Universität Bremen

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University of Bremen www.marum.de

Dr. Oscar E. Romero
Senior Scientist
MARUM
D-28359 Bremen
Germany

Tel. +49 421 218 – 65 645
E-Mail oromero@uni-bremen.de
www www.marum.de

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Biogeosciences
Associate Editor
Prof. Emilio Marañón
Universidad de Vigo
Spain

Dear Emilio,

We submit the revised version of our manuscript "*Flux variability of phyto-and zooplankton communities in the Mauritanian coastal upwelling between 2003 and 2008*" (bg-2019-314). We have endeavored to deal with all of the issues raised by both referees. Following both reviews, several changes were made to the text, figures and tables. In addition to the point-by-point response to the remarks raised by Dr. Manuel Bringué, an anonymous referee and yourself, we have included following changes:

(1) The title has been rephrased.
(2) A new co-author has been added (Prof. Vera Pospelova).
(3) Two new tables have been added (now Tables 3 and 4).

In addition to our Reply and the point-by-point reply to the comments, the following documents are submitted:

(1) a copy of the revised manuscript (the marked-up version shows all changes made throughout the text as highlighted in red), and,
(2) all files in publication-ready formats (including high-resolution files of figures).

We greatly appreciate the helpful reviewers' insights. We hope that this revised version will merit your positive consideration and the editorial requirements of *Biogeosciences*.

Best regards,

Oscar E. Romero
(on behalf of all co-authors)

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

bg-2019-314

Authors = Oscar E. Romero, Karl-Heinz Baumann, Karin A. F. Zonneveld, Barbara Donner, Jens Hefter, Bambaye Hamady, Vera Pospelova and Gerhard Fischer

Reply to the Interactive Discussion

As required by BG, the response to the Referees is structured in the following sequence: (1) comments from Referees (RC), (2) author's response (AR), (3) author's changes in manuscript (ACM).

1) Comments from Dr. M. Bringué's

1.1) General comments

RC: One aspect I would like to see discussed further is the possibility of the trap record missing on some parts of the pelagic food web dynamics. All major groups (along with lithogenic particles) are recorded simultaneously, which seems to indicate co-occurrence. We also observed the same patterns in the Cariaco Basin (Bringué et al. 2019, Progress in Oceanography 171: 175-211). I think part of the issue was well discussed in section 5.1, but there seems to be a decoupling between Chla and the trap record (RDA in Fig. 5 suggests that). Could it be that planktonic groups are only exported to the depths when 'ballasting minerals' are present (biogenic carbonates and silica, or lithogenics brought in by winds), but we are missing on all primary and secondary production that takes place without those denser particles? It would not undermine the data or findings, I just think it is worth discussing.

AR: *We agree with Dr. Bringué on the possible 'ballasting minerals' impact on the downward flux of primary and secondary producers. This issue was partially addressed in our first submitted version (l. 516-522), but we will extend and clarify this paragraph. This issue has been already addressed in several of our previous publication dealing with the seasonal and interannual variability of fluxes off Mauritania* (e.g., Fischer et al., 2016, Biogeosciences, 13, 3071; Romero and Fischer, 2017, Prog. Oceanogr. 159, 31; Fischer et al., 2019, Global Biogeochem. Cy., 33, 1100–1128).

ACM: added to the revised version, *Further evidence of a possible ballasting effect on the flux of bulk components was recently presented by Fischer et al. (2019). These authors observed that individual high BSi maxima at site CBeu revealed a peak-to-peak correlation with the dust fluxes. This was interpreted to indicate a strong coupling between dust deposition (lithogenic flux) and the efficiency of the biological pump under dry depositional conditions in winter off Mauritania. Based on these observations, Fischer et al. (2019) proposed that the ballasted, organic-rich aggregates built in surface waters immediately react to any additional dust supply with aggregation followed by rapid sedimentation. Experimental studies on aggregate ballasting and scavenging off*

Mauritania (van der Jagt et al., 2018) support this view as well. (l. 550-558 in revised version).

RC: 2. Section 3.4: We usually need to justify the use of RDA by running a DCCA first (or at least a DCA on species data) – the length of the first gradient informs you on the linear vs unimodal character of the variability in the species data matrix. <2: linear and RDA is appropriate. 2-4: both ordination methods work. >4: unimodal and CCA should be used. See Canoco manual for instance. You also need to specify how the significance of the RDA ordination was tested (e.g., Monte-Carlo permutations and how permutations were done – should be the 'transect' option in Canoco because samples represent a time series; and whether the whole ordination is tested or just the first 1 or 2 axes…).

AR & ACM: *To determine if a linear or unimodal based ordination method should be applied on the data we performed a Detrended Correspondence Analysis previous to statistical analysis. Results of this analysis revealed a total length of gradient of 1.2 sd which indicates a linear species respond on environmental gradients. The methods PCA and RDA have been accordingly performed. Significance of the environmental variables have been tested with a Monte-Carlo permutation test with unrestricted permutations.* (l. 315-320 in revised version).

RC: In general, the manuscript would benefit from being revised by a native English speaker; I provide some suggestions that may help.

AR & ACM: *Dr. Bringué's language corrections are much appreciated and will be introduced. The corrected manuscript was reviewed by Prof. Vera Pospelova (Canada).*

RF: The notation $m^{-2}d^{-1}$ should be changed throughout the manuscript and figures to include the minus signs in superscript.

AR & ACM: *This was accordingly rephrased throughout the MS*.

1.2) Detailed comments/suggestions

All suggested language corrections will be considered.

RC: L. 109-111: Consider the following publications (Bringué et al. 2019, Progress in Oceanography 171: 175-211) that also provided multi-year records of several phytoplanktonic and (micro)zooplanktonic groups in a highly productive coastal ecosystem.

AR: *this suggestion, together with Referee #2's suggestion on 'multiannual records of microplankton and biogeochemical fluxes' was considered in the revised version. Unfortunately, there are not many long-term (longer than five years), continuous sediment trap experiments dealing with several groups of primary and secondary producers.*

ACM: *we mentioned and shortly discuss Bringué et al. (2019*.

RC: L. 298: Wind directions: please specify how the variable is defined (e.g., 360° from N? or relative to coastline?) This is important to understand what the ordination in the RDA of Fig. 5 means.

AR: *In terms of angle measurement in degrees, 0°/360° corresponds to North, 90° to East, 180° to South and 270° to West.*

ACM: *This was rephrased in Figure 7.*

RC: Figure 4: Unless the authors are planning to place this figure in one column only, the figure would greatly benefit from a legend, explaining what each color represents next to each panel. It is very difficult to refer to the caption to read the figure.

AR: *this suggestion is accepted.*

ACM: *The names of taxa or group of taxa was added to the right-hand side of each panel in the corrected Figure 4.*

RC: Figure 5: The authors need to specify what the color-coding for labels means, as well as black vs grey arrows. I also suggest the following:
- Use the abbreviation 'Chl-a' to be consistent with the text (in figure and L. 1156),

AR & ACM: *we are afraid this was an unwilling problem while uploading the figure during the submission process. We submitted an earlier version of this figure. All labels and arrows should have been in black. This is now corrected.*

RC: Figure 6: "C-up phot' in figure should be 'Co-up phot'.

AR & ACM: *This has been accordingly re-named.*

RC: Table 1: Vertical lines are usually omitted.

AR: *this suggestion is accepted.*

ACM: *Vertical lines in Table 1 are now omitted.*

Flux variability of phyto- and zooplankton communities in the Mauritanian coastal upwelling between 2003 and 2008 (bg-2019-314)

Authors = Oscar E. Romero, Karl-Heinz Baumann, Karin A. F. Zonneveld, Barbara Donner, Jens Hefter, Bambaye Hamady , Vera Pospelova and Gerhard Fischer

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Comments from Referee #2

RC: Title. The current title is somewhat misleading. As it reads now it seems that authors documented phyto- and zooplankton communities from the upper water column. Since phytoplankton and zooplankton assemblages can be severely altered before reaching the sediment traps I would suggest to find alternatives for the current title. Mentioning the terms sediment trap or fluxes would help to give the reader a better idea of the content of the article.

AR & ACM: *We rephrase the MS title as: 'FLUX variability of phyto- and zooplankton communities in the Mauritanian coastal upwelling between 2003 and 2008'.*

RC: Lines 20-21. Do authors mean calcareous and organic dinoflagellate cysts? Please revise.

AR & ACM: *This was accordingly rephrased.*

RC: Lines 55-60. Authors provide a short summary of previous long-term monitoring experiments in the global ocean. As stated in the text, this type of studies is scarce, however, there are several sites in the global ocean where multiannual records of microplankton and biogeochemical fluxes have been analysed. The IOC-UNESCO report only covers very few of these sediment trap experiments. Since the current work is based on sediment trap samples, it is important to include in the introduction some of these studies in order to provide the reader with better picture of previous similar work.

AR & ACM: *Please see our comment above on Dr. Bringué's comments on additional references for long-term trap-based studies.*

RC: Section "3.1 Moorings, sediment traps and fluxes". Can authors provide the depth of the water column at the study region? It is important to know the distance from the sea floor in order to assess the possible influence of resuspended sediments in the trap record.

AR & ACM: *We addressed this by adding an additional column in Table 1 with the ocean bottom depth corresponding to each mooring.*

RC: Line 184: "Uncertainties with the trapping efficiency due to strong currents (e.g. undersampling, Buesseler et al., 2007) and/or due to the migration and activity of zooplankton migrators ('swimmer problem') are assumed to be minimal in this depth range." Is this assumption based on Buesseler et al. (2007) paper? Or is this an assumption made by the authors? I would suggest to include the reference at the end of the sentence to support the whole statement and/or explain better.

AR & ACM: Buesseler et al. (2007) *was moved to the end of the sentence.*

RC: Line 246-248: Authors refer to a taxonomy key that they used for dinocyst identification. However, no names of dinocyst taxa are provided in the manuscript. Why do authors provide species names for all microplankton groups but not in the case of the dinocysts? Please clarify.

AR: *We are afraid that Referee #2 overlooked Table 3 (now Table 5). The originally submitted version of this Table includes all species of all groups found between June 2003 and February 2008 in samples collected with the CBeu trap.*

RC: Line 333: "On average, the carbonate fraction (CaCO3) dominates the mass flux (41% to the total mass flux)" Is this average a mean of all samples without considering the magnitude of the flux? Or is it an annual integrated average? I would recommend that authors provide annual values of main biogeochemical components of the flux, microplankton groups and major taxa in an additional figure. This information would greatly facilitate the comparison of the results of the current study with other investigations conducted in other regions of the world's ocean.

AR: averages depicted in Fig. 2 (horizontal dashed line for each parameter represented) and the values discussed in the MS refer to the entire sampled period (June 2003 – February 2008).

ACM*: We added two new tables with annual averages of (1) bulk components (Table 3), (2) flux of organisms, and (3) relative abundances of taxa (Table 4) represented in Figures 2-4 for those years with full calendar year sampled (2004-2007). In doing so, data will be available for future comparisons.*

RC: Lines 336-337. I do agree that the main contributors to CaCO3 and BSI must be the ones listed in the text. But how do authors know that the bulk of the organic carbon is delivered by diatoms coccolithophores and organic dinoflagellate cysts? Although this possibility is likely, the data provided in the current manuscript h is insufficient to reach such conclusion. In particular, in the case of diatoms, they were treated with chemicals that removed their organic content, a process that impedes the estimation of the number of cells that reached the trap with their cellular content intact. An important fraction of the organic matter could correspond to other phytoplankton or zooplankton groups, faecal matter or other components of the marine snow. Is this statement based on previous research in the study region or is it just an interpretation by the authors? I would suggest to either provide more evidence or be more cautious with this statement. Moreover, could authors provide some insights into the contribution of the different components of the CaCO3 flux to the total CaCO3? It would be really interesting to see which microplankton groups are the most important in CaCO3 export to the deep sea.

AR: *We agree with Referee #2 in that the sentence as originally written was misleading and did not express our observations properly. This was accordingly rephrased.*

ACM: We added the following sentence, *Coccolithophores, planktonic foraminifera, calcareous dinoflagellates and pteropods are main contributors to the $CaCO_3$ flux, while diatoms dominate the siliceous community*. (l. 356-58 in revised version)

RC: Line 404. Why not dinocyst species are presented? Authors should provide a list of species, not only groups.

AR: *as commented above, the originally submitted version of Table 3 (now T 5) includes all species of all groups found between June 2003 and February 2008 in samples collected with the CBeu trap.*

RC: Line 416. Defining Globigerina bulloides as an upwelling species is an oversimplification of the environmental preferences of this species. The contribution of this species is often higher at times and in regions of high primary productivity, but such conditions are not necessarily linked to upwelling. Please explain better and provide references to support the affinity of this species for certain environmental conditions. Please also note that planktonic foraminifera species distribution is also influenced by changes in primary productivity not only SST as suggested in the discussion (line 582).

AR: *we revised the ecological interpretation of G. bulloides' temporal occurrence at site CBeu. The planktonic foraminifera group including G. bulloides will be re-named 'high nutrient waters' (instead of 'upwelling').*

ACM: *We rephrased the corresponding sentences as follows: Globigerina bulloides, usually thriving in temperate to subpolar waters during intervals of enhanced primary productivity due to high nutrient availability (Schiebel and Hemleben, 2017), is generally most abundant between summer and fall (fig. 4e)* (l. 435-38 in revised version).

RC: Line 425. "*Heliconoides inflatus* (formerly known as *Limacina inflata*)" Why two names for the same species are provided? Please clarify and provide references supporting this statement.

AR & ACM: *this will be properly rephrased and only the name 'Heliconoides inflatus" will be used throughout the MS and Figures. The former name is only given in Table 3.*

RC: Lines 437-448. Authors do not mention the relationship between the different phytoplankton groups and Chlorophyll-a in Figure 5. Why? This is an important parameter that should be discussed.

AR: *we do agree with both Referees in that this should have been discussed in the first submitted version.*

ACM: following paragraph has been added, *Interestingly, the satellite-derived Chl-a data do not show a significant correlation with fluxes of major microorganism groups studied at site CBeu. This possibly indicates that (1) a large portion of satellite-measured chlorophyll concentration is delivered by microorganisms, which did not reach the CBeu trap, and/or (2) due to the strong ballasting effect, part of the microorganisms' remains reach the trap cups independent of intervals of highest satellite chlorophyll values. An alternative explanation is that (3) satellites measure the chlorophyll concentration in the uppermost centimeters of the water column while microorganisms collected with the CBeu traps thrive mostly in waters deeper than those reached by satellite sensors.* (l. 469-476 in revised version)

RC: Line 479. Many other studies (including sediment trap studies) have documented a simultaneous increase in the abundance of different microplankton groups during favorable conditions for phytoplankton growth. Perhaps authors could discuss their results in light of Barber and Hiscock (2006, GBC). Please consider this suggestion and incorporate if appropriate. I found interesting that dinocysts increase their fluxes together with those of diatoms and coccolithophores. I would expect that the cysts are developed at the end of the productive period. Could authors briefly summarize/mention previous studies that describe the environmental parameters that trigger dinocyst formation?

AR: *Barber and Hiscock (2006) and others are now discussed in the revised version.*

ACM: *Following paragraph was added, Although it is widely believed that the supply of resources regulates the marine community structure (Roelke and Spatharis, 2015), experimental data show that the competition of resources per se does not lead to succession of phytoplankton populations. For instance, Barber and Hiscock (2006) observed that marine picoplankton is not replaced by diatoms when chemical transient conditions (e.g., added iron) abruptly provide a more favorable growth setting. The enormous proportional increase in diatom biomass has fostered the misconception that diatoms replace the non-diatom taxa by succession as the bloom matures. Additional evidence is provided by observational studies. Bringué et al. (2018) observed that autotrophic dinoflagellates in the Cariaco Basin do not appear to compete with diatoms for resources as both groups respond positively to upwelling dynamics. Similarly, Anabalón et al. (2014) observed equal and simultaneous contributions of diatoms and pigmented dinoflagellates to total autotrophic biomass off Cape Ghir located in the northern CC-EBUEs. Contrary to conventional wisdom, Anabalón et al. (2014) demonstrate that groups of phytoplankton increase in growth rates and absolute abundance, but the biomass* *increase of the ambient non-diatom assemblage is modest, especially compared to the order of magnitude or more increase of diatom biomass.* (l. 569-583 in revised version).

Flux variability of phyto- and zooplankton communities in the Mauritanian coastal upwelling between 2003 and 2008 (bg-2019-314)

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Comments from Referee #2

RC: Just a last point to add to my review. Diatom flux data presented in this work seems to have been previously published (Romero and Fischer, 2017, Prog. Oceanogr. 159, 31-44). Could authors clarify which data is new and which data has been published before? Please note that Materials and Methods section has to be corrected accordingly. As it reads now it seems that all the diatom flux data is new. Please revise for diatoms and other microplankton groups if required.

AR: *All coccolithophore, dinoflagellate, planktonic foraminifera and pteropod data are new. Diatom data were previously published in Romero and Fischer (2019, Prog. Ocean 159, 31). We will make clear that our MS builds on previous work.*

ACM: *Detailed information about sampling and laboratory analysis is given in Mollenhauer et al. (2015), Romero and Fischer (2017) and Fischer et al. (2019). These papers present the bulk fluxes for the deployments CBeu 1-5 (Table 1). Alkenone-derived sea surface temperature (SST) for the CBeu deployments 1-4 were provided by Mollenhauer et al. (2015).* (l. 202-206 of the revised version).

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

Oscar E. Romero[1], Karl-Heinz Baumann[1,2], Karin A. F. Zonneveld[1], Barbara Donner[1], Jens Hefter[3], Bambaye Hamady[4], Vera Pospelova[5,6] and Gerhard Fischer[1,2]

[1]University of Bremen, Marum, Center for Marine Environmental Sciences, Leobener Str. 8, 28359 Bremen, Germany.

[2]University of Bremen, Department of Geosciences, Klagenfurter Str. 2-4, 28359 Bremen, Germany.

[3]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, 27568 Bremerhaven, Germany.

[4]IMROP, Institut Mauretanien de Recherches Océanographiques et des Pêches, BP 22, Nouadhibou, Mauritania.

[5]Department of Earth and Environmental Sciences, University of Minnesota, College of Science and Engineering, 116 Church Street SE, Minneapolis, MN 55455, USA.

[6]School of Earth and Ocean Sciences, University of Victoria, OEASB A405, P. O. Box 1700 16 STN CSC, Victoria, British Columbia, V8W 2Y2, Canada.

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

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

community.

1. Introduction

A way to obtain insights into the impact of climate variability on marine ecosystems is monitoring multiannual evolution and changes covering key species or groups of species representing different trophic levels. To date, multiyear continuous, *in situ* monitoring records of marine communities are scarce. Information about open ocean ecosystems is even more rare (*e.g.*, IOC-UNESCO TS129 IGMETS 2017; Bringué et al., 2019). Furthermore, records providing information about organism groups of different trophic levels are practically unknown or cover only a few species (*e.g.*, Schlüter et al., 2012; Rembauville et al., 2016).

Eastern Boundary Upwelling Ecosystems (EBUEs) are among the most important marine ecosystems, both ecologically and economically (Cropper et al., 2014). Despite the fact that they cover only 10% of the global surface ocean area, they provide about 25% of the global fish catch (Pauly and Christensen, 1995) and build extraordinary marine hotspots of high primary production and biodiversity (Arístegui et al., 2009). In doing so, they play a key role in the marine biological pump, as together with other continental margins may be responsible for more than 40% of the CO_2 ocean sequestration (Muller-Karger et al., 2005). As EBUEs are highly dynamic with large seasonal and interannual variability (*e.g.*, Chavez and Messié, 2009; Fischer et al., 2016), gaining information on their long-term variability is essential to understand their potential response to current global climate change.

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

This paper builds on the long-term studies of the variability of sea-surface temperature and fluxes (SST) at the site CBeu published by Mollenhauer et al. (2015), Romero and Fischer (2017), and Fischer et al. (2019). We describe the seasonal and interannual variability of fluxes of several primary and secondary producers in the Mauritanian coastal upwelling over a continuous trap experiment extending almost 1,900 days between June 2003 and March 2008 (Table 1). In addition to the previously reported diatom fluxes and reconstructed SST values, we present here new data of fluxes of coccolithophores, calcareous and organic-walled dinoflagellate cysts, planktonic foraminifera and pteropods as well as the species-specific composition of the assemblages that have been collected at the mooring site CBeu (*Cape Blanc eutrophic*), located around 80 nm west of the Mauritanian coastline below a giant chlorophyll filament (Fig. 1). The microorganisms producing the calcareous, opaline or organic remains have different water column habitats, life strategies, and use different nutrient sources (Romero et al., 1999, 2002; Baumann et al., 2005; Romero and Armand, 2010; Zonneveld et al., 2013), and are widely used as proxies in paleostudies carried on Mauritanian sediments (Jordan et al., 1996; Romero et al., 2008; McKay et al., 2014) and similar paleoenvironments (*e.g.*, Baumann and Freitag, 2004; Bouimetarhan et al., 2009; Romero et al., 2015; Weiser et al., 2016; Hardy et al., 2018). The emphasis of our multiannual trap experiment is on the comparison of temporal dynamics and the species-specific composition of the primary and secondary producer plankton community off Mauritania. The simultaneous assessment of fluxes of several microorganism groups collected over long intervals provides substantial information about potential changes in the coastal upwelling community. Results are discussed in the context of varying environmental conditions of the low-latitude Northeastern Atlantic. To our knowledge, this is the first multiyear trap-based record of major primary and secondary producers that provides multiyear information on the dynamics of major components of the plankton community in a highly productive EBUE.

2. Oceanographic setting of the study area

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

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

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

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

3. Material and Methods

3.1. Moorings, sediment traps and bulk flux assessment

Sediment trap moorings were deployed at site CBeu off Mauritania in the CC-EBUE (Fig. 1). Details on trap location and depth, sample amount, water depth and sampling intervals as well as the sample identification (cruise and GeoB numbers) are presented in Table 1. Large-aperture time-series sediment traps of the Kiel type were used with 20 to 40 cups (depending on ship-time availability) and 0.5 m² openings, equipped with a honeycomb baffle (Kremling et al., 1996). Traps were moored in intermediate waters (1,256 m – 1,296 m) and sampling intervals varied between 6.5 and 23 days (Table 1). Uncertainties with the trapping efficiency due to strong currents (*e.g.* undersampling) and/or due to the migration and activity of zooplankton migrators ('swimmer problem') are assumed to be minimal in the depth range of our trap experiments (Buesseler et al., 2007; Fischer et al., 2019).

Prior to each deployment, sampling cups were poisoned with 1 ml of concentrated $HgCL_2$ per 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 laboratory (University Bremen, Bremen) using a rotating McLANE wet splitter system. Larger swimmers, such as crustaceans, were handpicked with forceps and removed by carefully filtering through a 1-mm sieve. All flux data hereafter refer to the size fraction of <1 mm. Detailed information about sampling and laboratory analysis is given in Mollenhauer et al. (2015), Romero and Fischer (2017) and Fischer et al. (2019). These papers present the bulk fluxes for the deployments CBeu 1-5 (Table 1). Alkenone-derived sea surface temperature (SST) for the CBeu deployments 1-4 were provided by Mollenhauer et al. (2015).

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 for bulk (total mass), organic carbon (OC), calcium carbonate ($CaCO_3$) and biogenic silica (BSi, opal). Total organic carbon (TOC) and $CaCO_3$ were measured by combustion with a CHN-Analyzer (HERAEUS, Department of Geosciences, University of Bremen). TOC was measured after removal of carbonate with 2 N HCl. Overall analytical precision based on internal lab standards was better than 0.1% (±1σ). Carbonate was determined by subtracting OC from total carbon, the latter being measured by combustion without pre-treatment with 2N HCl. Organic matter was estimated by multiplying the content of total organic carbon by a factor of two as about 50-60% of marine organic matter is constituted by OC (Hedges et al., 2002).

BSi was determined with a sequential leaching technique with 1M NaOH at 85°C (Müller and Schneider, 1993). The precision of the overall method based on replicate analyses is mostly between ±0.2 and ±0.4%, depending on the material analyzed. The lithogenic fluxes were estimated by subtracting the masses of $CaCO_3$, BSi, and 2 x OC from the total mass flux.

3.2. Assessment of organism fluxes and species identification

3.2.1. Diatoms

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

3.2.2. Coccolithophores

Aliquots of each sample were 1/125. Depending on the total flux, samples were further split down to 1/625 to 1/2500 of the original sample volume and were filtered afterward onto polycarbonate membrane filters (Schleicher and Schuell^{TM} 47mm diameter, 0.45 µm pore size). A piece of the filter was cut and mounted on a Scanning Electron Microscopy stub. Qualitative and quantitative analyses of the trapped assemblages were performed using a *Zeiss*® DSM 940A at 10kV accelerating voltage (Department of Geosciences, University of Bremen, Bremen). In an arbitrarily chosen transect, coccoliths were counted until a total of at least 500 specimens were reached. The taxonomic classification of identified species was based on Young et al. (2003) as well as on Nannotax 3 (Young et al., 2019).

3.2.3. Calcareous and organic-walled dinoflagellate cysts

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

3.2.4. Planktonic foraminifera and pteropods

Depending on the absolute magnitude of the total mass flux, a 1/5 or a 1/25 split of the wet solution (fraction <1mm) was used to pick planktonic foraminifera and pteropods (pelagic mollusks). Specimens of both groups of calcareous microorganisms were rinsed three times by using tap water, dried at 50°C in an oven overnight and then separated from each other. Identification and count of shells were done by using a stereomicroscope *Zeiss*® Stemi 2000 (MARUM, Bremen). The foraminifera fluxes (all size fractions) were determined in mg per m^2 and day with a Sartorius BP 211D analytical balance. Additionally, the total amount of specimens/sample of foraminifera and pteropods (>150 μm) were manually counted. Planktonic foraminifera were identified and classified according to Hemleben et al. (1989) and Schiebel and Hemleben (2017). Out of 15 species of planktonic foraminifera identified, only six species were used as environmental indicators.

3.2.5. Alkenones

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

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

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

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

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

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

3.3. Environmental physical parameters

SST, Sea Surface Temperature Anomaly (SSTA), mixed layer depth (MLD) and upper ocean chlorophyll-a concentration data are based on satellite-derived data achieved from the NASA supported Giovanni project (https://giovanni.gsfc.nasa.gov/). SST is the mean of daily surface ocean temperature and MLD values of the sampling interval in a 4 km^2 area around the trap position (Table 1). In the study area, SST at the mooring location is influenced by seasonal air temperature changes as well as the presence of upheld water surfacing at the trap position.

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

3.4. Multivariate analyses

To determine if a linear or unimodal based ordination method should be applied on the data we performed a Detrended Correspondence Analysis previous to the statistical analysis. Results of this analysis revealed a total length of gradient of 1.2 sd, which indicates a linear species respond on environmental gradients. The ordination techniques Principal Component (PCA) and Redundancy Analysis (RDA) have been accordingly performed. Significance of the environmental variables has been tested with a Monte-Carlo permutation test with unrestricted permutations.

PCA and RDA have been performed with the software Package Canoco 5 (ter Braak and Smilauer, 2012; Smilauer and Leps, 2014). To obtain insights into the temporal relationship between fluxes of organism groups (diatoms, coccolithophores, calcareous and organic-walled dinoflagellate cysts, planktonic foraminifera and pteropods) and bulk components as well as the environmental conditions in surface waters and low atmosphere, a RDA has been performed. RDA compares the total flux of organism groups with environmental parameters and TOC, BSi, $CaCO_3$ and lithogenic fluxes (Table 2). Since the fluxes of the individual groups differ by several orders of magnitudes, it is essential to normalize their flux values prior to the statistical analysis in order to be able to determine temporal relationships of flux variability. As a consequence, the total flux of the organism groups has been normalized to values between 0 and 1000 previous to the analyses according to formula 1:

$nFl_i = (FL_{i\,/y} / FL_i \text{ max}) \text{ x } 1000n$

Fl_i = normalized flux of species group i

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

FL_i max = maximal flux observed in species group i

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

$nFl_j = (FL_{ij/y} / FL_i \text{ max}) \text{ x } 1000n$

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

$Flj_{/y}$ = accumulation rate of ecological entity j in sample yFL_j max = maximal accumulation rate observed in species group i

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

4. Results

4.1. Bulk fluxes and fluxes of organism groups

Independent of the year, the total mass flux of particulates at site CBeu is mainly composed of biogenic components (calcium carbonate, BSi and TOC, Table 3; Fischer et al., 2019). Calcium carbonate is the main bulk biogenic component. The daily average flux of $CaCO_3$ –calculated for each full calendar year sampled between 2004 and 2007- varies between 121.1 and 150.9 mg m^{-2} d^{-1} (Table 3). BSi is the second most important biogenic bulk component (35.8-54.61 mg m^{-2} d^{-1}, Table 3), followed by TOC (19.00-29.40 mg m^{-2} d^{-1}). Lithogenics is the main non-biogenic contributor to the total mass flux (84.6-134.2 mg m^{-2} d^{-1}, Table 3). Coccolithophores, planktonic foraminifera, calcareous dinoflagellates and pteropods are main contributors to the $CaCO_3$ flux, while diatoms dominate the siliceous community.

The fluxes of total mass, $CaCO_3$, TOC, BSi and lithogenics show major peaks in winter and spring (Fig. 2). Secondary maxima were found during late summer/fall, mainly in 2003, and less clearly in 2005, 2006 and 2007 (Fig. 2). However, the individual components reveal different flux amplitudes and point to some interannual variability (Table 3). $CaCO_3$ fluxes were exceptionally high in early winter 2005 compared to the other years. Fluxes of BSi and TOC match well the flux pattern of total mass and show less interannual variability (Fig. 2c, d). The flux of the lithogenic fraction has the highest amplitudes in spring 2006 and 2007 (Fig. 2e).

Fluxes of microorganisms are dominated by diatoms and coccoliths (Fig. 3a, b). These exceeded the fluxes of organic- and calcareous walled dinoflagellate cysts, planktonic foraminifera and pteropods by a factor of four to five. Highest coccolithophore 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 dinoflagellates reach up to 7.1×10^4 cysts m^{-2} d^{-1}, of planktonic foraminifera 0.9×10^4 shells m^{-2} d^{-1}, and of pteropods 1.1×10^4 shells m^{-2} d^{-1}.

Each group of microorganisms shows large seasonal and interannual variability (Table 5). Diatoms had their maximal flux in fall/winter 2005 and spring/summer 2006 (Fig. 3a). Coccolithophores had their highest 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 were observed fall and winter 2007/2008 (Fig. 3b). Calcareous dinoflagellate cysts were practically absent until fall 2005 (Fig. 3c). After September 2005, calcareous dinoflagellate cysts showed maximal export fluxes in fall/winter 2005/2006 and fall/winter 2006/2007 (Fig. 3c). Fluxes decreased again after spring 2007. Organic-walled dinoflagellate cysts had their highest export fluxes in summer 2003, spring/summer 2006 and summer 2007 (Fig. 3d). Planktonic foraminifera showed maximal fluxes in summer 2003, winter/spring 2004, 2005, 2007 and spring/summer 2006 (Fig. 3e). Pteropods had their maximal fluxes in summer 2003, fall/winter 2003/2004, 2004/2005 and 2006/2007 as well as summer 2005 and 2007 (Fig. 3f).

4.2. Species- and group-specific composition of assemblages

The studied plankton community at the CBeu site is highly diverse and is composed by at least 220 identified species. Table 5 presents the species-specific composition of groups depicted in Fig. 4.

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

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

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

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

The distribution and abundance of ***planktonic foraminifera*** species is linked to surface-water properties. We use prominent species as tracers of surface water properties: *Globigerina bulloides*, usually thriving in temperate to subpolar waters during intervals of enhanced primary productivity due to high nutrient availability (Schiebel and Hemleben, 2017), is generally most abundant between summer and fall (fig. 4e). Transitional and subpolar species *Globorotalia inflata* and *Neogloboquadrina incompta* are usually present throughout a year, only decreasing in abundance in fall and winter when warm water taxa peaked (*Globigerinoides ruber* pink, *G. ruber* white and *G. sacculifer*; Kucera, 2007, Schiebel and Hemleben, 2017) (Fig. 4e). The only exception is in fall and winter 2004/2005, when warm-water taxa are almost absent.

As large secondary carbonate producers off Mauritania, ***pteropods*** are important contributors to the carbonate flux in the CC-EBUE (Fischer et al., 2016). The community is composed of relatively few taxa. *Heliconoides inflatus* dominates the assemblage throughout most of the studied interval (Fig. 4f). It is often the only species found in the assemblage until winter 2005/2006, when a sudden and drastic shift in the relative contribution occurred. *Limacina bulimoides* appears for the first time in winter to spring 2006 - and again in fall and winter 2006/2007 - and dominates the assemblage together with a group of unspecified uncoiled pteropods. However, another occurrence of *L. bulimoides* is missing in winter 2007/2008.

4.3. Statistical analyses

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

All microorganism groups are ordinated on the positive part of the first axis showing a positive relationship with all bulk parameters (Fig. 5). This implies that the fluxes of total mass, TOC, BSi and $CaCO_3$ increased with increasing fluxes of all studied microorganism groups (Fig. 5, Tables 3 and 4). Fluxes of planktonic foraminifera, diatoms and –to a lesser extent– coccolithophores and organic dinoflagellate cysts are ordinated on the negative site of SST and, with the exception of organic dinoflagellate cysts, ordinated on the positive side of MLD (Fig. 5). This implies that their fluxes are enhanced whenever SST is low and MLD is deep, *i.e*. under a well-mixed uppermost water column. Diatoms, coccolithophores, organic dinoflagellate cysts and planktonic foraminifera also show a positive correlation with SSTA, implying that enhanced fluxes of these microorganisms occur when temperature anomalies between waters overlying site CBeu and the offshore pelagial is large. The flux of pteropods and calcareous dinoflagellate cysts are positively related to the average wind direction, and negatively to MLD and average wind speed (Fig. 5).

Interestingly, the satellite-derived Chl-a data do not show a significant correlation with fluxes of major microorganism groups studied at site CBeu. This possibly indicates that (1) a large portion of satellite-measured chlorophyll concentration is delivered by microorganisms, which did not reach the CBeu trap, and/or (2) due to the strong ballasting effect, part of the microorganisms' remains reach the trap cups independent of intervals of highest satellite chlorophyll values. An alternative explanation is that (3) satellites measure the chlorophyll concentration in the uppermost centimeters of the water column while microorganisms collected with the CBeu traps thrive mostly in waters deeper than those reached by satellite sensors.

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

- Groups 1 and 2 are ordinated at the negative side of the second axis. Group 1 (in blue, Fig. 6) is built by planktonic foraminifera characteristic of cooler or high nutrient water masses (For-cold, For-hinut); benthic and upwelling-related diatoms (Dia-bent and Dia-upw); organic dinoflagellates characteristic for upwelling regions (OD-upw), and the coccolithophore *Gephyrocapsa oceanica* (Co-*Gocean*). Group 2 (in brown, Fig. 6) consists of upwelling–related and other calcareous dinoflagellates cysts (CD-upw and CD-other), other coccolithophores (Co-other), and coastal planktonic and open-ocean diatoms (Dia-coast and Dia-ocean).
- Ordinated on the positive side of the second axis and central part of the first axis, group 3

assembles planktonic foraminifera mainly thriving in warm waters (For-warm), calcareous dinoflagellates characteristic of warm water conditions and those responding to mineral input (CD-warm, CD-min), and all pteropods taxa (in black, Fig. 6).

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

5. Discussion

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

Both the visual examination of the flux variability and the performed statistical analysis evidence that the seasonality of most microorganism groups at the CBeu site closely follows the temporal pattern of changes in upper water oceanographic conditions off Mauritania between June 2003 and March 2008. Fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera increase whenever the uppermost water column is well mixed (Fig. 7e), SSTs are low (Fig. 7d), and SSTA are high (Figs. 2, 3, 5). This strong match supports the scenario of simultaneous occurrence of intense upwelling off Mauritania and high microorganisms' fluxes at site CBeu. Several previous studies have separately documented enhanced production of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera occurring when the nutrient concentration in the uppermost water column off Mauritania increases (Baumann et al., 2005; Zonneveld et al., 2012; Guerreiro et al., 2017; Romero and Fischer, 2017; Pospelova et al., 2018).

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

Fluxes of total mass and biogenic bulk components ($CaCO_3$, BSi, TOC) are clearly seasonal in nature (Fig. 3 a-d; Fischer et al., 2019) and reflect the temporal productivity pattern of the Mauritanian upwelling region (Meunier et al., 2012; Cropper et al., 2014). The good temporal match between flux maxima of most of the studied microorganism groups and biogenic bulk components unambiguously evidences the contribution of primary and secondary producers to the total mass/biogenic mass fluxes off Mauritania (Figs. 2, 3). Higher absolute values of $CaCO_3$ over BSi (Fig. 2b, d, Table 3) support the scenario of calcareous primary and secondary producers (coccolithophores, planktonic foraminifera and pteropods) dominating the plankton community in the Mauritanian upwelling system (Fischer et al., 2019). Diatoms are the main contributors to the BSi flux (Fig. 3a, 2d; Romero et al., 2002; Romero and Fischer, 2017).

A strong match among fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera with lithogenic fluxes at times of intense upwelling is observed (Figs. 2e, 3 a-c, e). The RDA supports this correlation (Fig. 5). The good correlation between lithogenic and microorganisms' fluxes demonstrates that winds –responsible for the water column mixing off Mauritania (Mittelstaedt, 1983; Meunier et al., 2012)– might additionally enrich surface waters overlying site CBeu with land-derived nutrients. Primary and secondary producers may remarkably benefit from this eolian-transported pool of nutrients. Lithogenic material is brought into Mauritanian ocean waters in the form of dust that it is transported from the Sahara and the Sahel (Romero et al., 2003; Friese et al., 2017). Numerous studies have thoroughly documented that the particle flux off Mauritania predominantly occurs in the form of aggregates, often rich in lithogenic particles (*e.g.*, Karakaş et al., 2009; Iversen et al., 2010; Iversen and Ploug, 2010; Nowald et al., 2015; Fischer et al., 2016; van der Jagt et al., 2018). Recent experiments have also shown that aggregates' abundance and sinking velocities increase toward deeper waters when aggregates are ballasted with lithogenic particles, whereas aggregates are not able to scavenge lithogenic material from deeper waters (van der Jagt et al., 2018). Further evidence of a possible ballasting effect on the flux of bulk components was recently presented by Fischer et al. (2019). These authors observed that individual high BSi maxima at site CBeu revealed a peak-to-peak correlation with the dust fluxes. This was interpreted to indicate a strong coupling between dust deposition (lithogenic flux) and the efficiency of the biological pump under dry depositional conditions in winter off Mauritania. Based on these observations, Fischer et al. (2019) proposed that the ballasted, organic-rich aggregates built in surface waters immediately react to any additional dust supply with aggregation followed by rapid sedimentation. Experimental studies on aggregate ballasting and scavenging off Mauritania (van der Jagt et al., 2018) support this view as well.

A remarkable finding of our multiannual trap experiment is that flux maxima of diatoms, coccolithophores, organic-walled cysts producing dinoflagellates (all primary producers) and planktonic foraminifera (secondary producers) seem to occur fairly simultaneously (Figs. 3, 5). We propose three possible interpretations: (*i*) no clear short-term succession of the microorganism groups occurred (no temporal turnover in phytoplankton composition within a few days, Roelke and Spatharis, 2015), (*ii*) the succession is not properly captured due to low temporal resolution of some sediment trap intervals (Table 1), and/or (*iii*) the microorganisms –originally produced in surface and subsurface waters by different communities– sink with different velocities through the water column toward the ocean bottom and get 'mixed' during their sinking, mainly due to dissimilar weights and sizes of their remains.

Although it is widely believed that the supply of resources regulates the marine community structure (Roelke and Spatharis, 2015), experimental data show that the competition of resources *per se* does not lead to succession of phytoplankton populations. For instance, Barber and Hiscock (2006) observed that marine picoplankton is not replaced by diatoms when chemical transient conditions (*e.g.*, added iron) abruptly provide a more favorable growth setting. The enormous proportional increase in diatom biomass has fostered the misconception that diatoms replace the non-diatom taxa by succession as the bloom matures. Additional evidence is provided by observational studies. Bringué et al. (2018) observed that autotrophic dinoflagellates in the Cariaco

Basin do not appear to compete with diatoms for resources as both groups respond positively to upwelling dynamics. Similarly, Anabalón et al. (2014) observed equal and simultaneous contributions of diatoms and pigmented dinoflagellates to total autotrophic biomass off Cape Ghir located in the northern CC-EBUEs. Contrary to conventional wisdom, Anabalón et al. (2014) demonstrate that groups of phytoplankton increase in growth rates and absolute abundance, but the biomass increase of the ambient non-diatom assemblage is modest, especially compared to the order of magnitude or more increase of diatom biomass.

The first three CBeu trap experiments had long, low-resolution sampling intervals (>18 days/sample, June 2003 through September 2006, Table 1). However, the high-resolution intervals of CBeu deployments 4 and 5 (up to 7.5 days per sample, Oct 2006-March 2008, Table 1) should have captured a possible short-term succession of major groups (*e.g.*, diatoms quickly reacting to increasing nutrient availability, whereas photosynthetic dinoflagellates becoming more abundant during upwelling relaxation, Margalef, 1963; Jiménez-Quiroz et al., 2019). Although we do not dismiss the possibly occurrence of succession within studied populations at site CBeu, at this stage we do not disregard either its occurrence. It should also 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 hardly capture green algae or cyanobacteria thriving in surface waters. CBeu traps at ca. 1,300 m water depth capture a mixed signal of sinking particles from a surface catchment area of at least ca. 100 km^2 (Siegel and Deuser, 1997, Fischer et al., 2016,) due to (*i*) differential settling velocities of particles (Fischer and Karakaş, 2009; Iversen et al., 2010; van der Jagt et al., 2018), and (*ii*) highly heterogeneous and dynamic surface water conditions due to filament and eddy activity off Mauritania (Mittelstaedt, 1991; Gabric et al., 1993; Meunier et al., 2012; Cropper et al., 2014). Additionally, the trapped signal is always affected by dissolution of particular species and/groups of organisms sinking through the water column into deeper waters (*e.g.*, Romero et al., 1999, 2002).

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

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

Diatoms of coastal regions (Dia-coast, non-upwelling related) and those thriving in open ocean waters (Dia-ocean) together with other calcareous dinoflagellates (CD-other), cosmopolitan organic dinoflagellate cysts (OD-cosm) and 'other coccolithophores' (Co-other) are assigned to group 2 (in brown in Fig. 6). Except for the cosmopolitan organic dinoflagellate cysts, all components of group 2 are primary producers and occur more abundantly between early fall and late winter (Fig. 4), at times of deepening of the ML and upwelling relaxation (Fig. 7e). Group 2 represents a primary producer signal typical of meso- to oligotrophic waters conditions off Mauritania, occurring under weakened upwelling, when winds predominantly blow from the N-NE, SST start decreasing after their summer peak, and the uppermost water column stratifies (Fig. 7a, d, e).

Except for warm waters (CD-warm) and dust input-sensitive (CD-min) calcareous dinoflagellate cysts, group 3 is mainly composed by secondary producers: warm-water planktonic foraminifera and all pteropods (Fig. 4e, f). As such, this group represents the calcareous fraction of zooplankton feeding on (primary) phytoplankton, occurring mainly during phases of predominantly warmer

SSTs (Fig. 7d), N-NE-originated winds (Fig. 7a) and stratified uppermost water column (Fig. 7e). SST appears to be the most important factor controlling assemblage composition of planktonic foraminifera (Kucera, 2007). Large, symbiont-bearing specialists like *G. ruber and G. sacculifer* are adapted to more oligotrophic and warmer waters. They show their maximum abundance in warm waters with a deeper mixed-layer depth (Fig. 7e, f).

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

5.3. Shifts in the species-specific composition of assemblages between 2004 and 2006

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

1. Stage 1 (2004): (*i*) low total biogenic production (summer–fall 2004, Fig. 2b-d), and (*ii*) absence of warm-water foraminifera (Fig. 7f). These changes in production/flux were accompanied by (*iii*) a significant decrease in SST as reconstructed with $\mathrm{U}^{\mathrm{K}'}_{37}$ (Fig. 7d).
2. Stage 2 (late 2005/early 2006): (*i*) extraordinarily high relative contribution of the coccolithophore *U. anulus* (Fig. 7i); as well as (*ii*) the first high occurrence of *L. bulimoides* and uncoiled pteropods (Fig. 7h).

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

A certain degree of interannual variability of the physical setting (Mittelstaedt, 1983, 1991; Cropper et al., 2014) might explain the shifts in the species-specific composition of the assemblages. The near-disappearance of warm-water planktonic foraminifera in 2004 (Fig. 7f) was most probable the response to lower-than-usual water temperatures (Fig. 7d). However, the SST decrease is not recorded by satellite imagery. The overall climate evolution indicates a longer warm and dry period from 2001-2004 in the Sahel and Sahara (east of site CBeu) and anomalously warm temperatures in the Eastern Atlantic (Zeeberg et al., 2008; Alheit et al., 2014). 2004 is the only year of our study with noticeable temporal discrepancies between satellite and $U^{K'}_{37}$-based temperature (Fig. 7d). This temperature gap suggests a certain decoupling between the temperature signal of the uppermost centimeters of the water column (satellite) and subsurface waters where the alkenone-forming coccolithophores dwell (*E. huxleyi* and *G. oceanica*; Conte et al., 1995). As planktonic foraminifera mainly react to SST variability (Kucera, 2007), cooler than usual subsurface waters between middle winter and early fall 2004 (Fig. 7d) might have been responsible for the strong decrease of the warm-water planktonic foraminifera contribution (Fig. 7f). Additionally, all other plankton groups show lowest fluxes toward late summer. Neither the seasonal pattern nor the MLD show any significant change nor unusually high lithogenic fluxes occurred (Fig. 2e, 7e). Exceptionally, the winter season 2004/2005 is characterized by a high total mass flux (Fig. 2a); this extraordinarily high seasonal value matches well with the highest fluxes of TOC and $CaCO_3$ for the studied interval.

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

The shift in the pteropod composition from dominating *H. inflatus* towards the appearance of *L. bulimoides* between winter 2005 and spring 2006 –and again in fall and winter 2006/2007 (Fig. 7h)– can be also explained by the increased influence of warmer surface waters of southern origin. *Heliconoides inflatus* is known as a rather cosmopolitan species, occurring across a wide range of oceanic provinces (Bé and Gilmer, 1977; Burridge et al., 2017), whereas *L. bulimoides* seems to prefer waters of subtropical gyres (although it was also present in low numbers in the equatorial region, Burridge et al., 2017). A stronger transport of the MC from the south may have led to the deterioration of the adequate environmental conditions for *H. inflatus*, as can be seen by the extremely low total pteropods flux during winter 2005 to spring 2006 (Fig. 3e), and, thus, to the relative enrichment of *L. bulimoides*. The fact that the latter species is absent again in winter 2008 (Fig. 7h) represents a gradual return to previous (‘regular’) winter conditions. ‘Regular’ temperatures from early 2005 on allowed the reappearance of warm-water planktonic foraminifera in fall 2005 (Fig. 7f).

The exceptional increase in the contribution of the benthic diatoms in spring-summer 2006 (Fig. 7i) might have been possibly related to the intensification of lateral advection upon the intermediate-waters deployed CBeu trap (Romero and Fischer, 2017). Observational and model experiments show that the transport of particles from the Mauritanian shelf and the uppermost slope via nepheloid layers significantly contributes to the deposition upon the lowermost slope and beyond than the direct vertical settling of particles from the surface layer (Nowald et al., 2014; Karakaş et al., 2006; Fischer et al., 2009; Zonneveld et al., 2018). The relevance of advective processes within nepheloid layers has been already proposed for similar settings (Puig and Palanques, 1998; Inthorn et al., 2006). We speculate that the longer predominance of N-NE winds between 2005 and 2007 (Fig. 7a) might have possibly intensified the transport of benthic diatoms from the shallow coastal area into the hemipelagic CBeu trap via the MC (Fig. 1). Enhanced lateral transport has important environmental implications for the final burial of organic matter in EBUEs. As the organic matter can be effectively displaced from the area of production (Inthorn et al., 2006), carbon depocenters generally occur at the continental slopes between 500 and 2,000 m. In the CC-EBUE around Cape Blanc, the depocenter with up to 3% of organic carbon has a depth range between 1,000 and 2,000m (Fischer et al., 2019).

Most of the populations affected by and responding to shifting environmental conditions off Mauritania between 2004 and 2006 returned to their ‘regular’ seasonal pattern of occurrence after 2006 (Fig. 4). However, some shifts persisted after summer 2006. *Limacina bulimoides* still dominated the pteropod assemblage (Fig. 7h), the total pteropod flux showed the highest maxima for the entire studied interval (might be due to the large food supply and organic matter as represented by high total fluxes of diatoms, Fig. 3a, e), and warm-water calcareous dinoflagellate cysts 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 fully disregarded that the shift in the species-specific composition of the diatom community (also present after 2008; Romero and Fischer, 2017; Romero, unpublished observations) might be due to the natural long-term variability due to external forcings (*e.g.*, North Atlantic Oscillation) or due to on-going climate change.

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

6. Conclusions

- The seasonal amplitude of the flux variations of primary and secondary producers in the upper water column off Mauritania was well recorded in our continuous trap experiment that lasted 1,900 days. The repeated yearly pattern of higher fluxes of diatoms, coccolithophores, organic-walled dinoflagellate cysts and planktonic foraminifera between early spring and early/middle summer matched well the temporal occurrence of the most intense upwelling interval in waters overlying site CBeu. Conversely, fluxes of calcareous dinoflagellate cysts and pteropods were higher during intervals of upwelling relaxation (late summer through late fall).
- The good temporal match between maxima of (most of) studied microorganism groups and biogenic bulk components unambiguously evidences the contribution of primary and secondary producers to the total mass/biogenic mass fluxes. The notorious coupling between fluxes of lithogenics and major microorganism groups provides compelling evidence for the biological pump off Mauritania to be strongly dependent on the dust input from the Sahara/Sahel and the eolian-transported nutrient deposition.
- 1,900 days of continuous trap record of microorganism fluxes allowed for the recognition of a general sequence of seasonal variations of the main plankton populations thriving in coastal waters off Mauritania. The temporal turnover (succession) was better shown by the temporal variations of particular species or groups of species.
- A significant shift in the ‘regular’ seasonal pattern of populations’ occurrence was recognized in species relative contributions between 2004 and 2006. Several events altering the regular seasonal pattern were observed and occurred in three main stages: summer–fall 2004, late 2005/early 2006, and after fall 2006. Although most of the populations return ‘to normal’ after fall 2006, a few did not.
- Our multiannual trap experiment emphasizes the significance of long-term records on evaluating the impact of changing environmental conditions on living populations. Time-series trap experiments conducted over many years –as those currently conducted in the CC-EBUE by MARUM– deliver a broad observational basis on the occurrence of persistent seasonal and interannual patterns. They also help in the interpretation of long-lasting variations of population

changes in response to key environmental forcings, such as nutrient input, water masses variability, lateral transport and/or climate change. The applicability of the flux dynamics of primary and secondary producers here presented is not limited to the Mauritanian upwelling system, and it might comparable to other EBUEs.

Code and Data Availability

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

Author Contributions

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

Competing Interests

The authors declare that they have no conflict of interest.

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Figures

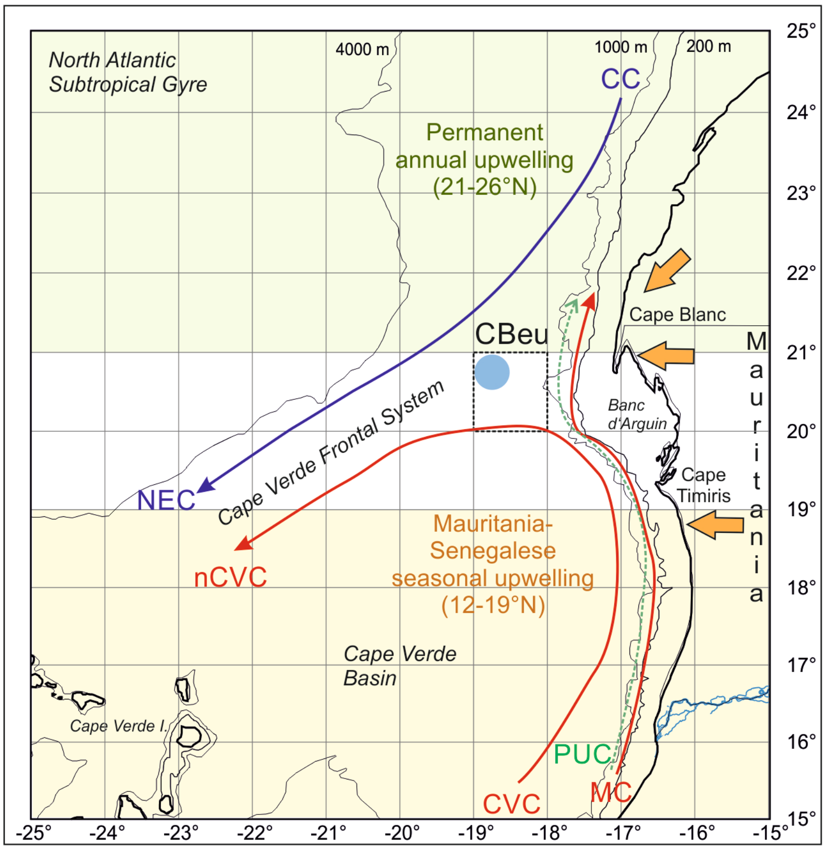

Figure 1. Map of the study area showing the location of trap site CBeu (full light blue dot), surface currents, and main wind system. Surface currents (Canary Current, CC, violet line; North Equatorial Counter Current, blue arrow; Mauritanian Current; red arrow), North Equatorial Current (NEC), Cape Verde Current (CVC), north Cape Verde Current (nCVC), PUC are depicted after Mittelstaedt (1983, 1991) and Zenk et al. (1991). The Cape Verde Frontal Zone (CVFZ) builds at the confluence of the NACW and the SACW (Zenk et al., 1991). Trade winds and Saharan Air Layer are represented by orange arrows (Nicholson, 2013). The upwelling zones are depicted after Cropper et al. (2014).

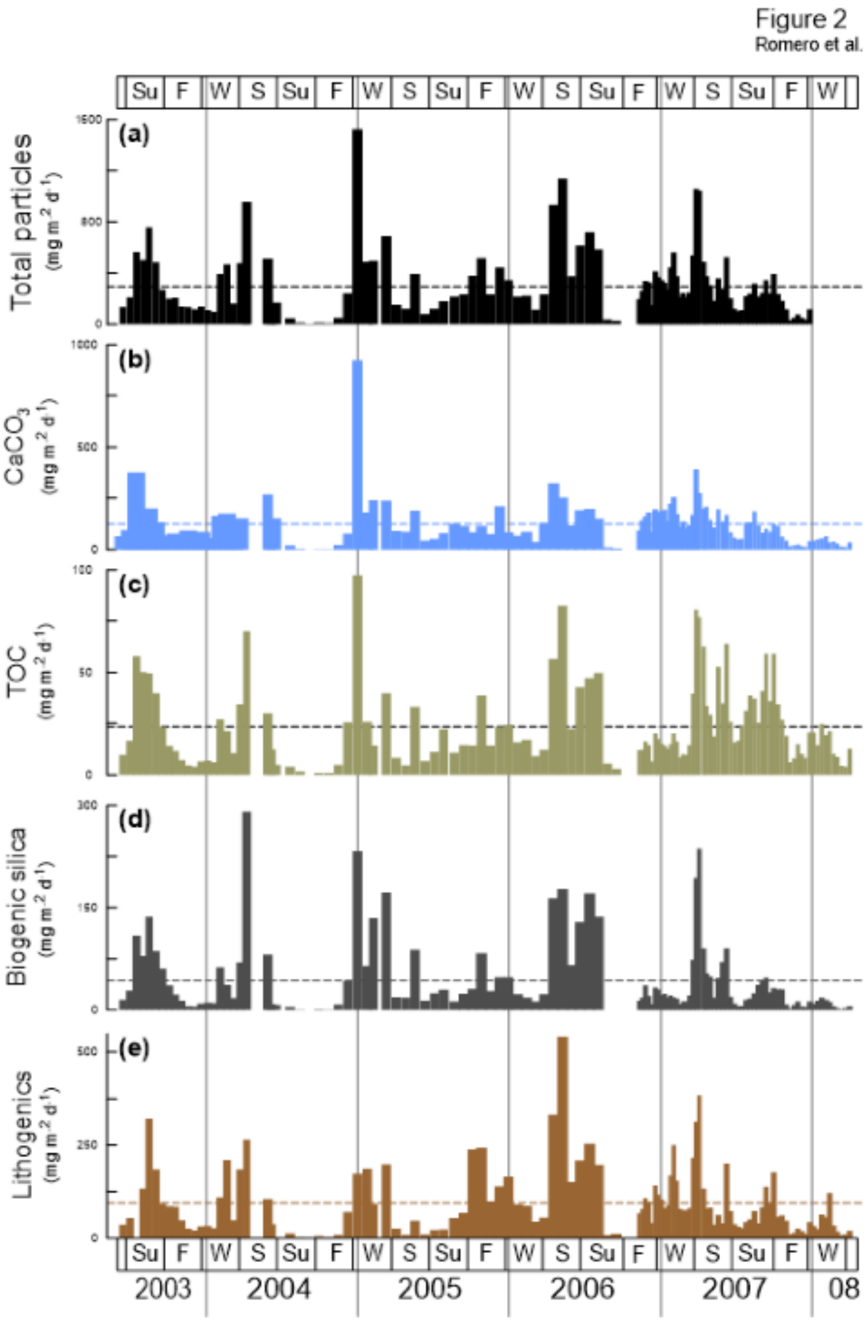

Figure 2. Total mass particle and bulk fluxes at the trap site CBeu between June 2003 and March 2008. From top to bottom: (a) total mass particle (mg m^{-2} d^{-1}, black bars), (b) calcium carbonate ($CaCO_3$, mg m^{-2} d^{-1}, light blue bars), (c) total organic carbon (TOC, mg m^{-2} d^{-1}, olive bars), (d) biogenic silica (BSi, opal, mg m^{-2} d^{-1}, dark grey bars), and (e) lithogenics (mg m^{-2} d^{-1}, brown bars). The horizontal stripped line for each parameter represents the average flux for the whole studied interval (Table 1). The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

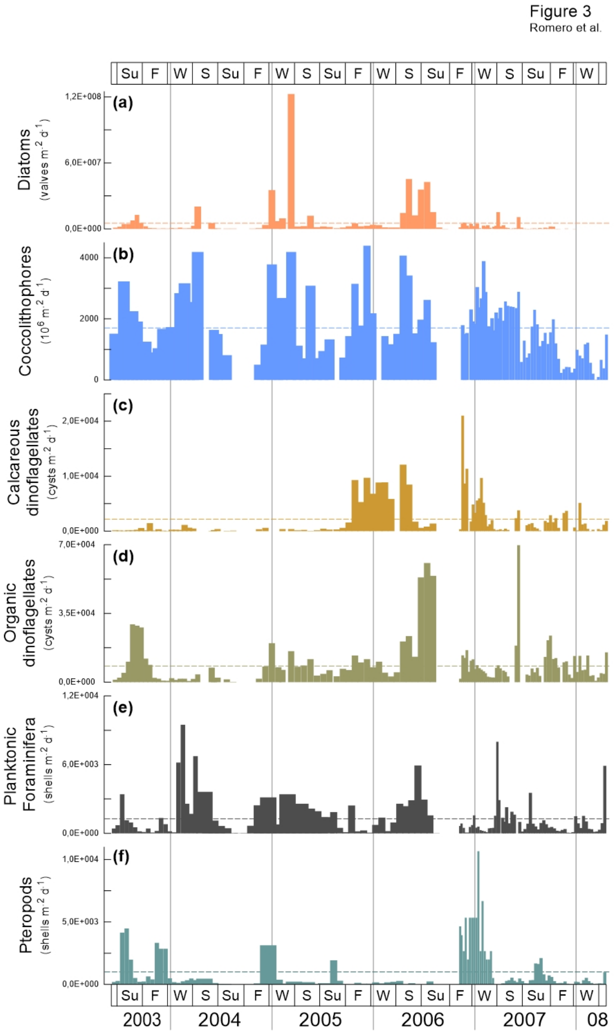

Figure 3. Fluxes of microorganisms at the trap site CBeu between June 2003 and March 2008. From top to bottom: (a) diatoms (valves m^{-2} d^{-1}, peach bars; note that ten samples corresponding to CBeu 5 –12/13/2007 through 03/17/2008– were not available for diatom analysis); (b) coccolithophores (coccoliths m^{-2} d^{-1}, light blue bars); (c) calcareous dinoflagellates (cysts m^{-2} d^{-1}; gold bars); (d) organic dinoflagellates (cysts m^{-2} d^{-1}; khaki bars); (f) planktonic foraminifera (shells m^{-2} d^{-1}; grey bars), and (f) pteropods (shells m^{-2} d^{-1}; ocean green bars). The horizontal stripped line for each group of organisms represents the average flux for the whole study interval. The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

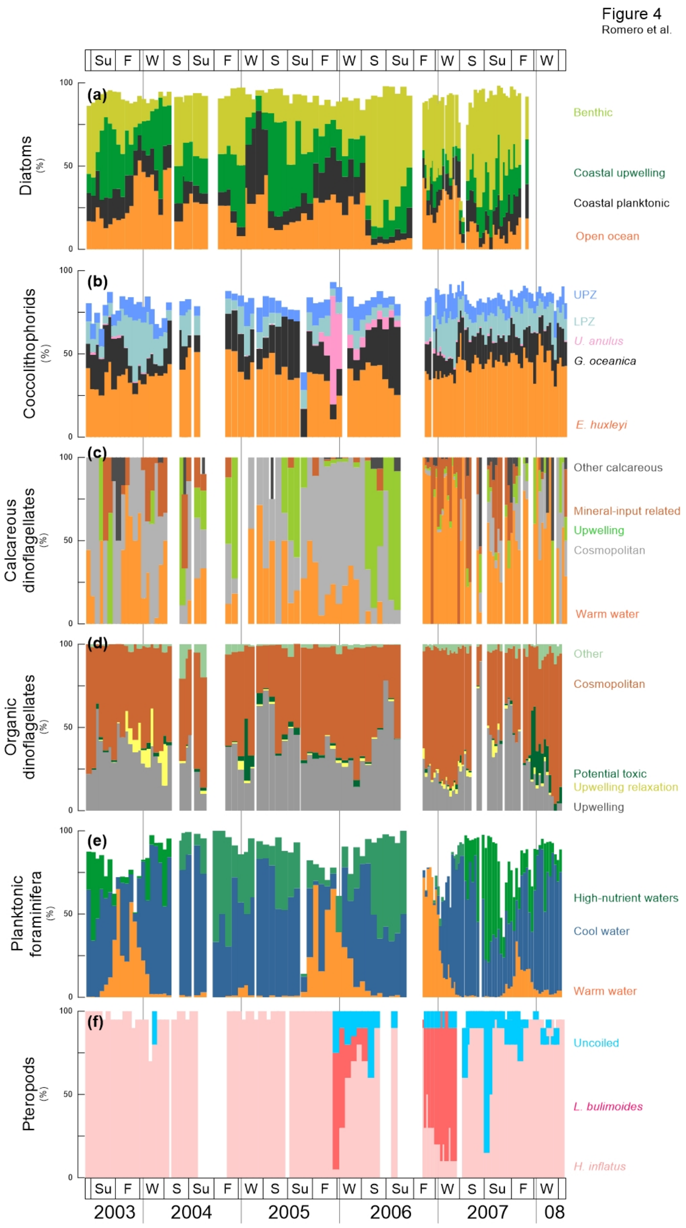

Figure 4. Cumulative relative abundance (%) of main species or group of species of diatoms, coccolithophores, dinoflagellates, planktonic foraminifera and pteropods at the trap site CBeu between June 2003 and March 2008 (Table 1). From top to bottom: (a) diatoms - benthic, light green bars; coastal upwelling, dark green bars; coastal planktonic, black bars; and open-ocean (%, orange bars; note that ten samples corresponding to CBeu 5 –12/13/2007 through 03/17/2008– were not available for diatom analysis); (b) coccolithophores –upper photic zone, blue bars; lower photic zone, moss green; *Umbilicosphaera anulus*, pink bars; *Gephyrocapsa oceanica*, black bars; *Emiliana huxleyi*, orange bars; (c) calcareous dinoflagellates – other calcareous, dark grey bars; mineral-input related, brown bars; upwelling, light green bars; cosmopolitan, light grey; warm water, orange bars; (d) organic dinoflagellates – upwelling

species (grey bars); upwelling relaxation species (light yellow bars); potential toxic (dark green bars); cosmopolitan, red brown bars; other, faded green bars; (e) planktic foraminifera – high nutrient water, green bars; cool water, blue bars; warm water, orange bars; and (f) pteropods – uncoiled species, light blue bars; *Limacina bulimoides*, red bars; *Heliconoides inflatus*, pink bars. Note that the relative contribution of diatoms, coccolithophores and planktonic foraminifera does not add up to 100% since the ecology of some taxa of these groups is not well known constrained. The species-specific composition of groups is presented in Table 5. The boxes in the upper and lower panels represent seasons (Su=summer, F=fall, W=winter, S=spring). The vertical background gray lines indicate calendar year separation. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Figure 5

Romero et al.

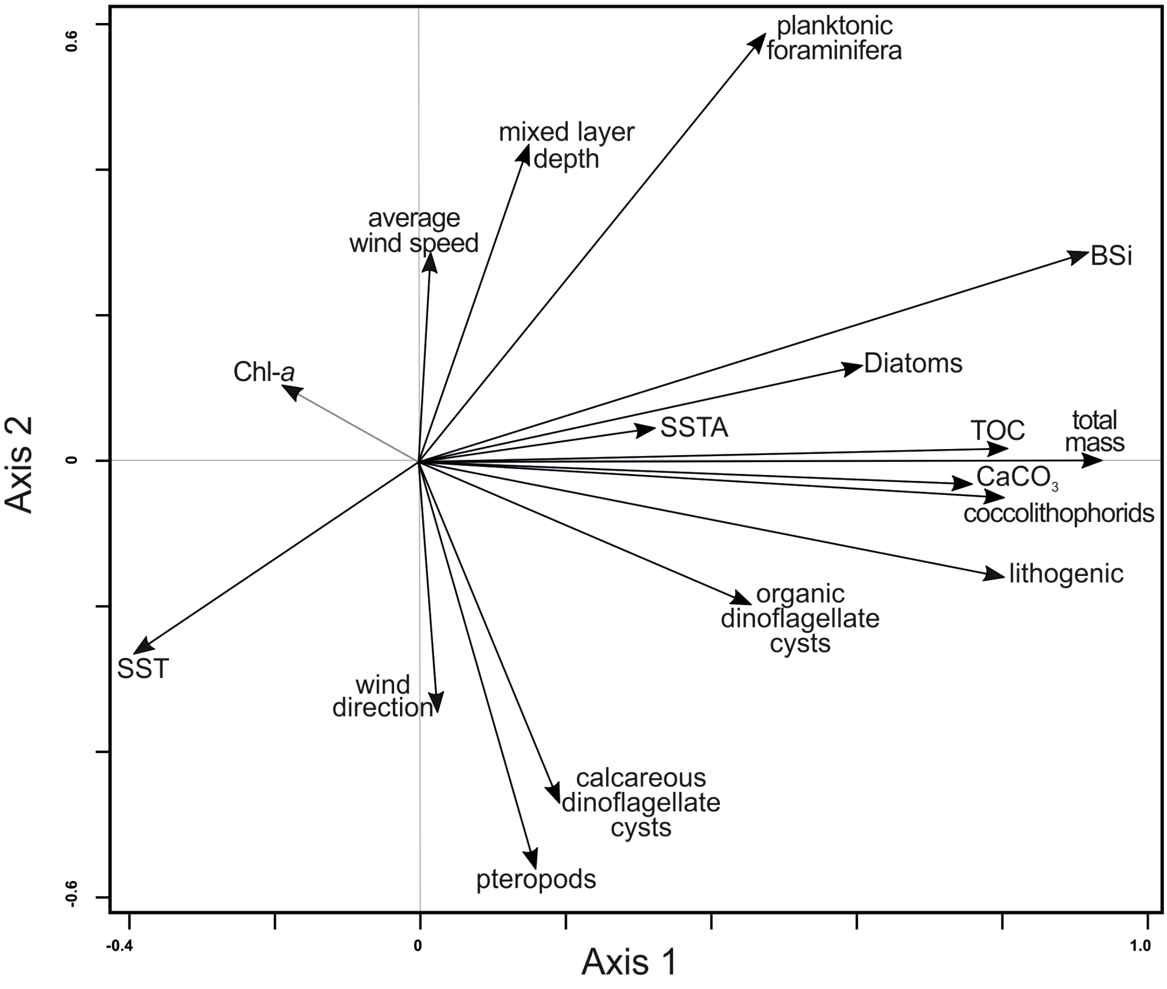

Figure 5. RDA ordination diagram depicting the relationship between the accumulation rates of organism groups and bulk fluxes and environmental conditions in upper waters. References: Av. wind speed=average wind speed; Chl-*a*=chlorophyll *a*; TOC=total organic carbon; $CaCO_3$=calcium carbonate; MLD=mixed layer depth; SST=sea surface temperature; SSTA=sea surface temperature anomalies. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Figure 6
Romero et al.

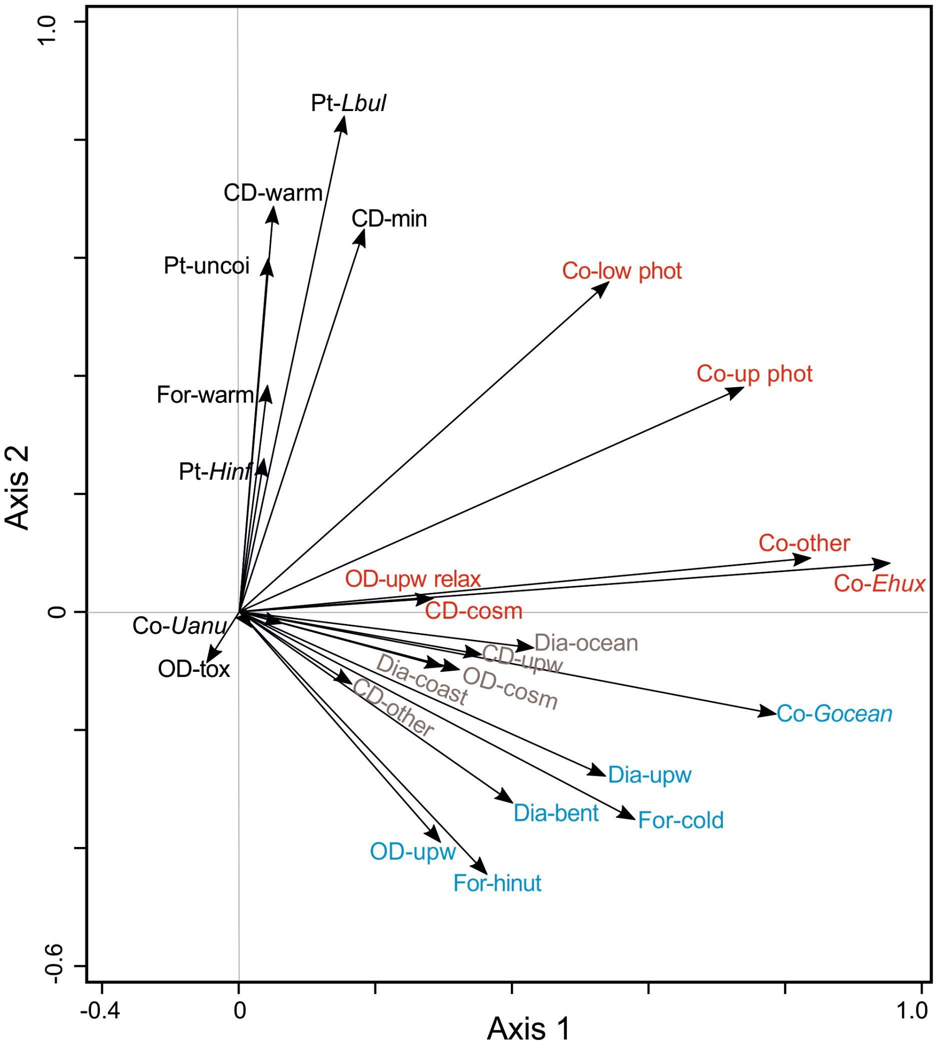

Figure 6. Results of a PCA analysis of ecological groups of the organism groups at the CBeu trap site between June 2003 and March 2008. References: Dia (diatoms): -bent = benthic, -coast = coastal planktonic, -ocean = open ocean, -upw = upwelling; Co (coccolithophores): -*Ehux* = *Emiliana huxleyi*, -*Gocean* = *Gephyrocapsa oceanica*, -low phot: low photic zone, -other: other coccolithophroids, -*Uanu* = *Umbilicosphaera anulus,* -up phot: upper photic zone; CD (calcareous

dinoflagellate cysts): -cosm = cosmopolitan group, -min = terrestrial mineral group, -other = species that do not fit in one of the other ecological groups, -upw = upwelling, warm: warm waters; OD (organic-walled dinoflagellate cysts): -cosm = cosmopolitan group, -other = species that do not fit in one of the other ecological groups, -tox = potential toxic group, -upw = upwelling, -upw relax = upwelling relaxation; For (plantonic foraminifera): -cold: cold water group, -hinut = high nutrient waters 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 5. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

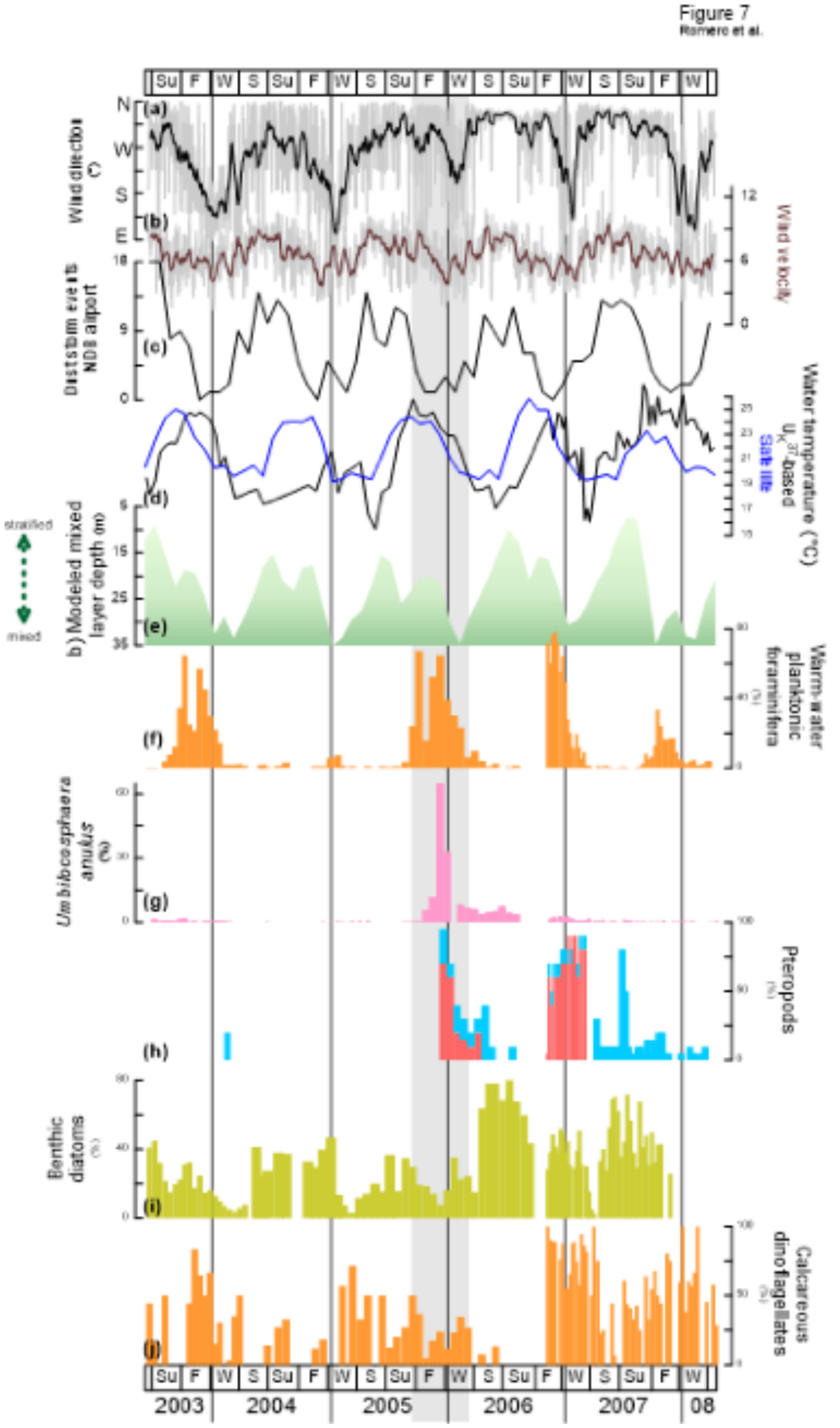

Figure 7. Comparison physical data (a-e) and relative abundance of selected species or group/s of species (f-j) at site CBeu between June 2003 and March 2008. Physical data: (a) origin of daily wind direction (the grey line are daily data, the thicker black line represent the 17-running point average); (b) daily wind velocity (m s^{-1}, the grey line are daily data, the thicker dark brown line represent the 17-running point average), (c) dust storm event (number of events) recorded at the

meteorological station of the Airport of Nouadhibou (ca. 20°57'N, 17°02'W, Mauritania); (d) seawater temperature (°C): $U_{37}^{K'}$-based reconstruction (black line) and satellite-imagery generated data (blue line); (e) mixed layer depth (m, grey line, https://modis.gsfc.nasa.gov for the area between 19°-18°W and 20°-21°N). Relative contribution (%) of (f) warm-water planktonic 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 5. 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.

Tables

Table 1 – Romero et al.

Mooring CB$_{eu}$	Coordinates	GeoB-#/ cruise	Trap depth (m)	Ocean bottom depth (m)	Sample amount	Capture duration (sample/days)	Sampling interval
1	20°45’N 18°42’W	- POS 310	1,296	2,714	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	2,714	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	2,693	20	21.5	07/25/05 – 09/28/2006
4	20°45.7’N 18°42.4’W	11835-2 MSM 04b	1,256	2,705	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	2,709	38	1, 2 = 6.5, 3-38 = 9.5	03/28/2007 – 03/17/2008

Table 1: Data deployment at site CBeu (Cape Blanc eutrophic, off Mauritania): coordinates, GeoB location and cruise, trap depth, ocean bottom 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.

Table 2 Romero et al.

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; PDA, Principal Component Analysis.

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

Table 3

Year	Total mass	CaCO3		TOC		Biogenic silica		Lithogenics	
	(mg m-2 d-1)	(mg m-2 d-1)	(%)	(mg m-2 d-1)	(%)	(mg m-2 d-1)	(%)	(mg m-2 d-1)	(%)
2004	309.5+403.9	150.9+360.2	48.75	21.93+39.7	7.15	54.61+85.6	17.57	84.6+66.5	27.33
2005	317.5+176.6	125.5+65.3	39.45	19.00+11.00	6.00	52,4+46.2	16.50	101.7+82.5	32.03
2006	377.9+281.9	142.8+79.1	37.79	23.3+20.6	6.19	54.07+60.2	14.31	134.2+122.6	35.51
2007	282.8+225.1	121.1+80.2	42.18	29.4+19.6	10.38	35.8+46.9	12.66	92.9+83.4	32.85

Table 3: Average daily fluxes of total mass, calcium carbonate ($CaCO_3$), total organic carbon (TOC), biogenic silica and lithogenics (mg m^{-2} d^{-1}) calculated at site CBeu for full calendar years 2004, 2005, 2006 and 2007.

Table 4

Year	Diatoms					Coccolithophores						Calcareous dinoflagellate cysts					
	Flux	Benthic	Coastal upwelling	Coastal planktonic	Open-ocean	Flux	*E huxleyii*	*G. oceanica*	Low photic zone	Upper photic zone	*A. anulus*	Flux	Other calcareous	Mineral input	Upwelling	Cosmopolitan	Warm waters
	(valves m^{-2} d^{-1})	Relative abundance (%)				(coccoliths *10^6 m^{-2} d^{-1})	Relative abundance (%)					(cysts m^{-2} d^{-1})	Relative abundance (%)				
2004	4770323±14831598	23.96±15.54	27.56±10.95	27.56±10.95	27.56±10.95	2094±1159	43.73±6.70	14.77±7.98	13.86±2.21	6.72±1.92	0.14±0.18	389±312	2.73±2.50	14.47±14.71	20.24±29.22	32.25±28.00	14.93±16.85
2005	11189496+29887484	17.66±9.31	27.26±17.40	27.26±17.40	27.26±17.40	2014±1224	36.95±9.23	20.19±8.21	9.87±3.09	9.45±3.14	7.41±17.53	2228±3457	1.68±6.23	1.23±3.07	10.17±18.84	51.47±29.53	29.20±21.69
2006	9699612+13964939	48.40±19.03	12.76±6.88	12.76±6.88	12.76±6.88	2056±833	37.29±5.22	21.63±9.70	10.45±5.11	10.16±3.85	3.93±2.22	5556±5490	1.85±2.92	11.83±24.40	21.16±32.24	25.73±33.54	39.42±38.65
2007	1785459+3114341	40.05±17.03	17.76±9.12	17.76±9.12	17.76±9.12	1616±872	44.72±6.53	15.35±5.17	14.61±5.75	9.64±2.63	0.53±0.44	1851±2104	4.27±10.39	20.57±23.73	6.26±8.67	9.57±13.36	53.61±28.29

Year	Organic dinoflagellate cysts					Planktonic Foraminifera				Pteropods			
	Flux	Upwelling	Upwelling relaxation	Potential toxic	Cosmopolitan	Flux	Upwelling	Cool waters	Warm waters	Flux	Uncoiled	*L. bulimoides*	*H. inflatus*
	(cysts m^{-2} d^{-1})	Relative abundance (%)				(shells m^{-2} d^{-1})	Relative abundance (%)			(shells m^{-2} d^{-1})	Relative abundance (%)		
2004	3823±5164	30.59±10.23	5.46±8.48	1.61±1.55	56.38±8.26	2286±2801	22.76±20.69	63.77±26.21	2.29±3.30	326±741	1.18±4.85	0.00±0.00	65.88±44.88
2005	8128±3626	40.42±15.41	0.73±0.62	4.92±8.90	52.04±14.46	1228±1129	19.00±13.57	49.42±28.58	17.53±24.59	221±838	1.56±6.25	4.38±17.50	86.88±33.01
2006	17160±17780	32.21±16.86	1.26±1.57	0.83±1.07	63.85±15.69	1287±1417	20.87±23.64	28.54±25.30	31.83±30.75	1962±2342	10.25±8.66	31.00±29.23	43.50±30.83
2007	9600±11757	33.00±20.06	2.12±2.07	4.13±9.75	57.33±18.81	996±1373	22.32±20.49	52.20±21.22	7.01±8.18	1034±1981	10.49±14.48	15.61±32.41	64.63±36.75

Table 4: Average daily fluxes diatoms (valves m^{-2} d^{-1}), coccolithophores (coccoliths m^{-2} d^{-1}), calcareous and organic dinoflagellate cysts (cysts m^{-2} d^{-1}), planktonic foraminifera and pteropods (shells m^{-2} d^{-1}) and average relative contribution of groups of taxa for each of the above-mentioned microorganisms calculated at site CBeu for full calendar years 2004, 2005, 2006 and 2007.

Table 5 Romero et al.

Diatoms	**References**
1) Benthic	
Actinoptychus spp.	Round et al. (1990)
Amphora spp.	
Cocconeis spp.	
Cymatosira belgica	
Delphineis surirella	
Grammatophora marina	
Licmophora sp.	
Odontella mobiliensis	
Psammodyction panduriformis	
Tabullaria spp.	
2) Coastal upwelling	
Resting spores of:	Hasle and Syvertsen (1996)
Chaetoceros affinis	
Chaetoceros cinctus	
Chaetoceros compresus	
Chaetoceros constrictus	
Chaetoceros coronatus	
Chaetoceros debilis	
Chaetoceros diadema	
Chaetoceros radicans	
3) Coastal planktonic	
Actinocyclus curvatulus	Crosta et al. (2012), Romero et al. (2009, 2012, 2016, 2017),
Actinocyclus octonarius	
Actinocyclus subtilis	
Chaetoceros concavicornis (vegetative cell.	
Chaetoceros lorenzianus (VC)	
Chaetoceros pseudobrevis (VC)	
Coscinodiscus argus	
Coscinodiscus decrescens	
Coscinodiscus radiatus	
Cyclotella litoralis	
Skeletonema costatum	
Thalassionema nitzschioides var. *capitulata*	
Thalassiosira angulata	
Thalassiosira conferta	
Thalassiosira oestrupii var. *venrickae*	
Thalassiosira poro-irregulata	
4) Open-ocean	
Asteromphalus flabellatus	Hasle and Syvertsen (1996), Romero et al. (2005), Crosta et al. (2012)
Asteromphalus sarcophagus	
Azpetia neocrenulata	
Azpetia nodulifera	
Azpetia tabularis	
Detonula pumila	
Dytilum brightwellii	
Fragilariopsis doliolus	
Hemiaulus hauckii	
Hemidiscus membranaceus	
Leptocyclindrus mediterraneus	
Neodelphineis denticula	
Nitzschia bicapitata	
Nitzschia capuluspalae	
Nitzschia interruptestriata	
Nitzschia sicula	
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)
Emiliania huxleyi	
Gephyrocapsa oceanica	
2) Lower photic zone	
Algirosphaera robusta	
Calciosolenia murrayi	
Florisphaera profunda	
Gladiolithus flabellatus	
Hayaster perplexus	
3) Warm oligotrophic surface waters	
Discosphaera tubifera	
Helicosphaera carteri	
Rhabdosphaera xiphos	
Umbellosphaera irregularis	
Umbellosphaera tenuis	
Umbilicosphaera anulus	
Umbilicosphaera sibogae	

4) Other miscellanous species	
Acanthoica quattrospina	
Calcidiscus leptoporus	
Calcidiscus leptoporus small	
Calcidiscus quadriperforatus	
Gephyrocapsa ericsonii	
Gephyrocapsa muellerae	
Ophiaster hydroideus	
Ophiaster hydroideus	
Rhabdosphaera stylifer	
Syracosphaera anthos	
Syracosphaera pulchra	
Calcareous dinoflagellates cysts	
1) Upwelling	Siggelkow et al. (2002); Richter et al. (2007); Kohn and Zonneveld (2010)
Calciodinellum operosum	
Scrippsiella trochoidea	
2) Warm waters	
Calciodinellum albatrosianum	
3) Mineral input	
Leonella granifera	
4) Cosmopolitan	
Thoracosphaera heimii	
5) Others	
Calciodinellum levantinum	
Melodemuncula berlinensis	
Pernambugia tuberosa	
Scrippsiella lacrymosa	
Scrippsiella regalis	
Scrippsiella trifida	
Organic dinoflagellates cysts	
1) Upwelling	Susek et al. (2005); Holzwarth et al. (2010); Trainer et al. (2010); Smayda (2010); Smayda and Trainer (2010); Zonneveld et al. (2010; 2013)
Echinidinium aculeatum	
Echinidinium granulatum	
Echinidinium transparantum	
Echinidinium zonneveldiae	
Echinidinium spp.	
cyst of *Protoperidinium americanum*	
cyst of *Protoperidinium monospinum*	
Stelladinium stellatum	
2) Upwelling relaxation	
Lingulodinium machaerophorum	
cyst of *Polykrikos schwartzii*	
cyst of *Polykrikos kofoidii*	
3) Potential toxic	
cysts of *Gymnodinium* spp.	
cysts of Alexandrium spp.	
4) Cosmopolitan	
Brigantedinium spp.	
Spiniferites species	
Impagidinium species	
Planktonic Foraminifera	
1) Warmer waters	Hemleben et al. (1989), Schiebel and Hemleben (2017)
Globigerinoides ruber (pink and white)	
Globigerinoides sacculifer	
2) Cooler waters	
Globorotalia inflata	
Neogloboquadrina incompta	
3) Upwelling	
Globigerina bulloides	
4) Additional secondary species	
Beella digitata (Brady 1879)	
Globigerinella calida (Parker 1962)	
Globigerinella siphonifera (d'Orbigny 1839)	
Globorotalia crassaformis (Galloway and Wissler 1927)	
Globorotalia menardii (Parker, Jones and Brady 1865)	
Globorotalia scitula (Brady 1882)	
Globorotalia truncatulinoides (d'Orbigny 1839)	
Neogloboquadrina dutertrei (d'orbigny 1839)	
Orbulina universa (d'Orbigny 1839)	
Pulleniatina obliquiloculata (Parker and Jones 1865)	
Pteropods	
Heliconoides inflatus (d'Orbigny 1835, formerly known as *Limacina inflata*)	WoRMS Editorial Board (2017)
Limacina bulimoides (d'Orbigny 1835)	

Table 5: Species composition of the assemblage of (a) diatoms, (b) coccolithophores, (c) calcareous and (d) organic dinoflagellate cysts, (e) planktonic foraminifera and (f) pteropods at site CBeu between June 2003 and March 2008.