



Variability of phyto- and zooplankton communities

in the Mauritanian coastal upwelling between 2003 and 2008

Oscar E. Romero¹, Karl-Heinz Baumann^{1,2}, Karin A. F. Zonneveld¹, Barbara Donner¹, Jens Hefter³,
Bambaye Hamady⁴ and Gerhard Fischer^{1,2}

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 Mauretaniien 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 CB_{eu} (*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
32 seasonal groups' contribution. Species of planktonic foraminifera, diatom, and organic
dinoflagellate cysts typical of coastal upwelling as well as cooler water planktonic foraminifera and
34 the coccolithophore *Gephyrocapsa oceanica* are abundant at times of intense upwelling (late
winter through early summer). Planktonic foraminifera and calcareous dinoflagellate cysts
36 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
38 zone, together with *Emiliana 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
42 diatom assemblage during main upwelling season. Additional evidence for a change in population
dynamics are the short dominance of the coccolithophore *Umbilicosphaera annulus*, the
44 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
46 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
48 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
50 community.

52 1. Introduction

A way to obtain insights into the impact of climate variability on marine ecosystems is
54 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
56 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



Plankton variability off Mauritania

58 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
60 a few species (e.g., Schlüter et al., 2012; Rembauville et al., 2016).

Eastern Boundary Upwelling Ecosystems (EBUEs) are among the most important marine
62 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
64 (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
66 pump, as together with other continental margins may be responsible for more than 40% of the
CO₂ ocean sequestration (Muller-Karger et al., 2005). As EBUEs are highly dynamic with large
68 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
70 current global climate change.

One of the EBUEs that have been thoroughly studied over the past three decades is the coastal
72 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
74 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;
76 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
78 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
80 dynamics of primary and secondary producers communities in surface waters along the
Mauritanian coast. In this ecosystem, several long-term, continuous, sediment trap-based
82 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.,
84 1996, 2009, 2016, 2019; Bory et al., 2001; Marcello et al., 2011; Skonieczny et al., 2013), particular
groups of microorganisms (Lange et al. 1998; Romero et al., 1999, 2002, 2003; Köbrich and
86 Baumann, 2008; Romero and Armand, 2010; Zonneveld et al., 2010; Köbrich et al., 2016; Romero



Plankton variability off Mauritania

and Fischer, 2017; Guerreiro et al., 2019) or sea-surface temperature (Müller and Fischer, 2001;
88 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
90 experiments has not been performed in this region and is rare in other EBUEs or other ocean
areas as well.

92 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
94 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
96 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
98 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,
100 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
102 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.,
104 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
106 secondary producer plankton community off Mauritania. The simultaneous assessment of fluxes of
several microorganism groups collected over long intervals provides substantial information about
108 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
110 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.



114 **2. Oceanographic setting of the study area**

115 The CC-EBUE is located in the eastern part of the North Atlantic Subtropical Gyre (Fig. 1;
116 Arístegui 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,
118 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
120 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
122 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
124 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).

126 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
128 (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
130 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
132 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
134 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
136 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
138 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
140 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-
142 driven offshore divergence (Pelegrí et al., 2017). North of Cape Blanc (ca. 21°N), the intense



Plankton variability off Mauritania

northeasterly winds cause the coastal upwelling to move further offshore and the upper slope is
144 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
146 Timiris (ca. 19°30'N), the PUC intensifies during summer-fall and remains at the subsurface during
winter–spring (Pelegrí et al., 2017). The encountering of the northward flowing MC-PUC system
148 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
150 filament (Gabric, 1993; Pelegrí et al., 2006; Pelegrí 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
152 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,
154 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
156 particulate coastal 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
158 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
160 strongly advected by lateral transport (Fischer and Karakaş, 2009; Karakaş et al., 2006, Fischer et
al., 2009).

162 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
164 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
166 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
168 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
170 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



Plankton variability off Mauritania

172 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.,
174 1991).

176 **3. Material and Methods**

3.1. Moorings, sediment traps and fluxes

178 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
180 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)
182 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
184 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
186 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
188 100 ml of filtered seawater. Pure NaCl was used to increase the density in the sampling cups up to
40 ‰. Upon recovery, samples were stored at 4°C and wet-split in the MARUM sediment trap
190 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
192 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
194 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.

196 Using ¼ or 1/5 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
198 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
200 (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
202 than 0.1% ($\pm 1\sigma$). 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
204 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).

206 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
208 between ± 0.2 and $\pm 0.4\%$, 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.

210 **3.2. Assessment of organism fluxes and species identification**

3.2.1. Diatoms

212 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
214 sediment trap samples were processed. Each split was treated with potassium permanganate,
hydrogen peroxide, and concentrated hydrochloric acid following previously used methodology
216 (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
218 *Zeiss*® Axioscop with phase-contrast illumination (MARUM, Bremen). The counting procedure and
definition of counting units follows Schrader and Gersonde (1978). Depending on valve
220 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
222 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
224 taxa (absolute and relative) as well as daily fluxes of valves per $\text{m}^{-2} \text{d}^{-1}$, calculated according to
Sancetta & Calvert (1988).

226 **3.2.2. Coccolithophores**

Aliquots of each sample were 1/125 of the <1 mm fraction. Depending on the total flux, samples
228 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, 0.45 μm



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
232 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
234 500 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
238 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
240 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
242 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
244 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
246 microscopy (Axiovert, x400 magnification). Taxonomy of organic walled dinoflagellate cysts is
according to Zonneveld and Pospelova (2015), taxonomy of calcareous dinoflagellate cysts is
248 according to Vink et al. (2002) and Elbrächter et al. (2008)

3.2.4. Planktonic foraminifera and pteropods

250 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
252 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.
254 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
256 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
258 were identified and classified according to Hemleben et al. (1989) and Schiebel and Hemleben



Plankton variability off Mauritania

(2017). Out of 15 species of planktonic foraminifers identified, only six species were used as
260 environmental indicators.

3.2.5. Alkenones

262 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
264 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).

266 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
268 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
270 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
272 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
274 (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
276 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
278 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
280 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
282 sample composed of known compounds. Peak areas were determined by integrating the
respective peaks.

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

$$U_{37}^{K'} = \frac{C_{37:2}}{C_{37:2} + C_{37:3}}$$



286 and converted to SST using the global surface water calibration from Conte et al. (2006):

$$\text{SST} = \frac{U_{37}^K - 0.0709}{0.0322}$$

3.3. Environmental physical parameters

288 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
290 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
292 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.

294 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
296 intervals in a 4km² block 200m 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
298 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 Mauretaniien de Recherches
300 Océanographiques et des Pêches, Nouadhibou, Mauritania). For statistical analyses, the means of
daily values during the trap sampling intervals were calculated.

302 3.4. Multivariate analyses

The ordination techniques Principal Component (PCA) and Redundancy (RDA) analyses have
304 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
306 (diatoms, coccolithophores, organic-walled dinoflagellate cysts, calcareous dinoflagellate cysts,
planktonic foraminifera and pteropods) and bulk components as well as the environmental
308 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
310 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
312 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

314 according to formula 1:

$$nFl_i = (Fl_{i,y} / Fl_i \text{ max}) \times 1000n$$

316 Fl_i = normalized flux of species group i

$Fl_{i,y}$ = flux of species group i in sample y

318 $Fl_i \text{ max}$ = maximal flux observed in species group i

To better understand the relationship within the individual organism groups, a PCA has been
320 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:

$$nFl_j = (Fl_{j,y} / Fl_j \text{ max}) \times 1000n$$

Fl_j = normalized accumulation rate of ecological entity j in species group i

324 $Fl_{j,y}$ = accumulation rate of ecological entity j in sample y
 $Fl_j \text{ max}$ = maximal accumulation
rate observed in species group i

326 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
328 been excluded from the analysis and the $Fl_j \text{ max}$ in this group is determined by excluding this
outlier.

330

4. Results

332 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
334 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%,
336 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
338 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
340 Mollenhauer et al. (2015; Table 1) in combination with fluxes of the lipid fraction and SST



Plankton variability off Mauritania

reconstructions. The SST record is extended with new alkenone data until March 2008 (CBeu
342 deployment 5, Table 1).

The fluxes of total mass, CaCO₃, TOC, BSi and lithogenics show major peaks in winter and
344 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
346 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
348 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).

350 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
352 and pteropods by a factor of four to five. Highest coccoliths and diatom fluxes reach 4.2×10^9
coccoliths m⁻² d⁻¹, and 1.2×10^8 valves m⁻² d⁻¹, respectively. Maximal fluxes of organic-walled
354 dinoflagellates reach up to 7.1×10^4 cysts m⁻² d⁻¹, and of planktonic foraminifera 0.9×10^4 shells
m⁻² d⁻¹, and 1.1×10^4 pteropods shells m⁻² d⁻¹.

356 Each group of organisms shows large seasonal and interannual variabilities. Diatoms had their
maximal flux in fall/winter 2005 and spring/summer 2006 (Fig. 3a). Coccolithophores had their
358 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
360 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
362 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
364 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
366 (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).

368 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
370 220 identified species. Table 3 presents the species-specific composition of groups depicted in Fig.
4.

372 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
374 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
376 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
378 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
380 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
382 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).

384 **Coccolithophores** are consistently dominated by *Emiliana huxleyi* and *Gephyrocapsa*
oceanica, whose contribution is always higher 50% of the community throughout the sampling
386 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
388 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
390 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
392 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.

394 **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
396 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



398 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
400 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.
402 Whereas upwelling species are most abundant in spring and fall, warm water and mineral
indicators are more abundant in fall/winter (Fig. 4).

404 **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
406 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
408 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
410 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
412 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
414 observed for many other groups.

The distribution and abundance of **planktonic foraminifera** species is linked to surface-water
416 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*
418 *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
420 (*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
422 taxa are almost absent.

As large secondary carbonate producers off Mauritania, **pteropods** are important contributors
424 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
426 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
428 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
430 uncoiled pteropods. However, another occurrence of *L. bulimoides* is missing in winter 2007/2008.

4.3. Statistical analyses

432 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,
434 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,
436 respectively (Table 2).

All microorganism groups are ordinated at the positive part of the first axis showing a positive
438 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
440 CaCO₃ (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
442 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
444 column. Diatoms, coccolithophores, organic dinoflagellates and planktonic foraminifera also show
a positive correlation with SSTA, implying that enhanced fluxes of these microorganisms occur
446 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
448 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
450 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
452 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.
454 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

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

- Ordinated at the positive side of the second axis and central part of the first axis, group 3
462 assembles planktonic foraminifera mainly thriving in warm waters (For-warm), calcareous
dinoflagellates characteristic of warm water conditions and those responding to mineral
464 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
466 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-
468 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).

470

5. Discussion

472 5.1. Relationship between microorganisms fluxes at site CBeu and the physical and biogeochemical settings off Mauritania

474 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
476 changes in upper water oceanographic conditions off Mauritania between June 2003 and March
2008. Fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic
478 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
480 simultaneous occurrence of intense upwelling off Mauritania and high microorganisms fluxes and
production at site CBeu. Several previous studies have separately documented enhanced
482 production of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic
foraminifera occurring when the nutrient concentration in the uppermost water column off
484 Mauritania increases (Baumann et al., 2005; Zonneveld et al., 2012; Guerreiro et al., 2017;



Romero and Fischer, 2017; Pospelova et al., 2018; Jiménez-Quiroz et al., 2019).

486 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.
488 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
490 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
492 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
494 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
496 (increasing SSTA in late winter and throughout the spring season). Throughout the period
investigated, this SST cyclicity remains fairly constant.

498 Fluxes of total mass and biogenic bulk components (TOC, BSi, CaCO₃) are clearly seasonal in
nature (Fig. 3 a-d; Fischer et al., 2019) and reflect the temporal productivity pattern of the
500 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
502 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 CaCO₃ over
504 BSi (Fig. 2b, d) support the scenario of calcareous primary and secondary producers
(coccolithophores, foraminifera and pteropods) dominating the plankton community in the
506 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).

508 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.
510 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
512 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



514 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
516 (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
518 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
520 aggregates' abundance and sinking velocities increase toward deeper waters when aggregates
are ballasted with lithogenic particles, whereas aggregates are not able to scavenge lithogenic
522 material from deeper waters (van der Jagt et al., 2018).

A remarkable finding of our multiannual trap experiment is that flux maxima of diatoms,
524 coccolithophores, organic-walled dinoflagellate (all primary producers) and planktonic foraminifera
(secondary producers) seem to occur fairly simultaneously (Figs. 3, 5). We propose three possible
526 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),
528 (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
530 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
532 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
534 succession of major groups (e.g., diatoms quickly reacting to increasing nutrient availability,
whereas photosynthetic dinoflagellates becoming more abundant during upwelling relaxation,
536 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
538 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
540 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 km² (Siegel and
542 Deuser, 1997, Fischer et al., 2016,) due to (i) differential settling velocities of particles (Fischer and



Plankton variability off Mauritania

Karakaş, 2009; Iversen et al., 2010, van der Jagt et al., 2018), and (ii) highly heterogeneous and
544 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
546 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).

548 **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
550 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
552 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
554 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
556 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
558 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
560 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
562 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 has been
564 separately presented in previous biogeographical/ecological studies (Romero et al., 2002; Kucera,
2007; Köbrich et al., 2008, 2016; Zonneveld et al., 2013; Romero and Fischer, 2017).

566 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
568 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
570 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



Plankton variability off Mauritania

572 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
574 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
576 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
578 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
580 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
582 assemblage composition of planktonic foraminifera (Kucera, 2007). Large, symbiont-bearing
specialists like *Globigerinoides ruber* and *G. sacculifer* are adapted to more oligotrophic and
584 warmer waters. They show their maximum abundance in warm waters with a deeper mixed-layer
depth (Fig. 7e,f).

586 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
588 producers. These populations dominate the plankton community during intervals of weakened
upwelling, shallow MLD and predominantly oligotrophic water conditions. Similar to group 3, group
590 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
592 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
594 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
596 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*
598 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



600 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
602 group species at site CBeu, were observed between late 2004 and late 2006 (Fig. 7f-j). We identify
three main shift stages in the species-specific composition of assemblages:

- 604 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
606 accompanied by (iii) a significant decrease in SST as reconstructed with $U_{37}^{K'}_t$ (Fig. 7d).
- 608 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).
- 610 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
612 occurrence and highest relative abundance of *L. bulimoides* (fall 2006/winter 2007, Fig.
7h).

614 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
616 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
618 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
620 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 $U_{37}^{K'}_t$ -based temperature
622 (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
624 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
626 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
628 other plankton groups show lowest fluxes toward late summer. Neither the seasonal pattern nor



Plankton variability off Mauritania

the MLD show any significant change nor unusual high fluxes of lithogenic occurred (Fig. 2e, 7e).

630 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 CaCO₃ for the studied
632 interval.

The extraordinary high relative abundance of *U. anulus* in fall 2005 has not yet been observed
634 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
636 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
638 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
640 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
642 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
644 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.*
646 *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.
648 *Heliconoides inflatus* is known as a rather cosmopolitan species, occurring across a wide range of
oceanic provinces (Bé and Gilmer, 1977; Burrige et al., 2017), whereas *L. bulimoides* seems to
650 prefer waters of subtropical gyres (although it was also present in low numbers in the equatorial
region, Burrige et al., 2017). A stronger transport of the MC from the south may have led to the
652 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
654 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'
656 temperatures from early 2005 on allowed the reappearance of warm-water planktonic foraminifera
in fall 2005 (Fig. 7f).



658 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
660 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
662 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;
664 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
666 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
668 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.
670 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
672 the CC-EBUE around Cape Blanc, the depocenter with up to 3% of organic carbon has a depth
range between 1,000 and 2,000m (Fischer et al., 2019).

674 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
676 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
678 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
680 cyst increased during late fall 2006 (Fig. 7j). 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
682 fully disregard 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
684 to the natural long-term variability due to external forcings (e.g., North Atlantic Oscillation) or due to
on-going climate change.

686 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
688 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-
690 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
692 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
694 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.

696

6. Conclusions

- 698 - 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
700 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
702 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
704 upwelling relaxation (late summer through late fall).
- The good temporal match between maxima of (most of) studied microorganism groups and
706 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
708 lithogenics 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
710 eolian-transported nutrient deposition.
- 1,900 days of continuous trap record of microorganism fluxes let recognizing a general
712 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
714 particular species or group of species.



Plankton variability off Mauritania

716 - 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
718 2005/early 2006, and after fall 2006. Although most of the populations return 'to normal' after fall
2006, a few did not.

720 - 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
722 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
724 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
726 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.

728

Code and Data Availability

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

732 Author Contributions

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

736 Competing Interests

The authors declare that they have no conflict of interest.

738

Acknowledgements

740 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,
742 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



744 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
746 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
748 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”
750 (University of Bremen, Bremen, Germany).

752 **References**

- Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M. T. G., Slotte, A.,
754 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.*,
756 133, 88-102, 2014.
- Aristegui, J., Barton, E.C., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S.,
758 Hernández-León, S., Mason, E., Machú, E., Demarcq, H.: Sub-regional ecosystem variability in
the Canary Current upwelling, *Prog. Oceanogr.*, 83, 33–48, 2009.
- 760 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.
- 762 Baumann, K.-H., Freitag, T.: Pleistocene fluctuations in the Benguela Current system as revealed
by coccolith assemblages, *Mar. Micropaleontol.*, 52, 195-215, 2004.
- 764 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
766 paleoproductivity: a review, *Paläontolog. Zeitschr.*, 79/1, 93-112, 2005.
- Baumann, K.-H., Boeckel, B.: Spatial distribution of living coccolithophores in the southwestern
768 Gulf of Mexico. *J. Micropaleontol.*, 32, 123-133, 2013.
- Baumann, K.-H., Saavedra-Pellitero, M., Böckel, B., Ott, C.: Morphometry, biogeography and
770 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

- 772 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,
774 733–808, 1977.
- Böckel, B., Baumann, K.-H.: Vertical and lateral variations in coccolithophore community structure
776 across the subtropical frontal zone in the South Atlantic Ocean, *Mar. Micropaleontol.*, 67, 255-
273, 2008.
- 778 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
780 different productivity regimes off the Mauritanian upwelling zone (EUMELI program), *Deep-Sea
Res. I*, 48, 2251-2282, 2001.
- 782 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,
784 freshwater 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.,
786 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-
788 416, 2007.
- Burridge, A. K., Goetze, E., Wall-Palmer, D., Le Double, S. L., Huisman, J., Peijnenburg, K. T. C.
790 A.: Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the
Atlantic Ocean, *Prog. Oceanogr.*, 158, 213-223, 2017.
- 792 Chavez, F. P., Messié, M.: A comparison of Eastern Boundary Upwelling Ecosystems, *Prog.
Oceanogr.*, 83, 80-96, 2009.
- 794 Conte, M. H., Thompson, A., Egrinton, G., Green, J. C.: Lipid biomarker diversity in the
coccolithophorid *Emiliana huxleyi* (Prymnesiophyceae) and the related species *Gephyrocapsa*
796 *oceanica*, *J. Phycol.*, 31, 272–282, 1995.
- Conte, M. H., Sicre, M., Rühlemann, C., Weber, J. C., Schulte, S., Schulz-Bull, D., Blanz, T.:
798 Global temperature calibration of the alkenone unsaturation index (UK'37) in surface waters and
comparison with surface sediments, *Geochem. Geophys. Geosy.*, 7(2),
800 <https://doi.org/10.1029/2005GC001054>, 2006.



Plankton variability off Mauritania

- 802 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.
- 804 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.
- 806 Elbrächter, M., Gottschling, M., Hildebrand-Habel, T., Keupp, H., Kohring, R., Lewis, J., Meier, K.
J. S., Montresor, M., Streng, M., Versteegh, G.J.M., Willems, H., Zonneveld, K., Establishing an
agenda for calcareous dinoflagellate research (Thoracosphaeraceae, Dinophyceae) including a
808 nomenclatural synopsis of generic names, *Taxon*, 57, 1289-1303, 2008.
- 810 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.
812 pone.0151699, 2016.
- 814 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.
- 816 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 $\delta^{18}\text{O}$ -deduced sea-surface
818 temperatures and trade winds, *J. Mar. Res.*, 54, 73–98, 1996.
- 820 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.
- 822 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*,
824 13, 3071-3090, 2016.
- 826 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
828 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

- 830 changes in present-day Saharan dust collected in and off Mauritania, *Atmos. Chem. Phys.*, 17,
10163-10193, 2017.
- 832 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
834 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
836 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.
- 838 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
840 of the Amazon river and of Saharan dust deposition, *Biogeosciences*, 14, 4577-4599,
<https://doi.org/10.5194/bg-14-4577-2017>, 2017.
- 842 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.*,
844 176, <https://doi.org/10.1016/j.pocean.2019.102140>, 2019.
- Hagen, E.: Northwest African upwelling scenario, *Oceanol. Acta*, 24 (Supplement), S113-S128,
846 2001.
- Hardy, W., Marret, F., Penaud, A., le Mézo, P., Droz, L., Marsset, T., Kageyama, M.: Quantification
848 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.
850 2018.
- Hasle, G. A., Syvertsen, E. E.: Marine diatoms, in: Identifying marine diatoms and dinoflagellates,
852 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
854 biochemical and elemental compositions of marine plankton: A NMR perspective, *Mar. Chem.*,
78, 47-63, 2002.
- 856 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,
858 [doi:10.1029/2004GB002265](https://doi.org/10.1029/2004GB002265), 2005.



Plankton variability off Mauritania

- 860 Hemleben, C., Spindler, C., Anderson, O. R.: Modern Planktonic Foraminifera, pp. 363, New York
(Springer), 1989.
- 862 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.
- 864 Inthorn, M., Wagner, T., Scheeder, G., Zabel, M.: Lateral transport controls distribution, quality,
and burial of organic matter along continental slopes in high-productivity areas, *Geology*, 34,
866 205-208, doi: 210.1130/G22153.22151, 2006.
- Iversen, M. H., Nowald, N., Ploug, H., Jackson, G. A., Fischer, G.: High resolution profiles of
868 vertical particulate organic matter export off Cape Blanc, Mauritania: Degradation processes
and ballasting effects, *Deep-Sea Res. I*, 57, 771-784, 2010.
- 870 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-
872 2624, 2010.
- IOC-UNESCO TS129 IGMETS: What are Marine Ecological Time Series telling us about the
874 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.,
876 García-Romaro, F. d. J., Hernández-Trujillo, S., Hernández-Becerril, D. U., González-Armas, L.
V., Martell-Dubois, R., Cerdeira-Estrada, S., Fernández-Mémdez, J., González-Ania, L. V.,
878 Vásquez-Ortiz, M., Barrón-Barraza, F. J.: Impact of "The Blob" and "El Niño" in the SW Baja
California Peninsula: Plankton and environmental variability of Bahía Magdalena, *Front. Mar.*
880 *Sci.*, 6, 1-23, 2019.
- Jordan, R. W., Zhao, M., Eglinton, G., Weaver, P. P. E.: Coccolith and alkenone stratigraphy and
882 palaeoceanography at an upwelling site off NW Africa (ODP 658C) during the last 130,000
years, in: *Microfossils and oceanic environments*, edited by Mokuilevsky, A., Whatley, R.,
884 University of Wales, Aberystwyth Press, London, pp. 111–130, 1996.
- Karakaş, G., Nowald, N., Blaas, M., Marchesiello, P., Frickenhaus, S., Schlitzer, R.: High-
886 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

- 888 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.
890 Oceanogr., 83, 331-341, 2009.
- Köbrich, M. I., Baumann, K.-H.: Coccolithophore flux in a sediment trap off Cape Blanc (NW
892 Africa), J. Nannopl., 30, 2, 83-96, 2008.
- Köbrich, M. I., Baumann, K.-H., Fischer, G.: Seasonal and inter-annual dynamics of
894 coccolithophore fluxes from the upwelling region off Cape Blanc, Northwest Africa, J.
Micropaleontol, doi:10.1144/jmpaleo2014-024, 2016.
- 896 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,
898 2010.
- Kremling, K., Lentz, U., Zeitzschell, B., Schulz-Bull, D. E., Duinker, J. C.: New type of time-series
900 sediment trap for the reliable collection of inorganic and organic trace chemical substances,
Rev. Sci. Instrument., 67, 4360–4363, 1996.
- 902 Kucera, M.: Planktonic foraminifera as tracers of past oceanic environments: in, Developments in
Marine Geology, Volume 1, Proxies in Late Cenozoic Paleoceanography, edited by Hillaire–
904 Marcel, C., De Vernal, A., Elsevier, Amsterdam, 213-262, 2007.
- Lange, C. B., Romero, O. E., Wefer, G., Gabric, A. J.: Offshore influence of coastal upwelling off
906 Mauritania, NW Africa, as recorded by diatoms in sediment traps at 2195 m water depth, Deep-
Sea Res. I, 45, 985-1013, 1998.
- 908 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,
910 doi:10.1029/2007/JC004433, 2008.
- Marcello, J., Hernández-Guerra, A., Eugenio, F., Fonte, A.: Seasonal and temporal study of the
912 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.
- 914 McKay, C. L., Filipsson, H. L., Romero, O. E., Stuetz, J.-B. W., Donner, B.: Pelagic-benthic coupling
within an upwelling system of the subtropical northeast Atlantic over the last 35 ka BP., Quat.
916 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
918 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.
- 920 Mittelstaedt, E.: The upwelling area off Northwest Africa - a description of phenomena related to
coastal upwelling, *Prog. Oceanogr.*, 12, 307-331, 1983.
- 922 Mittelstaedt, E.: The ocean boundary along the northwest African coast: Circulation and
oceanographic properties at the sea surface, *Prog. Oceanogr.*, 26, 307-355, 1991.
- 924 Mollenhauer, G., Basse, A., Kim, J.-H., Sinninghe Damsté, J. S., Fischer, G.: A four-year record of
U^K₃₇ - and TEX₈₆-derived sea surface temperature estimates from sinking particles in the
926 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
928 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
930 Cape Blanc, NW Africa, and a comparison with distributions in underlying sediments, *Deep-Sea*
Res. I, 48, 1877-1903, 2001.
- 932 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. Res. Lett.*, 32, L01602,
934 doi:10.1029/2004GL021346, 021341_021341-021341_021344, 2005.
- Nicholson, S. E.: The West African Sahel. A review of recent studies on the rainfall regime and its
936 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
938 properties and sediment trap fluxes in the coastal upwelling filament off Cape Blanc, Mauritania,
Prog. Oceanogr., 137, 1-11, 2014.
- 940 Pauly, D., Christensen, V.: Primary production required to sustain global fisheries, *Nature*, 374,
255-257, 1995.
- 942 Pelegrí, J. L., Marrero-Díaz, A., Ratsimandresy, A. W.: Nutrient irrigation of the North Atlantic,
Prog. Oceanogr., 70, 366-406, 2006.
- 944 Pelegrí, 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
950 sediment trap studies, *Palynology*, 42, 1, 162-182, 2018.
- Poulton, A. J., Holligan, P. M., Charalampopoulou, A., Adey, T. R.: Coccolithophore ecology in the
952 tropical and subtropical Atlantic Ocean: New perspectives from the Atlantic meridional transect
(AMT) Programme, *Progr. Oceanogr.*, 158, 150-170, 2017.
- 954 Prah, 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.: Nepheloid structure and hydrographic control on the Barcelona continental
margin, northwestern Mediterranean, *Mar. Geol.*, 149, 39–54, 1998.
- 958 Rembauville, M., Meilland, 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*
960 *Res. I*, 111, 91–101, <https://doi.org/10.1016/j.dsr.2016.02.017>, 2016.
- Richter, D., Vink, A., Zonneveld, K. A. F., Kuhlman, H., Willems, H.: Calcareous dinoflagellate cyst
962 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, e0121392, 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:
968 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,
970 Heidelberg, 365-392, 1999.
- Romero, O. E., Lange, C.B., Wefer, G.: Interannual variability (1988-1991) of siliceous
972 phytoplankton fluxes off northwest Africa, *J. Plank. Res.*, 24, 10, 1035-1046,
doi:10.1093/plankt/1024.1010.1035, 2002.
- 974 Romero, O. E., Dupont, L., Wyputta, U., Jahns, S., Wefer, G.: Temporal variability of fluxes of



Plankton variability off Mauritania

- 976 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.
- 978 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. Palaeocl.*,
980 223, 49-65, 2005
- Romero, O. E., Kim, J., Donner, B.: Submillennial-to-millennial variability of diatom production off
982 Mauritania, NW Africa, during the last glacial cycle, *Paleoceanography*, 23, PA3218,
doi:10.1029/2008PA001601, 2008.
- 984 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.
- 986 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-
988 82, 2009b.
- Romero, O. E., Armand, L.K.: Marine diatoms as indicators of modern changes in oceanographic
990 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-
992 400, 2010.
- Romero, O. E., Crosta, X., Kim, J.-H., Pichevin, L., Crespin, J.: Rapid longitudinal migrations of the
994 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.
- 996 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.
- 998 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
1000 (2003 – 2010), *Prog. Oceanogr.*, 159, 31-44, 2017.
- Round, F. E., Crawford, R.M., Mann, D.G.: *The diatoms*, Cambridge University Press, Cambridge,
1002 pp. 747, 1990.



- 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.
- 1004
- 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.
- 1006
- Schiebel, R., Hemleben, C.: *Planktic Foraminifers in the Modern Ocean*, Springer-Verlag GmbH Berlin, Heidelberg, 2017.
- 1008
- 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., Brokman, M. J., Schrader, H., Gersonde, R., Drooger, M. M., Broekman, J. A, Utrecht Micropaleontological Bulletin, Utrecht, 17, 129-176, 1978.
- 1010
- 1012
- 1014
- 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.
- 1016
- Siggelkow, D., Vink, A., Willems, H.: Calcareous dinoflagellate cyst production, vertical transport and preservation off Cape Blanc during 1990: a sediment-trap study, *J. Nanoplankton Res.*, 24, 160, 2002.
- 1018
- 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.
- 1020
- 1022
- Smayda, T. J.: Ecological features of harmful algal blooms in coastal upwelling ecosystems, *African J. Mar. Sci.*, 219-253, 2010.
- 1024
- 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.
- 1026
- Smilauer, P., Leps, J.: *Multivariate analysis of ecological data using Canoco 5*, Cambridge University Press, Cambridge, 1-362, 2014.
- 1028



Plankton variability off Mauritania

- 1030 Steinmetz, J. C.: Calcareous nanoplankton biocoenosis: sediment trap studies in the Equatorial
Atlantic, Central Pacific, and Panama Basin, Woods Hole Oceanographic Institution, U.S.A., 1,
1032 1-85, 1991.
- Susek, E., Zonneveld, K. A. F., Fischer, G., Versteegh, G. J., Willems, H.: Organic-walled
1034 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.
- Trainer, V. L., Pitcher, G. C., Reguera, B., Smayda, T. J.: The distribution and impacts of harmful
1038 algal bloom species in eastern boundary upwelling systems, *Prog. Oceanogr.*, 85, 33-52, 2010.
- Van Camp, L., Nykjær, L., Mittelstaedt, E., Schlittenhardt, P.: Upwelling and boundary circulation
1040 off Northwest Africa as depicted by infrared and visible satellite observations, *Prog. Oceanogr.*,
26, 357–402, 1991.
- 1042 van der Jagt, H., Friese, C., Stuu, J., Fischer, G., Iversen, M.: The ballasting effect of Saharan
dust deposition on aggregate dynamics and carbon export: Aggregation, settling, and
1044 scavenging potential of marine snow, *Limnol. Oceanogr.*, 63, 1386-1394, 2018.
- Vink, A., Brune, A., Höll, C., Zonneveld, K. A. F., Willems, H.: On the response of calcareous
1046 dinoflagellates to oligotrophy and stratification of the upper water column in the equatorial
Atlantic Ocean, *Palaeogeogr., Palaeoecol.*, 178, 53-66, 2002.
- 1048 Vink, A.: Calcareous dinoflagellate cysts in South and equatorial Atlantic surface sediments:
diversity, distribution, ecology and potential for palaeoenvironmental reconstruction, *Mar.*
1050 *Micropaleontol.*, 50, 43-88, 2004.
- Weiser, J., Baumann, K.-H., Hahn, A., Zabel, M.: Late Holocene paleoceanographic changes off
1052 south-western Africa as inferred from nanofossil assemblages, *J. Nannoplankton Res.*, 36, 2,
161-171, 2016.
- 1054 WoRMS Editorial Board, <http://www.marinespecies.org>, 2017.
- Young, J., Geisen, M., Cross, L., Kleijne, A., Sprengel, C., Probert, I., Østergaard, J.: A guide to
1056 extant coccolithophore taxonomy, *J. Nannoplankton Res.*, Special Issue 1, International
Nannoplankton Association, 124 pp., 2003.
- 1058 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.

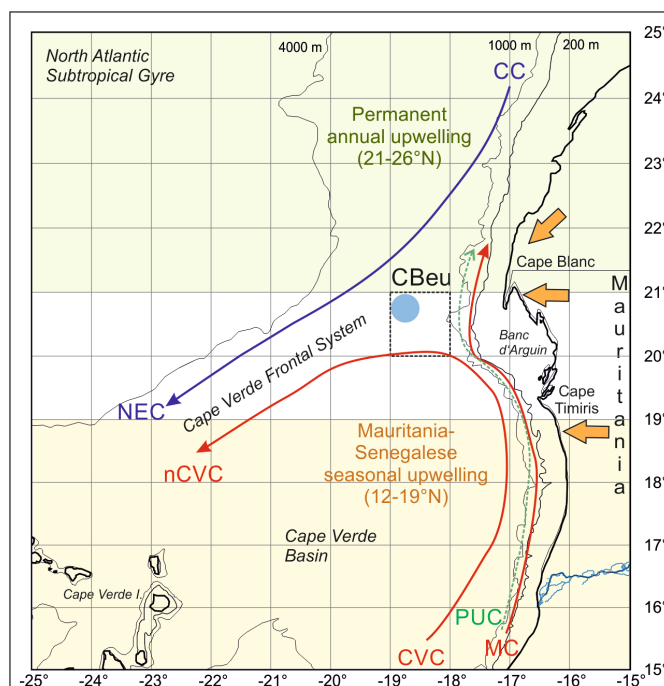
- 1060 Zeeberg, J., Corten, A., Tjoe-Awie, P., Coca, J., Hamady, B.: Climate modulates the effects
of *Sardinella aurita* fisheries off Northwest Africa, *Fish. Res.*, 89, 65–75, 2008.
- 1062 Zenk, W., Klein, B., Schröder, M.: Cape Verde Frontal Zone, *Deep-Sea Res.*, 38, Suppl. 1, S505–
S530, 1991.
- 1064 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,
1066 *J. Phycol.*, 46, 202-215, 2010.
- Zonneveld, K. A. F., Chen, L., Elshanawany, R., Fischer, H. W., Hoins, M., Ibrahim, M. I.,
1068 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
1070 centuries, *Mar. Pollut. Bull.*, 64, 114-132, 2012.
- Zonneveld, K. A. F., Marret, F., Versteegh, G. J. M., Bogus, K., Bonnet, S., Bouimetarhan, I.,
1072 Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K.,
Henry, M., Holzwarth, U., Kieft, J.-F., Kim, S.-Y., Ladouceur, S., Ledu, D., Chen, L., Limoges,
1074 A., Londeix, L., Lu, H., Mahmoud, M. S., Marino, G., Matsouka, K., Matthiessen, J., Mildenthal,
C., Mudie, P., Neil, L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F.,
1076 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,
1078 2013.
- Zonneveld, K. A. F., Pospelova, V.: A determination key for modern dinoflagellate cysts, *Palyno-*
1080 *logy*, 39, 387-409, 2015.
- Zonneveld, K. A. F., Ebersbach, F., Maeke, M., Versteegh, G.J.M.: Transport of organic-walled
1082 dinoflagellate cysts in nepheloid layers off Cape Blanc (N-W Africa), *Deep Sea Res. I*, 139,
55-67, 2018.

1084

1086



1088 **Figures**



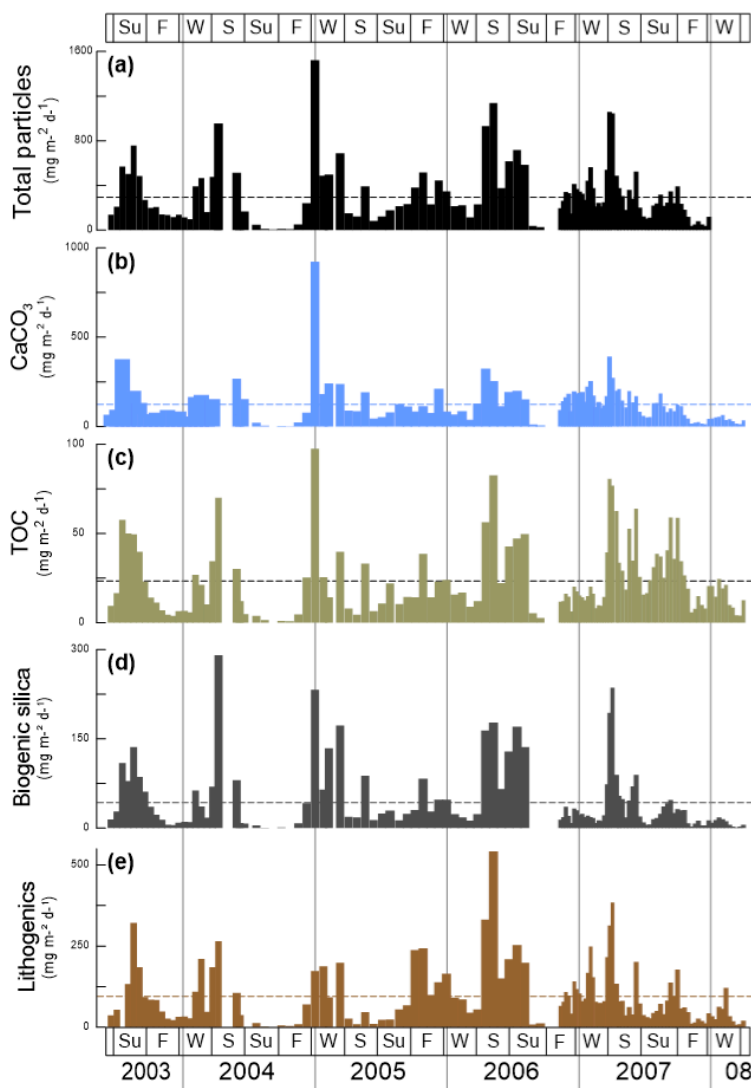
1090

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).

1100



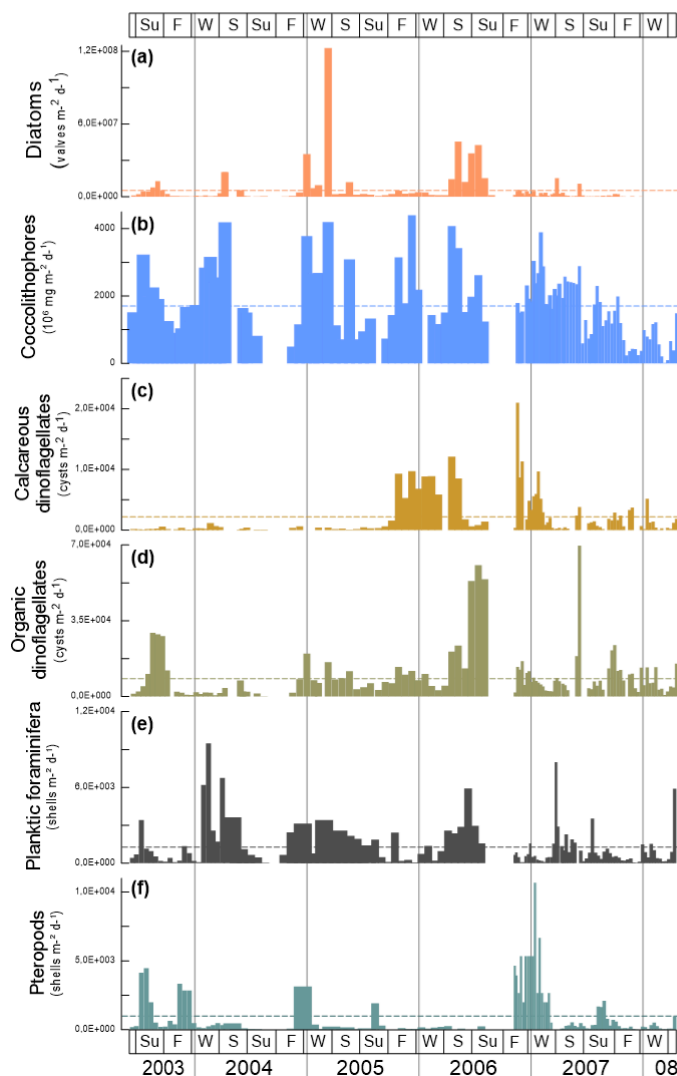
Figure 2
Romero et al.



1102 Figure 2. Total particle and bulk fluxes at the trap site CBeu between June 2003 and March 2008.
1104 From top to bottom: (a) total particle ($\text{mg m}^{-2} \text{d}^{-1}$, black bars), (b) calcium carbonate (CaCO_3 ,
1104 $\text{mg m}^{-2} \text{d}^{-1}$, light blue bars), (c) total organic carbon (TOC, $\text{mg m}^{-2} \text{d}^{-1}$, olive bars), (d) biogenic
1106 silica (BSi, opal, $\text{mg m}^{-2} \text{d}^{-1}$, dark grey bars), and (e) lithogenics ($\text{mg m}^{-2} \text{d}^{-1}$, brown bars). The
1106 horizontal striped line for each parameter represents the average flux for the whole studied
1108 interval (see Table 1). The boxes in the upper and lower panels represent seasons
1108 (Su=summer, F=fall, W=Winter, S=spring). The vertical background gray lines indicate calendar
1110 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
 Romero et al.



1112

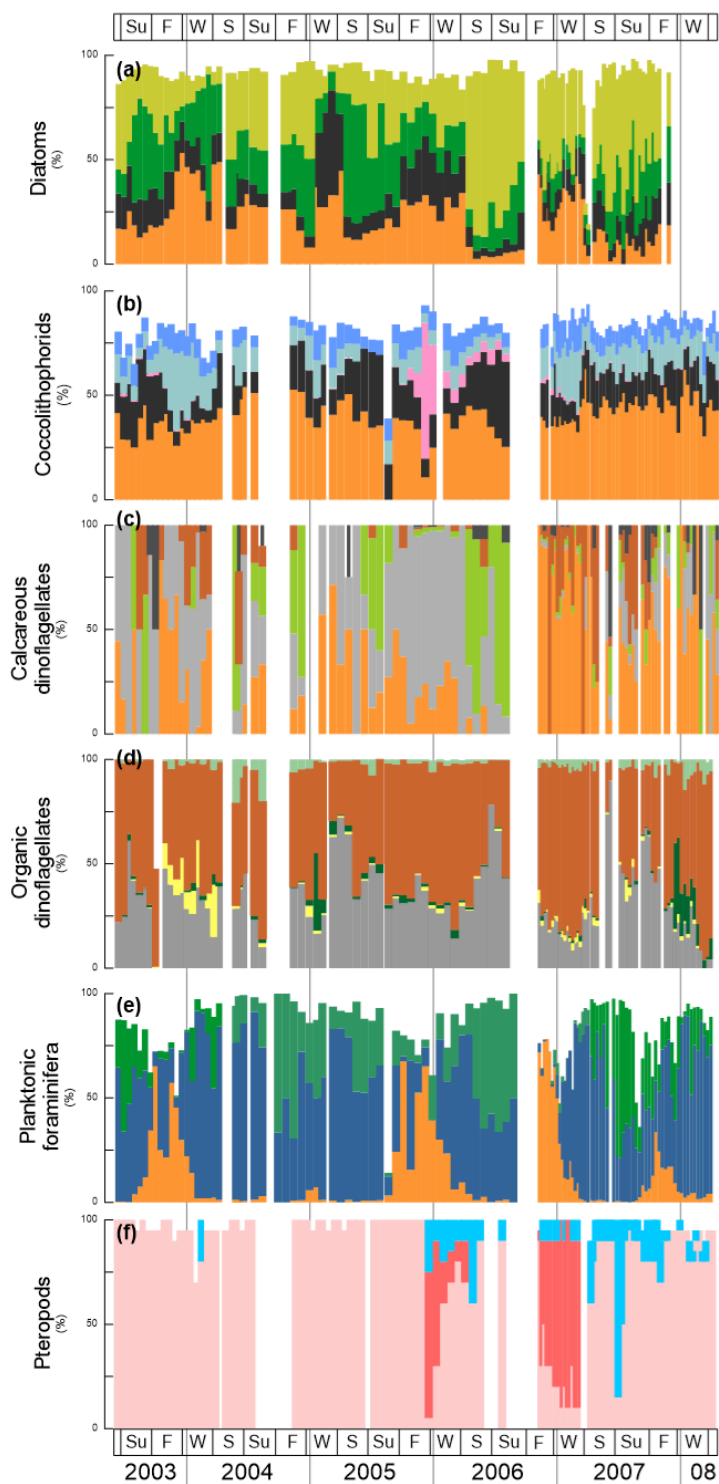
Figure 3. Fluxes of microorganisms at the trap site CBeu between June 2003 and March 2008.

1114 From top to bottom: (a) diatoms ($\text{valves m}^{-2} \text{d}^{-1}$, peach bars; note that ten samples
 1116 corresponding to CBeu 5 –12/13/2007 through 03/17/2008– were not available for diatom
 1118 analysis); (b) coccolithophores (coccoliths $\text{m}^{-2} \text{d}^{-1}$, light blue bars); (c) calcareous dinoflagellates
 1120 (cysts $\text{m}^{-2} \text{d}^{-1}$; gold bars); (d) organic dinoflagellates (cysts $\text{m}^{-2} \text{d}^{-1}$; khaki bars); (e) planktic
 1122 foraminifera (shells $\text{m}^{-2} \text{d}^{-1}$; grey bars), and (f) pteropods (shells $\text{m}^{-2} \text{d}^{-1}$; ocean green bars). The
 1124 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.



Plankton variability off Mauritania

Figure 4
Romero et al.

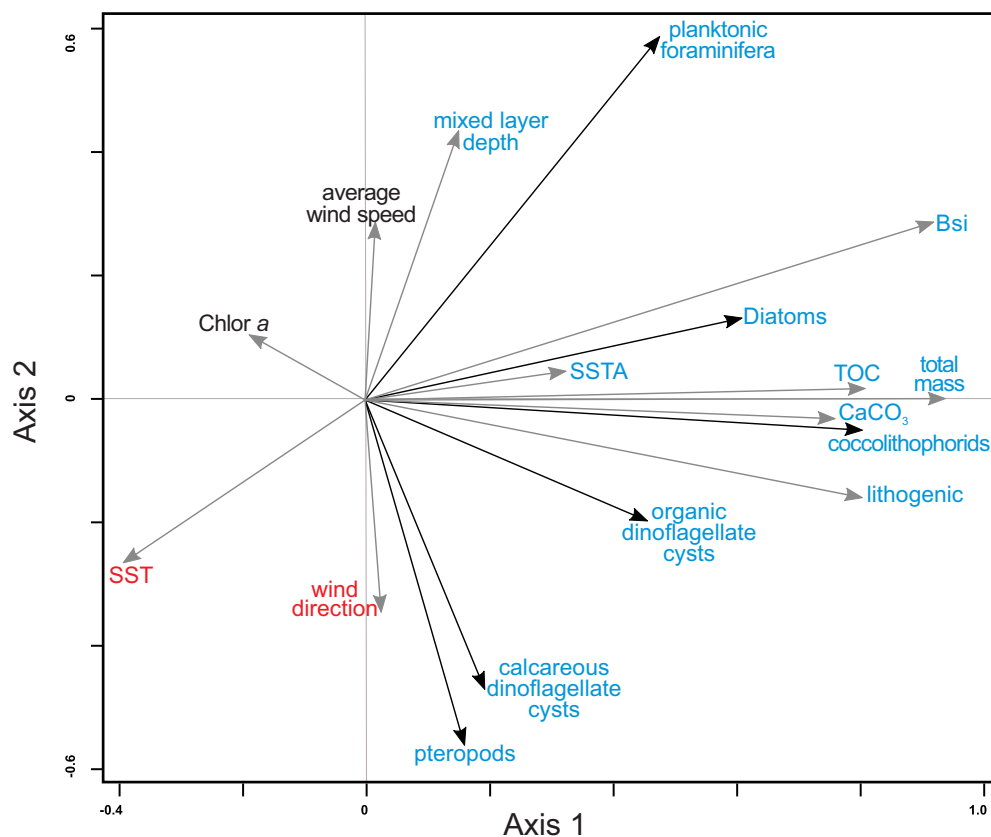




1128 Figure 4. Cumulative relative abundance (%) of main species or group of species of
1129 diatoms, coccolithophores, dinoflagellates, planktonic foraminifera and pteropods at the trap
1130 site CBeu between June 2003 and March 2008 (Table 1). From top to bottom: (a) diatoms -
1131 benthic, light green bars; coastal upwelling, dark green bars; coastal planktonic, black bars;
1132 and open-ocean (% , orange bars; note that ten samples corresponding to CBeu 5 –12/13/2007
1133 through 03/17/2008– were not available for diatom analysis); (b) coccolithophores –upper
1134 photic zone, blue bars; lower photic zone, moss green; *Umbilicosphaera anulus*, pink bars;
1135 *Gephyrocapsa oceanica*, black bars; *Emiliana huxleyi*, orange bars; (c) calcareous
1136 dinoflagellates – other calcareous, dark grey bars; mineral-input related, brown bars; upwelling,
1137 light green bars; cosmopolitan, light grey; warm water, orange bars; (d) organic dinoflagellates
1138 – upwelling species (grey bars); upwelling relaxation species (light yellow bars); potential toxic
1139 (dark green bars); cosmopolitan, red brown bars; other, faded green bars; (e) planktic
1140 foraminifera – upwelling, green bars; cool water, blue bars; warm water, orange bars; and (f)
1141 pteropods – uncoiled species, light blue bars; *Limacina bulimoides*, red bars; *Heliconoides*
1142 *inflatus*, pink bars. The species-specific composition of groups is presented in Table 3. The
1143 boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=Winter,
1144 S=spring). The vertical background gray lines indicate calendar year separation. For
1145 interpretation of the references to color in this figure legend, the reader is referred to the web
1146 version of this article.
1147
1148
1149
1150



Figure 5
Romero et al.

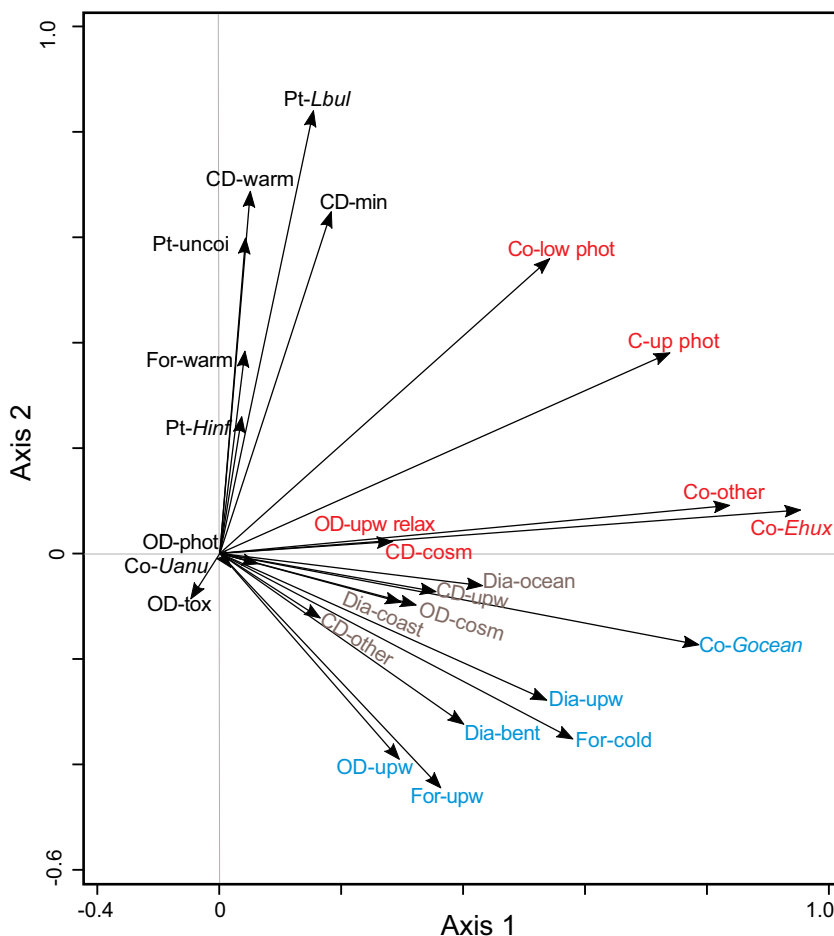


1152

1154 Figure 5. RDA ordination diagram depicting the relationship between the accumulation rates of
1155 organism groups and bulk fluxes and environmental conditions in upper waters. References: Av.
1156 wind speed=average wind speed; Chlor-*a*=chlorophyll *a*; TOC=total organic carbon;
1157 CaCO₃=calcium carbonate; mixed layer depth; SST=sea surface temperature; SSTA=sea
1158 surface temperature anomalies. For interpretation of the references to color in this figure
1159 legend, the reader is referred to the web version of this article.
1160



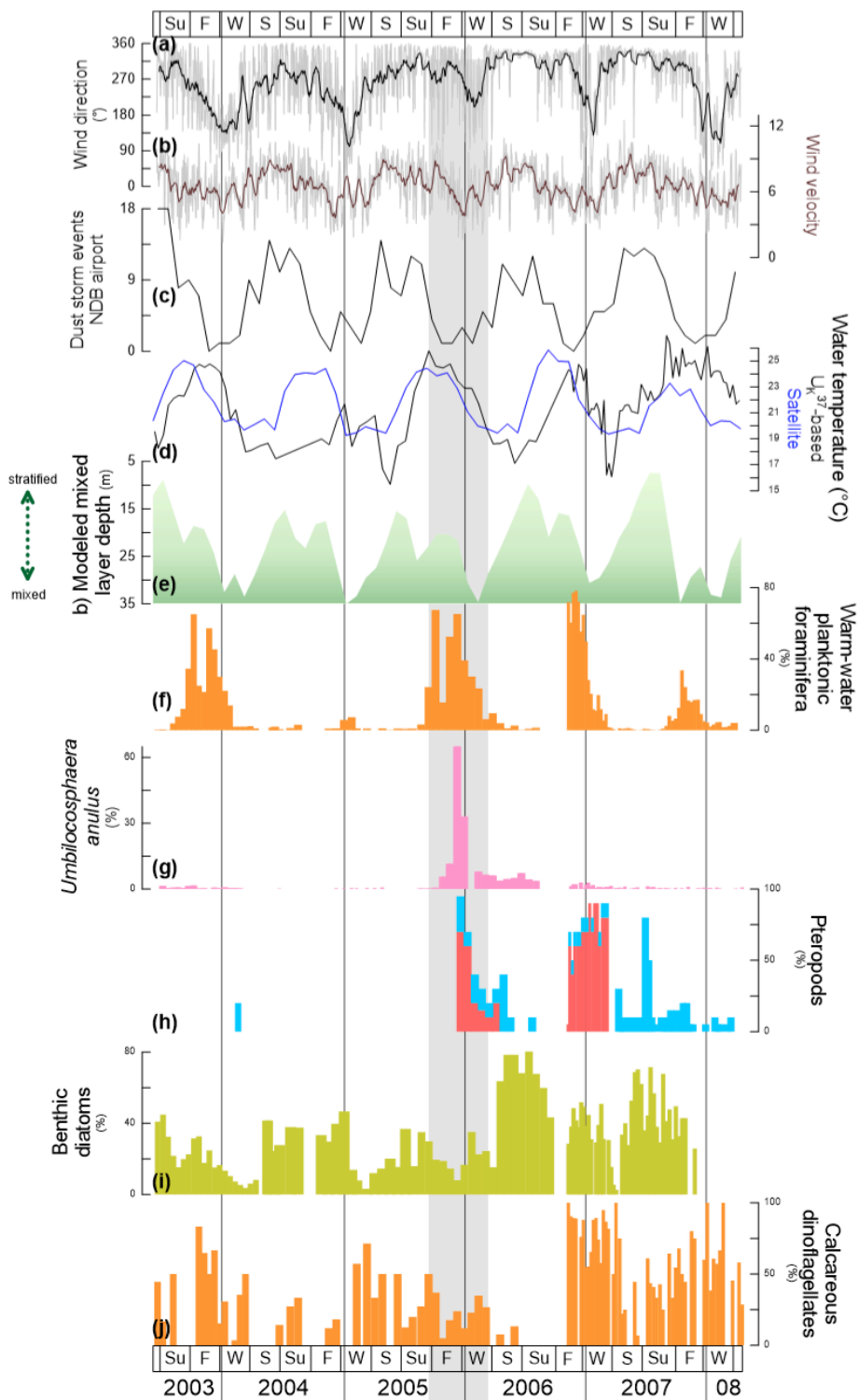
Figure 6
 Romero et al.



1162 Figure 6. Results of a PCA analysis of ecological groups of the organism groups at the CBeu trap
 1164 site between June 2003 and March 2008. References: Dia (diatoms): -bent = benthic, -coast =
 1166 coastal planktonic, -ocean = open ocean, -upw = upwelling; Co {coccolithophores): -Ehux =
 1168 *Emiliana huxleyi*, -Gocean = *Gephyrocapsa oceanica*, -low phot: low photic zone, -other: other
 1170 coccolithophroids, -Uanu = *Umbilicosphaera anulus*, -up phot: upper photic zone; CD
 1172 (calcareous dinoflagellate cysts): -cosm = cosmopolitan group, -min = terrestrial mineral group,
 1174 -other = species that do not fit in one of the other ecological groups, -upw = upwelling, warm:
 1176 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.



Figure 7
 Romero et al.





Plankton variability off Mauritania

1178 Figure 7. Comparison physical data (a-e) and relative abundance of selected species or group/s
1180 of species (f-j) at site CBeu between June 2003 and March 2008. Physical data: (a) daily wind
1182 direction ($^{\circ}$, the grey line are daily data, the thicker black line represent the 17-running points
1184 average); (b) daily wind velocity (m s^{-1} , the grey line are daily data, the thicker dark brown line
1186 represent the 17-running points average), (c) dust storm event (number of events) recorded at
1188 the meteorological station of the Airport of Nouadhibou (ca. $20^{\circ}57'N$, $17^{\circ}02'W$, Mauritania); (d)
1190 seawater temperature ($^{\circ}C$): U_{37}^{Kl} -based reconstruction (black line) and satellite-imagery
1192 generated data (blue line); (e) mixed layer depth (m, grey line, <https://modis.gsfc.nasa.gov>
1194 for the area between 19° - $18^{\circ}W$ and 20° - $21^{\circ}N$). 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.

1196

1198

1200

1202

1204

1206

1208

1210

1212

1214



Tables

1216 Table 1: Data deployment at site CBeu (Cape Blanc eutrophic, off Mauritania): coordinates, GeoB
 1218 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 CBeu	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	9630-2 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	11404-3 POS 344-	1,277	20	21.5	07/25/05 – 09/28/2006
4	20°45.7'N 18°42.4'W	11835-2 MSM 04b	1,256	20	1 = 3.5, 2-20 = 7.5	10/28/2006 – 03/23/2007
5	20°44.9'N 18°42.7'W	12910-2 POS 365-	1,263	38	1, 2 = 6.5, 3-38 = 9.5	03/28/2007 – 03/17/2008

1220

1222

1224 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
 1226 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	

References: RDA, Redundancy Analysis; PCA, Principal Component Analysis.

1228

1230

1232

1234

1236



1238 Table 3: Species composition of the groups of (a) diatoms, (b) coccolithophores, (c) calcareous
 1240 and (d) organic dinoflagellate cysts, (e) planktonic foraminifera and (f) pteropods at Site CBeu
 between June 2003 and March 2008.

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



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 tessellata
Stellarima 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 subtilis
Thalassiosira symmetrica

Coccolithophores

- | | |
|--|---|
| 1) Cosmopolitan | Boeckel and Baumann (2008),
Baumann and Boeckel (2013),
Poulton et al. (2017), Young et al.
(2019) |
| <i>Emiliana huxleyi</i>
<i>Gephyrocapsa oceanica</i> | |
| 2) Lower photic zone | |
| <i>Algirosphaera robusta</i>
<i>Calciosolenia murrayi</i>
<i>Florisphaera profunda</i>
<i>Gladiolithus flabellatus</i>
<i>Hayaster perplexus</i> | |
| 3) Warm oligotrophic surface waters | |
| <i>Discosphaera tubifera</i>
<i>Helicosphaera carteri</i>
<i>Rhabdosphaera xiphos</i>
<i>Umbellosphaera irregularis</i>
<i>Umbellosphaera tenuis</i>
<i>Umbilicosphaera anulus</i>
<i>Umbilicosphaera sibogae</i> | |
| 4) Other miscellaneous species | |
| <i>Acanthoica quattropsina</i>
<i>Calcidiscus leptoporus</i>
<i>Calcidiscus leptoporus</i> small
<i>Calcidiscus quadriperforatus</i>
<i>Gephyrocapsa ericsonii</i>
<i>Gephyrocapsa muelleriae</i>
<i>Ophiaster hydroideus</i>
<i>Ophiaster hydroideus</i>
<i>Rhabdosphaera stylifer</i>
<i>Syracosphaera anthos</i>
<i>Syracosphaera pulchra</i> | |

Calcareous dinoflagellates cysts

- | | |
|-------------------------------|---|
| 1) Upwelling | Siggelkow et al. (2002); Richter
et al. (2007); Kohn and |
| <i>Calcidinellum operosum</i> | |



Plankton variability off Mauritania

	<i>Scrippsiella trochoidea</i>	Zonneveld (2010)
2) Warm waters	<i>Calciodinellum albatrosianum</i>	
3) Mineral input	<i>Leonella granifera</i>	
4) Cosmopolitan	<i>Thoracosphaera heimii</i>	
5) Others	<i>Calciodinellum levantinum</i> <i>Melodermuncula berlinensis</i> <i>Pernambugia tuberosa</i> <i>Scrippsiella lacrymosa</i> <i>Scrippsiella regalis</i> <i>Scrippsiella trifida</i>	
Organic dinoflagellates cysts		
1) Upwelling	<i>Echinidinium aculeatum</i> <i>Echinidinium granulatum</i> <i>Echinidinium transparentum</i> <i>Echinidinium zonneveldii</i> <i>Ecginidinium</i> spp. cyst of <i>Protoperidinium americanum</i> cyst of <i>Protoperidinium monospinum</i> <i>Stelladinium stellatum</i>	Susek et al. (2005); Holzwarth et al. (2010); Trainer et al. (2010); Smayda (2010); Smayda and Trainer (2010); Zonneveld et al. (2010; 2013)
2) Upwelling relaxation	<i>Lingulodinium machaerophorum</i> cyst of <i>Polykrikos schwarzii</i> cyst of <i>Polykrikos kofoidii</i>	
3) Potential toxic	cysts of <i>Gymnodinium</i> spp.	
4) Cosmopolitan	<i>Brigantedinium</i> spp. <i>Spiniferites</i> species <i>Impagidinium</i> species	
Planktonic Foraminifera		
1) Warmer waters	<i>Globigerinoides ruber</i> (pink and white) <i>Globigerinoides sacculifer</i>	Hemleben et al. (1989), Schiebel and Hemleben (2017)
2) Cooler waters	<i>Globorotalia inflata</i> <i>Neogloboquadrina incompta</i>	
3) Upwelling	<i>Globigerina bulloides</i>	
4) Additional secondary species	<i>Beella digitata</i> (Brady 1879) <i>Globigerinella calida</i> (Parker 1962) <i>Globigerinella siphonifera</i> (d'Orbigny 1839) <i>Globorotalia crassaformis</i> (Galloway and Wissler 1927) <i>Globorotalia menardii</i> (Parker, Jones and Brady 1865) <i>Globorotalia scitula</i> (Brady 1882) <i>Globorotalia truncatulinoidea</i> (d'Orbigny 1839) <i>Neogloboquadrina dutertrei</i> (d'Orbigny 1839) <i>Orbulina universa</i> (d'Orbigny 1839) <i>Pulleniatina obliquiloculata</i> (Parker and Jones 1865)	
Pteropods		
	<i>Heliconoides inflatus</i> (d'Orbigny 1835) <i>Limacina bulimoides</i> (d'Orbigny 1835)	WoRMS Editorial Board (2017)