Leibniz Center for Marine Tropical Ecology, Bremen, Germany

Academic year 2012

Changes on the abundance of pelagic foraminifera in relation to calcite saturation state Ω

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Master thesis submitted for the partial fulfillment of the title of

Master of Science in Marine Biodiversity and Conservation

Within the ERASMUS MUNDUS Master Programme EMBC

Abstract

Considerable attention is now being focused on the responses of marine organisms to the environmental scenarios predicted for climate change (ocean acidification and warming), which result from man-induced CO_2 increase in the atmosphere. The decrease of aragonite (Ωa) and calcite (Ωc) saturation states associated with an increase in pCO_2 is affecting calcifying organisms that are sensitive to changes in saturation state, such as planktic foraminifera, which are among the main carbonate producers in the pelagic realm and act as import ballast material in sink particles. Upwelling systems such as those off Namibia reveal already today CO_2 concentrations similar to those predicted for the year 2100 that make them excellent sites to investigate the possible variations in the abundance of pelagic foraminifera as a response to changes of the calcite saturation state. In this study, the abundance of foraminifera was evaluated in relation to calcite saturation state and chlorophyll a concentration, as well as among different sampling methods (vertical and horizontal cast), with the aim of determining which factors are mainly controlling the distribution patterns of different foraminifera species within the Benguela upwelling system, more specifically is calcite saturation state as a effect on abundance as it has for shell weight. The results showed that the two sampling methods gave different results in terms total abundance, species composition and numerically dominant species, highlighting the need for developing sampling strategies with standardized sampling methods in order to avoid biasing of ecological information. Also, they suggest that chlorophyll a concentration was the main factor controlling foraminiferal abundances rather than changes in the calcite saturation state, which is a different trend of what have been observed in the majority of the studies for the shell weight of planktic foraminifera. After this study, further investigation is suggested on the calcification mechanisms of planktic foraminifera, in order to better understand how does carbonate chemistry and food availability affects the foraminiferal abundances in natural waters.

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Introduction

Considerable attention is now being focused on the responses of marine organisms to the environmental scenarios predicted for climate change (ocean acidification and warming), which result from man-induced CO_2 increase in the atmosphere since the industrial revolution (e.g., Orr et al., 2005; de Moel et al., 2009). Approximately between 1980 and 1999, one third of the anthropogenic CO_2 has been taken up by the oceans (Sabine et al., 2004) and due to its sea-air interface exchange, its highest concentrations are found in near-surface waters (Sabine et al., 2004). With the intrusion of CO_2, the surface ocean becomes the water less alkaline, and the carbonate ion concentration and therewith the aragonite (Ωa) and calcite (Ωc) saturation state decreases. This process is called "ocean acidification". Various experiments have shown that many marine calcifying organisms respond to a decrease in aragonite or calcite saturation state by reducing their calcifying rates (e.g., Beaufort et al, 2011). Ocean acidification has been projected into the future by modeling different CO_2 emission scenarios (e.g., Caldeira and Wickett, 2003), indicating that higher pCO_2 would lead to a decrease in the growth rates of important marine calcifying organisms, such as pteropods (i.e., marine opisthobranch gastropods; e.g., Comeau et al., 2012) and corals (e.g., Gattuso et al., 1998; Kleypas et al., 1999). Other studies have also focused on planktic foraminifera (e.g., Barker and Elderfield, 2002; de Moel et al., 2009; de Nooijer et al., 2009); however, field observation is scarce to our knowledge. Foraminifera are relatively large protozoa that are widespread in the marine environment, with benthic and pelagic species. Most of the pelagic species are found in the euphotic zone, as their subsistence is depending on plankton and/or their symbionts (Bé, 1982). Among these pelagic species, the majority precipitates a calcite shell, which can be very simple with one or only few chambers or it can be complex with many chambers arranged in various three-dimensional configurations structures, which have the appearance of a chambered snail shell.

Planktic foraminifers form a minor part in the total marine plankton; nevertheless, they are among the major producers of calcareous particles in the pelagic realm through the formation of their shells, which after reproduction or death act as import ballast material in sinking particles, carrying carbon from the surface ocean into the deep sea and further into the sediments (Milliman, 1993; Schiebel, 2002; Schiebel et al., 2007).

This component of the carbon pump caused by the sinking of calcareous hard parts into the deep sea and sediments is called the inorganic carbon or carbonate pump. As sedimentary biogenic calcite is such a large carbon reservoir, fluctuations in its production at the ocean surface and its burial or dissolution at the ocean floor is one of the dominant processes involved in neutralizing excess atmospheric CO_2 in the ocean, by reabsorbing it after dissolution at deeper layers and upwelling to the surface (Erez, 2003; Kwon et al., 2009). As they exert these important stabilizing feedbacks for the ocean as well as for the atmosphere, it can be inferred that planktic foraminifera have an important role in regulating our climate. Globally, the planktic foraminifera calcite export out of the productive zone is estimated at 1.3 – 3.2 Gt y^{-1} (Schiebel, 2002), which is equivalent between 25 to 50 % of the total open marine $CaCO_3$ flux (Milliman, 1993). On a global average, about 25 % of the test calcite produced in surface waters has been assumed to arrive the sea floor, i.e., 0.71 Gt y^{-1} (Schiebel et al., 2007), which may account up to 65 % of the total deep-marine calcite budget (estimated at 1.1 Gt y^{-1}; Milliman and Droxler, 1996).

Shell weight of planktic foraminiferal species is positively affected by temperature, pH, Ca^{+2} and CO_3^{2-} concentrations and total alkalinity of the ambient sea water, as well as by symbiont activity and the formation of secondary calcite crusts (Schiebel and Hemleben, 2005). Lower carbonate concentration decreases the calcification rate of planktic foraminifers (Bijma et al., 1999); however, it has been shown that they are able to perform calcification in low ambient carbonate concentrations by elevating their pH at the site of calcification (de Nooijer et al., 2009). This process is accompanied by the fixation of organic carbon, and the ratio of biogenic calcium carbonate (inorganic carbon) to particulate organic carbon formation determines the $CaCO_3$ to POC flux ratio, or "rain" ratio. Therefore, a decrease in water pH would tend to the need of more energy by foraminifers to precipitate calcite and consequently to the formation of a lighter shell, which may generate variations in their abundance, the deposition flux of dissolved inorganic carbon to the sea bottom, and the preservation of $CaCO_3$ in deep sea sediments.

In terms of distribution, some species or a complete assemblage of planktic foraminifera can be classified into five different biogeographical provinces: (1) polar, (2) subpolar, (3) transition (template), (4) subtropical, and (5) tropical (Hemleben et al., 1989). This modern biogeographical provinces show a clear correlation with the surface circulation

pattern (Murray, 1991); however, other multiple factors exert control in foraminiferal distribution and abundance. Generally, these other factors include hydrographic conditions, such as salinity (Schmuker and Schiebel, 2002; Bergami et al., 2009; Retailleau et al., 2009), temperature (Mohiuddin et al., 2005; Bergami et al., 2009), chlorophyll a concentration (Fairbanks and Wiebe, 1980; Schiebel et al., 2001; Bergami et al., 2009; Retailleau et al., 2009; Siccha et al., 2009), nutrient content (Marchant et al., 1998; Schiebel et al., 2001), or even natural events such as El Niño (Marchant et al., 2004) or the occurrence of a storm (Schiebel et al., 1995). Shell formation of planktic foraminifera is directly coupled to carbonate equilibrium of ambient seawater (Schiebel and Hemleben, 2005) and to nutrient concentrations (Aldridge et al., 2011) that would also determine the quality and quantity of their food; nevertheless, to our knowledge, it has not been documented the effects that changes in calcite saturation state may have on the abundance of planktic foraminifera.

Eastern boundary current systems are highly productive areas associated to upwelling zones, which are characterized by strong physical, chemical, and biological variability at interannual to decadal timescales (Quiñones, 2010). Upwelling systems such as the Benguela upwelling system off Namibia (between 17°S and 30°S), show nowadays CO_2 concentrations similar to those predicted for the year 2100 (Rixen et al., in prep.) that make it an excellent site to investigate under natural conditions the possible variations in the abundance of pelagic foraminifera as a response to changes of the calcite saturation state, which tend to increase from the upwelling cells along the coast towards the open ocean.

In this study, the abundances of different planktic foraminifera species of the Benguela Upwelling System off Namibia were evaluated in relation to calcite saturation state and chlorophyll a concentration, by using surface plankton samples from three different years (RV *Africana*, cruise 258, December 2009; RRS *Discovery*, cruise 356, September-October 2010; and RRS *Maria S. Merian*, cruise MSM17/3, January-March 2011). The main objective was to investigate their response in terms of abundance to changes in the calcite saturation state and chlorophyll a concentration due to upwelling of acidic and nutrient enriched subsurface waters. For one period (MSM 17-3, January-March of 2011) the results were derived from an Apstein net (vertical cast) as well as from a multiple opening/closing net (horizontal cast); therefore, it will be also evaluated if the results of these two different sampling methods are comparable among them.

Materials and Methods

Site description The Benguela upwelling system (Figure 1) is one of the four most productive wind-driven eastern boundary upwelling systems, and has the highest potential to export carbon from the euphotic zone (Monteiro, 2010). It is considered as a two-sector system (northern and southern subsystems) separated at 26°S by the powerful Lüderitz upwelling cell. Its temporal variability varies from mesoscale events of a few days' duration (e.g., upwelling) to decadal scale changes in its subsystems, which act as a crucial driver for the variability of plankton development (Hutchings et al., 2006; Hutchings et al., 2009; Monteiro, 2010). Moreover, it shows CO_2 concentrations similar to those predicted for the year 2100 (Rixen, in prep.), tending to increase the calcite saturation state from the upwelling cells along the coast towards the open ocean. In the continental margin of the Benguela upwelling system, a surface equatorward current that flows from its southern boundary in Cape Peninsula (at approximately 34°S) dominates the system, being its northern boundary the Angola–Benguela front (Hutchings et al, 2009), which has a seasonally and interannually driven meridional displacement between 14 and 17°S (Monteiro et al., 2010). It is uniquely bounded on both northern and southern ends by warm water current systems: the equatorial eastern Atlantic and the Indian Ocean's Agulhas Current (Shannon and O'Toole, 2003). The transport linkages between the slope and the shelf are considered to be largely driven by the advection of South Atlantic Central Water (SACW) at three points: Cape Frio at 17°S, Lüderitz at 26°S and Cape Columbine at 33°S, marking the three main components of the this system (Monteiro et al, 2010). The SACW is originated from Antarctic Intermediate Water (AAIW) that is formed at the surface in polar and subpolar regions and have distinct characteristics in the northern and southern Benguela, with the entrance through the Angola Basin of a high salinity AAIW into the northern Benguela in a poleward undercurrent along the shelf edge; whereas the southern Benguela has a low salinity AAIW close to the subtropical front (Shillington et al., 2006 and references therein). A combination of the equatorward Benguela Current and the southeast trade winds result in upwelling of nutrient-rich water South Atlantic Central Water along the west coast of southern Africa. Together with shelf width and coastal topography, discrete upwelling cells are created between the Cape of Good Hope and the Kunene River mouth (17 and 34°S, respectively; Hutchings et al., 2009), which make it difficult to define delimited spatial and temporal seaward boundaries of the

Benguela upwelling system (Monteiro, 2010). The Benguela upwelling system is also characterized for having low oxygen waters, which is a key environmental factor for variability of the ecosystem as well as for the commercial viability of fisheries (Monteiro and van der Plas, 2006). The seasonal oxygen balance over the Namibian shelf depends to a high extent on the water mass composition of the upper central water layer, controlled by the large scale and local circulation. In the north, a poleward undercurrent, which is the continuation of the Angola Current, flows into the northern Benguela. In austral summer hypoxic, nutrient rich South Atlantic central water (SACW) from the Angola Gyre is transported into the northern Benguela, whereas during the winter season the oxygen rich Eastern SACW (ESACW) spreads northward. During the austral summer, anoxic bottom waters together with hydrogen sulphide events are observed at the central Namibian shelf, which correlate to an SACW fraction >55% (Mohrholz et al., 2008).

2009   2010   2011
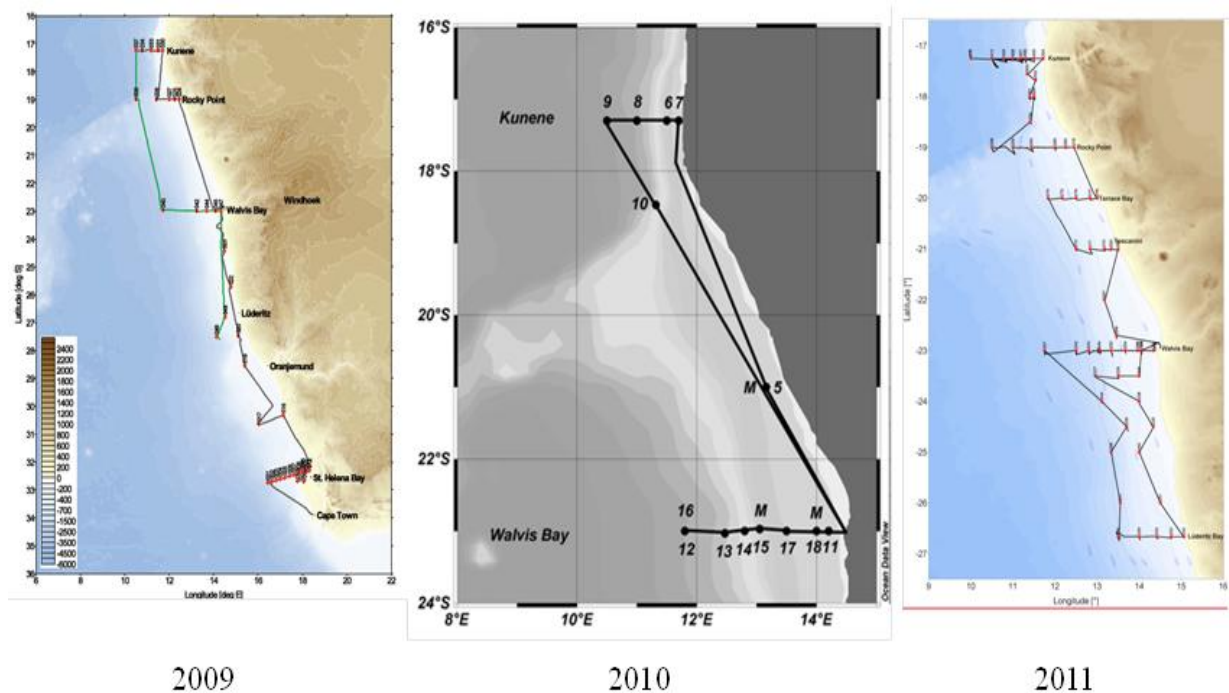
Figure 1: Maps of the Benguela Upwelling System off Namibia, showing the sampling area of the three cruises at each year. 2009: cruise 258 on board of RV *Africana*, during December, 2009; 2010: cruise 356 on board of RRS *Discovery*, during September-October, 2010; 2011: cruise on board of RRS *Maria S. Merian*, during January-March, 2011.

Methods and instruments During each cruise, surface (40 m – 0 m) plankton samples were taken at each station using an obliquely towed 55μm mesh net that was placed inside a multiple opening/closing net (Figure 2), during three different cruises: RV *Africana*, cruise 258, December 2009; RRS *Discovery*, cruise 356, September-October 2010; and RRS *Maria S. Merian*, cruise MSM17/3, January-March 2011 (Figure 1). The volume of water that went through was estimated by the multiplication of the area of the opening of the net times the distance it travelled at each station, thus obtaining abundance data as the number of foraminifera per cubic meter (forminifera m^{-3}). Also, for the MSM17-3 cruise in January-March 2011, the data available, which was obtained with a multiple opening/closing net (horizontal cast), will be evaluated with regard to what was obtained for the same period with an Apstein net (vertical cast).

The samples were fixed with buffered 10% formalin and kept in plastic containers to be later sorted, identified and counted by the use of a stereoscope (Zeiss Stemi SV6 and Zeiss SteREO Discovery V8).
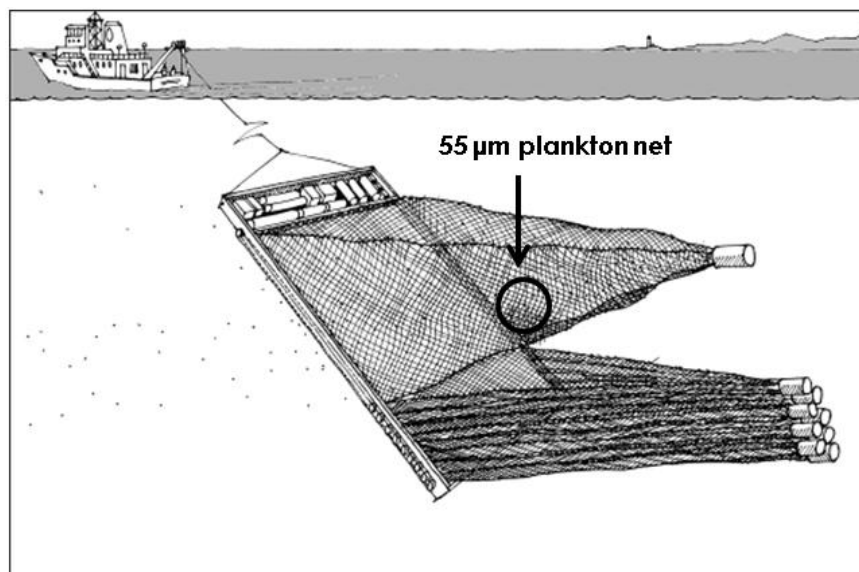
Figure 2: Schematic view of the placement of the 55 µm mesh size phytoplankton net in the multiple opening/closing net. Image modified from: http://octopus.gma.org/onlocation/mocness.html.

Data obtained Foraminifera were sorted individually from the wet samples with a pipette, washed and finally dried at 60°C. Later, they were divided into two size fractions: <150 μm and >150 μm (i.e., juveniles and adults, respectively). All fractions were counted and the >150 μm fraction was identified. This abundance data were compared to the calcite saturation state (obtained from total alkalinity (TA) and the concentrations of dissolved inorganic carbon (DIC)) and chlorophyll a concentration data obtained from the CTD (except for the year 2010).

Carbonate System The mole fraction of CO_2 (xCO_2) was continuously measured in the ocean and the atmosphere by using an "*underway carbon dioxide analyzer*" SUNDANS. Sea water temperatures (SST), salinity (SSS), wind speeds and the atmospheric pressure were continuously recorded by each research vessel. The collected data were evaluated and used to convert xCO_2 into the fugacity of CO_2 (fCO_2) which is required to calculate the CO_2 flux across the sea water interface. At the sampling sites, water samples were collected by Niskin bottles attached to the CTD in order to analyze TA and DIC which in addition to SST and SSS were used to calculate calcite saturation states. Chlorophyll a concentrations were taken from the CTD.

Data analysis A comparison of different data sets was done by producing figures with a scientific graphing software (Grapher 4) and by performing multiple regression analyses with R (www.r-project.org).

Results

Environmental settings

The environmental conditions during each period are described from the cruise reports of each year. According to the Cruise Report of Africana 258: Geochemistry and Ecology of the Namibian Upwelling System (GENUS) and St Helena Bay Monitoring Line (SHBML), there was occurrence of upwelling during December of 2009 in terms of changing water temperature and conductivity, which could be observed along the coastline from approximately 27° to 23°S as well as at approximately17°S. However, for the area between 27° to 23°S there was no direct correlation between the extent and intensity of upwelling and the geochemical state of the respective water mass at the surface, showing a patchy chemical composition together with small-scale variations. Around 17°S, physical and chemical properties showed more correlation, i.e. low water temperature, enhanced nutrient concentrations, oxygen depletion and elevated pH and CO_2 levels (Figure 3).
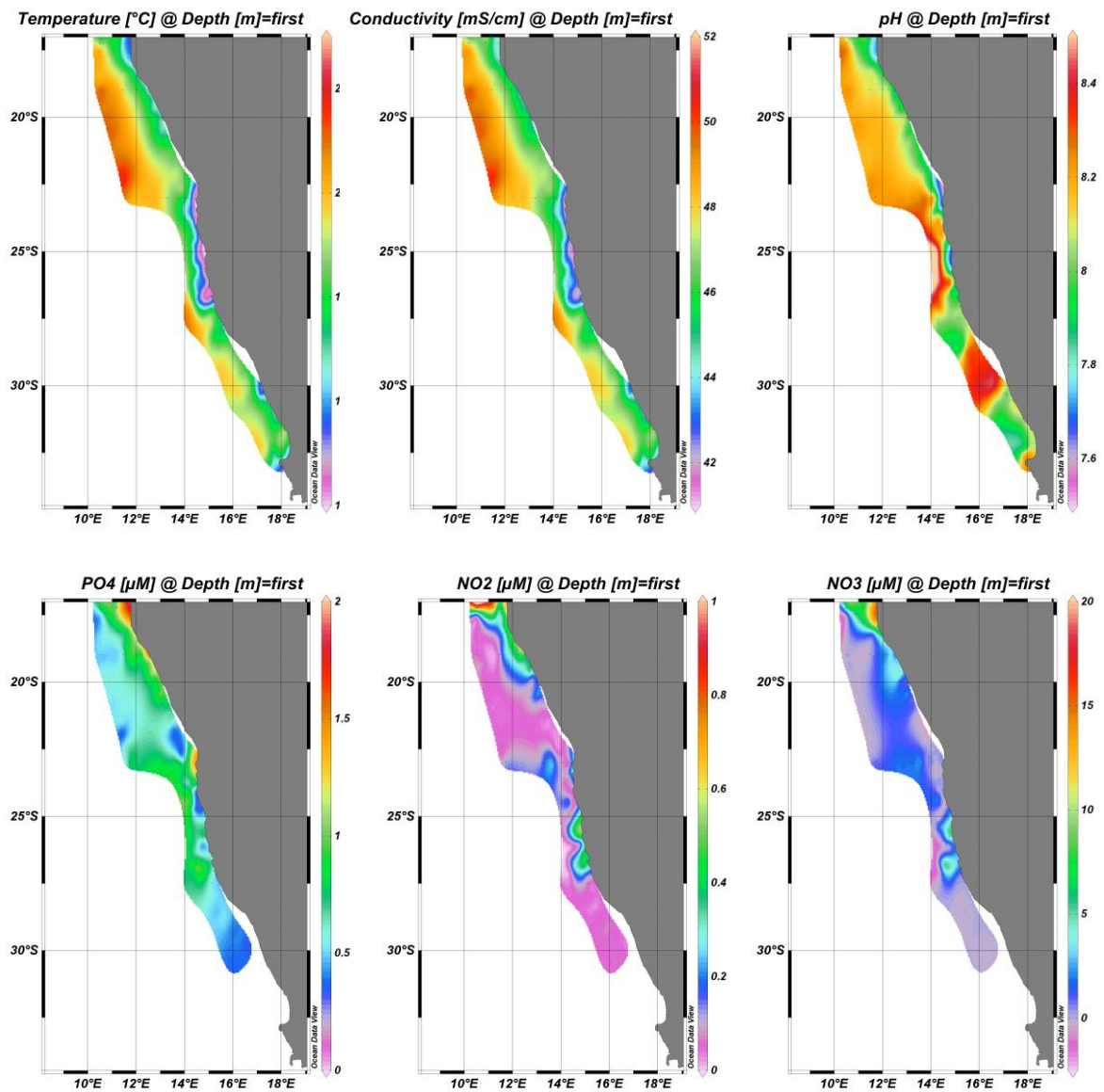
Figure 3: Physical and chemical properties of the Benguela upwelling system off Namibia during December of 2009 obtained from continuous measurements (>17 000 data points) of a Ferrybox and *Systea* autoanalyser installed on RV *Africana*. (Source: Cruise Report GENUS *Africana* 2009, p. 43)

According to the Cruise Report of D356 RRS *Discovery*: 10 September (Walvis Bay) – 13 October 2010 (Cape Town), the hydrographic investigations during the first leg of D356 covered two transects in the northern Benguela, one off the Kunene river mouth at 17° 30' S and one off Walvis Bay at 23°S, which corresponds to the sampling area for the samples analyzed in this study. The cruise started during strong winds favoring coastal upwelling followed by a rather calm period when the Kunene transect was

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worked. Synoptic figures of the Kunene transect show cold and less saline upwelled water near the coast and warm saline waters of tropical origin more off-shore (Figure 4).
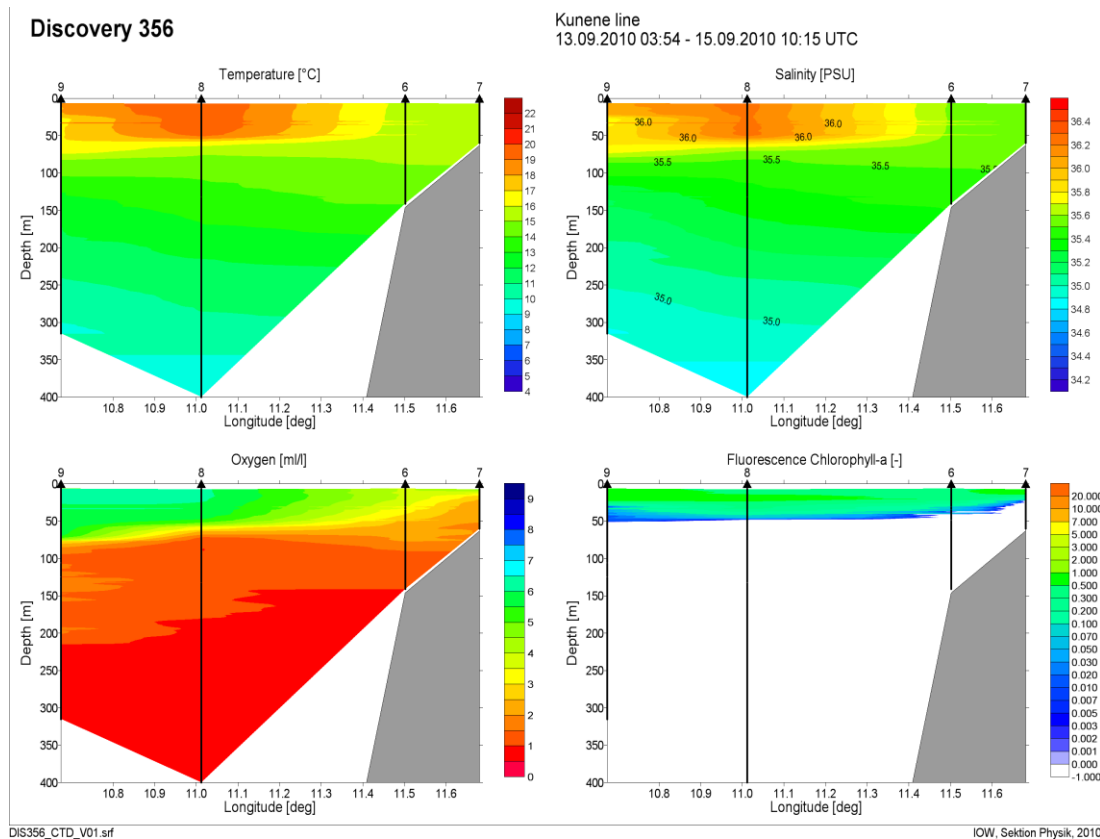
Figure 4: Physical properties of the Benguela upwelling system off Namibia during September-October of 2010 obtained from the measurements of a CTD (SeaBird 911+) deployed from RRS *Discovery*. (Source: Cruise Report *Discovery* 2010, p. 4)

The CTD casts reach the core of the oxygen minimum zone, which extends to sub-surface waters at the in-shore station. The horizontal gradient in the surface water reflects the reduced saturation concentration with increasing temperature. The mole fraction of CO_2 (xCO_2) in the surface water revealed an extreme spatial variability caused by the complex interplay of upwelling of CO_2 enriched deep water, the biological uptake and the CO_2 emission.

According to the cruise report Maria S. Merian, in the surface layer at 20 m depth the temperature distribution shows a west east gradient with the cooler water at the coast indicating recent or active coastal upwelling along the entire coast. This pattern is

superimposed by a north south gradient due to the transition from tropical conditions near the Kunene to the subtropics in the south of the investigation area. The off shore waters north of 20°S depicted a higher temperature than usual for this season, pointing to an intensified southward transport of tropical waters. The salinity distribution was characterized by a southward decrease in salinity from 36 (PSU) at the Kunene mouth down to 35 (PSU) near Lüderitz. This depicts the distribution of the two dominating central water masses. High salinities in the north are associated with SACW, the low saline water in the south is ESACW. The transition zone between both water masses stretches from the Rocky Point transect southward to at least Walvis Bay. Surface oxygen concentrations were reduced in a narrow coastal belt along the entire coast, indicating coastal upwelling of water from subthermocline layers.

The maximum chlorophyll a fluorescence in the surface layer was located in a belt 40 to 80 nautical miles off the coast. This shift is caused by the temporal delay between the physical process of upwelling and the development of phytoplankton bloom in the upwelled waters (Figure 5).
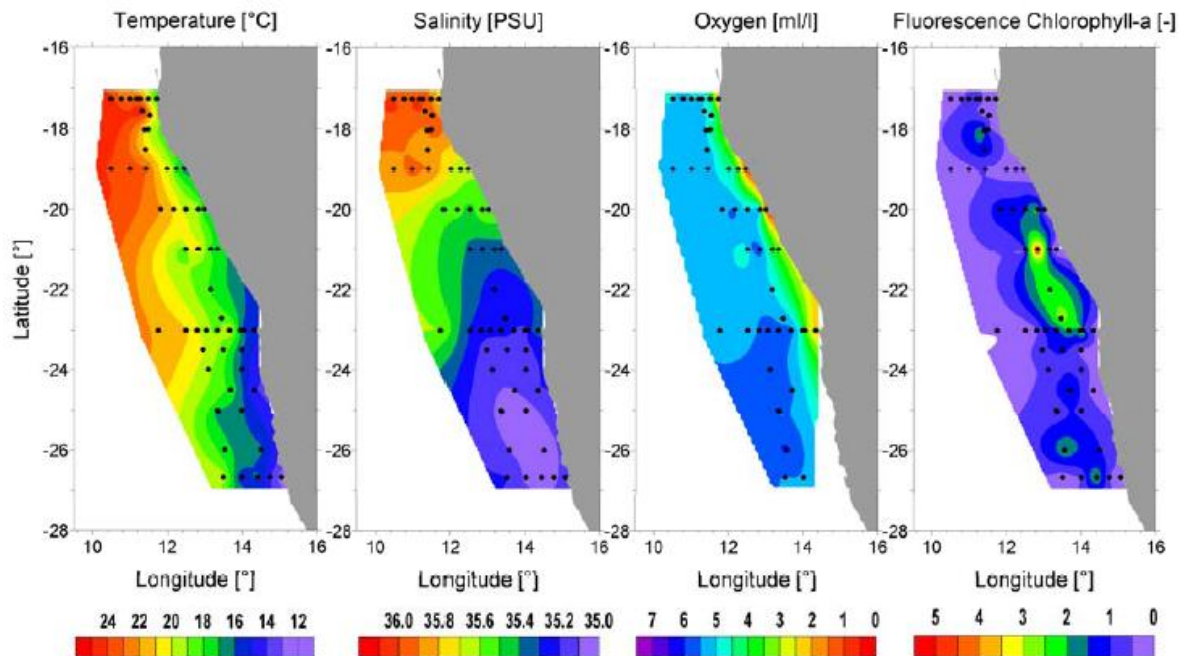
Figure 5: Horizontal distribution of temperature, salinity, oxygen and chlorophyll a fluorescence off Namibia at 20 m depth (based on CTD data). (Source: Maria S. Merian-Berichte xx-y, Cruise 17, Leg 3, Walvis Bay - Dakar, Jan 30 – Mar 07, 2011; p. 8).

Foraminiferal abundance

For the three cruises, there was in general more individuals in the <150 µm size fraction (i.e., juveniles) than in the >150 µm fraction (i.e., adults; Figure 6, Table 1). Total abundances (adults + juveniles) ranged from 6122,63 to 63,84 individuals m^{-3}; 2409,81 to 18,92 individuals m^{-3}; 1755,35 to 0 individuals m^{-3} for Afri258 (2009), Discovery356 (2010) and MSM17-3 (2011), respectively. Regarding adults' abundances, they ranged from 925,90 to 9,93; 847,40 to 3,78 and 1041,35 to 0 adults m^{-3} for Afri258, Discovery356 and MSM17-3, respectively (Table 1).
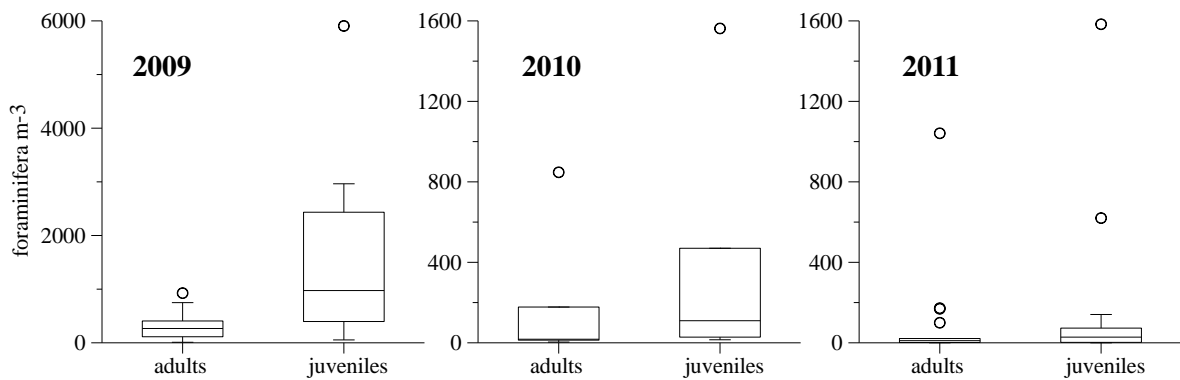
Figure 6: Boxplot of adults and juveniles data from the three cruises. 2009: cruise 258 on board of RV *Africana*, during December, 2009; 2010: cruise 356 on board of RRS *Discovery*, during September-October, 2010; 2011: cruise on board of RRS *Maria S. Merian*, during January-March, 2011. Open circles indicate outliers.

Table 1: Foraminifera abundance at each station per cruise, together with information on environmental settings (calcite saturation state and mean of chlorophyll a). Afr258: cruise 258 on board of RV *Africana*, during December, 2009. D356: cruise Discovery 356 on board of RV RRS *Discovery*, during September-October, 2010. MSM17/3: cruise on board of RV *Maria S. Merian*, during January-March, 2011. Ω calcite: calcite saturation state. mean Chla-a: mean chlorophyll a concentration (mg m^{-3}). n.a.: data not available.

| cruise	Station	adults m^{-3}	juveniles	total ind.	Ω calcite	mean Chl-a
Afr258	30246	242,55	219,36	461,91	4,90	1,23
(2009)	30247	561,78	1316,50	1878,29	5,03	2,68
	30248	407,09	879,31	1286,40	4,56	0,19
	30249	217,11	5905,51	6122,63	2,80	3,46
	30251	749,04	2434,39	3183,44	2,90	4,27
	30252	80,25	624,20	704,46	4,34	3,06
	30260	9,93	53,91	63,84	4,16	0,90
	30261	294,62	489,38	784,00	5,59	1,12
	30262	112,76	2963,96	3076,72	5,10	1,17
	30263	54,51	397,38	451,89	4,77	5,37
	30264	925,90	1401,86	2327,76	4,67	7,14
	30266	136,04	1069,15	1205,19	3,41	1,91
D356	6	16,49	28,27	44,75	2,19	n.a
(2010)	7	3,78	15,13	18,92	3,77	n.a
	15	13,38	63,54	76,91	3,27	n.a
	17	847,40	1562,40	2409,81	3,42	n.a
	24	19,51	156,05	175,56	2,86	n.a
	25	177,74	469,74	647,48	3,04	n.a
MSM17-3	232	99,65	140,85	240,50	1,32	0,13
(2011)	233	0,00	2,08	2,08	2,53	0,42
	235	0,00	0,00	0,00	4,62	0,53
	243	0,00	0,73	0,73	4,68	0,63
	246	2,90	1,49	4,39	3,36	1,92
	250	1,49	1,73	3,22	4,29	2,30
	254	1,73	5,55	7,28	4,51	2,30
	266	172,00	1583,35	1755,35	4,69	2,30
	270	1041,35	619,90	1661,25	4,80	5,20
	271	12,91	59,92	72,84	1,79	4,87
	279	19,97	41,61	61,59	2,41	0,67
	282	7,80	32,22	40,02	3,53	2,49
	285	5,31	2,29	7,61	4,15	0,21
	292	0,62	0,76	1,38	4,98	0,56
	295	0,27	0,45	0,72	4,04	0,36
	304	0,00	0,76	0,76	2,77	0,47
	305	0,67	1,38	2,05	4,26	0,18
	306	0,46	2,54	3,00	5,04	0,84

In relation to calcite saturation state, the foraminifera showed a tendency to increase their abundance at calcite saturation state over 3,5 for the cruises Afri 258 (2009) and MSM 17-3 (2011), whereas for the cruise D-356 (2010) they increased in abundance from a calcite saturation state of 3 (Figure 7a). For the MSM 17-3 cruise from January to March of 2011, the samples from both the Apstein net and the phytoplankton net placed inside the multiple opening/closing net showed a higher abundance of foraminifera within a similar range of calcite saturation state; nevertheless, compared to the Apstein net's samples, the abundances were one order of magnitude higher for the multiple opening/closing net samples (Figure 7b).

Between foraminifers' abundance and chlorophyll a concentration, the results do not show a clear relationship for both 2009 and 2011 cruises (Figure 7c), nor for the Apstein net and the multiple closing net of the year 2011 (Figure 7d). Moreover, there were some zero values of abundance (Figure 7) that cannot be related for either the calcite saturation state or the chlorophyll a.

Species Composition

Regarding species composition, four species showed numerical dominance for the three periods: *Neogloboquadrina pachyderma*, *Globigerina bulloides*, *Globorotalia inflata* and *Turborotalita quinqueloba* (Figure 8). Also, during the three cruises, the dextral coiling form of *G. pachyderma* occurred in a much higher proportion than its sinistral coiling form (Figure 9).
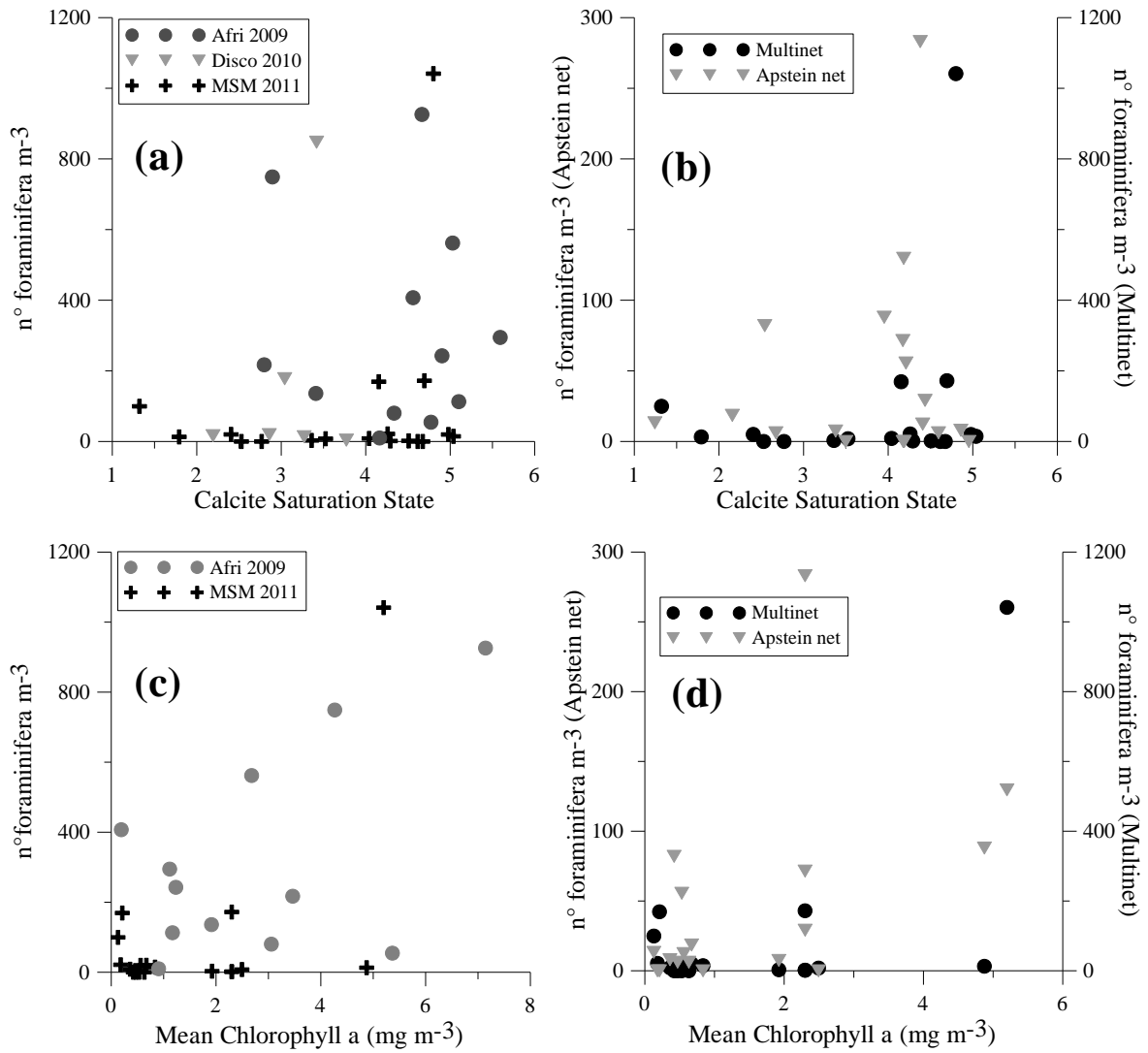
Figure 7: (a) Foraminifera abundances in relation to calcite saturation state for the three cruises. (b) Foraminifera abundances in relation to calcite saturation state for a comparison between the two different nets used in 2011. (c) Foraminifera abundances in relation to chlorophyll a for two cruises. (d) Foraminifera abundances in relation of chlorophyll a for a comparison between the two different nets used in 2011. Afri 2009: cruise 258 on board of RV *Africana*, during December, 2009. Disco 2010: cruise 356 on board of RRS *Discovery*, during September-October, 2010. MSM 2011: cruise on board of RRS *Maria S. Merian*, during January-March, 2011.
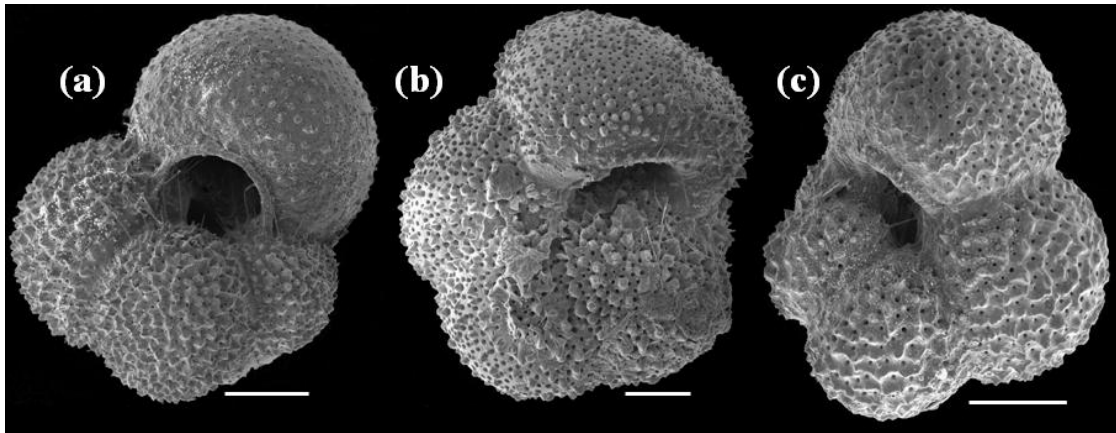
Figure 8: Scanning electron microscope pictures of three numerically dominant foraminifera species. (a) *Globigerina bulloides*; (b) *Globorotalia inflata*; (c) *Neogloboquadrina pachyderma* (dextral coiling). Scale bar: 50 µm.
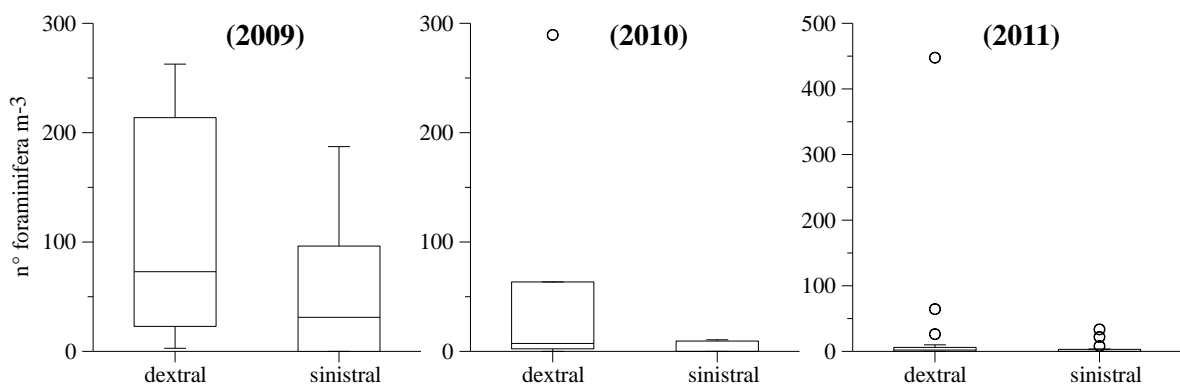
Figure 9: Boxplot of the dextral and sinistral coiling form of the foraminifera species *Neogloboquadrina pachyderma* from the three cruises. 2009: cruise 258 on board of RV *Africana*, during December, 2009; 2010: cruise 356 on board of RRS *Discovery*, during September-October, 2010; 2011: cruise on board of RRS *Maria S. Merian*, during January-March, 2011. Open circles indicate outliers.

The numerically dominant species showed higher abundances from a value of calcite saturation state of 3.5 for the cruises Africana 2009 and Maria S. Merian 2011 (Figure 10a,d) whereas for the cruise Discovery 2010, they showed higher abundances from a value of calcite saturation state of 2,5 (Figure 10c). The abundance did not show a clear tendency with respect to chlorophyll a concentration during the cruises Africana (2009) and Maria S. Merian (2011; Figures 10b,e). Moreover, there were some zero values of

abundance (Figure 10) that cannot be related for either the calcite saturation state or the chlorophyll a.
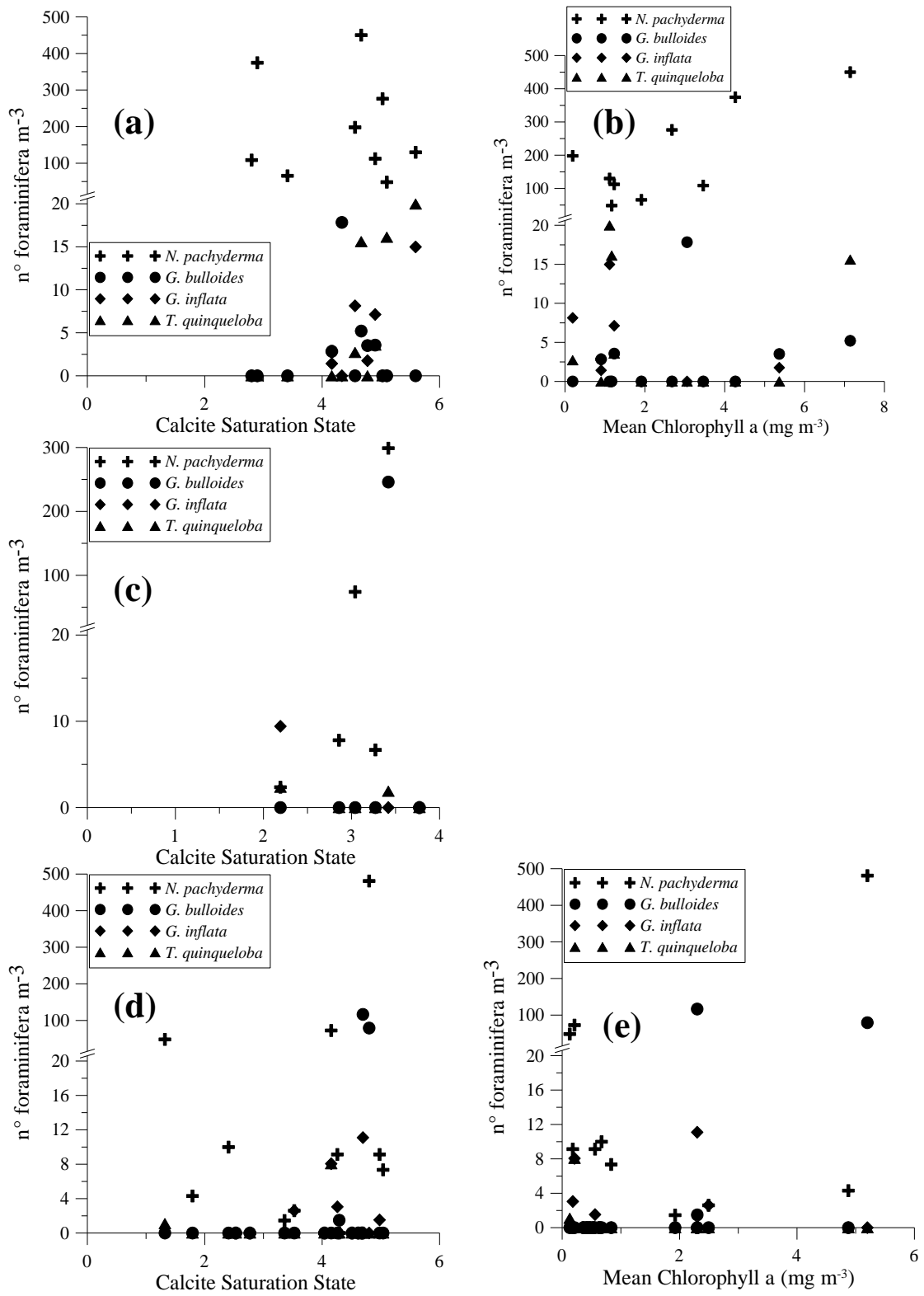
Figure 10: Abundances of the four numerically dominant species in relation to calcite saturation state (left panel) and chlorophyll a concentration (right panel) for the cruises on board of RV *Africana* (2009; a,b), RRS *Discovery* (2010; c) and RRS *Maria S. Merian* (2011, d,e).

Comparison of results among net types in Maria Merian (2011) cruise

Regarding the number of adult foraminifera caught, the phytoplankton net placed inside the multiple opening/closing net caught up to one order of magnitude more adult foraminifera than the Apstein net in some stations, or did not catch any adult foraminifera at all (Table 2). In total, the phytoplankton net placed inside the multiple opening/closing net caught almost twice the amount of adult foraminifera than the Apstein net.

Table 2: Abundances of adult foraminifera caught with two different types of nets and casts (Apstein net-vertical cast; phytoplankton net inside a multiple opening/closing net-horizontal cast) during the cruise on board of RRS *Maria S. Merian*, on 2011.

	Number of Adults m^{-3}	
Station	Multinet	Apstein net
232	99,65	13,23
233	0,00	82,01
235	0,00	55,56
243	0,00	6,17
246	2,90	7,41
250	1,49	29,10
254	1,73	71,43
266	172,00	283,07
270	1041,35	129,63
271	12,91	87,96
279	19,97	18,52
282	7,80	0,00
285	169,14	0,00
292	19,79	12,35
295	8,67	7,94
304	0,00	6,17
305	21,31	0,00
306	14,69	0,00
Total	1593,43	810,54

The number of species that occurred in the samples taken with both nets was five (*Neogloboquadrina pachyderma*, *Globigerina bulloides*, *Globorotalia infalata*, *Globorotalia menardii* and *Orbulina universa*), Also, there were differences in terms of numerically dominant species composition between the samples caught with the Apstein and the mutiple opening/closing net. *N. pachyderma* and *G. bulloides* were numerically dominant species common for both nets; whereas *O. universa* and *Neogloboquadrina dutertrei*, which were numerically dominant species for the Apstein net, were also caught with the phytoplankton net placed inside the multiple opening/closing net, but were not numerically dominant for it. *G. inflata* was caught by both nets, but was numerically dominant only for the phytoplankton net placed inside the multiple opening/closing net. Finally, *Turborotalita quiqueloba*, the fourth dominat species caught by the phytoplankton net placed inside the multiple opening/closing net, was not caugth with Apstein net (Figure 11).
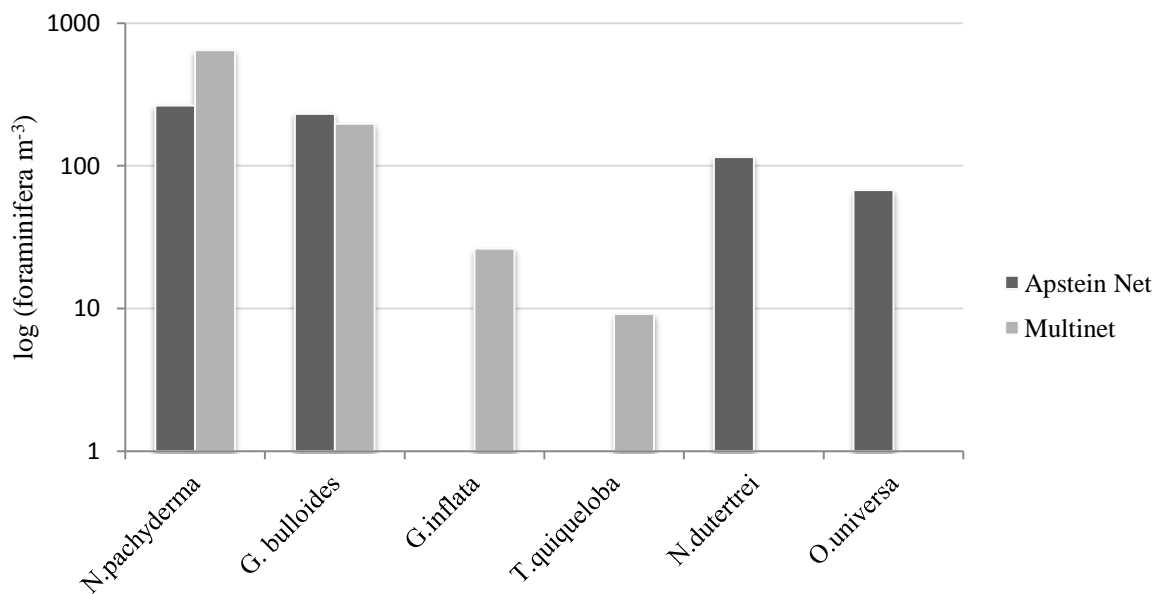
Figure 11: Abundances of numerically dominant species for two different sampling gears used in the cruise on board of *Maria S. Merian* in 2011.

Moreover, focusing on the numerically dominant species that were common for both nets (i.e., *N. pachyderma* and *G. bulloides*), a difference in the amount of individuals caught and their respective abundances could be observed, being some species underestimated at with respect to the other net and vice versa (Table 3).

Multiple regression analyses

In order to determine which of the two variables were affecting more the abundance of foraminifera and at which extent, multiple regression analyses were done with multiplicative and additive models. The predictors used were calcite saturation state, chlorophyll a concentration and CO_2 concentration. Only the additive models were selected after their Bayesian information criterion. The results showed that there is no relationship between the three predictors used for the analysis, and that chlorophyll a is a dominant factor explaining approximately 40 % of the variability of *Neogloboquadrina pachyderma* abundance and the total adults' abundance. The variability in abundance of *Globigerina bulloides* could not be explained by any of the three variables.

Table 3: Abundance of the numerically dominant species caught by both nets during the cruise on board of RV *Maria S. Merian* on 2011.

| station | *N. pachyderma* (individuals m^{-3}) | | *G.bulloides* (individuals m^{-3}) | |
	Apstein net	Multinet	Apstein net	Multinet
232	0,00	48,18	0,00	0,00
233	31,75	0,00	23,81	0,00
235	6,17	0,00	33,95	0,00
243	0,00	0,00	3,09	0,00
246	0,00	1,45	1,85	0,00
250	13,23	0,00	10,58	1,49
254	21,16	0,00	21,16	0,00
266	103,17	0,00	37,04	116,52
270	37,04	481,09	37,04	79,17
271	46,30	4,30	32,41	0,00
279	0,00	9,99	18,52	0,00
282	0,00	2,60	0,00	0,00
285	0,00	72,49	0,00	0,00
292	0,00	9,13	9,26	0,00
295	5,29	0,00	0,00	0,00
304	0,00	0,00	3,09	0,00
305	0,00	9,13	0,00	0,00
306	0,00	7,34	0,00	0,00

Discussion

Species composition

It has been documented in former studies that the species assemblages composition of foraminifera varies seasonally (e.g., Marchant et al., 1998; Schiebel and Hemleben, 2000; Peeters and Brummer, 2002; Marchant et al., 2004; Mohiuddin et al., 2005). In this study, the three samplings were performed during different seasons (December (early austral summer), September-October (austral spring) and January-March (late austral summer) for 2009, 2010 and 2011, respectively); however, in terms of species composition, no seasonality could be observed, as for almost all the samples of each cruise, the most abundant species was *Neogloboquadrina pachyderma* dextral, followed by *Globigerina bulloides*. This would be concordant with the hydrographic conditions of the sampling area, as non-spinose species such as *N. pachyderma* are more abundant in eutrophic waters with high phytoplankton productivity, such as upwelling regions (Hemleben et al., 1989); and, *G. bulloides* is a well known upwelling indicator (e.g., Thiede, 1975; Ufkes et al., 1998). Also, these results are concordant with a sediment traps study performed at the same area by Lončarić et al. (2007), in which the absence of warm water species and an increase in the dominance of *Globigerina bulloides* together with *Neogloboquadrina pachyderma* dextral, accompanied by it sinistral form and by *Turborotalita quiqueloba*, indicated the transition from mesotrophic conditions to the eutrophic coastal ocean. Therefore, it can be affirmed that in the Benguela upwelling system off Namibia there is a foraminiferal assemblage dominated by *Neogloboquadrina pachyderma* dextral and *Globigerina bulloides*, indicating the influence of subpolar and transitional (intermediate) water masses and upwelling conditions, which are typical for this system (Hutchings et al., 2009) and concordant with the previous description of biogeographical provinces (Hemleben et al., 1989; Murray, 1991).

Sampling method

For the cruise of the year 2011, the sampling of foraminifera was performed at each station by using two different nets: an Apstein net (vertical cast) and a phytoplankton net placed inside a multiple opening/closing net (horizontal cast). The results showed 1)

different species composition between the samples caught for each net, 2) different numerically dominant species, and 3) abundances of foraminifera one order of magnitude higher for the samples caught with the multiple opening/closing net. These aspects may be explained by the type of cast was different for each net (horizontal vs. vertical), which may have tended to under- or over-estimate the occurrence and abundance of certain species with respect to the other net, as different species dwell at distinct depths even in the mixed layer. The light penetration depth and deep chlorophyll maximum (DCM), might play an important role in this context. The third aspect may be explained by the type of nets. The Apstein net was directly opened to the water, whereas the phytoplankton net was placed inside a multiple opening/closing net. This location of the phytoplankton net may have served to catch a water sample with a higher concentration of organisms, as the water coming inside may have created advective waves that would not allowed smaller organisms to escape out of the multiple opening/closing net before being caught by the phytoplankton net. Another aspect that may be of importance is the tow speed that was used to do each cast at each station. It has been stated that the velocity at which a net is pulled may have an effect on the type of organisms caught, as it may cause damage and/or extrusion of some organisms through the mesh if too fast (Tranter and Smith, 1968).

Despite the dissimilarities between the results given by these two nets, they coincided in the two most important numerically dominant species for this study (*Neogloboquadrina pachyderma* and *Globigerina bulloides*), although their abundance in some stations was underestimated by one of the nets if compared to the abundance obtained with the other. These aspects may be tested by the implementation of a combined sampling method that includes vertical and horizontal cast for one station (e.g., an oblique cast), which may help to integrate the different data given by these two nets in one sample.

Juveniles vs. adults

The number of juveniles was, despite some exceptions, higher than the number of adults for the three cruises, as well as for the samples caught with the Apstein net during 2011. These observations are concordant with the ontogeny of planktic foraminifera, which after recruitment at depth they grow and mature in the upper layer where food (i.e., phytoplankton and zooplankton) and symbiotic algae are abundant, to sink down to the

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depth when maturity is reached to release gametes in the darkness (Taniguchi and Bé, 1985; Schiebel and Hemleben, 2000). Another alternative would be the fact that the majority of the samples were taken on the shelf where upwelling was active. At such sites, plankton blooms start to develop and thereby increase the calcite saturation state by taking up CO_2. Foramifera seem to follow this development only if the calcite saturation state increase above 2.5 – 3.5 so that it is assumed that the dominance of juveniles over adults indicates young blooms of foraminifera.

Abundance in relation to environmental settings

For the three cruises done for this study, there were two environmental factors available: the calcite saturation state and the chlorophyll a concentration. Calcite saturation state gives information on how much carbonate is available for calcification, whereas chlorophyll a is a proxy of food. As lower carbonate concentration decreases the calcification rate of planktic foraminifers (Bijma et al., 1999) and therefore the shell weight (Schiebel and Hemleben, 2005), in this study it was expected to find an analogous relationship between changes in calcite saturation state and foraminiferal abundance, with a decrease in the number of foraminifera as the calcite saturation state is lower and vice versa. The results pointed to an increase in the foraminiferal abundance after calcite saturation states of 2,5 to 3,5 for the cruise on 2010 and 2009 and 2011, respectively; highlighting the possible existence of a threshold in oversaturated calcite conditions at which foraminifera may thrive better. Nevertheless, after performing multiple regression analyses, the calcite saturation state did not appear to be a controlling factor of the abundance of planktic foraminifera, whereas chlorophyll a concentration could explain approximately 40 % of their abundance variability. This observation is concordant with previous studies for other areas (e.g., Fairbanks and Wiebe, 1980; Taniguchi and Bé (1985); Schiebel and Hemleben, 2000; Schiebel et al., 2001; Fraile et al., 2008; Bergami et al., 2009; Retailleau et al., 2009; Siccha et al., 2009) and highlights the importance that food (and possibly light for their symbionts) have for the abundance of planktic foraminifera. Also, hydrographical conditions are of importance, as they determine the variation in productivity enhancing or not favorable conditions for foraminiferal development. As hydrographical conditions can present variations in different time scales (from day-to-day to interannual), more frequent

sampling (e.g., monthly time series and/or sediment trap moorings) would supply better resolution of the abundance and distribution patterns of planktic foraminifera of the Benguela upwelling system off Namibia.

Statistical analyses

Although it was found that chlorophyll a plays a significant role in the abundance of planktic foraminifera of the Benguela upwelling system off Namibia, more detailed analysis for each numerically dominant species needs to be done with the aim of elucidate which factors affect in more or less extent their abundance and distribution. To do so, more representative data would be better in order to compare different years, through the performance of more casts per station at the same time to obtain more than one replicate per sample.

Conclusions

In this study, it was showed that total abundance of planktic foraminifera varies by up to two orders of magnitude over the three years; however, the species composition of the assemblages appeared to be similar between the different sampling periods (especially for the numerically dominant species) when sampled with the same method. Regarding the two different sampling methods, they showed different results in terms total abundance, species composition and numerically dominant species, highlighting the need for developing sampling strategies with standardized methods in order to avoid biasing of ecological information. However, the factor that exerts a primary control in the abundance of foraminifera in the Benguela upwelling system off Namibia seems to be the chlorophyll a concentration rather than changes in the calcite saturation state. Apart from improving better sampling strategies, it would be necessary to have a larger amount of replicates per sample, in order to have more representative and homogeneous data sets and thus avoid these biases, which may occur by using small sample sizes (number of replicates) and/or different net types or casts (horizontal vs. vertical). Sediment trap moorings, together with time series data on hydrography (calcite saturation state, chlorophyll a concentration, depths of the deep chlorophyll maxima, temperature, oxygen, plankton community description) would serve to obtain a larger and more continuous description of the ecology of planktic foraminifera of the Benguela upwelling system.

Acknowledgements

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