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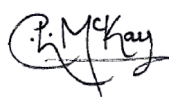
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Title and subtitle Benthic environmental responses to climatic changes during the late Quaternary: a micropalaeontological and geochemical approach

Abstract

There is a limited understanding of how the benthic environment within upwelling regions responded to past rapid climatic changes. Within this thesis, a multiproxy approach is applied to two marine sediment cores from two coastal upwelling sites in the low latitude subtropical Atlantic. With a focus on benthic foraminiferal faunal analyses, the response of the benthic environment to rapid climatic changes and the degree of coupling with surface primary production was reconstructed for the last 35 ka for the Mauritanian upwelling system and 70 ka for the Benguela upwelling system.

Benthic foraminiferal faunal composition shifts occurred within both records, in the case of the Mauritanian upwelling site four shifts occurred: during late MIS3 (35-28 ka), across Heinrich event 2 and the Last Glacial Maximum (28 to 19 ka), throughout Heinrich event 1, the Bølling Allerød and the Younger Dryas (18-11.5 ka) and throughout the Holocene (11 ka – present). From the Benguela Upwelling System, six benthic foraminiferal assemblages were documented within the record: the first two during MIS4 and early MIS3 (70-59 and 59-40 ka), late MIS3 (40-30 ka), early-late MIS2 (30-16 ka), the termination of MIS2 to the onset of MIS1 (16 – 12 ka) and the Holocene (12 ka - present).

Perhaps the most striking finding from both records was the abundance of low oxygen tolerant benthic foraminiferal species *Eubuliminella exilis* being so tightly correlated with diatom accumulation rate. From this coupling, low oxygen conditions at the seafloor were inferred to be caused by extreme levels of productivity export which actually hindered the benthos in terms of benthic foraminiferal diversity and accumulation rate; during Heinrich Event 1 and the Younger Dryas within the Mauritanian upwelling system and during late MIS4 and MIS3 within the Benguela upwelling system.

In conclusion, major changes in deep-sea benthic foraminiferal faunas over the late Quaternary were attributed not only to upwelling intensity influenced by trade wind strength but also a complex balance between surface water productivity, sea level and deep water circulation. Therefore, this thesis demonstrates the rapidity of the benthic environmental response to these factors induced by global scale climatic change.

To investigate the interplay between the surface and bottom water o further, a geochemical approach using the elemental composition of foraminiferal shells (tests) to develop a proxy of bottom water oxygen content was undertaken. The analytical methods of Secondary Ion Mass Spectrometry (SIMS) and Flow-Through Inductively Coupled Plasma Optical Emission Spectroscopy (FT-ICP-OES) were used to measure redox sensitive element manganese (Mn) and the results indicate that foraminiferal Mn/Ca in might prove to be a valuable proxy for oxygen in the bottom and pore waters when influenced by different productivity regimes.

Lastly this thesis explores the concept of size fractions used for benthic foraminiferal analyses. By performing size fraction studies on samples from the Benguela record and reviewing the literature, an underrepresentation of opportunistic taxa such as *Epistominella exigua* occurred when the finer (>63-125 μm) fraction was not analysed. However, the relative abundances of the benthic foraminiferal species does not alter sufficiently and therefore the palaeoecological interpretation does not change within this specific record.

Overall, the findings within this thesis contribute to a gap in the knowledge regarding the seafloor responses to surface productivity dynamics during rapid climate changes, which need to be better understood in order to comprehend upwelling regions and predict future benthic environmental changes.

Key words: benthic foraminifera, upwelling, productivity, Mauritania, Benguela, rapid climate change, late Quaternary

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"The Ocean is more ancient than the mountains, and freighted with the memories and the dreams of Time."

- H.P. Lovecraft -

Contents

List of papers

This thesis is based on four papers listed below, which have been appended to the thesis. Paper I has been published in a special issue of *Quaternary Science Reviews* entitled "Dating, Synthesis, and Interpretation of Palaeoclimatic Records and Model-data Integration: Advances of the INTIMATE project (INTegration of Ice core, Marine and TErrestrial records, COST Action ES0907)", and is reprinted with the permission of Elsevier. Papers II and III have been submitted to the indicated journals and are under consideration. Paper IV is an unpublished manuscript.

Paper I: McKay, C.L., Filipsson, H.L., Romero, O.E., Stuut, J.-B.W., Donner, B., 2014. Pelagic-benthic coupling within an upwelling system of the subtropical northeast Atlantic over the last 35 ka BP. *Quaternary Science Reviews*, 106, 299-315 .

Paper II: McKay, C.L., Filipsson, H.L., Romero, O.E., Stuut, J.-B.W., Björck, S., Donner, B., (submitted). The interplay between the surface and bottom water environment within the Benguela Upwelling System over the last 70 ka. Submitted to *Paleoceanography.*

Paper III: McKay, C.L., Groeneveld, J., Filipsson, H.L., Gallego-Torres, D., Whitehouse, M., Toyofuku, T., A comparison of benthic foraminiferal Mn/Ca and sedimentary Mn/Al as proxies of bottom water oxygenation in the low latitude NE Atlantic upwelling system. Accepted in *Biogeoscience Discussions* (for a special issue in *Biogeosciences*: "Low oxygen environments in marine, fresh and estuarine waters").

Paper IV: McKay, C.L., Filipsson, H.L., Björnfors, O., Size fractions and faunal assemblages of deep-water benthic foraminifera - a case study from the Benguela Upwelling System. To be submitted to *Journal of Foraminiferal Research.* Manuscript.

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From the bottom of my heart, a special thanks to my parents Gill and John for all of your help and utmost, constant support and to the rest of my family for believing in me over the years: *Manu forti*!

Last but not least, thank you Sweden for being my home.

Abbreviations

AABW	Antarctic Bottom Water
AAIW	Antarctic Intermediate Water
ACR	Antarctic Cold Reversal
AMOC	Atlantic Meridional Overturning Circulation
AMS	Accelerator Mass Spectrometry
BA	Bølling Allerød
BC	Benguela Current
BEST	Bio-Env + STepwise
BFAR	Benthic foraminiferal accumulation rate
BUS	Benguela upwelling system
CC	Canary Current
DAR	Diatom accumulation rate
EBCS	Eastern Boundary Current System
EMMA	End member model algorithm
EM	End member
FT-ICP-OES	Flow-Through Inductively Coupled Optical Emission Spectroscopy
H1	Heinrich Event 1
H2	HeinrichEvent 2
H3	Heinrich Event 3
ITCZ	Intertropical Convergence Zone
LGM	Last Glacial Maximum
MIS	Marine Isotope Stage
NACW	North Atlantic Central Water
NADW	North Atlantic Deep Water
SACW	South Atlantic Central Water
SAL	Saharan Air Layer
SAR	Sediment accumulation rate
SEM	Scanning electron microscope
SIMS	Secondary Ion Mass Spectrometry
SST	Sea surface temperature
TC	Total carbon
THC	Thermohaline circulation
TOC	Total organic carbon
UCDW	Upper Circumpolar Deep Water
YD	Younger Dryas

1.   Introduction

1.1   Context of upwelling regions

Coastal ocean upwelling systems generally represent the most productive marine ecosystems of the world's oceans in terms of primary productivity, despite their relatively small area. These systems sustain upper trophic levels of complex food webs and are a key component of climate-active biogeochemical cycles (Mariotti et al., 2012). Therefore, the state of these highly productive areas is of great importance not only in terms of ecosystem dynamics but also for the fishing industry, socioeconomic value and the carbon cycle.

Coastal upwelling systems occur along the eastern boundaries of ocean basins and are a function of the strength of alongshore winds, defined by the characteristic trade wind system which depends on the seasonal migration of the inter-tropical convergence zone (ITCZ). Over the low latitudes, the surface trade winds are largely directed towards the west and equatorwards as part of the Hadley circulation. The Coriolis effect results in currents being deflected to the right in the northern hemisphere and to the left in the southern hemisphere. Furthermore, the mean transport direction of sea surface waters is at right angles to the wind direction due to the combined influence of Ekman motion (friction) and the Coriolis effect (Murray, 1995). Winds displace surface waters offshore via Ekman transport and thus cause the ascendancy (upwelling) of nutrient-rich, colder, deeper sourced waters (Figure 1). Upwelling manifests itself in a number of distinct cells and filaments in a continuous belt along the coastline. Enhanced productivity is concentrated at the filament front and overall they represent an effective mechanism for nutrient export from the productive inner shelf to the less nutrient rich offshore areas (Shillington, 1998) as depicted in figure 2. The intensity of this process determines the dynamics of primary productivity that can be dispersed hundreds of kilometres offshore. This
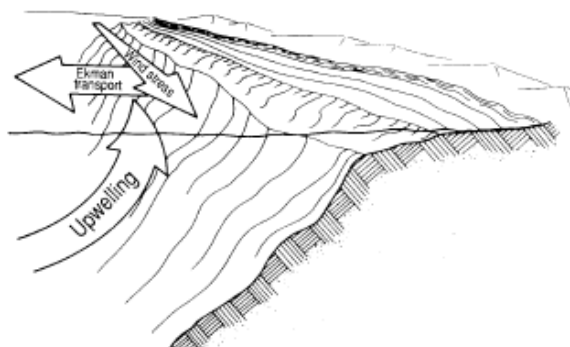
Figure 1. A conceptual diagram of the coastal upwelling process. The coast is represented in cutaway view, with offshore transport in the surface Ekman layer, driven by the alongshore stress of the wind on the sea surface which is replaced by upwelled waters from depth (Bakun, 1990).
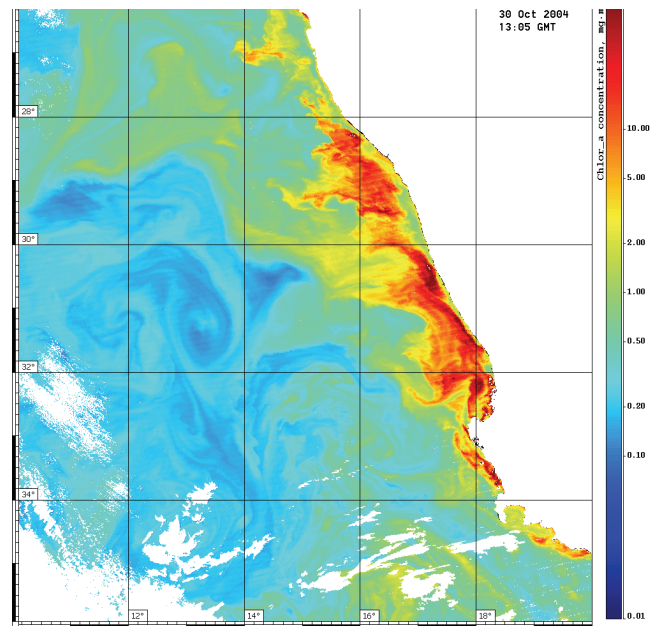
Figure 2. Chl a data determined by MODIS-Aqua satellite, highlighting the upwelling filaments along the southwest coast of Africa (26-35 ºS) during October 2004. (NASA Earth Observations, 2004).

offshore transport of nutrients can be spatially affected by turbulent mixing generated by the interaction of currents and eddies. Moreover, productivity is exported through the water column to the seafloor and thus has impact upon the benthic environment. In particular, oxygen minimum zones (OMZs), characterised as O_2 deficient layers in the ocean water column (Paulmier and Ruiz-Pino, 2009) commonly occur in upwelling regions due to the sheer amount of productivity export which initiates oxygen consumption during its decomposition (Suess, 1980).

Studying upwelling (and productivity) patterns is vital since upwelling is connected to all the major processes and elements defining the ocean during the past and therefore has implications for a variety of disciplines from oceanography, biology, geochemistry to geology and palaeo-research. From a geological perspective, the role of upwelling in sequestering organic carbon at high depositional rates is an important aspect (Schneider and Müller, 1995) for a better understanding of the global carbon cycle and also the chemistry of the ocean. From the point of view of palaeo-related studies of the ocean and ecosystems, coastal upwelling environments provide high resolution marine sediment archives to document past shifts in productivity and ocean dynamics. Also, copious research is being undertaken to determine how global climate variability will impact upwelling regions (McGregor et al., 2007; Bakun et al., 2010). In order to make robust predictions concerning the future of these areas, we need to increase our knowledge of past changes in these systems by analysing their marine sediment archives. Marine sediment cores from upwelling regions characterised by high sedimentation rates and well preserved microfossils provide a unique opportunity for their palaeo-reconstructions.

Two of the highest productive upwelling systems of the world's ocean are presented: the Mauritanian upwelling system off the coast of Mauritania, NW Africa and the Benguela upwelling system off the coast of Namibia, SW Africa (Figure 3). The rationale for my research is to increase our understanding of how the marine environment within these subtropical upwelling settings responded to past rapid climate change.

The project has three focus areas:

• The reconstruction of the coupling between the pelagic (surface primary productivity) and benthic (seafloor) environment during the late Quaternary. A multiproxy approach is applied to two marine sediment records; one from the Mauritanian upwelling system (Paper I) and a second from the Benguela upwelling system (Paper II).

• To investigate the interplay between the surface and bottom water environment further, a geochemical investigation using the elemental composition of foraminiferal shells (tests) to develop a proxy for bottom water oxygen content was undertaken. The analytical methods of Secondary Ion Mass Spectrometry (SIMS) and Flow-Through Inductively Coupled Plasma Optical Emission Spectroscopy (FT-ICP-OES) were used to measure the redox sensitive element manganese (Mn) and are a relatively new approach (Paper III).

• Finally, a size fraction comparison study was undertaken by the means of both a literature review and faunal analyses in an attempt to highlight what minimum foraminiferal test size is most representative for benthic foraminiferal faunal studies (Paper IV).

2. Background

2.1 Palaeo records

Upwelling regions can present vast sedimentary archives for reconstructing long term changes in the marine environment and the climate of the adjacent land mass at high temporal resolution. In this project, a multiproxy approach was employed to reconstruct the past environment and climatic conditions. The following proxies have been utilised: species composition of benthic foraminifera and diatoms, stable oxygen and carbon isotopes and trace elemental composition of benthic foraminiferal species *Eubuliminella exilis*, grain-size analysis, total organic carbon (TOC), biogenic silica and calcium carbonate content. To obtain a chronology of the
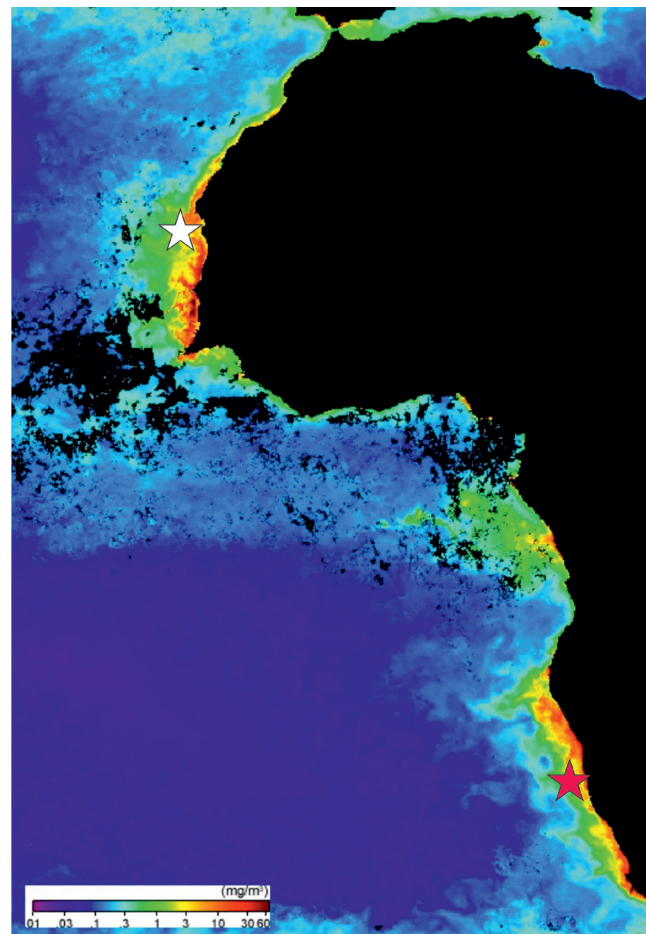
Figure 3. Study locations: site GeoB7926 (white star) and site GeoB3606 (red star). The MODIS data depicts chlorophyll concentrations (mg/m^3) over one month off the west African coast, highlighting the upwelling and high productivity regions of the Atlantic's eastern boundary (NASA Earth Observations, 2009).

sediments, radiocarbon dating has been performed.

By analysing the benthic foraminiferal assemblages, important environmental conditions such as oxygen levels and nutrient input can be inferred. As benthic foraminifera are the focus of this thesis, a more detailed synthesis can be found in the subsequent section (2.2).

A substantial part of the ocean's primary productivity is in the form of diatoms (Tréguer et al., 1995) hence, by accounting for diatom accumulation, productivity levels and upwelling intensity can be reconstructed (e.g. Romero et al., 2008). A number of biologically derived substances other than diatoms can also be useful in assessing productivity fluctuations. In this work we also consider total organic carbon, biogenic silica (opal) and $CaCO_3$ to infer information about productivity levels and nutrient source.

Besides the conditions of the ocean, climate and environmental conditions of the adjacent land mass can also be reconstructed from the marine sediment records. Wind-transported particles are a function of wind intensity (controlled by temperature and pressure gradients in the atmosphere) and availability (terrestrial

aridity). Therefore, particle-size analysis, being dependent on the carrying capacity of the wind or transport by rivers can ideally reflect past climatic conditions. Here the grain-size analysis results were processed into an end-member model (Weltje, 1997) in order to categorise particle provenance to interpret climatic conditions deducing humidity from fine, fluvial muds and wind strength and aridity from the coarsest sediment fractions.

Radiocarbon (^{14}C) dating is the most common age determination tool utilised in the field of Quaternary stratigraphy and the method is suitable for estimating the age of carbon bearing samples of less than 50 ka in age. Since the production of ^{14}C is not constant in time, radiocarbon ages require calibration in order to infer a true age in calibrated years before present (where "present" is defined as 1950 AD). Calibration curves, the most recent being IntCal13 (Reimer et al., 2013) provide a means of determining the calibrated age. However, ^{14}C dating on marine derived material requires the consideration of so-called reservoir ages; oceanic mixing processes are slower than atmospheric mixing, giving an offset from the atmospheric calibration curve (Bronk Ramsey, 2008). Therefore a marine ^{14}C calibration curve has been constructed for the oceans, with the most recent version being Marine13 (Reimer et al., 2013). Caution is required with marine reservoir ages, as they vary locally and are influenced by ocean ventilation. This complicates ^{14}C dating in upwelling regions, as changes in upwelling intensity lead to a varying supply of ^{14}C-depleted deeper waters and hence reservoir ages through time. For example, the upwelling of older subsurface waters with increased upwelling intensity could mean that reservoir ages may be larger (deMenocal et al., 2000). By the use of a chronological (depth/age) model the sedimentation accumulation rate can be accounted for (cm ka^{-1}).

2.2   Benthic foraminiferal assemblages

2.2.1   *Ecology*

Foraminifera are single-celled organisms with an order (Foraminiferida) in the Phylum Protista. These protists reside in the modern ocean as either planktonic (surface dwelling) or benthic (seafloor inhabitants) species. Benthic species can be epifaunal, i.e. they live at the sediment-water interface or infaunal, i.e. they live within the sediment. Despite their small size (<1 mm) they are extremely valuable as a micro-palaeontological tool since the majority of specimens have a shell (test) with high fossilisation potential (Cambrian to recent). Their test wall structure can be either calcareous (secreted calcite) or agglutinated (constructed from inorganic or organic particles), a few species can even build their test out of silica.

Foraminiferal species are defined primarily on their test morphology (Murray, 1991) according to taxonomic tomes and to date, approximately 2140 extant benthic foraminiferal species have been formally described (Murray, 2007). As important components of the meiofauna (45µm - 1 mm), foraminiferal biomass can exceed that of nematodes (Bernhard et al., 2008) and they are proposed to be as efficient as bacteria at recycling detritus (Moodley et al., 2002). Their faunal distribution and abundance is determined by different abiotic (i.e. temperature, oxygen, salinity, substrate) and biotic (i.e. inter-species competition, food supply) factors. The two major factors which play the most integral role in controlling the benthic microhabitat and subsequently, foraminifera assemblages are (i) the flux and temporal fluctuations of organic matter (food) to the sea floor and (ii) bottom and pore water oxygen content (Mackensen, 1995). The TROX model (Jorissen et al., 1995) demonstrates the interplay between oxygen concentration and food availability and how these two factors affect the vertical distribution of the foraminiferal microhabitat in various ecosystems (Figure 4). This conceptual model highlights that in oligotrophic settings, a critical food level determines the microhabitat depth of most species, whereas in eutrophic settings, a critical oxygen threshold determines this depth. However, the tolerance limits varies amongst species and furthermore, a particular species may live deep in the sediment at one site, but much closer to the sediment-water interface at a different site (Sen Gupta, 1999). In particular, certain species do not only survive but also calcify in low oxygen (even anoxic) conditions (Alve and Bernhard, 1995; Nardelli et al., 2014) suggesting that oxygen concentration is not a critical factor for all taxa.

Since different benthic foraminiferal species have different environmental niches and specific preferences we can use their ecology as a tool to reconstruct past environmental conditions. Key examples of the ecological significance of the most common species discussed in Papers I and II are summarised in table 1 and figure 5.

Figure 4. Hypothetical model showing the depth of the benthic foraminiferal microhabitat as a function of food availability in the sediment and/or oxygen. Note that many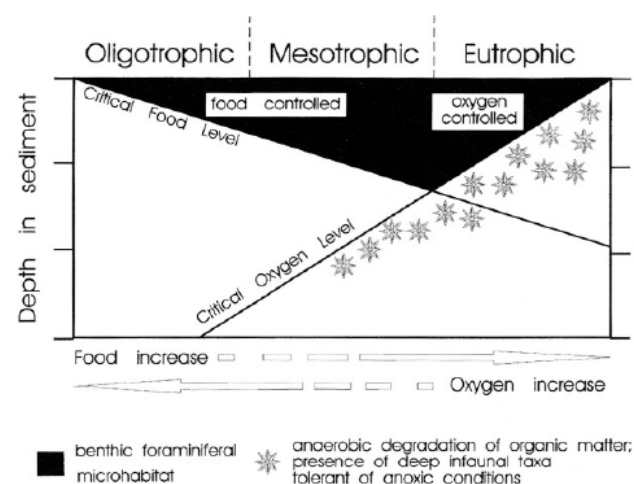 deep infaunal taxa may be found in completely anoxic condtions (represented by the star symbols). (Jorissen et al., 1995).

Table 1. The ecological significance of the most common benthic foraminiferal species found in the GeoB7926-2 and GeoB3606-1 records.

Species	Ecological significance	Reference
Bulimina aculeata	Limited phytodetritus input, intermittant organic carbon flux	Caulle et al. (2014)
Cassidella bradyi	Fresh phytodetritus input	Personal comm. W. Austin.
Cassidulina laevigata	Moderate oxygen depletion in the bottom and pore water, high organic matter input	Suhr and Pond (2006)
Cibicides wuellerstorfi	Consumes labile organic matter. Prefers well oxygenated bottom water conditions	Gooday (1988), Jorissen et al. (1995), Schmiedl et al. (1997)
Elphidium macellum	Shallow water, epiphytic, indicates downward transportation	Personal comm. M. Seidenkrantz
Eubuliminella exilis	Phytodetritus input and low oxygen conditions in the pore water	Caralp (1989)
Melonis barleeanum	Tolerates moderate oxygen depletion in the bottom and pore water, adapted to degraded organic matter	Lutze and Coulbourn (1984), Corliss (1985), Caralp, (1989)
Melonis pompilioides	Organic rich environment	Fariduddin and Loubere (1997)
Nonionella iridea	High phytodetritus input	Polovodova Asteman et al. (2013)
Uvigerina peregrina	Associated with high organic matter input combined with low to moderate oxygen depletion in the bottom and pore water	Lutze and Coulbourn (1984), Sen Gupta and Machain-Castillo (1993), Murray (1991)

2.2.2   Foraminiferal geochemistry

In addition to the ecology of foraminifera, the stable oxygen and carbon isotopic and trace elemental composition of their test are integral palaeoceanographical tools which have played a pivotal role in paleoceanography since the field was pioneered.

The classical marker for global ice sheet volume and temperature is the stable oxygen isotope ratio ^{18}O to ^{16}O (expressed as δ^{18}O) recorded by carbonate secreting organisms. δ^{18}O is defined as the relative deviation of the ratio compared to the standard, measured in permil, (‰). Seawater δ^{18}O is intimately linked to the hydrological cycle, consisting of evaporation, atmospheric vapour transport and the return of freshwater to the ocean via precipitation, fluvial input or ice sheet melting. The δ^{18}O of the global ocean is primarily influenced by changes in the amount of water stored in ice sheets (Shackleton, 1967). Preferential uptake of lighter isotopes during evaporation which can be stored in ice sheets increases the δ^{18}O values in the remaining surface waters during glacial conditions. Therefore sea water δ^{18}O values are dependent on global ice volume and also local δ^{18}O variability, as presented in numerous palaeo-temperature equations (e.g. Kim and O'Neil, 1997; McCorkle, et al., 1997). Thus, as the oxygen isotopic composition of foraminifera depends on the temperature of sea water during calcification, together with the composition of the δ^{18}O in sea water and therefore their δ^{18}O values reflect global climate and local hydrological processes.

A major part of the organic carbon cycle is CO_2 fixation into the organic biomass via photosynthesis in both the marine and terrestrial biospheres. The ratio of 13C to ^{12}C (expressed as δ^{13}C) can be used as a proxy of water mass circulation and nutrient input related to primary productivity export. Within seawater this stable isotopic ratio of carbon is set by competing processes of CO_2 exchange with the atmosphere, fractionation during photosynthesis, removal of carbon by export production and resupply of dissolved carbon from subsurface waters (Wefer et al., 1999). Since photosynthetic organisms preferentially uptake the lighter ^{12}C isotope, surface waters are generally enriched in ^{13}C. This strong discrimination in favour of ^{12}C results in ^{13}C depleted marine organic matter being exported to deeper waters. Upon remineralisation of the organic matter, an effective transfer of ^{12}C has occurred from the surface to the benthos, in turn affecting the foraminiferal signature. Therefore, the δ^{13}C composition in benthic foraminiferal tests reflects the δ^{13}C values of the dissolved inorganic carbon of the ambient deep and bottom water in which the test calcified (Mackensen and Bickert, 1999). Thus, more negative δ^{13}C values indicate an increase in export productivity.

As well as changes in productivity, water mass formation and circulation can also strongly influence δ^{13}C values at a given location. For example, North Atlantic Deep Water (NADW) has relatively high (more positive) δ^{13}C values due to its North Atlantic surface water source whereas Antarctic Bottom Water (AABW) has relatively

Figure 5. Scanning electron microscope images of common, recurrent and transported (*E. macellum* and *T. hanzawai*) benthic foraminiferal species from the >150 μm fraction picked from the GeoB7926-2 record. Each scale bar represents 100 μm. **1.** *Bulimina aculeata* d'Orbigny, 1826. **2.** *Eubuliminella exilis* (Brady, 1884). **3.** *Cassidella bradyi* (Cushman, 1922). **4.** *Uvigerina peregrina* Cushman, 1923. **5.** *Cassidulina laevigata* d'Orbigny 1826. **6.** *Cibicides wuellerstorfi* (Schwager, 1866). **7.** *Elphidium macellum* (Fichtel and Moll, 1798); Knudsen (1973). **8.** *Melonis pompilioides* (Fichtel and Moll, 1798); Eberwein (2006). **9.** *Melonis barleeanum* (Williamson, 1858); Eberwein (2006). **10.** *Nonionella iridea* Heron-Allen and Earland, 1932. **11.** *Tosaia hanzawai* Takayanagi, 1953. **12.** *Quinqueloculina seminulum* (Linnaeus, 1758); Ingle et al. (1980). **13.** *Pyrgo murrhina* (Schwager, 1866). **14.** *Triloculina tricarinata* d'Orbigny, 1826.
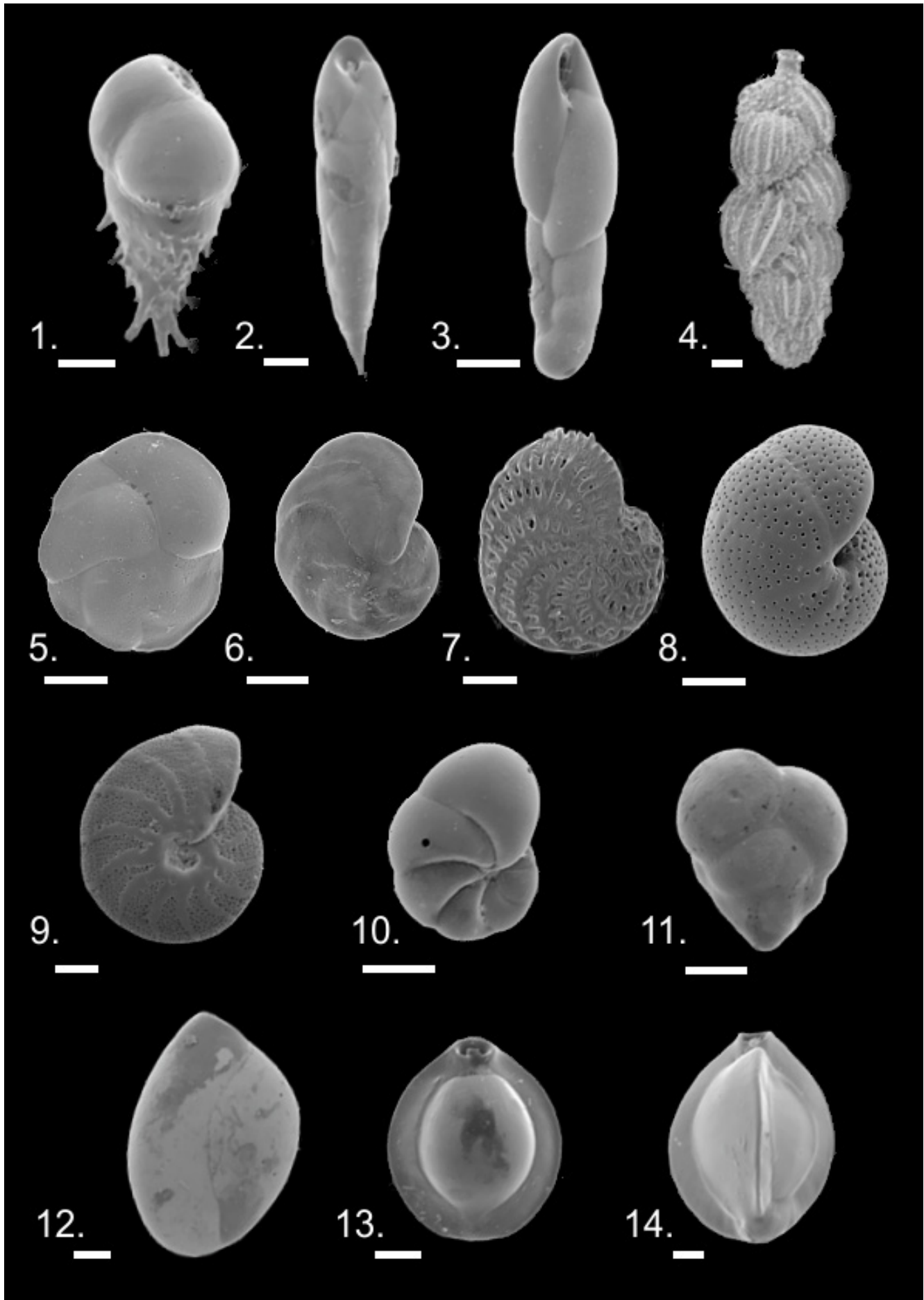
Figure .5.

low (more negative) $\delta^{13}C$ values, owing to its composition of Southern Ocean surface water and deep water from all basins which have relatively low $\delta^{13}C$ values. Since different water masses have certain $\delta^{13}C$ signatures (Figure 6) studying the $\delta^{13}C$ values of benthic foraminfera provide a way to reconstruct past deep-water mass distribution and changes in bottom water ventilation.

On a final note, the $\delta^{13}C$ of benthic foraminifera is also dependent on their microhabitat (Woodruff et al., 1980). Several studies have confirmed that generally, epifaunal taxa have a higher $\delta^{13}C$ value, whereas infaunal taxa have a lower $\delta^{13}C$ (e.g. Grossman, 1987; McCorkle et al., 1990). This is due to the isotopic composition of infaunal taxa being strongly influenced by that of the pore water, opposed to the bottom water. In addition, a productivity induced overprint, the so called "Mackensen effect" (Mackensen et al., 1993) can cause $\delta^{13}C$ values of up to 0.6 ‰ lower than ambient bottom water. These species specific issues are discussed in paper II and depicted in figure 7.

As well as the use of stable oxygen and carbon isotopes, the trace elemental composition of benthic foraminiferal tests can enable us to reconstruct past bottom water conditions. Perhaps one of the most conventional approaches is the reconstruction of seawater temperatures using Mg/Ca (e.g. Nürnberg et al., 1996; Elderfield et al., 2006). Within this thesis, however, the redox element Mn in foraminiferal calcite is explored as a potential proxy of past bottom water oxygenation (Paper III). At the sediment-water interface, redox sensitive elements respond under a hypoxic (<2 ml l⁻¹ dissolved oxygen) setting (i.e relatively higher Mn concentrations are present in the pore waters). Since certain species of benthic foraminifera tolerate and continue to calcify in low oxygen conditions (Nardelli et al., 2014), their tests have potential to record these signals.
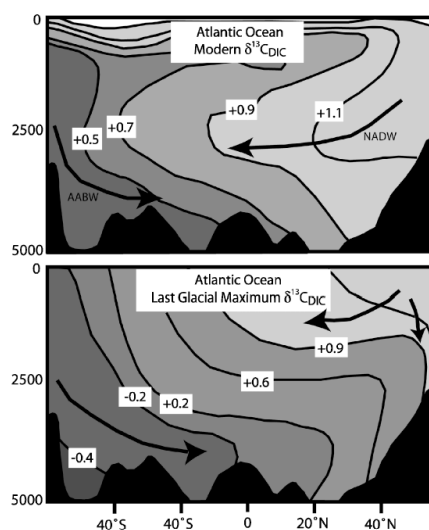
Figure 6. LGM vs. modern conditions in the Atlantic Ocean, based on $\delta^{13}C$ values in benthic foraminifera from variable depths (Duplessy et al., 1988; Labeyrie et al., 1992). A much shallower distribution of the NADW is apparent during the LGM (Ravelo and Hillaire-Marcel, 2007).
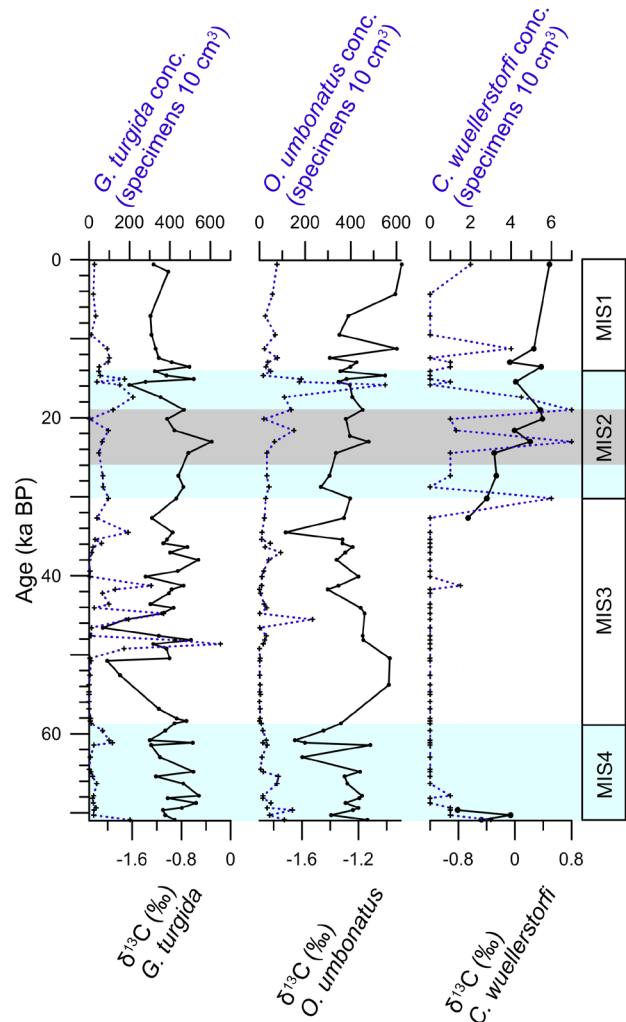
Figure 7. $\delta^{13}C$ for the three benthic foraminiferal species: infaunal *G. turgida*, shallow infaunal - epifaunal *O. umbonatus* and epifaunal *C. wuellerstorfi* (black lines) from the Benguela upwelling system (GeoB3606-1) record. Species concentrations are also shown (dotted blue lines). Shadings are as follows: late MIS4:70-59 ka, MIS2: 30-14 ka, LGM: 26-19 ka. Note that infaunal *G. turgida* exhibits relatively more negative $\delta^{13}C$ values than shallow infaunal – epifaunal *O. umbonatus* during early MIS3; when primary productivity export is high.

2.3   Primary productivity

Diatoms, among the most common type of phytoplankton, are a substantial part of the ocean's primary productivity (Tréguer et al., 1995) with a relative contribution of up to 75% in coastal upwelling areas. Furthermore, diatoms are siliceous organisms, accounting for over half of the total suspended biogenic silica (opal) (Nelson et al., 1995). In a similar manner to benthic foraminiferal taxa are indicative of former environmental conditions, the composition of diatom assemblages varies according to hydrographic conditions. Therefore diatom concentration and accumulation rate are used as a proxy of primary productivity and past upwelling conditions. For example, resting spores of *Chaetoceros affinis* (Figure 8) are typically found during times of intense upwelling whereas *Fragilariopsis doliolus* is indicative of warmer, less productive waters.
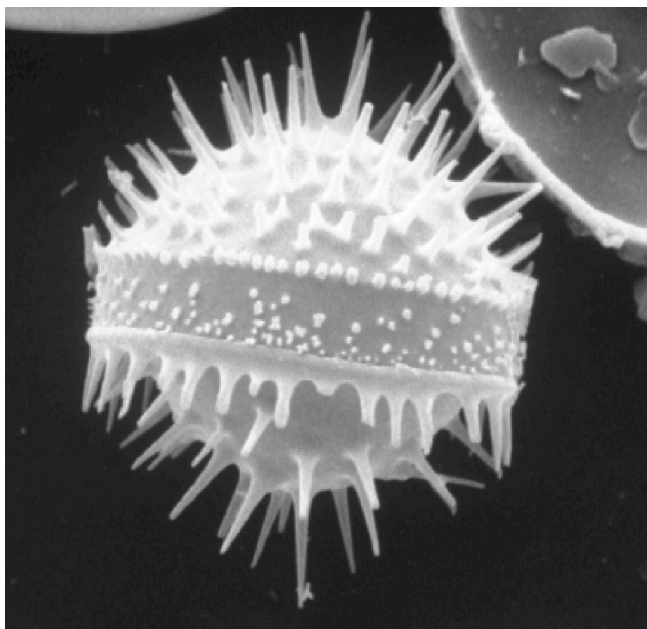
Figure 8. Scanning electron microscope image of the resting spore of diatom species *Chaetoceros affinis* (image courtesy of Oscar Romero).

Figure 9. Location of core GeoB7926-2 (black star) off the coast of Mauritania in the NE Atlantic Ocean. The proximity of site ODP658 (black dot) is also shown. Arrows indicate the currents and water masses. Black arrows show surface water circulation (Canary Current and North Equatorial Countercurrent), orange show North Atlantic Central Water (NACW), green show South Atlantic Central Water (SACW), light grey show Arctic Intermediate Water (AIW) and dark grey show Antarctic Intermediate Waters (AAIW). Inset is the present day position of the ITCZ for August and February (Romero et al., 2008).

3.   Study sites

3.1   Mauritanian Upwelling System

The Mauritanian upwelling system of the NE Atlantic is situated 200 km off the modern Mauritanian coastline, northwest Africa. From this area, a 1068 cm long gravity core GeoB7926-2 (Figure 9) was retrieved at 20°13'N, 18°27'E, on the upper continental slope at 2500 m water depth (Meggers and Cruise Participants, 2003). This 35 ka record is now archived at MARUM, University of Bremen, Germany.

The atmospheric circulation patterns and climate of the region is determined by the northeast trade winds and the easterly Saharan Air Layer. With regards to the hydrography of the system, the Canary Current is underlain by subsurface water masses which ascend into the surface layers through the upwelling process. A transition zone exists just north of Cape Blanc (24°N) whereby to the north, North Atlantic Central Water (NACW) is an important constituent of the upwelled waters and to the south of this convergence, the upwelled waters contain a significant portion of South Atlantic Central Waters (SACW). The southward-flowing, deeper-running NACW (Fütterer, 1983) is nutrient depleted in comparison to the northward-flowing SACW, which is less saline and more nutrient rich (Gardener, 1977). Shifts in this transition impact upon the surface productivity at core site GeoB7926, adding another dimension to the changes in the benthic environment.

3.2   Benguela Upwelling System

The Benguela Upwelling System is situated in the south-eastern subtropical Atlantic. From this system, a 1074 cm long gravity core GeoB3606-1 (Figure 10) was retrieved 175 km off the modern Namibian coastline (25°28'S, 13°05'E), southwest Africa, on the upper continental slope at 1785 m water depth (Bleil and Cruise Participants, 1996). This 70 ka record is archived at MARUM, University of Bremen, Germany.

The atmospheric dynamics of the Benguela area is influenced by the southeast trade winds. The hydrography of the Benguela upwelling system is multifaceted with different water masses entering the system. Mainly SACW is the upwelling component with waters of sub-Antarctic origin and also the Indian Ocean via the Agulhas Current being important constituents. Together with upwelling intensity, the inflow of these water masses change over time, coupled to climatic shifts; such as the Southern Hemisphere subtropical front location which influences the reactivation of the oceanic thermohaline circulation. Both impact the nutrient levels of the surface waters and accordingly the productivity at core site GeoB3606.
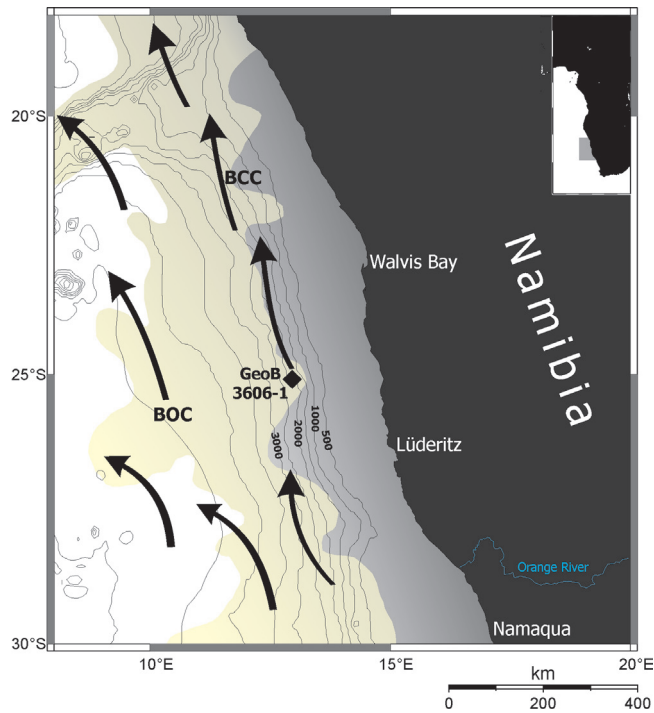
Figure 10. Location of site GeoB3606 (black diamond). Black arrows represent surface water circulation in the BUS (after Shannon, 1985; Lutjeharms and Stockton, 1987). Darker shading indicates the area of strong coastal upwelling and light shading represents the extensions of the upwelling filaments. Inset is the locality of the Benguela upwelling system off the coast of Namibia in the SE Atlantic Ocean.

4. Methods and Data

4.1 Benthic foraminiferal faunal analysis

For benthic foraminiferal faunal analyses, 10 cm^3 of sediment was sampled, freeze-dried, wet sieved and oven dried at 40ºC. The >150 µm size fraction was used for analyses on the GeoB7926-2 core (Paper I).

Samples from core GeoB3606-1 were analysed separately in the following sample size fractions in order to investigate potential differences in abundance data between different size fractions: 63-125 µm, 125-250 µm, 250-500 µm, >500 µm (paper IV).

A minimum of 300 specimens per sample were identified to species level for a representation of the fauna under a binocular microscope at 112.5 x magnification. Taxonomic identification follows Loeblich and Tappan (1987), Jones (1994) and the World Register of Marine Species (WoRMS) database. Counts were adjusted accordingly for large samples that required splitting. A total of 60 samples from core GeoB7926-2 were analysed to add to an existing dataset (Filipsson et al., 2011). 70 samples (a total of 231 samples when taking the four different fractions into account) from core GeoB3606-1 were analysed. In order to determine benthic foraminiferal response to primary productivity and climatic changes, samples were selected at 10 cm resolution and higher (5

cm) where surface productivity export (in the form of diatoms) exhibited major shifts. Taxa with an abundance of >5% were considered for statistical analyses. Benthic foraminiferal accumulation rate (BFAR), traditionally used as an indirect measure of surface-water productivity (Herguera and Berger, 1991), is a measure of the accumulation of individuals per unit area of seafloor per unit interval in time and was calculated as follows: BFAR (number of specimens cm^{-2} ka^{-1}) = benthic foraminifera (specimens cm^{-3}) x sediment accumulation rate (cm ka^{-1}).

From core GeoB7926-2 individuals of *Eubuliminella exilis* (>150 µm, Figure 11) were picked for determining Mn/Ca by Secondary Ion Mass Spectrometry (SIMS) and bulk samples of several specimens per sample depth for analysis by Flow-through Inductively Coupled Plasma Optical Emission Spectroscopy (FT-ICP-OES).

For core GeoB3606-1individual foraminiferal tests of the epifaunal *Cibicides wuellerstorfi*, deep infaunal *Globobulimina turgida* and epifauna - shallow infaunal *Oridisalis umbonatus* were also picked for stable oxygen and carbon isotope analysis (250-500 µm). For radiocarbon dating planktonic foraminifera specimens were selected from both sediment cores (>150 µm from core GeoB7926-2 and from all fractions >63 µm from GeoB3606-1 since planktonic foraminifera were scarce).
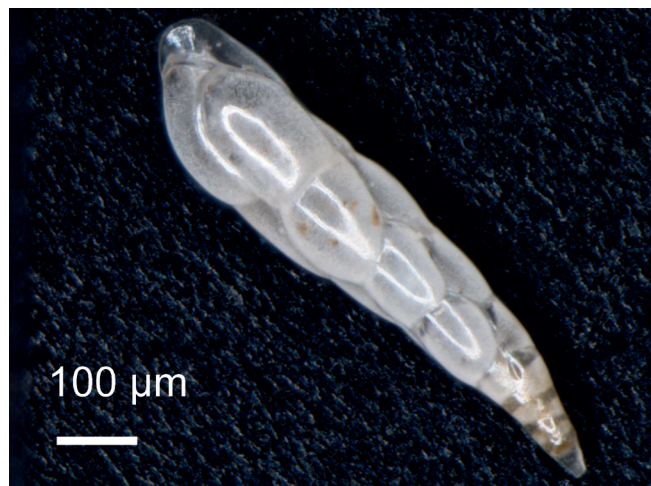
Figure 11. Focus-stacked image of benthic foraminiferal species Eubuliminella exilis from the >150 µm fraction.

4.2 Radiocarbon dating

Radiocarbon dating was performed on planktonic foraminifera species *Globigerina bulloides* and *Globigerina inflata* to add to the pre-existing dates (Romero et al., 2003; Romero et al., 2008) in order to increase the temporal resolution and confirm or improve the original age models (Romero et al., 2008; Romero, 2010). These supplementary AMS ^{14}C samples were measured at Lund University Radiocarbon Dating Laboratory, Sweden.

Ages were calibrated using OxCal 4.2 and the Marine09

and Marine13 curves (Ramsey, 2008; Reimer et al., 2009; Reimer et al., 2013). A reservoir age of 400 years was employed as a mean for both the North and South Atlantic Ocean (Bard, 1988; Mollenhauer et al., 2003). However, we acknowledge that this is the best accuracy we can achieve since dating is problematic within upwelling regions due to the exact reservoir age being unknown and not constant through time. All ages are reported in calendar years before present (BP), where present is 1950 AD and in unit thousand years (ka).

4.3   Multi proxy approach

4.3.1   *Stable O and C isotopes*

The benthic foraminiferal species *Cibicides wuellerstorfi*, *Globobulimina turgida* and *Oridisalis umbonatus* were used for the stable O and C isotopic analyses for core GeoB3606-1. Epifaunal *C. wuellerstorfi* is the classic species used for stable O and C isotope analysis, however as it was not present throughout the entire record, additional species were analysed that had higher abundances. The samples (approximately 2 mg per sample) were measured at the Bjerknes Centre for Climate Research, University of Bergen, Norway, using a Finnigan Mat 253 mass spectrometer. Isotope values are reported as $\delta^{13}C$ and $\delta^{18}O$, relative to the Vienna-Peedee Belemnite (VPDB) standard with a precision of over 0.08‰ for $\delta^{18}O$ and 0.03‰ for $\delta^{13}C$ respectively.

4.3.2   *Diatom analysis*

The diatom records for both marine sediment cores were previously published (Romero et al., 2003; Romero et al., 2008; Romero, 2010). Sample preparation and counting procedure followed methods of Schrader and Gersonde (1978). Analyses were carried out at x 1000 magnification using a Zeiss Axioscope with phase-contrast illumination at 5 cm intervals for both cores.

4.3.3   *Grain-size analysis and End-Member Modelling*

For both cores, 0.5 g of sediment was subsampled at 5 cm intervals for grain-size analysis. Biogenic compounds were removed from the sediment. Organic carbon was removed by heating the sample to 100°C in H_2O_2 (35%). Subsequently, the samples were treated for 1 minute with HCl (10%) at 100°C to remove $CaCO_3$ and biogenic opal was removed with NaOH. Measurements were performed in demineralised and degassed water in order to improve the signal-to-noise ratio of the particle-size analysis. Particle size distributions were measured on a Beckman Coulter laser particle sizer LS200 at MARUM, University of Bremen, Germany.

Numerical end-member modelling was employed to differentiate between distinctive sediment sub-populations within the grain-size distribution using an End Member Modelling Algorithm (EMMA; Weltje, 1997). The end-members are selected based on goodness of fit statistics. Further details are provided in Weltje and Prins (2003).

4.3.4   Bulk geochemical analysis

Samples for bulk geochemistry were taken at 5 cm intervals, freeze dried and ground in an agate mortar. After decalcification of the samples with 6 N HCl, the TOC content was determined by combustion at 1050°C. Carbonate ($CaCO_3$) was calculated from the difference between total carbon and TOC and expressed as calcite. Opal content was obtained using the sequential leaching technique of DeMaster (1981) with adjustments by Müller and Schneider (1993).

4.4   Trace elemental test composition

From the GeoB7926-2 core, well-preserved specimens of benthic foraminifera species *Eubuliminella exilis* were picked from samples with high and low surface productivity regimes to determine if past oxygen conditions could be quantified by the use of Mn/Ca measurements.

4.4.1   *Secondary Ion Mass Spectrometry (SIMS)*

42 specimens of benthic foraminifera species *Eubuliminella exilis* were pre-treated following the method of Glock et al., (2012) to remove any diagenetic coatings which may be formed post-mortem. Foraminifera specimens were embedded in low viscosity epoxy resin at JAMSTEC, Japan. The foraminifera were then ground to expose a cross-section through the test wall using 16 μm silicon carbide paper at the Department of Geosciences, University of Edinburgh, UK. Resin pieces were then mounted into low viscosity epoxy resin disks (Struers) at the NORDSIM laboratory, Laboratory for Isotope Geology at the Swedish Museum of Natural history, Stockholm, Sweden. The mounts were then polished using 3 μm diamond paper first with 3 μm diamond suspension and finally with 1 μm diamond suspension. Between each grinding and polishing step, mounts were cleaned with ethanol and after final polishing; mounts were coated in a 20 nm thick layer of high purity Au.

The reference material used for the SIMS was a polished piece of OKA calcite crystal supplied from Geomar, Kiel University, Germany (E. Hathorne, pers. comm). The Mn/Ca analyses of the test cross-sections were performed using a Cameca IMS 1270 ion microprobe at the NORDSIM laboratory, Laboratory for Isotope Geology at the Swedish Museum of Natural history, Stockholm, Sweden. A $^{16}O^-$ ion beam accelerated at 10 kV was used and focussed to a diameter of 5 μm on the sample surface.
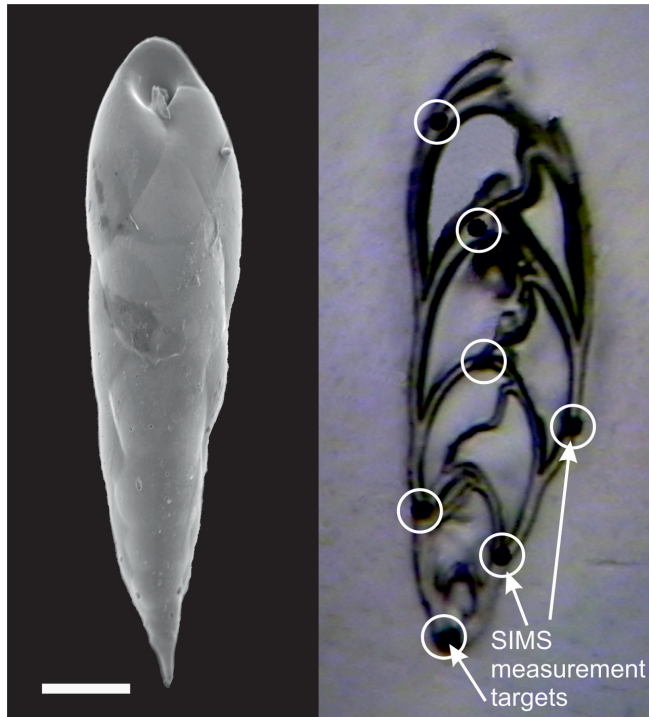
Figure 12. Figure 2. Scanning electron microscope image (scale bar: 100 µm) and cross section image during SIMS analysis of a single *Eubuliminella exilis* specimen. Black spots indicated by the white circles are examples of selected locations for SIMS analyses, measuring 5 µm in diameter.

Several of these analysis points were undertaken upon each individual test of *E. exilis* (ca. 6-10 targets per individual specimen, Figure 12). Further operational details of the SIMS can be found in Paper III.

4.4.2   Flow-Through Inductively Coupled Plasma Optical Emission Spectroscopy (FT-ICP-OES)

For FT-ICP-OES, 20-50 specimens of *Eubuliminella exilis* from the GeoB7926-2 record were selected from samples contemporaneous with Heinrich Event 1 (H1), the Bølling Allerød (BA) and the Younger Dryas (YD) for comparisons with the SIMS data. These three climatic intervals encompassed the only samples where a sufficient number of pristine *E. exilis* individuals were present. The tests were gently crushed in a 0.5 ml vial and fragments were transferred into a PTFA filter with 0.45 µm mesh. For analysis, the filters were connected to a Flow-Through – Automated Cleaning Device (Klinkhammer et al., 2004) to prevent the loss of material which occurs with traditional cleaning allowing the analysis of very small samples (~20 µg). The Flow-Through was then connected to an ICP-OES (Agilent Technologies, 700 Series with autosampler (ASX-520 Cetac) and micro-nebulizer) Time Resolved Analysis (TRA; the dissolution technique) was used to analyze the samples at MARUM, University of Bremen, Germany. Details of the solution process and calibration can be found in Paper III.

5.   Summary of Papers

The author contributions to the following papers are enlisted in Table 2.

5.1   Paper I

C.L. McKay, H.L. Filipsson, O.E. Romero, J.-B.W. Stuut and B. Donner., 2014. "Pelagic-benthic coupling within an upwelling system of the subtropical northeast Atlantic over the last 35 ka BP". Quaternary Science Reviews, 106, 299-315.

The aim of this article was to directly account how the coupling between the surface and bottom water environments in the Mauritanian upwelling system responded to past rapid climate change. Based on data obtained from sediment core GeoB7926-2, this high-resolution, multiproxy study dates back to 35 ka. Over this time period, high latitude cold events and global scale changes in atmospheric and oceanographic dynamics influenced upwelling intensity. Subsequently, processes including sea-level changes which displaced upwelling filament position and changes in trade wind intensity caused shifts in primary productivity regime. These productivity changes impacted upon the benthic environment, resulting in four main community shifts within the record (Figure 13). The first one occurred during late Marine Isotope Stage 3 (MIS3, 35-28 ka) where strong pelagic-benthic coupling is apparent from the relatively moderate diatom input and the dominance of benthic foraminiferal species which prefer fresh phytodetritus. The second benthic foraminiferal assemblage occurred from 28 to 19 ka (including Heinrich event 2; H2 and the Last Glacial Maximum; LGM) resulted from a proportionately larger amount of older, degraded matter and lower phytodetritus export. A third benthic foraminiferal assemblage is apparent throughout 18-11.5 ka (across H1, BA and YD) whereby extreme levels of primary productivity actually hindered the benthos by promoting low oxygen conditions. This is inferred from the dominance of low oxygen tolerant benthic foraminiferal species *Eubuliminella exilis*. Finally, a sudden shift in the benthic faunal composition is apparent throughout the Holocene (11 ka – present). More oxygenated bottom water conditions due to relatively low diatom accumulation occurred during this most recent period with weaker upwelling intensity.

This study demonstrates the rapidity of which the benthic environment can respond to changes in the surface waters and related productivity export. Furthermore, a compilation of other records from the region (both marine and terrestrial) as well as comparison with the NGRIP ice core record provided insight on this particular upwelling system.
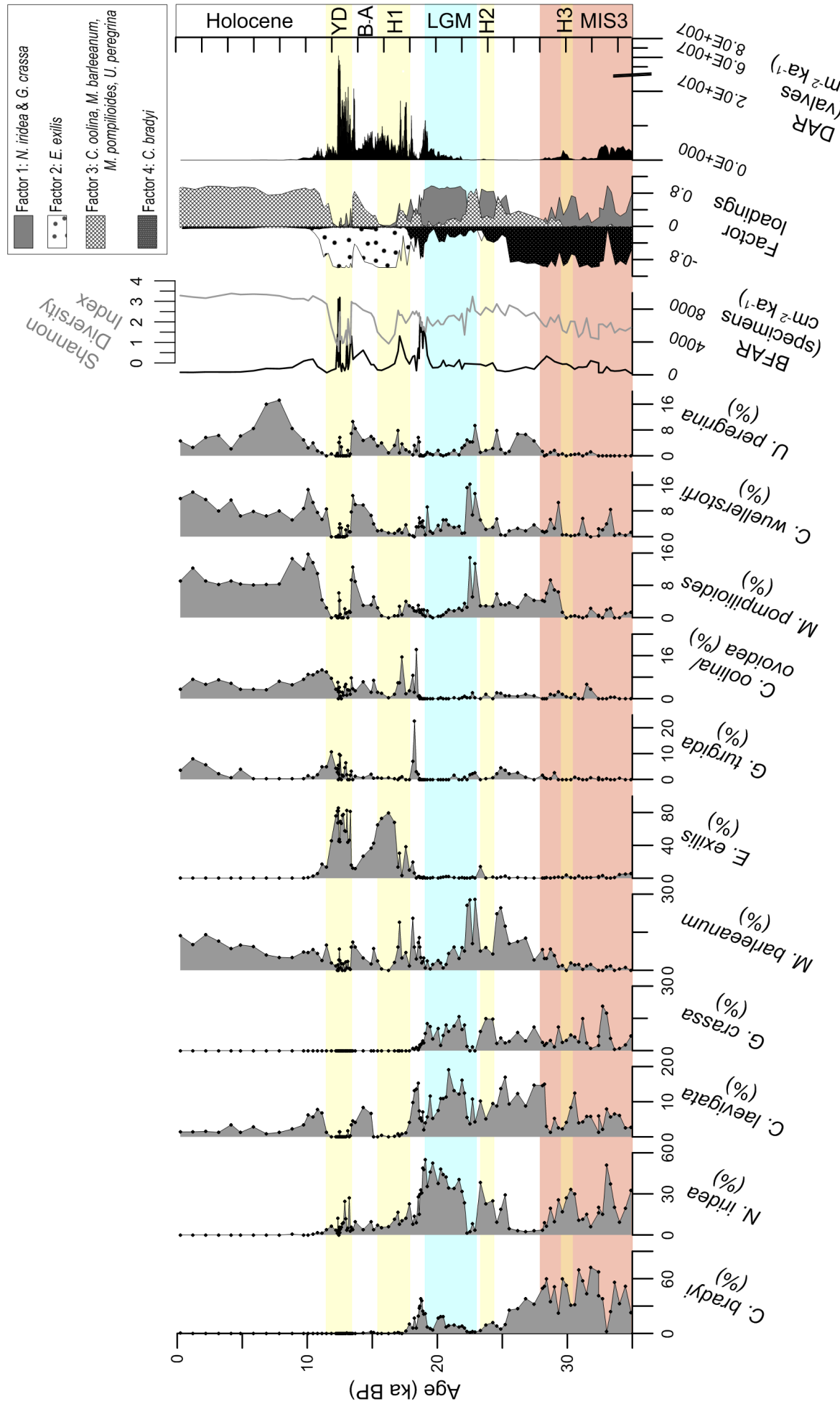
Figure 13. GeoB7926-2 down-core changes in relative abundance (%) of the most common benthic foraminifera species (17-0 ka BP after Filipsson et al., 2011), benthic foraminiferal accumulation rate (specimens cm^{-2} ka^{-1}), Shannon diversity index, factor analysis loadings and diatom accumulation rate (valves cm^{-2} ka^{-1}). Shadings are as follows: light orange, late MIS3, (Marine Isotope Stage 3: 35-28 ka BP); light yellow, H3 (Heinrich event 3: 30.6-29.6 ka BP), H2 (Heinrich event 2: 24.5-23.25 ka BP), H1 (Heinrich event 1: 18-15.5 ka BP) and the YD (Younger Dryas; 13.5-11.5 ka BP); light blue, LGM (Last Glacial Maximum: 23-19 ka BP); unshaded B-A (Bølling-Allerød: 15.5-13.5 ka BP) and the Holocene (11.5-0 ka BP). Note the different size x-axes of the benthic foraminiferal abundance data to emphasize the more abundant taxa.

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5.2   Paper II

C.L. McKay, H.L. Filipsson, O.E. Romero, J.-B.W. Stuut, S. Björck and B. Donner., "The interplay between the surface and bottom water environment within the Benguela Upwelling System over the last 70 ka". Submitted to Paleoceanography.

In the second article, a multi-proxy study of a 70 ka record from sediment core GeoB3606-1 retrieved from the Benguela upwelling system is presented. This work represents the first extensive quantitative study of benthic foraminiferal response and direct coupling to export productivity in the region. Significant shifts in benthic foraminiferal assemblage composition occurred and tight coupling existed between the surface and bottom water environment especially throughout MIS4 and MIS3.

Overall, six benthic foraminiferal assemblages were documented within the record (Figure 14). The first two assemblages occurred during MIS4 and early MIS3 and are representative of severe hypoxic conditions, evident from the dominance of low oxygen tolerant *Eubuliminella exilis*. Whilst site GeoB3606 has experienced continuous low oxygen conditions, the extremely high export production in the form of diatoms during these two climatic periods exacerbated these conditions. Furthermore this coincided with an inverse relationship between diatom and benthic foraminifera accumulation, highlighting that during times of extremely high phytodetritus export, the benthic productivity can become strongly suppressed. It is during these high productivity periods that *E. exilis* is strongly coupled with primary productivity. A third benthic foraminiferal faunal shift towards an assemblage consisting of *Cassidulina laevigata* and *Nonionella iridea* occurred during late MIS3 as a response to a relative decrease in nutrient input and decreased competition with *E. exilis*. The fourth assemblage followed during the LGM when species typical of a high organic carbon input, highlighting food source as a controlling factor upon the benthic community. During the Antarctic Cold Reversal (ACR, 14.5 – 12.8 ka) a rapid shift in the benthic foraminiferal fauna is notable whereby *Bulimina aculeata* responds rapidly to fresh organic matter input and emphasizes that bottom water oxygenation did not degrade to previous levels within the records where *E. exilis* could out-compete all other species during MIS3. Finally, throughout the Holocene benthic foraminiferal species which were previously of low abundance dominated the assemblage, which transpired in tandem with the demise of both *E. exilis* and *B. aculeata*. More opportunistic species such as Epistominella exigua increased, potentially as a result in the decline in diatom export.

The responses of the benthos to such dynamic shifts in export productivity recorded in GeoB3606-1 are attributed not only to upwelling intensity influenced by trade wind intensity, but also to sea level and oceanographic circulation changes.

Figure 14. GeoB3606-1 down-core changes in diatom accumulation rate (valves cm⁻² ka⁻¹), benthic foraminiferal accumulation rate (specimens cm⁻² ka⁻¹), relative abundance (%) of the most common benthic foraminifera species Shannon diversity index and factor analysis loadings. Shadings are as follows: late MIS4:70-59 ka, MIS2: 30-14 ka, LGM: 26-19 ka. Benthic foraminiferal assemblages are labelled A-F and dotted lines represent their boundaries according to the factor analysis. Note the different size x-axes of the benthic foraminiferal abundance data to emphasize the more 1025 abundant taxa.

5.3 Paper III

C.L. McKay, J. Groeneveld, H.L. Filipsson, D. Gallego-Torres, M. Whitehouse, T. Toyofuku and O.E. Romero., "A comparison of benthic foraminiferal Mn/Ca and sedimentary Mn/Al as proxies of bottom water oxygenation in the low latitude NE Atlantic upwelling system". Submitted to Biogeosciences.

The third article was initiated from the results of papers I and II. Because both upwelling systems were prone to low oxygen conditions at the seafloor during times of excessively high diatom accumulation rate (inferred from the dominance of low oxygen tolerant *Eubuliminella exilis*), Paper III aims to develop a proxy of the former bottom water oxygen levels. A geochemical approach of analysing redox sensitive Mn incorporated into foraminiferal calcite (Mn/Ca) was explored in attempt to evaluate its potential for bottom water oxygen reconstruction.

Mn/Ca analysis by Secondary Ion Mass Spectrometry (SIMS) was used to analyse cross sections of benthic foraminiferal tests. This is a relatively new method of analysing trace elements in foraminiferal calcite and is a useful tool where only a few specimens are available. 42 individuals (from five different climatic intervals) of *E. exilis* from sediment core GeoB7926-2 were selected from periods of high and low primary productivity. By analysing specimens from contrasting productivity regimes (samples derived from intervals of low diatom accumulation rate during MIS3 and LGM and high diatom input during H1 - YD), we aimed to detect the oxygen conditions previously interpreted solely from the benthic foraminiferal assemblage data. As SIMS is

a relatively new method of analysing foraminiferal tests, a comparison with Flow-Through Inductively Coupled Plasma Optical Emission Spectroscopy (FT-ICP-OES) was undertaken to determine if the results were representative. Both methods gave comparable results. Furthermore, foraminiferal Mn/Ca was compared with published sediment bulk Mn/Al data from the same sediment core (Gallego-Torres et al., 2014).

The results indicate that shifts in oxygen levels occurred during different productivity regimes between MIS3 and the YD (35 and 11.5 ka). The highest foraminiferal Mn/Ca and greatest Mn variability within individual tests were obtained during the YD and indicate Mn enrichment which coincides with very high primary productivity (Figure 15). The foraminiferal Mn/Ca results are consistent with benthic foraminiferal faunal data.

5.4 Paper IV

C.L. McKay, H.L. Filipsson and O.J.H. Björnfors., "Size fractions and faunal assemblages of deep-water benthic foraminifera – a case study from the Benguela Upwelling System". Manuscript to be submitted to Journal of Foraminiferal Research.

The fourth manuscript within this thesis reviews the various size fractions of benthic foraminiferal assemblages which have been undertaken over the years. Paper IV presents a literature study on this topic and also compares actual faunal data generated when using the >63 µm and>125 µm fractions from samples taken from sediment core GeoB3606-1.
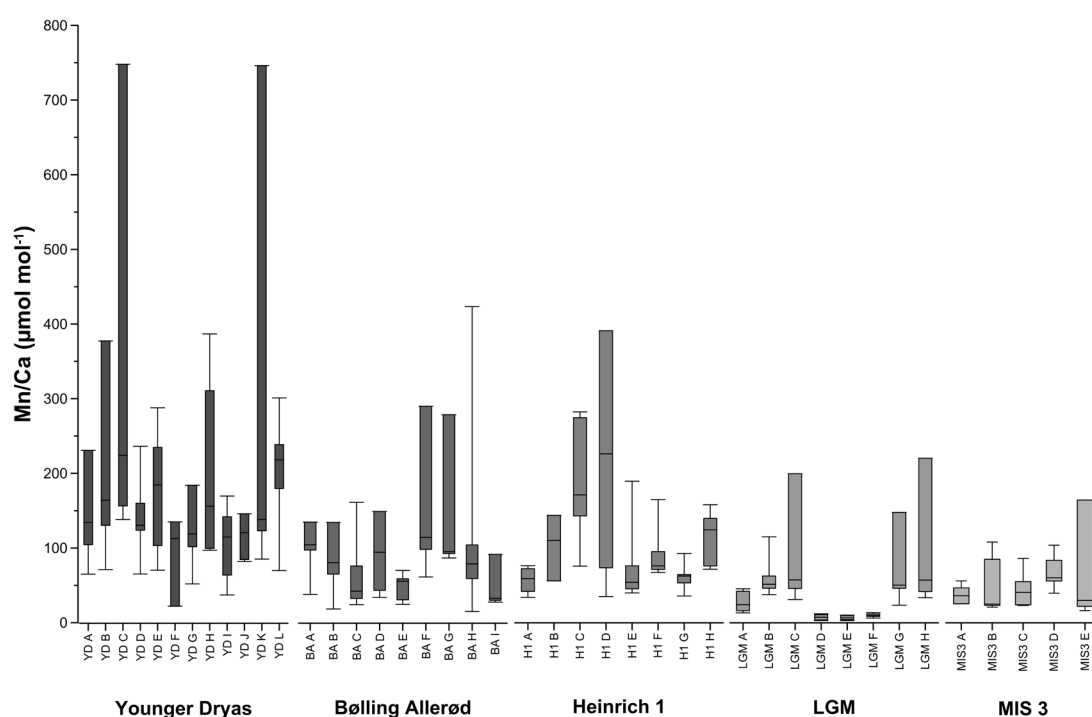

Figure 15. The Mn/Ca (µmol mol^{-1}) variability within each individual *Eubuliminella exilis* specimen for each climatic interval (labelled on the x-axis), determined by SIMS.

The literature review of similar palaeoecological studies (in terms of study site and research questions) to the analyses of Paper IV revealed that a range of minimum size fractions has continued to be analysed over the years. However, the majority of publications used the >125 µm fraction. From the benthic foraminiferal faunal analyses, our results highlight that overall benthic foraminiferal concentrations and accumulation rates can be much higher when including the 63-125 µm fraction. The most significant finding when observing the abundance of species is the underrepresentation of opportunistic taxa such as *Epistominella exigua* and juveniles of *Nonionella iridea* (Figure 16). Furthermore, as the abundances of these species were previously missed when only accounting for the >125 µm fraction, the dominant *Eubuliminella exilis* was inflated and slightly overrepresented. When the smaller size limit is included, this species decreases in relative abundance. In spite of this however, the overall species composition and patterns remain the same and therefore the inclusion of the 63-125 µm fraction does not impact upon the ecological interpretation of this particular record (Paper II).

The outcome of this work emphasizes the importance of considering the >63 µm fraction. However, as the analysis of the lower size limit is meticulous and time consuming, perhaps spot-checks of a few samples per record ought to provide sufficient ecological information to determine if the larger size fractions are truly representative. On a final note, from the range of size fractions used throughout the literature, an agreed, standardised protocol of which minimum size fraction to analyse is required in the style of biomonitoring studies upon live foraminifera (Schönfeld et al., 2012) if we are to have comparable datasets between different studies.

6.   Discussion

6.1   Productivity regimes and benthic faunal community shifts in response to large scale climatic change

In general, large scale climatic shifts and corresponding atmospheric dynamics impact upon low latitudes. Namely, increased trade wind vigour occurred during glacial periods (e.g. Stuut et al., 2002) when the polar ice sheets advanced, shifting the ITCZ south. In turn, trade wind-driven upwelling intensified, increasing primary productivity in general. However, as highlighted in Paper I and II, the productivity dynamics and benthic responses are more multifaceted.

Subsequently, large scale atmospheric processes, can act upon ocean circulation. The equatorward (poleward) expansion (contraction) of the subtropical gyres can alter the advection of water masses, therefore changing the source of the upwelled waters. In the case of the Benguela upwelling system, such an equatorward expansion supplies the upwelling system with warm, more nutrient depleted Agulhas waters sourced from the Indian Ocean (Peterson and Stramma, 1991; Peeters et al., 2004). As for site GeoB7926 in the Mauritanian upwelling system, being located at a convergence between NADW (nutrient depleted) and SACW (silica enriched), it can experience shifts in upwelling source by this same large scale process. Changes in the source of the upwelled waters impact upon the intensity and type of primary productivity blooming at the two study sites; be it more siliceous (diatomaceous) or calcareous (coccolithoforids) based producers. As demonstrated within this thesis, both upwelling systems exhibit the same benthic response to intense export productivity in the form of diatoms (Figures 13 and 14). During exceedingly high diatom export, the benthic

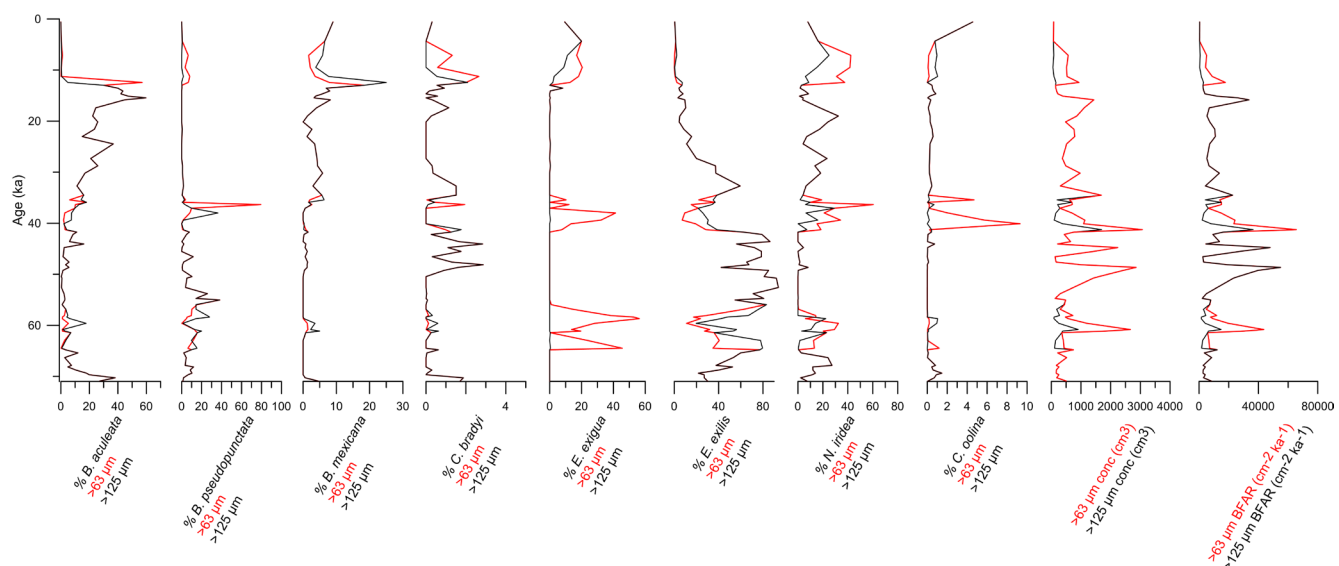

Figure 16. Relative abundances (%) of benthic foraminiferal species and difference in benthic foraminiferal concentrations (cm^{-3}) and accumulation rate (specimens cm^{-2} ka^{-1}) analysed from the >63 µm and >125 µm size fractions.

Table 2. Author contributions for Papers I to IV

Author contributions	Paper I	Paper II	Paper III	Paper IV
Benthic foraminiferal faunal analyses	C. McKay	C. McKay		O. Björnfors C. McKay
Benthic foraminiferal taxonomic checks	H. Filipsson			
Benthic foraminiferal stable O and C isotope analysis selection		C. McKay		
Planktonic foraminiferal ^{14}C selection	C. McKay	C. McKay		
Diatom analyses	O. Romero	O. Romero		
Grain-size analysis	C. McKay			
End-member modelling	J.-B. Stuut	J.-B. Stuut		
Age modelling		C. McKay		
Foraminiferal sample selection and cleaning for SIMS and FT-ICP-OES			C. McKay	
Foraminiferal sample mounting for SIMS			T. Toyofuku	
SIMS analysis			M. Whitehouse C. McKay	
FT-ICP-OES analysis			J. Groeneveld	
Mn/Al bulk data			D. Gallego-Torres	
Data interpretation	C. McKay H. Filipsson O. Romero J.-B. Stuut B. Donner	C. McKay, H. Filipsson O. Romero J.-B. Stuut S. Björck B. Donner	C. McKay J. Groeneveld H. Filipsson D. Gallego-Torres M. Whitehouse T. Toyofuku O. Romero	C. McKay H. Filipsson

foraminiferal community responds with rapidly and the dominant benthic foraminiferal faunal species within the assemblage was *Eubuliminella exilis* during such periods. From the dominance of this low oxygen tolerant species, we infer that the seafloor experienced hypoxic conditions due to exceedingly high diatom export which led to oxygen consumption via decomposition.

In addition to surface productivity being exported to the seafloor and affecting the benthic environment, deep ocean circulation changes also have an impact. During times of low diatom production, benthic foraminifera respond to a shift in food source. Species with a preference for a fresh phytodetritus diet decline in abundance and are replaced by species typical of a more refractory organic matter setting. Such shifts in species composition occurred at both study sites during MIS2. Whilst refractory organic matter can already be present, changes in deep water circulation can import additional, older material when the bottom water is well ventilated. As a result, the benthic foraminiferal assemblage shifted in species composition.

6.2 Productivity regimes and benthic faunal community shifts in response to local environmental changes

Although productivity variations in coastal upwelling are mainly attributed to changes in wind strength,

productivity dynamics in the Mauritanian and Benguela upwelling sites studied within this thesis are less straightforward due to their complex atmospheric and hydrographic settings. Other interplaying mechanisms defined the temporal variations in productivity in both of these systems.

Upwelling filaments themselves can affect the dynamics and intensity of the primary productivity over much of the continental slope by transporting nutrients up to 750 km seaward (Shillington, 1998). For example, within the Benguela upwelling system, the heterogeneous spatial distribution of nutrients presents a marked east-west productivity gradient off SW Africa (Shannon, 1985). Furthermore, the seaward-shoreward (i.e. westward-eastward) migration of the filament front position leads to shifts in the locality of the enhanced productivity area. Therefore, upwelling and its corresponding primary productivity can be more intense in the overlying waters of a particular study site, which is reflected in its sediment record. As highlighted within this thesis, the surface productivity directly impacts the underlying seafloor environment.

The position of the upwelling filament front magnifies the effect of intensified upwelling caused by increased wind strength. The migration of upwelling filaments is linked to large scale changes having regional effects; namely atmospheric forcing, sea level changes and also coastal morphology. In addition to these links between large scale

atmospherics and ocean circulation changes discussed in the previous section, regional trade wind forcing also has potential to cause displacement of the upwelling filament position. Both the strength and latitudinal position of the trade winds have triggered changes in upwelling intensity at both study sites, for example during the LGM, H1 and the YD in the Mauritanian upwelling system.

A potential amplifier of filament front migration and according productivity is sea level variability (Giraud and Paul, 2010). Again, global climate is the determining factor of sea level change, with a sea level low stand of ca. 125 m below modern sea level during the LGM (Siddall et al., 2008); the upwelling filaments would be displaced offshore. Suffice to say that sea level rise shifts the filament position shoreward. Furthermore, sea level variability shifted the former coastline, also altering its morphology and exposing the shelf (Holzwarth et al., 2010). In particular, upwelling off the NW coast of Africa is concentrated off a series of prominent capes and therefore the locality and geometry of the enhanced productivity areas within the subtropical northeast Atlantic upwelling system dramatically shifted in position over time (Giraud and Paul, 2010).

The mechanisms and factors that can incur strong fluctuations in primary productivity of a particular site within an upwelling system have significant implications for the underlying sea floor environment. As with global scale factors, the level of export production in the overlying waters is affected by the regional dynamics discussed here and accordingly, results in benthic foraminferal faunal assemblage changes. In the case of the Benguela upwelling system, offshore filament displacement impacted the diatom accumulation rate during MIS3 in a two-step

manner. A shift to relatively lower diatom accumulation rate at 40 ka was in accordance with a sea level fall of ca. 20 m from previous levels in MIS3 (Ninneman et al., 1999). Concurrently, the benthic foraminiferal fauna exhibited an assemblage composition shift (Figure 14).

6.3 Food or oxygen as the dominant controlling factor upon benthic foraminiferal communities?

It is widely accepted that the main two factors contributing to benthic foraminiferal faunal distributions are food and oxygen availability (e.g. Schmiedl et al., 1997; Jorissen et al., 1999). Furthermore, it is not only the amount of food but also the source and quality. For example, *Melonis barleeanum* has a preference for refractory organic matter opposed to fresh phytodetritus material such as *Eubuliminella exilis*. One difficulty within the two ecological studies within this thesis is that the dominance of *E. exilis* indicates low oxygen conditions. However, its strikingly close correlation with diatom accumulation rate in both the Mauritanian and the Benguela upwelling systems (Figure 17) represent a dietary based preference as well. Therefore, it is arguable that this species responds more to the fresh phytodetritus as opposed to the low oxygen conditions induced by excessive productivity export. The Benguela upwelling system is renowned for being poorly oxygenated at the seafloor and therefore it could be plausible that *E. exilis*' ability to survive low oxygen conditions leads to it out-competing other species.
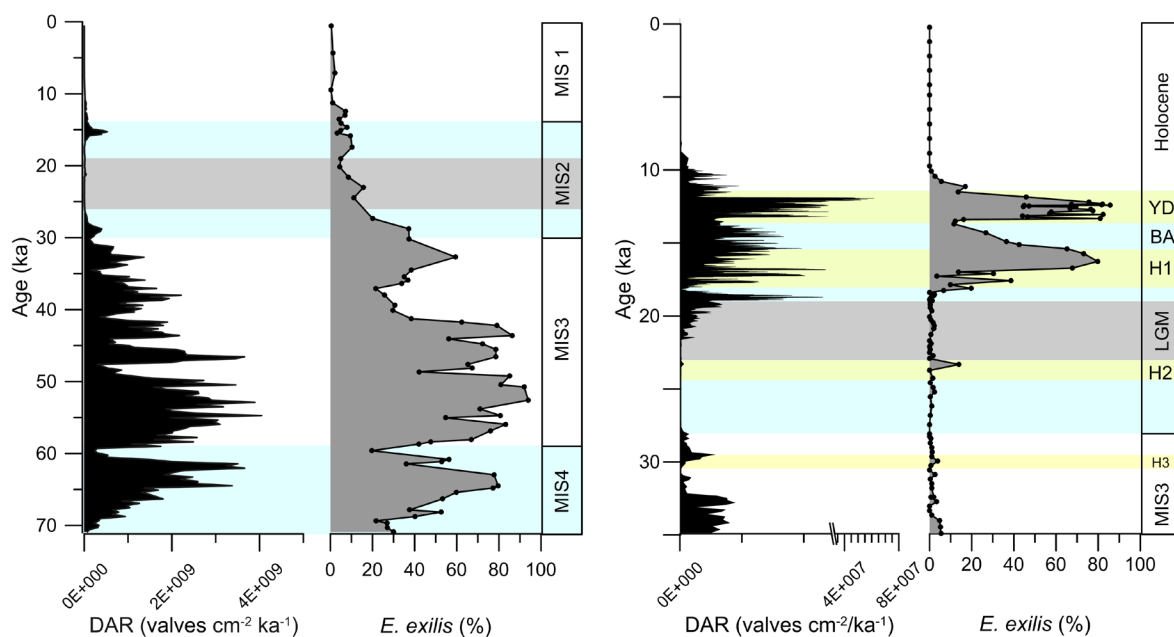
Figure 17. Down-core relationship between diatom accumulation rate (valves cm^{-2} ka^{-1}) and the relative abundance of low oxygen tolerant and fresh phytodetritus feeder species *Eubuliminella exilis* (%) for both the GeoB3606-1 record (shadings represent: unshaded: MIS3 and the Holocene, blue: Marine Isotope 4 and 2, grey: Last Glacial Maximum) and GeoB7926-2 records (shadings represent: unshaded: MIS3 and the Holocene, yellow: Heinrich events 1-3 and the Younger Dryas, blue: MIS2 and the Bølling Allerød).

7.   Research outlooks and implications

Reconstructing the past dynamics of upwelling induced productivity and the coupling with the underlying benthic environment during rapid climate changes has implications for demonstrating potential impending environmental changes. A majority of recent model-based research predicts anthropogenic-associated intensification of wind-driven ocean upwelling in coastal upwelling regions of the world's oceans (McGregor et al., 2007; Bakun et al., 2010; Cropper et al., 2014). Since coastal upwelling operates predominately during spring and summer in subtropical latitudes when much greater heat storage capacity of the ocean waters compared with land surfaces is accentuated, the air temperature over the adjacent landmass tends to increase relative to that over the sea (Bakun et al., 2010). This leads to a strong pressure gradient to form between the land surface and the cooler ocean which promotes an alongshore geostrophic wind which enhances offshore transport of the surface waters and according upwelling. Whilst this is predicted for the low latitude NE Atlantic upwelling systems for example, Benguela upwelling is predicted to decrease in intensity. As climate change proceeds, the Benguela coastline might be expected to become less humid meaning a reduced greenhouse effect within the region (Bakun et al., 2010). Thus the coastal thermal low-pressure cell would relax rather than intensify. Whichever consequence occurs, upwelling intensity changes are likely to occur under anthropogenic warming, leading to shifts in primary production. To add to these contrasting scenarios, considering that the trade winds plays a key role in the upwelling process (particularly at glacial-interglacial timescales), we still need to consider trade wind strength for a representative outlook of future upwelling intensity, opposed to just regional-local atmospheric effects.

Potential consequences to the future of marine ecosystems would not only be apparent in the surface waters, but also within the water column and the underlying seafloor. Increased export production onto the seafloor may result in more intense hypoxia and the release of noxious products from anaerobic decomposition, such as poisonous hydrogen sulphide (Bakun et al., 2010). If benthic foraminiferal accumulation rates were to become suppressed under high export productivity regimes in the future, as noted in the Benguela upwelling system during MIS3, this could also have implications for higher organisms and their community structure.

Intense upwelling and strong nutrient recycling that influence primary productivity variations play a significant role in atmosphere-ocean CO_2 exchange, as well as carbon recycling and export to the open ocean (Longhurst et al., 1995). Upwelling intensification has been reported to occur concurrently with atmospheric CO_2 rise (Anderson et al., 2009) but in contrast, phytoplankton (diatoms) plays a role in CO_2 drawdown (Hales et al. 2005). Thus,

implications for the future ocean uptake of CO_2 together with deoxygenation and rising temperature are presently a subject of intense debate and research (e.g. Gruber, 2011). Overall, given the importance of these highly productive marine ecosystems, this thesis contributes to further understanding of their past dynamics during rapid climate change. It is hoped that we can apply this insight into the past to the major knowledge gap of how upwelling systems will change in the future.

The implications of developing Mn/Ca as a proxy of former bottom water oxygen conditions mean that additional analyses are required upon modern foraminifera specimens in order to calibrate with modern pore water values. Unfortunately, within core GeoB7926-2 there were no *E. exilis* specimens present within the samples corresponding to recent times. Furthermore, culturing experiments on live foraminifera under varying oxygen concentration and productivity regimes are integral for comparing with in situ pore water data to develop it into a robust proxy. On a final note, we also acknowledge that the incorporation of trace metals into the foraminiferal test is species specific (Lear et al., 2002; McKay unpublished) and therefore calibrations need to be established for different foraminiferal species.

Finally, the results of Paper IV suggest that accounting for the 63-125 μm fraction does not impact upon relative abundance patterns, at least for our specific study site. Regardless of the ecological interpretation of the foraminiferal data being unaffected by the inclusion of the finer fraction, it is hoped that a standardised minimum size fraction protocol is introduced for future benthic foraminiferal studies for fair comparisons between datasets.

8. Summary and Conclusions

The main focus of this thesis investigates the response of the benthic environment of upwelling areas to past periods of climate change. More specifically, by utilising a multiproxy approach we have demonstrated how the benthos has been subject to shifts in productivity regimes and bottom water oxygen changes during the late Quaternary. In addition, I examine the protocol used for benthic foraminiferal faunal analysis as well as the development of a new proxy for reconstructing past bottom water oxygen conditions.

The following main conclusions of this work are based on the discussion and the results of the papers appended within this thesis and can be summarised as follows:

- The benthic foraminiferal fauna displays several community shifts corresponding to rapid climatic events. In the case of the Mauritanian upwelling system, four assemblages were apparent within the 35 ka record (Figure 13): first during late MIS3 (35-

28 ka), across H2 and the LGM (28-19 ka), within H1, BA and YD (18-11.5 ka) and finally during the Holocene (11.5-0 ka). Within the Benguela upwelling system, six assemblages occur within the 70 ka record (Figure 14): during late MIS4 (70-59 ka), early MIS3(59-40 ka), late MIS3 (40-30 ka), early-late MIS2 (30-16 ka), the termination of MIS2 and the onset of MIS1 (16-12 ka) and finally, the Holocene (12-0 ka).

• Both the Mauritanian and Benguela records exhibit correlations between productivity export (in the form of diatoms) and the benthic foraminiferal faunal assemblage composition (Figures 13, 14 and 17). The distinct coupling between the surface and benthic environments is governed by the specific upwelling dynamics, such as former upwelling filament locality influenced by sea level changes. When the Mauritanian record is compared to other studies within the region (Paper I), it becomes apparent that substantial variations in primary productivity occur within locally confined area. Therefore the benthic environmental response is also expected to be heterogeneous across these upwelling systems.

• Whilst upwelling intensity and related production are usually attributed to trade wind strength, the results of papers I and II give further insight into how global scale climate change can impact upwelling dynamics and the underlying seafloor environment at a regional scale. The substantial ecological inter-relationships between the pelagic and benthic realms are governed by a complex, interchanging set of factors of trade wind strength, nutrient source and hydrographic conditions.

• More specifically, former benthic environmental conditions were reconstructed and low oxygen conditions were inferred from the dominance of *Eubuliminella exilis* during H1 to the YD within the Mauritanian upwelling system and during MIS3 within the Benguela upwelling system. Ocean circulation changes also played a role in determining the benthic foraminiferal distributions, such as during the Antarctic Cold Reversal in the Benguela upwelling system whereby nutrient depleted bottom waters potentially inhibited the benthic productivity. Relatively more oxygenated conditions were indicated during the Holocene in both upwelling systems.

• Overall, both palaeoecological studies (Papers I and II) evidence that bottom water oxygen and food source are the utmost important factors determining the benthic foraminiferal faunal composition. On a final note, during extremely high phytodetritus export, hypoxic periods, (such as during late MIS4 and MIS3 within the Benguela upwelling system), can strongly suppress the benthic productivity.

• Mn/Ca in benthic foraminiferal calcite might prove to be a valuable proxy for oxygen in the bottom and pore waters. The analytical technique of SIMS has the potential to provide reliable results from a few individuals to compensate for when a sufficient amount of benthic foraminiferal specimens are not available in sediment samples for solution-based analyses.

• Foraminiferal Mn/Ca data reveals that shifts in oxygen levels occurred during different productivity regimes between 35 and 11.5 ka (Figure 15) and thus can assist our understanding of the past environment in the Mauritanian upwelling system in the low latitude NE Atlantic. The Mn/Ca results are well in line with the benthic foraminiferal faunal composition and productivity data.

• Size fraction data highlights that whilst characteristically smaller benthic foraminifera species can be under-represented and lost from the >125 μm fraction (Figure 16), this does not alter the overall species relative abundances and therefore has little impact upon the paleoecological interpretation inferred from the faunal assemblage composition.

Svensk sammanfattning

Genom att använda marina sedimentkärnor från havbotten kan vi dyka ner i forna tiders hav och förstå hur klimat och havsmiljö har utvecklats över tid. Sedimenten och dess innehåll av olika mikrofossil utgör ett fantastiskt miljöarkiv och ju längre ner i sedimenten vi kommer desto äldre är de vanligtvis. I mitt doktorandprojekt har jag studerat marina sediment från kusten utanför NV och SV Afrika, och då särskilt med avseende på en mikrofossil grupp som heter foraminiferer, detta för att bättre förstå hur havsmiljön i dessa områden har utvecklats de senaste 70 000 åren.

Kustområdena utanför Mauretanien, NV Afrika och Namibia, SV Afrika kännetecknas av väldigt rikt fiske och hög produktivitet, dvs. det finns gott om näring i havsvattnet, mycket växtplankton och olika slags organismer. Detta beror på att kustområdena är uppvällningsområden där kallt, näringsrikt vatten från större djup kommer nära ytan. Uppvällningsområden utgör en försvinnande liten del av världshavens yta men har stor socioekonomisk betydelse bland annat för fiskeindustrin. Dessutom är uppvällningsområden en viktig del i den globala kolcykeln just därför att deras produktivitet är så hög. Men har det alltid varit så? Och hur var produktionen under andra tidsperioder när klimatet var annorlunda än vad vi har idag? Kan vi använda kunskap om forna tiders havsmiljö för att förstå pågående och framtida miljö- och klimatförändringar?

Jag har bidragit till ökad förståelse kring just kring de frågorna genom att, tillsammans med mina kollegor, studera en rad olika mikrofossil och deras geokemiska sammansättning från sedimentkärnor från uppvällningsområden. Jag har använt mig av foraminiferer, vilka är encelliga organismer som ofta har ett skal av kalk. Olika arter trivs i olika miljöer vilket kan ge viktiga ledtrådar om forna tiders hav. Dessutom gör kalkskalen att de bevaras väldigt väl i sedimenten. Århundranden efter århundraden ansamlas de i bottensedimenten och vi kan använda dem för att förstå exempelvis hur produktivet i ytvattnet och syreförhållanden i bottenvattnet har varierat. Dessutom kan vi använda skalens geokemiska sammansättning och olika isotoper för att bestämma exempel temperatur i omgivande havsvatten. Foraminiferer fungerar i det fallet som en slags minitermometrar som har spelat in forna tiders havstemperaturer.

Jag kan konstatera att både utanför Mauretanien och utanför Namibia har bottenmiljön varierat avsevärt under de senaste 70 000 åren, vi kan se det genom att foraminiferernas artsammansättning har varierat kraftigt. Dessa variationer stämmer ganska så väl i tid med när vi har andra dokumenterade klimatförändringar. Förändringarna på havsbotten kan vi koppla till variationer i ytvattnets produktion, främst mängden kiselalger - diatoméer. Hur mycket kiselalger som produceras beror i sin tur på hur intensiv uppvällningen är, dvs. hur mycket

kallt och näringsrikt vatten som kommer upp nära ytan. Andra faktorer som kan ha spelat roll är havsnivå förändringar vilket i sin tur styrs av omfattningen av inlandsisars utbredning.

Från både områdena gjorde jag en mycket spännande upptäckt: att särskilt en bottenlevande foraminiferart *Eubuliminella exilis* förekom i stora mängder under tider när mängden diatoméer var mycket stor. *Eubuliminella exilis* verkar gilla diatoméer som mat överallt annat. Däremot minskade de flesta andra foraminiferarter i stor omfattning under samma tidsperiod. Det är mycket möjligt att mängden organiskt material från diatoméer var så stor att den orsakade syrebrist på havsbotten, genom att syre konsumeras när organiskt material ska brytas ner. Detta är särskilt tydligt under perioder med snabba klimatförändringar som exempelvis under Yngre Dryas, vilket är en kortvarig kall period på norra halvklotet, i Mauretaniens uppvällningssystem och under slutet av marin isotop stadie 3 och 4, vilket är omväxlande varma och kalla perioder i jordens tidigare klimat, inom uppvällning systemet utanför Namibia.

Jag ville fortsätta att undersöka de låga syreförhållandena och även utveckla nya metoder och det ledde mig in på spåret Mangan (Mn) och Calcium (Ca) kvoter i foraminiferernas skal. Vi analyserade Mn/Ca i skalen genom att använda avancerad mätutrustning och vi kan konstatera att högre Mn koncentrationer uppmättes under perioder med större mängd kiselalger och större andel av foraminiferer som tål låga syrgashalter i bottenvattnet. Jag vill fortsätta att utveckla den här metoden som en indikator för att återskapa tidigare bottenvattenförhållanden då särskilt med avseende på syrgasförhållanden.

Min avhandling visar på hur tätt kopplat sambanden är mellan ytvatten- och bottenmiljön, även när vattendjupet är flera tusen meter samtidigt som det är mycket komplexa system. Avhandlingen lyfter även fram betydelsen att studera flera olika variabler samtidigt för att bättre förstå hur havsmiljö och klimat har varierat över tid.

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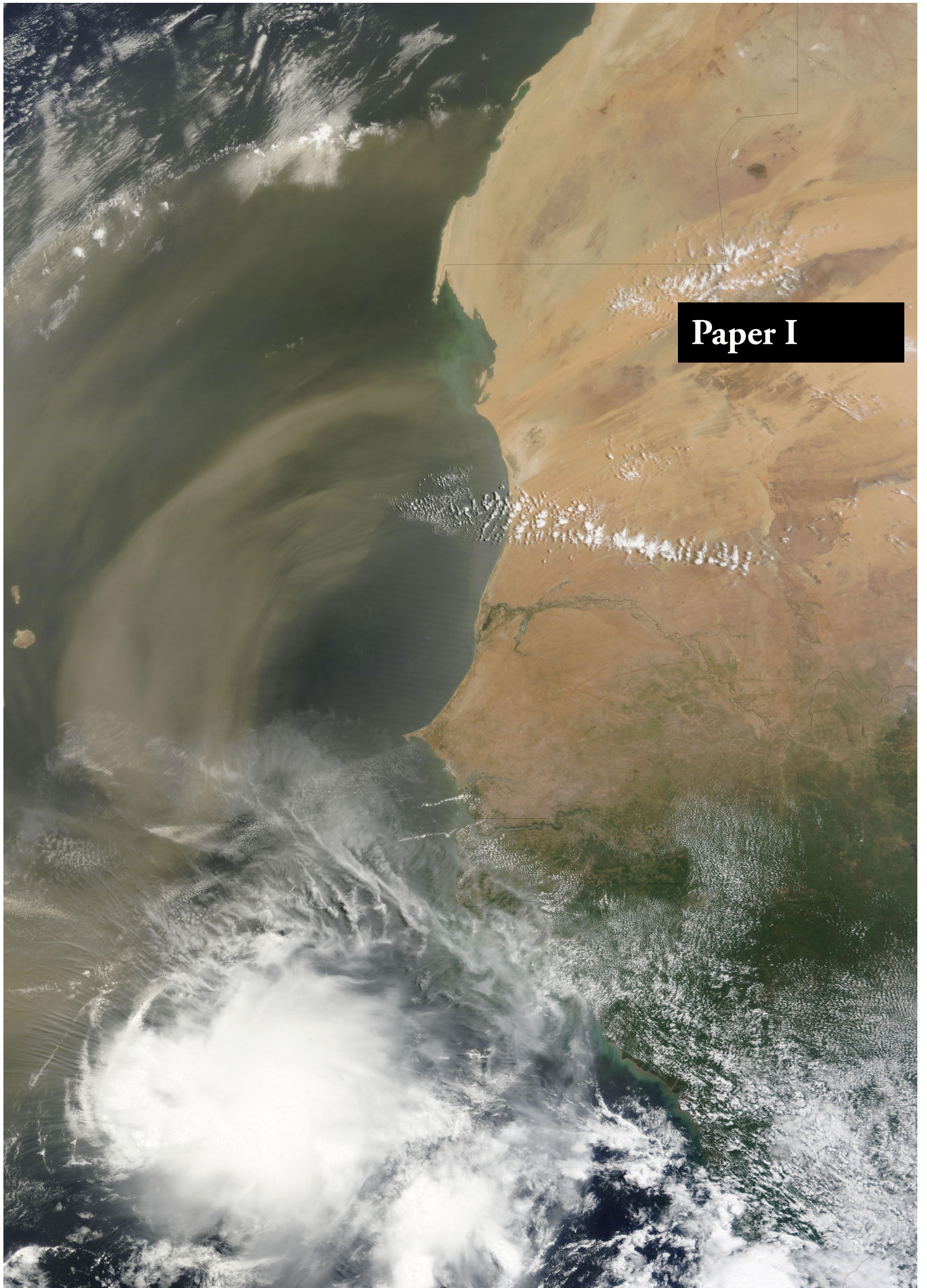
Overleaf: The Mauritanian upwelling region viewed with MODIS imagery. © NASA.