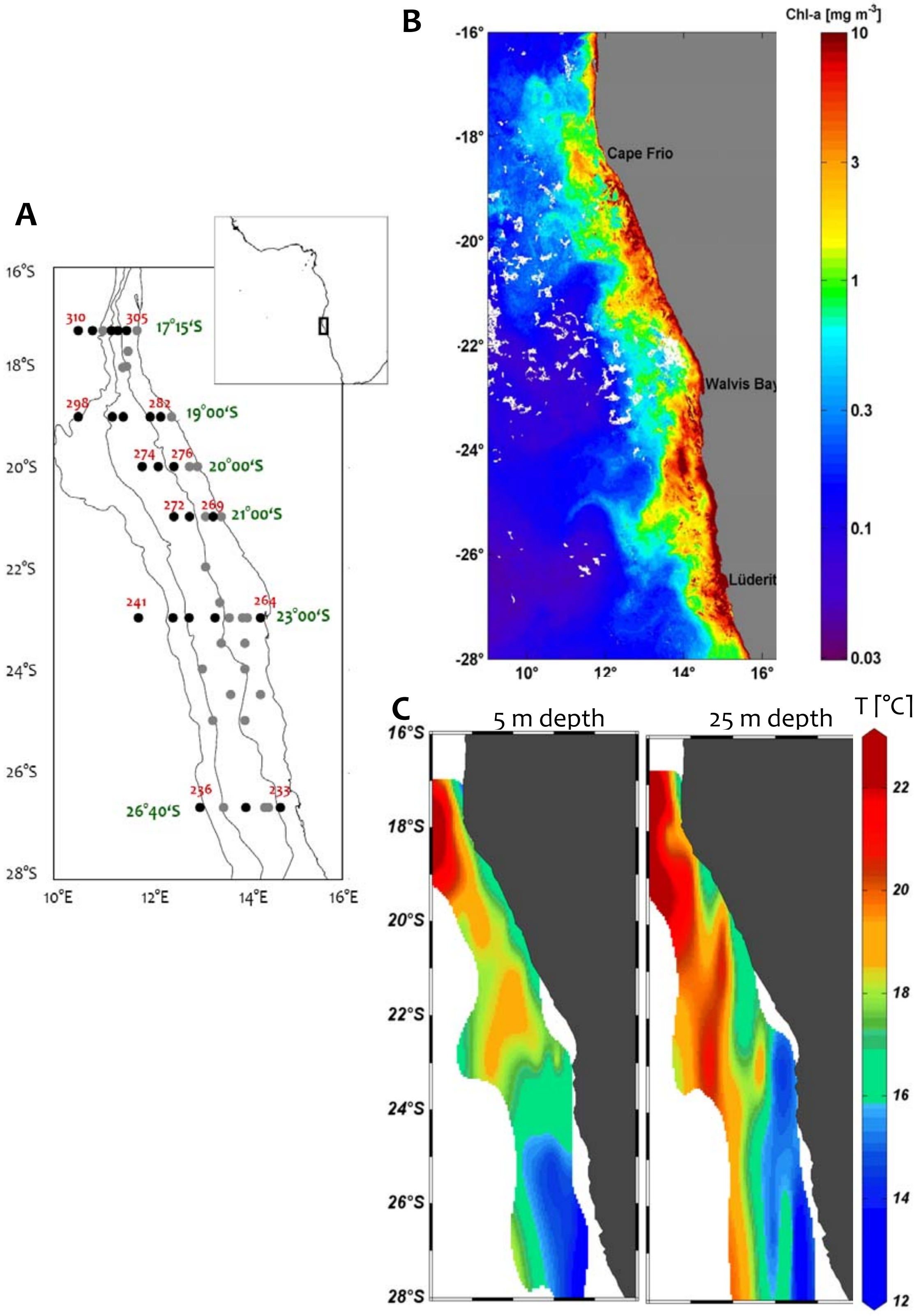


Figure 4-1: Sampling stations along the Namibian coast (A; black = MCN stations, grey = additional CTD stations) with the transect names (green) and ending stations (red), the chl *a* values (B; MODIS data) and the temperature profile in 5 and 25 m depth (C; CTD data) generated using the Ocean Data View.

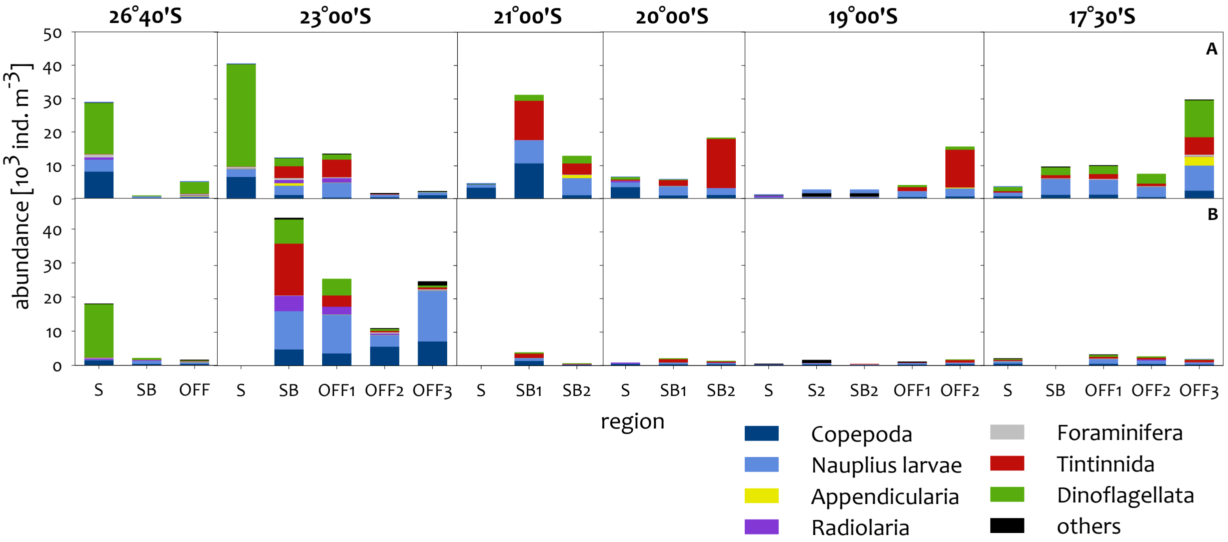


Figure 4-2: Distribution of the main detected microzooplankton groups on the six transects in 0-50 m depth (A) and 50-100 m depth (B). S = shelf, SB = shelf break, OFF = offshore.

4.3.2. Spatial patterns of total abundance and species richness

Most of the microzooplankton organisms were generally detected in the upper 50 m (see figure 4-2 and appendix 4-1). Based on these findings, we decided to focus on the community occurring in the upper 50m for further analyses. The highest abundances of microzooplankton were found in the upper surface layer along the shelf of the 26°40’S and 23°00’S transect with values of 48.3 x 10^3 ind. m^{-3} and 79.9 x 10^3 ind. m^{-3}, respectively (figure 4-2). The northern part of the investigated region (19°00’S and 17°15’S transect) revealed opposite conditions and an increasing trend in abundance of microzooplankton from the shelf to the open ocean in the upper 50 m with highest abundances of microzooplankton of 25.4 x 10^3 ind. m^{-3} and 53.4 x 10^3 ind. m^{-3}, respectively. The trend surface analysis of total abundance confirmed a general longitudinal trend, but also patterns at finer scales as indicated by the significant 2nd order polynomial of the longitude and a significant interaction between longitude and latitude (table 4-2). This spatial pattern can be best explained by the Chl *a* concentration (29% of the total variability), while the temperature, depth, and salinity had no significant effect.

The distribution of species richness, which ranged from 26 to 37, showed a less clear pattern but was generally lower in the South. Latitude was also the best predictor in the trend surface analysis explaining 28% of the total variation (table 4-2). For species richness, temperature explained best the observed latitudinal gradient, with a similar explanatory power (31%).

4.3.3. Description of the microzooplankton community

The microzooplankton community of the southern part of the study area, including the 26°40'S transect and 24°00'S transect, was dominated by Dinoflagellata and Copepoda (figure 4-2). Interestingly, also very high abundances, especially Copepoda, were found in the deeper layer (50-100 m depth) at the 23°00'S transect. In contrast, the microzooplankton communities along the northern transect were concentrated in the upper 50 m. At the 24°00'S, 20°00'S and 19°00'S transect, the microzooplankton composed mainly of Copepoda and Tintinnida. The 17°15'S transect was different to the other transects because the microzooplankton community consisted of almost equal amounts of Copepoda, Tintinnida and mixo- and heterotrophic Dinoflagellata.

Focusing on Copepoda, differences between the southern and the northern part of the study area are obvious (figure 4-3A). Whereas the Copepoda on the 26°40'S and 23°00'S transects were mainly composed of *Oncaea* spp., the 21°00'S and 20°00'S transects were dominated by *Microsetella* spp. and the 17°15'S transect by small calanoid Copepoda and copepodite stages of larger calanoid Copepoda. Copepoda on the 19°00'S transect were relatively low mainly consisting of *Oncaea* spp., whereas *Oithona* spp. was mainly found near the coast in the northern part of the study area.

Very low abundances of Tintinnida (> 0.1 x 10^3 ind. m^{-3}) were detected on the whole 26°40'S transect and on the shelf of the 23°00'S transect (figure 4-3B). In contrast, this group was very abundant at the shelf break of the 21°00'S and 20°00'S transect with a maximum abundance of 14.7 x 10^3 ind. m^{-3}. The abundance of Tintinida decreased from the shelf to the open ocean along the northern transect. In the southern part of the study area (26°40' S and 23°00'S), the community was dominated by the cosmopolitan species *Codonella galea* whereas the 21°00'S and 20°00'S transects were dominated by the cosmopolitan species *Codonellopsis morchela*. Further in the north on the 19°00'S transect, the warm-temperate species *Rhabdonella spiralis* dominated the Tintinnida community. The 17°30'S transect, showed a very heterogeneous distribution of Tintinnida group compared to the other transects.

The highest abundances of mixo- and heterotrophic Dinoflagellata in the upper 50 m was detected in the southern part of the study area (figure 4-3c). The heterotrophic Dinoflagellata group Peridinae was most abundant at the shelf station of the 26°40’S transect (11.9 x 10^3 ind. m^{-3}) and the mioxotrophic Dinoflagellata, represented by *Ceratium* species, were found on the shelf of the 23°00’S transect. With decreasing latitude, the abundances of Dinoflagellata decreased. However, increased abundances of this group were found again on the northernmost transect 17°15’S (11.1 x 10^3 ind. m^{-3}). Overall, the abundances in the deeper layers (50-100 m) were very low (< 0.1 x 10^3 ind. m^{-3}) with an exception at the shelf station of the southernmost transect 26°40’S (14.9 x 10^3 ind. m^{-3}).

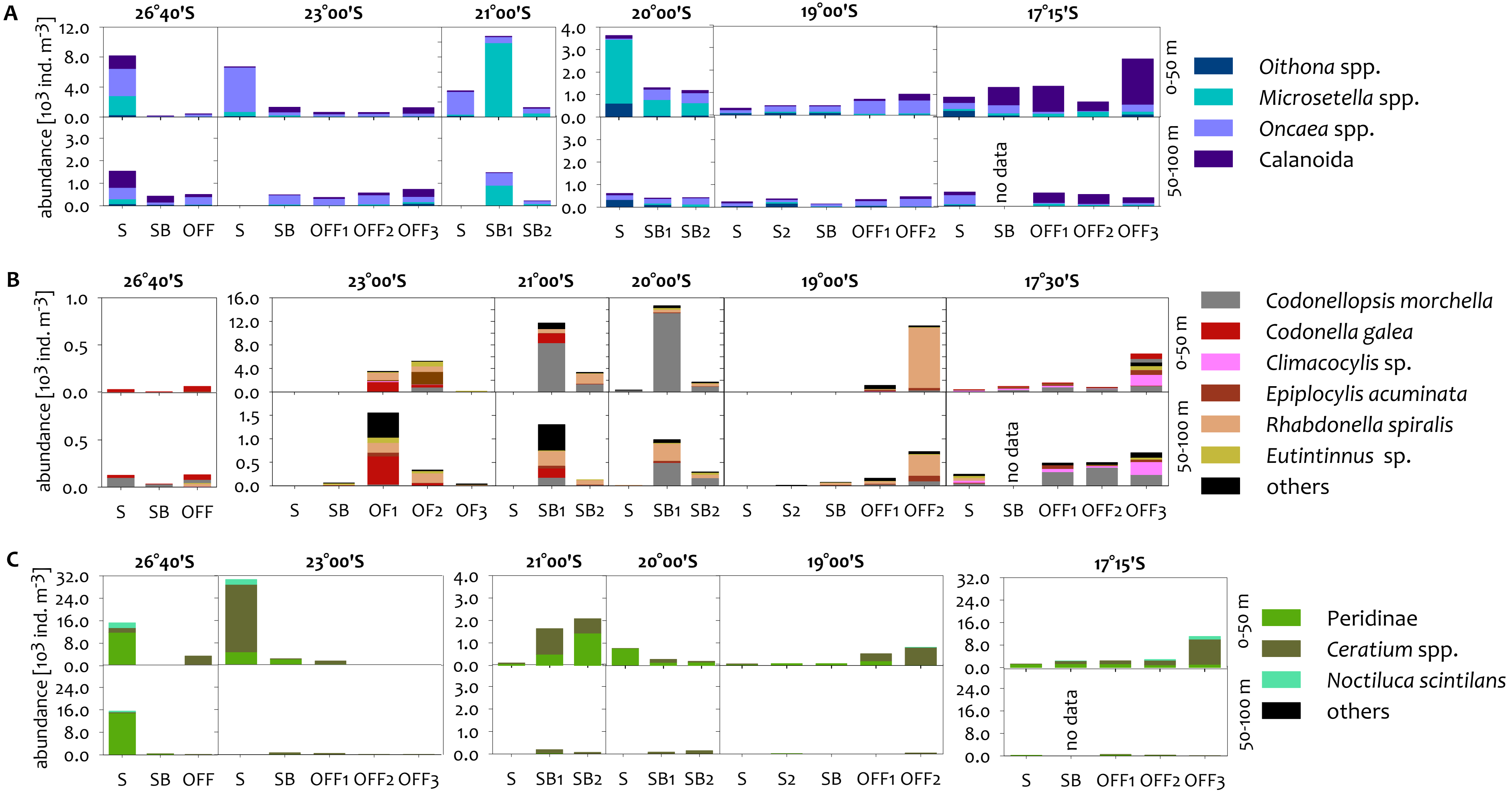


Figure 4-3: Taxa distribution of the Copepoda group (A), the Tintinnida group (B) and the Dinoflagellata group (C) on the six transects in two different depth intervals along the Namibian coast. S = shelf, SB = shelf break, OFF = offshore.

4.3.4. Spatial patterns of taxonomic groups and potential drivers

The entire community level and the composition of main taxa and their relative abundances vary in space and reveal two patterns at finer spatial scales instead of a gradient (figure 4-4). However, the polynomial RDA explained in total only 13% of the overall variation indicating that the identified spatial patterns were not so pronounced.

Two linearly independent models were obtained from the polynomial RDA. The first (representing the first canonical axes) explained 54% of the constrained variance and showed a strong difference between the centre region vs. the northern/southern regions. The taxa that contributed most to this pattern were the mixo- and heterotrophic Dinoflagellata, Protoperidiniae and *Ceratium* spp., both being more dominant in the outer regions, as well as Tintinnida being more dominant in the centre (figure 4-5). The second model explained 46% of the constrained variance and displayed significant similarities between the offshore stations of the southernmost transect (26°40’S) as well as 19°00’S transect and all stations of the northernmost transect (17°30’S). This pattern was mainly caused by the two copepod species *Oncaea* spp. and *Microsetella* spp. in the offshore and northern region (figure 4-5). In contrast, *Ceratium* spp. showed higher abundances in the shelf region.

While the first spatial structure could not be explained by any of the tested environmental drivers, the second structure was best explainable by the temperature and Chl *a* combined (54% expl. variance, see table 4-2). A variation partitioning analysis, however, showed no effect of the environmental matrix on the community matrix overall.

Table 4-2: Results of linear regression models linking diversity indices and significant RDAs from Trend-Surface-Analysis with spatial, i.e. longitude X, latitude Y and the 2nd and 3rd order polynomial terms, and/or environmental variables. Significant variables in final models that best explain the observed spatial pattern in diversity and community structure are provided together with the adjusted R^2.

Model	**Response Variable**	**Explanatory variable in final model**	**adj. R^2**
Spatial model	Species Richness S	X**	0.28
Environmental model	Species Richness S	Temperature **	0.31
Spatial model	Total Abundance N	X**, X^{2***}, XY*	0.49
Environmental model	Total Abundance N	ln-transformed Chl *a* *	0.28
Environmental model	$RDA1_{main\ taxa}$	-	
	$RDA2_{main\ taxa}$	Temp. + ln-Chl *a*	0.54
Environmental model	$RDA1_{tintinnids}$	Temp. + Salinity + Depth	0.66
	$RDA2_{tintinnids}$	Depth	0.23
	$RDA3_{tintinnids}$	Temp. + Salinity	0.44
	$RDA4_{tintinnids}$	-	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4.3.5. Spatial pattern of Tintinnida composition and potential drivers

Zooming into the group of Tintinnida shows a more pronounced spatial distribution at various broad and fine scales. Here, the polynomial RDA explained 29% of the total variation with four structures identified (represented by the four significant canonical axes; appendix 4-3).

The first explains 40% of the constrained variance and represents mainly a gradient from South to North and from East to West in latitude and longitude. This pattern is particularly driven by *Codonellopsis morchella* and *Cymatocyclis vanhoffen* in the North and "other Tintinnida" in the South (appendix 4-4).

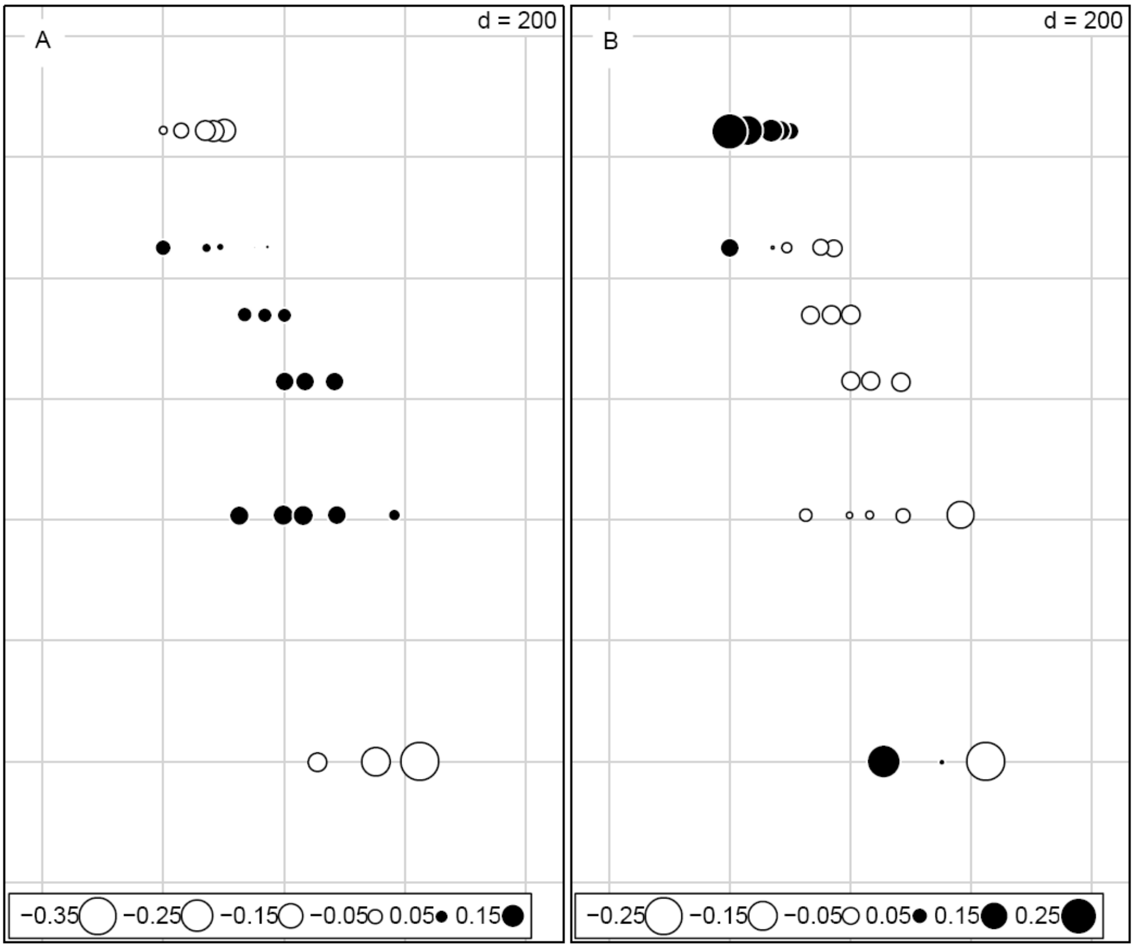


Figure 4-4: Two linearly independent spatial structures were found for the main microzooplankton taxa based on the cubic trend-surface analysis of the Hellinger-transformed data. RDA1 (A) and RDA2 (B). The circles are arranged at the latitudinal and longitudinal coordinates of the stations.

The second, explaining 23%, represents a spatial pattern at a finer spatial scale (indicated by the high loadings of 2nd and 3rd order Y polynomials) with greater differences between the offshore stations at the 19°00'S and 23°00'S transect and all shelf stations. Mainly *Cymacocylis vanhoffeni* (offshore) as well as *Rhabdonella* spp. and *Codonellopsis morchella* (both at the shelf) contributed to this pattern.

The other two finer-scaled structures detected by the polynomial RDA explained 19% (RDA3) and 18% (RDA4), and were driven by high values of *Rhabdonella* spp. (RDA3) and *Eutintinnus* sp. (RDA4) and low values of *Favella ehrenbergii* and respectively *Codonellopsis morchella*.

The broad scale distribution (i.e. RDA1) of the Tintinnida group could be best explained (66%) by the combination of three environmental conditions (temperature, salinity and depth; table 4-2). The finer scale patterns could be less (RDA2 and 3) or not at all (RDA4) explained by the environmental variables. The results of the combined polynomial RDA with a variation partitioning (Venn diagram; figure 4-6) showed that the variation in Tintinnida abundances is mainly explainable by smaller scaled spatial dynamics (14.1%) and then by broad-scale dynamics (5.7%, i.e. latitudinal and longitudinal gradient). Temperature was the only significant driver in the separate environment-community RDA and contributed alone, i.e. independent of any spatial structure found, only little to the Tintinnida variation (<0.1%). Most of the temperature effect is also spatially structured, either at the same broad scale (3.7%) or at the finer scales (5.1%).

4.4. Discussion

In this study, we present for the first time a detailed and complex analysis on microzooplankton composition, distributional patterns at different spatial scales and associations to environmental conditions for one of the major upwelling systems of the world, the Benguela Upwelling System (BUS).

Our results show that the total abundance distribution of microzooplankton is arranged in broad spatial scales in the range of tenth to hundreds of kilometers and influenced by chl *a* concentrations. The influence of high primary production on the total abundance distribution could be an indicator for a bottom-up control. In high upwelling areas, the phytoplankton bloom grow faster and reach higher densities and biomass, which supports the subsequent high productivity within the higher trophic levels. However, the bottom-up effects are difficult to detect through many other biotical factors and interactions. The distribution patterns of zooplankton and structure of the food web is rather influenced by a combination of the bottom-up and top-down control. From the top-down view, the reduction in predation by declining stocks of pelagic fish due to overfishing in the BUS could have a fundamental effect on the zooplankton biomass (Verheye & Richardson 1998).

The diversity of microzooplankton is more likely influenced by environmental conditions. Temperature (31%) and broad spatial scales (28%) best explained the variations in the diversity distribution. The nearshore assemblages are dominated by few taxa, which may reach high abundances, whereas oceanic communities comprise many species at low abundances. Zooplankton diversity reflects the complexity of the food web (Gibbons & Hutchings 1996). We assume that the food web associated with fresh upwelled water is relatively simple structured with few trophic levels. The species abundance and assemblages diversity in nearshore waters changes with intensity of upwelling. An active Ekman transport, the water is moved further offshore and replaced by fresh upwelled water with low number of species (Gibbons & Hutchings 1996). In contrast, complex food chains containing many micro-heterotrophic links prevail further offshore.

Additionally, we analyzed the influence of environmental parameters on the distribution of the main taxa (RDA; table 4-2). The environmental parameters could not explain the first spatial structure (RDA1) within the main taxa, which could be a consequence of groupings of the taxa in taxonomical groups for the analysis. However, the second structure (RDA2) was best explained by the combination of temperature and chl *a* concentrations. Remarkable is the distribution of *Ceratium* species and the copepods *Microsetella* spp. and *Oncae*a spp. (RDA 2, figure 4-4). *Ceratium* spp. generally prefers higher temperatures and relatively high irradiance (Baek et al. 2008) and was mainly found in the northern part of the study area, which is influenced by intrusions of warm water from the Angola Dome. *Oncaea* spp. and *Microsetella* spp. are worldwide distributed copepods (Gonzales & Broman 1965; Paffenhöfer 1993; Bradford-Grive et al. 1999; Davis 1949) and were mainly detected in the colder center region.

Strong differences were detected between the center region vs. northern/southern regions. The northern and southern region was composed at similar main groups resulting in similarities between these areas in the RDA analysis. However, the southern and northern part of the area is influenced by different environmental conditions. In the south, high upwelling intensity occurs all year long in the permanent upwelling cell off Lüderitz. Due to this high upwelling intensity, the phytoplankton bloom develops further offshore and is dominated by small Flagellata and Coccolitophora. Further into the open ocean, the phytoplankton bloom reaches highest concentrations and is dominated by large Diatomea (Hansen 2014). The composition of phytoplankton and the concentration of different phytoplankton species directly impacts the microzooplankton community. Heterotrophic Dinoflagellata are the most suitable grazers of Diatomea. Due to their plasticity, they are able to feed on organisms even larger as themselves (Lessard 1991; Hansen 1992) and may take control over the phytoplankton bloom (top-down control). The northern part of the investigated area is influenced by intrusions of warm and low oxygenated tropical water from the North and by weak upwelling. On the 17°30'S transect, high abundances of the mixotrophic dinoflagellates *Ceratium* spp. were found further offshore. The high offshore abundances of *Ceratium* spp. could be caused by their ability to survive also at low nutrient conditions (Baek 2007). Some species of *Ceratium* are able to use additional nutrient sources by mixotrophic feeding. They are also strongly influenced by the vertical and horizontal distribution of ciliate prey in stratified waters. They may even remove in average 67% of the ciliate population per day (Smalley and Coast 2002).

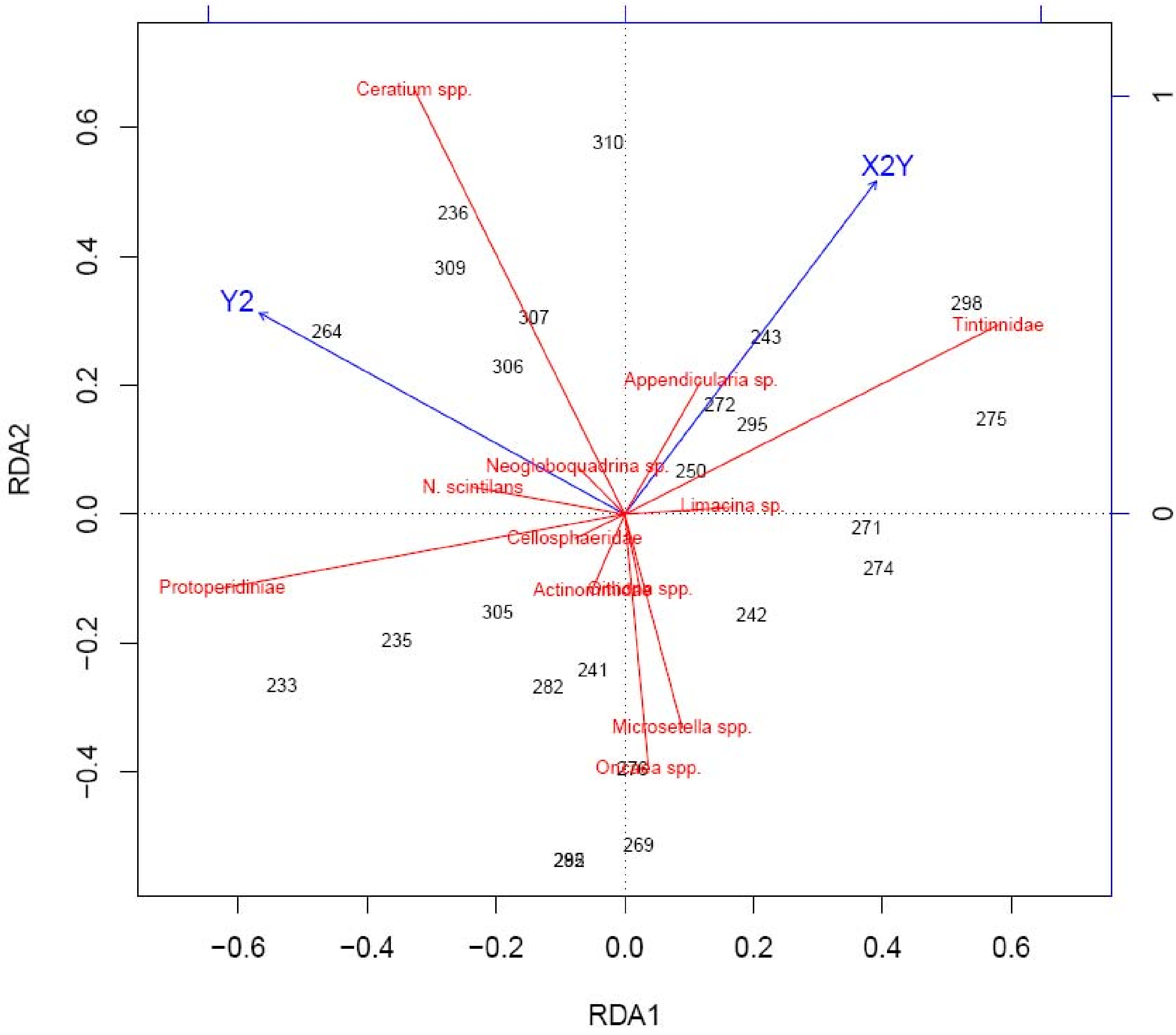


Figure 4-5: RDA triplot of the Hellinger-transformed data of main microzooplankton taxa, constrained by two polynomial terms of X-Y coordinates. The bottom and left-hand scales are for the objects and the response variables, the top and right-hand scales are for the explanatory variables. Both, species and station scores have been scaled.

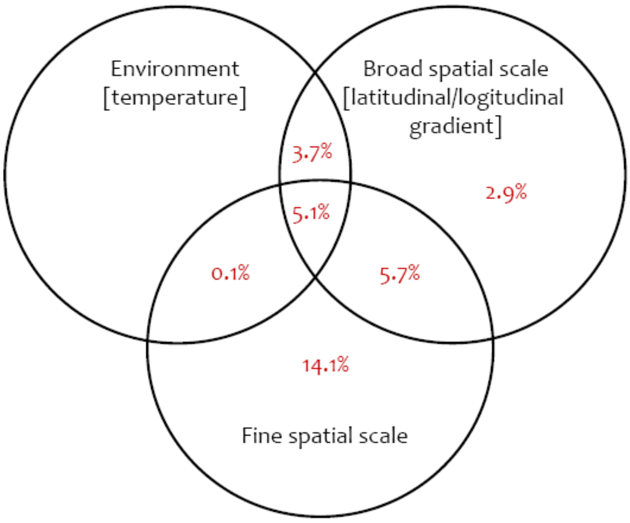


Figure 4-6: Variation partitioning of the Tintinnida into an environmental component (upper left-hand circle), a linear trend (upper right-hand circle), a broad scale (lower circle) and fine scale (disjoined rectangles) PCNM spatial components. The empty fractions in the plots have small negative R^2 values. Values < 0 not shown.

The differences between the two transects are an indicator for a different design of the food web, which is also reflected in the distribution of other microzooplankton taxa. In comparison to the other transects, the northernmost transect (17°30'S) was also characterized by high abundances of Tintinnida, Appendicularia and Copepoda. These findings suggest that the food web between the northern and southern part of the study area is not only a result of the upwelling intensity but also, on the broad spatial scale, it is influenced by the intrusions of water from the Angola dome.

We detected spatial patterns within the Tintinnida group caused by the combination of environamental parameters, temperature and salinity, and depth ($R^2 = 66\%$). This high relation of the Tintinnida species to different water masses could be used for an assesment of biological/environmental conditions in the northern BUS. Some authors already described the dependence of Tintinnida species to different biological and physical parameters in marine ecosystems (see Kchaou et al. 2009; Xu et al. 2011; Jiang et al. 2012). Different Tintinnida communities can be found in two water masses detetcted in the northern BUS, the Eastern South

Atlantic Central Water (ESACW) in the south and a mixture of the South Atlantic Central Water (SACW) and the ESACW in the north (Bohata et al. in prep). The cosmopolitan species are associated with the almost pure ESACW and the warm-temperate species are associated with the mixed water mass. Therefore we assume that the northern part of the study area, the 19°00'S and the 17°30'S transect, is more influenced by the SACW with high nutrient content and low oxygen. The southern part, exclusively from the 21°00'S transect, is affected by almost pure ESACW.

To asses the importance of biological and environmental drivers to zooplankton distribution in upwelling systems requires an understanding of the distribution patterns. The total abundance distribution in upwelling systems is mainly driven by broad spatial scales (latitudinal and longitudinal gradients), whereas the primary production seems to have an important effect not only on the total abundance distribution but also on the distribution of different microzooplannkton groups. Some zooplankton species could be used for biological/environmental condition assesment due to their connection to environmental parameters. To create links between the zooplankton distribution patterns across broad and fine spatial scales is nessesary for the understanding of the complexity of variable ecosystems such as upwelling systems.

4.5. References

Akaike H (1974) A new look at the statistical model identification. Automatic Control, IEEE Transactions on 19:716-723

Anger K (2003) Salinity as a key parameter in the larval biology of decapod crustaceans. . Invertebrate Reproduction & Development 43:29-45

Baek HS, Shimode S, Han M-S, Kikuchi T (2008) Growth of dinoflagellates, Ceratium furca and Ceratium fusus in Sagami Bay, Japan: The role of nutrients. Harmful Algae:729-739

Bohata K, Koppelmann R, Möllmann C (inn prep) Microzooplankton communities: fluctuating fundamental components of upwelling filaments

Bohata K, Koppelmann R, Mohrholz V, Möllmann C (in perp.) Mikrozooplankton communities: fluctuating fundamental components of upelling filaments.

Blanchet F, Legendre P, Borcard D (2008) Forward selection of explanatory variables. Ecology 89:2623-2632

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51-68

Borcard D, Gillet D, Legendre P (2011) Numerical Ecology with R, Vol. Springer Science & Business Media

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826-1832

Bradford-Grive JM, Markhaseva EL, Rocha CEF, Abiaky B (1999) Copepoda. In: Baltovskoy (ed) South Atlantic Zooplankton, Vol 2. Backhuys Publishers, Leiden, p 869-1009

Buck KR, Newton J (1995) Fecal pellet flux in Dabob Bay during a diatom bloom: Contribution of microzooplankton Limnology and Oceanography 40:306-315

Calbet A (2001) Mesozooplankton Grazing Effect on Primary Production: A Global Comparative Analysis in Marine Ecosystems. Limnology and Oceanography 46:1824-1830

Calbet A, Landry MR (2004) Phytoplankton Growth, Microzooplankton Grazing, and Carbon Cycling in Marine Systems. Limnology and Oceanography 49:51-57

Campbell RG, Sherr EB, Ashjian CJ, Ploudre S, Sherr BF, Hill V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 56:1274-1289

Caron DA, Goldman JC (1990) Protozoan nutrient regeneration. In: GM C (ed) Ecology of marine protozoa. Oxford University Press, New York, p 283-306

Castellani C, Irigoien X, Harris RP, Lampitt RS (2005) Feeding and egg production of Oithona similis in the North Atlantic. Marine Ecology Progress Series 288:173-182

Davis CC (1949) The pelagic Copepoda of the northeastern Pacific Ocean, Vol 14. Univ. Wash. Publ. Biol., Washington

Dolan JR (1997) Phosphorus and ammonia excretion by planktonic protists. . Marine Geology 139:109-122

Dolan JR, Pérez MT (2000) Costs, benefits and characteristics of mixotrophy in marine oligotrichs. Freshwater Biology 45:227-238

Dray Sp, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483-493

Fenchel T (1987) Ecology of protozoa: the biology of free-living phagotrophic protists. Vol. Springer Verlag, Berlin

Folt CL, Burns CW (1999) Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution 14:300-305

Gaudy R, Cervetto G, Pagano M (2000) Comparison of the metabolism of Acartia clausi and A. tonsa: influence of temperature and salinity. Journal of Experimental Marine Biology and Ecology 247:51-65

Gibbons MJ, Hutchings L (1996) Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system, Vol. Academy of Science of South Africa 92(2): 63-75

Gifford DJ, Dagg MJ (1988) Feeding of the estuarine copepod Acartia tonsa Dana: carnivory vs. herbivory in natural microplankton assemblages. Bulletion of Marine Science 43:458-468

González JG, E. BT (1965) Planktonic Copepods from Bahía Fosforescente, Puerto Rico, and adjacent waters. Proceedings of the United States National Museum 117

Halsband-Lenk C, Hirche H-Jr, Carlotti Fo (2002) Temperature impact on reproduction and development of congener copepod populations. Journal of Experimental Marine Biology and Ecology 271:121-153

Hansen A, Ohde T, Wasmund N (2014) Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. Journal of Marine Systems 140, Part B:130-137

Hansen PJ (1992) Particle size selection, feeding rates and growth dynamics of marine heterotrophic dinoflagellates, with special emphasis on *Gyrodinium spirale*. Marine Biology 114:327-334

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods : global rates and patterns. Marine Ecology - Progress Series 230:195-209

Horner RA, Postel JR, Halsband-Lenk C, Pierson JJ, Pohnert G, Wichard T (2005) Winter-spring phytoplankton blooms in Dabob Bay, Washington. Progress In Oceanography 67:286-313

Hu C, Lee Z, Franz BA (2012) Chlorophyll-a algorithms for oligotrophic oceans: A novel approach based on three-band reflectance difference, Journal of Geophysical Resources 117

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15:56-61

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress In Oceanography 83:15-32.

Jeong HJ, Kim JS, Kim JH, Kim ST, Seong KA, Kim TH, Song JY, Kim SK (2005) Feeding and grazing impact of the newly described heterotrophic dinoflagellate *Stoeckeria algicida* on the harmful alga *Heterosigma akashiwo*. Marine Ecology Progress Series 295:69-78

Jiang Y, Xu H, Zhang W, Zhu M, Al-Rasheid KS (2012) Can body-size patterns of ciliated zooplankton be used for assessing marine water quality? A case study on bioassessment in Jiaozhou Bay, northern Yellow Sea. Environmental Science and Pollution Research 19:1747-1754

Jonsson PR (1986) Particle size seletion, feeding rates and growth dynamics of marine planktonic oligotrochous ciliates (Ciliophora: Oligotrochina). Marine Ecology Progress Series 33:265-277

Kato S, Taniguchi A (1993) Tintinnid ciliates as indicator species of different water masses in the western North Pacific Polar Front. Fisheries Oceanography 2:166-174

Kchaou N, Elloumi J, Drira Z, Hamza A, Ayadi H, Bouain A, Aleya L (2009) Distribution of ciliates in relation to environmental factors along the coastline of the Gulf of Gabes, Tunisia. Estuarine, Coastal and Shelf Science 83:414-424

Kiørboe T, Saiz E (1996) Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. Oceanographic Literature Review 43:58-59

Klein-Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. Marine Biology 135:191-198

Kleppel GS (1993) On the diets of calanoid copepods. Marine Ecology Progress Series 99:183-195

Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280

Leonardo SM, Queiroga H, Rodríguez-Grana L, Tiselius P (2006) Temperature dependent development and somatic growth in two allopatric populations of *Acartia clausi*. Marine Ecology - Progress Series 322:189-197

Lessard EJ, Swift E (1986) Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. Journal of Plankton Research 8:1209-1215

Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. Marine Microbial Food Webs 5:49-58

Lynn DH, Montagnes DHS (1991) Global Production of Heterotrophic Marine Planktonic Ciliates. In: Reid PC, Turley CM, Burkill PH (eds) Protozoa and Their Role in Marine Processes, Vol 25. Springer Berlin Heidelberg, p 281-307

Oksanen J, Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, *al. e* (2015) vegan: Community Ecology Package R package version 2. http://CRANR-projectorg/package=vegan.

Paffenhöfer G-A (1993) On the ecology of marine cyclopoid copepods. Journal of Plankton Research 15:37-55

Parrish RH, Bakun A, Husby DM, Nelson CS (1983) Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction., FAO Fisheries Report

Pinel-Alloul B (1995) Spatial heterogeneity as a multiscale characteristic of zooplankton community. In: Balvay G (ed) Space Partition within Aquatic Ecosystems, Vol 104. Springer Netherlands, p 17-42

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Marine Ecology Progress Series 172:253-264

Pitcher GC, Horstman DA, Calder D, de Bruyn J, Post B (1993b) he first record of diarrhetic shellfish poisoning on the South African coast. . South African Journal of Science 89:512-514.

Queiroga H, Blanton J (2004) Interactions Between Behaviour and Physical Forcing in the Control of Horizontal Transport of Decapod Crustacean Larvae. In: Advances in Marine Biology, Vol Volume 47. Academic Press, p 107-214

Roddie BD, Leakey RJG, Berry AJ (1984) Salinity-temperature tolerance and osmoregulation in Eurytemora affinis (Poppe) (Copepoda : Calanoida) in relation to its distribution in the zooplankton of the upper reaches of the Forth estuary. Journal of Experimental Marine Biology and Ecology 79:191-211

Rovinsky AB, Adiwidjaja H, Yakhnin VZ, Menzinger M (1997) Patchiness and Enhancement of Productivity in Plankton Ecosystems due to the Differential Advection of Predator and Prey. Oikos 78:101-106

Saito H, Ota T, Suzuki K, Nishioka J, Tsuda A (2006) Role of heterotrophic dinoflagellate Gyrodinium sp. in the fate of an iron induced diatom bloom. Geophysis

Saiz E, Kiørboe T (1996) Predatory and suspension feeding of the copepod Acartia tonsa in turbulent environments. Oceanographic Literature Review 43:59

Sanders RW (1987) Tintinnids and other microzooplankton - seasonal distributions and relationships to resources and hydrography in a Maine estuary. Journal of Plankton Research 9:65-77

Shannon LV (1985) The Benguela Ecosystem, I., Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology 23:105-182

Shannon LV, Nelson G (1996) The Benguela: Large Scale Features and Processes and System Variability. In: The South Atlantic. Springer Berlin Heidelberg, p 163-210

Shannon LV, Pillar SC (1986) The Benguela Ecosystem: Part III. Plankton. Oceanography and Marine Biology 24:65-170

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Marine Ecology Progress Series 352:187-197

Smalley GW, Wayne Coats D (2002) Ecology of the Red-Tide Dinoflagellate Ceratium furca: Distribution, Mixotrophy, and Grazing Impact on Ciliate Populations of Chesapeake Bay. The Journal of Eukaryotic Microbiology 49:63-73

Steedman H (1976) General and applied data on formaldehyde fixation and preservation of marine zooplankton. In: Steedman H (ed) Zooplankton Fixation and Preservation, p 103-154

Steele JH, Henderson EW, Mangel M, Clark C (1994) Coupling between Physical and Biological Scales [and Discussion]. Philosophical Transactions: Biological Sciences 343:5-9

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the opwen Subarctic Pacific Ocean. Marine Ecology Progress Series 78:103-113

Strom SL, Strom MW (1996) Microplankton growth, grazing, and community structure in the northern Gulf of Mexico. Marine Ecology Progress Series 130:229-240

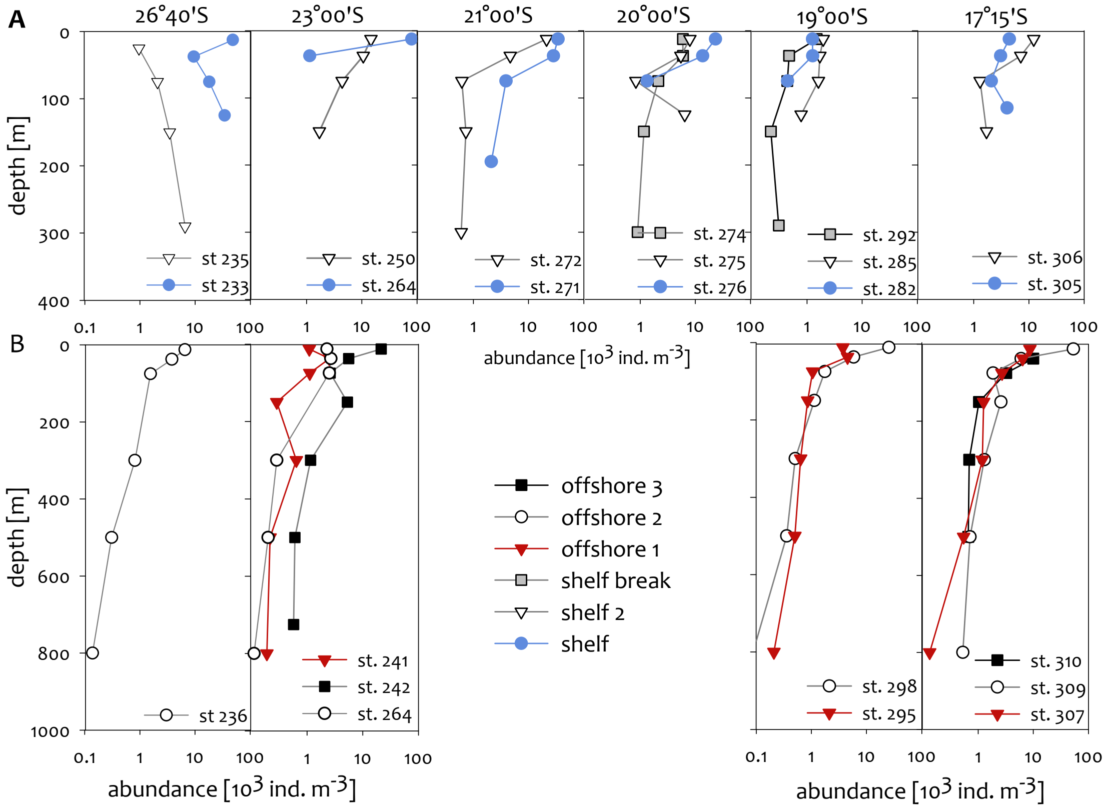
Verheye HM, Richardson AJ (1998) Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951-1996): bottom-up or top-down control? ICES Journal of Marine Science: Journal du Conseil 55:803-807

Walker DR, Peterson WT (1991) Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. South African Journal of Marine Science 11:289-305

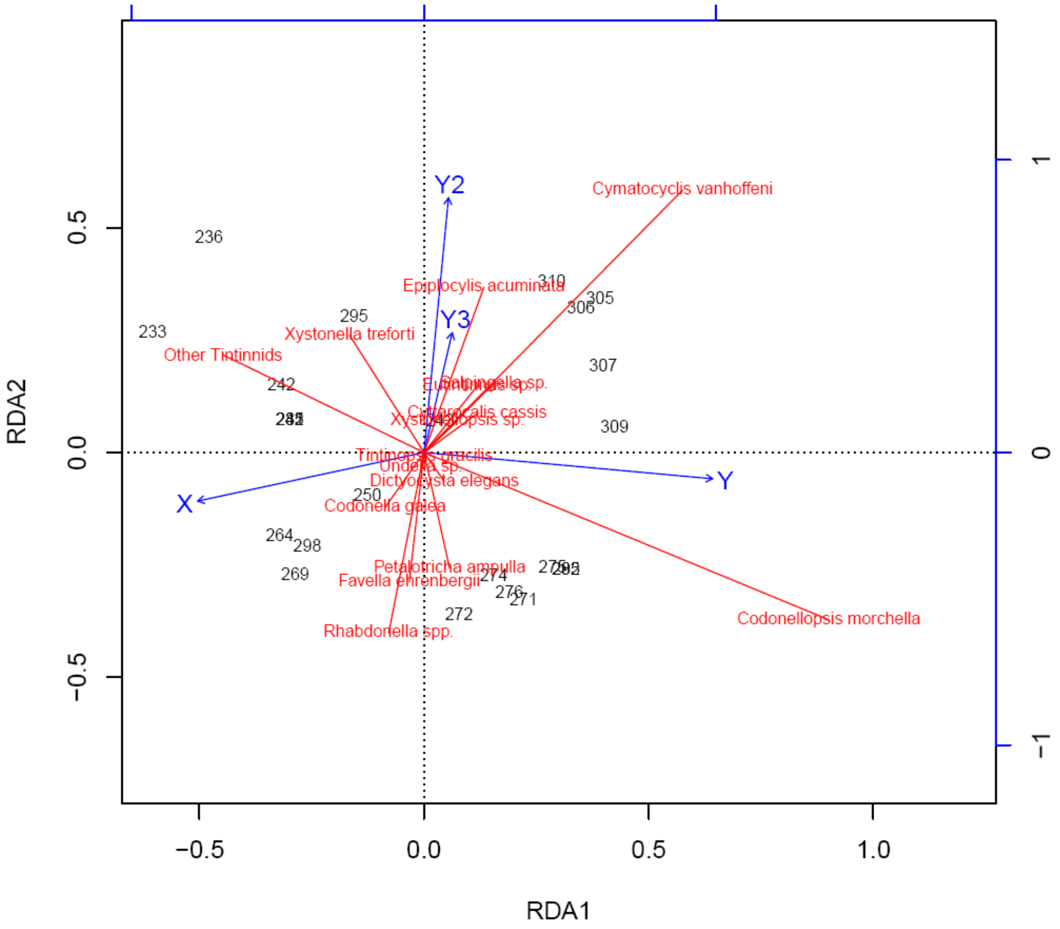
Yamazaki H, Osborn TR, Squires KD (1991) Direct numerical simulation of planktonic contact in turbulent flow. Journal of Plankton Research 13:629-643

Xu H, Jiang Y, Al-Rasheid KS, Song W, Warren A (2011) Spatial variation in taxonomic distinctness of ciliated protozoan communities at genus-level resolution and relationships to marine water quality in Jiaozhou Bay, northern China. Hydrobiologia 665:67-78

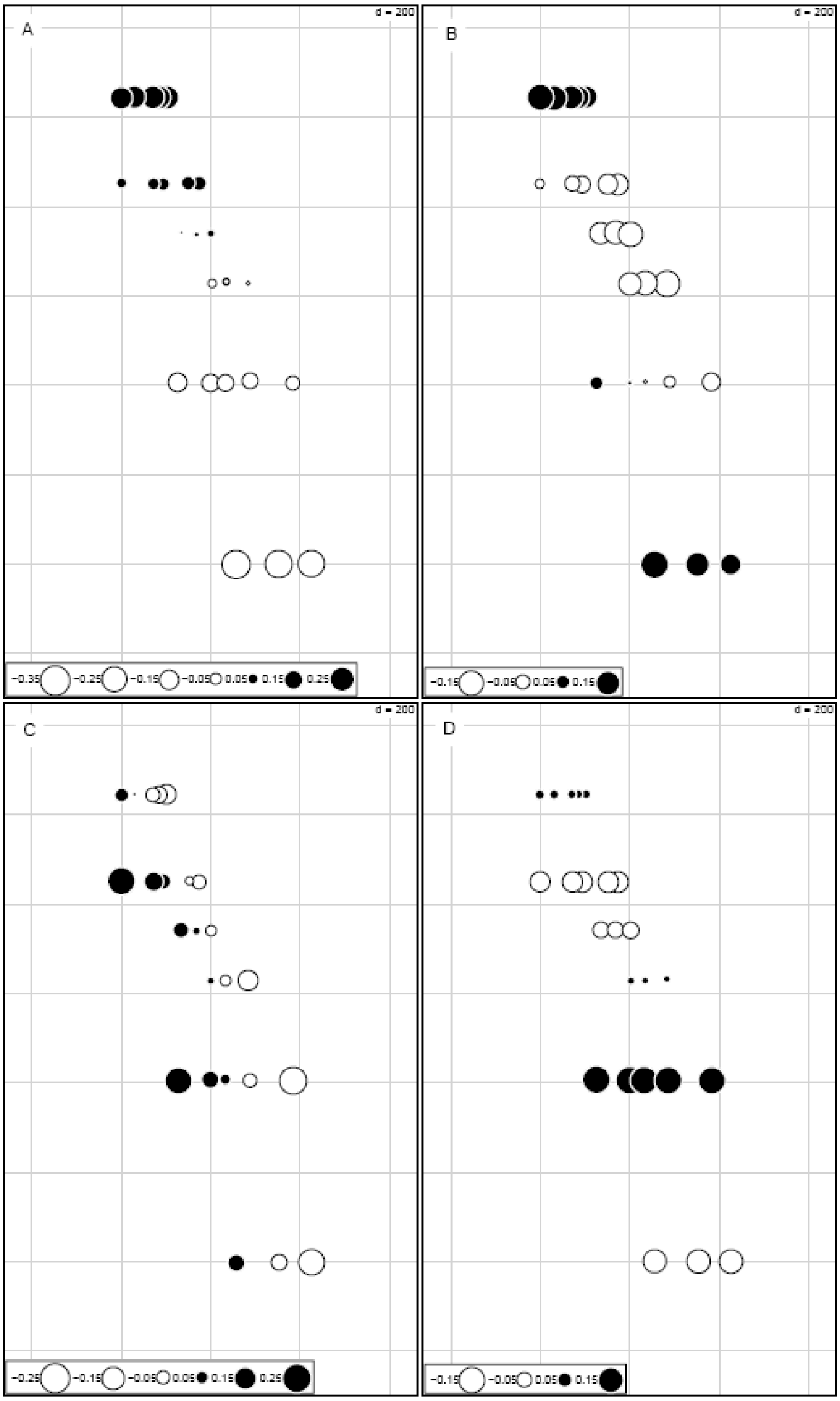
4.6. Appendix



Appendix 4-1: Overall microzooplankton abundances along the six transects on the shelf and shelf break (A) and offshore (B).



Appendix 4-2: RDA triplot of the Hellinger-transformed data of Tintinnida, constrained by two polynomial terms of X-Y coordinates. The bottom and left-hand scales are for the objects and the response variables, the top and right-hand scales are for the explanatory variables. Both, species and station scores have been scaled.



Appendix 4-3: Four linearly independent spatial structures were found for the Tintinnida taxa based on the cubic trend-surface analysis of the Hellinger-transformed data. RDA1 (A) , RDA2 (B), RDA3 (C) and RDA4 (D). The circles are arranged at the latitudinal and longitudinal coordinates of the stations.

Chapter 5

Microzooplankton communities: fluctuating fundamental components of upwelling filaments

Karolina Bohata, Rolf Koppelmann, Volker Mohrholz*, Christian Möllmann

Institute for Hydrobiology and Fisheries Science, Center for Earth Systems Research and Sustainability, University of Hamburg, Hamburg, Germany

*Leibniz-Institute for Baltic Sea Research Warnemünde, Germany

Abstract

Microzooplankton abundance, species composition and distribution were studied along and across an upwelling filament off the south-west coast of Africa at approximately 20°S using water bottle samples and 55 µm net samples. The filament was located in the mixing and transition area of two different central water masses, the Eastern South Atlantic Central Water (ESACW) and South African Central Water (SACW). Differences in the distribution of some microzooplankton species in relation to the ESACW and SACW were detected. A rapid change was found within the tintinnid group, from cosmopolitan species in the south (pure ESACW) to warm-temperate species in the north (mixture of SACW and ESACW). Therefore this group could be used as an indicator of different water masses. High microzooplankton abundances were observed at the southern front and in the upper layers of the filament centre, whereas low abundances were found at the northern front of the filament, probably a result of currents associated with the filament. As a result of changing phytoplankton composition, the microzooplankton composition changed from ciliates-dominated in the centre of the filament to dinoflagellate-dominated further offshore along the filament. Such a shift also affects the efficiency of the organic matter transfer from primary producers to higher trophic levels since more steps are nessesary within the food chain.

5.1. Introduction

Upwelling filaments transport cold and nutrient rich waters perpendicularly from the coast to hundreds of kilometres offshore (Brink 1983) and have been described for Eastern Boundary Currents (EBC) off southern Africa (Lutjeharms and Meeuwis 1987; Muller et al. 2013), northwest Africa (Navarro-Pérez 1998; Marchesiello 2009), California (Brink 1983; Mackas et al. 2006), Chile (Marín et al. 2001; Sobarzo & Figueroa 2001) and Portugal (Haynes et al. 1993; Cravo 2010). Such upwelling filaments are important hydrographic structures for the dynamics of EBC systems transporting nutrients and plankton to the open ocean (Strub 1991; Álvarez-Salgado 2001; García-Muñoz 2004; Mackas 2006). On regional scales, upwelling filaments occasionally transport more volume of water offshore than the Ekman transport alone (Barton et al. 1998; Muller et al. 2013). At the same time, filaments tend to transport a large fraction of coastal primary production even during low upwelling intensity. However, the dimension and nature of transported organic matter depends largely on the species composition and the related size structure of the plankton community. Usually small dinoflagellates, coccolithophores and microflagellates dominate fresh-upwelled, nutrient-rich water inshore, whereas larger diatoms are more abundant in the matured upwelled water with exhausted nutrient concentrations (Hart & Currie 1960; Pitcher et al. 1991; Shannon 1986; Hansen et al. 2014). Farther offshore, the abundance of larger diatoms decreases again and the phytoplankton community is dominated by small dinoflagellates (Hansen et al. 2014).

The community composition and the dynamics of microzooplankton is generally insufficiently understood in EBC systems and especially in upwelling filaments. Microzooplankton consist of many groups of organisms like ciliates, hetero- and mixotrophic dinoflagellates, foraminiferas, pteropods, radiolarians, nauplius larvae and several copepodite stages in the size range from 20 to 200 µm. Microzooplankton attracted increasing attention as an important part of the food web, since the seminal publication of Landry and Hasset (Landry & Hassett 1982) which introduced the dilution method to estimate microzooplankton grazing rates on phytoplankton and Azam *et al.* (1983) who defined the 'microbial loop',. Microzooplankton may consume up to 75% of the primary production (Calbet & Landry 2004) and forms also large fractions of the diets of planktonic organisms such as copepods (Batten at al. 2001; Calbet & Saiz 2005), krill (Levinsen & Nielsen 2002; Campbell et al. 2009), fish larvae (Figueiredo et al. 2007; Montagnes et al. 2010) and meroplanktonic invertebrates (Lavrentyev et al. 1995). Microzooplankton is further able to adapt to changing environmental conditions due to its variety of feeding mechanisms including omnivory, mixotrophy and bacterivory and fast reproduction cycles (Dolan & Pérez 2000).

Our material was collected during southern winter/spring in September 2013 in the Benguela Upwelling System (BUS), a highly productive upwelling system off South Africa and Namibia (Blamey et al. 2012). The BUS is separated into two subsystems by the permanent Lüderitz upwelling cell (at 27°S) which is characterised by strong winds, high turbulence and strong offshore advection (Hutchings et al. 2009). The northern part of the BUS is influenced by the South Atlantic Central Water (SACW) from the north and the Eastern South Central Water from the south. The SACW is characterized by high nutrient content and oxygen depletion, whereas the ESACW is characterized by high oxygen values and a poor nutrient content (Mohrholz et al 2014).

To overcome the lack of information about microzooplankton community in upwelling filaments, we provide detailed information on the distribution and abundance of the microzooplankton community with a closer consideration of naked ciliates and tintinnids in the Benguela Upwelling System. We hypothesise that: (1) the microzooplankton community differs between the northern and southern part of the filament reflecting the two water masses (ESACW and SACW) entering the area, (2) the highest abundance of microzooplankton can be found in the fronts of the upwelling filament as a result of mixing of water masses with different hydrographic characteristics, (3) the microzooplankton community differs along the filament due to hydrographic variability, and (4) the ratio of ciliates vs. heterotrophic dinoflagellates decreases along the filament from the shelf to wardsoffshore reflecting changes in phytoplankton composition.

Table 5-1: Stations sampled along and across the filament.

station name	station no.	latitude	longitude	date	water depth
filament centre	1874	20°04'S	11°58'E	8 September 2013	346
southern front	1876	20°21'S	12°08'E	8 September 2013	315
southern outside	1877	20°48'S	12°22'E	9 September 2013	412
northern front	1894	19°56'S	11°54'E	11 September 2013	364
northern outside	1895	19°30'S	11°40'E	11 September 2013	367
filament centre - offshore	1898	20°36'S	11°44'E	13 September 2013	1043
filament centre - shelf	1906	20°00'S	12°20'E	15 September 2013	210

5.2. Methods

The data were collected as a part of the GENUS project (Geochemistry and Ecology of the Namibian Upwelling System) during southern winter/spring in September 2013 on RV Meteor at cruise no. 100/1 off the western coast of southern Africa.

5.2.1. Hydrography

Temperature, salinity and oxygen concentrations were recorded with a towed CTD system (a ScanFish), a vertically operating SeaBird 911+ CTD system and a microstructure profiler MSS90L. The ScanFish was initially towed undulating within the upper 120m of the water column along a transect parallel to the coast to locate the upwelling filament. One vertical cycle was finished approximatelly 1 km of towing. Vertical casts of the CTD and the microstructure profiler were conducted concurrently to microzooplankton sampling at the stations (table 5-1, figure 5-1). For a detailed description of the hydrographic measurements and data processing refer to Buchholz (2014). The calculation of the SACW fraction was carried out according to Mohrholz et al. (2008).

The data collection was performed during the main upwelling season in the Northern Benguela. The wind forcing was dominated by the SE trade wind during the entire September 2013. Northward directed averaged wind speeds of about 10 ms^{-1} favoured strong coastal upwelling.

5.2.2. Microzooplankton sampling

Stations for microzooplankton sampling were selected based on the hydrographical data. Five stations were set across the centre of the filament (stations locations in figure 5-1; station details in table 1), located outside of the filament (stations 1877 and 1895), in the northern and southern frontal zones (stations 1876 and 1894) and in the centre of the filament (station 1874). Two additional stations were located at the base and at the distal part of the filament (station 1898 and 1906).

Smaller microzooplankton (20-100 µm), mainly ciliates and small mixo- and heterotrophic dinoflagellates, were collected with a rosette water sampler equipped with 10 L free flow bottles. At each station samples were taken in the surface layer as well as in 20 and 40 m depth. 200 ml (surface, 20 m) or 500 ml (40 m) seawater were fixed with acidic Lugol's solution. All samples were kept in darkness at 5°C until analysis in the home laboratory. Larger microzooplankton samples were collected using a multi-closing-net (MCN, Hydrobios) with an opening of 0.25 m^2 and a mesh size of 55 µm.

Vertical hauls in five 20 m intervals (max. haul depth: 100 m) were conducted with a heaving speed of 0.3 m s^{-1}. These samples were preserved in a 4% formaldehyde-seawater solution buffered with sodium-tetraborate until analysis in the laboratory.

5.2.3.Sample analyses

In the home laboratory, a volume of 50 or 100 mL (depending on the richness of the sample) of the water samples for smaller microzooplankton was filled in settling chambers for 24 and 48 h, respectively, and analyzed using an inverted microscope. Organisms of the *small size fraction* (20 and 100 µm) were counted and identified to the species level or to the nearest taxonomic unit that morphological characteristics and settled position allowed. The final concentration of this microzooplankton group was expressed as 10^3 cells L^{-1}.

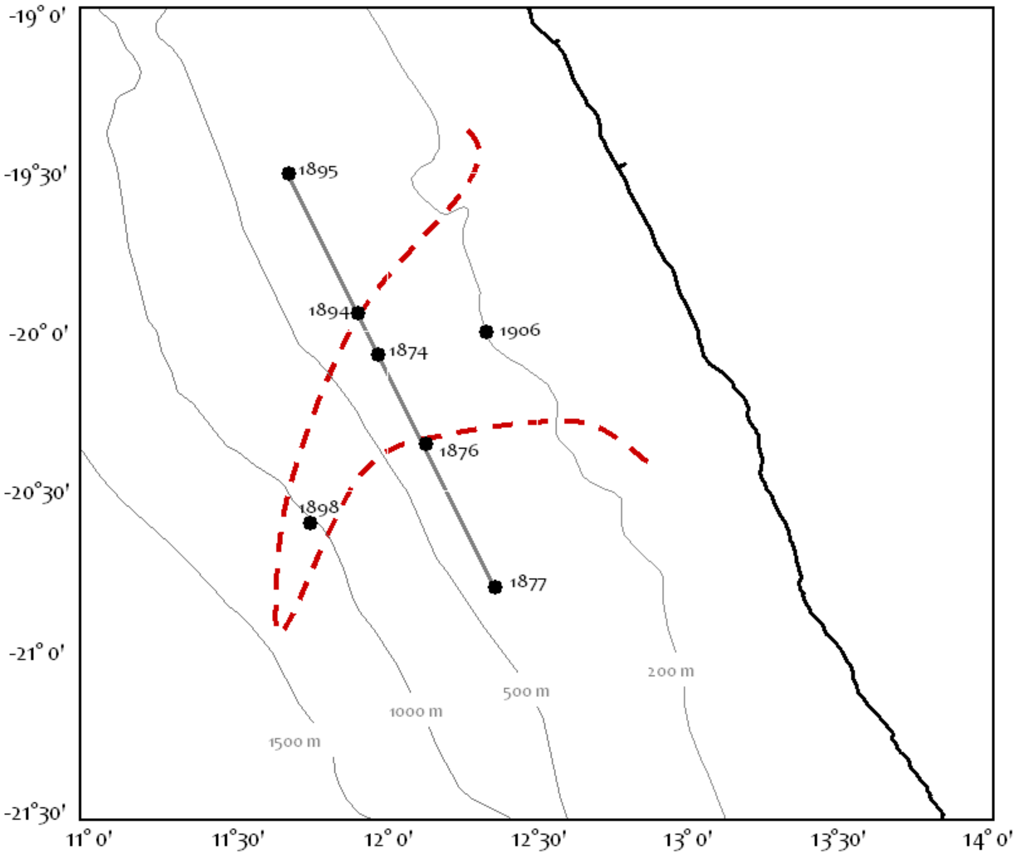


Figure 5-1: Sampling stations off the western coast of Africa (scattered red line = filament structure; solid grey line = microstructure profiler transect); source: GEBCO

The fixed MCN net samples containing the *large size fraction* (55-200 µm) were transferred into a sorting fluid composed of 94.5% fresh water, 5% propylene glycol and 0.5% propylene phenoxetol (Steasman's solution). Samples were fractionated using 55 µm and 200 µm sieves and organisms were counted and identified to the species level or to the nearest taxonomic level that morphological characteristics allowed. Copepods and their different life stages were first split into non-calanoid copepods (Cyclopoida and Harpacticoida) and calanoid copepods. Copepod life-stages were divided into nauplius larvae and a copepod group including copepodite stages and adults. The final abundance of this microzooplankton group was computed using the the volume filtered by the MCN and expressed as 10^3 ind. m^{-3}.

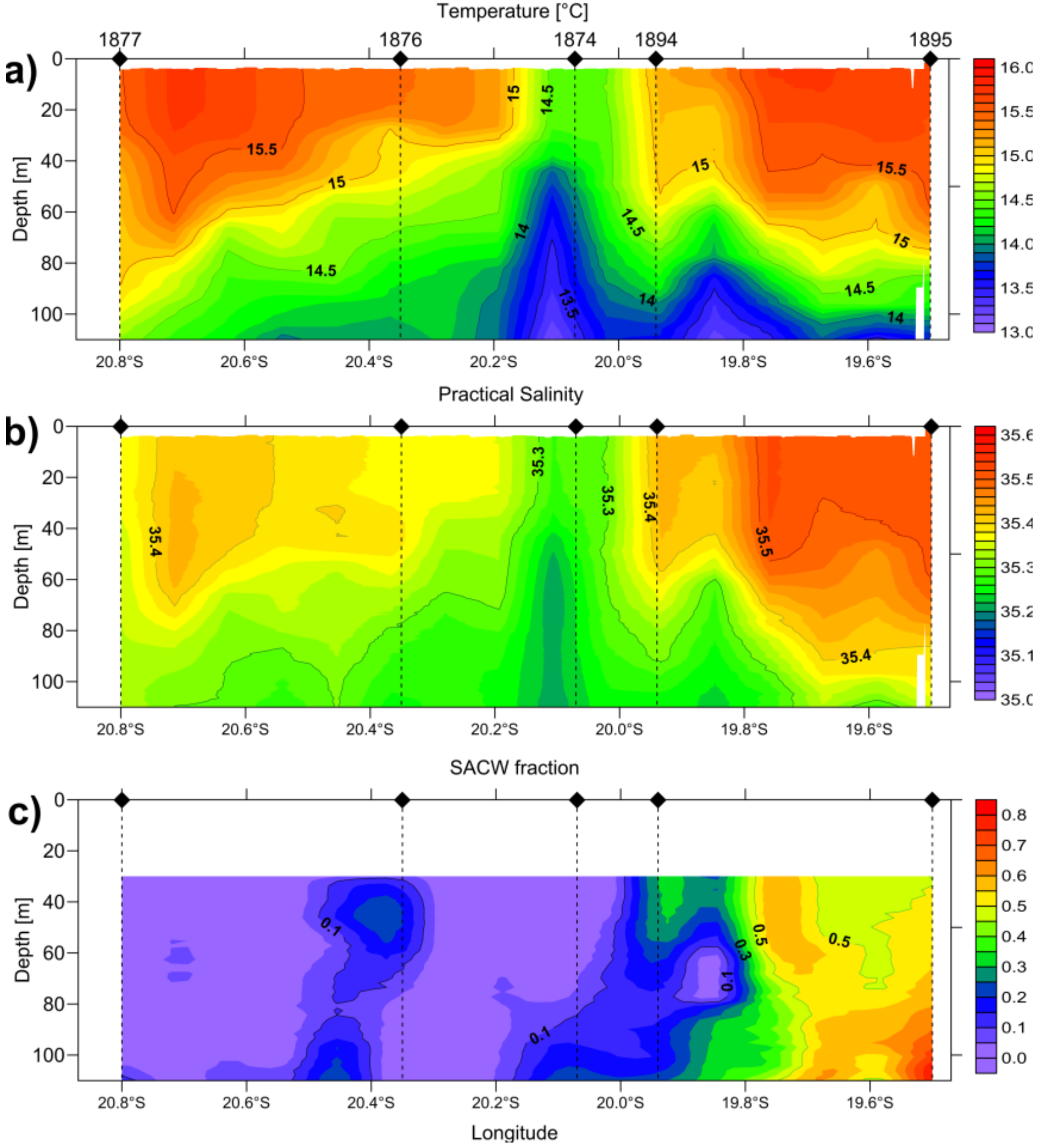


Figure 5-2: Filament structure (ScanFish transect): vertical distribution environmental parameters across the filament. a) temaperature, b) practical salinity, c) SACW fraction. Dashed line = stations across the filament.

5..4. Data analyses

We analysed the hydrographical structure in the study area by grouping water masses according to their hydrographic properties (temperature and salinity) for both size classes. Here we applied agglomerative hierarchical cluster analysis based on Bray–Curtis similarities of square-root transformed abundance data using the PRIMER software (version 6). Hierarchical clustering is a commonly applied approach and provides intuitive similarity relationships between any sample and the entire data set.

We tested for relationships between temperature and several microzooplankton groups from both size fractions, considering the latter as the main indicator for the different water masses in and out the filament (figure 5-6). After log-transformation of the microzooplankton abundance data we first tested for non-linear effects using Generalized Additive Modelling (GAM; Hastie & Tibshirani 1990, Wood 2006). GAMs have the advantage of not requiring an a priori specification of the relationship between the response variable (Y) and the explanatory variable (X). Each Y_i is here linked with X_i by a smoothing function instead of a coefficient as in traditional regression techniques and hence relationships do not have to be linear. If we found relationships to be linear in a GAM (effective degrees of freedom, edf = 1) the relationships have been refitted using a linear regression. All regression analyses were conducted using R (R Statistical Computing Software, http://www.rproject.org/) and the mgcv package (Wood 2004).

5.3. Results

5.3.1. Hydrographic conditions

The data collected with the ScanFish, identified a well developed upwelling filament centred at 20°S off the Namibian coast. The diameter of the cold water body along the transect extended to about 35 nautical miles offshore and covered the upper 100m. From 9th to 10th September 2013 the hydrographic sampling along the transect was repeated with the microstructure profiler (figure 5-2). Due to a short calm period from 6th to 8th September the filament structure was decaying. At the surface the filament diameter declined to about 20 n.m. on 10th September. The temperature difference between the filament core and the ambient oceanic water was about 1.0°C. The northern front of the filament was a border between the two central water masses. The filament structure was mainly influenced by ESACW coming from the South. A rapid change with a higher fraction of SACW (30-50%) was observed at the northern part of the hydrographical transect at approximately 19°40'S.

5.3.2. Spatial variability in the microzooplankton community across the filament

The highest abundance of microzooplankton of the smaller size fraction (20-100 µm) was detected in the upper 20 m at the station located in the southern front (up to 19.4 x 10^3 cells L^{-1}) and in the centre of the filament (up to 15.4 x 10^3 cells L^{-1}; appendix 5-1). A similar pattern was also detected for the larger microzooplankton fraction (55-200 µm) with abundances 2.26 x 10^3 ind. m^{-3} in the upper 40 m of the southern front station and 2.1 x 10^3 ind. m^{-3} in the centre of the filament (figure 5-3). The southern and northern outside station were characterized by a lower abundance of both microzooplankton size fractions. Interestingly, at the northern front station, the abundance of the larger microzooplankton (55-200 mm) increased with depth up to 1.9 x 10^3 ind. m^{-3}. In total, 10 groups of microzooplankton were detected: dinoflagellates, naked ciliates, tintinnids, radiolarians, foraminiferans, polychaets larvae, pteropods, tunicates, copepods and nauplius larvae.

Based on the vertical distribution pattern (figure 5-3), the allocation of the different water masses (figure 5-2) was difficult, partly due to missing data (figure 5-3). As a consequence, we decided to focus our further analyses on the microzooplankton community in 5 m depth for the smaller size fraction (CTD-rosette; 20-100 µm) and in the upper 40 m for the larger size fraction (MCN; 55-200 µm).

The *smaller size fraction* of the microzooplankton was dominated by protists, i.e. naked ciliates, tintinnids and small dinoflagellates (figure 5-3). Other groups such as small nauplius larvae were found in negligible concentrations. Naked ciliates were the dominating protist group with highest abundances in the filament centre and the southern front. The community of naked ciliates was dominated by *Strombidium* species with > 87% of the abundance of all stations and peak abundance in the filament centre (figure 5-4B). The second most abundant ciliate species was *Myrionecta rubra* with the highest abundance in the southern front, but as well at the northern station outside the filament. The composition of the small dinoflagellate group was more homogeneous (figure 5-4C). *Katodinium glaucum* dominated overall with about 30% of the total abundance at all stations and peak abundance at the southern station outside the filament. The secondmost abundant group *Protoperidinae* was equally found at all stations with gradinets of abundance decreasing from the centre of the filament to the outside stations. *Prorocentrum* spp. was also found at all stations peaking at the southern front.

The *larger size fraction* of the microzooplankton consisted of protists and metazoans. Nauplius larvae and copepods were the most abundant group (figure 5-3). Substantial population sizes were additionally found for tintinnids and foraminiferans, mainly in the south, as well as heterotrophic dinoflagellates in the centre and outside (north) of the filament. The tintinnid community was dominated by *Codonella galea* at the southern outside and southern front stations and in the centre of the filament (figure 5-4B). In contrast *Rhabdonella spiralis* dominated in the north both at the front station and outside of the filament. The copepod community consisted of four groups, Cyclopoida (*Oithona* sp. and *Oncaea* sp.), Harpacticoida (*Microsetella* sp.) and small species and copepodite stages of Calanoida. *Oncaea* sp. dominated the community across all stations (figure 5-4C). *Microsetella* sp. were important mainly in the south (outside and front) and in the centre of the filament. Additionally the *Calanoida* group constituted an imported fraction of the copepod community in the north (front and outside).

5.3.3. Microzooplankton community along the filament

The distribution pattern of the two size fractions differed along the filament. For the smaller size fraction (20-100 µm), we detected highest abundance at the middle station (filament centre; 15.2 x 10^3 cells L^{-1}) and lowest on the shelf (5.5 x 10^3 cells L^{-1}). These differences were found in the naked ciliate community which accounted to more than 95% of the microzooplankton in the smaller size fraction. Small mixo- and hetrotrophic dinoflagellates were most abundant at the offshore station (0.9 x 10^3 cells L^{-1}) and on the shelf (0.7 x 10^3 cells L^{-1}).

The abundances of the larger size fraction (55-200 µm) increased from the shelf (1.2 x 10^3 ind. m^{-3}) towards the open ocean (2.5 x 10^3 ind. m^{-3}). The abundances of mixo- and hetrotrophic dinoflagellates increased along the filament from the shelf (0.3 x 10^3 ind. m^{-3}) to offshore (1.3 x 10^3 ind. m^{-3}). This distribution pattern was also evident for the foraminiferans with max. abundance offshore (0.2 x 10^3 ind. m^{-3}). Copepods dominated all stations with highest abundance at the filament centre station (0.5 x 10^3 ind. m^{-3}), whereas the abundance of nauplius larvae increased from the shelf (0.6 x 10^3 ind. m^{-3}) to offshore (0.9 x 10^3 ind. m^{-3}).

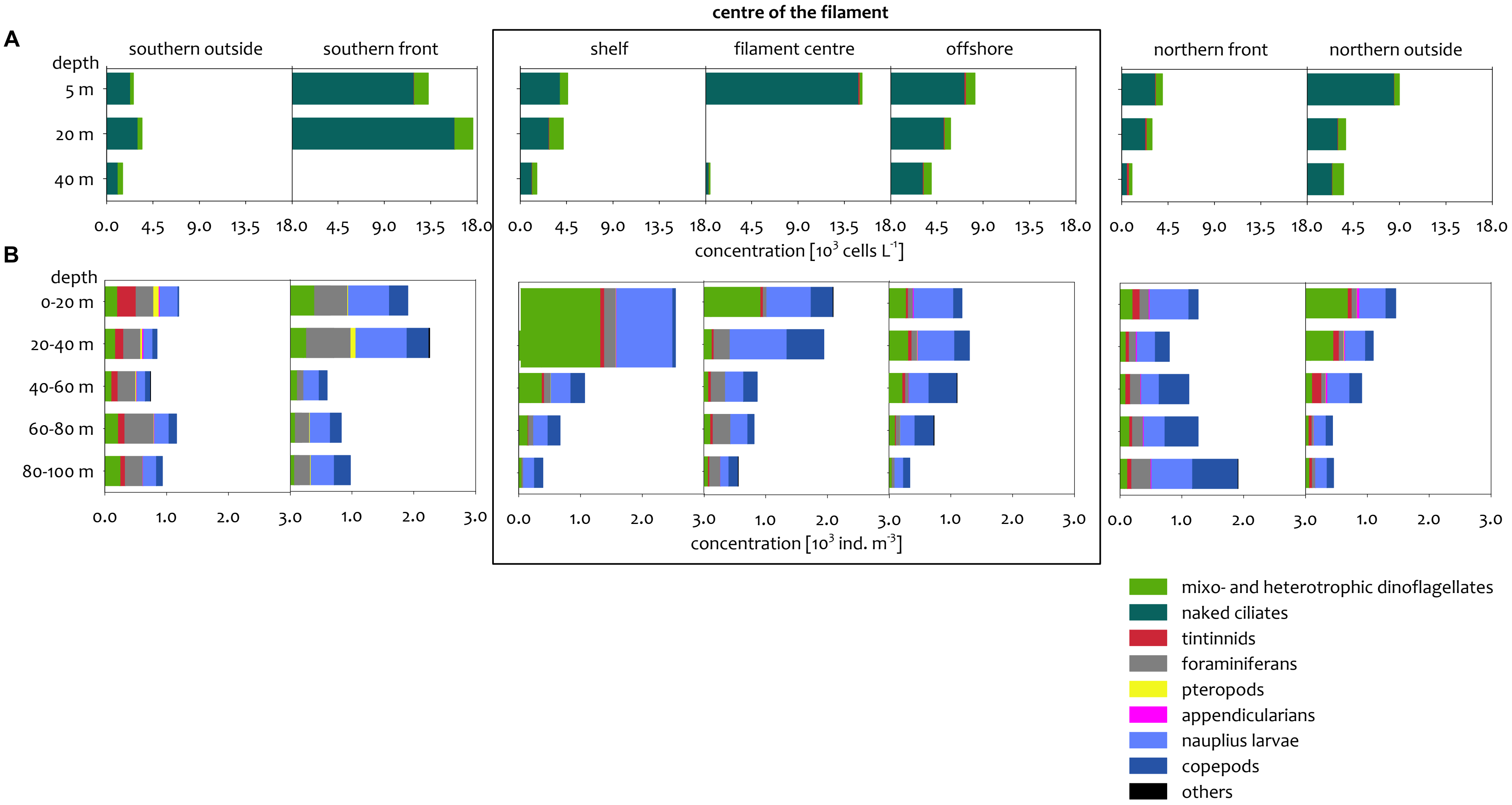


Figure 5-3: The vertical distribution of microzooplankton sampled with a CTD-rosette (A; size fraction: 20-100 µm) and a MCN (B; size fraction: 55-200 µm) across and along the filament.

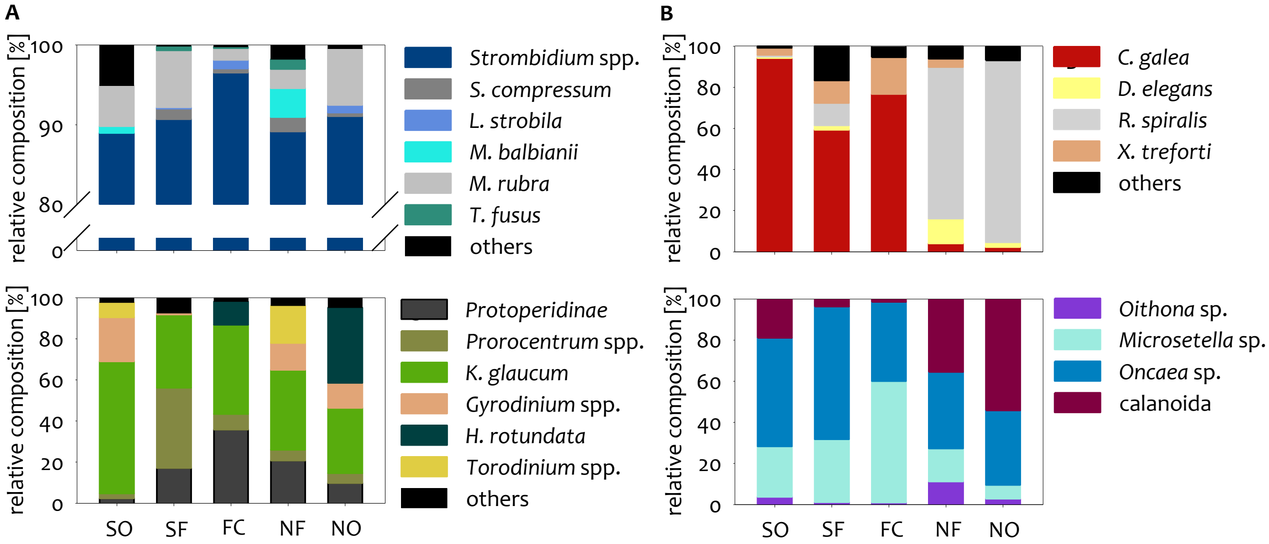


Figure 5-4: Distribution and relative composition of the main microzooplankton groups sampled by a CTD-rosette (A), a MCN (B).

5.3.4. Statistical analyses

The cluster analysis revealed that some stations could be grouped due to the community composition of the microzooplankton (figure 5-5). Samples with a linkage distance lower than 50 for the smaller size fraction and 70 for the larger size fraction allowed a division of both dendrograms into two clusters, which indicate differences between the samples from the southern front station, the upper layer of the centre of the filament and the other samples. The agglomerative cluster analyses based on the data for the larger size fraction (55-200 mm) showed a clear forming of pairs which were mainly composite of the samples from the same station but different depth with an exception of the filament centre station.

We used GAMs to explore the relationship between temperature on the different stations in and around the upwelling filament and microzooplankton groups (figure 5-6, table 5-2). We found three of the eight relationships modelled to be non-linear (figure 5-6C,G), while five found to be linear (figure 5-6A,B,E,G) and hence we refitted these using linear regression. Two relationships were found not to be statistically significant (figure 5-6D, F). We excluded some data points as outliers from the analyses (figure 5-6). These data points are high abundances detected in the southern front station and upper layer of the filament centre station. These samples were also identified as significantly different from all other stations (figure 5-5). Clear positive linear relations with temperature were detected for naked ciliates, dinoflagellates and tintinnids, while a negative relationship was observed for non-calanoid copepods. Non-linear relationships with temperature being strongly positive at the highest temperatures were derived for mixotrophic dinoflagellates and appendicularians.

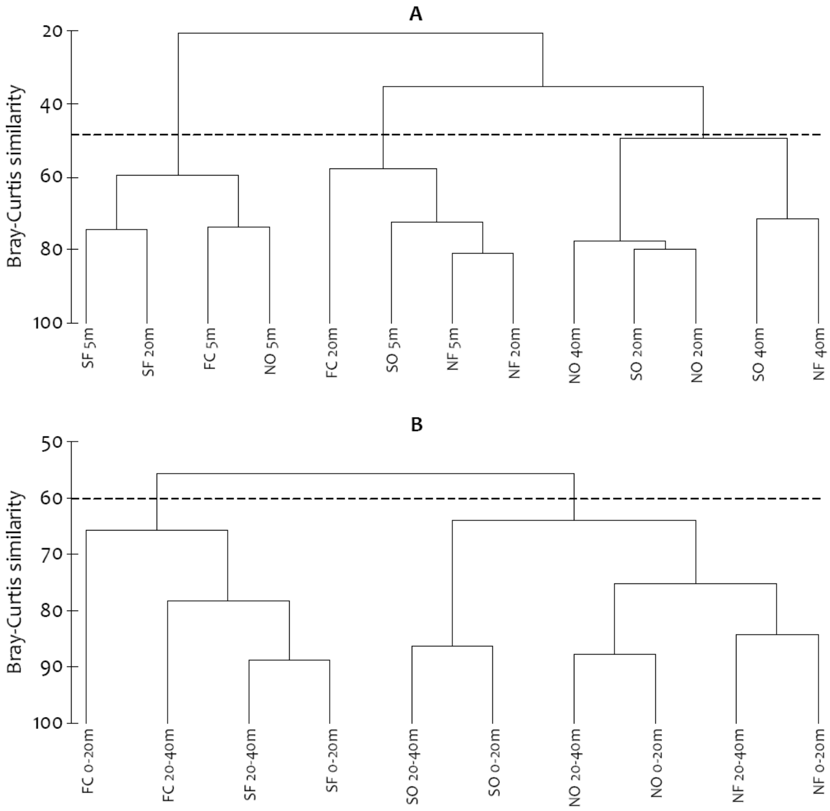


Figure 5-5: A hierarchical cluster analyses – natural grouping of stations based on similarity in microzooplankton composition group average linkage. A) a CTD-rosette samples (20-100 µm) and B) a MCN samples (55-200 µm); the line indicates the ≥ 50% and ≥ 60% similarity cut-off; SO = southern outside , SF = southern front, FC = filament centre, NF = northern front, NO = northern outside

5.4. Discussion

We present for the first time data set on the composition and vertical distribution of microzooplankton across an upwelling filament off the western coast of southern Africa.

We confirmed the hypothesis that that the microzooplankton community differs between the northern and southern part of the filament as a result of different water masses entering the area. The studied upwelling filament extended from the Namibian coast towards the open ocean with a slight shift to the southwest. The filament was influenced by two water masses: the northern water mass, a mixture of ESACW and SACW, which was characterized as a warm and high saline water, and the southern water mass, of pure ESACW, with warm and less saline water. The sharp change between these two water bodies was detected at the northern front. The northern front was also an area of changes in composition of some microzooplankton groups. In the tintinnid community, a rapid change from a community dominated by species *C. galea* south of the filament to a community dominated by warm temperate species *R. spiralis* in the northern part was observed. These two species have a different biogeographic distribution. *C. galea* is known as a cosmopolitan species, whereas *R. spiralis* is commonly found in warm tropical and sub-tropical waters (Dolan & Pierce 2013). We could detect changes in the community composition for other microzooplankton groups. The northern front and northern outside stations, copepods were mostly represented by the the calanoid group. In contrast, the harpacticoid copepod *Microsetella* sp. prevailed in the centre of the filament.

We found relationships between the occurrence of some microzooplankton groups and water temperature. We used temperature as indicators for the filament centre and the surrounding water masses (figure 5-6). Protists, naked ciliates, small dinoflagellates and tintinnids showed clear preferences for warmer water masses surrounding the filament whereas the copepods, *Microsetella* sp, *Oithona* sp. and *Oncaea* sp., were related to the cold filament water. Dvoretsky & Dvoretsky (2009) speculated that temperature is the major factor limiting the distribution and fecundity of small copepod *Oithona* spp. However, we assumed that the distribution of the small copepod species in the filament is rather driven by food conditions. Small copepod species such as *Oithona* spp. prefer to feed on small dinoflagellates and ciliates within the 10-40 µm size range (Castellani et al. 2005; Zamora-Terol & Saiz 2013). High abundances of small ciliates and dinoflagellates as well as increased abundances of copepods in the centre of the filament were observed during this study (figure 5-3).

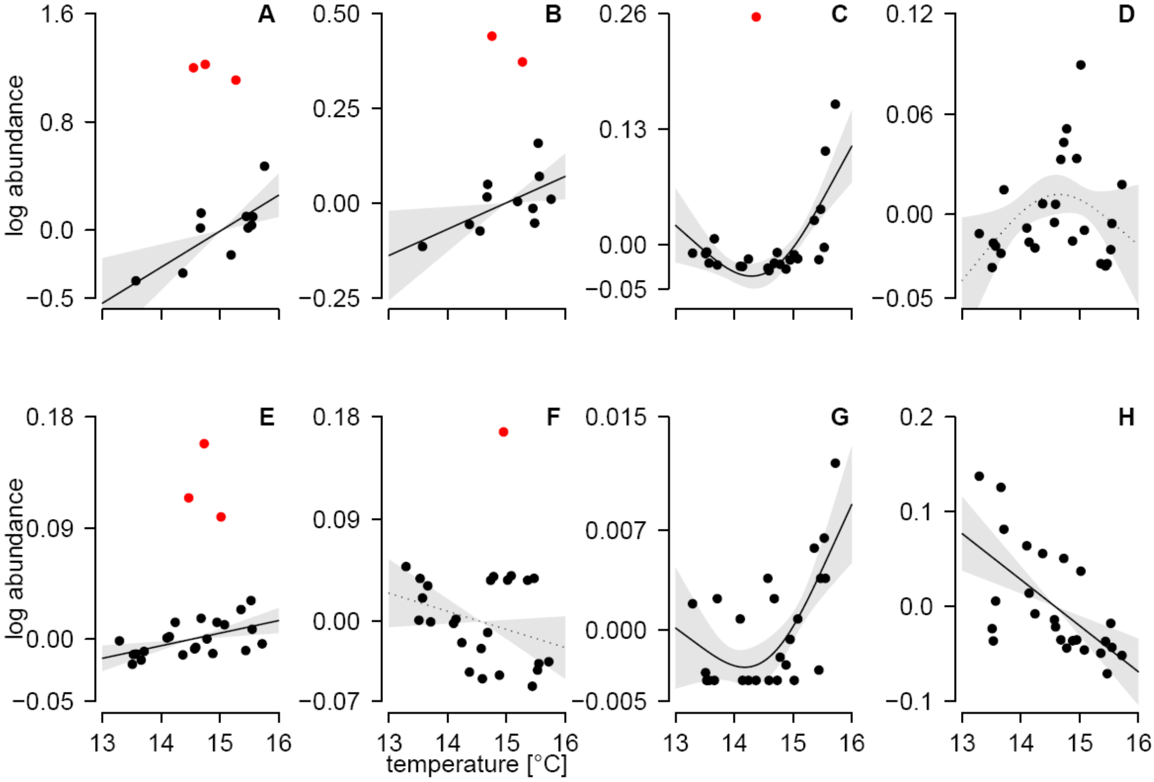


Figure 5-6: Results of generalized additive models (GAM) of abundance of different microzooplankton groups in relation to temperature (data from CTD-rossette and MCN combined). Small size fraction (20-100 µm; CTD-rossette): naked ciliates (A), dinoflagellates (B); larger size fraction (55-200 µm; MCN): mixotrophic dinoflagellates (C), heterotrophic dinoflagellates (D), tintinnids (E), foraminiferans (F), appendicularians (G), non-calanoid copepods (H). Dotted line = n.s., solid line = s. (<0.05). Red dots = excluded data from the model. 95% confidence limits are shown as a shadow.

Furthermore, we confirmed the hypothesis that the filament fronts were areas of high abundance and therefore associated with high productivity. We detected distinct fronts in the south (20°30'S) and north (19°30'S). Fronts are, generally considered, highly productive areas with high abundances of many plankton groups and fish (Hernández-León et al. 2002; Marańón & Fernández 1995; Sverdrup 1938). Some microzooplankton taxa are mainly connected to the frontal zones. Some species of dinoflagellates such as *Dinophysis* sp., *P. gracile*, *Torodinium* spp., *O. scolopax* were found predominantly in the southern front. Also polychaete larvae and some groups of radiolarians were mostly found in the frontal zones (figure 5-3, appendix 5-1). Interestingly, the highest abundances of microzooplankton were not detected at the northern front where the high nutrient SACW meets the filament. Enhanced abundances were detected instead the southern front and also in the centre of the upwelling filament (figure 5-3). Our data showed that the upper layers of theses two stations distinguished from all other stations and analysed depths (figure 5-5). This could be a result of differential currents associated with the filament. ScanFish data (figure 5-7) demonstrated that the water mass at the southern front moved strongly from the coast to the open ocean, transporting coastal zooplankton away from the coast. In contrast, at the northern front, the water moved backwrds towards the coast, which could reduce an expansion of plankton from the coast to the open ocean.

Table 5-2: Summary statistics of GAM; n = number of samples included in the model, edf = equivalent degrees of freedom.

group	size fraction	n	model	edf	R^2	variable effect	p-value	explained deviance
naked ciliates	20-100 µm	10	linear	1	0.51	positive	0.011	56.8%
small dinoflagellates	20-100 µm	11	linear	1	0.31	positive	0.043	37.9%
heterotrophic dinoflagellates	55-200 µm	24	GAM	1.94	0.56		<0.001	59.6%
mixotrophic dinoflagellates	55-200 µm	25	GAM	1.80	0.14		0.095	20.1%
tintinnids	55-200 µm	22	linear	1	0.28	positive	0.007	31.0%
foraminiferans	55-200 µm	24	linear	1	0.07	negative	0.109	11.3%
appendicularians	55-200 µm	25	GAM	1.90	0.44		0.001	48.2%
copepods (w/o calanoida)	55-200 µm	25	linear	1	0.38	negative	<0.001	40.4%

The biological activity at the fronts of upwelling filaments is driven only partially by the environmental conditions as described above but more likely by local biological processes occurring in the fronts. One of those factors is the feeding pressure and grazing selectivity of mesozooplankton. Many mesozooplankton groups such as copepods are selective feeders and may ingest prey non-proportionally to ambient densities (Kleppel 1993; Castellani et al. 2008). The feeding selectivity is mainly affected by the trophic state of the ''ecosystem'' (Atkinson 1995), the food size (Frost 1972) and quality (Berggreen et al. 1988; Löder et al. 2011). When the phytoplankton quality as food for mesozooplankton decreases, the copepod diet switches from phytoplankton-dominated to microzooplankton-dominated (Löder et al. 2011).

We further hypothesized that the ratio of ciliates vs. mixo- and heterotrophic dinoflagellates decreased along the filament from the shelf to offshore. The phytoplankton composition and its quality as food source for mesozooplankton changes with increasing distance from the shelf and ciliates become more important than phytoplankton as a food source for larger organisms like copepods (Hernández-León et al. 2002). During our study, the abundance of ciliates along the filament rapidly increased from the shelf to the centre of the filament and decreased again at the offshore station (figure 5-3). This distribution pattern probably results from the composition of the phytoplankton. At the source of an upwelling filament, the community is often dominated by small dinoflagellates and nanoflagellates (Hansen et al. 2014) which is an optimal food source for small microzooplankton groups like ciliates (Hernández-León et al. 2002). Furthermore, we detected an increasing trend in the abundance of dinoflagellates in the offshore direction which could have been caused by an increasing abundance of larger diatoms (Hansen et al. 2014). This is the only group of microzooplankton able to feed on larger organisms as themselves such as diatoms (Lessard & Swift 1986; Hansen 1992; Horner et al. 2005; Saito et al. 2006; Sherr & Sherr 2007) and may take advantage of this situation. In this study, we could not substantiate our third hypothesis about increasing ratios of ciliates vs. dinoflagellates, but we detected an increasing abundance of larger mixo- and heterotrophic dinoflagellates, whereas the abundance of naked ciliates was highest in the filament centre and decreased at the offshore station.

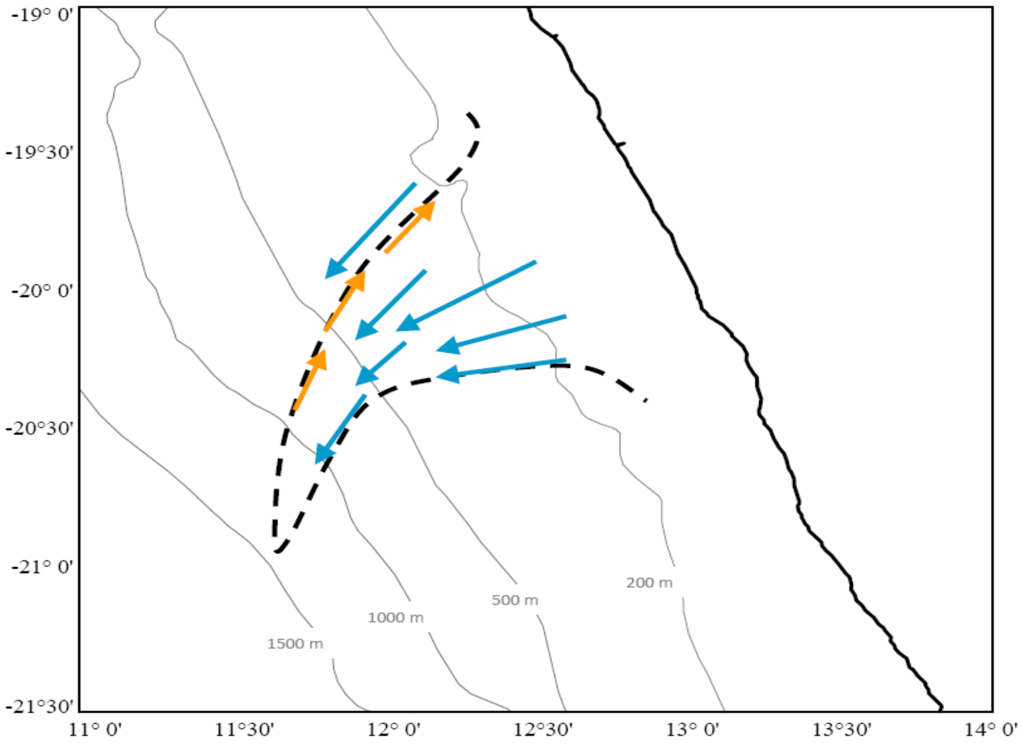


Figure 5-7: Scheme of the water currents associated with the filament according to ScanFish data.

Generally, the community of microzooplankton related to the upwelling filament was partially associated with environmental parameters and conditions. We could see clear small-scale differences in distribution of some microzooplankton species, mainly within the tintinnid group, in dependence of the fraction of SACW and ESACW. Therefore we assume, that tintinnids could be used as indicators of the two different water masses in this area. We could prove that fronts of an upwelling filament are not necessarily an area with high abundances and diversity. The functioning of upwelling filaments are very complex and the changes of zooplankton community connected to the fronts depends on physiological parameters related to properties of the entering water masses, the water circulation within the filament and many biological parameters such as the composition of the original community at the beginning of the filament or predator pressure. The composition of microzooplankton community also changed with the age of the filament. The abundances of large microzooplankton groups such as large heterotrophic dinoflagellates, tintinnids, foraminiferans and nauplius larvae increased toward the open ocean, whereas the abundances of naked ciliates was highest in the centre of the filament and strongly decreased offshore.

We conclude that a shift to more ciliates and heterotrophic dinoflagellates observed in the southern front could have an effect on the biogeochemical cycle as multiple steps within the microbial food web which may reduce the efficiency of the transfer of organic matter to higher trophic levels (Pomeroy et al. 2007). Diverse distributions of microzoolankton taxa could serve as indicators for different pattern in the food web between the different parts of the filament.

5.5. References

Álvarez-Salgado XA, Doval MD, Borges AV, Joint I, Frankignoulle M, Woodward EMS, Figueiras FG (2001) Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System. Progress in Oceanography 51:321-337

Atkinson A (1995) Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. ICES Journal of Marine Science: Journal du Conseil 52:385-396

Azam F, Fenchel T, Field GJ, Gray JS, Mayer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10:257-263

Barton ED, Arístegui J, Tett P, Cantón M, García-Braun J, Hernández-León S, Nykjaer L, Almeida C, Almunia J, Ballesteros S, Basterretxea G, Escánez J, García-Weill L, Hernández-Guerra A, López-Laatzen F, Molina R, Montero MF, Navarro-Pérez E, Rodríguez JM, van Lenning K, Vélez H, Wild K (1998) The transition zone of the Canary Current upwelling region. Progress in Oceanography 41:455-504

Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepodAcartia tonsa during development: Implications for determination of copepod production. Marine Biology 99:341-352

Blamey LK, Howard JAE, Agenbag J, Jarre A (2012) Regime-shifts in the southern Benguela shelf and inshore region. Progress in Oceanography 106:80-95

Brink KH (1983) The near-surface dynamics of coastal upwelling. Progress in Oceanography 12:223-257

Buchholz F (2014) Cruise Report RV Meteor M100/1 Walvis Bay-Walvis Bay 1st September to 1st October 2013

Calbet A, Landry MR (2004) Phytoplankton Growth, Microzooplankton Grazing, and Carbon Cycling in Marine Systems. Limnology and Oceanography 49:51-57

Calbet A, Saiz (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Campbell RG, Sherr EB, Ashjian CJ, Ploudre S, Sherr BF, Hill V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 56:1274-1289

Liu H, Dagg MJ, Strom S (2005) Grazing by the calanoid copepod Neocalanus cristatus on the microbial food web in the coastal Gulf of Alaska. Journal of Plankton Research 27:647-662

Castellani C, Irigoien X, Mayor DJ, Harris RP, Wilson D (2008) Feeding of Calanus finmarchicus and Oithona similis on the microplankton assemblage in the Irminger Sea, North Atlantic. Journal of Plankton Research 30:1095-1116

Cravo A, Relvas P, Cardeira S, Rita F, Madureira M, Sánchez R (2010) An upwelling filament off southwest Iberia: Effect on the chlorophyll a and nutrient export. Continental Shelf Research 30:1601-1613

Dolan JR, Pérez MT (2000) Costs, benefits and characteristics of mixotrophy in marine oligotrichs. Freshwater Biology 45:227-238

Dolan JR, Pierce RP (2013) Diversity and distributions of tintinnids. In: Dolan JR, Montagnes DJS, Agatha S, Coats DW, Stoecker DK (eds) The biology and ecology of tintinnid ciliates. John Wiley & Sons, Ltd., Chichester, p 296

Dvoretsky VG, Dvoretsky AG (2009) Lify cycle of *Oithona similis* (Copepoda: Cyclopoida) in Kola Bay (Barents Sea). Marine Biology 156:1433-1446

Figueiredo GM, Nash RDM, Montagnes DJS (2007) Do protozoa contribute to the diet of larval fish in the Irish sea? Journal of the Marine Biological Association of the United Kingdom 87:843-850

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography 17:805-815

García-Muñoz M, Arístegui J, Montero MF, Barton ED (2004) Distribution and transport of organic matter along a filament-eddy system in the Canaries â€“ NW Africa coastal transition zone region. Progress in Oceanography 62:115-129

Hansen A, Ohde T, Wasmund N (2014) Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. Journal of Marine Systems 140, Part B:130-137

Hansen PJ (1992) Particle size selection, feeding rates and growth dynamics of marine heterotrophic dinoflagellates, with special emphasis on *Gyrodinium spirale*. Marine Biology 114:327-334

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Haynes R, Barton ED, Pilling I (1993) Development, persistence, and variability of upwelling filaments off the Atlantic coast of the Iberian Peninsula. Journal of Geophysical Reasearch 98:681-692

Hernández-León S, Almeida C, Portillo-Hahnefeld A, Gómez M, Rodríguez JM, Arístegui J (2002) Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off northwest Africa. Journal of Marine Research 60:327-346

Horner RA, Postel JR, Halsband-Lenk C, Pierson JJ, Pohnert G, Wichard T (2005) Winter-spring phytoplankton blooms in Dabob Bay, Washington. Progress In Oceanography 67:286-313

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress In Oceanography 83:15-32.

Kleppel GS (1993) On the diets of calanoid copepods. Marine Ecology Progress Series 99:183-195

Landry MR, Hassett RP (1982) Estimating the grazing impact of marine micro-zooplankton. Marine Biology 67:283-288

Lavrentyev PJ, Gardner WS, Cavaletto JF, Beaver JR (1995) Effects of the zebra mussel (*Dreissena polymorpha* Pallas) on protozoa and phytoplankton from Saginaw Bay, lake Huron. Journal of Great Lakes Research 21:545-557

Lessard EJ, Swift E (1986) Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. Journal of Plankton Research 8:1209-1215

Levinsen H, Nielsen TG (2002) The trophic role of marine pelagic ciliates and heterotrophic 22 dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison. Limnology and Oceanography 47:427-439

Löder MJ, Meunier C, Wiltshire KH, Boersma M, Aberle N (2011) The role of ciliates, heterotrophic dinoflagellates and copepods in structuring spring plankton communities at Helgoland Roads, North Sea. Marine Biology 158:1551-1580

Lutjeharms JRE, Shillington FA, Duncombe Rae CM (1991) Observations of extreme upwelling filaments in the southeast atlantic ocean. Science 253:774-776

Mackas DL, Peterson WT, Ohman MD, Lavaniegos BE (2006) Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophysical Research Letters 33:L22S07

Marańón E, Fernández E (1995) Changes in phytoplankton ecophysiology across a coastal upwelling front. Journal of Plankton Research 17:1999-2008

Marchesiello P, Estrade P (2009) Eddy activity and mixing in upwelling systems: a comparative study of Northwest Africa and California regions. International Journal of Earth Sciences 98:299-308

Marín VR, Escribano R, Delgado LE, Olivares G, Hidalgo P (2001) A numerical study of the upwelling circulation off central Chile. Continental Shelf Research 21:1317-1329

Mohrholz V, Bartholomae CH, van der Plas AK, Lass HU (2008) The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Continental Shelf Research 28:424-441

Mohrholz V, Eggert A, Junker T, Nausch Gn, Ohde T, Schmidt M (2014) Cross shelf hydrographic and hydrochemical conditions and their short term variability at the northern Benguela during a normal upwelling season. Journal of Marine Systems 140, Part B:92-110

Montagnes DJS, Dower JF, Figueiredo GM (2010) The Protozooplankton–Ichthyoplankton Trophic Link: An Overlooked Aspect of Aquatic Food Webs1. Journal of Eukaryotic Microbiology 57:223-228

Muller AA, Mohrholz V, Schmidt M (2013) The circulation dynamics associated with a northern Benguela upwelling filament during October 2010. Continental Shelf Research 63:59-68

Navarro-Pérez E (1998) The physical structure of an upwelling filament off the North-west African coast during august 1993. African Journal of Marine Science 19

Pitcher GC, Walker DR, Mitchell-Innes BA, Moloney CL (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton dynamics. Progress In Oceanography 28:39-64

Pomeroy LR, Williams PJ, Azam F, Hobbie JE (2007) The Microbial Loop. Oceanography 20:28-33

Saito H, Ota T, Suzuki K, Nishioka J, Tsuda A (2006) Role of heterotrophic dinoflagellate Gyrodinium sp. in the fate of an iron induced diatom bloom. Geophysis

Shannon LV, Pillar SC (1986) The Benguela Ecosystem: Part III. Plankton. Oceanography and Marine Biology 24:65-170

Shannon CE, Weaver W (1949) The Mathematical Theory of Information, Vol. University of Illinois Press, Urbana

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Marine Ecology Progress Series 352:187-197

Sobarzo M, Figueroa D (2001) The physical structure of a cold filament in a Chilean upwelling zone (Peninsula de Mejillones, Chile, 23°S). Deep Sea Research Part I: Oceanographic Research Papers 48:2699-2726

Strub PT, Korso PM, Huyer A (1991) The nature of the cold filaments in the California Current System. Journal of Geophysical Reasearch 96:743-768

Sverdrup HU (1938) On the process of upwelling. Journal of Marine Research 1:115-164

Zamora-Terol S, Saiz E (2013) Effects of food concentration on egg production and feeding rates of the cyclopoid copepod Oithona davisae. Limnology and Oceanography 58:376-387

5.6. Appendix

Appendix 5-1: Relative distribution of identified taxa (MSN, CTD), the sum of all individuals belonging to one taxa in the five different water bodies in one size fraction is 100%: ○ < 25%, ◔ 25-50%, ◑ 50-75%, ◕ > 75% and ● 100%; SO = southern outside, SF = southern front, FC = filament centre; NF = northern front, NO = northern outside.

		CTD data (20-100 µm)					MSN data (55-200 µm)				
		SO	SF	FC	NF	NO	SO	SF	FC	NF	NO
Dinoflagellata											
Thecate Dinophytes	*Ceratium* sp.	○	◔	○	○	○	○	◔	○	◔	○
	Dinophysis spp.		◕		○						
	Heterokapsa rotundata	○		○	○	◕					
	Oxytoxum spp.	○	◑		○	◔					
	Prorocentrum spp.	○	◕	○	○	○					
	Protoperidinium sp. <50 µm	○	◑	○	○	○					
	Protoperidinium sp. > 50 µm	○	◕	○	○	○	◑	○	○	○	○
Athecate Dinophytes	*Gyrodinium* spp.	◔	○	○	◔	○					
	Katodinium glaucum	○	◔	○	○	◔					
	Noctiluca scintillans								◔	◑	
	Polykrikos sp.	◔			○	◔					
	Torodinium spp..	○	◑	○	◔						
Ciliophora	*Cyrtostrombidium* sp.	◑				◔					
	Laboea strobila	○		◔		◑					
	Monodinium balbianii	○	○	○	◑	○					
	Myrionecta rubra	○	◑	○	○	○					
	Strombidium crassulum	○	◕	○	○	○					
	Strombidium compressum	○	◔	○	○	◔					
	Strombidium sp.	○	◔	◔	○	○					
	Tiarina fusus			◔	◑						

		CTD data (20-100 µm)					MSN data (55-200 µm)				
		SO	SF	FC	NF	NO	SO	SF	FC	NF	NO
Tintinnida											
	Ascampbeliella sp.			◔	◑						
	Codonella galea	◑	○	○	◑		◔	◔	○	○	○
	Codonellopsis morchella									○	◕
	Cymatocyclis vanhoffeni									●	
	Cyttarocalis cassis						○	◑	○	○	○
	Dadayiella ganymedes			◔	◑	○					
	Dictyocysta elegans				●		◔	○		◔	○
	Epiplocylis acuminata							○		○	◑
	Eutintinus sp.		◕			○		●			
	Favella ehrenbergii				●					●	
	Ormosella sp.				●						
	Petalotricha ampulla			●							
	Rhabdonella sp.		◔		◔	◔	○	○		◔	◑
	Stenosemella sp.				●						
	Tintinnopsis gracilis			◕	○				●		
	Xystonella treforti						◑	◔	○	○	○
Radiolaria											
Actinommidae							◔	◔	○	◔	○
Astrobiidae								●			
Cellosphaeridae									●		
Challengeridae							●				
Collodaria									●		
Pterocorythidae								●			
Spongodididae								○	◔		◑
Theoperidae								◑	◔	○	○
Copepoda											
Calanoida							○	○	○	◔	◔
Cyclopoida	*Oithona* sp.						○	○	○	◑	○
	Oncaea sp.						○	◔	◔	◔	○
Harpacticoida	*Microsetella* sp.						○	○	◔	◔	○
Foraminifera	*Neogloboquadrina* sp.						◔	○	○	○	○
Polychaeta Larvae							○	◔	○		○
Pteropoda	*Limacina* sp.						◑	◔			○
Tunicata	*Appendicularia* sp.						◔		○	○	◑

Chapter 6

Microzooplankton patchiness: short-time series

Bohata Karolina, Koppelmann Rolf, Louw Deon*, van der Plas Anja*

Institute for Hydrobiology and Fisheries Science, Centre for Earth Systems Research and Sustainability, University of Hamburg, Hamburg, Germany

*National Marine Information and Research Centre, Swakopmund, Namibia

Abstract

Small scale variations within the microzooplankton community over a short-time period have been estimated in the northern Benguela Upwelling System. The distribution of microzooplankton species, especially tintinnids, was relatively patchy due to complex biological-physical interactions. The diversity of microzooplankton was very low directly on the shelf and increased with increasing distance from the shore as a result of chl *a* concentrations and a more complex food web offshore. The concentrations of naked ciliates increased with increasing chl *a* values, whereas the concentration of mixo- and heterotrophic dinoflagellates decreased. Significant differences between the community occupying the warm surface layer and the community occupying deeper colder water below the thermocline have been detected. These differences are caused by stratification between the surface water warmed up by solar radiation with high primary production as a result of incoming nutrients and deeper fresh upwelled cold water streaming upward.

6.1. Introduction

The Benguela Upwelling System (BUS; Blamey et al. 2012) is one of the major eastern boundary upwelling systems of the world (Hutchings et al. 2009). The BUS is situated off the west coast of Africa and spans from Cape of Good Hope in the south along the coast of Southern African and Namibian into Angolan waters (Shannon & O'Toole 2003). A high pressure system over the central South Atlantic Ocean induces south-eastern winds along the African coast, modified by seasonal low pressure over the continent and eastward moving cyclones to the south (Nelson & Hutchings, 1983). This supports the upwelling-favourable south-easterly winds during the spring and summer seasons in the southern part of the BUS and during southern autumn and spring in the northern BUS. The central BUS between about 26°S and 28°S experiences almost perennial upwelling-favourable conditions (Summehayes et al. 1995; Shannon & Nelson 1996).

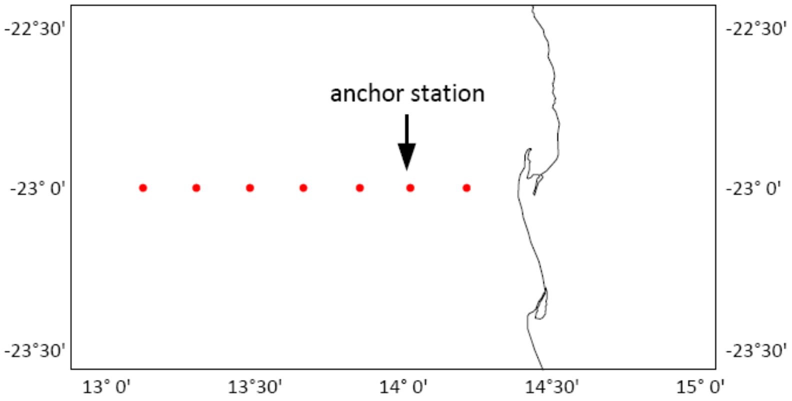


Figure 6-1: The study area off Walvis Bay, Namibia. Station location: 10, 20, 30, 40, 50, 60, 70 nm off the coast.

Table 6-1: Sampled stations on the transect off Walvis Bay; T1 = leg 1, T2 = leg 2.

transect	station	date	time	latitude	longitude
T1	10nm	1/15/2013	21:55 (UTC)	S 23°00,044'	E 14°13,789'
T1	20nm	1/16/2013	00:26 (UTC)	S 23°00,0356	E 14°02,674'
T1	30nm	1/16/2013	04:20 (UTC)	S 23°00,066'	E 13°51,920'
T1	40nm	1/16/2013	04:55 (UTC)	S 23°00,195'	E 13°40,737'
T1	50nm	1/16/2013	07:00 (UTC)	S 23°00,012'	E 13°29,904'
T1	60nm	1/16/2013	09:15 (UTC)	S 23°00,005'	E 13°19,203'
T1	70nm	1/16/203	11:25 (UTC)	S 23°00,134'	E 13°08,142'
T2	10nm	1/25/2013	21:50 (UTC)	S 22°59,874'	E 14°13.659'
T2	20nm	1/25/2013	19:40 (UTC)	S 23°00,155'	E 14°02.592'
T2	30nm	1/26/2013	00:39 (UTC)	S 23°00.112'	E 13°51,808'
T2	40nm	1/26/2013	02:35 (UTC)	S 23°00.000'	E 13°40.840'
T2	50nm	1/26/2013	04:22 (UTC)	S 23°00.137'	E 13°29.966'
T2	60nm	1/26/2013	06:25 (UTC)	S 22°59.995'	E 13°19.095'
T2	70nm	1/26/2013	08:40 (UTC)	S 22°59.941'	E 13°07.989'

The southern region of the BUS is influenced by oceanographic processes from the South Atlantic and Indo-Pacific Oceans, ring-formation from the Agulhas current enter the Atlantic Ocean (Shannon & O'Toole 2003). The northern region of the BUS is affected by the Angola-Benguela front as a result of seasonal and inter-annual changes of the intensity of upwelling cells at Cape Frio (Clarke & Gorley 2006) and Lüderitz (26°40'S; Hutchings et al. 2009).

Microzooplankton plays an important role as main grazers of phytoplankton production in oligotrophic as well as in nutrient-rich ocean regions (Calbet 2001; McManus et al. 2007, Sherr & Sherr 2007). In upwelling regions, the understanding of microzooplankton as a part of the food web was long time underestimated. It has been accepted that short food chains prevail in this high productive areas, with high production of large phytoplankton cells passing directly to the mesozooplankton and than to larger animals such as fish. In the last two decades, the evidence of an importance of microzooplankton as an essential part of the food web increased (Painting 1992; Neuer & Cowles 1995; Vargas et al. 2007). Microzooplankton is an important link between small primary producers and larger consumers. They can rapidly respond to changes in phytoplankton abundance (Strom et al. 2001) and due to their selective feeding behavior they are able to change the structure of phytoplankton communities (Burkill et al. 1987). Microzooplankton also contribute to the diet of organisms of higher trophic levels such as copepods (Batten et al. 2001; Calbet & Saiz 2005), fish larvae (Pepin & Penney 2000; Figueiredo et al. 2007; Montagnes et al. 2010) and krill (Levisen & Nielsen 2002; Campbell et al. 2009).

To characterize the trophic interactions in the ecosystem, it is important to understand whether the food web is driven by bottom-up or top-down mechanisms. Until now, the interactions between bottom-up and top-down control is poorly understood. Verheye and Richardson (1998) proposed several mechanisms, which probably influence long-term increase in abundance of zooplankton in the BUS. From the bottom-up view, the increase in upwelling favorable wind stress and associated processes could be related to this increase in zooplankton abundance. However, from the top-down view, this increase could be related to a long-term decrease in abundance of pelagic fish as a result of increasing fishing effort. These suggestions could be applied to smaller scale interactions between environmental parameters, primary producers, microzooplankton and mesozooplankton.

The trophic structure of the ecosystem is determined also by the diversity of the ecosystem. Increasing predator size spectra enhance the strength of top-down control on prey through diet niche partitioning (Ye et al. 2013). The diversity of microzooplankton is influenced by the size-class diversity of potential phytoplankton prey (Dolan et al. 2002). Small phytoplankton cells, mainly small diatoms and dinoflagellates, are well adapted to high nutrient fresh upwelled water, whereas larger cells and dinoflagellates adapted to stratified and nutrient poor waters are associated with matured offshore water (Hansen et al. 2014). Therefore the diversity of microzooplankton is supposed not to be highest in the fresh upwelled water near the coast or further offshore, but above the deeper shelf and at the shelf break. This would be in contrast to other studies, which reported an increasing diversity of different plankton groups in direction from the shelf to offshore (Miloslavić et al. 2012; Bohata & Koppelmann 2013; Koppelmann et al. 2013).

As mentioned above the physical environment is not only affecting the trophic interactions in the ocean but also the temporal and spatial distribution, growth, and dominance of species. Flow patterns in the ocean are important by influencing the distribution of organisms on all spatial scales (Mann & Lazier 2005). The distribution of species in the ocean is also driven by biological dynamics such as food availability or sexual encounters among individuals of relatively rare species (Franks 2005). These biological and physical drivers are responsible for the patchy distribution of plankton, but still not well understood.

This study presents a detailed analysis of the dynamics of the microzooplankton community during a short-time series study off the Namibian coast. We hypothesize that (1) the highest diversity of microzooplankton can be found further from the shore in matured upwelled water; (2) the ratio ciliates vs. mixo- and heterotrophic dinoflagellates decreases with increasing distance from the shore as a result of changes in phytoplankton community; (3) the distribution of microzooplankton is patchy and correlates with the distribution of chl *a*; (4) the microzooplankton community is split/separated by the thermocline into two subgroups as a result of different environmental parameters with a focus on temperature and changes in the food web. The results obtained in this study will be useful not only to implement our knowledge about the interaction between the different trophic levels in this complex ecosystem, but also to better understand the dynamics of plankton patchiness.

6.2 Methods

The data were collected as a part of the GENUS project (Geochemistry and Ecology of the Namibian Upwelling System) in cooperation with the Namibian National Marine Information and Research Centre. The samples were taken during southern summer in January 2013 on the RV Mirabilis off the Namibian coast (figure 6-1). Environmental data (temperature and salinity) were gathered with a SeaBird 911+ CTD system.

6.2.1 Field sampling and laboratory analysis

To determine the spatial and temporal differences in phytoplankton and microzooplankton composition, a transect off Walvis Bay was sampled two times with 10 days time gap. Stations were situated every 10 nm apart between 10 and 70 nm in direction from the coast. To determine the temporal changes and patchiness in microzooplankton distribution, an anchor station 20 nm from the coast was sampled every 24 h for 7 days (table 6-2).

For Chl *a* analyses, 200 ml water samples were taken at the surface (1-2 m), 10 m, 20 m and 30 m depth. The water was vacuum filtered on WhatmanTM GF/F filters and stored at -20°C on the ship to be analysed in the laboratory within the next 1-2 weeks. Chl *a* pigment was extracted by adding 90% acetone and sonicating the sample in a water bath for seven minutes where the temperature did not exceed 10-12°C. The samples were put back at -20°C for complete extraction for another 24 hours. Raw fluorometer readings were obtained after blanking it with 90% acetone with a Turner Model 10 fluorometer, following the Welschmeyer (1994) protocol, which uses the non-acidification optical kit (P/N 10-040R) from Turner. The fluorometer was calibrated on a regular basis with a Chl *a* standard (Sigma-Aldrich, St. Louis, USA) and the final Chl *a* concentrations were calculated as mg m^{-3} in reference to a calibration curve of the Chl *a* standard.

Microzooplankton samples were collected in 5, 10, 40 and 70 m depth on the transects and in 5 and 10 m at the anchor station using the rosette water sampler of the CTD system, which was equipped with 10 L free flow bottles (table 6-1 and 6-2). Depending on the sampled depth, 200 ml (5 m, 20 m depth) or 500 ml (40 m, 70 m depth) of seawater were fixed with acidic Lugol's solution and kept in darkness at 5°C for further analyses in the home laboratory. In the home laboratory, a volume of 50 mL or 100 mL of the fixed water samples were filled in settling chambers for 24 h and analysed using an inverted microscope. The organisms between 20-200 µm on a microscope scale were counted and identified to the species level or the nearest taxonomic level that the settled position and the visible characteristics allowed.

Table 6-2: Sampling design during the anchor station 20 nm off Walvis Bay.

time	date	latitude	longitude
0 h	1/17/2013 20:00 (UTC)	S 23°00583'	E 14°03,796'
24 h	1/18/2013 20:00 (UTC)	S 23°00,596'	E 14°03,761'
48 h	1/19/2013 20:25 (UTC)	S 23°00,407'	E 14°03,631'
72 h	1/20/2013 20:38 (UTC)	S 23°00,520'	E 14°03,659'
96 h	1/21/2013 20:25 (UTC)	S 23°00,403'	E 14°03,887'
120 h	1/22/2013 20:20 (UTC)	S 23°00,441'	E 14°03,762'
144 h	1/23/2013 20:25 (UTC)	S 23°00.487'	E 14°03.971'

6.2.2 Statistical analyses

To test our fourth hypothesis on two different communities split by the thermocline, we applied the ANOSIM (Analyses of Similarity). This analysis was performed to identify the level of significant difference between the different communities found in different depths. Due to the small sample size, interpretation of ANOSIM-R value was also used to evaluate the differential level between groups, with R values >0.75 indicating clear separation among groups, R= 0.75-0.25 indicating separate groups with overlapping values and R<0.25 indicating barely separated groups (Clarke & Gorley 2006). SIMPER (Similarity Percentages) was used to identify the contribution of each species to similarities within a group and dissimilarities amongst different groups. We used a non-metric multi-dimensional scaling (MDS) plots to visualise groupings within and among the groups. ANOSIM, SIMPER and MDS analyses were generated using PRIMERv6 (PRIMER-E, UK).

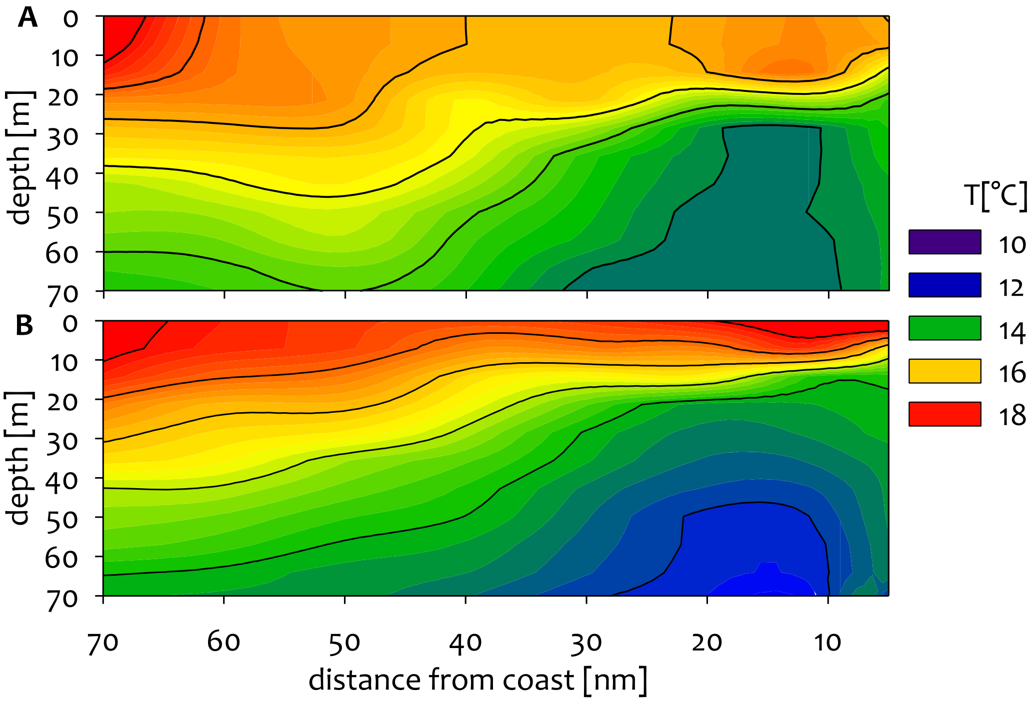


Figure 6-2: Temperature profiles along the transect during the first (A) and second leg (B).

6.3 Results

6.3.1 Transect: first and second leg

Environmental conditions

Temperatures on the transect were quiet similar during the first and the second leg (figure 6-2). A relatively shallow thermocline in about 20 m depth was situated near the coast. With increasing distance from the coast, the thermocline sank to 40 m. The temperature above the thermocline reached more than18.0°C and 19.0°C and decreased below the thermocline to less than 13.5°C and 13.0°C during the first and second leg, respectively.

Abundance and composition of microzooplankton

Naked ciliates were mainly distributed in the upper 40 m during both legs and reached high densities further from the shore with up to 24.0 x 10^3 cells L^{-1} at 60 nm on the first leg and about 12.7 x 10^3 cells L^{-1} at 50 nm during the second leg (figure 6-3). During both legs, the densities of naked ciliates near the coast did not exceed 5.4 x 10^3 cells L^{-1}. Tintinnids occurred very patchy. During the first leg, one hot-spot was detected at 10 nm with densities above 22.0 x 10^3 cells L^{-1}. During the second leg, the hot-spot was found more offshore at 30 nm with lower densities of up to 1.9 x 10^3 cells L^{-1}. At all other stations, the tintinnid densities were very low and did not exceed 0.7 x 10^3 cells L^{-1} on the first leg and 0.6 x 10^3 cells L^{-1} on the second leg.

Mixo- and heterotrophic dinoflagellates were abundantly found in the upper 40 m with very high densities at two stations during the first leg with densities up to 5.3 x 10^3 cells L^{-1} at 10 nm and 6.0 x 10^3 cells L^{-1} at 60 nm (figure 6-3). During the second leg, the distribution of mixo- and heterotrophic dinoflagellates was more uniform. The majority of the individuals were found in the upper 20 m with densities of up to 9.0 x 10^3 cells L^{-1} at 40 nm.

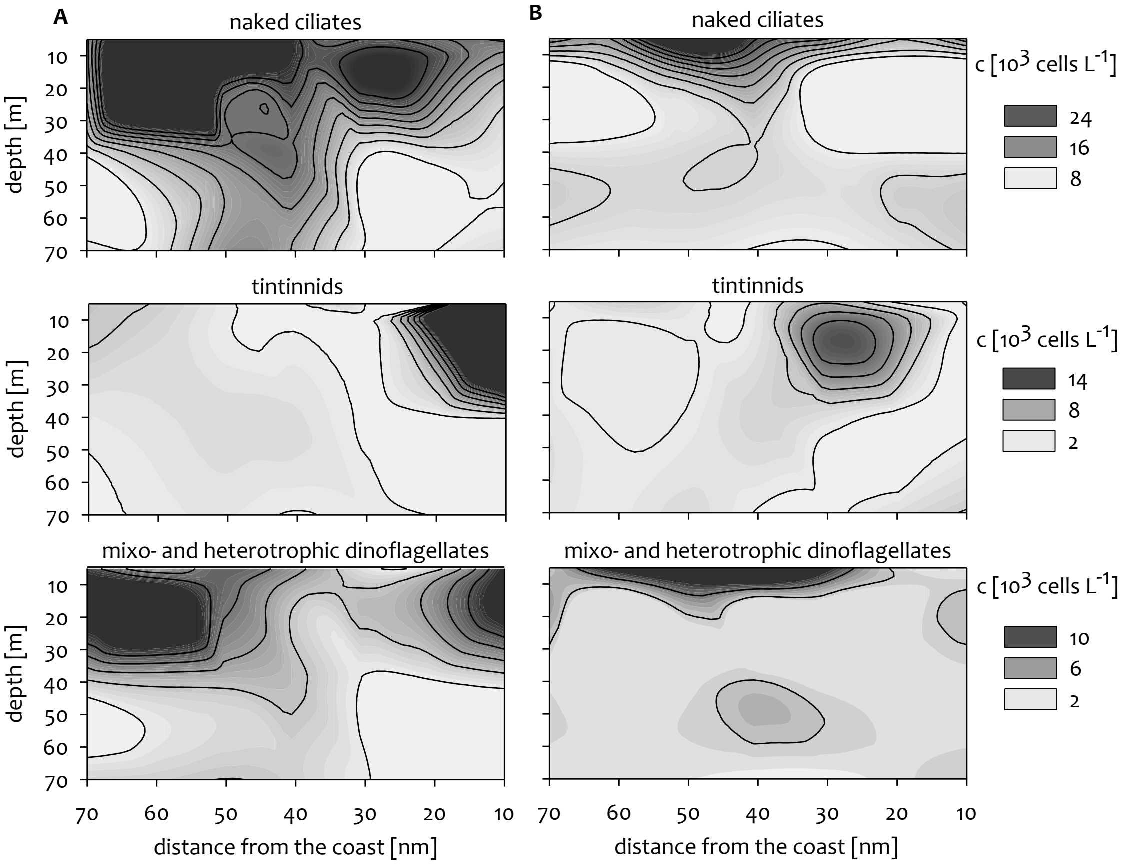


Figure 6-3: Distribution of the main microzooplankton groups along the study transect during the first (A) and second leg (B).

The ratio of naked ciliates vs. mixo- and heterotrophic dinoflagellates

The ratio between naked ciliates and mixo- and heterotrophic dinoflagellates followed the distribution of chl *a* (figure 6-4). It was very low near the shore and increased rapidly at the 20 and 30 nm stations and dropped again further offshore during the first leg. During the second leg, the ratio was highest at the 10 nm station, dropped rapidly further offshore and stayed at the same level along the remaining transect.

Microzooplankton density and chl a

Mixo- and heterotrophic dinoflagellates accounted for about half of the total microzooplankton densities at low chl *a* conditions (figure 6-5). With increasing chl *a* values, the relative amount of mixo- and heterotrophic dinoflagellates decreased and the importance of naked ciliates increased and represented more than 80% of the total microzooplankton density. Tintinnids played only a minor role due to their low densities. Tintinnids were detected in high abundances during the two legs only at single spots; therefore no clear preference was detected.

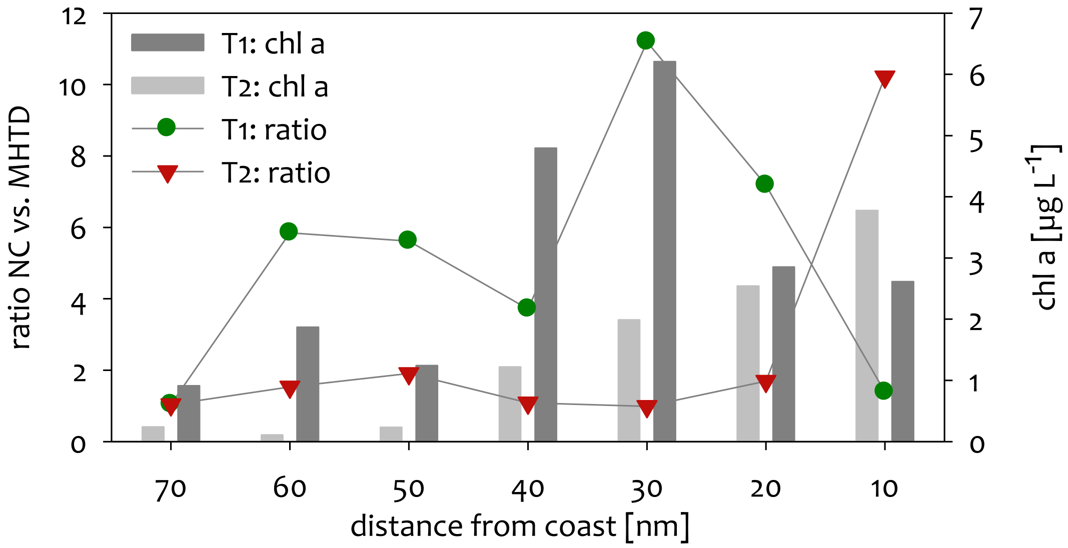


Figure 6-4: The ratio of naked ciliates (NC) vs. mixo- and heterotrophic dinoflagellates (MHTD) and chl a values along the transect during the first (T1) and second leg (T2).

Microzooplankton richness

The species richness was low near the coast during both legs, but the number of species increased rapidly behind the 30 nm stations (figure 6-6). No clear pattern was found for evenness and dominance, due to a high species variability and patchiness. The analyses of the chl *a* content and the number of species revealed a clear correlation for both legs (figure 6-7). The number of species decreased with increasing chl *a* level.

Effects of the thermocline on the microzooplankton community

Significant differences in community structure were detected between the four different depths (ANOSIM, R-value = 0.319, P = 0.1%). However, no differences were obvious between 5 and 10 m (R-value = -0.049, P = 86.1%), and 40 and 70 m (R-value = 0.003, P = 39.9%), but the pairwise tests of ANOSIM revealed significant differences between the community above (5 and 10 m depth) and below the thermocline (40 and 70 m depth, table 6-3). The R-values ranged between 0.403 and 0.589 which suggests groupings with overlapping values. This result was supported by the MDS plotting of the communities found in the different depths (figure 6-8). However, the MDS plot showed also a clear selection of four stations, which were located at 10 and 20 nm off the coast in 70 m depth during the first and second leg.

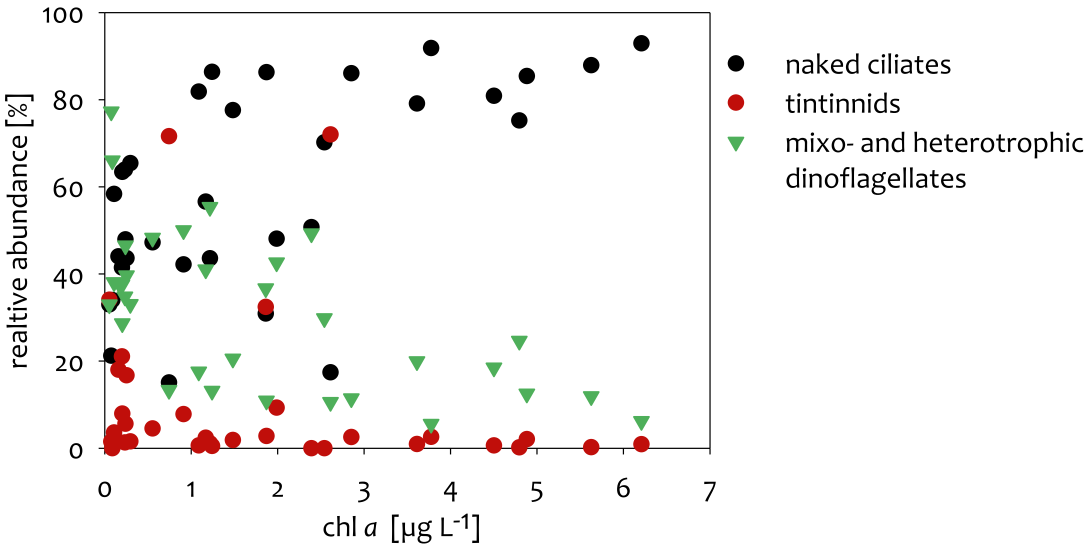


Figure 6-5: Relative abundances of the main microzooplankton groups in relation to chl a.

The groups above (5 and 10 m depth) and below the thermocline (40 and 70 m depth) were pooled together for further SIMPER analyses (appendix 6-1). Both communities were dominated by *Strombidium* spp. (>25%), *Katodinium* sp. (>17%), *Gyrodinium* sp. (9%) and *Monodinium balbianii* (4%). The differences between the groups were caused by less abundant species. Besides the main taxa, the community below the thermocline was characterized by a high number of different tintinnid species, whereas the community above the thermocline was completely dominated by species belonging to the naked ciliates.

6.3.2 Anchor station

At the anchor station, the thermocline varied in depth between 12 and 20 m as a result of low and high tides (figure 6-9). However, the depth of the fluctuating thermocline had no influence on the microzooplankton vertical distribution, since we analyzed micro-zooplankton community above the thermocline, in the upper 10 m depths (figure 6-9). No large differences in composition of all three main groups (naked ciliates, tintinnids and mixo- and heterotrophic dinoflagellates) were observed during the short time period (144 h). The surface layer (5 m depth) was more patchy with higher fluctuations in total abundances over the time period. The deeper layer (10 m depth) was characterized by more stable conditions with less difference in abundances and composition of microzooplankton groups between the samplings.

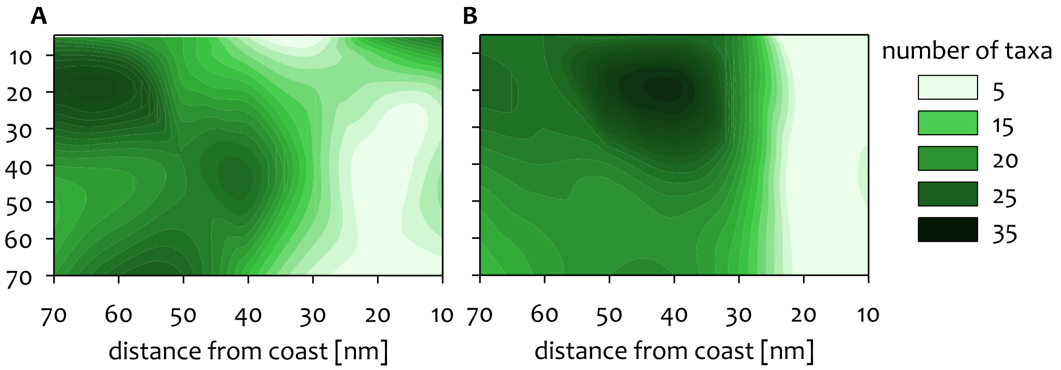


Figure 6-6: Species richness along the first (A) and second leg (B).

The naked ciliates community was more abundant in the deeper layer (> 8.86 x 10^3 cells L^{-1}) and was mainly composed of *Strombidium* spp. Another two species, *L. strobila* and *Spirostrombidium* sp. were detected during the whole sampling period. Abundance of *L. strobila* decreased with time, whereas *Spirostrombidium* sp. became more abundant. The community of tintinnids was temporally patchier. The abundances fluctuated between 0.01 x 10^3 cells L^{-1} (48 h) and 0.22 x 10^3 cells L^{-1} (144 h) in the surface layer. The community detected in the deeper layer was more stable with low abundance of to 0.04 x 10^3 cells L^{-1}. The main contributors to this group were *Favella ehrenbergii* and *Tintinnopsis gracilis*. The community of mixo- and heterotrophic dinoflagellates was also relatively uneven over time. The maximal abundances were observed at 48, 72 and 96 h with > 1.54 x 10^3 cells L^{-1}. This group was dominated by *Katodinium* sp., however, less abundant dinoflagellate *Gyrodinium* sp. was detected during the whole time period.

6.4 Discussion

Detailed analyses of the microzooplankton community and short-time changes are presented for the first time in the Benguela Upwelling System. The intensity of the upwelling has an effect on the phytoplankton composition and thereby influences also the microzooplankton community.

In fresh upwelled water with high nutrient concentrations, mainly small phytoplankton cells (small diatoms and small flagellates) can be detected (Hansen et al. 2014; Pitcher et al. 1998; Walker & Peterson 1991). Larger diatoms are well adapted to conditions with a reduced nutrient content and are generally found in the matured upwelled water. Further offshore, the water masses contain very low nutrient concentrations, which is an optimal environment for small dinoflagellates

(Hansen et al. 2014; Hart & Currie 1960). These variations in phytoplankton influenced the composition and diversity of the microzooplankton community. Supporting our hypothesis that the highest diversity of microzooplankton can be found further offshore in matured upwelled water, we detected low microzooplankton diversity near the shore. This feature rapidly changed beyond the 30 nm line on the Walvis Bay transect during both legs. However, the species diversity was very patchy behind 30 nm, which probably arises from the high variability in composition of different microzooplankton groups (appendix 6-2). Additionally, the number of species increased with decreasing chl *a* values. With increasing distance from the coast, the food web became more complex, whereas in fresh upwelled water a relatively simple food web existed. The high concentration of small phytoplankton cells occurring in fresh upwelled water is good food source for small ciliates.

As stated in our second hypothesis, the ratio between naked ciliates vs. mixo- and heterotrophic dinoflagellates rapidly changes during the first leg with increasing distance from the shore. During the second leg, however, the ratio between naked ciliate vs. mixo- and heterotrrophic dinoflagellates was highest near the coast at 10 nm. Nevertheless, the ratio between naked ciliates vs. mixo- and heterotrophic dinoflagellates followed the chl *a* concentrations, which was probably caused by high concentrations of small phytoplankton cells. These findings are in contrast to other studies describing occurrence of high concentrations of mixo- and heterotrophic dinoflagellates under conditions of high chl *a* concentrations (Sherr & Sherr 2007). However, we assumed that the low concentration of mixo- and heterotrophic dinoflagellates during our study are a result of their ability to survive in low food concentrations either feeding on alternative prey, or reducing their metabolic rate. Additionally, mixotrophic dinoflagellates are able to switch from heterotrophic to autotrophic nutrition under low prey concentrations (Sherr & Sherr 2007). Therefore, we detected high concentrations of these protists at low chl *a* concentrations suspecting higher concentrations of larger diatom cells. Mixo- and heterotrophic dinoflagellates are able to ingest prey ranging in size from ca. 1 µm (Jeong et al. 2005; Strom 1991; Strom & Strom 1996) to several times of their body size (Sherr & Sherr 2007; Strom & Strom 1996), and even graze over dense diatom blooms (top-down control; Jeong et al. 2005).

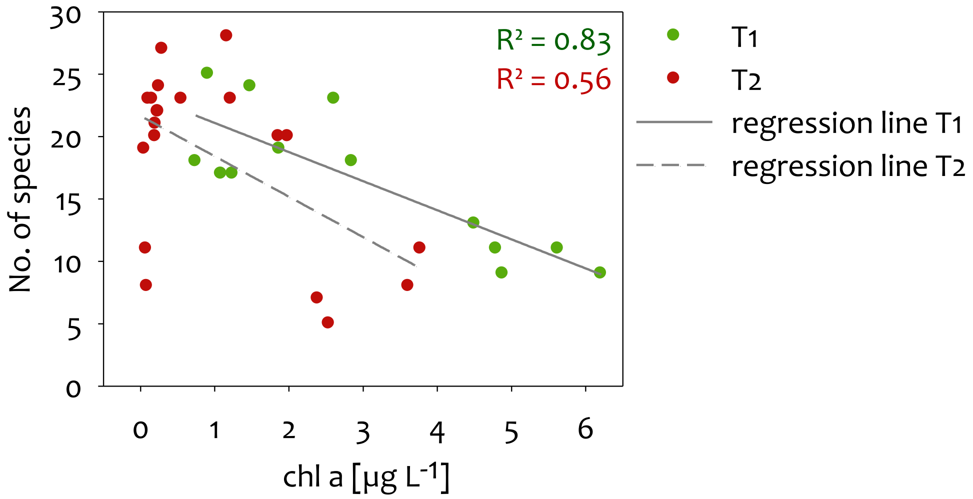


Figure 6-7: Number of species in relation to the chl *a* values during the first (T1) and second leg (T2).

We assumed differences between two microzooplankton communities occupying the warm and more saline upper surface layer above the thermocline and the deeper surface layer with lower temperatures below the thermocline. Nutrients are transported into the euphotic zone with the upwelled water and become part of the mixed layer. This upwelled water that reaches the surface over the shelf has its primary source in the central water masses from ca. 180 m depth (Shannon & Nelson 1996). Due to a high nutrient availability in the surface layer, a phytoplankton bloom may develop (Barlow et al. 2009; Pitcher et al. 1991). Consequently, the deeper layer is more influenced by the fresh upwelled water, whereas the surface layer above the thermocline alters by the biological dynamics as described above. These circumstances probably led to significant differences between the microzooplankton community above and below the thermocline. Interestingly, the MDS plot showed clear differentiation of two stations located at 10 and 20 nm from the coast in 70 m depth. These stations were located in deep colder water (<12°C), which spreads upward the surface layer.

Table 6-3: Differences between communities of the different depths. Results of ANOSIM (global test: R-value = 0.319, P = 0.1%); n.s. = no significant differences.

groups	R Statistic	significance level
5 m x 10 m	-0.049	n.s.
5 m x 40 m	0.513	0.1
5 m x 70 m	0.589	0.1
10 m x 40 m	0.403	0.1
10 m x 70 m	0.451	0.1
40 m x 70 m	0.003	n.s.

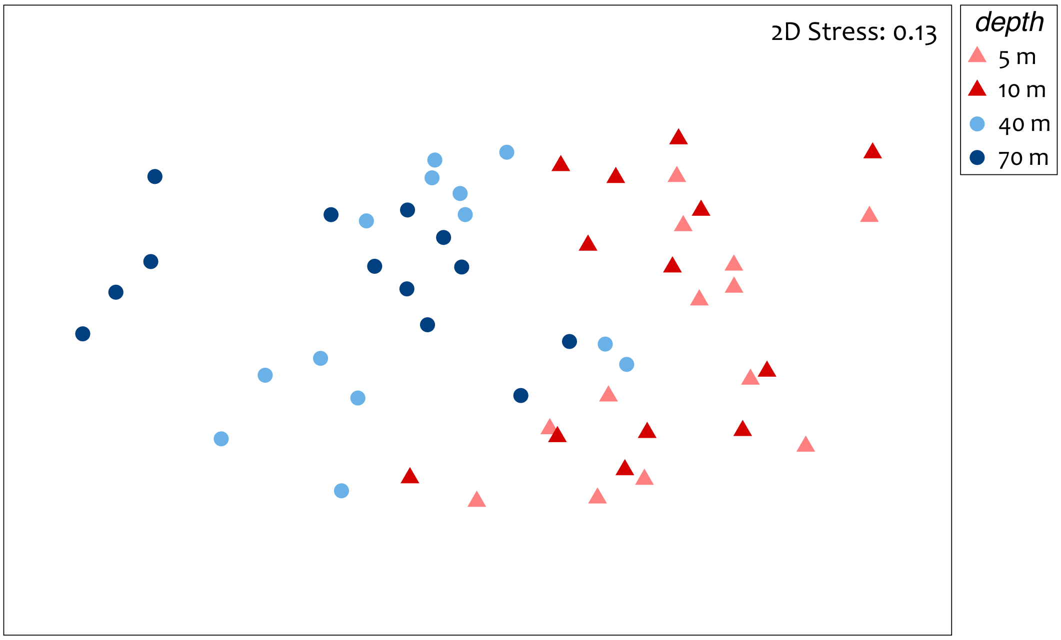


Figure 6-8: MDS plot of the microzooplankton in the different depths. Red = above the thermocline, blue = below the thermocline.

Overall, the distribution of different microzooplankton taxa, especially of tintinnid taxa, was very patchy (appendix 6-2). Generally, the spatial distribution of microzooplankton species is very variable and is affected not only by biological factors, but also primarily by biological-physical interactions, especially by flow patterns in the ocean (Mann & Lazier 2005). Since Abraham (1998) presented the importance of stirring and mixing in the ocean on plankton patchiness and blooms, this topic became an important part of the current research. We assume that the distribution of microzooplankton is primarily influenced by relationship between phytoplankton size distribution and feeding ability of diverse microzooplankton groups, e.g. ciliates are able to consume only prey smaller as themselves whereas mixo- and heterotrophic dinoflagellates are able to feed over phytoplankton cells in different size classes. Also, the predation pressure by copepods on microzooplankton may play an important role in high productive areas such us upwelling systems. High abundances of copepods may impact not only the biomass of microzooplankton but also benefit some species of microzooplankton, especially ciliates, with behavioural responses to avoid predation (Calbet & Saiz 2005).

In conclusion, our analyses show small-scale variations of the microzooplankton community over a short-time period in the Benguela Upwelling System. The distribution of microzooplankton is relatively patchy due to complex biological-physical interactions. The diversity of microzooplankton is generally high further offshore caused by more complex food-web relations. However, the concentration of mixo- and heterotrophic dinoflagellates increases with increasing chl *a* values as an evidence of high predator pressure of mixo- and heterotrophic dinoflagellates on large blooming diatoms. We also found significant differences between the community occupying the surface layer and the community occupying the deeper layer below the thermocline. These differences are caused by stratification between the (1) deeper fresh upwelled water with high nutrient concentrations streaming upward and (2) surface water warmed up by solar radiation with high primary production as a result of incoming nutrients.

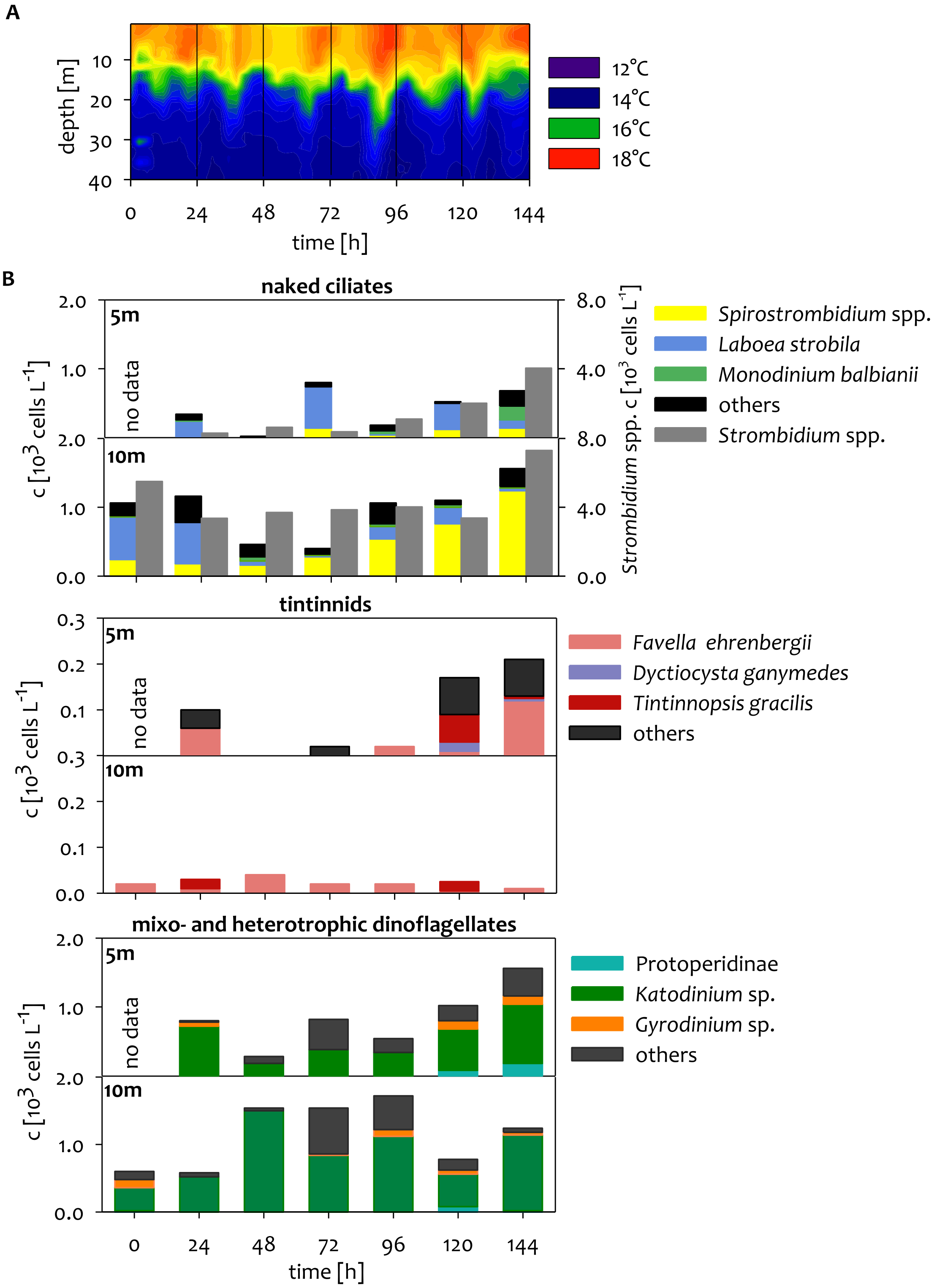


Figure 6-9: Temperature profile (A) and abundances and composition of the main microzooplankton groups during the anchor station (B).

6.5 References

Abraham ER (1998) The generation of plankton patchiness by turbulent stirring. Nature 391:577-580

Barlow R, Lamont T, Mitchell-Innes B, Lucas M, Thomalla S (2009) Primary production in the Benguela ecosystem, 1999-2002. African Journal of Marine Science 31:97-101

Batten SD, Fileman ES, Halvorsen E (2001) The contribution of microzooplankton to the diet of mesozooplankton in an upwelling filament off the northwest coast of Spain. Progress In Oceanography 51:385-398

Blamey LK, Howard JAE, Agenbag J, Jarre A (2012) Regime-shifts in the southern Benguela shelf and inshore region. Progress in Oceanography 106:80-95

Bohata K, Koppelmann R (2013) Chaetognatha of the Namibian Upwelling Region: Taxonomy, Distribution and Trophic Position. PLoS ONE 8:e53839

Burkill PH, Mantoura RFC, Llewellyn CA, Owens NJP (1987) Microzooplankton grazing and selectivity of phytoplankton in coastal waters. Marine Biology 93:581-590

Calbet A (2001) Mesozooplankton Grazing Effect on Primary Production: A Global Comparative Analysis in Marine Ecosystems. Limnology and Oceanography 46:1824-1830.

Calbet A, Saiz (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Campbell RG, Sherr EB, Ashjian CJ, Ploudre S, Sherr BF, Hill V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 56:1274-128

Clarke RK, Gorley RN (2006) Primer V6: User Manual - Tutorial, Vol. Plymouth Marine Laboratory, Plymouth

Dolan JR, Claustre H, Carlotti F, Plounevez S, Moutin T (2002) Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean. Deep Sea Research Part I: Oceanographic Research Papers 49:1217-1232

Figueiredo GM, Nash RDM, Montagnes DJS (2007) Do protozoa contribute to the diet of larval fish in the Irish sea? Journal of the Marine Biological Association of the United Kingdom 87:843-850

Franks PJS (2005) Plankton patchiness, turbulent transport and spatial spectra. Marine Ecology Progress Series 294:295-309

Hansen A, Ohde T, Wasmund N (2014) Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. Journal of Marine Systems 140, Part B:130-137

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress In Oceanography 83:15-32

Jeong HJ, Kim JS, Kim JH, Kim ST, Seong KA, Kim TH, Song JY, Kim SK (2005) Feeding and grazing impact of the newly described heterotrophic dinoflagellate *Stoeckeria algicida* on the harmful alga *Heterosigma akashiwo*. Marine Ecology Progress Series 295:69-78

Koppelmann R, Jung SA, Lahajnar N (2014) Abundance and trophic position of gelatinous zooplankton in the Namibian Upwelling Region. In: Kehayias G (ed) Zooplankton: species diversity, distribution and seasonal dynamics. Nova Science Publishers, New York

Koppelmann R, Kullmann B, Lahajnar N, Martin B, Mohrholz V (2013) Onshore-offshore distribution of Thecostomata (Pteropoda) in the Benguela Current Upwelling Region off Namibia: species diversity and trophic position. Journal of the Marine Biological Association of the United Kingdom

Levinsen H, Nielsen TG (2002) The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison. Limnology and Oceanography 47:427-439

Mann KH, Lazier JRN (2005) Biology and Boundary Layers. In: Dynamics of Marine Ecosystems. Blackwell Publishing Ltd., p 512

McManus G, Costas B, Dam H, Lopes R, Gaeta S, Susini S, Rosetta C (2007) Microzooplankton grazing of phytoplankton in a tropical upwelling region. Hydrobiologia 575:69-81

Miloslavić M, Lučić D, Njire J, Gangai B, Onofri I, Garić R, Žarić M, Miri Osmani F, Pestorić B, Nikleka E, Shumka S (2012) Zooplankton composition and distribution across coastal and offshore waters off Albania (Southern Adriatic) in late spring. Acta Adriatica 52:165-180

Montagnes DJS, Dower JF, Figueiredo GM (2010) The Protozooplankton–Ichthyoplankton Trophic Link: An Overlooked Aspect of Aquatic Food Webs1. Journal of Eukaryotic Microbiology 57:223-228

Nelson G, Hutchings L (1983) The Benguela Upwelling Area. Progress in Oceanography 12:333-35

Neuer S, Cowles TJ (1995) Comparative cell-specific grazing rates in field populations of ciliates and dinoflagellates. Marine Ecology Progress Series 125:259-267

Painting SJ, Moloney CL, Probyn TA, Tibbles B (1992) Microheterotrophic pathways in the southern Benguela upwelling system. South African Journal of Marine Science 12:527-543

Parrish RH, Bakun A, Husby DM, Nelson CS (1983) Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction., FAO Fisheries Report

Pepin P, Penney R (2000) Feeding by larval fish community: impact on zooplankton. marine Ecology Progress Series 204:199-212

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Marine Ecology Progress Series 172:253-264

Pitcher GC, Walker DR, Mitchell-Innes BA, Moloney CL (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton dynamics. Progress In Oceanography 28:39-64

Shannon LV (1985) The Benguela Ecosystem, I., Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology 23:105-182

Shannon LV, Nelson G (1996) The Benguela: Large Scale Features and Processes and System Variability. In: The South Atlantic. Springer Berlin Heidelberg, p 163-210

Shannon LV, O'Toole M (2003) Sustainability of the Benguela: ex Africa semper aliquid novi. In: Hempel G, Sherman K (eds) Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research. Elsevier, p 423

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Marine Ecology Progress Series 352:187-197

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the opwen Subarctic Pacific Ocean. Marine Ecology Progress Series 78:103-113

Strom SL, Brainard MA, Holmes JL, Olson MB (2001) Phytoplankton blooms are strongly impacted by microzooplankton grazing in coastal North Pacific waters. Marine Biology 138:355-368

Strom SL, Strom MW (1996) Microplankton growth, grazing, and community structure in the northern Gulf of Mexico. Marine Ecology Progress Series 130:229-240

Summerhayes CP, Kroon D, Rosell-Melé A, Jordan RW, Schrader HJ, Hearn R, Villanueva J, Grimalt JO, Eglinton G (1995) Variability in the Benguela Current upwelling system over the past 70,000 years. Progress in Oceanography 35:207-251

Vargas CA, Martínez RA, Cuevas LA, Pavez MA, Cartes C, González HE, Escribano R, Daneri G (2007) The Relative Importance of Microbial and Classical Food Webs in a Highly Productive Coastal Upwelling Area. Limnology and Oceanography 52:1495-1510

Verheye HM, Richardson AJ (1998) Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951-1996): bottom-up or top-down control? ICES Journal of Marine Science: Journal du Conseil 55:803-807

Walker DR, Peterson WT (1991) Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. South African Journal of Marine Science 11:289-305

Welschmeyer NA (1994) Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnology and Oceanography 39:1985-1992

Ye L, Chang C-Y, García-Comas C, Gong G-C, Hsieh C-h (2013) Increasing zooplankton size diversity enhances the strength of top-down control on phytoplankton through diet niche partitioning. Journal of Animal Ecology 82:1052-1061

6.6 Appendix

Appendix 6-1: Results of the SIMPER analysis for the group above the thermocline (A; average similarity: 50.69%) and below the thermocline (B; average similarity: 49.46). Av.Abund.= average abundance, Av.Sim. = average similarity, SD = standard deviation, Contr. = contribution of the species to the group, Cum. = cumulative contribution.

A

Species	Av.Abund.	Av.Sim.	Sim./SD	Contrib [%]	Cum.[%]
Strombidium spp.	2.19	18.86	2.39	37.21	37.21
Katodinium *sp.*	0.98	8.63	2.04	17.02	54.24
Gyrodinium sp.	0.78	4.55	1.48	8.97	63.21
Monodinium balbianii	0.34	2.21	1.05	4.36	67.57
Protoperidinium sp. (<50µm)	0.49	1.95	0.65	3.84	71.41
Spirostrombidium sp.	0.30	1.66	1.07	3.27	74.69
Laboea strobila	0.28	1.56	1.15	3.08	77.76
Strombidium crassulum	0.32	1.51	0.82	2.97	80.73
Myrionecta rubra	0.21	1.20	1.00	2.37	83.11
Cyrtostrombidium sp.	0.22	0.89	0.73	1.75	84.86
Tiarina fusus	0.20	0.72	0.64	1.42	86.28
S. conicum	0.29	0.71	0.56	1.40	87.69
other Ciliophora	0.19	0.69	0.64	1.36	89.04
Stenosemella sp.	0.18	0.61	0.65	1.20	90.25

B

Species	Av.Abund.	Av.Sim.	Sim./SD	Contrib[%]	Cum.[%]
Strombidium spp.	0.73	12.53	3.53	25.33	25.33
Katodinium *sp.*	0.53	11.04	2.71	22.33	47.66
Gyrodinium *sp.*	0.34	5.41	2.19	10.93	58.59
Monodinium balbianii	0.21	2.54	1.16	5.13	63.71
Favella ehrenbergii	0.12	1.93	0.94	3.91	67.63
Stenosemella sp.	0.15	1.74	0.82	3.51	71.14
other Ciliophora	0.12	1.69	1.07	3.42	74.56
Protoperidinium sp. (<50µm)	0.13	1.48	0.83	2.99	77.55
Dadayiella ganymedes	0.10	1.31	0.71	2.64	80.19
Salpingela acuminata	*0.09*	*1.15*	*0.76*	2.32	*82.51*
Strombidium crassulum	0.09	0.90	0.67	1.83	84.34
Protoperidinium sp. (<20µm)	0.09	0.88	0.49	1.77	86.11
Myrionecta rubra	0.09	0.84	0.60	1.69	87.80
Spirostrombidium sp.	0.11	0.62	0.36	1.26	89.06
Tiarina fusus	0.09	0.56	0.50	1.14	90.20

Appendix 6-2: Distribution and concentration [10^3 cells L^{-1}] of taxa along the first (A) and second leg (B). Blue = naked ciliates, red = tintinnids, green = mixo- and heterotrophic dinoflagellates. Taxa with total abundance below 5.00 cells x 10^3 cells L^{-1} are not shown.

A

Distance [nm]	10	10	10	20	20	20	30	30	30	30	40	40	40	40	50	50	50	50	60	60	60	70	70	70	70
Depth [m]	surf.	10	40	surf.	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	70	surf.	10	40	70
Strombidium spp.	4.9	3.6	0.4	3.7	0.4	0.1	5.5	7.4	0.3	0.9	7.2	6.7	4.2	1.8	14.4	13.1	4.0	3.5	15.7	17.5	0.4	1.3	2.7	0.4	0.5
Strombidium crassulum				0.9	0.2		0.8	0.1	0.3		0.1	0.2	0.2	0.2	0.3	0.2	0.1	0.9	0.7	0.6	0.1	1.4	0.3		0.1
Strombidium conicum				0.2					0.3		0.1	0.4	0.5	0.1	7.8	1.6	0.4	0.1	0.1	0.3	0.3				0.1
Spirostrombidium sp.				0.2	0.1	0.6	0.4	0.6	0.2		0.4	0.4				0.4				0.1	0.1	0.1	0.4		0.1
Cyrtostrombidium sp.	0.6	0.2		0.4		0.1				0.1					0.4				0.5	0.3	0.1	0.2	0.3		0.1
Laboea strobila	0.1	0.4		0.2				0.2			0.2	0.2	0.4		1.0	0.3	0.2		0.1	0.1		0.5	0.1		
Uronema marinum	0.1		0.4	0.6			0.4																		
Monodinium balbianii	0.1	0.1	0.2	0.3	0.3		0.6	0.3	0.9		0.3	0.2	0.1	0.6	0.5	0.4	0.4	0.3	0.2	0.5	0.8	0.2	0.2	0.1	0.1
Myrionecta rubra	0.4	0.2	0.2	0.1	0.4		0.8	0.2			0.2		0.1	0.7	0.2	0.2	0.4	0.9	0.1	0.2		0.2	0.4	0.2	0.3
Tiarina fusus	0.2			0.2				0.4	0.3			0.2	0.4	0.2	0.9	0.4	0.4	0.1		0.2	0.1	0.8			0.8
Eutintinus sp.									0.2								0.1	0.1	0.4	0.4	0.3	0.8			
Favella ehrenbergii				0.2		0.2				0.4			0.1	0.1				0.4			0.1	0.4	0.4	0.2	0.1
Helicostomella subulata	1.6	3.5	0.4		0.2	0.3				0.1			0.1	0.2	0.4										
Salpingela acuminata			0.2										0.1	0.2				0.3						0.4	0.1
Stenosemella sp.	0.4	0.5	0.4			0.1	0.2		0.2			0.2	0.1	0.1	0.8	0.8	0.2	0.3	0.3	0.2	0.3		0.4		
Acanthostomella conicoides													0.3						0.4	0.2		0.2	0.4	0.4	0.1
Dadayiella ganymedes						0.1			0.1	0.1		0.4	0.7		0.2	0.2	0.3	0.1	0.8	0.6	0.2	0.4	0.4		
Tintinnopsis gracilis	18.7	12.6	0.6	0.8			0.4	0.2			0.2		0.7	0.1		0.2		0.1							
Rhabdonella amor																	0.2	0.2	0.4	0.2	0.1	0.2	0.1	0.6	0.2
Eutinntinus sp.	0.8	0.4								0.2				0.1			0.2	0.3		0.4					

Distance [nm]	10	10	10	20	20	20	30	30	30	30	40	40	40	40	50	50	50	50	60	60	60	70	70	70	70
Depth [m]	surf.	10	40	surf.	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	70	surf.	10	40	70
Ceratium spp.	0.1	0.1												0.1		0.2	0.2	0.4	0.8	0.8	0.3		0.6	0.3	0.2
Protoperidinae	2.0	2.5	0.6	0.2	0.2			0.6	0.2	0.4	0.2	0.2	0.1	0.5	0.4	0.3	0.1	0.1	0.4	0.4	0.6	1.6	2.2	0.6	0.6
Katodinium sp.	0.6	0.2	0.4	0.5	0.8	0.4	0.4	1.2	0.6	0.2	2.3	1.6	0.9	0.6	2.1	2.5	0.6	0.7	1.8	4.0	0.5	0.7	0.6	0.4	0.7
Gyrodinium sp.	0.3	0.4	0.1	0.1	0.2	0.1			0.4		0.6	0.1	0.2	0.2	1.2	0.6	0.6	0.3	0.6	0.7	0.3	0.8	1.2	0.4	0.5
Oxytoxum scolopax										0.1					0.4		0.4	0.1			0.6		0.5	0.2	
Prorocentrum gracile	0.6	0.4							0.1				0.1										0.6		0.1
Dinophysis sp.	0.2	0.1	0.2									0.4	0.1		0.4	0.8	0.4		0.8	0.8		0.6	0.8		
Nauplius larvae	0.4	0.3	0.2	0.6			0.6	0.8			0.4	0.4	0.4		0.8	0.6	0.4	0.1			0.1		0.6	0.1	
Copepoda	0.6	0.8			0.2			0.2				0.4	0.1												

B

Distance [nm]	10	10	10	10	20	20	20	20	30	30	30	30	40	40	40	40	50	50	50	50	60	60	60	70	70	70	70
Depth [m]	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	10	40	70	surf.	10	40	70
Strombidium spp.	4.6	4.9	0.8	0.8	2.2	1.0	0.1	0.1	3.7	1.9	0.2	0.4	4.8	2.6	0.4	0.2	11.2	6.6	0.6	0.4	2.0	0.5	0.3	4.2	1.1	0.5	0.2
Strombidium crassulum	0.2		0.1				0.1		0.1		0.2		0.2	0.5	0.1	0.1		0.5	0.1	0.1	0.1	0.1		0.2	0.1		
Strombidium conicum	0.2	0.1	0.1						0.3	0.2			0.4	0.2		0.2		0.1		0.2	0.2	0.2					
Spirostrombidium sp.	0.6					0.2			0.7	0.2		0.2	1.0	1.5	0.6		0.2	0.3	0.2	0.7	0.4	0.2	0.1	0.2	0.5		
Cyrtostrombidium sp.						0.1				0.2			0.2	0.7		0.1	0.2	0.6	0.5	0.7	0.6	0.1	0.1	0.1	0.2		
Laboea strobila	0.8					0.1			0.2	0.2				0.1	0.3	0.8	0.3	0.2	0.3	0.9	0.2		0.2	0.4	0.6	0.1	
Uronema marinum								0.1		0.2	0.1	0.1		0.4	0.4		0.6	0.1	0.2		0.2	0.3			0.1	0.1	
Monodinium balbianii	0.2	0.7	0.1		0.4		0.1		0.2	0.4	0.5	0.4	0.2	0.5	0.2	0.4	0.2		0.2	0.2	0.1		0.3	0.2		0.1	0.2
Myrionecta rubra		0.3	0.2						0.2		0.1	0.1	0.2		0.1		0.2	0.1	0.1		0.2	0.3	0.2	0.4	0.1		
Tiarina fusus										0.8	0.1		0.6	0.1	0.4	0.1	0.5	0.3			0.8	0.3	0.2		0.3	0.3	
Eutintinus sp.									0.2	0.3	0.1		0.2	0.6	0.6	0.1	0.2	0.9	0.2	0.1	0.5	0.8	0.1	0.6	0.1	0.6	0.3
Favella ehrenbergii	0.1	0.4	0.1	0.2				0.1	0.4	0.3	0.6	0.2	0.4	0.5	0.6		0.6	0.4	0.6	0.7	0.4	0.1	0.1	0.1	0.2	0.1	0.1
Helicostomella subulata									0.8	0.2	0.3	0.3	0.2		0.2												
Salpingela acuminata				0.1				0.1			0.2	0.2			0.8	0.1		0.1	0.1	0.3		0.2	0.2	0.4		0.3	
Stenosemella sp.								0.2	0.1	0.8	0.1	0.1	0.2	0.3	0.1	0.5	0.6	0.1	0.2	0.9		0.3	0.3				0.2
Acanthostomella conicoides											0.7		0.4		0.4		0.6	0.1			0.1	0.2	0.2	0.3	0.7	0.3	0.1
Dadayiella ganymedes	0.2	0.2		0.1				0.4	0.7	1.6	0.1	0.6	0.2	0.3	0.4	0.4	0.2	0.1		0.2						0.1	0.3
Tintinnopsis gracilis												0.1		0.1		0.2											
Rhabdonella amor											0.1			0.2	0.4		0.4	0.1	0.1	0.1	0.5	0.7	0.1	0.6	0.3	0.6	0.4
Xystonella treforti																										0.2	
Eutinntinus sp.																						0.3	0.2			0.1	0.3

Distance [nm]	10	10	10	10	20	20	20	20	30	30	30	30	40	40	40	40	50	50	50	50	60	60	60	70	70	70	70
Depth [m]	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	surf.	10	40	70	10	40	70	surf.	10	40	70
Ceratium spp.									0.2				0.6	0.7	0.2	0.1	0.6	0.9	0.1	0.1	0.3	0.1		0.2	0.6	0.2	0.1
Protoperidinae	0.2		0.1		0.2		0.3	0.2	0.8	0.5	0.1	0.3	1.9	0.7	0.1	0.3	0.5	0.8	0.1	0.4	0.3	0.1	0.9	1.2	0.4	0.6	0.2
Katodinium sp.	0.2	1.1	0.5	0.9	0.9	1.0	0.3	0.8	2.6	0.5	0.2	0.3	1.2	0.2	0.1	0.5	2.2	0.8	0.1	0.2	0.4	0.2	0.2	1.8	0.2	0.3	0.3
Gyrodinium sp.	0.1	0.2	0.2	0.2	0.2	0.1	0.3	0.1	1.2	1.6	0.1	0.1	5.9	3.0	0.8	0.6	4.0	2.2	0.3	0.2	0.9	0.2	0.1	0.8	0.3	0.2	0.6
Oxytoxum scolopax										0.1				0.1	0.2	0.1	0.1	0.9	0.2		0.1			0.5	0.2	0.5	
Prorocentrum gracile			0.1				0.2								0.1			0.3	0.2	0.1	0.1	0.1		0.8	0.2	0.2	0.1
Dinophysis sp.										0.4							0.2	0.3			0.2		0.1		0.2		
Nauplius larvae		0.3	0.2					0.1	0.2	0.4		0.2	0.4	0.7	0.4		0.6	0.1	0.1	0.1	0.5		0.2	0.6	0.3		0.2
Copepoda								0.1			0.1				0.1				0.2			0.1				0.1	

Chapter 7

Benthic structures in the Namibian Upwelling Region and the pelago-benthic coupling

Mertzen Mathias[a], Koppelmann Rolf[a], Bohata Karolina[a], Martin Bettina[a], Werner Johanna[a], Neumann Andreas[b], Müller Anja[c], Eckhardt Andre[a], Möllmann Christian[a]

[a] University of Hamburg, Center for Earth System Research and Sustainability,
Institute for Hydrobiology and Fisheries Science,
Große Elbstraße 133, 22767 Hamburg, Germany.

[b] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung,
Hafenstraße 43, 25992 List/Sylt, Germany.

[c] Carl von Ossietzky Universität Oldenburg,
Carl-von-Ossietzky-Straße 9-11, 26129 Oldenburg

Abstract

Benthic megafauna was observed with an remotely operated vehicle in the northern Benguela Upwelling System at three locations on the shelf off Namibia ca 60 and 90 nm in latitudinal direction apart from each other at depths between 100 and 210 m. One station off Terrace Bay, two stations off Rocky Point and one station off the Kunene River mouth were analysed. Additionally two stations on the slope off Kunene in 500 m and 800 m depth were investigated. The analysis revealed a high heterogeneity of the benthic megafauna between the stations. Bacterial mats were detected off Rocky Point in 110 and 210 m depth under low oxygen conditions together with bearded gobies (*Sufflogobius bibarbatus*). The highest concentration of particles was observed on the shelf off Kunene in 150 m depth. The megafauna composition showed a depth-dependent succession in composition down the slope. Visual particle abundance was decreasing with depth, but highest megafauna concentrations were detected in 500 m depth. Exemplarily performed analyses of benthic macrofauna, however at different depths, showed a similar heterogeneity between the locations. Bottom concentrations of biogeochemical proxies like C_{org}-content correlate with the abundance of benthic macro- and megafauna. Structuring processes in the water column like primary production as exemplified by satellite images of chlorophyll indicated higher values at the northern stations than at the southern stations contradicting the abundance of the benthic fauna. The abundance of micro- and mesozooplankton was very variable and allowed no correlation. The composition of these faunal elements, however, showed a bloom of tunicates off Rocky Point. These animals are highly-effective filter feeders and modify the sinking flux. Sinking of dead and moribund bodies and large fecal pellets stochastically provide enhanced fluxes which may have an effect on the benthic community on a longer time-scale. The intrusion of oxygen-depleted water from the north and oxygen consumptions by decomposing organic material are causing extenxed oxygen minimum zones which affect the benthic community. Another factor forming the benthic community is the shape of the shelf and slope which is smaller and steeper off Kunene than at the other stations as well as inputs of organic material from the Kunene River.

7.1. Introduction

The Benguela Current (BC) flows along the southwestern coast of Africa and forms the eastern part of the South Atlantic subtropical gyre (Peterson & Stramma 1991). The Benguela Upwelling System (BUS), located between 15-37° S and 0-20° E (Shannon & O'Toole 2003), is one of the four large eastern oceanic upwelling systems which are very productive regions of the ocean. The northern boundary is at the Angola-Benguela Frontal Zone (ABFZ) which is formed by the northern BUS and the southern part of the Angola Current. From the Angola Dome, the South Atlantic Central Water (SACW) streams southwards along the shelf and is characterized by higher nutrient concentration as well as higher temperature and salinity than the water masses from the south (Poole & Tomczak, 1999; Mohrholz et al. 2001). The southern boundary is formed by the Agulhas Current at the Cape of Good Hope. This current originates from the Indian Ocean and contributes nutrient-rich water into the BUS in form of rings (Shannon & O'Toole 2003). The main source of water to the BUS, however, is the South Atlantic Current which transports cold, oxygenated water from the south-west into the system, called Eastern South Atlantic Central Water (ESACW; Mohrholz et al. 2001). This water body is transported from the Cape of Good Hope through the BUS along the South African coast towards the equator (Shannon & O'Toole 2003). Further north (27° S), the BC splits into two branches. The larger stream becomes part of the South Equatorial Current and the smaller stream, located near the coast, builds together with the northern Angola Current the ABFZ (Stramma & England 1999; Meeuwis & Lutjeharms 1990). When the two water masses from the north and south collide, the SACW flows below the ESACW, due to its higher density. The oxygen and nutrient concentration depends on the mixing ratio of SACW and ESACW (Mohrholz et al. 2008).

Upwelling along the Namibian coast has its maximum between August and October (southern winter) and its minimum between January and March (southern summer; Hart & Currie 1960). The main upwelling cell off Lüderitz (26.6° S) characterizes the boundary between the southern and the northern BUS (Lass et al. 2000; Shannon 1985). The upwelled water is rich in nutrients (10-30 mmol m^{-3} nitrate, 2-3 mmol m^{-3} phosphate, 20-50 mmol m^{-3} silicate; Wasmund et al. 2005) and low in oxygen (Chapman & Shannon 1985), resulting in high primary production along the Namibian coast with up to 1.2 g C m^{-2} d^{-1} (Brown et al. 1991), exceeding that of other eastern boundary current regions (Gruber & Sarmiento 1997; Carr 2002). However, the phytoplankton production is highly variable in the BUS due to spatial and temporal variations of meteorological, hydrographical, chemical and biological parameters.

In marine systems, generally 60-70 % of the primary production is consumed by microzooplankton and 10-40 % by mesozooplankton, in particular by copepods (Calbet 2001; Calbet & Landry 2004). Microzooplankton itself is an important diet in mesozooplankton feeding (Rollwagen-Bollens and Landry 2000; Calbet & Saiz 2005). This grazing mainly occurs in a thin surface layer of 50 m, but also influences the oceanic region below the euphotic zone, because the vertical and horizontal movement of the predating mesozooplankton contributes to the vertical particle flux, thereby influencing the input of organic material in deeper layers (Martin et al. 1987; Burd & Jackson, 2009; Vinogradov 1968). At greater depth, vertically migrating mesozooplankton excrete faecal pellets which is one way for organic material to enter the deeper ocean. Other ways of organic material entering the deeper layer are mixing, advection, diffusion and passive sinking. In particular, sedimentation of sinking particles like living and dead phytoplankton cells, dead animals, faeces and marine snow are the main links between the primary production at the eutrophic zone and the benthic community (see Koppelmann & Frost 2008). This particle flux can be reduced by heterotrophic consumption when particulate organic carbon (POC) is partly transformed into dissolved organic carbon (DOC) by metabolic activity (Koppelmann et al. 2000; Robinson et al. 2010). The concentrations of POC decrease in the depth interval from 100 to 1000 m by a factor of approximately 10 (Suess 1980).

One characteristic of the northern BUS are frequently occurring oxygen minimum zones (OMZ; Hamukuaya et al., 1998) due to the consumption of O_2 during the decomposition of settling organic matter (Chapman and Shannon, 1985) and biogeochemical processes like strong denitrification (Perry et al., 1993; Shannon and Weaver, 1949). The OMZ is located on the shelf and at the shelf break down to 300 m (Hart and Currie, 1960) and covers up to 50 % of the shelf (Brüchert et al., 2006). The extensions of the OMZs are limited by physical barriers such as fronts and seasonal changes in biotic and abiotic parameters (Monteiro and van der Plas, 2006). Furthermore, temporary hypoxic and anoxic events are caused by seasonal changes in the amount of oxygen-deficient SACW which is entering the BUS from the north (Poole and Tomczak, 1999; Mohrholz et al., 2001; Hutchings et al., 2009). Besides the lack of oxygen, the seafloor conditions in this habitat are influenced by other important processes as transformations of oxygen, nitrate and sulphate into carbon dioxide, dinitrogen, hydrogen sulphide and methane in the sediment-water interface (Emeis et al., 2004). These processes favour the development of chemolithoautotrophic and sulphide oxidizing bacterial mats on the seafloor (Schulz et al., 1999). Anaerobic bacterial mats reduce the sulphide and produce hydrogen sulphide gas (H_2S).

The distribution of benthic organisms is influenced by physical, chemical and biological processes (Siegel et al., 2008) like hydrographic conditions, the occurrence of toxic gas, the OMZ and the input of organic material via sedimentation, lateral advection and river discharge (Parsons et al., 1984; Ricklefs, 1987; Roughgarden, 2006). Preliminary investigations (Werner, 2012) indicated a heterogeneous distribution and structure in different regions and at different depths in the northern BUS. This raised the question which factors cause the high mesoscale heterogeneity in benthic structures. The following parameters and water column data will be analysed and interpreted to foster our understanding of processes forming the distribution and abundance of the benthic fauna:

1. physical water parameters
2. Chl *a* distribution
3. vertical and horizontal distribution and composition of micro- and mesozooplankton
4. chemical parameters like the concentration of oxygen, phosphate, nitrogen oxide, nitrite, ammonium, dissolved inorganic nitrogen (DIN), total organic carbon and total nitrogen in the sediment-water interface
5. benthic macrofauna of the top 5 cm of the sediment
6. distribution of the benthic megafauna and bacterial mats

7.2. Materials and Methods

7.2.1. Research area

Samples were taken on three transects (Terrace Bay, Rocky Point and Kunene) in the northern BUS from the shelf to the continental slope (figure 7-1; table 7-1) during the expedition 17/3 of the RV MARIA S. MERIAN in February 2011. Different gears were deployed (table 7-1) at five stations between 50 m and 400 m depth on the Terrace Bay transect (20° S) and six stations between 38 m and 2080 m depth on the Rocky Point transect (19° S). At the Kunene transect (17.5° S), nine stations at depths between 35 m and 3200 m were sampled. The latter area is characterized by a narrow shelf and a steeper slope compared to the other transects and the outflow of the Kunene River.

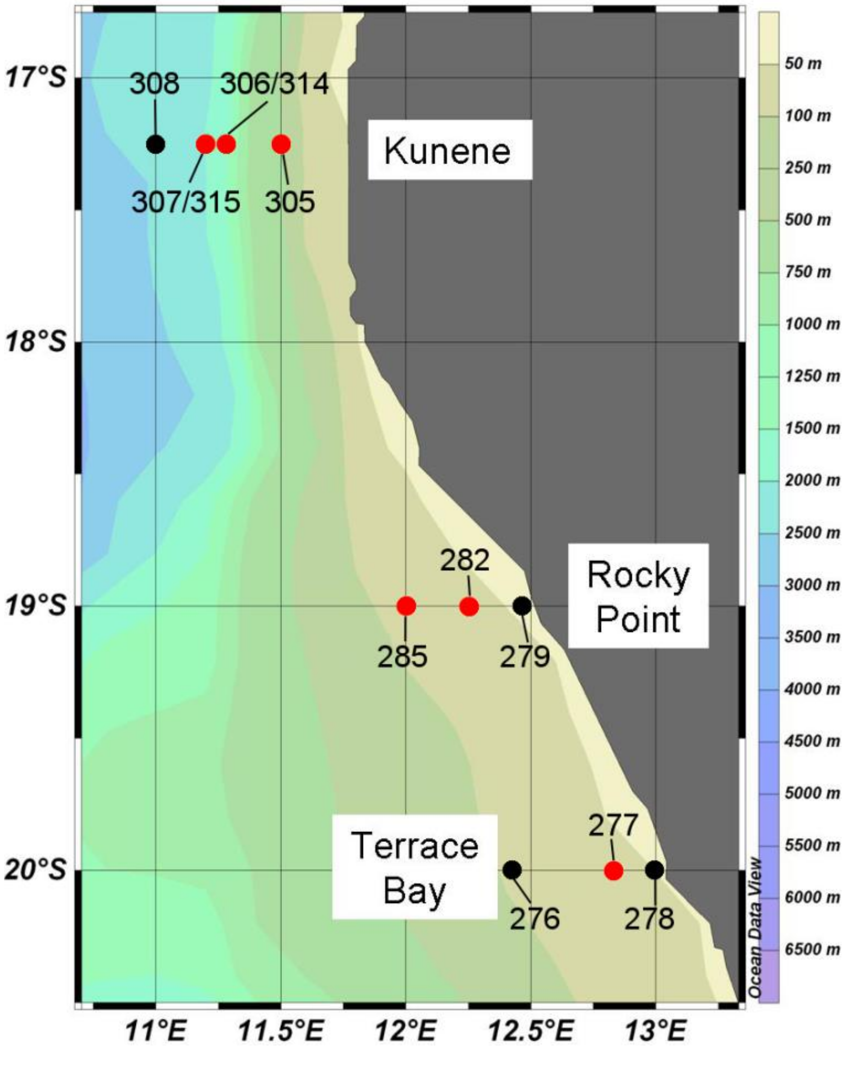


Figure 7-1: Research area with sampled stations (stations where the ROV was deployed are marked in red).

Table 7-1: Overview of samples taken at the stations.

Station	Station name	Date	Time period	longitude	latitude	Depth [m]	Samples
274	Terrace Bay, slope	12.02.2011	19:28 – 23:48	20° 01.50' S	11° 51.80' E	412	Hydro
275	Terrace Bay, shelf	13.02.2011	01:32 – 05:19	20° 0.00' S	12° 12.60' E	274	Hydro
276	Terrace Bay, shelf	13.02.2011	07:00 - 09:40	20° 0.00' S	12° 30.00' E	155	Hydro, Micro,
277	Terrace Bay, shelf	13.02.2011	11:43 - 14:49	20° 0.00' S	12° 50.00' E	104	Hydro, Biogeo, Mega
278	Terrace Bay shelf	13.02.2011	16:51 - 18:04	20° 0.00' S	13° 00.00' E	34	Hydro, Biogeo, Macro
279	Rocky Point, shelf	14.02.2011	00:11 - 01:12	18° 59.97' S	12° 27.00' E	38	Hydro, Biogeo, Macro
282	Rocky Point, shelf	14.02.2011	04:34 - 07:32	18° 59.97' S	12° 15.00' E	112	Hydro, Micro, Mega
285	Rocky Point, shelf	14./15.02.2011	12:53 – 10:46	18° 59.98' S	12° 00.06' E	210	Hydro, Micro, Meso, Mega
292	Rocky Point, slope	15.02.2011	21:13 – 04:10	19° 00.00' S	11° 28.06' E	418	Hydro
295	Rocky Point, slope	16.02.2011	09:27 – 22:08	18° 59.99' S	11° 02.96' E	488	Hydro
298	Rocky Point, offshore	17.02.2011	04:00 – 22:17	19° 00.00' S	10°30.00’ E	2045	Hydro
304	Kunene, shelf	17.02.2011	01:38 – 04:08	17° 15.00’S	11°43.00’ E	40	Hydro
305	Kunene, shelf	19.02.2011	05:44 – 13:17	17° 15.00' S	11° 30.00' E	150	Hydro, Micro, Meso, Biogeo, Macro, Mega
306	Kunene, slope	19./20.02.2011	15:07 – 00:11	17° 15.01' S	11° 17.25' E	500	Hydro, Micro, Meso, Biogeo,
314	Kunene, slope	23.02.2011	07:24 – 12:24	17° 15.05' S	11° 17.34' E	500	Mega
307	Kunene, slope	20.02.2011	01:37 – 11:57	17° 15.00' S	11° 10.96' E	890	Hydro, Micro, Meso,
315	Kunene, slope	23.02.2011	13:34 – 18:38	17° 15.02' S	11° 11.34' E	775	Mega
308	Kunene, offshore	20.02.2011	14:53 - 21:46	17° 15.55' S	11° 0.00' E	2000	Hydro, Biogeo, Macro
309	Kunene, offshore	21.02.2011	00:02 – 14:01	17° 15.42' S	10° 47.10' E	3018	Hydro
310	Kunene, offshore	21.02.2011	16:12 – 18:05	17° 15.04' S	10° 29.00' E	3200	Hydro

Hydro: Hydrography, Micro: Microzooplankton, Meso: Mesozooplankton, Marco: benthic Macrofauna, Mega: benthic Megafaun, Biogeo: Biochemistry.

7.2.2. Field sampling, laboratory work and calculations

Hydrography

A pumping CTD system (SBE 911plus SEABIRD-ELECTRONICS, USA) was used to obtain vertical profiles of the following abiotic parameters: salinity, temperature, pressure, and oxygen concentration (Tab. 1). The data was monitored and stored with Seasave (Version 7) software.

Satellite Data

Near-surface chlorophyll *a* concentrations (Chl *a*; mg m^{-3}) were obtained by the Moderate Resolution Imaging Spectroradiometer (MODIS) level-3 product. The MODIS data are produced by Remote Sensing Systems sponsored by the NASA Earth Science MEaSUREs DISCOVER Project (data source: http://oceancolor.gsfc.nasa.gov/; Feldman and McClain, 2012).

The data was integrated for the months January and February. The spatial resolution was set to 4 km. To consider the influence of the temporarily changing concentrations and to close the time lack of Chl *a* data, this data was collected one month before the actual sampling period, to get information about the conditions that influence the development of the zooplankton.

Microzooplankton

Microzooplankton was sampled by vertical hauls with a multinet (HYDROBIOS, Kiel, Germany). The multinet was equipped with four nets with a mesh size of 55 µm, which can be opened and closed at defined water depths, allowing a fine vertical resolution of the water column. Sampling was obtained during heaving from the maximum sampling depth at a winch speed of 0.5 m s^{-1}. At shallow stations, the intervals were 200/150-100-50-25-0 m. At deeper stations, the additional intervals were 600-400-200-0 m depending on the total water depth (table 7-1). The samples were fixed in 4% formaldehyde-seawater solution buffered with sodium-tetraborate. In the home laboratory, the microzooplankton samples were transferred into a sorting fluid consisting of 0.5 % propylene phenoxetol, 5 % propylene glycol and 94.5 % tap water (Steedman, 1976). The samples were split using Hensen-pipettes. Main groups were identified and the abundance (ind. m^{-3}) and standing stock (ind. m^{-2}) was determined.

Mesozooplankton

Mesozooplankton samples were taken with a 1 m^2-Double Multiple Opening/Closing Net and Environmental Sensing Systems (MOCNESS; BESS, North Falmouth Mass, USA; Wiebe et al., 1985). The gear was equipped with 2*9 nets parallel to each other with a mesh size of 330 µm. The opening and closing system allowed sequential sampling similar to microzooplankton (table 7-1).

The filtered volume of each net was measured by a flow-meter. Veering and heaving speed of the winch was 0.5 m s^{-1} and was reduced to 0.2-0.3 m s^{-1} in the upper 200 m by maintaining a MOCNESS-frame angle of ~ 45° and an effective opening of 1 m^2. Changes in tilt were measured with an inclinometer and considered in the calculation of the filtered volume. The towing speed was 2 knots. After recovery of the gear, the samples were fixed in 4% formaldehyde-seawater solution buffered with sodium-tetraborate. The fixed samples were separated into five size categories (> 5 mm, 2 to 5 mm, 1 to 2 mm, 0.5 to 1 mm, < 0.5 mm) using a sieve chain. In this study, the results of all fractions were combined for further analyses.

For taxonomical analysis, the samples were transferred into Steedman solution, and the sample was divided according to density into smaller, more easily countable fractions using a Motodo plankton splitter (Motodo, 1959). The organisms were identified, if possible to family level, and the numbers of individuals were counted and standardized to concentration (ind. m^{-3}) and standing stock (ind. m^{-2}).

Biogeochemical analyses

Profiles of biogeochemical parameters such as inorganic nitrogen, phosphate and organic carbon were analyzed in the sediment as well as in the water above the sediment in muticorer cores at five stations on the three transects (table 7-1) using a multicorer (Oktopus, Kiel) equipped with eight acrylic glass polymethylmethacrylate (PMMA) tubes with an inner diameter of 0.1 m (0.0078 m^2) and a length of 0.6 m. Oxygen profiles in the sediment were measured via microprobes (PRESENS) and an automated micromanipulator (PYRO SCIENCE). To prevent instabilities and to avoid increased reaction rates caused by warming of the sediment, both setups were kept in a temperature controlled laboratory. Furthermore, pore water was sampled with rhizon core solution samplers (Rhizophere Research), using core liners prepared with sealed ports for nutrients analysis (for further details see Neumann et al., subm.). Simultaneously, overlying water of the sediment cores was sampled for nutrients and dissolved organic carbon (DOC). The profiles of oxygen and dissolved inorganic nitrogen concentration across the sediment-water interface are the basis for flux calculation according to Berg et al. (1998).

Benthic macrofauna sampling

Benthic fauna was sampled with the above-described multicorer (table 7-1). The first 5 cm of the cores were sieved through a 500 µm mesh. Macrozoobenthic organisms were immediately presorted on the sieve. Empty conches were arranged with the concave part (blank) facing up. Broken and open shells were not included in the counts. Living bivalves were deposited with the convex side up. Samples with over 80 bivalves were not arranged. Complete photos as well as some close-ups were taken from each sieve and standardized to ind. m^{-2}.

Benthic megafauna observation

A modified remotely operated vehicle (ROV; MOHAWK Sub-Atlantic, Aberdeen, UK) operated from the ship was used to observe the benthic megafauna (table 7-1). The vehicle was equipped with a color and a black/white camera system. The depth and distance to the sea bottom were overlaid on the screen and two laser point markers defined a distance of 10 cm on the sea-bottom. A positioning system (IXSEA) was used to determine the position and track length of the ROV. Four tracks on the shelf off Terrace Bay, Rocky Point and Kunene as well as two tracks at the slope off Kunene were taken (table 7-2).

Table 7-2: Depth and track length of ROV stations.

Station number	Station name	Depth [m]	track length (m)
277	Terrace Bay, shelf	100	119
282	Rocky Point, shelf	110	279
285	Rocky Point, shelf	205	343
305	Kunene shelf	150	421
314	Kunene, slope	500	596
315	Kunene, slope	775	335

Organisms detected on the ROV videos were identified and counted. The numbers of individuals per taxon were standardized to 100 m of the track route. At stations with an abundance of more than 500 ind. 100 m^{-1}, subsamples were evaluated and individuals were counted every 10 minutes for 30 seconds while the distance traveled during this time was also determined. The results were standardized to one meter and the average was calculated. Bacterial mats were assessed using still images taken every 10 m on the track and categorized into percentage of coverage.

7.3. Results

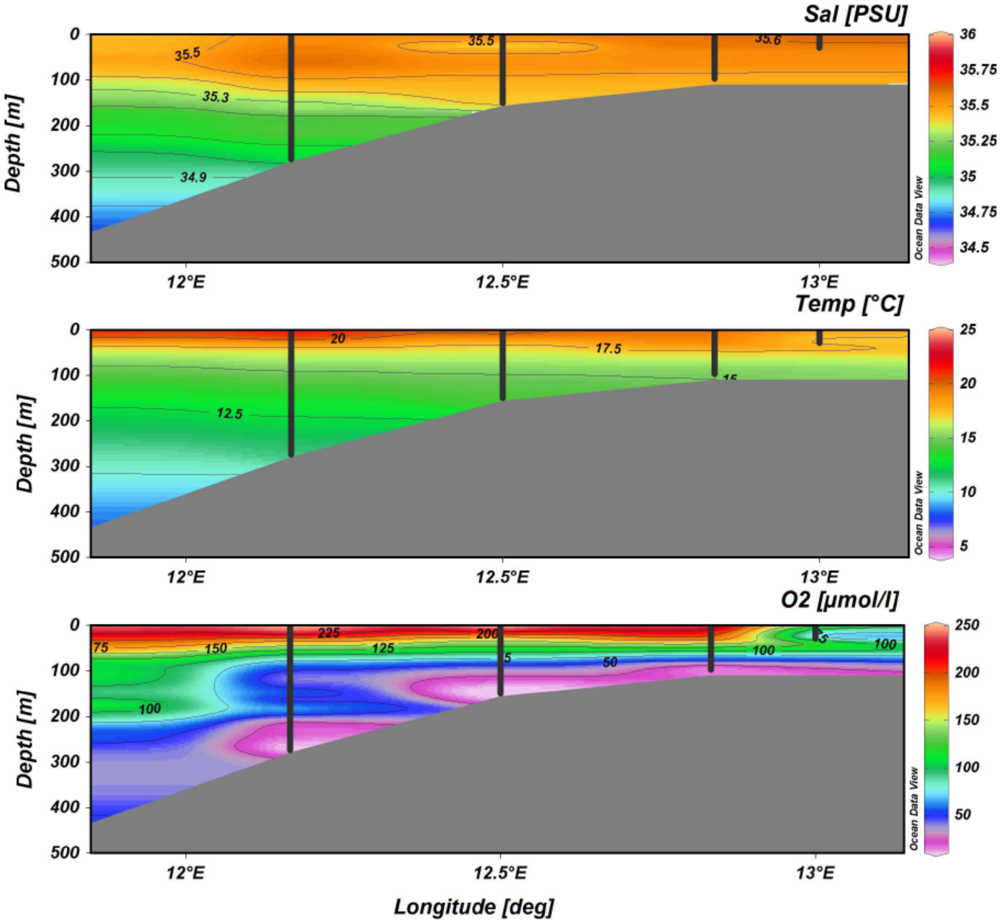
7.3.1. Physical parameters on the three investigated transects

All three transects were characterized by stratified waters with high salinity and temperature values in the upper 50 m (34-36 PSU; 18-22 °C). On the Terrace Bay transect (figure 7-2A) salinity was high near the surface layer (5 m; ~35.5 PSU) and decreased with depth to 34.7 PSU near the bottom (400 m). The temperature showed also a decreasing trend with 21.5 °C at the surface to 7.5 °C at 400 m depth. On the shelf of the Terrace Bay transect, oxygen decreased below a well oxygenated (200 µmol l^{-1}) surface layer (0-100 m; figure 7-2A) to almost 0 µmol l^{-1} on the seafloor. On the Rocky Point transect (figure 7-2B), salinity was slightly higher (35.7 PSU) and temperature slightly lower (~18.5 °C) than on the Terrace Bay transect at the surface but similar at greater depths. Oxygen was similar distributed. The Kunene transect (figure 7-2C) was sampled down to 1000 m. Salinity and temperature were marginally higher with 36 PSU and 22.5 °C similar to the Terrace Bay transect. The main difference to the other transects was the slightly deeper oxygen minimum zone between 150 m and 500 m depth. At greater depths (~850 m), the oxygen concentration was higher with 150 µmol l^{-1}.

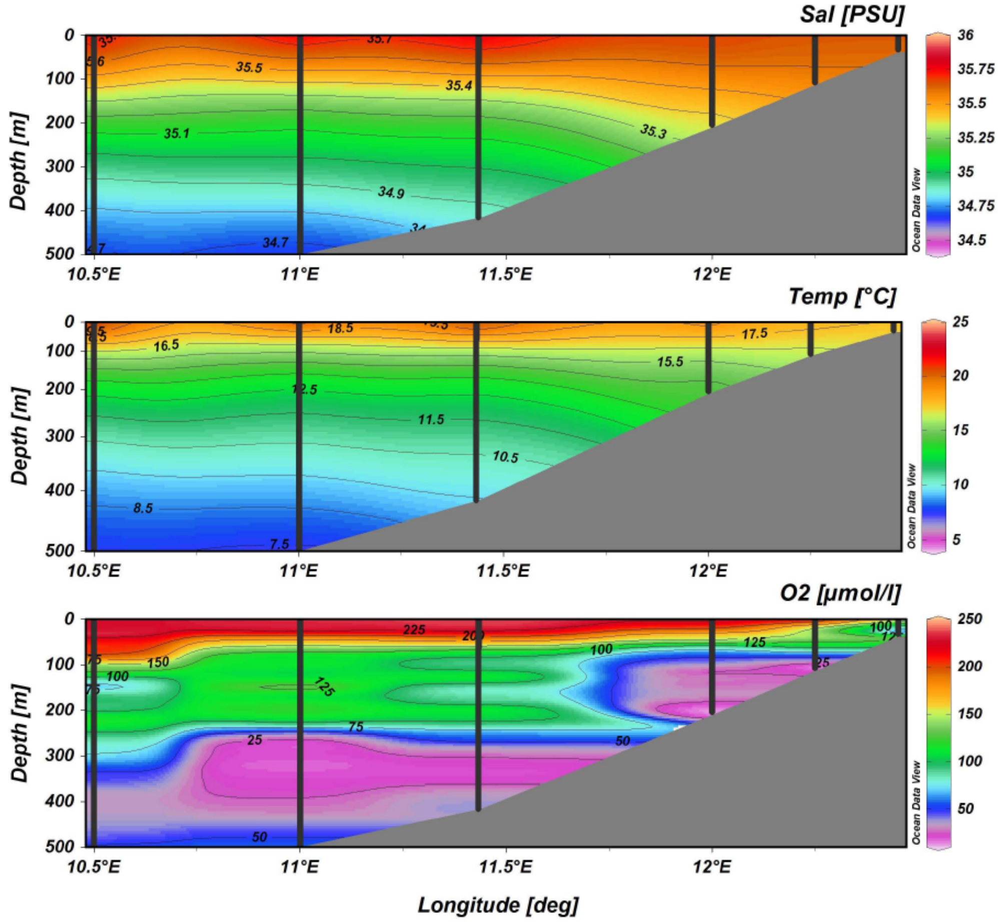
7.3.2. Chlorophyll *a* concentrations

Chl *a* concentrations were generally higher inshore (6-10 mg m^{-3}) than offshore (0.1-1 mg m^{-3}) in the studied area in January and February 2011. The lowest Chl *a* concentrations were detected on the Kunene transect (1-6 mg m^{-3}) compared to higher concentrations on the Terrace Bay and Rocky Point transects (1-10 mg m^{-3}) inshore and above the slope.

A


Sal [PSU]
Depth [m]
0
100
200
300
400
500
35.5
35.3
34.9
35.6
12°E
12.5°E
13°E
36
35.75
35.5
35.25
35
34.75
34.5
Ocean Data View
Temp [°C]
20
17.5
15
12.5
25
20
15
10
5
O2 [µmol/l]
225
200
150
125
100
75
50
250
Longitude [deg]

B


Sal [PSU]
Depth [m]
0
100
200
300
400
500
35.7
35.6
35.5
35.4
35.3
35.1
34.9
34.7
10.5°E
11°E
11.5°E
12°E
36
35.75
35.5
35.25
35
34.75
34.5
Ocean Data View
Temp [°C]
18.5
17.5
16.5
15.5
12.5
11.5
10.5
8.5
7.5
25
20
15
10
5
O2 [µmol/l]
225
200
150
125
100
75
50
25
250
Longitude [deg]

C

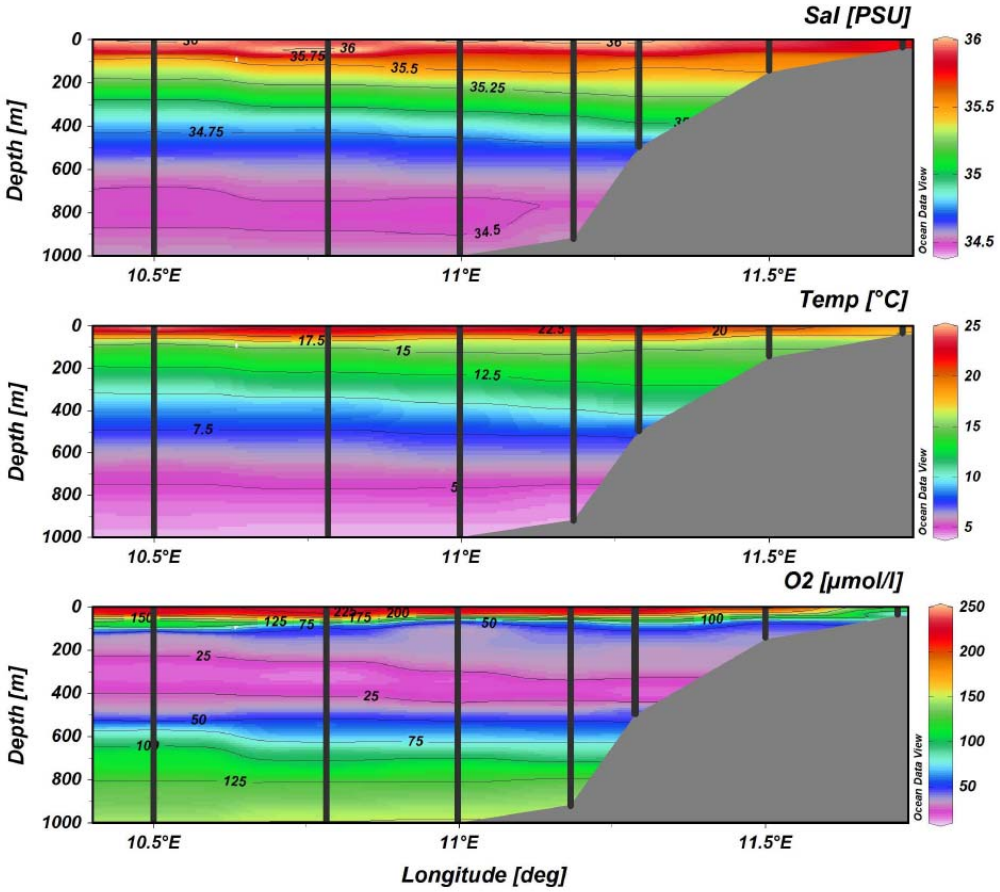


Figure 7-2A-C: Distribution of salinity (PSU), temperature (°C) and oxygen (µmol l^{-1}1) on the Terrace Bay (A), Rocky Point (B) and Kunene (C) transects. Black lines: CTD stations. Note the different depth scaling in 2C.

7.3.3. Microzooplankton and mesozooplankton abundance

Microzooplankton abundance

At the Terrace Bay shelf station (155 m; st. 276), the microzooplankton abundance decreased from 7900 ind. m^{-3} in the surface water (0-25 m) to 840 ind. m^{-3} between 50-100 m and increased again below 100 m depth to 6400 ind. m^{-3} during daytime (figure 7-3). At the Rocky Point inner shelf station (112 m; st. 282), the microzooplankton concentrations ranged around 1300 ind. m^{-3} in the upper 50 m and decreased to 450 ind. m^{-3} in 50-100 m during night. At the outer shelf station (210 m; st. 285), the microzooplankton abundance reached 2000 ind. m^{-3} in the upper 25 m and decreased slowly to 800 ind. m^{-3} in 100-150 m depth during daytime.

At the shelf station (150 m; st. 305) of the Kunene transect, the near surface (0-25 m) microzooplankton abundance was 4400 ind. m^{-3} during day and decreased with depth to 2100 ind. m^{-3} in 50-100 m. Below this depth, the concentration increased again to 4000 ind. m^{-3}. At the slope station (500 m; st. 306) of the Kunene transect, the microzooplankton abundance declined from 12200 ind. m^{-3} in the surface layer (0-25 m) to 1700 ind. m^{-3} in 100-200 m during night. At the deeper slope station (2000 m; st. 307) of the Kunene transect, the microzooplankton abundance decreased from 10000 ind. m^{-3} in the upper layer (25-50 m) to 660 ind. m^{-3} in the 400-600 m layer during daytime. Sampling in the upper 25 m failed.

Mesozooplankton abundance

At the Rocky Point inner shelf station (112 m; st. 282), the mesozooplankton abundance was 550 ind. m^{-3} in 0-25 m, increased to 1300 ind. m^{-3} between 25 and 50 m, and then decreased to 80 ind. m^{-3} in the depth interval from 100 to 150 m at this station during daytime. During night, peaks of 2700 ind. m^{-3} and 2100 ind. m^{-3} in mesozooplankton abundance were observed in 25-50 m and 100-150 m between values of 400-500 ind. m^{-3}. At the shelf station (150 m; st. 305) of the Kunene transect, the mesozooplankton abundance decreased from 2200 ind. m^{-3} at the surface to 140 ind. m^{-3} in the 50-100 m depth interval during daytime (figure 7-3). At the slope station (500 m; st. 306) of the Kunene transect, the mesozooplankton abundance was lower at the surface with 170 ind. m^{-3} and highest in 25 to 50 m with 360 ind. m^{-3} and showed a decreasing trend with depth.

At the deeper slope station (2000 m; st. 307) of the Kunene transect, low mesozooplankton abundances of approximately 50 ind. m^{-3} were detected near the surface (0-50 m) decreasing with depth to a minimum of 0.1 ind. m^{-3}, while the abundance increased again to 140 ind. m^{-3} in the depth interval 400-600 m.

Overall, standing stocks of microzooplankton in the upper 100 m increased from inshore to offshore whereas mesozooplankton decreased. Highest microzooplankton stocks were detected on the shelf off Terrace Bay and Kunene, lowest values were observed off Rocky Point. Mesozooplankton standing stocks were similar on the shelf off Kunene and Rocky Point.

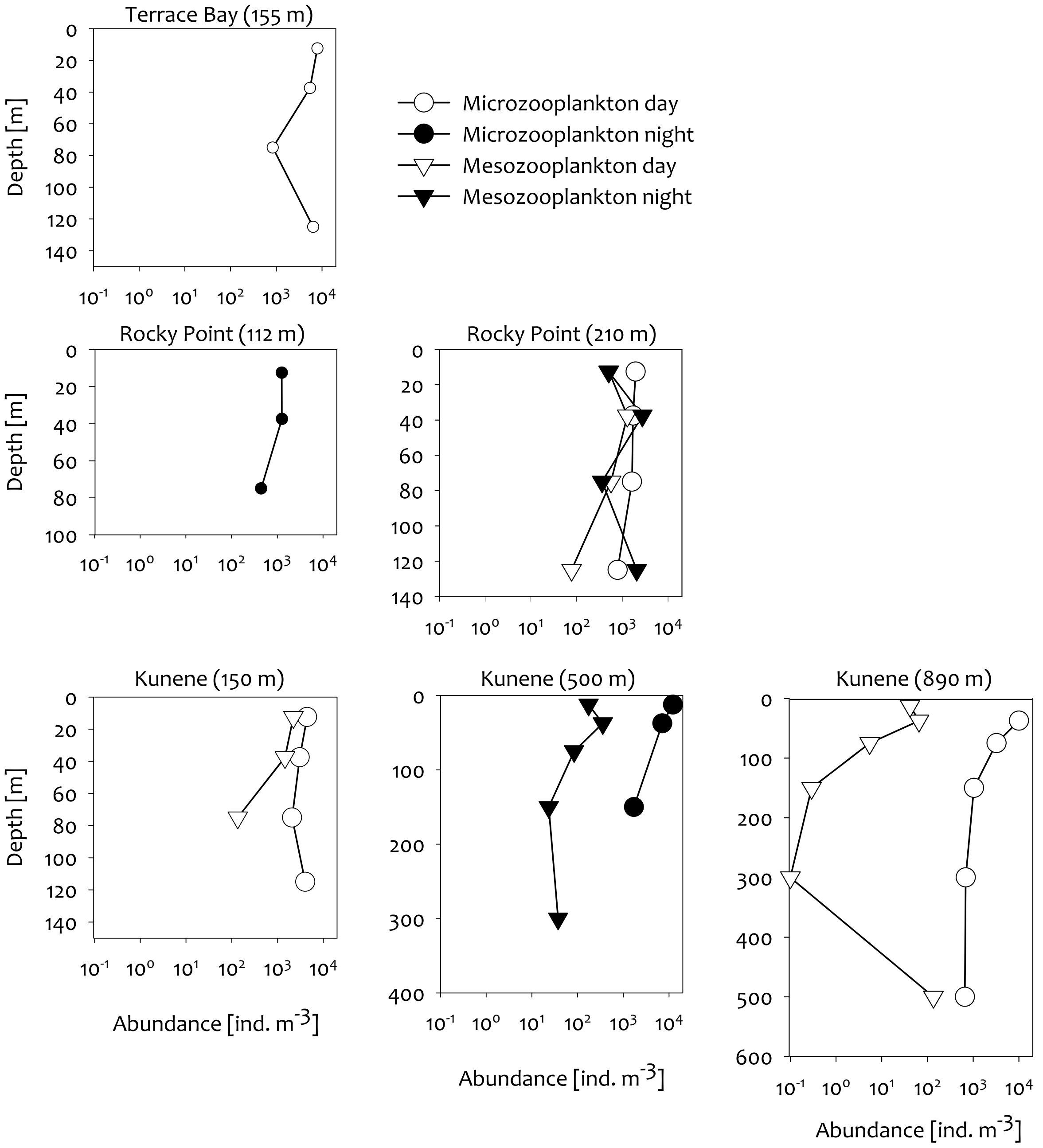


Figure 7-3: Vertical distribution of micro- and mesozooplankton abundance.

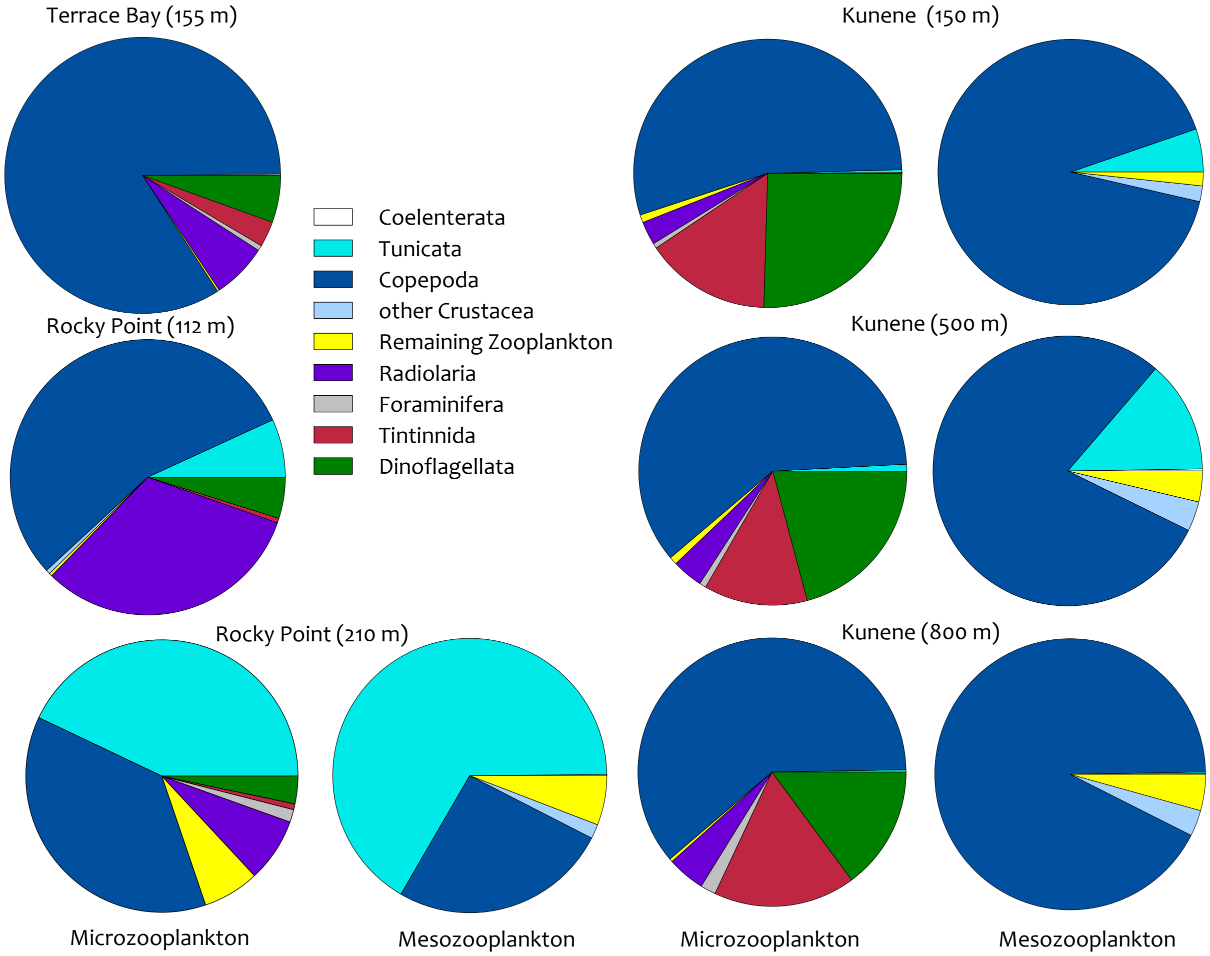


Figure 7-4: Micro- and mesozooplankton composition.

7.3.4. Microzooplankton and mesozooplankton taxa composition

The microzooplankton taxa composition at the Terrace Bay shelf station (155 m; st. 276; figure 7-4) was dominated by Copepoda (84.0 %), followed by Radiolaria (6.5 %), Dinoflagellata (5.5 %) and Tintinnida (3.0 %). At the Rocky Point shelf station (38 m; st. 282), the main microzooplankton taxon was Copepoda (55.0 %) followed by Radiolaria (31.9 %), Tunicata (6.8 %, mainly Salpida und Doliolida). and Dinoflagellata (4.8 %). At the deeper shelf station (210 m; st. 285) of this transect, Tunicata was the major taxon of the microzooplankton composition with 43.0 %. Copepoda made up 37.2 % of the microzooplankton composition and Radiolaria contributed with 6.7 %. On the Kunene transect, Copepoda were the main taxon with 54.6-61.0 % of the microzooplankton community. Dinoflagellata and Tintinnida ranked next with contributions between 12.5 and 25.4 %.

At the deeper shelf station of the Rocky Point transect (210 m; st. 285), the mesozooplankton composition at this station was similar to microzooplanlton composition dominated by Tunicata with 66.5 % followed by Copepoda (25.8 %). On the Kunene transect, Copepoda contributed to the mesozooplankton composition with 79.0-92.3 %.

7.3.5. Biogeochemistry

Data from stations close to the ROV stations were evaluated for bottom nutrient concentration and elemental composition (table 7-3). In general, the bottom concentrations of oxygen and mono-nitrogen oxides were higher on the shelf than on the slope. In particular, at the Rocky Point shelf station (38 m; st. 279), the highest bottom concentration of all stations were measured for phosphate (PO_4), nitrogen oxide (NO_x), nitrite ion (NO_2^-), ammonium ion (NH_4^+) and dissolved inorganic nitrogen (ammonium, nitrate, nitrite; DIN). On the Kunene transect, the bottom concentration of NO_x was highest at the slope station (2000 m; st. 308) and lowest at the shelf (150 m; st. 305) and slope station (500 m; st. 306). At the Kunene slope station (2000 m; st. 308), the lowest concentration of PO_4 (1.93 µmol l^{-1}) was measured, while the lowest concentration of NO_2^- (-0.02 µmol l^{-1}) was detected at the Kunene shelf station (150 m; st. 305). Ammonium showed a generally increasing trend from the shelf (11.54 µmol l^{-1}; 38 m; st. 279) down the slope (1.10 µmol l^{-1}; 2000 m; st. 308)

N_{tot} and C_{org} in the sediment were correlated. At the Terrace Bay shelf station (104 m; st. 277), the highest contributions of N_{tot} (1.0 %) and also of C_{org} (7.3 %) to the total sample mass were detected, while the lowest percentages of N_{tot} (0.1 %) and C_{org} (1 %) were measured at the slope station (500 m; st. 306) on the Kunene transect. The Terrace Bay and Kunene transect shelf stations (st. 279, st. 305) were characterized by similar amounts of N_{tot} (table 7-3). However, the C_{org} differed between these two stations with lower values at the Kunene shelf station (150 m; st. 305).

Table 7-3: Bottom concentrations [µmol l^{-1}] of the different elements: phosphate (PO_4), nitrogen oxide (NO_x), nitrite ion (NO_2^-), ammonium ion (NO_4^+), dissolved inorganic nitrogen (ammonium, nitrate, nitrite) (DIN) and percentage of total nitrogen (N_{tot}) and organic carbon (C_{org}) in the sediment (molar ratio of both elements). Oxygen concentration compared to oxygen consumption. st.= station number

st.	name	bottom c. [PO_4]	bottom c. [NO_x]	bottom c. [NO^-_2]	bottom c. [NO^+_4]	bottom c. [DIN]
278	Terrace Bay, shelf	3.28	23.40	0.49	6.85	30.25
279	Rocky Point, shelf	5.91	19.23	0.93	11.54	30.77
305	Kunene, shelf	2.16	13.45	-0.02	3.11	16.56
306	Kunene, slope	2.78	12.01	0.34	2.38	14.39
308	Kunene, slope	1.93	23.75	0.36	1.10	25.75

st.	name	N_{tot} % (sediment)	C_{org} % (sediment)	$C_{org} : N_{tot}$ (molar ratio)	bottom water oxygen (µM)	oxygen consumption (µmol m^{-2} d^{-1})
277	Terrace Bay, shelf	1.0	7.28	8.45	1.90	
278	Terrace Bay, shelf	0.5	3.57	8.83	1.33	769.48
279	Rocky Point, shelf	0.22	1.59	8.62	16.38	
305	Kunene, shelf	0.21	1.88	10.21	46.66	2023.06
306	Kunene, slope	0.14	1.00	10.33	42.58	2160.69
308	Kunene, slope	0.38	3.05	9.26	239.25	3065.04

Generally, oxygen concentrations in the sediment were low on the shelf (for example 1.9 µM; 104 m; st. 277) with increasing trends to the north (Terrace Bay to Kunene) and further offshore (for example 239.3 µM; 2000 m; st. 308). The oxygen consumption presented the same trend: 769 µmol m^{-2} d^{-1} at the Terrace Bay shelf station (34 m; st. 278) and 3065 µmol m^{-2} d^{-1} at the Kunene slope station (2000 m; st. 308) were measured.

7.3.6. Benthic macrofauna distribution

Benthic macrofauna samples at four stations on the Terrace Bay (34 m; st. 278), Rocky Point (38 m; st. 279) and Kunene transects (150 m; st. 305 and 2000 m; st. 308) were evaluated (figures 7-5, 7-6). The shelf stations of all three transects were characterized by abundances between 3177 and 11282 ind. m^{-2} of benthic macrofauna. At the Terrace Bay inshore station (34 m; st. 278), the highest total number (11282 ind. m^{-2}) was detected. The two main fractions of this sample consisted of undefined tubeworms (1538 ind. m^{-2}) and other undefined organisms (7948 ind. m^{-2}). The identified organisms were Polychaeta (769 ind. m^{-2}), Holothuroidea (897 ind. m^{-2}) and the bivalve c.f. *Telina sp.* (128 ind. m^{-2}). Mollusca were very abundant at the Rocky Point and Kunene shelf stations (38 m; st. 279 and 150 m; st. 305); a not defined species of Gastropoda (taxon A) was found at these stations with 769 ind. m^{-2}. However, the highest abundance of Mollusca was detected at the shelf station of the Rocky Point transect (38 m; 3718 ind. m^{-2}; st. 279). Bivalvia (2820 ind. m^{-2}) were separated into undetermined (1410 ind. m^{-2}) and whole c.f. *Telina sp*. (1410 ind. m^{-2}). Whereas at most station only single sediment cores were evaluated, nine sediment cores were examined at the Kunene shelf station (150 m; st. 305). The total abundance of all individuals reached 3177 ±3463 SD ind. m^{-2}, dominated by Gastropoda (taxon A; 1382 ±229 SD ind. m^{-2}). The Bivalvia consisted of c.f. *Telina sp*. (57 ±113 SD ind. m^{-2}), c.f. *Nuculana sp.* (869 ±344 SD ind. m^{-2}) and not further identified Bivalvia (14 ±43 SD ind. m^{-2}). Mollusca and Polychaeta (812 ±484 SD ind. m^{-2}) indicated a high variability in the analyzed sediment cores. The lowest macrofauna abundance was observed at the slope station (2000 m; st. 308) with less than 1410 ind. m^{-2}. Here, *Scaphopoda sp*. dominated the samples (769 ind. m^{-2}), followed by unidentified species (513 ind. m^{-2}) and Amphipoda (128 ind. m^{-2}).

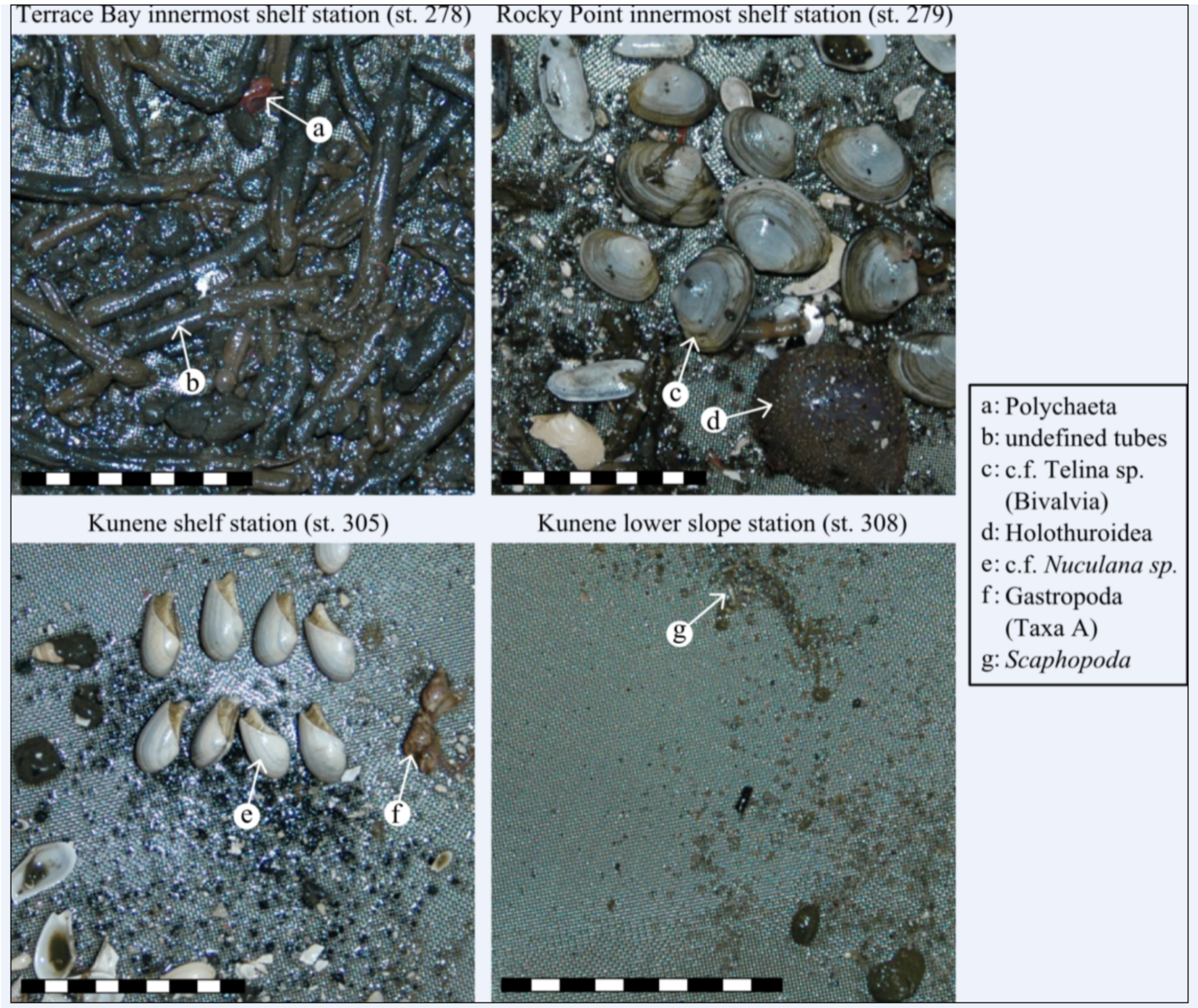

Terrace Bay innermost shelf station (st. 278)
Rocky Point innermost shelf station (st. 279)
Kunene shelf station (st. 305)
Kunene lower slope station (st. 308)

Figure 7-5: Benthic macrofauna composition of the first 5 cm of the sediment. Scale: 5 cm.

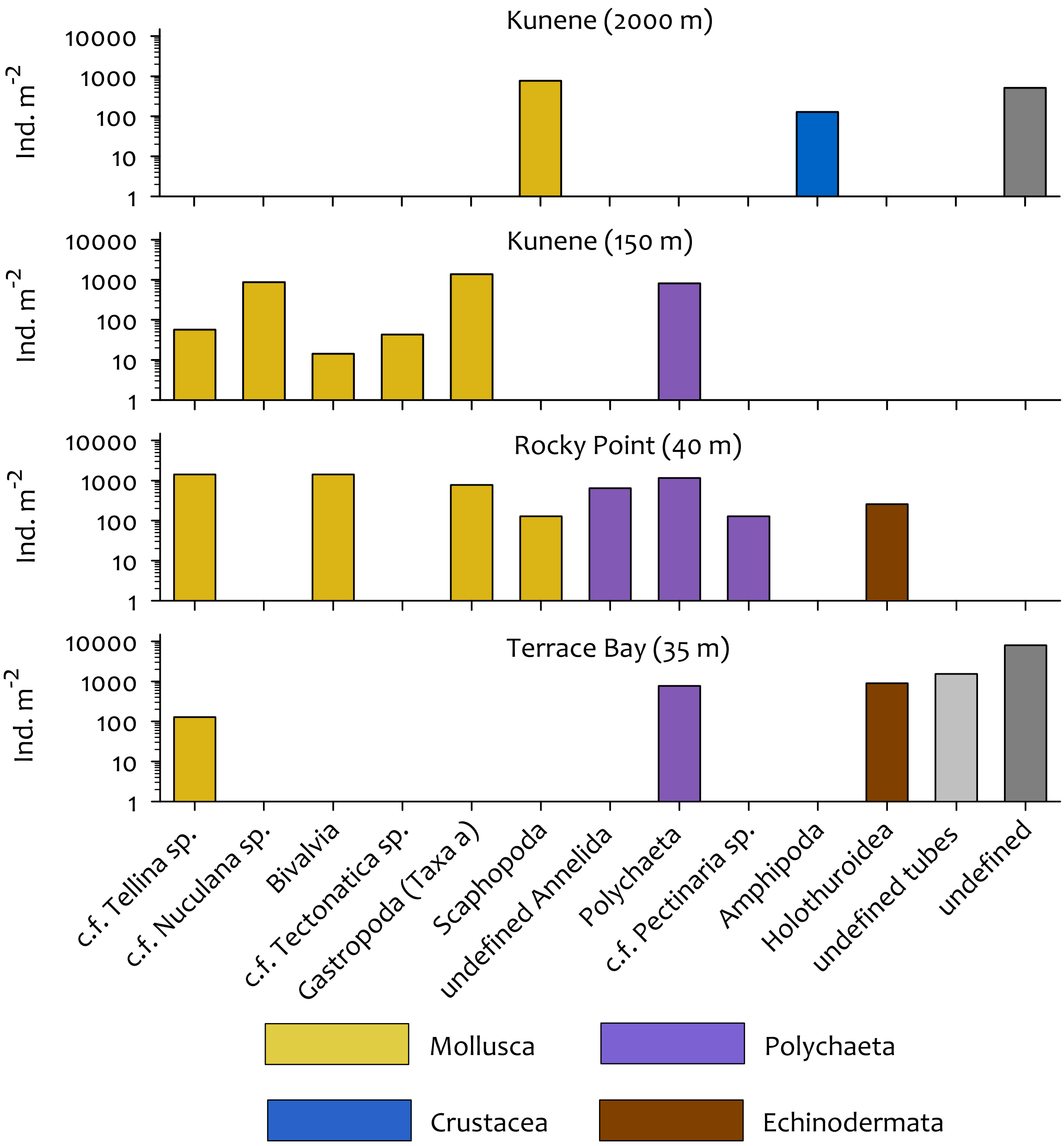


Figure 7-6: Abundance of benthic macrofauna groups (ind. m^{-2}) derived from the sieve pictures of the first 5 cm of the sediment cores.

7.3.7. ROV video analysis of the benthic megafauna

All locations showed distinct differences in sediment structure (figure 7-7), near bottom particle density and megafauna composition. At the Terrace Bay shelf station (104 m; st. 277), the sediment was very fluffy and each movement of the ROV caused a plume of dust in the water column. Particles were not counted but showed an intermediate density compared to the other stations. Off Rocky Point the sediment was much firmer at both stations in 112 and 210 m depth. The particle density was moderate and bacterial mats were detected in decreasing abundance with increasing depth. The highest particle density was detected on the shelf off Kunene in 150 m depth causing a bad visibility. Particle density was decreasing with increasing depth on the slope but still higher as at the other locations.

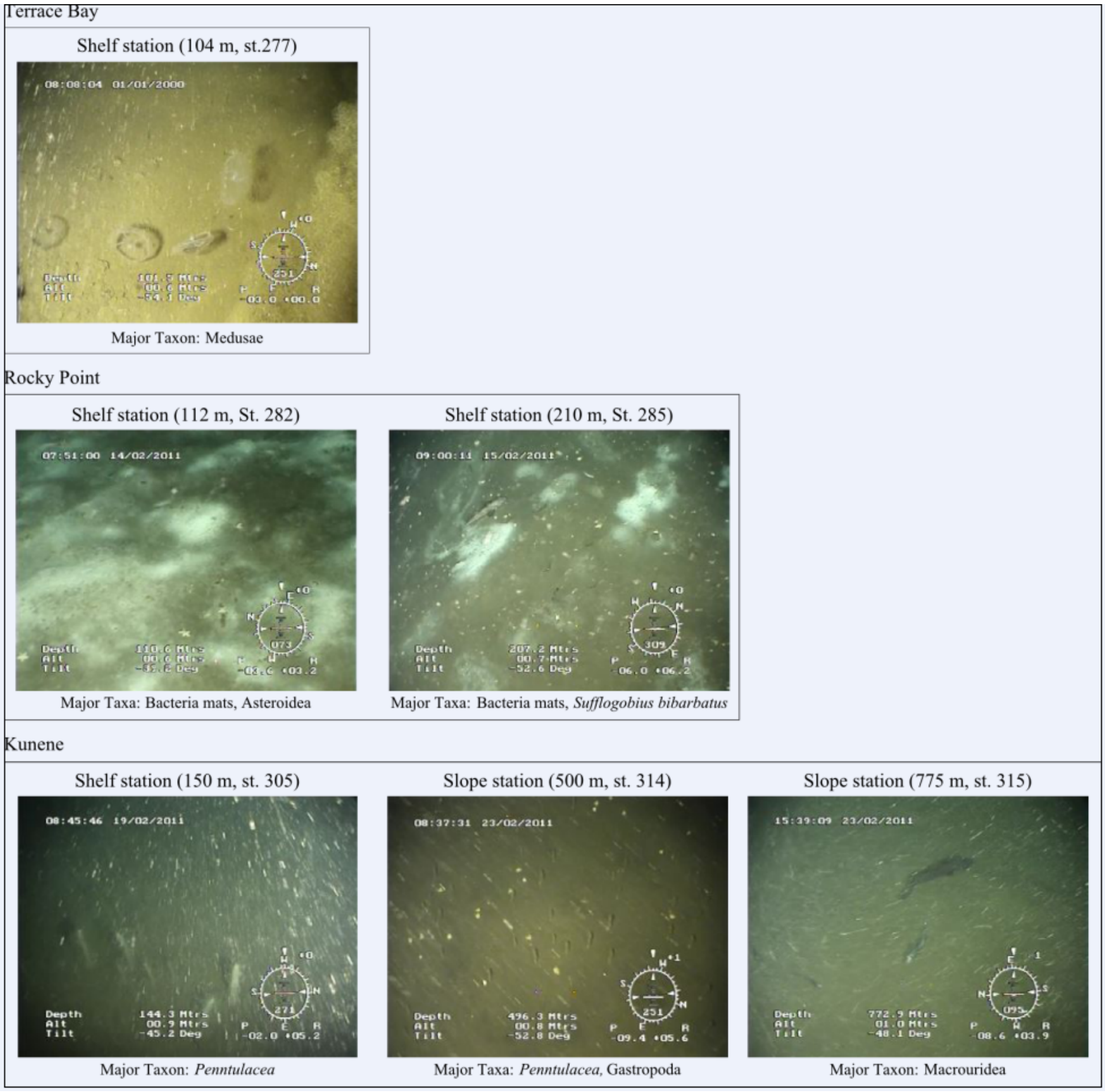


Figure 7-7: Overview of the benthic megafauna on the northern Namibian shelf via ROV.

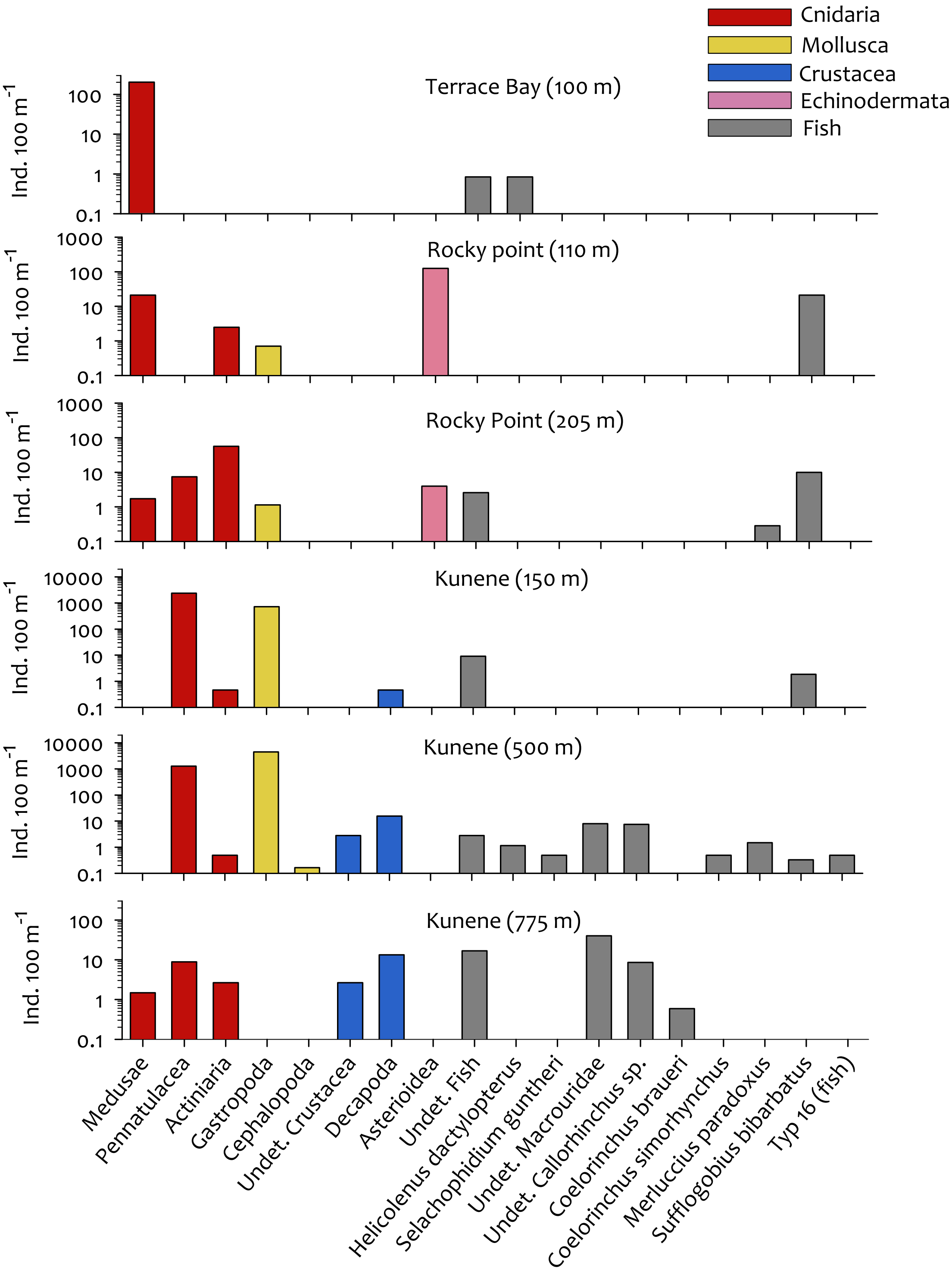


Figure 7-8: Abundance of benthic megafauna (ind. 100 m^{-1}) derived from ROV observations. Note the different scaling of the y-axis.

Mainly Medusa with an abundance of 203 ind. 100 m^{-1} were detected at the Terrace Bay shelf station (figure 7-8). Most of the Medusa had their tentacles pointed up to the surface. One Blackbelly Rose fish (*Helicolenus dactylopterus*) was found per 100 m track length.

On the Rocky Point transect, Asteroidea were the most common group with 124 ind. 100 m^{-1} at the inner shelf station (112 m; st. 282), followed by Medusa and gobies (*Sufflogobius bibarbatus*, Bearded Goby) with 21 ind. 100 m^{-1}, each. At the outer shelf station (210 m; st. 285), Actiniaria was the dominating taxon in the benthic megafauna with 56 ind. 100 m^{-1}, followed by *Sufflogobius bibarbatus* with 10 ind. 100 m^{-1}. In contrast to the other stations on this transect, Actinopterygii (3 ind. 100 m^{-1}), Pennatulacea (7 ind. 100 m^{-1}) and *Merluccius capensis* (hake; 1 ind. 100 m^{-1}) were additionally detected at the 210 m shelf station (st. 285).

On the Kunene transect, the composition of the benthic megafauna differed again from the other transects. Pennatulacea (Vertillidae) followed by Gastropoda (728 ind. 100 m^{-1}) were most common at the shelf station with 2397 ind. 100 m^{-1} (150 m; st. 305; figure 7-8). Unidentified taxa of Actinopterygii (9 ind. 100 m^{-1}) were also detected. Similar to the shelf station, Gastropoda (4463 ind. 100 m^{-1}) and Pennatulacea (Virgulariidae; 1278 ind. 100 m^{-1}) were the most common taxa at the 500 m slope station (st. 314), but the species composition was different. Moreover, a higher abundance of Decapoda (16 ind. 100 m^{-1}) was observed compared to the shelf station (150 m; st. 305). Macrouridae (rattails) were found with 16 ind. 100 m^{-1} of which 8 ind. 100 m^{-1} were further classified as *Callorhinchus spp.*

In contrast to the other stations of the Kunene transect, no Gastropoda were detected and only 9 ind. 100 m^{-1} of Pennatulacea were observed at the deeper slope station (775 m; st. 315). The most common taxon was Macrouridae with 49 ind. 100 m^{-1}; 9 of them were determined as *Callorhinchus spp.*, one was defined as *Coelorinchus simorhynchus*. Less Decapoda (13 ind. 100 m^{-1}) than at the slope station were observed.

Overall, the highest benthic megafauna abundance was detected on the Kunene transect. The distribution pattern on this transect was characterized by an abundance of 3137 ind. 100 m^{-1} at the shelf station (150 m; st. 305), a peak of 5783 ind. 100 m^{-1} at the upper slope station (500 m; st. 314) and reduced values of 95 ind. 100 m^{-1} at the deeper slope station (775 m; st. 315).

7.4. Discussion

The three investigated transects, which are 60 and 90 NM in latitudinal direction apart from each other, showed clear differences in the abundance and composition of benthic megafauna and macrofauna. However, it has to be noted that macrofauna samples at Terrace Bay and Rocky Point were taken closer to the coast. These stations could be affected by coastal processes like greater mixing events and changes in ventilation. Despite these facts, differences in species composition were obvious between transects. Structuring factors can be the shape and width of the shelf, the food supply by phytoplankton, micro- and mesozooplankton and particles as well as the availability of oxygen (see also Parsons et al., 1984; Roughgarden, 2006). Also riverine inputs have to be considered. This study identified factors forming the benthic community in the northern Benguela Upwelling System by focussing on local peculiarities.

Food supply to the benthos

Food to the benthos is mainly supplied by the primary production in the euphotic and the subsequent deposition of organic particles to the sea floor.

A recent and moderate coastal upwelling took place along the entire Namibian coast throughout the investigation period. The detection of moderate upwelling conditions on the Terrace Bay transect was supported by an absence of an intermediate salinity maximum, which was often detected during upwelling conditions (Mohrholz et al., 2008). Higher water temperatures than usual in February, caused by a drift of the South Atlantic Central Water (SACW) from the Angola Dome into the northern BUS, were observed. Ohde and Mohrholz (2011) depicted a strong downward sloping of isotherms and isohalines towards the coast between 100 m and 400 m in the central water layer, which is typical for a strong geostrophic adjusted southward flow along the shelf edge. Temperature, salinity and oxygen indicated a moderate coastal upwelling from water layers between 50 m and 80 m on the Kunene transect and from below 100 m at the Terrace Bay and Rocky Point transects.

Upwelling occurring in different depths could lead to divergences in nutrient supply for phytoplankton growth which could be the reason for the lower total Chl *a* concentration on the Kunene shelf than in the shelf regions of the two other transects (Nogueira et al., 1997). On all transects, a decreasing trend of Chl *a* concentrations from the coast to offshore was detected (see also Demarcq et al., 2003; Weeks and Shillington, 1996), which was most probably caused by the considerable nutrient supply and the resulting production due to coastal upwelling. Barlow et al. (2005) detected that the phytoplankton production is very variable in this region. In contrast to the Peruvian upwelling system, only a weak relationship between the seasonal maximum of the Chl *a* concentrations and the seasonal maximum of the upwelling activity exists in the BUS (Nixon and Thomas 2001).

Clear relationships between Chl *a* and micro- and mesozooplankton concentrations were not detected due to the coarse data resolution. Remarkable is the low mesozooplankton concentration at the lower slope site off Kunene in intermediate depths (figure 7-3) which can be related to the oxygen minimum zone. The taxa composition of micro- and mesozooplankton is much more notable. Generally, a dominance of Copepoda was observed at most stations. The strong dominance of Copepoda may be triggered by the increased food uptake on phytoplankton during active upwelling (Timonin et al., 1992) with an average of 25 % of the available daily phytoplankton production (Verheye et al., 1992). Hansen et al. (2013) detected that on the Walvis Bay transect (23° S), further south of Terrace Bay, copepods were usually most abundant between March and June, while abundances were lower during the rest of the year. The high concentrations of Tunicata at the Rocky Point outer shelf station is remarkable. This may have been caused by high primary production at this station. These highly effective filter-feeding organisms occur stochastically in blooms and contribute largely to the vertical particle flux (Irigoien, 2005).

Overall, the supply of food to the benthos is controlled by primary production in the upper water column and the subsequent sinking of organic matter. The composition and abundance of sinking particles is controlled and affected by micro- and mesozooplankton grazing. Stochastic events like salp blooms may have an enormous influence on the particle flux both in abundance and composition (Pfannkuche and Lochte, 1993).

Geomorphology and riverine input

Differences in particle flux from the coast towards the open water lead to a diverse sediment structure from the shelf downwards the continental slope. Bremner (1978) divided the seafloor off Namibia's coast into three zones with high organic matter deposits: (i) the inner mud belt, especially diatom mud in 50-150 m water depth (inner shelf) with the highest concentration of organic matter (7-25 %), (ii) the middle shelf with a sand-mud sediment at depths between 150 m and 500 m, and (iii) the outermost belt, at depths between 500 and 1400 m on the slope with a sand-mud to mud sediment below 1000 m. The upper slope area (around 500 m) is additionally supplied with organic material which is transported down the slope from the high production on the shelf (Inthorn et al., 2006; Mollenhauer et al., 2007). Based on the definition above, the Terrace Bay and Kunene shelf stations at 104 m (st. 277) and in 150 m (st. 305) as well as the Rocky Point shelf station at 112 m (st. 282) are located in the inner mud belt, whereas the Rocky Point shelf station at 210 m (st. 285) is located in the sand-mud area. Both Kunene slope stations at 500 m (st. 306) and in 890 m (st. 307) are located in the outer belt. The shelf of the Terrace Bay and Rocky Point transects is wide and smooth, whereas it is narrow and steep at the Kunene transect, probably leading to an enhanced downward particle flux at the latter site.

In contrast to the Terrace Bay and Rocky Point transects, the Kunene transect is influenced by the outflow of the Kunene River (annual mean discharge rate: 550 m^{-3} s^{-1}, Hogan, 2012), which, however, is low compared to other rivers like the Congo (41200 m^{-3} s^{-1}, Gupta, 2007). Nevertheless, the outflow may increase the nutrient flow and the particle flux rates (Eggers, 1990; Lass et al., 2000) due to the high load of particulate and dissolved organic matter (Emery et al. 1973).

Nutrient chemistry of the northern Namibian shelf

The northern Namibian shelf is seasonally exposed to relatively warm and low-oxygenated bottom water (SACW), which permits intensive microbial activity and results in high rates of nutrient turnover (Neumann et al., subm.). A frequent consequence of the high remineralisation rates is the successive consumption of available electron acceptors such as oxygen, nitrate, sulphate etc. by bacteria. This condition may be supported by high particle densities. On the Kunene transectect, ROV observations visually indicated a lower particle density at the upper slope station (500 m; st. 306) than on the shelf which could result in the lower C_{org} sediment concentrations. Rowe (1981) mentioned that the total benthic biomass is influenced by the surface productivity and tends to decrease with distance from the shore and with depth. For the macrofauna, Kröncke and Türkay (2003) found a significant positive correlation between the abundance and biomass in the sediment and the total organic carbon (TOC) in the Angola Basin. In this study both C_{org} and N_{tot} rates decline from the shelf to the slope at different rates, but N_{tot} rates decline more slowly than those of C_{org}. These differences induce a shift in the dominance of C_{org} and N_{tot} resulting in an increasing C_{org}:N_{tot} ratio, which can be found on the Kunene transect. In the process of C_{org} depletion, ammonium is released; therefore the ammonium concentration follows the same decreasing pattern as C_{org}. The decreasing trend of C_{org} is also similar to the distribution pattern of macro- and megafauna, implying an influence of C_{org} onto those organisms. Furthermore, a higher turnover of C_{org} than N_{tot} via organisms implies fresh organic material with a lower C_{org}:N_{tot} ratio on the shelf. This turnover of fresh organic material leads to a higher ammonium release than for refractory organic material with a high C_{org}:N_{tot} ratio.

Additionally, high remineralisation rates are positively correlated with the water temperature which influences poikilothermal bacteria and invertebrates (Kristensen et al., 1992). This is present on the shelf and leads to high concentrations of phosphate, DIN and C_{org} as by-products. Furthermore, warm bottom temperatures (13-15 °C) enhance the accumulation of carbon dioxide, di-nitrogen, hydrogen sulphide and methane in the surface sediment and the bottom water (Neumann et al., subm.).

Hypoxic/anoxic areas

Large areas of the BUS are affected by seasonal changing hypoxic/anoxic events and oxygen minimum zones (OMZ). The reduction in oxygen can be caused by the bacterial decomposition of organic matter and/or by the intrusion of already oxygen depleted waters mainly on the central shelf. The OMZ can have an enormous influence on the distribution of species in the water column and at the sea floor since few species can tolerate these oxygen deficiencies, thereby constraining the vertical habitat of most marine organisms (Wishner et al., 1990, Prince and Goodyear, 2006; Bertrand et al., 2010).

The oxygen poor SACW caused the existence of suboxic to anoxic zones (OMZ) on the Kunene transect between 150 and 500 m water depth beginning at the shelf break. Warm saline surface water of tropical origin was detected above the thermocline (50 m), indicating a southward shift of the Angola Benguela Frontal Zone (ABFZ) to the Kunene transect (see Lahajnar et al., 2012). Even though the front affected the whole transect, a limitation of the extended OMZ could only be detected on the Kunene shelf due to a shallower water body compared to the other transects. Here, this front acts as a physical barrier as described by Monteiro and van der Plas (2006).

The OMZ seems to have less influence on the distribution of microzooplankton than on mesozooplankton as exemplified off Kunene. Due to the location of the OMZ close to the bottom at Rocky Point and Terrace Bay, it could not be detected whether depth or the OMZ was the reason for decreasing mesozooplankton abundance (Auel and Hagen, 2002).

The shallow Terrace Bay station (34 m; st. 278) showed a different benthic macrofauna composition than the other stations with Holothuroidea and Polychaeta as abundant organisms. Similar findings were detected by Zettler et al. (2009) in an OMZ at depths between 150 m and 200 m on the Namibia shelf. Sako (1998) and Sanders (1968) detected that the macrofauna species diversity was reduced in the OMZ off Namibia. The Gastropoda *Nassarius vinctus*, a long-living species adapted to the occurrence of nearly anoxic and hypoxic conditions in this region, showed high abundances in the OMZ (see also Zettler et al. 2009). Zettler et al. (2009) classified this Gastropod as an indicator species of OMZs. The Gastropod taxon A, which was detected in the Rocky Point hypoxic area may belong to *Nassarius vinctus,* but could not be further identified in the pictures.

Resulting structures in the benthic macro- and megafauna community

The high overall productivity on the Namibian shelf results in a high benthic biomass and a benthic community well adapted to a constant and massive organic material input (Aspetsberger et al., 2007). Nevertheless, there are differences in the habitat structure of the benthos caused by physical, chemical and biological processes (Siegel et al., 2008).

The benthic macrofauna abundance decreased from the coast towards the lower slope (2000 m; st. 308), confirming results from other benthic studies (Aspetsberger et al., 2007; Heip et al., 2001) which could be caused by the lower particle flux rates offshore than onshore (Martin and Sayles, 2004). The relatively high abundance of benthic macrofauna on the shelf could be caused by the coverage of diatomaceous mud (Bremner, 1978) since it contains high concentrations of organic matter and reduced sulphur as a food source.

At the Terrace Bay shelf station (104 m; st. 277), the high benthic megafauna abundance of the major taxon Medusa (203 ind. 100 m^{-1}) was also detected by Flynn et al. (2012), who reported a peak of jellyfish abundance in the central region of the Namibian shelf (19.5°S-21.5°S at 100-200 m depth). Jellyfish are probably more abundant in areas with high particle concentrations (Bailey and Batty, 1984) caused by phytoplankton detritus (Estrada and Marrasé, 1987; Brown et al., 1991) and zooplankton biomass (Shannon and Pillar, 1986; Olivar and Barange, 1990). The ROV videos showed that many Medusa pointed their tentacles upwards, maybe to catch the marine snow fall at the Terrace Bay shelf station (see also Berryman et al., 2005;

Calvert and Price, 1970). However, we could not identify the Medusa in this area, but it was neither *Chrysaora* spp. nor *Aequorea* spp. which are common on the Namibian shelf (Flynn et al. 2012). The increase in the abundance of jellyfish along the Namibian coast from the Kunene River in the north to the Orange River in the south (Venter, 1988; Fearon et al., 1992) with the highest abundances at water depths of <200 m coincides with a decrease of abundances of small pelagic fishes as predators and food competition since the 1970s (Boyer et al., 2001). Moreover, Polyps and Medusa may have an advantage since they can cope with the low oxygen conditions on the shelf (Purcell et al., 2001; Condon et al., 2001, Roux et al., 2013).

The Rocky Point transect was the only transect where bacteria mats (*Thiomargarita namibiensis*) were recorded, which were located in the upper centimetres of the sediment. This bacteria are facultative aerobic sulphur bacteria which oxidize bottom water into environmentally harmless colloidal sulphur and sulphate (Lavik et al., 2009). The coverage decreased from the inner shelf to the outer shelf. This could be caused by higher amounts of diatoms in the mud with high amounts of sulphide at the inner shelf station (Bremner, 1978). The bacteria probably increased the sulphur concentrations via decomposition which results in hydrogen sulphides (H_2S) and methane (CH_4) in the sediment and in the deep water. *Thiomargarita namibiensis* (Schulz and Schulz, 2005; Goldhammer et al., 2011), among others, is responsible for the accumulation of phosphate in the sediment at oxygen concentrations above 40 µmol O_2 l^{-1} (Schulz and Jørgensen, 2001). Otherwise the metabolism of *Thiomargarita namibiensis* switches to anaerobic, flexibly adapting to the lower oxygen conditions (Schulz and Schulz, 2005). Due to the temperature and oxygen conditions (12-15 °C and < 40 µmol O_2 l^{-1}), the highest phosphate concentrations in the water column were detected on the Rocky Point transect, implying an incapability of *Thiomargarita namibiensis* to accumulate the phosphate. These suboxic conditions are also tolerated by the bearded goby *Sufflogobius bibarbatus* (Utne-Palm et al., 2010). In our study *Sufflogobius bibarbatus* was more common at the inner shelf than at the outer shelf. The inner shelf with low oxygen concentrations seems to be a refuge-zone for *Sufflogobius bibarbatus* since predators like *Merluccius capensis* avoid these low oxygen environments (Utne-Palm et al., 2010). *Sufflogobius bibarbatus* mainly feeds on zooplankton, medusae and benthic species like Polychaeta and also on diatom mud which is associated with *Thiomargarita namibiensis* (Utne-Palm et al., 2010).

Pennatulacea were more abundant at the slope and the shelf stations of the Kunene transect compared to the other transects. The highest abundance of Pennatulacea was recorded on the shelf with a decreasing trend towards the lower slope, whereas Vertillidae were detected mainly on the shelf and Virgulariide at the slope station (figure 7-7). The highest diversity and abundance of fish was detected at the Kunene slope station (775 m; st. 315), which could be caused by the combination of increasing oxygen concentration down the slope and total high particle flux rates on the Kunene transect caused by the Kunene River outflow. Macrouridae were abundantly found in 800 m depth. They are generally common near the bottom at depth from <2000 to more than 4000 m (Martin and Christiansen, 1997; Marschall and Iwamoto, 1973). The higher abundance of megafauna at the Kunene slope stations compared to the shelf might be explained by the Kunene River outflow which could have increased the nutrient input and accelerated the offshore transport of nutrients and particles or by the narrow shelf, causing a higher organic sedimentation on the slope.

Oceanic upwelling systems with high nutrient concentrations are generally assumed to have short trophic food chains and a low number of links per species which makes them more vulnerable to extinctions or changes in species composition (Dunne et al., 2004). Considering this background information, it is crucial to understand how the pelagic components impact the benthic structure in the different regions and depths off the Namibian coast. Benthic structures seem to be strongly influenced by oxygen conditions in the water column and at the bottom and by differences in production and processes in the water column. It became visible that higher abundances of benthic fauna were detected in areas with higher pelagic biomass, enhanced particle flux rates and the resulting increase of food. Alterations in the pelagic environment are not reflected in the benthic community within short time-scales (Aspetsberger et al., 2007) but over a longer time span, which makes these communities more conservative than the pelagic ones.

The three transects showed a large diversity in the benthic macro- and megafauna which was mainly driven by the differences in particle flux and by hypoxic/anoxic events. Moreover, the sediment structure and the chemical processes at the sediment-water-interface, the width of shelf and the Kunene River outflow are additional factors for the diverse benthic community structures.

7.5. References

Yang EJ, Kang H-K, Yoo S, Hyun J-H (2009) Contribution of auto- and heterotrophic protozoa to the diet of copepods in the Ulleung Basin, East Sea/Japan Sea. Journal of Plankton Research 31:647-659

Aspetsberger F, Zabel M, Ferdelman T, Struck U, Mackensen A, Ahke A, Witte U (2007) Instantaneous benthic response to different organic matter quality: in situ experiments in the Benguela Upwelling System. *Marine Biological Research,* 3: 342-356.

Auel H, Hagen W (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Marine Biology 140:1013-1021

Bailey KM, Batty RS (1984) Laboratory study of predation by Aurelia aurita on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Marine Biology 83:287-291

Barlow R, Sessions H, Balarin M, Weeks S, Whittle C, Hutchings L (2005) Seasonal variation in phytoplankton in the southern Benguela: pigment indices and ocean colour. African Journal of Marine Science 27:275-287

Berryman M, Wood JB, and Zeeh K (2005). Marine Invertebrates of Bermuda, Upside-down Jellyfish Cassiopeaxamachana. http://www.thecephalopodpage.org/MarineInvertebrateZoology/Cassiopeaxamachana.html (last accessed 25. Feb 2015).

Bertrand A, BallÃ³n M, Chaigneau A Acoustic Observation of Living Organisms Reveals the Upper Limit of the Oxygen Minimum Zone. PLoS ONE 5:e10330

Boyer DC, Boyer HJ, Fossen I, Kreiner A (2001) Changes in abundance of the northern Benguela sardine stock during the decade 1990-2000, with comments on the relative importance of fishing and the environment. South African Journal of Marine Science 23:67-84

Bremner JM (1978) Sediments on the continental margin off south west Africa between the latitudes 17° and 25° S. South Africa: PhD Thesis, University of Cape Town, 233 pp.

Brown PC, Painting SJ, Cochrane KL (1991) Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. South African Journal of Marine Science 11:537-564

Brüchert V, Currie B, Peard K, Lass U, Endler R, Dübecke A, Julies E, Leipe T, Zitzmann S (2006) Biogeochemical and physical control on shelf anoxia and water column hydrogen sulphidein the Benguela upwelling system off Namibia. Past and Present Water Column Anoxia. In: Neretin LN (ed) Past and Present Water Column Anoxia, Vol 64. Springer Netherlands, p 161-193

Calbet A (2001) Mesozooplankton Grazing Effect on Primary Production: A Global Comparative Analysis in Marine Ecosystems. Limnology and Oceanography 46:1824-1830

Calbet A, Landry MR (2004) Phytoplankton Growth, Microzooplankton Grazing, and Carbon Cycling in Marine Systems. Limnology and Oceanography 49:51-57

Calbet A, Saiz (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Calvert SE and Price NB (1970) Minor metal contents of recent organic-rich sediments off South West Africa. Nature, 227: 593-595.

Carr M-E (2001) Estimation of potential productivity in Eastern Boundary Currents using remote sensing. Deep Sea Research Part II: Topical Studies in Oceanography 49:59-80

Chapman P, Shannon LV (1985) The Benguela ecosystem. Part II. Chemistry and related processes. Oceanography and Marine Biology, Annual Review, 23: 183-251.

Condon, R. H., Decker, M. B. and Purcell, J. E. (2001). Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (Chrysaora quinquecirrha). Hydrobiologia, 451: 89-95.

Demarcq H, Barlow RG, Shillington FA (2003) Climatology and Variability of Sea Surface Temperature and Surface Chlorophyll in the Benguela and Agulhas Ecosystems As Observed by Satellite Imagery. African Journal of Marine Science 25:363-372

Dunne JA, Williams RJ and Martinez ND (2004) Network structure and robustness of marine food webs. Marine Ecology Progress Series, 273: 291-302.

Emeis KC, Brüchert V, Currie B, Endler R, Ferdelman T, Kiessling A, Leipe T, Noli-Peard K, Struck U, Vogt T (2004) Shallow gas in shelf sediments of the Namibian coastal upwelling ecosystem. Continental Shelf Research 24:627-642

Emery KO, Milliman JD, Uchupi E (1973) Physical properties and suspended matter of surface waters in the southeastern Atlantic Ocean. Journal of Sedimentary Research, 43: 822-837.

Estrada M, Marrasé C (1987) Phytoplankton biomass and productivity off the Namibian Coast. South African Journal of Marine Science 5:347-356

Fearon JJ, Boyd AJ and Schülein FH (1992). Views on the biomass and distribution of Chrysaora hysoscella (Linne, 1766) and Aequorea aequorea (Forskal, 1775) off Namibia, 1982-1989. Indian Journal Marine Science, 56: 75-85.

Flynn BA, Richardson AJ, Brierley AS, Boyer DC, Axelsen BE, Scott L, Moroff NE, Kainge PI, Tjizoo BM, Gibbons MJ Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. African Journal of Marine Science 34:131-146

Goldhammer T, Brunner B, Bernasconi SM, Ferdelman TG, Zabel M Phosphate oxygen isotopes: Insights into sedimentary phosphorus cycling from the Benguela upwelling system. Geochimica et Cosmochimica Acta 75:3741-3756 56.

Gruber N, Sarmiento JL (1997) Global patterns of marine nitrogen fixation and denitrification. Global Biogeochemical Cycles, 11: 235-266.

Gupta A (2007). Large rivers: Geomorphology and management. John Wiley and Sons, Chicester, 689 pp.

Hamukuaya H, O'Toole MJ, Woodhead PMJ (1998) Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. South African Journal of Marine Science 19:57-59

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Hansen FC, Cloete RR, Verheye HM (2005) Seasonal and spatial variability of dominant copepods along a transect off Walvis Bay (23°S), Namibia. African Journal of Marine Science 27:55-63

Heip CHR, Duineveld G, Flach E, Graf G, Helder W, Herman PMJ (2001) The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic). Deep-Sea Research Part II: Topical Studies in Oceanography, 48: 32-43.

Hogan CM (2012) Kunene River. In: The Encyclopedia of Earth. http://www.eoearth.org/view/article/174385/ (last accessed 25 Feb 2015).

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress In Oceanography 83:15-32

Inthorn M, Wagner T, Scheeder G, Zabel M (2006) Lateral transport controls distribution, quality and burial of organic matter along continental slopes in high-productivity areas. Geology, 34: 205-208.

Irigoien X, Flynn KJ, Harris RP (2005) Phytoplankton blooms: a "loophole" in microzooplankton grazing impact? Journal of Plankton Research 27:313-321

Koppelmann R, Schäfer P, Schiebel R (2000) Organic carbon losses measured by heterotrophic activity of mesozooplankton and CaCO3 flux in the bathypelagic zone of the Arabian Sea. Deep Sea Research Part II: Topical Studies in Oceanography 47:169-187

Koppelmann R, Frost J (2008) The ecological role of zooplankton in the twilight and dark zones of the ocean. In: Mertens, L.P. (Ed.), Biological Oceanography Research Trends, Nova Science, New York, 67-130.

Kristensen E, Andersen FØ, Blackburn TH (1992) Effects of benthic macrofauna and temperature on degradation of macroalgal detritus: The fate of organic carbon. Limnology and Oceanography 37:1404-1419

Kröncke IM, Türkay M (2003) Structural and functional aspects of the benthic communities in the deep Angola Basin. Marine Ecology Progress Series, 260: 43-53.

Lahajnar N, Ankele M, Annighöfer M, Bode M, Bohata K, Buchholz F, Eckhardt A, Ekau W, Flohr A, Geist S, Gumbo A, Hansen A, Heene T, Hünerlage LK, Jung S, Kandjii I, Koppelmann R, Kullmann B, Kutter J, Langenberg F, Martin B, Mohrholz V, Muller A, Neumann A, Schukat A, Steigüber C, Teuber L, Verheye H, Waldthausen CV, Wencke P and Werner T (2012) Geochemistry and Ecology of the Namibian Upwelling System. MARIA S. MERIAN Cruise: No. 17, Leg 3 (2011), DFG-Senatskommission für Ozeanographie, Bremen, 62 pp.

Lass HU, Schmidt M, Mohrholz V, Nausch G (2000) Hydrographic and Current Measurements in the Area of the Angolaâ€“Benguela Front. Journal of Physical Oceanography 30:2589-2609

Lavik G, Stuhrmann T, Bruchert V, Van der Plas A, Mohrholz V, Lam P, Muszmann M, Fuchs BM, Amann R, Lass U, Kuypers MMM (2009) Detoxification of sulphidic African shelf waters by blooming chemolithotrophs. Nature 457:581-584

Marshall NB and Iwamoto T (1973) Family Macrouridae. In: Cohen DM, Ebeling AW, Iwamoto T, McDowell SB, Marshall NB, Rosen DE, Sonoda P, Weed WH and Woods LP, Fishes of the Western North Atlantic. Memoirs of the Sears Foundation of Marine Research, New Haven, 496-665.

Martin JH, Knauer GA, Karl DM, Broenkow WW (1987) VERTEX: carbon cycling in the northeast Pacific. Deep Sea Research Part A Oceanographic Research Papers 34:267-285

Martin B, Christiansen B (1997) Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 44:541-558

Martin WR, Sayles FL (2004) Organic matter cycling in sediments of the continental margin in the northwest Atlantic Ocean. Deep Sea Research Part I: Oceanographic Research Papers 51:457-489

Meeuwis JM, Lutjeharms JRE (1990) Surface thermal characteristics of the Angola-Benguela front. South African Journal of Marine Science 9:261-279

Mohrholz V, Bartholomae CH, van der Plas AK, Lass HU (2008) The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Continental Shelf Research 28:424-441

Mohrholz V, Bartholomae CH, van der Plas AK, Lass HU (2008) The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Continental Shelf Research 28:424-441

Mollenhauer G, Inthorn M, Vogt T, Zabel M, Sinninghe Damsté JS, Eglinton TICQ (2007) Aging of marine organic matter during cross-shelf lateral transport in the Benguela upwelling system revealed by compound-specific radiocarbon dating. Geochemistry, Geophysics, Geosystems 8:n/a-n/a

Monteiro PM and van der Plas AK (2006) Low oxygen water (LOW) variability in the Benguela system: Key processes and forcing scales relevant to forecasting in Large Marine Ecosystems. Elsevier, 14: 71-90.

Motodo S (1959) Devices of simple plankton apparatus. Memoirs of Faculty of Fisheries, Hokkaido University, 7: 73-94.

Neumann A, Lahajnar N and Emeis KC (subm.) Benthic remineralisation rates in shelf and slope sediments of the northern Benguela upwelling margin. Continental Shelf Research.

Nixon S. and Thomas A (2001) Research Note On the size of the Peru upwelling ecosystem. Deep-Sea Research I, 48: 2521-2528.

Nogueira E, Pérez FF, Ríos AF (1997) Seasonal Patterns and Long-term Trends in an Estuarine Upwelling Ecosystem (Ría de Vigo, NW Spain). Estuarine, Coastal and Shelf Science 44:285-300

Ohde T, Mohrholz V Interannual variability of sulphur plumes off the Namibian coast. International Journal of Remote Sensing 32:9327-9342

Olivar MP. and Barange M (1990) Zooplankton of the northern Benguela region in a quiescent upwelling period. Journal of Plankton Research, 12: 1023-1044.

Parsons TR, Takahashi M and Hargrave B (1984) Biological oceanographic. Pergamon Press, Oxford, 330 pp.

Perry RI, Harding GC, Loder JW, Tremblay MJ, Sinclair MM, Drinkwater KF (1993) Zooplankton distributions at the Georges Bank frontal system: retention or dispersion? Continental Shelf Research 13:357-38

Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. Progress in Oceanography 26:1-73

Pfannkuche O and Lochte K (1993) Open ocean pelago-benthic coupling: cyanobacteria as tracers of sediementing salp faces. Deep Sea Research I., 40: 727-737.

Poole R, Tomczak M (1999) Optimum multiparameter analysis of the water mass structure in the Atlantic Ocean thermocline. Deep Sea Research Part I: Oceanographic Research Papers 46:1895-1921

Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. Fisheries Oceanography 15:451-464

Purcell J, Arai M (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27-44

Ricklefs RE (1987) Community Diversity: Relative Roles of Local and Regional Processes. Science 235:167-171

Rollwagen-Bollens GC and Landry MR (2000) The biological response to ironfertilization in the easternequatorial Pacific (IronEx II). II. Mesozooplankton abundance, biomass, depth distribution and grazing. Marine Ecology Progress Series, 201: 43-56.

Roughgarden J (2006) Marine Metapopulations, Foreword. In: Kritzer, J. and Sale, P.F. (eds.), Marine metapopulations. Elsevier, San Diego, 17-20.

Rowe, GT (1981) The deep-sea ecosystem. In: Longhurst, A. R. (ed.), Analysis of marine ecosystems. Academic Press, London, 235–267.

Sakko AL (1998) The influence of the Benguela upwelling system on Namibia's marine biodiversity. Biodiversity & Conservation 7:419-433

Sanders HL (1968) Marine benthic diversity: A comparative study. American Naturalist, 102: 243-282.

Schulz HN, Brinkhoff T, Ferdelman TG, Mariné MH, Teske A, Jorgensen BB (1999) Dense Populations of a Giant Sulfur Bacterium in Namibian Shelf Sediments. Science 284:493-495

Schulz HN and Jørgensen BB (2001) Big bacteria. Annual Review of Microbiology, 55: 105-137.

Schulz HN, Schulz HD (2005) Large Sulfur Bacteria and the Formation of Phosphorite. Science 307:416-418

Shannon CE and Weaver W (1949) The mathematical theory of communication. Champaign Il: University of Illinois Press, Urbana, 144 pp.

Shannon LV (1985) The Benguela Ecosystem, I., Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology 23:105-182

Shannon LV, O'Toole M (2003) Sustainability of the Benguela: ex Africa semper aliquid novi. In: Hempel G, Sherman K (eds) Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research. Elsevier, p 423

Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR and Winters KB (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences, 105: 8974-8979.

Stramma L, England M (1999) On the water masses and mean circulation of the South Atlantic Ocean. Journal of Geophysical Research: Oceans 104:20863-20883

Suess E (1980) Particulate organic carbon flux in the oceans-surface productivity and oxygen utilization. Nature, 288: 260-263.

Timonin AG, Arashkevich EG, Drits AV, Semenova TN (1992) Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod Calanoides carinatus. South African Journal of Marine Science 12:545-560

Utne-Palm AC, Salvanes AGV, Currie B, Kaartvedt S, Nilsson GrE, Braithwaite VA, Stecyk JAW, Hundt M, van der Bank M, Flynn B, Sandvik GK, Klevjer TA, Sweetman AK, BrÃ¼chert V, Pittman K, Peard KR, Lunde IG, StrandabÃ¸ RnAU, Gibbons MJ Trophic Structure and Community Stability in an Overfished Ecosystem. Science 329:333-336

Venter GE (1988) Occurrence of jellyfish on the west coast off South West Africa / Namibia. Report of the South African national Science Program, 157: 56-61.

Verheye HM, Hutchings L, Huggett JA, Painting SJ (1992) Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. South African Journal of Marine Science 12:561-584

Vinogradov ME (1968) Vertical distribution of the Oceanic zooplankton. Academy of Science of the U.S.S.R.. Institute of Oceanography, Moscow, 339 pp.

Wasmund N, Lass HU, Nausch G (2005) Distribution of nutrients, chlorophyll and phytoplankton primary production in relation to hydrographic structures bordering the Benguela-Angolan frontal region. African Journal of Marine Science 27:177-190

Weeks SJ, Shillington FA (1996) Phytoplankton pigment distribution and frontal structure in the subtropical convergence region south of Africa. Deep Sea Research Part I: Oceanographic Research Papers 43:739-768

Werner J (2012) Untersuchungen zur Benthosbesiedlung auf dem Schelf und am Schelfhang im Auftriebsgebiet vor Namibia mit Hilfe eines ferngesteuerten Tauchfahrzeugs (Remotely Operated Vehicle, ROV). Germany: Bachelor Thesis, University of Hamburg, Hamburg, 61 pp.

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New development in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology 87:313-323

Wishner K, Levin LA, Growing M, Mullineaux L (1990) Involvement of the oxygen minimum in benthic zonation on a deep seamount. Nature, 346: 57-59.

Zettler M, Bochert R, Pollehne F (2009) Macrozoobenthos diversity in an oxygen minimum zone off northern Namibia. Marine Biology 156:1949-1961

Chapter 8

General Discussion

Many studies about microzooplankton distribution and composition (Beers et al. 1980; Stoecker et al. 1984; Dolan & Pierce 2013) and its grazing impact on phytoplankton have been published (Strom 1991; Calbet 2001; Calbet & Landry 2004; Strom et al. 2001; Suffrian 2008; Löder 2010; Cáceres et al 2013). However, detailed information about the role of microzooplankton in upwelling systems and its position within the food web in these productive areas is still missing. This knowledge, however, is essential to understand biological processes in upwelling systems, the food web design and interactions between physical and biological components. Gaining this information will help us to allow predictions of ecological changes in ecosystems associated with climate change. This study focuses on microzooplankton in the Benguela Upwelling System (BUS) by yielding complex information about its distribution, composition, relation to the water masses and its essential role in this highly productive ecosystem.

Key topics of this thesis are microzooplankton distribution patterns depending on environmental and biological parameters, the influence of upwelling structures on the microzooplankton community, short-time dynamics and patchiness of microzooplankton and interactions between microzooplankton, mesozooplankton and the benthic community. In total 81 taxa were detected, belonging to 16 groups. The main groups were: mixo- and heterotrophic dinoflagellates (17 taxa), naked ciliates (18 taxa), tintinnids (22 taxa), and copepods (5 taxa).

8.1. Microzooplankton – the drivers and distribution patterns

This study presents for the first time detailed information on the distribution and composition of microzooplankton in the BUS. Upwelling systems are highly variable ecosystems, which are characterized by changes in temperature, salinity, oxygen concentrations and food availability. The northern BUS is characterized by intense seasonal patterns in upwelling intensity with highest values during southern winter (Bartholomae & van der Plas 2007). We analysed the dependence of microzooplankton on different environmental and biological drivers. The total abundance distribution of microzooplankton in the northern BUS is spanning broad spatial scales (ranging from ten to hundreds of kilometers) and is highly influenced by chl *a* concentrations (*manuscript 1*). The influence of high primary production on the total abundance distribution could be an indicator for a bottom-up control. The phytoplankton blooms grow faster and reach higher densities and more biomass in high upwelling areas, which supports the subsequent high productivity within the higher trophic levels. However, the bottom-up effects are difficult to detect due to influences and interactions of many other biotic factors.

The diversity of microzooplankton is more likely influenced by environmental conditions. The nearshore assemblages are dominated by a few taxa only, which may reach high abundances, whereas oceanic communities comprise a lot more species at low abundances. Zooplankton diversity reflects the complexity of the food web (Gibbons & Hutchings 1996). We assume that the food web associated with fresh upwelled water is relatively simple structured with only a few trophic levels. The species abundance and assemblage diversity in nearshore waters changes with the intensity of upwelling. An active Ekman transport, where the water is moved further offshore and replaced by fresh upwelled water features only a low number of species (Gibbons & Hutchings 1996). In contrast, complex food webs containing many micro-heterotrophic links prevail further offshore.

The dependence between the occurrence of some microzooplankton taxa and water temperature was additionally analysed. The ciliates and small heterotrophic dinoflagellates, composed mainly by *Ceratium* spp., showed a clear preference for the warm offshore waters. This species are generally detected in warm water masses with relatively high irradiance (Baek et al. 2008). In contrast, small copepods, mainly composed by worldwide distributed *Oncaea* spp. and *Microsetella* spp., were mainly detected in fresh upwelled cold water and the filament centre (*manuscript 1 and 2*).

However, the interaction of the drivers controlling the distribution and composition of microzooplankton in upwelling systems is very complex. The distribution is driven by the interaction of many physical and biological parameters. Distinct species may react differently on changes within the environment. Some species are controlled by temperature (Dvoretsky & Dvoretsky 2009), whereas others are influenced by pH (Russell et al. 2004; Lombard et al. 2010), food availability (Castellani et al. 2005; Zamora-Terol & Saiz 2013) or food quality (Berggreen et al. 1988, Löder et al. 2011).

8.1.1. The north-south gradient

The taxa composition was similar between the northernmost and southernmost area of the northern BUS. However, the similar microzooplankton structure is caused by different reasons like for instance contrasting environmental conditions and different food web designs. The southern part of the study area is characterized by permanent intensive upwelling (permanent upwelling cell off Lüderitz). The high nutrient concentrations favour the development of a strong phytoplankton bloom with large diatoms. The microzooplankton of this area is mainly composed of heterotrophic and some mixotrophic dinoflagellates and small copepods. Heterotrophic dinoflagellates are the most suitable grazers of large phytoplankton cells due to their plasticity to feed on organisms larger then themselves (Lessard, 1991; Hansen 1992; Strom & Strom 1996; Saito et al. 2006; Sherr and Sherr 2007).

The northern BUS is influenced by two different water masses: (1) almost pure Eastern South Atlantic Central Water (ESACW) entering the area from the South and (2) a mixture of ESACW and South Atlantic Central Water (SACW) originating from the Angola Dome. Chl *a* values remain very low during low upwelling intensity. This region is mainly dominated by mixotrophic dinoflagellates belonging to the *Ceratium* group and copepodite stages of larger calanoid copepods. Some *Ceratium* species are able to survive at low nutrient conditions (Baek et al. 2008) due to their ability to use additional nutrient sources by mixotrophic feeding. They are also strongly influenced by the vertical and horizontal distribution of ciliate prey in stratified waters. They may even remove approximately 67% of the ciliate population per day (Smalley and Coast 2002).

Spatial differences in the distribution of different taxa was especially detected within the tintinnid group (figure 8-1). The southern part of the study area is dominated by two cosmopolitan species (*Codonella galea* and *Codonellopsis morchela*; (*manuscript 1*) whereas the warm-temperate species *Rhabdonella spiralis* is dominating in the northern part. This distribution pattern is also similar during the season of high upwelling intensity, in the southern winter (*manuscript* 2). Tintinnids can be used as indicators for biological/environmental condition assessments in the marine ecosystem (Kchaou et al. 2009, Jiang et al. 2012, Xu et al. 2011). Water mass features have been shown to be very relevant in determining the natural patterns in tintinnid appearance (Thompson et al. 1999). The cosmopolitan tintinnid species are associated with the ESACW and the warm-temperate species are associated with the warmer mixture of ESACW and SACW. When the two different water masses meet, the physical and chemical properties of the water change. Also plankton connected to these water masses mixes. The individuals carried by the different water masses remain unchanged and are discernible until they die and decompose. Due to the relation of tintinnids to different water properties, tintinnids can not only be used as indicators for different water masses, but also as indicators for the origin of these different water masses.

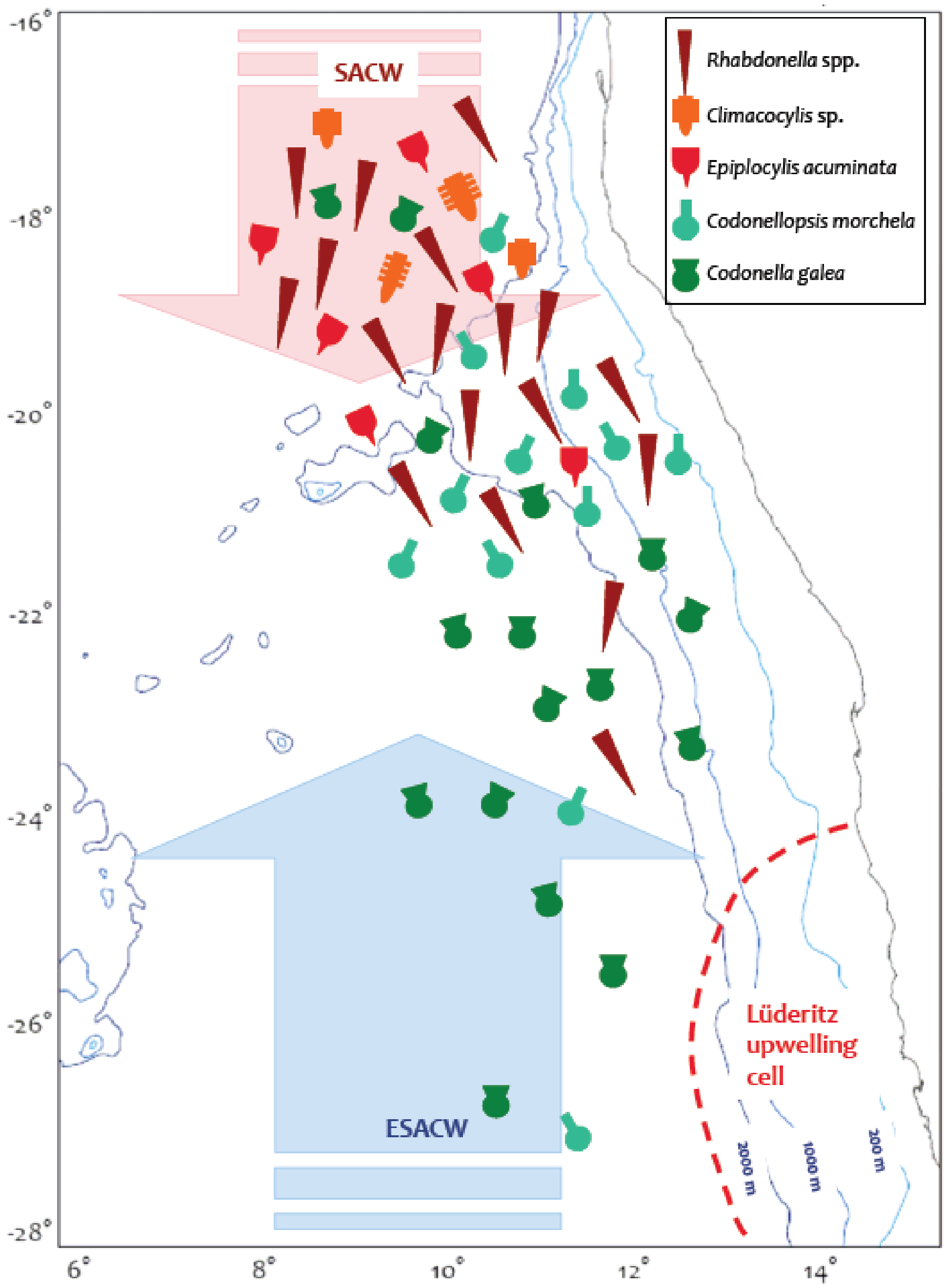


Figure 8-1: Conceptual view of the tintinnid distribution in the northern Benguela Upwelling System. Red = warm-temperate species, green = cosmopolitan species. ESACW = Eastern South Atlantic Central Water, SACW = South Atlantic Central Water.

8.1.2. The shelf – offshore gradient

Variations in phytoplankton community structure and chl *a* concentrations directly influence the composition and diversity of the microzooplankton community. Generally mainly small phytoplankton cells (small diatoms and small dinoflagellates) exist in fresh upwelled water with high nutrient concentrations (figure 8-2A; Hansen et al. 2014; Pitcher et al. 1998, Walker & Peterson 1991). Larger diatoms are well adapted to conditions with reduced nutrient content and are generally detected in high concentrations in matured upwelled water (figure 8-2B). Small dinoflagellates are most abundant further offshore, where the water masses contain very low nutrient concentrations (figure 8-2C; Hansen et al. 2014; Hart & Currie 1960).

High abundances of microzooplankton were generally associated with high chl a concentrations (*manuscript 3*). Naked ciliates and small dinoflagellates dominate the fresh upwelled water, whereas high abundances of larger mixo- and heterotrophic dinoflagellates were present further offshore (figure 8-2; *manuscript 1,* 2). This is the only group of microzooplankton able to feed on larger organisms as themselves such as diatoms (Hansen 1992; Horner et al. 2005; Lessard & Swift 1986; Saito et al. 2006; Sherr & Sherr 2007) and they may take advantage of this situation. The phytoplankton composition and its quality as a food source for mesozooplankton changes with increasing distance from the shelf and ciliates become more important than phytoplankton as a food source for larger organisms like for instance copepods (Hernández-León et al. 2002). The microzooplankton community in offshore waters is mainly dominated by smaller mixotrophic dinoflagellates due to their ability to switch from heterotrophic to autotrophic nutrition under low prey concentration. But also small heterotrophic dinoflagellates are relatively abundant. Heterotrophic dinoflagellates may survive in low food concentrations either feeding on alternative prey, or reducing their metabolic rate (Sherr & Sherr 2007).

The ratio between naked ciliates and mixo- and heterotrophic dinoflagellates changes in direction from the shelf to offshore (*manuscript* 2 *and 3*). The ratio is very low close to the shore and increases further from the shelf and drops again offshore following the chl *a* concentrations (*manuscript 3*). There is also evidence that ciliates are often present under conditions of high chl *a* concentrations due to high concentrations of small phytoplankton species.

Additionally, the microzooplankton diversity increases with increasing distance from the coast. The community on the shelf is mainly comprised of only a few microzooplankton taxa, whereas the community at the shelf break and further offshore is composed of almost five times more taxa, which is related to the fact that the food web becomes more complex with increasing distance from the coast, whereas a relatively simple food web exists in fresh upwelled water masses.

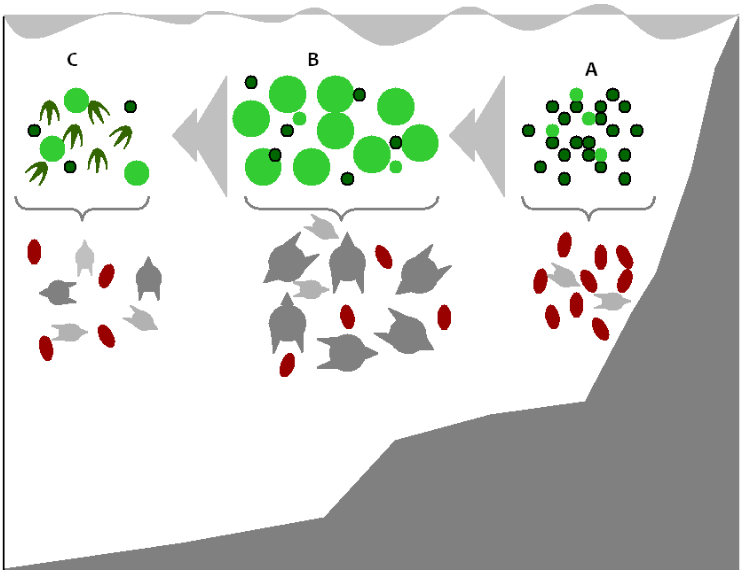


Figure 8-2: Conceptual model of phytoplankton and microzooplankton interactions in direction from the shelf to offshore in the Benguela Upwelling Systems. (A) small nanoflagellates and diatoms develop on the shelf and are consumed by ciliates; (B) large diatoms dominate the phytoplankton further offshore and are mainly consumed by large heterotrophic dinoflagellates; (C) small autotrophic dinoflagellates and smaller diatoms are well adapted to low nutrient concentrations and are mainly consumed by small mixo- and heterotrophic dinoflagellates. Dark green = nanoflagellates and autotrophic dinoflagellates, light green = diatoms, red = ciliates, dark grey = heterotrophic dinoflagellates, light grey = mixotrophic dinoflagellates.

8.2. Microzooplankton in relation to upwelling structures

Upwelling filaments may develop due to the wind stress and water circulation. Filaments are important hydrographic structures for the dynamics of Eastern Boundary Upwelling Systems and transport nutrients and plankton to the open ocean (Álvarez-Salgado 2001, García-Muñoz 2004, Mackas 2006, Strub 1991). Until now, only few studies about microzooplankton in association to upwelling filaments have been published (Batten et al. 2001; Halvorsen et al. 2001).

Some microzooplankton groups are connected to the filament fronts or the cold filament centre (*manuscript* 2). The protists, naked ciliates, small mixo- and heterotrophic dinoflagellates and tintinnids, prefer the warmer water masses surrounding the filament, whereas small copepods as for instance *Microsetella* sp., *Oithona* sp. and *Oncaea* sp. are connected to the cold filament water. Dvoretsky & Dvoretsky (2009) speculated that temperature is the major factor limiting the distribution and fecundity of the small copepod *Oithona* spp. However, on the basis of our findings, we assume that the distribution of the small copepod species in the filament is rather driven by the food conditions. Species such as *Oithona* spp. prefer to feed on small dinoflagellates and ciliates within the 10-40 µm size range (Castellani et al. 2005; Zamora-Terol & Saiz 2013). High abundances of small ciliates and dinoflagellates as well as increased abundances of copepods can be observed in the centre of the filament (*manuscript* 2).

During the filament study distinct fronts were detected north and south of a filament. Fronts are generally considered to be very productive areas with high abundances of different plankton groups and fish (Hernández-León et al. 2002; Marańón & Fernández 1995; Sverdrup 1938). Some microzooplankton taxa concentrate in frontal zones. Differences in microzooplankton composition between the northern and southern fronts have been detected. Interestingly, the highest abundances of microzooplankton were not detected at the northern front, where the high nutrient SACW meets the filament. Instead, enhanced abundances were detected in the southern front and also in the centre of the upwelling filament (*manuscript* 2). The distribution of microzooplankton in relation to the upwelling filament is rather a result of water currents associated with the filament. During the filament study, the water mass at the southern front moved strongly from the coast to the open ocean, transporting coastal zooplankton away from the coast (see *manuscript* 2). In contrast, the water moved back towards the coast at the northern front, which could hamper an expansion of plankton from the coast to the open ocean.

The biological activity at the fronts of upwelling filaments is driven only partially by the environmental conditions as described above, but also by local biological processes occurring in the fronts. One of those factors is the feeding pressure and feeding selectivity of mesozooplankton. Many mesozooplankton groups such as copepods are selective feeders and may ingest prey non-proportionally to ambient densities (Castellani et al. 2008; Kleppel 1993). The feeding selectivity is mainly affected by the trophic state of the ‘’ecosystem” (Atkinson 1995), the food size (Frost 1972) and quality (Berggreen et al. 1988; Löder et al. 2011). The copepod diet switches from phytoplankton-dominated to microzooplankton-dominated, when the phytoplankton quality as food for mesozooplankton decreases (Löder et al. 2011).

The functioning of upwelling filaments is very complex and changes of the zooplankton community connected to the fronts depend on physiological parameters such as properties of the entering water masses, the water movement associated to the filament and many biological parameters such as the composition of the original community at the beginning of the filament or predation pressure.

8.3. Dynamics and patchiness of microzooplankton

We detected high variability in microzooplankton abundance and composition during an anchor station in January 2013. These variations were relatively high within the naked ciliate and tintinnid group (*manuscript 3*). Many physical and biological dynamics and interactions control plankton distribution and patchiness. Plankton patchiness is an important feature in the oceanic ecosystem. Mesoscale hydrodynamics impact the growth, coexistence and dominance of species (Hernández-Garcia & López 2004, Neufeld & Hernández-Garcia 2009). The survival of zooplanktonic organisms is closely associated with the ability to locate patches (Mullin & Brooks 1976; Daro 1988). Zooplankton organisms search for food particles by means of multiple strategies; they can use physical gradients and chemical signals to locate them (Kiørboe 2001). Therefore we assume that the distribution of microzooplankton is influenced by interactions between phytoplankton size, distribution and feeding ability of diverse microzooplankton groups, since we detected changes in microzooplankton composition with altering water masses (*manuscript 1, 2 and 3*) and a strong dependence on chl *a* concentrations (*manuscript 3*). Also, the predation pressure by copepods on microzooplankton may play an important role in high productive areas such as the northern BUS. High abundances of copepods may impact not only the biomass of microzooplankton, but also benefit from some species of microzooplankton, especially ciliates, with behavioural responses to avoid predation (Calbet & Saiz 2005), which could lead to agglomerations of some species.

8.4. Connections between microzooplankton, mesozooplankton and the benthic fauna

It is crucial to understand how the pelagic components impact the benthic structure in the different regions and depths in upwelling regions. Food for the benthos is mainly supplied by primary production in the euphotic zone and subsequent deposition of organic particles to the sea floor. Although clear relationships between microzooplankton and other planktonic and benthic organisms were not detected, it is notable that abundances of the benthic fauna were higher in areas with higher pelagic biomass (*manuscript* 4). Alterations in the pelagic environment are not reflected in the benthic community within short time-scales (Aspetsberger et al. 2007) but over a longer time span, which makes these communities more conservative than the pelagic ones.

To understand the functioning of a highly variable ecosystem like the BUS, it is essential to comprehend the relationships within the food web. Mesozooplankton directly consume 10-15% of the primary production (Calbet 2001), while microzooplankton may consume 60-80% (Calbet and Landry 2004). Microzooplankton is an important food source for mesozooplankton and in some regions even more important than phytoplankton. Ciliates have been recognized as an essential component of the copepod diet. Their contribution to copepod daily food rations is disproportionally high and increases with the trophic status of the ecosystem (Calbet & Saiz 2005). Based on this knowledge, it is evident the strength and importance of the heterotrophic link between the microbial food web and the 'classical' food chain (Sherr et al. 1987). Overall, the quality and quantity of organic matter from the pelagial reaching the bottom in form of sedimenting particles is one of the major factors influencing the benthic fauna (Mills 1975).

8.5. Climate change and expected changes within the microzooplankton community

A general wind-driven ocean upwelling intensification in the Eastern Boundary Upwelling System is expected as a result of global warming and intensified thermal low-pressure cells over the coastal land of upwelling regions (Bakun et al. 2010). The direct impact of climate change on microzooplankton distribution, composition and activities is a result of interactions between biological and physical drivers.

Decreased pH and increased CO_2 in the ocean affects some microzooplankton groups such as calcifying organisms, the planktonic foraminifera (Russell et al. 2004; Lombard et al. 2010), molluscs (Bamber 1990; Comeau et al. 2009) and bivalves (Welladsen et al. 2010). Indirect influence of this intensification on microzooplankton will be generated by changes in the phytoplankton community. A dense phytoplankton bloom can develop due to higher nutrient concentrations at the surface. Mixo- and heterotrophic dinoflagellates may benefit from this dense phytoplankton bloom consisting mainly of large diatoms. Generally, harmful and toxic dinoflagellates bloom (red tides) may cause severe commercial and recreational problems, as well as faunal mortalities (Horstman 1981) and human illness through consumtion of contaminated fish (Grindley & Sapeika 1969; Popkiss 1979; Pitcher 1993b). Furthermore, high accumulated organic matter sinks to the bottom and causes hypoxia and releases noxious products of anaerobic decomposition that include poisonous hydrogen sulfide and methane (Bakun 2010), which may negatively influence the fish stocks in this area. Due to this extension of oxygen minimum zones, the relative importance of microzooplankton as grazers of phytoplankton may increase since most meso- and macrozooplankton cannot cope with such low oxygen concentrations over longer time periods. Many protistan zooplankton may survive even in anoxic conditions through anaerobic respiration (Marcus 2001).

8.6. Conclusion and future perspectives

This study enlightens the role of microzooplankton in the BUS. It revealed a complex set of information about microzooplankton distribution and composition in relation to the biological and physical parameters, the influence of upwelling structures on microzooplankton community, short-time dynamics and patchiness of microzooplankton and interactions between microzooplankton, mesozooplankton and the benthic community. However, the understanding of the importance of microzooplankton in this productive area is still not complete.

It is important to learn more about the relationships within the food web in upwelling systems in order to be able to understand the responses of the ecosystem to changes within the environment due to the anthropogenic influence. Many studies have been undertaken to picture the food web in the northern BUS (Travers et al. 2010; Bohata & Koppelmann 2013; Schukat et al. 2014; Werner et al. 2014). However, basic data about the microzooplankton position in the food chain was so far still missing. Many authors described the grazing impact of microzooplankton on phytoplankton all around the World. Information about microzooplankton grazing in upwelling systems is still rare (Böttjer & Morales 2005; Mcmanus et al. 2007). Traditionally, the dilution method after Landry and Hassett (1982) is the most commonly applied method for estimating the rates of microzooplankton grazing on primary production (Calbet and Landry 2004) but this technique contains many difficulties (Calbet & Saiz 2013). It is necessary to develop a modification of this technique, which will make the experimental set up and interpretation easier. Additionally, grazing impact of mesozooplankton on phytoplankton and microzooplankton should be estimated. As already mentioned, the grazing impact of mesozooplankton on phytoplankton is very low in comparison to the grazing impact of microzooplankton. However, the information about the mesozooplankton grazing, species-specific preference to prey over microzooplankton e.g. mesozooplankton selectivity is still incomplete. Also the trophic position using stable isotope analyses has been proven to be difficult due to the small size of microzooplankton species. Traditionally the smallest size of plankton in the aquatic environments, has been used as a baseline without separating the microzooplankton and phytoplankton apart (Bode et al. 2003; Bode et al. 2004; Schukat 2014).

On the basis of our findings, the distribution of microzooplankton in upwelling regions is relatively patchy due to complex biological-physical interactions. For some species we could estimate temperature/water masses preference. However, these datasets represent only a temporary picture of the state of the ecosystem. We detected during our short-time study that the phytoplankton and microzooplankton communities are very variable. Further studies focusing on long-term observations have to be undertaken for gaining a deeper insight and a better understanding of the responses of microzooplankton on biological and physical drivers.

8.7. References

Álvarez-Salgado XA, Doval MD, Borges AV, Joint I, Frankignoulle M, Woodward EMS, Figueiras FG (2001) Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System. Progress in Oceanography 51:321-337

Aspetsberger F, Zabel M, Ferdelman T, Struck U, Mackensen A, Ahke A, Witte U (2007) Instantaneous benthic response to different organic matter quality: In situ experiments in the Benguela Upwelling System. Marine Biology Research 3:342-356

Atkinson A (1995) Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. ICES Journal of Marine Science: Journal du Conseil 52:385-396

Bakun A, Field DB, Redondo-Rodriguez ANA, Weeks SJ (2010) Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Global Change Biology 16:1213-1228

Bamber RN (1990) The effects of acidic seawater on three species of lamellibranch mollusc. Journal of Experimental Marine Biology and Ecology 143:181-191

Bartholomae CH, van der Plas AK (2007) Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. African Journal of Marine Science 29:25-35

Baek HS, Shimode S, Han M-S, Kikuchi T (2008) Growth of dinoflagellates, Ceratium furca and Ceratium fusus in Sagami Bay, Japan: The role of nutrients,. Harmful Algae:729-739

Batten SD, Fileman ES, Halvorsen E (2001) The contribution of microzooplankton to the diet of mesozooplankton in an upwelling filament off the north west coast of Spain. Progress in Oceanography 51:385-398

Beers JR, Reid FMH, Stewart GL (1980) Microplankton of the North Pacific Central Gyre. Population structure and abundance, June 1973. Internationale Revue gesamten Hydrobiologie 60:607-638

Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepodAcartia tonsa during development: Implications for determination of copepod production. Marine Biology 99:341-352

Bode A, Carrera P, Lens S (2003) The pelagic foodweb in the upwelling ecosystem of Galicia (NW Spain) during spring: natural abundance of stable carbon and nitrogen isotopes. ICES Journal of Marine Science: Journal du Conseil 60:11-22

Bode A, Barquero S, González N, Alvarez-Ossorio MT, Varela M (2004) Contribution of heterotrophic plankton to nitrogen regeneration in the upwelling ecosystem of A Corua (NW Spain). Journal of Plankton Research 26:11-28

Bohata K, Koppelmann R (2013) Chaetognatha of the Namibian Upwelling Region: Taxonomy, Distribution and Trophic Position. PLoS ONE 8:e53839

Böttjer D, Morales CE (2005) Microzooplankton grazing in a coastal embayment off Concepción, Chile, (36° S) during non-upwelling conditions. Journal of Plankton Research 27:383-391

Cáceres C, Taboada FG, Höfer J, Anadón R (2013) Phytoplankton Growth and Microzooplankton Grazing in the Subtropical Northeast Atlantic. PLoS ONE 8:e69159

Calbet A (2001) Mesozooplankton Grazing Effect on Primary Production: A Global Comparative Analysis in Marine Ecosystems. Limnology and Oceanography 46:1824-1830

Calbet A, Landry MR (2004) Phytoplankton growth, Microzooplankton grazing, and carbon cycling in marine systems. Limnol Oceanog 40:51 – 57

Calbet A, Saiz (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Castellani C, Irigoien X, Harris RP, Lampitt RS (2005) Feeding and egg production of Oithona similis in the North Atlantic. Marine Ecology Progress Series 288:173-182

Castellani C, Irigoien X, Mayor DJ, Harris RP, Wilson D (2008) Feeding of Calanus finmarchicus and Oithona similis on the microplankton assemblage in the Irminger Sea, North Atlantic. Journal of Plankton Research 30:1095-1116

Comeau S, Gorsky G, Jeffree R, Teyssié JL, Gattuso JP (2009) Impact of ocean acidification on a key Arctic pelagic mollusc (Limacina helicina). Biogeosciences 6:1877-1882

Daro MH (1988) Migratory and Grazing Behavior of Copepods and Vertical Distribution of Phytoplankton. Bulletin of Marine Science 43:710-729

Dolan JR, Pierce RP (2013) Diversity and distributions of tintinnids. In: Dolan JR, Montagnes DJS, Agatha S, Coats DW, Stoecker DK (eds) The biology and ecology of tintinnid ciliates. John Wiley & Sons, Ltd., Chichester, p 296

Dvoretsky VG, Dvoretsky AG (2009) Lify cycle of *Oithona similis* (Copepoda: Cyclopoida) in Kola Bay (Barents Sea). Marine Biology 156:1433-1446

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography 17:805-815

García-Muñoz M, Arístegui J, Montero MF, Barton ED (2004) Distribution and transport of organic matter along a filament-eddy system in the Canaries â€“ NW Africa coastal transition zone region. Progress in Oceanography 62:115-129

Gibbons MJ, Hutchings L (1996) Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system, Vol. Academy of Science of South Africa 92(2): 63-75

Grindley J, Sapeika N (1969) The cause of mussel poisoning in South Africa. . South African Medical Journal 43:276-279

Halvorsen E, Pedersen OP, Slagstad D, Tande KS, Fileman ES, Batten SD (2001) Microzooplankton and mesozooplankton in an upwelling filament off Galicia: modelling and sensitivity analysis of the linkages and their impact on the carbon dynamics. Progress in Oceanography 51:499-513

Hansen A, Ohde T, Wasmund N (2014) Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. Journal of Marine Systems 140, Part B:130-137

Hansen PJ (1992) Particle size selection, feeding rates and growth dynamics of marine heterotrophic dinoflagellates, with special emphasis on *Gyrodinium spirale*. Marine Biology 114:327-334

Hart TJ, Currie RI (1960) The Benguela current, Vol 31. University Press, Cornell

Hernández-García E, López C (2004) Sustained plankton blooms under open chaotic flows. Ecological Complexity 1:253-259

Hernández-León S, Almeida C, Portillo-Hahnefeld A, Gómez M, Rodríguez JM, Arístegui J (2002) Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off northwest Africa. Journal of Marine Research 60:327-346

Horner RA, Postel JR, Halsband-Lenk C, Pierson JJ, Pohnert G, Wichard T (2005) Winter-spring phytoplankton blooms in Dabob Bay, Washington. Progress In Oceanography 67:286-313

Horstmann K (1981) Revision der europäischen tersilochinen (Hymenoptera, Ichneumonidae). Spixiana Suppl 4

Jiang Y, Xu H, Zhang W, Zhu M, Al-Rasheid KS (2012) Can body-size patterns of ciliated zooplankton be used for assessing marine water quality? A case study on bioassessment in Jiaozhou Bay, northern Yellow Sea. Environmental Science and Pollution Research 19:1747-1754

Kchaou N, Elloumi J, Drira Z, Hamza A, Ayadi H, Bouain A, Aleya L (2009) Distribution of ciliates in relation to environmental factors along the coastline of the Gulf of Gabes, Tunisia. Estuarine, Coastal and Shelf Science 83:414-424

Kiørboe T (2001) Formation and fate of marine snow: small-scale processes with large- scale implications. Scienta Marina 65

Kleppel GS (1993) On the diets of calanoid copepods. Marine Ecology Progress Series 99:183-195

Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. Marine Microbial Food Webs 5:49-58

Lessard EJ, Swift E (1986) Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. Journal of Plankton Research 8:1209-121

Löder MGJ (2010) The role of heterotrophic dinoflagellate and ciliate grazers in the food web at Helgoland Roads, North Sea Jacobs University

Löder MJ, Meunier C, Wiltshire KH, Boersma M, Aberle N (2011) The role of ciliates, heterotrophic dinoflagellates and copepods in structuring spring plankton communities at Helgoland Roads, North Sea. Marine Biology 158:1551-1580

Lombard F, de Rocha RE, Bijma J, Gattuso J-P (2010) Effect of carbonate ion concentration and irradiance on calcification in planktonic foraminifera. Biogeosciences 7:247-255

Mackas DL, Peterson WT, Ohman MD, Lavaniegos BE (2006) Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophysical Research Letters 33:L22S07

Marańón E, Fernández E (1995) Changes in phytoplankton ecophysiology across a coastal upwelling front. Journal of Plankton Research 17:1999-2008

Marcus NH (2001) Zooplankton: Responses to and Consequences of Hypoxia. In: Coastal Hypoxia: Consequences for Living Resources and Ecosystems. American Geophysical Union, p 49-60

Mills EL (1975) Benthic organisms and the structure of marine ecosystems. Journal of the Fisheries Research Board of Canada 32:1657-1663

Mullin MM, Brooks ER (1976) Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnology and Oceanography 21:784-796

Neufeld Z, Hernández-García E (2009) Chemical and biological processes in fluid flows : a dynamical systems approach., Vol. Eorld Scientific, Singapore

Pitcher GC, Horstman DA, Calder D, de Bruyn J, Post B (1993b) he first record of diarrhetic shellfish poisoning on the South African coast. South African Journal of Science 89:512-514

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Marine Ecology Progress Series 172:253-264

Popkiss M, Horstman DA, Harpur D (1979) Paralytic sheUfish poisoning: a report of 17 cases in Cape Tow. South African Medical Journal 55

Russell AD, Hönisch B, Spero HJ, Lea DW (2004) Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera. Geochimica et Cosmochimica Acta 68:4347-4361

Saito H, Ota T, Suzuki K, Nishioka J, Tsuda A (2006) Role of heterotrophic dinoflagellate Gyrodinium sp. in the fate of an iron induced diatom bloom. Geophysis

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Marine Ecology Progress Series 352:187-197

Sherr EB, Sherr BF, Albright LJ (1987) Bacteria: link or sink? Science 235:88-89

Sherr EB, Sherr BF (2002) Significant of predation by protists in aquatic microbial food webs. Antonie Leeuwenhoek 81:293 – 308

Schukat A, Auel H, Teuber L, Lahajnar N, Hagen W Complex trophic interactions of calanoid copepods in the Benguela upwelling system. Journal of Sea Research 85:186-196

Smalley GW, Wayne Coats D (2002) Ecology of the Red-Tide Dinoflagellate Ceratium furca: Distribution, Mixotrophy, and Grazing Impact on Ciliate Populations of Chesapeake Bay. The Journal of Eukaryotic Microbiology 49:63-73

Stoecker D, Davis LH, Anderson DM (1984) Fine scale of spatial correlations between planktonic ciliates and dinoflagellates. J Plankton Res 6:829 – 842

Strom SL (1991) Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the opwen Subarctic Pacific Ocean. Marine Ecology Progress Series 78:103-113

Strom SL, Brainard MA, Holmes JL, Olson MB (2001) Phytoplankton blooms are strongly impacted by microzooplankton grazing in coastal North Pacific waters. Marine Biology 138:355-368

Strom SL, Strom MW (1996) Microplankton growth, grazing, and community structure in the northern Gulf of Mexico. Marine Ecology Progress Series 130:229-240

Strub PT, Korso PM, Huyer A (1991) The nature of the cold filaments in the California Current System. Journal of Geophysical Reasearch 96:743-768

Suffrian K, Simonelli P, Nejstgaard JC, Putzeys S, Carotenuto Y, Antia A (2008) Microzooplankton grazing and phytoplankton growth in marine mesocosms with increased CO2 levels. Biogeosciences 5:1145-1156

Sverdrup HU (1938) On the process of upwelling. Journal of Marine Research 1:115-164

Thompson GA, Alder VA, Boltovskoy D, Brandini F (1999) Abundance and biogeography of tintinnids (Ciliophora) and associated microzooplankton in the Southwestern Atlantic Ocean. Journal of Plankton Research 21:1265-1298

Travers M, Watermeyer K, Shannon LJ, Shin YJ (2010) Changes in food web structure under scenarios of overfishing in the southern Benguela:

Comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems 79:101-111

Walker DR, Peterson WT (1991) Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. South African Journal of Marine Science 11:289-3

Welladsen HM, Southgate PC, Heimann K (2010) The effects of exposure to near-future levels of ocean acidification on shell characteristics of Pinctada fucata (Bivalvia: Pteriidae). molluscan Research 30:125-130

Xu H, Jiang Y, Al-Rasheid KS, Song W, Warren A (2011) Spatial variation in taxonomic distinctness of ciliated protozoan communities at genus-level resolution and relationships to marine water quality in Jiaozhou Bay, northern China. Hydrobiologia 665:67-78

Zamora-Terol S, Saiz E (2013) Effects of food concentration on egg production and feeding rates of the cyclopoid copepod Oithona davisae. Limnology and Oceanography 58:376-387

9 Acknowledgements

I would like to thank my supervisors Prof Dr. Christian Möllmann and Prof. Dr. Friedrich Buchholz for their support and scientific guidance.
Christian, for supporting me during the past years and many fruitful discussions.
Fritz, for helpful comments and support during all the cruises and scientific meetings.

Very special thanks go to Dr. Rolf Koppelmann for the opportunity to conduct this thesis, his continuous support, scientific guidance, many discussions during the last years, and the very positive and pleasant working atmosphere.

I am very grateful for the support and help from Dr. Bettina Martin during all the years of my study and very pleasant time during many research cruises.

Special thanks go to Sarah Schnurr and Anna Schukat for their helpful comments on my thesis and their support during the last phase.

I would like to thank to all my colleagues from the GENUS project for their help during the research cruises, Frauke Langenberg , Anita Flohr, Simon Geist, Thorsten Werner, Niko Lahajnar, Volker Mohrholz, Thoralf Heene, Martin Schmidt, Werner Ekau, Norbert Wasmund, and all the others!

I am thankful for the support and pleasant discussions during our lunch breaks to all my 'IHF' colleagues, Betti, Dominik, Klas, Silke, Muriel, Justus, Margarethe and all others!

Furthermore, I would like to thank to all my co-authors, especially Saskia Otto for her support and ideas during the last period of this thesis.

I want to thank the Federal Ministry of Education and Reasearch (BMBF, Project No. 03F0497E) for the financial support of this thesis.

Finally, I want to thank to my family and friends for their endless encouragement and loving support through all my life.

10 Eidesstattliche Versicherung

Hiermit erkläre ich, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den 30.06.2016

Darlegung zum Eigenanteil an den wissenschaftlichen Manuskripten

Thema der Dissertation: Microzooplankton of the northern Benguela Upwelling System

Manuskript 1: **Spatial patterns of microzooplankton in the northern Benguela Upwelling system** (Bohata Karolina, Otto Saskia A., Koppelmann Rolf, Brust-Möbius Juliane, Mertzen Matthias, Müller Anja)**:** Die Planung der Probenahme, die Gewinnung des Materials und dessen taxonomischen Analysen wurden eigenständig von Karolina Bohata unter Betreuung von Dr. Rolf Koppelmann durchgeführt. Das Verfassen des Textes und die Anfertigung der Graphiken wurden überwiegend von Karolina Bohata mit Hilfe von Dr. Saskia A. Otto durchgeführt. Dr. Juliane Brust-Möbius stellte Chlorophylldaten aus Satellitenaufnahmen bereit und Matthias Mertzen und Anja Müller halfen bei der Probenaufarbeitung.

Manuskript 2: **Microzooplankton communities: fluctuating fundamental components of upwelling filaments** (Bohata Karolina, Koppelmann Rolf, Mohrholz Volker, Möllmann Christian): Die Planung der Probenahme, die Aufnahme der Mikrozooplanktondaten, deren Analyse und das Verfassen des Textes wurden eigenständig von Karolina Bohata unter Anleitung von Dr. Rolf Koppelmann and Prof. Dr. Christian Möllmann durchgeführt. Dr. Volker Mohrholz stellte die Analyse der hydrographischen Daten bereit.

Manuskript 3: **Mikrozooplankton patchiness: short-time series** (Bohata Karolina, Koppelmann Rolf, Louw Deon, van der Plas Anja): Die Planung der Probenahme, die Aufnahme der Mikrozooplanktondaten, deren Analyse und das Verfassen des Textes wurden eigenständig von Karolina Bohata unter Betreuung von Dr. Rolf Koppelmann durchgeführt. Die Aufnahme der physikalischen Daten und Phytoplankton-Daten und deren Analyse wurden mit Hilfe der Ko-Autoren Deon Louw und Dr. Anja van der Plas durchgeführt.

Manuskript 4: **Benthic structures in the Namibian Upwelling Region and the pelagobenthic coupling** (Mertzen Mathias, Rolf Koppelmann, Bohata Karolina, Martin Bettina, Werner Johanna, Neumannn Andreas, Müller Anja, Eckhardt Andre, Möllmann Christian): Die Laboranalyse des Mikrozooplanktons, die Betreuung der Analyse des Mikrozooplanktons und Modifizierungen des Textes wurden von Karolina Bohata durchgeführt. Das Manuskript wurde von Matthias Mertzen unter Betreuung von Dr. Rolf Koppelmann verfasst. Dr. Bettina Martin analysierte das Mesozooplankton und Anja Müller half bei der Analyse des Mikrozooplanktons. Dr. Andreas Neumann stellte Makrozoobenthosdaten und biogeochemische Analysen bereit. André Eckhardt hat die ROV-Einsätze technisch betreut und Prof. Dr. Christian Möllmann modifizierte den Text.