Variability of phyto- and zooplankton communities
in the Mauritanian coastal upwelling between 2003 and 2008

Oscar E. Romero¹, Karl-Heinz Baumann¹², Karin A. F. Zonneveld¹, Barbara Donner¹, Jens Hefter³,
Bambaye Hamady⁴ and Gerhard Fischer¹²

¹University of Bremen, Marum, Center for Marine Environmental Sciences, Leobener Str. 8, 28359 Bremen, Germany.
²University of Bremen, Department of Geosciences, Klagenfurter Str. 2-4, 28359 Bremen, Germany.
³Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, 27568 Bremerhaven, Germany.
⁴IMROP, Institut Mauretanien de Recherches Océanographiques et des Pêches, BP 22, Nouadhibou, Mauritania.

Keywords: Eastern Boundary Upwelling Ecosystems, fluxes of microorganisms, interannual variability, northwest Africa, primary producers, secondary producers, sediment traps

Abstract

Continuous multiyear records of sediment trap-gained microorganism fluxes are scarce. Such studies are important to identify and to understand the main forcings behind seasonal and multiannual evolution of microorganism flux dynamics. Here, we assess the long-term flux variations and population dynamics of diatoms, coccolithophores, calcareous and organic dinoflagellates, foraminifera and pteropods in the Eastern Boundary Upwelling Ecosystem (EBUE) of the Canary Current. A multiannual, continuous sediment trap experiment was conducted at the mooring site CBeu (Cape Blanc eutrophic, ~20°N, 18°W; trap depth = ca. 1,300 m) off Cape Blanc, Mauritania (northwest Africa), between June 2003 and March 2008. Throughout the study, the reasonably consistent good match of fluxes of microorganisms and bulk mass reflects the seasonal occurrence of the main upwelling season and the contribution of microorganisms to mass flux off Mauritania. A clear successional pattern of microorganisms, i.e. primary producers followed by secondary producers, is not observed. High fluxes of diatoms, coccolithophores, organic dinoflagellates cysts, and planktonic foraminifera occur simultaneously. Peaks of calcareous
Plankton variability off Mauritania

30 dinoflagellate cysts and pteropods mostly occurred during intervals of upwelling relaxation. A striking feature of the temporal variability of populations’ occurrence is the persistent pattern of seasonal groups’ contribution. Species of planktonic foraminifera, diatom, and organic dinoflagellate cysts typical of coastal upwelling as well as cooler water planktonic foraminifera and the coccolithophore Gephyrocapsa oceanica are abundant at times of intense upwelling (late winter through early summer). Planktonic foraminifera and calcareous dinoflagellate cysts dominant in warm pelagic surface waters and all pteropod groups are more abundant in fall and winter, when the mixed layer deepens. Similarly, coccolithophores of the upper- and lower photic zone, together with Emiliania huxleyi, and organic dinoflagellate cysts dominate the assemblage during phases of upwelling relaxation and deeper layer mixing.

40 A significant shift in the ‘regular’ seasonal pattern of species relative contributions is observed between 2004 and 2006. Benthic diatoms strongly increased after fall 2005 and dominated the diatom assemblage during main upwelling season. Additional evidence for a change in population dynamics are the short dominance of the coccolithophore Umbilicosphaera annulus, the occurrence of the pteropod Limacina bulimoides, and the strong increase in the flux of calcareous dinoflagellate cysts, abundant in tropical, warm oligotrophic waters south of the research area after fall 2005. Altogether, this suggests that pulses of southern waters were transported to the sampling site via the northward Mauritania Current. Our multiannual trap experiment provides a unique opportunity to characterize temporal patterns of variability that can be extrapolated to other EBUEs, which are experiencing or might experience similar future changes in the plankton community.

52 1. Introduction

A way to obtain insights into the impact of climate variability on marine ecosystems is monitoring multiannual evolution and changes covering key species or groups of species representing different trophic levels. To date, continuous in situ long-term, monitoring records of marine communities are scarce. Information about open oceanic ecosystems is even more rare (see e.g. overview of currently available long-term time series of phytoplankton community
abundance and composition IOC-UNESCO TS129 IGMETS 2017). Furthermore, records providing information about organism groups of different trophic levels are practically unknown or cover only a few species (e.g., Schlüter et al., 2012; Rembauville et al., 2016).

Eastern Boundary Upwelling Ecosystems (EBUEs) are among the most important marine ecosystems, both ecologically and economically (Cropper et al., 2014). Despite the fact that they cover only 10% of the global surface ocean area, they provide about 25% of the global fish catch (Pauly and Christensen, 1995) and build extraordinary marine hotspots of high primary production and biodiversity (Aristegui et al., 2009). In doing so, they play a key role in the marine biological pump, as together with other continental margins may be responsible for more than 40% of the CO$_2$ ocean sequestration (Muller-Karger et al., 2005). As EBUEs are highly dynamic with large seasonal and interannual variability (e.g., Chavez and Messié, 2009; Fischer et al., 2016), gaining information on their long-term variability is essential to understand their potential response to current global climate change.

One of the EBUEs that have been thoroughly studied over the past three decades is the coastal ecosystem off Mauritania (northwest Africa), which is part of the Canary Current (CC) EBUE (Cropper et al., 2014). The Mauritanian system is characterized by intense offshore Ekman transport and strong mesoscale heterogeneity, which facilitate the exchange of neritic and pelagic water masses (Mittelstaedt, 1983; Zenk et al., 1991; Van Camp et al., 1991; Aristegui et al., 2009; Chavez and Messié, 2009; Meunier et al., 2012; Cropper et al., 2014). In addition, regional factors such as nutrient trapping efficiency (Aristegui et al., 2009), the giant chlorophyll filament (Gabric et al., 1993; Barton, 1998; Lange et al., 1998; Helmke et al., 2005); dust deposition (Fischer et al., 2016, 2019) and/or the shelf width (Hagen, 2001; Cropper et al., 2014) strongly affect the temporal dynamics of primary and secondary producers communities in surface waters along the Mauritanian coast. In this ecosystem, several long-term, continuous, sediment trap-based monitoring records are available since the late 1980s. Until now, studies monitoring variability of this seasonally dynamic ecosystem mostly focused on the variability of bulk fluxes (Fischer et al., 1996, 2009, 2016, 2019; Bory et al., 2001; Marcello et al., 2011; Skonieczy et al., 2013), particular groups of microorganisms (Lange et al. 1998; Romero et al., 1999, 2002, 2003; Köbrich and Baumann, 2008; Romero and Armand, 2010; Zonneveld et al., 2010; Köbrich et al., 2016; Romero
and Fischer, 2017; Guerreiro et al., 2019) or sea-surface temperature (Müller and Fischer, 2001; Mollenhauer et al., 2015). However, the simultaneous comparison of the seasonal and interannual dynamics of several phyto- and zooplankton communities by means of multiyear sediment trap experiments has not been performed in this region and is rare in other EBUEs or other ocean areas as well.

In this study, we describe the seasonal and interannual variability of fluxes of several primary and secondary producers in the Mauritanian coastal upwelling over a continuous trap experiment extending almost 1,900 days between June 2003 and March 2008 (Table 1). We present fluxes of diatoms, coccolithophores, calcareous and organic-walled dinoflagellate cysts, planktonic foraminifera and pteropods as well as the species-specific composition of the assemblages that have been collected at the mooring site CBeu (Cape Blanc eutrophic), located around 80 nm west of the Mauritanian coastline below a giant chlorophyll filament (Fig. 1). The organisms producing the calcareous, opaline or organic remains have different water column habitats, life strategies, and use different nutrient sources (Romero et al., 1999, 2002; Baumann et al., 2005; Romero and Armand, 2010; Zonneveld et al., 2013), and are widely used as proxies in paleostudies carried on Mauritanian sediments (Jordan et al., 1996; Romero et al., 2008; McKay et al., 2014) and similar paleoenvironments (e.g., Baumann and Freitag, 2004; Bouimetarhan et al., 2009; Romero et al., 2015; Weiser et al., 2016; Hardy et al., 2018). The emphasis of our multiannual trap experiment is on the comparison of temporal dynamics and the species-specific composition of the primary and secondary producer plankton community off Mauritania. The simultaneous assessment of fluxes of several microorganism groups collected over long intervals provides substantial information about potential changes in the coastal upwelling community. Results are discussed in the context of varying environmental conditions of the low-latitude Northeastern Atlantic. To our knowledge, this is the first multiyear trap-based record of primary and secondary producers that provides multiyear information on the dynamics of populations in a highly productive coastal upwelling system.
2. Oceanographic setting of the study area

The CC-EBUE is located in the eastern part of the North Atlantic Subtropical Gyre (Fig. 1; Aristegui et al., 2009; Chavez and Messié, 2009; Cropper et al., 2014). Both the temporal occurrence and the intensity of the upwelling along northwestern Africa depend on the shelf width, the seafloor topography, and wind direction and strength (Mittelstaedt, 1983; Hagen, 2001). The Mauritanian shelf is wider than the shelf northward and southward and gently slopes from the coastline into water depths below 200 m (Fig. 1b; Hagen, 2001). The shelf break zone with its steep continental slope extends over a distance of approximately 100 km (Hagen, 2001). As a result of the coastal and bottom topography, and the ocean currents and wind systems, the coastal region off Mauritania is characterized by almost permanent upwelling. Its intensity varies throughout the year (Lathuilière et al., 2008; Cropper et al., 2014). Our trap site CB_eu is located at the southern boundary of this permanent upwelling zone (Fig. 1; Table 1).

The surface hydrography is strongly influenced by two wind-driven surface currents: the southwestward-flowing CC and the poleward-flowing coastal countercurrent or Mauritania Current (MC) (Fig. 1). The eastern branch of the subtropical gyre, the surficial CC detaches from the continental slope between 25° and 21°N and supplies waters to the North Equatorial Current. The CC water is relatively cool because it entrains upwelled water from the coast as it moves southward (Mittelstaedt, 1991). The MC gradually flows northward along the coast up to about 20°N (Mittelstaedt, 1991), bringing warmer surface waters from the equatorial realm into the study area. Towards late autumn, the MC is gradually replaced by a southward flow associated with upwelling water due to the increasing influence of trade winds south of 20°N (Zenk et al., 1991), and becomes a narrow strip of less than 100 km width in winter (Mittelstaedt, 1983). The MC advances onto the shelf during summer and is enhanced by the relatively strong Equatorial Countercurrent and the southerly monsoon (Mittelstaedt, 1983). The presence of strong coastal currents during the upwelling season causes substantial horizontal shear within the surface layer, where currents tend to converge (Mittelstaedt, 1983). This convergence favors the formation of the Cape Verde Frontal Zone (CVFZ, Fig. 1; Zenk et al., 1991).

A coastal countercurrent, the Poleward Undercurrent (PUC; Fig. 1) occurs mainly due to wind-driven offshore divergence (Pelegrí et al., 2017). North of Cape Blanc (ca. 21°N), the intense
northeasterly winds cause the coastal upwelling to move further offshore and the upper slope is filled with upwelling waters. South of Cape Blanc (Fig. 1), northerly winds dominate year through but surface waters remain stratified and the PUC occurs as a subsurface current. South of Cape Timiris (ca. 19°30’N), the PUC intensifies during summer-fall and remains at the subsurface during winter–spring (Pelegri et al., 2017). The encountering of the northward flowing MC-PUC system with the southward flowing currents in the Canary Basin leads to flow confluence at the CVFZ (Zenk et al., 1991) and the offshore water export visible as the giant Mauritanian chlorophyll filament (Gabric, 1993; Pelegri et al., 2006; Pelegri et al., 2017). This filament extends over 300 km offshore (e.g., Van Camp et al., 1991; Arístegui et al., 2009; Cropper et al., 2014) and carries South Atlantic Central Water (SACW) offshore through an intense jet-like flow (Meunier et al., 2012; Fig. 1). Intense offshore transport forms an important mechanism for the export of cool, nutrient-rich shelf and upper slope waters offshore Mauritania. Based on satellite imagery and in situ data, it has been estimated that the giant Mauritanian filament could export about 50% of the particulate new production offshore toward the open ocean during intervals of most intense upwelling, while coastal phytoplankton at the surface might be transported as far as 400 km offshore (Gabric et al., 1993; Barton, 1998; Lange et al., 1998; Helmke et al., 2005). The transport effect could extend to even more distant regions in the deep ocean, since sinking particles are strongly advected by lateral transport (Fischer and Karakaş, 2009; Karakaş et al., 2006, Fischer et al., 2009).

The nutrient concentration of the upwelled waters off Mauritania varies depending on their origin (Fütterer, 1983; Mittelstaedt, 1991; Zenk et al., 1991). The source of upwelling waters off Mauritania are either North Atlantic Central Water (NACW), north of about 23°N, or SACW (south of 21°N, Fig. 1). Both water masses are mixed in the filament area off Cape Blanc. The SACW occurs in layers between 100 and 400 m depth off Cape Blanc and the Banc d’Arguin. The hydrographic properties of the upwelling waters on the shelf suggest that they ascend from depths between 100 and 200 m south off the Banc d’Arguin (Mittelstaedt, 1983). North of it, the SACW merges gradually into deeper layers (200-400 m) below the CC (Mittelstaedt, 1983). During intense upwelling, the stratification of the shelf waters weakens, and so is the stratification further offshore, usually within the upper 100 m (Mittelstaedt, 1991). The biological response is drastically
accelerated in the upwelling waters when the SACW of the upper part of the undercurrent feeds the onshore transport of intermediate layers to form mixed-water types on the shelf (Zenk et al., 1991).

3. Material and Methods

3.1. Moorings, sediment traps and fluxes

Sediment trap moorings were deployed at site CBeu off Mauritania in the CC-EBUE (Fig. 1; Table 1). Details on trap depth, sample number, and sampling intervals as well as the sample identification (cruise and GeoB numbers) are presented in Table 1. Large-aperture time-series sediment traps of the Kiel type with 20 to 40 cups (depending on ship-time availability, Table 1) and 0.5 m² openings, equipped with a honeycomb baffle (Kremling et al., 1996), were used. Traps were moored in intermediate waters (between 1,256 m and 1,296 m) and sampling intervals varied between 6.5 and 23 days (Table 1). Uncertainties with the trapping efficiency due to strong currents (e.g. undersampling, Buesseler et al., 2007) and/or due to the migration and activity of zooplankton migrators (‘swimmer problem’) are assumed to be minimal in this depth range.

Prior to each deployment, sampling cups were poisoned with 1 ml of concentrated HgCl₂ per 100 ml of filtered seawater. Pure NaCl was used to increase the density in the sampling cups up to 40 °C. Upon recovery, samples were stored at 4°C and wet-split in the MARUM sediment trap laboratory (University Bremen, Bremen) using a rotating McLane wet splitter system. Larger swimmers, such as crustaceans, were handpicked with forceps and removed by carefully filtering through a 1-mm sieve. All flux data hereafter refer to the size fraction of <1 mm. Detailed information about sampling and laboratory analysis is given in Mollenhauer et al. (2015) where the bulk fluxes are given for the deployments CBeu 1-4. Additionally to the fluxes, alkenone derived sea surface temperature (SST) for the CBeu deployments 1-4 were provided by these authors.

Using ¼ or ¹/₁₆ wet splits, analysis of the <1 mm fraction was carried out (Fischer and Wefer, 1991; Fischer et al., 2016). Samples were freeze-dried and homogenized before being analyzed for bulk (total mass), organic carbon (OC), calcium carbonate (CaCO₃) and biogenic silica (BSi, opal). Total organic carbon (TOC) and CaCO₃ were measured by combustion with a CHN-Analyzer (HERAEUS, Dept. of Geosciences, University of Bremen). TOC was measured after removal of
Plankton variability off Mauritania carbonate with 2 N HCl. Overall analytical precision based on internal lab standards was better than 0.1% (±1σ). Carbonate was determined by subtracting OC from total carbon, the latter being measured by combustion without pre-treatment with 2N HCl. Organic matter was estimated by multiplying the content of total organic carbon by a factor of two as about 50-60% of marine organic matter is constituted by OC (Hedges et al., 2002).

BSi was determined with a sequential leaching technique with 1M NaOH at 85°C (Müller and Schneider, 1993). The precision of the overall method based on replicate analyses is mostly between ±0.2 and ±0.4%, depending on the material analyzed. The lithogenic fluxes were estimated by subtracting the masses of CaCO$_3$, BSi, and 2 x OC from the total mass flux.

### 3.2. Assessment of organism fluxes and species identification

#### 3.2.1. Diatoms

For this study 1/25 and 1/125 splits of the original samples were used. Samples were prepared for diatom studies following the method proposed by Schrader and Gersonde (1978). A total of 185 sediment trap samples were processed. Each split was treated with potassium permanganate, hydrogen peroxide, and concentrated hydrochloric acid following previously used methodology (Romero et al., 2002, 2009a, b, 2016, 2017). Identification and count of the species assemblage were done on permanent slides (Mountex® mounting medium) at x1000 magnification using a Zeiss® Axioscop with phase-contrast illumination (MARUM, Bremen). The counting procedure and definition of counting units follows Schrader and Gersonde (1978). Depending on valve abundances in each sample, several traverses across each slide were examined. Total amount of counted valves per slide ranged between 300 and 800. At least two cover slips per sample were scanned in this way. Valve counts of replicate slides indicate that the analytical error of concentration estimates is ca. 10%. The resulting counts yielded abundance of individual diatom taxa (absolute and relative) as well as daily fluxes of valves per m$^2$ d$^{-1}$, calculated according to Sancetta & Calvert (1988).

#### 3.2.2. Coccolithophores

Aliquots of each sample were 1/125 of the <1 mm fraction. Depending on the total flux, samples were further split down to 1/625 to 1/2500 of the original sample volume and were filtered afterward onto polycarbonate membrane filters (Schleicher and Schuell™ 47mm diameter, 0.45µm
Plankton variability off Mauritania

230  pore size). A piece of the filter was cut and mounted on a Scanning Electron Microscopy (SEM) stub. Qualitative and quantitative analyses of the trapped assemblages were performed using a Zeiss® DSM 940A at 10kV accelerating voltage (Department of Geosciences, University of Bremen, Bremen). In an arbitrarily chosen transect, coccoliths were counted until a total of at least 500 specimens were reached. The taxonomic classification of identified species was based on Young et al. (2003) as well as on Nannotax 3 (Young et al., 2019).

236  **3.2.3. Organic-walled and calcareous dinoflagellate cysts**

1/125 splits of the original trap material was ultrasonically treated and sieved with tap water through a high precision metal sieve (Storck-Veco®) with a 20µm pore size. The residue was transferred to Eppendorff cups and concentrated to 1 ml of suspension. After homogenization of the material, a known aliquot was transferred to a microscope slide where it was embedded in glycerin-gelatine, covered with a cover slip and sealed with wax to prevent oxidation of the organic material. After counting, cyst fluxes were calculated by multiplying the cyst counts with the aliquot fraction and the split size (1/125) and dividing through the amount of days during which the trap material was sampled as well as the trap-capture surface. No chemicals were used to prevent dissolution of calcite and silicate. Cyst assemblages were determined by light microscopy (Axiovert, x400 magnification). Taxonomy of organic walled dinoflagellate cysts is according to Zonneveld and Pospelova (2015), taxonomy of calcareous dinoflagellate cysts is according to Vink et al. (2002) and Elbrächter et al. (2008).

250  **3.2.4. Planktonic foraminifera and pteropods**

Depending on the absolute magnitude of the total mass flux, a 1/5 or a 1/25 split of the wet solution (fraction <1mm) was used to pick planktonic foraminifers and pteropods (pelagic mollusks). Specimens of both groups of calcareous microorganisms were rinsed three times by using tap water, dried at 50°C in an oven overnight and then separated from each other. Identification and count of shells were done by using a stereomicroscope Zeiss® Stemi 2000 (MARUM, Bremen). The foraminifera fluxes (all size fractions) were determined in mg per m² and day with a Sartorius BP 211D analytical balance. Additionally, the total amount of specimens/sample of foraminifera and pteropods (>150 µm) were counted manually. Foraminifera were identified and classified according to Hemleben et al. (1989) and Schiebel and Hemleben...
3.2.5. Alkenones

1/5 wet splits of the <1mm fraction were used for alkenone analysis. Briefly, freeze-dried CBeu 1-4 samples were solvent extracted. The resulting total lipid extracts (TLEs) saponified and the alkenone fractions were obtained by means of column chromatography of the neutral lipid fractions from the saponification. Details are given in Mollenhauer et al. (2015).

A slightly different, miniaturized analysis procedure has been applied for the CBeu trap 5 samples. 1/5 wet splits of the freeze-dried <1mm fraction were weighted in 10 ml Pyrex tubes and a known amount of an internal standard (n-Nonadecan-2-one) was added. Samples were then 3x ultrasonically extracted with a mixture of 3 ml dichloromethane/methanol (9:1 vol./vol.), centrifuged and the supernatant solvent combined as total lipid extract (TLE). TLEs were evaporated to dryness and saponified in a 0.1M potassium hydroxide solution in methanol/water (9:1 vol./vol.) for two hours at 80°C. Neutral lipids, recovered with hexane, were afterwards separated into fractions of different polarity by silica gel chromatography and elution with hexane, dichloromethane/hexane (1:1 vol./vol.) and dichloromethane/methanol (9:1 vol./vol.), respectively. The second fraction containing the alkenones was dried, re-dissolved in 20µl hexane and analyzed on a 7890A gas chromatograph (GC, Agilent Technologies) equipped with a cold on-column injection system, a DB-5MS fused silica capillary column (60 m, ID 250 µm, 0.25 µm film coupled to a 5 m, ID 530 µm deactivated fused silica precolumn) and a flame ionization detector (FID). Helium was used as carrier gas (constant flow, 1.5 mL/min) and the GC oven was heated using the following temperature program: 60 °C for 1 min, 20 °C/min to 150 °C, 6 °C/min to 320 °C and a final hold time of 35 min. Alkenones were identified by comparison of the retention times with a reference sample composed of known compounds. Peak areas were determined by integrating the respective peaks.

The U_{37^k} index was calculated using the following equation (Prahl and Wakeham, 1987)

$$U_{37^k} = \frac{C_{37:2}}{C_{37:2} + C_{37:3}}$$
and converted to SST using the global surface water calibration from Conte et al. (2006):

\[
\text{SST} = \frac{U_{37}^{5} - 0.0709}{0.0322}
\]

### 3.3. Environmental physical parameters

SST, Sea Surface Temperature Anomaly (SSTA), mixed layer depth (MLD) and upper ocean chlorophyll-a concentration data are based on satellite-derived data achieved from the NASA supported Giovanni project (https://giovanni.gsfc.nasa.gov/). SST is the mean of daily surface ocean temperature and MLD values of the sampling interval in a 4km² area around the trap position (Table 1). In the research area, SST at the trap position is influenced by seasonal air temperature changes as well as the presence of upheld water surfacing at the trap position.

To compensate for seasonal air temperature changes the SSTA is calculated by subtracting the above-calculated SST at the trap position from mean SST values of simultaneous sampling intervals in a 4km² block 200nm west of the trap position. Both SSTA and MLD are parameters reflecting active upwelling in the study area. Upper ocean chlorophyll a data and MLD represent monthly mean values in a 9km² block around the trap position. Wind speed and wind directions are provided by Nouadhibou airport (20°56’N, 17°2’W) (Institut Mauretanien de Recherches Océanographiques et des Pêches, Nouadhibou, Mauritania). For statistical analyses, the means of daily values during the trap sampling intervals were calculated.

### 3.4. Multivariate analyses

The ordination techniques Principal Component (PCA) and Redundancy (RDA) analyses have been performed with the software Package Canoco 5 (ter Braak and Smilauer, 2012; Smilauer and Leps, 2014). To obtain insights into the temporal relationship between fluxes of organism groups (diatoms, coccolithophores, organic-walled dinoflagellate cysts, calcareous dinoflagellate cysts, planktonic foraminifera and pteropods) and bulk components as well as the environmental conditions in surface waters and low atmosphere a RDA has been performed. RDA compares the total flux of organism groups with environmental parameters and TOC, BSi, CaCO₃ and lithogenic fluxes (Table 2). Since the fluxes of the individual groups differ by several orders of magnitudes, it is essential to normalize their flux values prior to the statistical analysis in order to be able to determine temporal relationships of flux variability. As a consequence, the total flux of the
Plankton variability off Mauritania

organism groups have been normalized to values between 0 and 1000 previous to the analyses according to formula 1:

\[ nF_l = \left( \frac{F_l}{F_{l,y}} / F_{l,\text{max}} \right) \times 1000n \]

\[ F_l = \text{normalized flux of species group } i \]
\[ F_{l,y} = \text{flux of species group } i \text{ in sample } y \]
\[ F_{l,\text{max}} = \text{maximal flux observed in species group } i \]

To better understand the relationship within the individual organism groups, a PCA has been performed (Table 2). For these analyses, the total flux of the organisms/species groups have been normalized to values between 0 and 1000 according to formula 2:

\[ nF_j = \left( \frac{F_{j,\text{y}}}{F_{l,\text{max}}} \right) \times 1000n \]
\[ F_{j,\text{y}} = \text{normalized accumulation rate of ecological entity } j \text{ in species group } i \]
\[ F_{l,\text{max}} = \text{maximal accumulation rate observed in species group } i \]

Within coccolithophores, *Umbilicosphaera anulus* had exceptionally large fluxes in one sample only. This flux exceeded the maximal flux of the other species by a factor of three. This value has been excluded from the analysis and the \( F_{l,\text{max}} \) in this group is determined by excluding this outlier.

4. Results

4.1. Bulk fluxes and fluxes of organism groups

On average, the carbonate fraction (CaCO\(_3\)) dominates the mass flux (41% to the total mass flux) and is mainly composed of coccolithophores, foraminifera, calcareous dinoflagellates and pteropods (see also Fischer et al., 2009, 2016). CaCO\(_3\) is followed by BSi (average = 14.5%, mostly diatoms, Romero and Fischer, 2017), and organic carbon (6.5%, delivered by diatoms, coccolithophores and organic dinoflagellate cysts). The lithogenic fraction –mostly composed of mineral dust– makes up 31.5% of the total mass for the entire sampling period of CBeu 1-5 (2003-2008, Table 1). Bulk fluxes for the CBeu deployments 1 to 4 were already presented in Mollenhauer et al. (2015; Table 1) in combination with fluxes of the lipid fraction and SST.
reconstructions. The SST record is extended with new alkenone data until March 2008 (CBeu
deployment 5, Table 1).
The fluxes of total mass, CaCO₃, TOC, BSi and lithogenics show major peaks in winter and
spring (Fig. 2). Secondary maxima were found during late summer/fall, mainly in 2003, and less
clear in 2005, 2006 and 2007 (Fig. 2). However, the individual components reveal different flux
amplitudes and point to some interannual variability. Carbonate fluxes were exceptionally high in
early winter 2005 compared to the other years. Fluxes of BSi and organic carbon match well the
total flux pattern and show less interannual variability (Fig. 2c, d). The flux of the lithogenic fraction
has the highest amplitudes in spring 2006 and 2007 (Fig. 2e).
Fluxes of microorganisms are dominated by diatoms and coccoliths (Fig. 3a, b). These
exceeded the fluxes of organic- and calcareous walled dinoflagellate cysts, planktonic foraminifera
and pteropods by a factor of four to five. Highest coccoliths and diatom fluxes reach 4.2 x 10⁸
coccoliths m⁻² d⁻¹, and 1.2 x 10⁸ valves m⁻² d⁻¹, respectively. Maximal fluxes of organic-walled
dinoflagellates reach up to 7.1 x 10⁴ cysts m⁻² d⁻¹, and of planktonic foraminifera 0.9 x 10⁴ shells
m⁻² d⁻¹, and 1.1 x 10⁴ pteropods shells m⁻² d⁻¹.
Each group of organisms shows large seasonal and interannual variabilities. Diatoms had their
highest export fluxes mostly in winter/spring throughout the sampling interval and exceptionally in
July/August 2003 and 2007 and in fall 2005. On the long-term, low coccolithophore fluxes are
observed fall and winter 2007/2008 (Fig. 3b). Calcareous dinoflagellate cysts were practically
absent until fall 2005 (Fig. 3c). After September 2005, calcareous dinoflagellate cysts showed
maximal export fluxes in fall/winter 2005/2006 and fall/winter 2006/2007 (Fig. 3c). Fluxes
decreased again after spring 2007. Organic-walled dinoflagellate cysts had their highest export
fluxes in summer 2003, spring/summer 2006 and summer 2007 (Fig. 3d). Planktonic foraminifera
showed maximal fluxes in summer 2003, winter/spring 2004, 2005, 2007 and spring/summer 2006
(Fig. 3e). Pteropods had their maximal fluxes in summer 2003, fall/winter 2003/2004, 2004/2005
and 2006/2007 as well as summer 2005 and 2007 (Fig. 3f).

4.2. Species- and group-specific composition of assemblages
The studied plankton community at the CBeu site is highly diverse and is composed by at least 220 identified species. Table 3 presents the species-specific composition of groups depicted in Fig. 4.

Out of 170 marine diatom species, the 70 most abundant diatom taxa (average relative contribution >0.75% for the entire studied interval) were attributed in four groups, according to the main ecological conditions they represent: (1) benthic, (2) coastal upwelling, (3) coastal planktonic, and (4) open-ocean waters (see also Romero and Fischer, 2017). The diatom groups show a clear seasonal pattern (Fig. 4a) with benthic diatoms having higher relative contributions during spring and summer, whereas the coastal upwelling group mainly occurred between late spring and early fall. Open-ocean diatoms were more abundant from fall to early spring while the coastal planktonic taxa tended to be more abundant during fall and winter. Most noticeable, a drastic shift in the relative contribution of the benthic diatoms occurred in spring-summer 2006 when the abundance of benthic diatoms strongly increased from 2006 onward, compared to 2003–2005 (Fig. 4a). In spite of the increased relative contribution of benthic diatoms after 2005, the seasonal pattern of the predominantly high spring-summer total diatom flux remained unaltered (Fig. 3a).

Coccolithophores are consistently dominated by Emiliania huxleyi and Gephyrocapsa oceanica, whose contribution is always higher 50% of the community throughout the sampling period (Fig. 4b). Oligotrophic upper photic zone (UPZ, e.g., Umbellosphaera tenuis, U. irregularis) and lower photic zone species (LPZ, e.g., Florisphaera profunda, Gladiolithus flabellatus) make up the majority of the remaining species. Whereas E. huxleyi showed a less clear seasonal pattern, G. oceanica tends to be more abundant during late spring and early fall (Fig. 4b). In contrast, UPZ and LPZ taxa have higher relative contributions during winter and spring. The appearance of Umbilicosphaera anulus (present in consistently low relative abundances of 5-10% until the summer of 2006) accounts for up to 65% of the community in winter 2005/06. Other common taxa with an average relative contribution >0.75% for the entire studied interval are listed in Table 3.

Calcareous dinoflagellates can be attributed to five groups based according to the main ecological conditions they represent (Siggelkow et al., 2002; Richter et al., 2007; Kohn and Zonneveld, 2010): (1) upwelling, (2) warm waters, (3) terrestrial mineral input, (4) cosmopolitan and (5) other species (Table 3). Until fall 2005 abundances are very low such that the
recognition of a seasonal pattern is hampered (Fig. 4c). After fall 2005, their occurrence shows a more distinguished seasonal pattern. In spring-summer of 2006 upwelling species dominate the association. After fall 2006, the community is composed by the interplay of cosmopolitan species, warm water taxa and upwelling-dependent species, where warm water taxa dominate. Whereas upwelling species are most abundant in spring and fall, warm water and mineral indicators are more abundant in fall/winter (Fig. 4).

Organic dinoflagellates can be attributed to five groups based on the relationship between their geographic distribution in surface sediments from the Cape Blanc area and the environmental conditions in surface and subsurface waters as well as long-term surveys of their seasonal cyst production (Susek et al., 2005; Holzwarth et al., 2010; Smayda, 2010; Smayda and Trainer, 2010; Trainer et al., 2010; Zonneveld et al., 2012, 2013): (1) upwelling, (2) upwelling relaxation, (3) potential toxic, (4) cosmopolitan, and (5) other species. Throughout the investigated time interval upwelling species are abundant in spring and fall/winter whereas upwelling relaxation species have higher relative abundances in fall (Fig. 4d). Potential toxic species are abundant in fall/winter 2004/2005 and 2007/2008. Organic-walled dinoflagellate cysts do not show a clear change in their composition between 2005 and early 2006 as observed for many other groups.

The distribution and abundance of planktonic foraminifera species is linked to surface-water properties. We use prominent species as tracers of surface water properties: Globigerina bulloides (upwelling species) is generally most abundant between summer and fall (Fig. 4e). Globorotalia inflata and Neogloboquadrina incompta (transitional and subpolar species) are present mostly throughout, only decreasing in abundance in fall and winter when warm water taxa peaked (Globigerinoides ruber pink, G. ruber white and G. sacculifer; Kucera, 2007, Schiebel and Hemleben, 2017) (Fig. 4e). The only exception is in fall and winter 2004/2005, when warm-water taxa are almost absent.

As large secondary carbonate producers off Mauritania, pteropods are important contributors to the carbonate flux in the CC-EBUE (Fischer et al., 2016). The community is composed of relatively few taxa. Heliconoides inflatus (formerly known as Limacina inflata) dominates the assemblage throughout most of the studied interval (Fig. 4f). It is often the only species found in
Plankton variability off Mauritania

the assemblage until winter 2005/2006, when a sudden and drastic shift in the relative contribution occurred. *Limacina bulimoides* appears for the first time in winter to spring 2006 - and again in fall and winter 2006/2007 - and dominates the assemblage together with a group of unspecified uncoiled pteropods. However, another occurrence of *L. bulimoides* is missing in winter 2007/2008.

4.3. Statistical analyses

Comparison of the fluxes of the microorganism groups, bulk fluxes and the environmental conditions in surface waters and the lower atmosphere (MLD, average wind speed, wind direction, chlorophyll-a concentration (Chl-a), SST and SSTA) resulted in a significant relationship within the first and second RDA axes that correspond to 34 % and 11% of the variance within the dataset, respectively (Table 2).

All microorganism groups are ordinated at the positive part of the first axis showing a positive relationship with all bulk parameters (Fig. 5). This implies that the fluxes of all studied microorganisms groups increase with increasing fluxes of total mass, TOC, lithogenic, BSi and CaCO$_3$ (Fig. 5). Fluxes of planktonic foraminifera, diatoms and –to a lesser extent– coccolithophores and organic dinoflagellates are ordinated at the negative site of SST and, with exception of organic dinoflagellates, positive side of MLD (Fig. 5). This implies that their fluxes are enhanced whenever SST is low and MLD is deep, i.e. under a well-mixed uppermost water column. Diatoms, coccolithophores, organic dinoflagellates and planktonic foraminifera also show a positive correlation with SSTA, implying that enhanced fluxes of these microorganisms occur when temperature anomalies between waters overlying site CBeu and the offshore pelagial is large. The fluxes of pteropods and calcareous dinoflagellate cysts are positively related to the average wind direction, and negatively to MLD and average wind speed (Fig. 5).

To better understand the correlation of the fluxes of the species groups within the organism groups, PCA has been performed (Fig. 6, Table 2). The first two axes correspond to 26.3 % and 16.2% of the variance within the dataset respectively. Based on their ordination on the first and second axis, three groups are recognized (Fig. 6):

- Groups 1 and 2 are ordinated at the negative side of the second axis. Group 1 (in blue, Fig. 6) is built by planktonic foraminifera characteristic of cooler or upwelled water masses (For-cold, For-upw); benthic and upwelling-related diatoms (Dia-bent and Dia-upw); organic...
Plankton variability off Mauritania

dinoflagellates characteristic for upwelling regions (OD-upw), and the coccolithophore *Gephyrocapsa oceanica* (Co-Gocean). Group 2 (in brown, Fig. 6) consists of upwelling-related and other calcareous dinoflagellates cysts (CD-upw and CD-other), other coccolithophores (Co-other), and coastal planktonic and open-ocean diatoms (Dia-coast and Dia-ocean).

- Ordinated at the positive side of the second axis and central part of the first axis, group 3 assembles planktonic foraminifera mainly thriving in warm waters (For-warm), calcareous dinoflagellates characteristic of warm water conditions and those responding to mineral input (CD-warm, CD-min), and all pteropods groups or species (in black, Fig. 6).

- Group 4 is ordinated at the central/positive part of the second axis and positive site of the first axis. Species assigned to group 4 are: organic walled dinoflagellate cysts typical of the upwelling relaxation (OD-upw relax); UPZ and LPZ coccolithophores (Co-up phot and Co-low phot); *E. huxleyi* (Co-Ehux), other coccolithophores (Co-other), *U. anulus* (Co-Uanu), and cosmopolitan calcareous dinoflagellate cysts (CD-cosm) (in red, Fig. 6).

5. Discussion

5.1. Relationship between microorganisms fluxes at site CBeu and the physical and biogeochemical settings off Mauritania

Both the visual examination of the flux variability and the statistical analysis document that the seasonality of most microorganism groups at the CBeu site closely follows the temporal pattern of changes in upper water oceanographic conditions off Mauritania between June 2003 and March 2008. Fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera increase whenever the uppermost water column is well mixed (Fig. 7e), SSTs are low (Fig. 7d), and SSTA are high (Figs. 2, 3, 5). This strong match supports the scenario of simultaneous occurrence of intense upwelling off Mauritania and high microorganisms fluxes and production at site CBeu. Several previous studies have separately documented enhanced production of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera occurring when the nutrient concentration in the uppermost water column off Mauritania increases (Baumann et al., 2005; Zonneveld et al., 2012; Guerreiro et al., 2017;
The atmospheric, hydrographic and biochemical conditions deliver the physical and nutrient frames that determine the temporal pattern of population dynamics as recorded by the CBeu trap.

Wind and upper water conditions off Mauritania show a clear seasonal pattern of variability (Fig. 7a-e). The highly stratified uppermost water column (above 40 m water depth) overlying site CBeu is an effect of winds blowing mainly from the N-NE between late winter and early summer (Fig. 7a, b, e). The stratification breaks down mostly in early to middle winter, when the predominant winds turn from N-NE into S-SE (Fig. 7a). Following this setting, upwelling off Mauritania reaches its highest intensity between late winter/early spring and early summer (Mittelstaedt, 1991; Meunier et al., 2012; Cropper et al., 2014). The SST record (Fig. 7d) matches well the seasonal evolution of stratification and mixing conditions: lowest temperatures mostly between winter and early spring (increasing SSTA in late winter and throughout the spring season). Throughout the period investigated, this SST cyclicity remains fairly constant.

Fluxes of total mass and biogenic bulk components (TOC, BSi, CaCO$_3$) are clearly seasonal in nature (Fig. 3 a-d; Fischer et al., 2019) and reflect the temporal productivity pattern of the Mauritanian upwelling region (Meunier et al., 2012; Cropper et al., 2014). The good temporal match between maxima of most of the studied microorganism groups and biogenic bulk components unambiguously evidences the contribution of primary and secondary producers to the total mass/biogenic mass fluxes off Mauritania (Figs. 2, 3). Higher absolute values of CaCO$_3$ over BSi (Fig. 2b, d) support the scenario of calcareous primary and secondary producers (coccolithophores, foraminifera and pteropods) dominating the plankton community in the Mauritanian upwelling system (Fischer et al., 2019). Diatoms are the main contributors to the BSi flux (Fig. 3a, 2d; Romero et al., 2002; Romero and Fischer, 2017).

A strong match among fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera with lithogenic fluxes at times of enhanced upwelling is observed (Figs. 2e, 3 a-c, e). The RDA supports this correlation (Fig. 5). The good correlation between lithogenic and microorganisms fluxes demonstrates that winds –responsible for the water column mixing off Mauritania (Mittelstaedt, 1983; Meunier et al., 2012)– might additionally enrich surface waters overlying site CBeu with land-derived nutrients. Primary and secondary producers may remarkably
benefit from this eolian-transported pool of nutrients. Lithogenic material is brought into
Mauritanian ocean waters in the form of dust that it is transported from the Sahara and the Sahel
(Romero et al., 2003; Friese et al., 2017). Numerous studies have thoroughly documented that the
particle flux off Mauritania predominantly occurs in the form of aggregates, often rich in lithogenic
particles (e.g., Karakaş et al., 2009; Iversen et al., 2010; Iversen and Ploug, 2010; Nowald et al.,
2015; Fischer et al., 2016; van der Jagt et al., 2018). Recent experiments have also shown that
aggregates’ abundance and sinking velocities increase toward deeper waters when aggregates
are ballasted with lithogenic particles, whereas aggregates are not able to scavenge lithogenic
material from deeper waters (van der Jagt et al., 2018).
A remarkable finding of our multiannual trap experiment is that flux maxima of diatoms,
coccolithophores, organic-walled dinoflagellate (all primary producers) and planktonic foraminifera
(secondary producers) seem to occur fairly simultaneously (Figs. 3, 5). We propose three possible
interpretations: (i) no clear short-term succession of the microorganism groups occurred (no
temporal turnover in phytoplankton composition within a few days, Roelke and Spatharis, 2015),
(ii) the succession is not properly captured due to low temporal resolution of some sediment trap
intervals (Table 1), and/or (iii) the microorganisms –originally produced in surface and subsurface
waters by different communities– sink with different velocities through the water column toward the
ocean bottom and get ‘mixed’ during their sinking, mainly due to dissimilar weights and sizes of
their remains. However, the high-resolution intervals of CBeu deployments 4 and 5 (up to 7.5 days
per sample, Oct 2006-March 2008, Table 1) should have captured a possible short-term
succession of major groups (e.g., diatoms quickly reacting to increasing nutrient availability,
whereas photosynthetic dinoflagellates becoming more abundant during upwelling relaxation,
Margalef, 1963; Jiménez-Quiroz et al., 2019). Although we do not observe a clear pattern of
succession within studied populations, at this stage we do not disregard either its occurrence. It
should be kept in mind that the deployed traps capture those microorganism remains that reach
the trap cups at around 1,300 m water depth, while they do not capture green algae or
cyanobacteria thriving in surface waters. CBeu traps at ca. 1,300 m water depth capture a mixed
signal of sinking particles from a surface catchment area of at least ca. 100 km$^2$ (Siegel and
Deuser, 1997, Fischer et al., 2016,) due to (i) differential settling velocities of particles (Fischer and
Plankton variability off Mauritania

Karakas, 2009; Iversen et al., 2010, van der Jagt et al., 2018), and (ii) highly heterogeneous and dynamic surface water conditions due to filament and eddy activity off Mauritania (Mittelstaedt, 1991; Gabric et al., 1993; Meunier et al., 2012; Cropper et al., 2014). Additionally, the trapped signal is always affected by dissolution of particular species and/groups of organisms sinking through the water column into deeper waters (e.g., Romero et al., 1999).

5.2. Temporal variations of the species-specific composition of the plankton community

We are aware that 1,900 days of continuous sampling cannot deliver a definite picture of all temporal changes affecting the composition of the plankton community in the very dynamic Mauritanian upwelling. However, the overall temporal pattern observed let us to propose a general sequence of seasonal variability. Most of the major microorganisms groups occur simultaneously and clear successional trends are not quite distinguishable (Fig. 3). A consistent seasonal pattern in the occurrence of species or groups of species is yet recognized. Figure 4 shows the seasonal evolution of populations responding to the temporal dynamics of nutrient availability, e.g. following short-period dust events (Fig. 2e) and/or vertical mixing events associated with stronger winds (Fig. 7a, e). Based on the visual data examination and the statistical analysis, four groups of species are recognized (Figs. 3, 6). Populations of group 1 (Dia-bent, Dia-upw, Co-Gocean, OD-upw, For-cold = in blue in Fig. 6) have higher relative contribution during the most intense phase of the upwelling season (mainly between late winter/early spring and early summer; Mittelstaedt, 1983, Cropper et al., 2014). Group 1 quickly responds to intense mixing and lowered SST at the CBeu site (Fig. 7d, e) and represents the typical upwelling-related association off Mauritania. This observation confirms the ecological characterization of the species groups that have been separately presented in previous biogeographical/ecological studies (Romero et al., 2002; Kucera, 2007; Kobrich et al., 2008, 2016; Zonneveld et al., 2013; Romero and Fischer, 2017).

Diatoms of coastal regions (Dia-coast, non-upwelling related) and those thriving in open ocean waters (Dia-ocean) together with other calcareous dinoflagellates (CD-other), cosmopolitan organic dinoflagellates (OD-cosm) and ‘other coccolithophores’ (Co-other) are assigned to group 2 (in brown in Fig. 6). Except for the cosmopolitan organic dinoflagellates cysts, all components of group 2 are primary producers and occur more abundantly between early fall and late winter (Fig. 4), at times of deepening of the ML and upwelling relaxation (Fig. 7e). Group 2 represents a
primary producers signal typical of meso- to oligotrophic waters conditions off Mauritania, occurring under weakened upwelling, when winds predominantly blow from the N-NE, SST start decreasing after their summer peak, and the uppermost water column stratifies (Fig. 7a, d, e). Except for warm waters (CD-warm) and dust input-sensitive (CD-min) calcareous dinoflagellates cysts, group 3 is mainly composed by secondary producers: warm-water planktonic foraminifera and all pteropods (Fig. 4e, f). As such, this group represents the calcareous fraction of zooplankton feeding on other (primary) phytoplankton, occurring mainly during phases of predominantly warmer SSTs (Fig. 7d), N-NE-originated winds (Fig. 7a) and stratified uppermost water column (Fig. 7e). The distribution and abundance of planktonic foraminifera species is strongly linked to surface-water properties. SST appears to be the most important factor controlling assemblage composition of planktonic foraminifera (Kucera, 2007). Large, symbiont-bearing specialists like *Globigerinoides ruber* and *G. sacculifer* are adapted to more oligotrophic and warmer waters. They show their maximum abundance in warm waters with a deeper mixed-layer depth (Fig. 7e,f).

The seasonal dynamics of group 4 is similar to that of group 3 (intervals of weakened upwelling conditions), but they differ in their composition: group 4 is mainly made of calcareous primary producers. These populations dominate the plankton community during intervals of weakened upwelling, shallow MLD and predominantly oligotrophic water conditions. Similar to group 3, group 4 consists mainly of coccolithophores (the dominant *E. huxleyi*, accompanied by UPZ and LPZ, *U. anulus*, Figs. 4b, 6), as well as organic dinoflagellate cysts characteristic for upwelling relaxation phases (CD-upw relax). The contribution of *E. huxleyi* and accompanying coccolithophore taxa, and upwelling-relaxation organic dinoflagellate cysts shows highest relative values from early fall through early spring and decreases into the most intense upwelling season (when *G. oceanica* increases, Fig. 4b). As such, this group also bears some resemblance to group 2, though coastal and open-ocean water diatoms are component of the latter, while diatoms are absent in group 4. This difference possibly reflects the distinct nutrient and water depth conditions in which *E. huxleyi* and other coccolithophores (group 4) and diatoms (group 2) typically thrive.

5.3. Shifts in the species-specific composition of assemblages between 2004 and 2006
The persistent seasonal pattern of the groups’ and species occurrence experiences occasional shifts. Several events, which altered the ‘regular’ pattern of temporal occurrence of species or group species at site CBeu, were observed between late 2004 and late 2006 (Fig. 7f–i). We identify three main shift stages in the species-specific composition of assemblages:

1. Stage 1 (2004): (i) low total biogenic production (summer–fall 2004, Fig. 2b–d), and (ii) absence of warm-water foraminifera (Fig. 7f). These changes in production/flux were accompanied by (iii) a significant decrease in SST as reconstructed with $U^{K}_{37}$ (Fig. 7d).

2. Stage 2 (late 2005/early 2006): (i) extraordinarily high relative contribution of the coccolithophore *U. anulus* (Fig. 7i); as well as (ii) the first high occurrence of *L. bulimoides* and uncoiled pteropods (Fig. 7h).

3. Stage 3 (after fall 2006): (i) strong increase of the relative contribution of benthic diatoms (Fig. 7i) and warm-water calcareous dinoflagellates (Fig. 7j), and (ii) highest longest occurrence and highest relative abundance of *L. bulimoides* (fall 2006/winter 2007, Fig. 7h).

A certain degree of interannual variability of the physical setting (Mittelstaedt, 1983, 1991; Cropper et al., 2014) might explain the shifts in the species-specific composition of the assemblages. The almost disappearance of warm-water planktonic foraminifera in 2004 (Fig. 7f) was most probable the response to lower-than-usual water temperatures (Fig. 7d). However, the SST decrease is not recorded by satellite imagery. The overall climate evolution indicates a longer warm and dry period from 2001-2004 in the Sahel and Sahara (east of site CBeu) and anomalously warm temperatures in the Eastern Atlantic (Zeeberg et al., 2008; Alheit et al., 2014). 2004 is the only year of our study with the largest lag between satellite and $U^{K}_{37}$-based temperature (Fig. 7d). This temperature gap suggests a certain decoupling between the temperature signal of the uppermost centimeters of the water column (satellite) and subsurface waters where the alkenone-forming coccolithophores dwell (*E. huxleyi* and *G. oceanica*; Conte et al., 1995). As planktonic foraminifera mainly react to SST variability (Kucera, 2007), cooler than usual subsurface waters between middle winter and early fall 2004 (Fig. 7d) might have been responsible for the strong decrease of the warm-water planktonic foraminifera contribution (Fig. 7f). Additionally, all other plankton groups show lowest fluxes toward late summer. Neither the seasonal pattern nor...
the MLD show any significant change nor unusual high fluxes of lithogenic occurred (Fig. 2e, 7e).

Exceptionally, the winter season 2004/2005 is characterized by a high total flux (Fig. 2a); this extraordinarily high seasonal value matches well highest fluxes of TOC and CaCO$_3$ for the studied interval.

The extraordinary high relative abundance of *U. anulus* in fall 2005 has not yet been observed in similar or other settings, although it is often listed in studies of large-scale distribution patterns of coccolithophores (e.g., Böckel and Baumann, 2008; Estrada et al., 2016; Poulton et al., 2017). So far only Steinmetz (1991) has found *U. anulus* (described as *U. calvata* and *U. scituloma*) in ‘frequent’ abundances in sediment traps deployed in the equatorial Atlantic, central Pacific, and in the Panama Basin, but without adding appropriate information such as fluxes, the timing of its occurrence or its ecological significance. In most of earlier trap studies, *U. anulus* has been grouped together with other umbilicosphaerids coccolithophores, since it did not reached high abundances (e.g., Köbrich et al., 2016; Guerreiro et al., 2017). Nevertheless, umbilicosphaerids seem to favor warm and more oligotrophic conditions (Baumann et al., 2016), so that the increased input of tropical surface waters transported northward via the MC (Mittelstaedt, 1991) can be possibly responsible for the advection of *U. anulus* upon the CBeu site.

The shift in the pteropod composition from dominating *H. inflatus* towards the appearance of *L. bulimoides* between winter 2005 and spring 2006 –and again in fall and winter 2006/2007 (Fig. 7h)– can be also explained by the increased influence of warmer surface waters of southern origin.

*Heliconoides inflatus* is known as a rather cosmopolitan species, occurring across a wide range of oceanic provinces (Bé and Gilmer, 1977; Burridge et al., 2017), whereas *L. bulimoides* seems to prefer waters of subtropical gyres (although it was also present in low numbers in the equatorial region, Burridge et al., 2017). A stronger transport of the MC from the south may have led to the deterioration of the adequate environmental conditions for *H. inflatus*, as can be seen by the extremely low total pteropods flux during winter 2005 to spring 2006 (Fig. 3e), and, thus, to the relative enrichment of *L. bulimoides*. The fact that the latter species is absent again in winter 2008 (Fig. 7h) represents a gradual return to previous (‘regular’) winter conditions. ‘Regular’ temperatures from early 2005 on allowed the reappearance of warm-water planktonic foraminifera in fall 2005 (Fig. 7f).
The outstanding increase in the contribution of the benthic diatoms in spring-summer 2006 (Fig. 7i) might have been possibly related to the intensification of lateral advection upon the intermediate-waters deployed CBeu trap (Romero and Fischer, 2017). Observational and model experiments show that the transport of particles from the Mauritanian shelf and the uppermost slope via nepheloid layers significantly contributes to the deposition upon the lowermost slope and beyond than the direct vertical settling of particles from the surface layer (Nowald et al., 2014; Karakaş et al., 2006; Fischer et al., 2009; Zonneveld et al., 2018). The relevance of advective processes within nepheloid layers has been already proposed for similar settings (Puig and Palanques, 1998; Inthorn et al., 2006). We speculate that the longer predominance of N-NE winds between 2005 and 2007 (Fig. 7a) might have possibly intensified the transport of benthic diatoms from the shallow coastal area into the hemipelagic CBeu trap via the MC (Fig. 1). Enhanced lateral transport has important environmental implications for the final burial of organic matter in EBUEs. As the organic matter can be effectively displaced from the area of production (Inthorn et al., 2006), carbon depocenters generally occur at the continental slopes between 500 and 2,000 m. In the CC-EBUE around Cape Blanc, the depocenter with up to 3% of organic carbon has a depth range between 1,000 and 2,000 m (Fischer et al., 2019). Most of the populations affected by and responding to shifting environmental conditions off Mauritania between 2004 and 2006 returned to their ‘regular’ seasonal pattern of occurrence after 2006 (Fig. 4). However, some shifts persisted still after summer 2006. *Limacina bulimoides* still dominated the pteropod assemblage (Fig. 7h), the total pteropod flux showed the highest maxima for the entire studied interval (might be due to the large food supply and organic matter as represented by high total fluxes of diatoms, Fig. 3a, e), and warm-water calcareous dinoflagellate cyst increased during late fall 2006 (Fig. 7i). An exception to this pattern is the high relative contribution of benthic diatoms (Figs. 4a, 7i; Romero and Fischer, 2017). At this stage, we cannot fully disregarded that the shift in the species-specific composition of the diatom community (also present after 2008; Romero and Fischer, 2017; Romero, unpublished observations) might be due to the natural long-term variability due to external forcings (e.g., North Atlantic Oscillation) or due to on-going climate change. Our multiannual trap experiment provides a unique opportunity to study the long-term evolution
Plankton variability off Mauritania

of the plankton community in an ecologically important EBUE. Rapid shifts in the population
contribution at the trap site CBeu demonstrate that calcareous, siliceous and organic plankton
microorganisms rapidly react to environmental changes in the CC-EBUE off Mauritania. Time-
series trap experiments continuously conducted over many years—as those currently in the CC-
EBUE (Fischer et al., 2016, 2019; Romero et al., 2002, 2016, 2017)—deliver a reliable
observational basis on the occurrence of long-lasting variations of populations in response to key
environmental forcings. Among others, our multiannual observations will be useful for future model
experiments on plankton dynamics and evolution in low- and mid latitude EBUEs and how
organisms influencing the global carbon cycle might react to global and ocean warming.

6. Conclusions

- The seasonal amplitude of the flux variations of primary and secondary producers in the upper
water column off Mauritania is well recorded in our 1,900 days continuous trap experiment. The
repeated yearly pattern of higher fluxes of diatoms, coccolithophores, organic-walled dinoflagellate
cysts and planktonic foraminifera between early spring and early/middle summer match well the
temporal occurrence of the most intense upwelling interval in waters overlying the trap site CBeu.
Instead, fluxes of calcareous dinoflagellate cysts and pteropods are higher during intervals of
upwelling relaxation (late summer through late fall).

- The good temporal match between maxima of (most of) studied microorganism groups and
biogenic bulk components unambiguously evidences the contribution of primary and secondary
producers to the total mass/biogenic mass fluxes. The notorious coupling between fluxes of
lithogenic and major microorganisms groups provides compelling evidence for the biological
pump off Mauritania to be strongly dependent on the dust input from the Sahara/Sahel and the
eolian-transported nutrient deposition.

- 1,900 days of continuous trap record of microorganism fluxes let recognizing a general
sequence of seasonal variations of the main plankton populations thriving in coastal waters off
Mauritania. The temporal turnover (succession) is better shown by the temporal variations of
particular species or group of species.
Plankton variability off Mauritania

- A significant shift in the ‘regular’ seasonal pattern of populations’ occurrence is recognized in species relative contributions between 2004 and 2006. Several events altering the regular seasonal pattern were observed and occurred in three main stages: summer–fall 2004, late 2005/early 2006, and after fall 2006. Although most of the populations return ‘to normal’ after fall 2006, a few did not.

- Our multiannual trap experiment emphasizes the significance of long-term records on evaluating the impact of changing environmental conditions on living populations. Time-series trap experiments conducted over many years—as those currently conducted in the CC-EBUE by MARUM—deliver a broad observational basis on the occurrence of persistent seasonal pattern as well long-lasting variations of microorganisms changes in response to key forcings, such as nutrient input, water masses variability, lateral transport and/or climate change. The applicability of the flux dynamics of primary and secondary producers here presented is not limited to the Mauritanian upwelling system, and it might comparable to other EBUEs.

Code and Data Availability

Data are available at https://doi.pangaea.de/10.1594/PANGAEA.904390

Author Contributions

All authors collected the data. Oscar E. Romero wrote the manuscript. All authors contributed to results interpretation and discussion.

Competing Interests

The authors declare that they have no conflict of interest.

Acknowledgements

We are greatly indebted to the masters and crews of the RVs Poseidon and MS Merian. We greatly appreciate the help of the RV Poseidon headquarters at Geomar (K. Lackschewitz, Kiel, Germany) during the planning phases of the research expeditions (Table 1) and the support by the German, Moroccan and Mauritanian authorities in Berlin, Rabat and Nouakchott. We also thank...
the IMROP and its director at Nouadhibou (Mauritania) for their general support and the help in getting the necessary permissions to perform our multiyear trap experiments in Mauritanian coastal waters. We thank G. Ruhland, N. Nowald and M. Klann (MARUM, Bremen) for mooring deployments and lab work on the samples (Table 1). This work was possible due to the long-term funding by the German Research Foundation (DFG) through SFB 261, the Research Center Ocean Margins (RCOM) and the MARUM Excellence Cluster "The Ocean in the Earth System" (University of Bremen, Bremen, Germany).

References

Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M. T. G., Slotte, A., Tsikliras, A.C.: Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic, J. Marine Syst., 133, 88-102, 2014.

Aristegui, J., Barton, E.C., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machú, E., Demarcq, H.: Sub-regional ecosystem variability in the Canary Current upwelling, Prog. Oceanogr., 83, 33–48, 2009.

Barton, E. D.: Eastern Boundary of the North Atlantic: Northwest Africa and Iberia, in: The Sea, edited by Robinson A. R., Brink, K. H., 11, 633-657, 1998.

Baumann, K.-H., Freitag, T.: Pleistocene fluctuations in the Benguela Current system as revealed by coccolith assemblages, Mar. Micropaleontol., 52, 195-215, 2004.

Baumann, K.-H., Andruleit, H., Böckel, B., Geisen, M., Kinkel, H.: The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity: a review, Paläontolog. Zeitschr., 79/1, 93-112, 2005.

Baumann, K.-H., Boeckel, B.: Spatial distribution of living coccolithophores in the southwestern Gulf of Mexico. J. Micropaleontol., 32, 123-133, 2013.

Baumann, K.-H., Saavedra-Pellitero, M., Böckel, B., Ott, C.: Morphometry, biogeography and ecology of Calcidiscus and Umbilicosphaera in the South Atlantic, Rev. Micropaleontol., 59, 239-251, doi:10.1016/j.revmic.2016.03.001, 2016.
Plankton variability off Mauritania

Bé, A. W. H., Gilmer, R. W.: A zoographic and taxonomic review of euthecosomatous pteropoda, in: Oceanic Micropalaeontology, Vol. 1, edited by Ramsay, A. T. S., Academic Press, London, 733–808, 1977.

Böckel, B., Baumann, K.-H.: Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean, Mar. Micropaleontol., 67, 255-273, 2008.

Bory, A., Jeandel, C., Leblond, N., Vangriesheim, A., Khripounoff, A., Beaufort, L., Rabouille, C., Nicolas, E., Tachikawa, F., Etcheber, H., Buat-Ménard, P.: Downward particle fluxes within different productivity regimes off the Mauritanian upwelling zone (EUMELI program), Deep-Sea Res. I, 48, 2251-2282, 2001.

Bouimetarhan, I., Marret, F., Dupont, L., Zonneveld, K. A. F.: Dinoflagellate cyst distribution in marine surface sediments off West Africa (17 – 6°N) in relation to sea-surface conditions, freshwatert input and seasonal coastal upwelling, Mar. Micropaleontol., 71, 113-130, 2009.

Buesseler, K.O., Antia, A.A., Chen, M., Fowler, S.W., Gardner, W.D., Gustafsson, O., Harada, K., Michaels, A.F., Rutgers van der Loeff, M., Sarin, M., Steinberg, D.K., Trull, T.: An assessment of the use of sediment traps for estimating upper ocean particle fluxes, J. Mar. Res., 65, 345-416, 2007.

Burridge, A. K., Goetze, E., Wall-Palmer, D., Le Double, S. L., Huisman, J., Peijnenburg, K. T. C. A.: Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean, Prog. Oceanogr., 158, 213-223, 2017.

Chavez, F. P., Messié, M.: A comparison of Eastern Boundary Upwelling Ecosystems, Prog. Oceanogr., 83, 80-96, 2009.

Conte, M. H., Thompson, A., Egrinton, G., Green, J. C.: Lipid biomarker diversity in the coccolithophorid Emiliania huxleyi (Prymnesiophyceae) and the related species Gephyrocapsa oceanica, J. Phycol., 31, 272–282, 1995.

Conte, M. H., Sicre, M., Rühlemann, C., Weber, J. C., Schulte, S., Schulz-Bull, D., Blanz, T.: Global temperature calibration of the alkenone unsaturation index (UK’37) in surface waters and comparison with surface sediments, Geochem. Geophy. Geosy., 7(2), 798 https://doi.org/10.1029/2005GC001054, 2006.
Plankton variability off Mauritania

Cropper, T. E., Hanna, E., Bigg, G. R.: Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981–2012, Deep-Sea Res. I, 86, 94-111, 2014.

Crosta, X., Romero, O. E., Ther, O., Schneider, R. R.: Climatically-controlled siliceous productivity in the eastern Gulf of Guinea during the last 40 000 yr, Clim. Past., 8, 415-431, 2012.

Elbrächter, M., Gottschling, M., Hildebrand-Habel, T., Keupp, H., Kohring, R., Lewis, J., Meier, K.

J. S., Montresor, M., Strengh, M., Versteegh, G.J.M., Willems, H., Zonneveld, K., Establishing an agenda for calcareous dinoflagellate research (Thoracosphaeraceae, Dinophyceae) including a nomenclatural synopsis of generic names, Taxon, 57, 1289-1303, 2008.

Estrada, M., Delgado, M., Blasco, D., Latasa, M., Cabello, A.M., Benítez-Barrios, V., Fraile-Nuez, E., Mozetic, P., Vidal, M.: Phytoplankton across Tropical and Subtropical Regions of the Atlantic, Indian and Pacific Oceans, PLoS ONE, 11, 3, e0151699. doi:10.1371/journal.pone.0151699, 2016.

Fischer, G., Wefer, G.: Sampling, preparation and analysis of marine particulate matter, in: The Analysis and Characterization of Marine Particles, Geophysical Monograph Series 63, edited by Hurd, D. C., Spencer, D. W., 391-397, 1991.

Fischer, G., Donner, B., Ratmeyer, V., Davenport, R., Wefer, G.: Distinct year-to-year particle flux variations off Cape Blanc during 1988–1991: Relation to δ18O-deduced sea-surface temperatures and trade winds, J. Mar. Res., 54, 73–98, 1996.

Fischer, G., Karakaş, G.: Sinking rates and ballast composition of particles in the Atlantic Ocean: implications for the organic carbon fluxes to the deep ocean, Biogeosciences, 6, 85-102, 2009.

Fischer, G., Romero, O. E., Merkel, U., Donner, B., Iversen, M., Nowald, N., Ratmeyer, V.,

Ruhland, G., Klann, M., Wefer, G.: Deep ocean mass fluxes in the coastal upwelling off Mauritania from 1988 to 2012: variability on seasonal to decadal timescales, Biogeosciences, 13, 3071-3090, 2016.

Fischer, G., Romero, O.E., Toby, E., Iversen, M., Donner, B., Mollenhauer, G., Nowald, N.,

Ruhland, G., Klann, M.: Hamady, B., Wefer, G.: Changes in the dust-influenced biological carbon pump in the Canary Current System: Implications from a coastal and an offshore sediment trap record off Cape Blanc, Mauritania, Global Biogeochem. Cycles, 2019.

Friese, C. A., Hateren, J. A. V., Vogt, C., Fischer, G., Stuut, J.-B. W.: Seasonal provenance
Plankton variability off Mauritania changes in present-day Saharan dust collected in and off Mauritania, Atmos. Chem. Phys., 17, 10163-10193, 2017.

Fütterer, D. K.: The modern upwelling record off Northwest Africa, in: Coastal Upwelling, its sediment record, Part B, Sedimentary records of ancient coastal upwelling, NATO Conference Series IV, Marine Science, edited by Thiede, J., Suess, E., pp. 105-121, 1983.

Gabric, A. J., García, L., Van Camp, L., Nykjaer, L., Eifler, W., Schrimpf, W.: Offshore Export of Shelf Production in the Cape Blanc (Mauritania) Giant Filament as Derived from Coastal Zone Color Scanner Imagery, J. Geophys. Res., 98, C3, 4697-4712, 1993.

Guerreiro, C. V., Baumann, K.-H., Brummer, G.-J. A., Fischer, G., Korte, L. F., Merkel, U., Sá, C., de Stigter, H., Stuut, J.-B.: Coccolithophore fluxes in the open tropical North Atlantic: influence of the Amazon river and of Saharan dust deposition, Biogeosciences, 14, 4577-4599, https://doi.org/10.5194/bg-14-4577-2017, 2017.

Guerreiro, C. V., Baumann, K.-H., Brummer, G.-J. A., Korte, L. F., de Sá, C., Stuut, J.-B.: Transatlantic gradients in calcifying phytoplankton (coccolithophores) fluxes, Progr. Oceanogr., 176, https://doi.org/10.1016/j.pocean.2019.102140, 2019.

Hagen, E.: Northwest African upwelling scenario, Oceanol. Acta, 24 (Supplement), S113-S128, 2001.

Hardy, W., Marret, F., Penaud, A., le Mézo, P., Droz, L., Marsset, T., Kageyama, M.: Quantification of last glacial-Holocene net primary productivity and upwelling activity in the equatorial eastern Atlantic with a revised modern dinocyst database, Palaeogeogr. Palaeoecol., 505, 410-427, 2018.

Hasle, G. A., Syvertsen, E. E.: Marine diatoms, in: Identifying marine diatoms and dinoflagellates, edited by Thomas, C., Academic Press, Inc. San Diego, CA, 1-385, 1996.

Hedges, J. I., Baldock, J. A., Gélinas, Y., Lee, C., Peterson, M. L., Wakeham, S. G.: The biochemical and elemental compositions of marine plankton: A NMR perspective, Mar. Chem., 78, 47–63, 2002.

Helmke, P., Romero, O. E., Fischer, G.: Northwest African upwelling and its effect on off-shore organic carbon export to the deep sea, Global Biogeochem. Cycles, 19, GB4015, doi:10.1029/2004GB002265, 2005.
Plankton variability off Mauritania

Hemleben, C., Spindler, C., Anderson, O. R.: Modern Planktonic Foraminifera, pp. 363, New York (Springer), 1989.

Holzwarth, U., Esper, O., Zonneveld, K. A. F.: Organic-walled dinoflagellate cysts as indicators of oceanographic conditions and terrigenous input in the NW African upwelling region, Rev. Palaeobot. Palyno., 159, 35-55, 2010.

Inthorn, M., Wagner, T., Scheeder, G., Zabel, M.: Lateral transport controls distribution, quality, and organic matter along continental slopes in high-productivity areas, Geology, 34, 205-208, doi: 210.1130/G22153.22151, 2006.

Iversen, M. H., Nowald, N., Ploug, H., Jackson, G. A., Fischer, G.: High resolution profiles of vertical particulate organic matter export off Cape Blanc, Mauritania: Degradation processes and ballasting effects, Deep-Sea Res. I, 57, 771-784, 2010.

Iversen, M. H., Ploug, H.: Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocity of marine snow aggregates, Biogeosciences, 7, 2613-2624, 2010.

IOC-UNESCO TS129 IGMETS: What are Marine Ecological Time Series telling us about the ocean? A status report, IOC Technical Series, 129. pp., 2017.

Jiménez-Quiroz, M. d. C., Cervantes-Duarte, R., Funes-Rodríguez, R., Barón-Campis, S. A., García-Romaro, F. d. J., Hernández-Trujillo, S., Hernández-Becerril, D. U., González-Armas, L. V., Martell-Dubois, R., Cerdeira-Estrada, S., Fernández-Méndez, J., González-Ania, L. V., Vásquez-Ortiz, M., Barrón-Barraza, F. J.: Impact of "The Blob" and "El Nino" in the SW Baja California Peninsula: Plankton and environmental variability of Bahia Magdalena, Front. Mar. Sci., 6, 1-23, 2019.

Jordan, R. W., Zhao, M., Eglinton, G., Weaver, P. P. E.: Coccolith and alkenone stratigraphy and palaeoceanography at an upwelling site off NW Africa (ODP 658C) during the last 130,000 years, in: Microfossils and oceanic environments, edited by Moguilevsky, A., Whatley, R., University of Wales, Aberystwyth Press, London, pp. 111–130, 1996.

Karakaş, G., Nowald, N., Blaas, M., Marchesiello, P., Frickenhaus, S., Schlitzer, R.: High-resolution modeling of sediment erosion and particle transport across the northwest African shelf, J. Geophys. Res., 111, C06025, doi.org/10.1029/2005JC003296, 2006.
Plankton variability off Mauritania

Karakaş, G., Nowald, N., Schäfer-Neth, C., Iversen, M., Barkmann, W., Fischer, G., Marchesiello, P., Schlitzer, R.: Impact of particle aggregation on vertical fluxes of organic matter, Prog. Oceanogr., 83, 331-341, 2009.

Köbrich, M. I., Baumann, K.-H.: Coccolithophore flux in a sediment trap off Cape Blanc (NW Africa), J. Nannopl., 30, 2, 83-96, 2008.

Köbrich, M. I., Baumann, K.-H., Fischer, G.: Seasonal and inter-annual dynamics of coccolithophore fluxes from the upwelling region off Cape Blanc, Northwest Africa, J. Micropaleontol, doi:10.1144/jmpaleo2014-024, 2016.

Kohn, M., Zonneveld, K. A. F.: Calcification depth and spatial distribution of Thoracosphaera heimii cysts Implications for palaeoceanographic reconstructions, Deep-Sea Res. I, 57, 1543-1560, 2010.

Kremling, K., Lentz, U., Zeitzschell, B., Schulz-Bull, D. E., Duinker, J. C.: New type of time-series sediment trap for the reliable collection of inorganic and organic trace chemical substances, Rev. Sci. Instrument., 67, 4360–4363, 1996.

Kucera, M.: Planktonic foraminifera as tracers of past oceanic environments: in, Developments in Marine Geology, Volume 1, Proxies in Late Cenozoic Paleoeceanography, edited by Hillaire-Marcel, C., De Vernal, A., Elsevier, Amsterdam, 213-262, 2007.

Lange, C. B., Romero, O. E., Wefer, G., Garibaldi, A. J.: Offshore influence of coastal upwelling off Mauritania, NW Africa, as recorded by diatoms in sediment traps at 2195 m water depth, Deep-Sea Res. I, 45, 985-1013, 1998.

Lathuilière, C., Echevin, V., Levy, M.: Seasonal and intraseasonal surface chlorophyll-a variability along the northwest African coast, J. Geophys. Res. Oceans, 13(C5), C05007, doi:10.1029/2007JC004433, 2008.

Marcello, J., Hernández-Guerra, A., Eugenio, F., Fonte, A.: Seasonal and temporal study of the northwest African upwelling system, Int. J. Remote Sens., 32, 1843-1859, 2011.

Margalef, R.: On certain unifying principles in ecology, Am. Nat., 97, 357-374, 1963.

McKay, C. L., Filipsson, H. L., Romero, O. E., Stuut, J.-B. W., Donner, B.: Pelagic-benthic coupling within an upwelling system of the subtropical northeast Atlantic over the last 35 ka BP., Quat. Sci. Rev., 106, 299-315, 2014.
Plankton variability off Mauritania

Meunier, T., Barton, E. D., Barreiro, B., Torres, R.: Upwelling filaments off Cape Blanc: interaction of the NW African upwelling current and the Cape Verde frontal zone eddy field?, J. Geophys. Res. Oceans, 117, C8, C08031, doi:10.1029/2012JC007905, 2012.

Mittelstaedt, E.: The upwelling area off Northwest Africa - a description of phenomena related to coastal upwelling, Prog. Oceanogr., 12, 307-331, 1983.

Mittelstaedt, E.: The ocean boundary along the northwest African coast: Circulation and oceanographic properties at the sea surface, Prog. Oceanogr., 26, 307–355, 1991.

Mollenhauer, G., Basse, A., Kim, J.-H., Sinninghe Damsté, J. S., Fischer, G.: A four-year record of U\(^{14}\) and TEX\(_{86}\)-derived sea surface temperature estimates from sinking particles in the filamentous upwelling region off Cape Blanc, Mauritania, Deep-Sea Res. I, 97, 67–79, 2015.

Müller, P.J., Schneider, R. R.: An automated leaching method for the determination of opal in sediments and particulate matter, Deep-Sea Res. I, 40, 425-444, 1993.

Müller, P., Fischer, G.: A 4-year sediment trap record of alkenones from the filamentous region off Cape Blanc, NW Africa, and a comparison with distributions in underlying sediments, Deep-Sea Res. I, 48, 1877-1903, 2001.

Muller-Karger, F., Varela, R., Thunell, R., Luerssen, R., Hu, C., Walsh, J. J.: The importance of continental margins in the global carbon cycle, Geophys. Rese. Lett., 32, L01602, doi:01610.01029/02004GL021346, 021341_021341_021344, 2005.

Nicholson, S. E.: The West African Sahel. A review of recent studies on the rainfall regime and its interannual variability. ISRN Meteorology, 453521, doi:10.1155/2013/453521, 2013.

Nowald, N., Iversen, M. H., Fischer, G., Ratmeyer, V., Wefer, G.: Time series of in-situ particle properties and sediment trap fluxes in the coastal upwelling filament off Cape Blanc, Mauritania, Prog. Oceanogr., 137, 1-11, 2014.

Pauly, D., Christensen, V.: Primary production required to sustain global fisheries, Nature, 374, 255-257, 1995.

Pelegri, J. L., Marrero-Díaz, A., Ratsimandresy, A. W.: Nutrient irrigation of the North Atlantic, Prog. Oceanogr., 70, 366-406, 2006.

Pelegri, J. L., Peña-Isquierdo, J., Machin, F., Meiners, C., Presas-Navarro, C.: Oceanography of the Cape Verde Basin and Mauritanian Slope Waters, in Research of Marine Biodiversity and
Plankton variability off Mauritania

946 Habitats in the Northwest African Margin 3, pp. 119-153, doi 10.1007/978-94-024-1023-5_3, Berlin: Springer. 2017

948 Pospelova, V., Zonneveld, K. A. F., Heikkilä, M., Bringué, M., Price, A. M., Esenkulova, S., Matsuoka, K.: Seasonal, annual, and inter-annual Spiniferites cyst production: a review of sediment trap studies, Palynology, 42, 1, 162-182, 2018.

950 Poulton, A. J., Holligan, P. M., Charalampopoulou, A., Adey, T. R.: Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: New perspectives from the Atlantic meridional transect (AMT) Programme, Progr. Oceanogr., 158, 150-170, 2017.

954 Prahl, F. G., Wakeham, S. G.: Calibration of unsaturation patterns in long-chain ketone compositions for palaeotemperature assessment, Nature, 330, 6146, 367, 1987.

956 Puig, P., Palanques, A.: Nepholoid structure and hydrographic control on the Barcelona continental margin, northwestern Mediterranean, Mar. Geol., 149, 39–54, 1998.

958 Rembauville, M., Meillard, J., Ziveri, P., Schiebel, R., Blain, S., Salter, I.: Planktic foraminifer and coccolith contribution to carbonate export fluxes over the central Kerguelen Plateau, Deep-Sea Res. I, 111, 91–101, https://doi.org/10.1016/j.dsr.2016.02.017, 2016.

962 Richter, D., Vink, A., Zonneveld, K. A. F., Kuhlman, H., Willems, H.: Calcareous dinoflagellate cyst distributions in surface sediments from upwelling areas off NW Africa, and their relationships with environmental parameters of the upper water column, Mar. Micropal., 63, 201–228, 2007.

964 Roelke, D.L., Spatharis, S.: Phytoplankton succession in recurrently fluctuating environments, PLoS One, 10, e012392, 2015.

966 Romero, O. E., Lange, C.B., Fischer, G., Treppke, U.F., Wefer, G.: Variability in export production documented by downward fluxes and species composition of marine planktonic diatoms: Observations from the tropical and equatorial Atlantic, in Use of Proxies in Paleoceanography, Examples from the South Atlantic, edited by Fischer, G., Wefer, G., Springer Verlag, Berlin, Heidelberg, 365-392, 1999.

Romero, O. E., Lange, C.B., Wefer, G.: Interannual variability (1988-1991) of siliceous phytoplankton fluxes off northwest Africa, J. Plank. Res., 24, 10, 1035-1046, doi:1010.1093/plankt/1024.1010.1035, 2002.

974 Romero, O. E., Dupont, L., Wyputta, U., Jahns, S., Wefer, G.: Temporal variability of fluxes of
eolian-transported freshwater diatoms, phytoliths, and pollen grains off Cape Blanc as reflection of land-atmosphere-ocean interactions in northwest Africa, J. Geophys. Res. Oceans, 108, C5, 3153, doi:10.1029/2000JC000375002003, 2003.

Romero, O. E., Armand, L.K., Crosta, X., Pichon, J.-J.: The biogeography of major diatom taxa in Southern Ocean surface sediments: 3. Tropical/Subtropical species, Palaeogeogr. Palaeoclim., 223, 49-65, 2005

Romero, O. E., Kim, J., Donner, B.: Submillennial-to-millennial variability of diatom production off Mauritania, NW Africa, during the last glacial cycle, Paleoceanography, 23, PA3218, doi:10.1029/2008PA001601, 2008.

Romero, O. E., Thunell, R. C., Astor, Y., Varela, R.: Seasonal and interannual dynamics in diatom production in the Cariaco Basin, Venezuela, Deep-Sea Res. I, 56, 571-581, 2009a.

Romero, O. E., Rixen, T., Herunadi, B.: Effects of hydrographic and climatic forcing on diatom production and export in the tropical southeastern Indian Ocean, Mar. Ecol. Prog. Ser., 384, 69-82, 2009b.

Romero, O. E., Armand, L.K.: Marine diatoms as indicators of modern changes in oceanographic conditions, in: The Diatoms, Applications for the Environmental and Earth Sciences (Second Edition), edited by Smol, J. P., Stoermer, E. F., Cambridge University Press, Cambridge, 373-400, 2010.

Romero, O. E., Crosta, X., Kim, J.-H., Picchevin, L., Crespin, J.: Rapid longitudinal migrations of the filament front off Namibia (SE Atlantic) during the past 70 kyr, Global Planet. Changes, 125, 1-12, http://dx.doi.org/10.1016/j.gloplacha.2014.1012.1001, 2015.

Romero, O. E., Fischer, G., Karstensen, J., Cermeño, P.: Eddies as trigger for diatom productivity in the open-ocean Northeast Atlantic, Prog. Oceanogr., 147, 38-48, 2016.

Romero, O. E., Fischer, G.: Shift in the species composition of the diatom community in the eutrophic Mauritanian coastal upwelling: Results from a multi-year sediment trap experiment (2003 – 2010), Prog. Oceanogr., 159, 31-44, 2017.

Round, F. E., Crawford, R.M., Mann, D.G.: The diatoms, Cambridge University Press, Cambridge, pp. 747,1990.
Plankton variability off Mauritania

Sancetta, C., Calvert, S. E.: The annual cycle of sedimentation in Saanich Inlet, British Columbia: implications for the interpretation of diatom fossil assemblages, Deep-Sea Res., 35, 1, 71-90, 1988.

Schlüter, M.H., Kraberg, A., Wiltshire, K. H.: Long-term changes in the seasonality of selected diatoms related to grazers and environmental conditions, J. Sea Res., 67, 91-97, 2012.

Schiebel, R., Hemleben, C.: Planktic Foraminifers in the Modern Ocean, Springer-Verlag GmbH Berlin, Heidelberg, 2017.

Schrader, H.-J., Gersonde, R.: Diatoms and silicoflagellates, In: Micropaleontological counting methods and techniques - an exercise on an eight meter section of the Lower Pliocene of Capo Rosello, Sicily, edited by Zachariasse, W. J., Riedel, W. R., Sanfilippo, A., Schmidt, R. R., Brolsma, M. J., Schrader, H., Gersonde, R., Droger, M. M., Broekman, J. A, Utrecht Micropaleontological Bulletin, Utrecht, 17, 129-176, 1978.

Siegel, D.A., Deuser, W.G.: Trajectories of sinking particles in the Sargasso Sea: modeling of statistical funnels above deep-ocean sediment traps, Deep-Sea Res. I, 44, 1519–1541, 1997.

Siggelkow, D., Vink, A., Willems, H.: Calcareous dinoflagellate cyst production, vertical transport and preservation off Cape Blanc during 1990: a sediment-trap study, J. Nannoplankton Res., 24, 160, 2002.

Skonieczny, C., Bory, A., Bout-Roumazeilles, V., Abouchami, W., Galer, S. J. G., Crosta, X., Diallo, A., Ndiaye, T.: A three-year time series of mineral dust deposits on the West African margin: Sedimentological and geochemical signatures and implications for interpretation of marine paleo-dust records, Earth Planet. Sc. Lett., 364, 145-156, 2013.

Smayda, T. J.: Ecological features of harmful algal blooms in coastal upwelling ecosystems, African J. Mar. Sci., 219-253, 2010.

Smayda, T. J., Trainer, V. L.: Dinoflagellate blooms in upwelling systems: Seeding, variability, and contrasts with diatom bloom behavior, Prog. Oceanogr., 85, 92-107, 2010.

Smilauer, P., Leps, J.: Multivariate analysis of ecological data using Canoco 5, Cambridge University Press, Cambridge, 1-362, 2014.
1030 Steinmetz, J. C.: Calcareous nannoplankton biocoenosis: sediment trap studies in the Equatorial Atlantic, Central Pacific, and Panama Basin, Woods Hole Oceanographic Institution, U.S.A., 1, 1-85, 1991.

1032 Susek, E., Zonneveld, K. A. F., Fischer, G., Versteegh, G. J., Willems, H.: Organic-walled dinoflagellate cyst production in relation to upwelling intensity and lithogenic influx in the Cape Blanc region (off north-west Africa), Phycol. Res., 53, 97-112, 2005.

1036 ter Braak, C.J., Smilauer, P.: Canoco 5. Biometris, Wageningen, pp. 1-496, 2012.

1038 Trainer, V. L., Pitcher, G. C., Reguera, B., Smayda, T. J.: The distribution and impacts of harmful algal bloom species in eastern boundary upwelling systems, Prog. Oceanogr., 85, 33-52, 2010.

1040 Van Camp, L., Nykjær, L., Mittelstaedt, E., Schlittenhardt, P.: Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations, Prog. Oceanogr., 26, 357–402, 1991.

1042 van der Jagt, H., Friese, C., Stuut, J., Fischer, G., Iversen, M.: The ballasting effect of Saharan dust deposition on aggregate dynamics and carbon export: Aggregation, settling, and scavenging potential of marine snow, Limnol. Oceanogr., 63, 1386-1394, 2018.

1044 Vink, A., Brune, A., Höll, C., Zonneveld, K. A. F., Willems, H.: On the response of calcareous dinoflagellates to oligotrophy and stratification of the upper water column in the equatorial Atlantic Ocean, Palaeoecogr., Palaeoecol., 178, 53-66, 2002.

1046 Vink, A.: Calcareous dinoflagellate cysts in South and equatorial Atlantic surface sediments: diversity, distribution, ecology and potential for palaeoenvironmental reconstruction, Mar. Micropaleontol., 50, 43-88, 2004.

1048 Weiser, J., Baumann, K.-H., Hahn, A., Zabel, M.: Late Holocene paleoceanographic changes off south-western Africa as inferred from nannofossil assemblages, J. Nannoplankton Res., 36, 2, 161-171, 2016.

1050 WoRMS Editorial Board, http://www.marinespecies.org, 2017.

1052 Young, J., Geisen, M., Cross, L., Kleijne, A., Sprengel, C., Probert, I., Østergaard, J.: A guide to extant coccolithophore taxonomy, J. Nannoplankton Res., Special Issue 1, International Nannoplankton Association, 124 pp., 2003.

1054 Young, J. R., Bown P. R., Lees J. A.: Nannotax3 website. International Nannoplankton
Plankton variability off Mauritania

Association. Accessed April 2019. URL: http://www.mikrotax.org/Nannotax3, 2019.

Zeeberg, J., Corten, A., Tjoel-Awie, P., Coca, J., Hamady, B.: Climate modulates the effects of *Sardinella aurita* fisheries off Northwest Africa, Fish. Res., 89, 65–75, 2008.

Zenk, W., Klein, B., Schröder, M.: Cape Verde Frontal Zone, Deep-Sea Res., 38, Suppl. 1, S505–S530, 1991.

Zonneveld, K. A. F., Susek, E., Fischer, G.: Seasonal variability of the organic-walled dinoflagellate cyst production in the coastal upwelling region off Cape Blanc (Mauritania): a five-year survey, J. Phycol., 46, 202-215, 2010.

Zonneveld, K. A. F., Chen, L., Elshanawany, R., Fischer, H. W., Hoins, M., Ibrahim, M. I., Pittauerova, D., Versteegh, G. J.: The use of dinoflagellate cysts to separate human-induced from natural variability in the trophic state of the Po River discharge plume over the last two centuries, Mar. Pollut. Bull., 64, 114-132, 2012.

Zonneveld, K. A. F., Marret, F., Versteegh, G. J. M., Bogus, K., Bonnet, S., Bouimetarhan, I., Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K., Henry, M., Holzwarth, U., Kietl, J.-F., Kim, S.-Y., Ladouceur, S., Ledu, D., Chen, L., Limoges, A., Londeix, L., Lu, H., Mahmoud, M. S., Marino, G., Matsouka, K., Matthiessen, J., Mildenhal, C., Mudie, P., Neil, L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.-L., Verleye, T., Wang, Y., Wang, Z., Young, M.: Atlas of modern dinoflagellate cyst distribution based on 2405 datapoints, Rev. Palaeobot. Palynol., 191, 1-197, 2013.

Zonneveld, K. A. F., Pospelova, V.: A determination key for modern dinoflagellate cysts, Palynology, 39, 387-409, 2015.

Zonneveld, K. A. F., Ebersbach, F., Maeke, M., Versteegh, G. J. M.: Transport of organic-walled dinoflagellate cysts in nepheloid layers off Cape Blanc (N-W Africa), Deep Sea Res. I, 139, 55-67, 2018.
Figure 1. Map of the study area showing the location of trap site CBeu (full light blue dot), surface currents, and main wind system. Surface currents (Canary Current, CC, violet line; North Equatorial Counter Current, blue arrow; Mauritanian Current; red arrow), North Equatorial Current (NEC), Cape Verde Current (CVC), north Cape Verde Current (nCVC), PUC are depicted after Mittelstaedt (1983, 1991) and Zenk et al. (1991). The Cape Verde Frontal Zone (CVFZ) builds at the confluence of the NACW and the SACW (Zenk et al., 1991). Trade winds and Saharan Air Layer are represented by orange arrows (Nicholson, 2013). The upwelling zones are depicted after Cropper et al. (2014).
Figure 2. Total particle and bulk fluxes at the trap site CBeu between June 2003 and March 2008. From top to bottom: (a) total particle (mg m\(^{-2}\) d\(^{-1}\), black bars), (b) calcium carbonate (CaCO\(_3\), mg m\(^{-2}\) d\(^{-1}\), light blue bars), (c) total organic carbon (TOC, mg m\(^{-2}\) d\(^{-1}\), olive bars), (d) biogenic silica (BSi, opal, mg m\(^{-2}\) d\(^{-1}\), dark grey bars), and (e) lithogenics (mg m\(^{-2}\) d\(^{-1}\), brown bars). The horizontal striped line for each parameter represents the average flux for the whole studied interval (see Table 1). The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=Winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Figure 3. Fluxes of microorganisms at the trap site CBeu between June 2003 and March 2008. From top to bottom: (a) diatoms (valves m$^{-2}$ d$^{-1}$, peach bars; note that ten samples corresponding to CBeu 5 –12/13/2007 through 03/17/2008– were not available for diatom analysis); (b) coccolithophores (coccoliths m$^{-2}$ d$^{-1}$, light blue bars); (c) calcareous dinoflagellates (cysts m$^{-2}$ d$^{-1}$; gold bars); (d) organic dinoflagellates (cysts m$^{-2}$ d$^{-1}$; khaki bars); (f) planktic foraminifera (shells m$^{-2}$ d$^{-1}$; grey bars), and (f) pteropods (shells m$^{-2}$ d$^{-1}$; ocean green bars). The horizontal striped line for each group of organisms represents the average flux for the whole study interval. The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=Winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Figure 4
Romeso et al.

(a) Diatoms
(b) Coccolithophoridae
(c) Calcareous dinoflagellates
(d) Organic dinoflagellates
(e) Planktonic foraminifera
(f) Peracarids

https://doi.org/10.5194/bg-2019-314
Preprint. Discussion started: 27 August 2019
© Author(s) 2019. CC BY 4.0 License.
Figure 4. Cumulative relative abundance (%) of main species or group of species of diatoms, coccolithophores, dinoflagellates, planktonic foraminifera and pteropods at the trap site CBeu between June 2003 and March 2008 (Table 1). From top to bottom: (a) diatoms - benthic, light green bars; coastal upwelling, dark green bars; coastal planktonic, black bars; and open-ocean, orange bars; note that ten samples corresponding to CBeu 5 –12/13/2007 through 03/17/2008 were not available for diatom analysis; (b) coccolithophores – upper photic zone, blue bars; lower photic zone, moss green; Umbilicosphaera anulus, pink bars; Gephyrocapsa oceanica, black bars; Emiliana huxleyi, orange bars; (c) calcareous dinoflagellates – other calcareous, dark grey bars; mineral-input related, brown bars; upwelling, light green bars; cosmopolitan, light grey; warm water, orange bars; (d) organic dinoflagellates – upwelling species (grey bars); upwelling relaxation species (light yellow bars); potential toxic (dark green bars); cosmopolitan, red brown bars; other, faded green bars; (e) planktic foraminifera – upwelling, green bars; cool water, blue bars; warm water, orange bars; and (f) pteropods – uncoiled species, light blue bars; Limacina bulimoides, red bars; Heliconoides inflatus, pink bars. The species-specific composition of groups is presented in Table 3. The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=Winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Figure 5. RDA ordination diagram depicting the relationship between the accumulation rates of organism groups and bulk fluxes and environmental conditions in upper waters. References: Av. wind speed=average wind speed; Chlor-a=chlorophyll a; TOC=total organic carbon; CaCO$_3$=calcium carbonate; mixed layer depth; SST=sea surface temperature; SSTA=sea surface temperature anomalies. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Figure 6. Results of a PCA analysis of ecological groups of the organism groups at the CBeu trap site between June 2003 and March 2008. References: Dia (diatoms): -bent = benthic, -coast = coastal planktonic, -ocean = open ocean, -upw = upwelling; Co (cocolithophores): -Ehux = Emiliana huxleyi, -Gocean = Gephyrocapsa oceanica, -low phot: low photic zone, -other: other cocolithophroids, -Uanu = Umbilicosphaera anulus, -up phot: upper photic zone; CD (calcaceous dinoflagellate cysts): -cosm = cosmopolitan group, -min = terrestrial mineral group, -other = species that do not fit in one of the other ecological groups, -upw = upwelling, warm: warm waters; OD (organic-walled dinoflagellate cysts): -cosm = cosmopolitan group, -other = species that do not fit in one of the other ecological groups, -tox = potential toxic group, -upw = upwelling, -upw relax = upwelling relaxation; For (foraminifera): -cold: cold water group, -upw = upwelling group; -warm = warm water group; and Pt (pteropods): -Hinf = Heliconoides inflatus, -Lbul = Limacina bulimoides, -uncoi: uncoiled. Groups of microorganisms are identified by colors (light blue, group 1; brown, group 2; black, group 3; and red, group 4). The species-specific composition of groups is presented in Table 3. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Plankton variability off Mauritania

Figure 7
Romero et al.
Figure 7. Comparison physical data (a-e) and relative abundance of selected species or group/s of species (f-j) at site CBeu between June 2003 and March 2008. Physical data: (a) daily wind direction (°, the grey line are daily data, the thicker black line represent the 17-running points average); (b) daily wind velocity (m s⁻¹, the grey line are daily data, the thicker dark brown line represent the 17-running points average), (c) dust storm event (number of events) recorded at the meteorological station of the Airport of Nouadhibou (ca. 20°57’N, 17°02’W, Mauritania); (d) seawater temperature (°C): U°K-based reconstruction (black line) and satellite-imagery generated data (blue line); (e) mixed layer depth (m, grey line, https://modis.gsfc.nasa.gov for the area between 19°-18°W and 20°-21°N). Relative contribution (%) of (f) planktonic warm-water foraminifera (orange bars); (g) the coccolithophore A. anulus (pink bars); (h) pteropods L. bulimoides (red bars) and uncoiled species (light blue bars); (i) benthic diatoms (banana yellow bars); and (j) calcareous dinoflagellates (light orange bars). The species-specific composition of groups is presented in Table 3. The vertical gray lines indicate years separation. The light grey shading in the background highlights the interval of main shift in fluxes values and/or the relative contribution of particular species or group of species (see discussion in 5.3.). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.
Plankton variability off Mauritania

Tables

Table 1: Data deployment at site CBeu (Cape Blanc eutrophic, off Mauritania): coordinates, GeoB location and cruise, trap depth, sample amount, capture duration of each sample and sampling interval. Two gaps in the sampling intervals occurred: 04/05/2004–04/18/2004, and 09/28/2006–10/28/2006.

| Mooring | Coordinates | GeoB-#/ cruise | Trap depth (m) | Sample amount | Capture duration (sample/days) | Sampling interval |
|---------|-------------|----------------|---------------|---------------|---------------------------------|------------------|
| 1       | 20°45'N 18°42'W | POS 310 | 1,296          | 20            | 1 = 10.5, 2-20 = 15.5          | 06/05/2003 – 04/05/2004 |
| 2       | 20°45'N 18°42'W | M 65-2      | 1,296          | 20            | 1-20 = 22, 2-19 = 23           | 04/18/2004 – 07/20/2005 |
| 3       | 20°45.5'N 18°41.9'W | POS 344-3 | 1,277          | 20            | 21.5                           | 07/25/05 – 09/28/2006 |
| 4       | 20°45.7'N 18°42.4'W | POS 365-2 | 1,263          | 38            | 1, 2 = 6.5, 3-38 = 9.5         | 03/28/2007 – 03/17/2008 |

Table 2: Main result values of the ordination techniques Redundancy (RDA) and Principal Component (PCA) analyses performed with the software Package Canoco 5 (ter Braak and Smilauer, 2012; Smilauer and Leps, 2014).

| Analysis | Method | Analysed Parameters | Length of gradient | Eigenvalue Axis 1 (%) | Eigenvalue Axis 2 (%) | Eigenvalue Axis 3 (%) | Eigenvalue Axis 4 (%) | P-value |
|----------|--------|---------------------|--------------------|----------------------|----------------------|----------------------|----------------------|---------|
| 1        | RDA    | Fluxes of microorganisms and bulk parameters, environmental parameters | 1.8                | 34.5                 | 10.7                 | 4.7                  | 2.1                  | 0.002   |
| 2        | PCA    | microorganisms      | 1.4                | 26.3                 | 16.2                 | 9.8                  | 6.9                  |         |
Table 3: Species composition of the groups of (a) diatoms, (b) coccolithophores, (c) calcareous and (d) organic dinoflagellate cysts, (e) planktonic foraminifera and (f) pteropods at Site CBeu between June 2003 and March 2008.

| Diatoms                      | References                          |
|------------------------------|-------------------------------------|
| 1) Benthic                   |                                     |
| Actinoptychus spp.           | Round et al. (1990)                 |
| Amphora spp.                 |                                     |
| Cocconeis spp.               |                                     |
| Cymatosira belgica           |                                     |
| Delphineis surirella         |                                     |
| Grammatophora marina         |                                     |
| Licmophora sp.               |                                     |
| Odontella mobilensis         |                                     |
| Psammodyction panduriformis  |                                     |
| Tabularia spp.               |                                     |
| 2) Coastal upwelling         |                                     |
| Resting spores of:           | Hasle and Syvertsen (1996)          |
| Chaetoceros affinis          |                                     |
| Chaetoceros cinctus          |                                     |
| Chaetoceros compressus       |                                     |
| Chaetoceros constrictus      |                                     |
| Chaetoceros coronatus        |                                     |
| Chaetoceros debilis          |                                     |
| Chaetoceros diadema          |                                     |
| Chaetoceros radicans         |                                     |
| 3) Coastal planktonic        | Crosta et al. (2012), Romero et al. |
| Actinocyclus curvatulus      | (2009, 2012, 2016, 2017),           |
| Actinocyclus octonarius      | Romero and Armand (2010)            |
| Actinocyclus subtilis        |                                     |
| Chaetoceros concavicornis (vegetative cell, VC) |                                     |
| Chaetoceros lorenzianus (VC) |                                     |
| Chaetoceros pseudobrevis (VC)|                                     |
| Coscinodiscus argus          |                                     |
| Coscinodiscus decrescens     |                                     |
| Coscinodiscus radiatus       |                                     |
| Cyclotella litoralis         |                                     |
| Skeletonema costatum         |                                     |
| Thalassionema nitzschioides var. capitulata |                     |
| Thalassiosira angulata       |                                     |
| Thalassiosira conferta       |                                     |
| Thalassiosira oestrupii var. vennckae |                           |
| Thalassiosira poro-irregulata|                                     |
| 4) Open-ocean                |                                     |
| Asteromphalus flabellatus    | Hasle and Syvertsen (1996),         |
| Asteromphalus sarcophagus    | Romero et al. (2005), Crosta et al.|
| Azpetia neocrenulata         | (2012)                              |
| Azpetia nodulifera           |                                     |
| Azpetia tabularis            |                                     |
| Detonula pumila              |                                     |
| Dytilum brightwellii         |                                     |
| Fragilariaopsis doliolus     |                                     |
| Hemilaus hauckii             |                                     |
| Hemidiscus membranaceus      |                                     |
| Leptocylindrus mediterraneus |                                     |
| Neodelphineis dentica        |                                     |
| Nitzschia bicapitata         |                                     |
| Nitzschia capuluspalae       |                                     |
| Nitzschia interruptestriata  |                                     |
| Nitzschia sicula             |                                     |
Plankton variability off Mauritania

Planktoniella sol
Pseudo-nitzschia inflata var. capitata
Pseudo-nitzschia pungens
Pseudo-nitzschia subfraudulenta
Pseudosolenia calcar-avis
Pseudotriceratium punctatum
Rhizosolenia acuminata
Rhizosolenia bergonii
Rhizosolenia imbricatae
Rhizosolenia setigera
Roperia tesselata
Stellarina stellaris
Thalassionema bacillare
Thalassionema frauenfeldii
Thalassionema nitzschioides var. capitulata
Thalassionema nitzschioides var. inflata
Thalassionema nitzschioides var. parva
Thalassiosira eccentrica
Thalassionema endoseriata
Thalassiosira ferelineata
Thalassiosira lineata
Thalassiosira nanolineata
Thalassiosira oestrupii var. oestrupii
Thalassiosira sacketii var. sacketii
Thalassiosira sacketii var. plana
Thalassiosira subtulis
Thalassiosira symmetrica

Coccolithophores

1) Cosmopolitan
   Emiliania huxleyi
   Gephyrocapsa oceanica

2) Lower photic zone
   Algoirosphaera robusta
   Calciosolenia murrayi
   Florisphaera profunda
   Gladiolithus flabellatus
   Hayaster perplexus

3) Warm oligotrophic surface waters
   Discosphaera tubifera
   Helicosphaera carteri
   Rhadospiochaera xiphos
   Umbellosphaera irregularis
   Umbellosphaera tenuis
   Umbilicosphaera anulus
   Umbilicosphaera sibogae

4) Other miscellaneous species
   Acanthoica quattrospina
   Calcidiscus leptoporus
   Calcidiscus leptoporus small
   Calcidiscus quadriperforatus
   Gephyrocapsa ericsonii
   Gephyrocapsa muellerae
   Ophiaster hydroideus
   Ophiaster hydroideus
   Rhadospiochaera stylifer
   Syracosphaera anthos
   Syracosphaera pulchra

Calcareous dinoflagellates cysts

1) Upwelling
   Calciodinellum operosum

Boeckel and Baumann (2008),
Baumann and Boeckel (2013),
Poulton et al. (2017), Young et al. (2019)

Calciodinellum operosum
Siggelkow et al. (2002); Richter et al. (2007); Kohn and
### Plankton variability off Mauritania

| Species                                      | Source               |
|----------------------------------------------|----------------------|
| *Scrippsiella trochoidea*                    | Zonneveld (2010)     |

#### 2) Warm waters

- *Calciodinellum albatrosianum*

#### 3) Mineral input

- *Leonella granifera*

#### 4) Cosmopolitan

- *Thoracosphaera heimii*

#### 5) Others

- *Calciodinellum levantinum*
- *Melodemuncula berlinensis*
- *Pernambugia tuberosa*
- *Scrippsiella lacrymosa*
- *Scrippsiella regalis*
- *Scrippsiella trifida*

### Organic dinoflagellates cysts

#### 1) Upwelling

- *Echinidinium aculeatum*
- *Echinidinium granulatum*
- *Echinidinium transparantum*
- *Echinidinium zonneveldii*
- *Ecgginidinium spp.*
- cyst of *Protoperidinium americanum*
- cyst of *Protoperidinium monospinum*
- *Stelladinium stellatum*

#### 2) Upwelling relaxation

- *Lingulodinium machaerophorum*
- cyst of *Polykrikos schwarzii*
- cyst of *Polykrikos kofoidii*

#### 3) Potential toxic

- cysts of *Gymnodinium spp.*

#### 4) Cosmopolitan

- *Brigantedinium spp.*
- *Spiniferites* species
- *Impagidinium* species

### Planktonic Foraminifera

#### 1) Warmer waters

- *Globigerinoides ruber* (pink and white)
- *Globigerinoides sacculifer*

#### 2) Cooler waters

- *Globorotalia inflata*
- *Neogloboquadrina incompta*

#### 3) Upwelling

- *Globigerina bulloides*

#### 4) Additional secondary species

- *Beella digitata* (Brady 1879)
- *Globigerinella calida* (Parker 1962)
- *Globigerinella siphonifera* (d’Orbigny 1839)
- *Globorotalia crassaformis* (Galloway and Wissler 1927)
- *Globorotalia menardii* (Parker, Jones and Brady 1865)
- *Globorotalia scitula* (Brady 1882)
- *Globorotalia truncatulinoides* (d’Orbigny 1839)
- *Neogloboquadrina dutertrei* (d’Orbigny 1839)
- *Orbulina universa* (d’Orbigny 1839)
- *Pulleniatina obliquiloculata* (Parker and Jones 1865)

### Pteropods

- *Heliconoides inflatus* (d’Orbigny 1835)
- *Limacina bulimoides* (d’Orbigny 1835)