Research paper

The effects of multidecadal-scale phytodetritus disturbances on the benthic foraminiferal community of a Western Boundary Upwelling System, Brazil

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ABSTRACT

Benthic foraminiferal assemblages, Shannon diversity, BFAR index, and oxygen and carbon stable isotopes from *Cibicides kullenbergi* and *Uvigerina peregrina* were analyzed in three sedimentary cores dating from the last two centuries from an oligotrophic area influenced by Cabo Frio Upwelling System events in the southwestern Atlantic. The geochemistry and ecology of the benthic foraminifera were compared to organic carbon flux and planktonic foraminiferal records in order to understand the impact of phytodetritus produced by upwelling events and disturbances on the benthic community on a multidecadal time-scale. Values of δ^{13}C for *C. kullenbergi* were lower (0.26 ± 0.10‰) compared to $\delta^{13}C_{DIC}$, suggesting the presence of phytodetritus in the sediment water where *C. kullenbergi* calcifies its test. Changes in the benthic foraminiferal assemblage suggest that distinct levels of disturbance differentially influence community-level diversity. Colonization and dominance by opportunistic species resulted in reduced diversity after 1960 CE, with low diversity being observed in areas under the influence of seasonal and intermittent phytodetritus inputs, and higher diversity in a less disturbed area. Certain species can compensate for the negative impact of opportunistic species in terms of disturbance across the community structure, supporting the spatial insurance hypothesis. This community seems to be far from a stable diversity, given the negative interactions between species over the past two centuries, with the r-selective species *G. subglobosa* and *A. weddellensis* limiting *B. marginata* growth during periods of high food availability.

1. Introduction

Apart from experiencing a broad range of instabilities such as tides, waves, temperature, salinity, and changes in sedimentation pattern, continental shelves are also subjected to catastrophic events that can disturb their benthic communities, such as seasonal pulses of phytodetritus derived from primary productivity in the surface and sub-surface waters (Gooday, 2002; Gooday et al., 2010). Phytodetritus (also known as labile carbon) is composed of aggregates of fresh phytoplankton, cyanobacteria, diatoms, and easily degradable pigments (Gooday, 2002). Once in the sediment, these materials can disturb the benthic ecosystem and permit colonization of the phytodetritus layer by opportunistic species. The abundance and the response to such opportunistic species are dependent on the intensity and spatial/temporal scale of disturbance, generating negative interactions between organisms (e.g., competition, predation, parasitism) that can be recorded in the community (Gooday, 2002; Norkko et al., 2006; Gooday et al., 2010).

The response of benthic foraminifera to phytodetritus has previously been reported through laboratory and in situ experiments in sediments (Heinz, 2001; Alve, 2010; Enge et al., 2011, 2014). Furthermore, seasonal variability in the response (Fariduddin and Loubere, 1997; Gooday and Rathburn, 1999; Fontanier et al., 2003; Fontanier et al., 2006; Corliss et al., 2009), as well as for decadal (13-yr) and glacial-interglacial time-scales (Ohkushi et al., 1999; Smart, 2008; Gooday et al., 2010), has also been described. We wanted to establish how community structure and biodiversity have evolved under phytodetritus pulses over the past two centuries, as well as assess the impact of these events on intraspecific competition between benthic foraminifera. Benthic foraminiferal assemblages and stable isotopes were analyzed in three box-cores from a cross-shelf transect of an oligotrophic continental margin subjected to periodic bouts of efficient biological pumping due to upwelling events in a western boundary upwelling system. The geochemistry and ecology of the benthic foraminifera were compared to accumulated organic carbon flux and

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planktonic foraminiferal records to establish the relationship between the phytodetritus produced by upwelling events and disturbances to the benthic community. Our results enhance our understanding of biological pump efficiency in western boundary upwelling systems, as well as the response of biological communities to ocean-atmosphere interactions and changes in the carbon cycle.

2. Methods

2.1. Study site and core locations

The Cabo Frio Upwelling System (CFUS) is located where the Campos and Santos sedimentary basins intersect, at the southeastern continental margin of Brazil at 23ºS (Castro and Miranda, 1998). The CFUS is influenced by the Brazil Current (BC), which is a South Atlantic western boundary current (Hogg and Johns, 1995). The BC carries warm and oligotrophic water at shallow depths, i.e., the Tropical Water (TW; temperature > 18 °C and salinity > 36), as well as cold and nutrient-rich water at intermediate depths from the South Atlantic Central Water (SACW; temperature < 18 °C and salinity 34–36) (Castro and Miranda, 1998; Stramma and England, 1999). Dilution of oceanic waters by terrigenous drainage creates the warm and low saline Subtropical Shelf Water (SSW; temperature ≥ 25 °C and salinity 32–34) that flows over the inner shelf (Castro and Miranda, 1998).

Due to geomorphological features, BC flux instabilities, the predominance of northeastern trade winds, and wind divergence, upwelling events are induced as the SACW is pumped over the continental shelf (Cerda and Castro, 2014). These events promote relatively high productivity within the oligotrophic realm of the Brazilian western boundary current. Unlike the Ekman transport observed in the inner shelf caused by the northeasterly winds (Valentin, 1984) and that generate increased seasonal primary productivity, SACW intrusions into the photic zone are intermittent in the mid-shelf and occur by wind stress curls, thermal front effects and eddies (Calado et al., 2010; Belem et al., 2013; Venancio et al., 2014). At the outer shelf and uppermost slope, current-driven upwelling is characterized by the SACW being pumped into the photic zone by breaking internal waves, tidal-induced vertical displacements, and a low pressure zone formed by BC mesoscale instabilities (Pereira and Castro, 2007; Lessa et al., 2016).

Three box-cores were recovered from the CFUS in 2010 aboard the Brazilian Navy Ship Diadorim. The cores were collected along a cross-shelf transect, with core BCCF10-01 being from the outer shelf (23°24′14.4″S, 41°35′24″W; 128 mbsl; 0.18 mbsf), BCCF10-09 was from the mid shelf (23°12′3.6″S, 41°44′9.6″W; 120 mbsl; 0.18 mbsf), and BCCF10-15 was obtained from the inner shelf (23°3′32.4″S, 41°52′33.6″W; 79 mbsl; 0.16 mbsf) (Fig. 1).

2.2. Sampling and laboratory procedures

Cores were sampled at 1 cm intervals for all analyses. The age model was estimated according to the sedimentation rate (SR) obtained by the Constant Initial Concentration dating method (Appleby and Oldfield, 1992), based on the downcore profiles of ^{210}Pb excess, run in gamma spectrometry and confirmed through $^{239 + 240}$Pu fallout activities (as described by Sanders et al., 2014). ^{210}Pb excess was fitted via the least squares procedure and the slope of the log-linear curve was used to calculate the SR (Supplementary material 1). Percentages of total organic carbon (TOC) and accumulated organic carbon flux (C_{org}) were also determined according to Sanders et al. (2014). Samples decarbonated in 1 M HCl were run in a CILAS 1064 laser particle analyzer to establish grain size.

The stable isotopes δ^{18}O and δ^{13}C were measured in 10 to 15 specimens of *Cibicides kullenbergi* (when available from the core samples) and *Uvigerina peregrina* from a > 150 μm-sieved size fraction. Analyses were performed in a Finning MAT 252 spectrometer with precisions of ± 0.03‰ and ± 0.07‰ for δ^{13}C and δ^{18}O, respectively. Samples

were reacted in supersaturated 105% H_3PO_4 at 90 °C using a Gilson Multicarbon Autosampler. The data were adjusted to Vienna Pee Dee Belemnite (VPDB) using the NBS-19 calcite standard. We used the calculation of Kim and O'Neil (1997) to measure $\delta^{18}O_{EQ}$, applying the $\delta^{18}O_W$ mean values for SACW from Venancio et al. (2014) and annual temperature data for the nearest location from the World Ocean Atlas 2013. Values of $\delta^{18}O_{EQ}$ SMOW (Standard Mean Oceanic Water) were converted to VPDB scale using the Friedman and O'Neil (1977) equation.

For our benthic foraminiferal analyses, we washed a sediment volume of 10 ml through a 63 μm mesh sieve. Samples were dried and split, and at least 300 specimens of benthic foraminifera were picked, identified, and numbers of species were estimated according to 1 ml sample volumes. The relative abundances of species were estimated, as well as their accumulation rates based on the number of specimens per 1 ml volume of sediment, the sedimentation rate (cm·yr^{-1}), and the dry bulk density (g·cm^{-3}). Shannon diversity (H′), benthic foraminifera accumulation rate (BFAR), and phytodetritus-free benthic foraminifera accumulation rate (BFAR$_{phfree}$) indexes were calculated according to Shannon (1948), Herguera and Berger (1991) and Diz and Barker (2016), respectively. We compared our data to δ^{13}C values for planktonic *Globigerinoides ruber* (pink) and the relative abundance of *Turborotalita quinqueloba* from the sites BCCF10-01 (outer shelf) and BCCF10-04 (mid shelf) according to data published by Venancio et al. (2016).

Statistical analyses including univariate (Kruskal-Wallis test to differentiate cross-shelf relative abundances and Spearman correlations) and multivariate analyses (cluster analysis and non-metric multi-dimensional scaling (MDS) of relative abundances of species) were conducted using the XLStat and PAST software, respectively. Cluster analysis was based on the Ward method and Euclidian distance was used to scale the similarities between species. MDS was performed to determine the spatial and temporal changes of the score for assemblages in each core. All statistical tests considered only those species with relative abundances > 2% in at least one sample.

3. Results

3.1. Benthic foraminiferal abundances and fluxes

Fifty-five samples were analyzed and 227 taxa of benthic foraminifera were identified, which mainly belonged to the orders Rotaliida and Buliminida. The assemblages were composed of species from the genera *Alabaminella*, *Bolivina*, *Bucella*, *Bulimina*, *Cassidulina*, *Cibicides*, *Discorbinella*, *Eponides*, *Evolvocassidulina*, *Globocassidulina*, *Gyroidina*, *Islandiella*, *Pseudononion*, *Rosalina*, *Rotorbis*, *Trifarina* and *Uvigerina*, together representing over 80% of the assemblage and each having an abundance of at least 2% in at least one sample. Plots of abundance and flux for representative species in the three cores are presented in Fig. 2 and the respective data are presented in Barbosa et al. (2017).

In the outer shelf core (BCCF10–01), the principal mean values for species fluxes were observed for *Alabaminella weddellensis* (147.3 ± 60.55 ind·cm^{-2}·yr^{-1}), *Bulimina marginata* (161.1 ± 48.93 ind·cm^{-2}·yr^{-1}), *Globocassidulina subglobosa* (925.4 ± 427.23 ind·cm^{-2}·yr^{-1}), and *Trifarina angulosa* (159.2 ± 55.71 ind·cm^{-2}·yr^{-1}). At the mid shelf site (BCCF10-09), the opportunistic species *A. weddellensis* and *G. subglobosa* showed higher mean fluxes (210.6 ± 48.89 ind·cm^{-2}·yr^{-1} and 1023.6 ± 291.63 ind·cm^{-2}·yr^{-1}, respectively), followed by *B. marginata* (128.0 ± 32.77 ind·cm^{-2}·yr^{-1}) and *T. angulosa* (124.3 ± 44.12 ind·cm^{-2}·yr^{-1}). *G. subglobosa* (1256.0 ± 356.13 ind·cm^{-2}·yr^{-1}), *Rotorbis auberii* (579.6 ± 195.20 ind·cm^{-2}·yr^{-1}) and *B. marginata* (225.5 ± 91.21 ind·cm^{-2}·yr^{-1}) exhibited the highest mean fluxes for the inner shelf core (BCCF10-15) (Fig. 2).

Analysis of relative abundances revealed the dominance of *G. subglobosa*, which was present in all samples in all three cores, representing
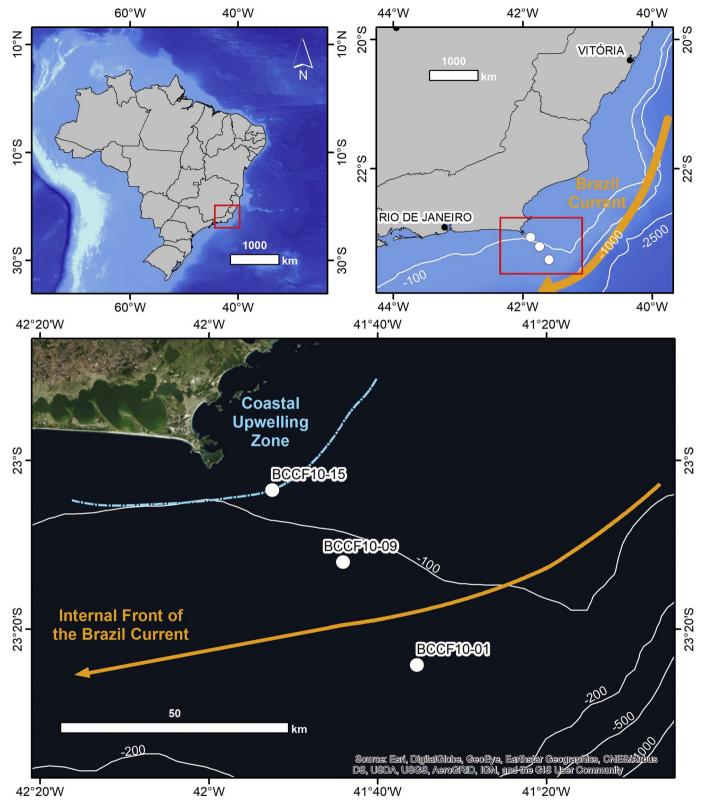
Fig. 1. Location of the study area and the three studied cores BCCF10-01, BCCF10-09, and BCCF10-15 in the western boundary upwelling system of Cabo Frio.

up to 54% of the total assemblage in some samples. *Globocassidulina subglobosa* presented average relative abundances of 35.69 ± 6.03%, 46.81 ± 4.63%, and 40.75 ± 4.92% respectively in the outer, mid and inner shelf cores (BCCF10-01, BCCF10-09 and BCCF10-15). Average relative abundances between cores were similar for *B. marginata*, with values of 6.76 ± 2.19%, 5.97 ± 1.31%, and

7.29 ± 1.74% for BCCF10-01, BCCF10-09, and BCCF10-15, respectively. Another opportunistic species, *A. weddellensis*, was highly abundant in the outer (BCCF10-01) (5.89 ± 1.60%) and mid shelf cores (BCCF10-09) (9.89 ± 2.18%), but less abundant in the inner shelf core (BCCF10-15) (2.79 ± 1.02%). The shallow inner core (BCCF10-15) presented a higher relative abundance (18.51 ± 1.77%)
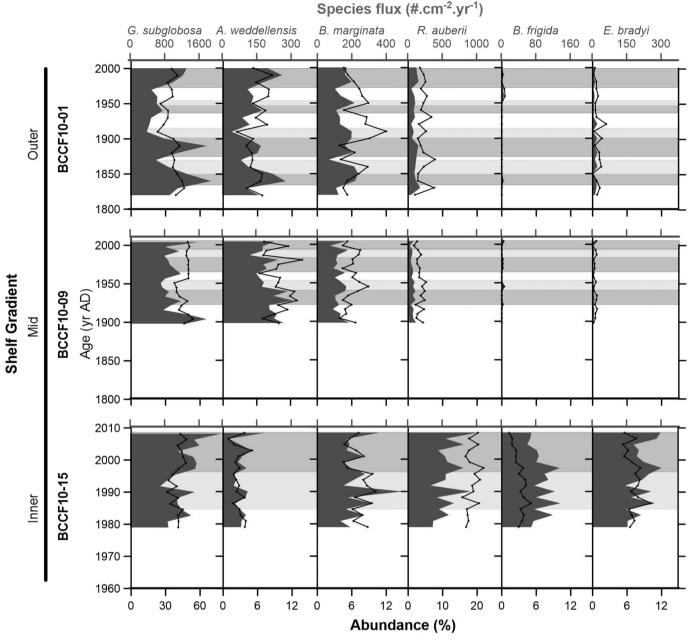
Fig. 2. Down-core comparison of the relative abundance (black line) and flux (dark gray shading) of benthic foraminiferal species at sites BCCF10-01, BCCF10-09 and BCCF10-15.

of *R. auberii* compared to the mid shelf (BCCF10-09) (3.40 ± 1.02%) and outer shelf core samples (BCCF10–01) (4.41 ± 0.49%) (Fig. 2). Abundance and flux of the opportunistic species *G. subglobosa* and *A. weddellensis* appeared to fluctuate according to abundance of *B. marginata*, as revealed by the gray bars of Fig. 2. A Kruskal-Wallis analysis revealed significant differences in the relative abundances of most species across the continental shelf (Fig. 3).

3.2. Benthic foraminiferal indexes

Mean BFAR values were higher for the inner shelf core (BCCF10-15) (3097.14 ± 864.50 ind·cm^{-2}·yr^{-1}) than for the mid shelf (BCCF10-09) (2172.82 ± 495.24 ind·cm^{-2}·yr^{-1}) and outer shelf cores (BCCF10-01) (2523.57 ± 886.10 ind·cm^{-2}·yr^{-1}). As for the BFAR values, BFAR$_{phfree}$ also showed the same trend for the inner (1755.80 ± 559.51 ind·cm^{-2}·yr^{-1}), mid (938.60 ± 214.56 ind·cm^{-2}·yr^{-1}) and outer shelf

cores (1450.89 ± 455.03 ind·cm^{-2}·yr^{-1}) (Fig. 4). However, these results are likely to be highly influenced by the differential sedimentation rates across the shelf, especially as established for the near-shore BCCF10-15 core (SR = 0.55 cm·yr^{-1}) and the mid (BCCF10-09; 0.14 cm·yr^{-1}) and outer shelf cores (BCCF10-01; 0.10 cm·yr^{-1}) (Sanders et al., 2014).

The outer shelf core (BCCF10-01) showed the highest Shannon-Wiener diversity index score (2.71 ± 0.19) compared to the mid shelf (BCCF10-09; 2.17 ± 0.14) and inner shelf cores (BCCF10-15; 2.18 ± 0.13) (Fig. 5). BFAR, BFAR$_{phfree}$ and Shannon diversity values showed similar trends for the BCCF10-01 and BCCF10-09 cores. After a phase of low diversity and high BFAR and BFAR$_{phfree}$ values until 1910 CE, both foraminiferal indexes declined and diversity was high from 1910 to 1960 CE. Thereafter, BFAR and BFAR$_{phfree}$ indexes increased and Shannon diversity decreased from 1950 to 2007 CE (Fig. 4).
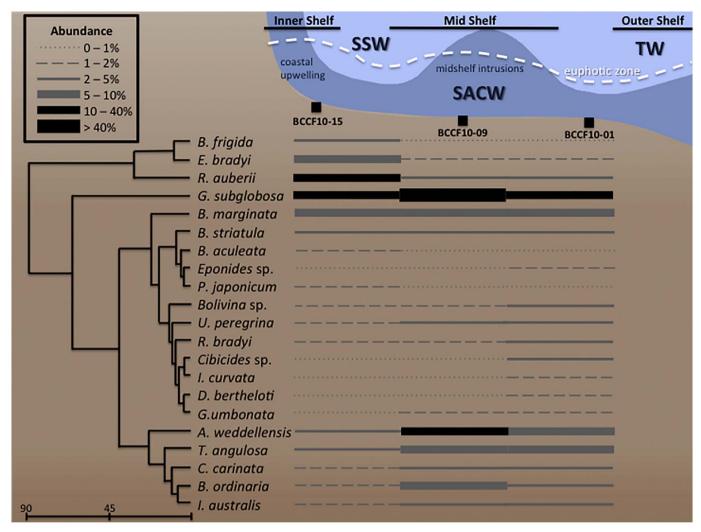
Fig. 3. Cluster analyses and spatial distribution of benthic foraminiferal species in the three cores BCCF10-01, BCCF10-09, and BCCF10-15 under the influence of different oceanographic processes.

(adapted from Venancio et al., 2014).

3.3. Stable isotopes and grain size analyses

Carbon isotopes of *Cibicides kullenbergi* ($\delta^{13}C_{Cib}$) were relatively stable for the outer shelf core (BCCF10-01) (between 0.73 and 1.18‰). The $\delta^{13}C$ values for *Uvigerina peregrina* ($\delta^{13}C_{Uv}$) varied between 0.09 and 0.40‰ for core BCCF10-01, between -0.15 and 0.41‰ for the mid shelf core (BCCF10-09), and between -0.11 and 0.30‰ for core BCCF10-15. The outer shelf and mid shelf exhibited low $\delta^{13}C_{Uv}$ values up to1900 AD, a slight increase between 1910 and 1960 CE, followed by a decrease thereafter (Fig. 4).

The species *C. kullenbergi* $\delta^{18}O$ values ($\delta^{18}O_{Cib}$) did not vary greatly for the outer shelf core (BCCF10-01; -0.13 to 0.96‰). *Uvigerina peregrina* $\delta^{18}O$ values ($\delta^{18}O_{Uv}$) varied between 0.52 and 1.17‰ for core BCCF10–01, between 0.79 and 2.16‰ for the mid shelf core (BCCF10-09), and between 0.98 and 1.17‰ for the inner shelf site (BCCF10-15) (Fig. 4).

Grain size analyses revealed a greater proportion of sand at the outer (average of 44.24 ± 10.06%) and inner shelf (39.87 ± 10.34%) compared to the mid shelf core BCCF10-09 (9.06 ± 5.73), with this latter exhibiting the largest proportion of silt (77.17 ± 3.93%). The proportion of clay sediments was higher in the mid shelf core BCCF10-09 (13.76 ± 2.97%), evidencing weaker hydrodynamics than for the BCCF10-01 (6.27 ± 0.76%) and BCCF10-15 (9.09 ± 1.47%) core locations (Fig. 4).

3.4. Multivariate analyses

Our MDS on the relative abundances of benthic foraminifera from the three sediment cores established a different pattern over the oceanographic conditions. The *R. auberii* assemblage explained MDS axis 1 (MDS1) variability and *G. subglobosa* explained MDS axis 2 (MDS2) variability (Fig. 6), with a stress of 0,05394 (Axis1: 0,6922; Axis 2: 0,2583). The *R. auberii* assemblage comprised *R. auberii*, *Evolvocassidulina bradyi* and *Bucella frigida*, all of which are species typical of continental shelf sediments at shallow depths of 35 to 220 m (Langer and Lipps, 2003; Parker and Gischler, 2011). The opportunistic *G. subglobosa* was separated from other species in MDS2 due to its quick response to phytodetritus (Heinz, 2001; Suhr and Pond, 2006; Smart et al., 2010) during periods of efficient biological pumping. Despite also being an opportunistic species, *A. weddellensis* abundance was not as important as *G. subglobosa* to MDS2, probably due to its lower relative abundance.

Cluster analysis separated relative species abundance responses in different groups (Fig. 3). The first group, the *R. auberii* assemblage, was formed by species typical of continental shelves in this region, i.e., *R. auberii*, *E. bradyi*, and *B. frigida*. The second group was formed by *G. subglobosa* alone, which is an opportunistic species that was present in high abundance in all three cores. The third group was subdivided into two subgroups: (a) the *Bulimina marginata* subgroup composed of *B.*
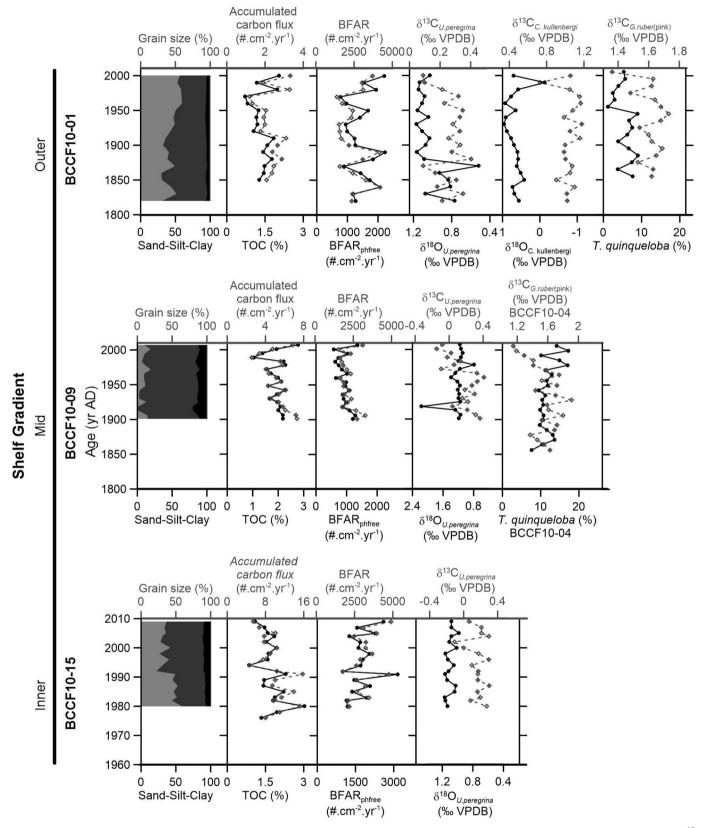
Fig. 4. Down-core variations of accumulated organic carbon (C$_{org}$) flux and total organic carbon (TOC) (Sanders et al., 2014); BFAR and BFAR$_{phfree}$ indexes; stable isotopes (δ^{13}C and δ^{18}O) of *Uvigerina peregrina* and *Cibicides kullenbergi*; stable isotope (δ^{13}C) of *Globigerinoides ruber*; and relative abundance of *Turborotalita quinqueloba* (Venancio et al., 2016) for the outer shelf core BCCF10-01, mid shelf core BCCF10-09 (and BCCF10-04), and inner shelf core BCCF10-15. Dashed gray lines referring to top labels; black lines referring to bottom labels.
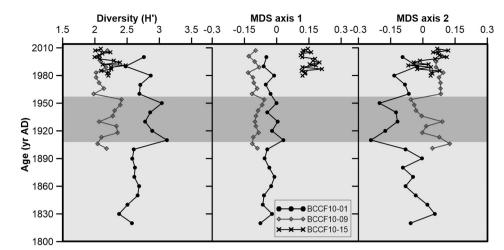
Fig. 5. Shannon diversity, MDS1 and MDS2 scores variation for the three studied cores BCCF10-01, BCCF10-09, and BCCF10-15.
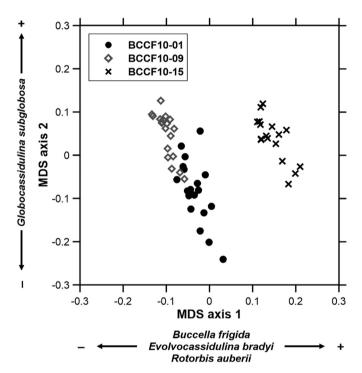

Fig. 6. Crossplot between scores of multi-dimensional scaling axes 1 (MDS1) and 2 (MDS2) for the outer shelf core BCCF10-01, mid shelf core BCCF10-09, and inner shelf core BCCF10-15.

marginata, *Bolivina striatula*, *Bulimina aculeata*, *Eponides* sp., *Pseudono-nion japonicum*, *Bolivina* sp., *Uvigerina peregrina*, *Rosalina bradyi*, *Cibi-cides* sp., *Islandiella curvata*, *Discorbinella bertheloti*, and *Gyroidina um-bonata* (Hayward et al., 2002; Eichler et al., 2014); and (b) the *Alabaminella weddellensis* subgroup comprising *A. weddellensis*, *Trifarina angulosa*, *Cassidulina carinata*, *Bolivina ordinaria*, and *Islandiella australis* (Fig. 3).

4. Discussion

4.1. Inputs of phytodetritus alter stable isotopes

Though $\delta^{13}C$ records for *C. kullenbergi* are constant and close to $\delta^{13}C_{DIC}$ values (DIC = dissolved inorganic content) over the past two centuries, $\delta^{18}O$ values from the epifaunal foraminifera analyzed here are not close to the $\delta^{18}O_{EQ}$ calcite calcification equilibrium, presenting an offset of 1.02‰ (Fig. 4; Table 1). The positive deviation might be related to inaccuracies in $\delta^{18}O_W$ and temperature estimations for sites

or in the $\delta^{18}O_{EQ}$ calculation (Kim and O'Neil, 1997). However, com-paring the values for stable oxygen isotopes from infaunal *U. peregrina* and epifaunal *C. kullenbergi*, we found a slight offset of 0.36 ± 0.28‰ that may be related to microhabitat differences. Despite the suggestion of Fontanier et al. (2006, 2008, 2017) that depth-related microhabitat cannot explain differences between the $\delta^{18}O$ values of shallow infaunal and epifaunal species, other authors have confirmed this relationship (Schmiedl et al., 2004; Theodor et al., 2016). Low pH and $[CO_3^{2-}]$ in pore waters facilitates ^{18}O enrichment in *U. peregrina* (Spero et al., 1997; Bemis et al., 1998), and different patterns of production and incorporation of oxygen isotopes into the shell (de Nooijer et al., 2014) might explain the observed offset.

Epifaunal species (such as some taxa from the genera *Cibicides* and *Planulina*) can secrete calcite very close to the $\delta^{13}C_{DIC}$ from bottom water (Schmiedl et al., 2004; Theodor et al., 2016). Lower values of $\delta^{13}C$ in *Cibicides wuellerstorfi* relative to $\delta^{13}C_{DIC}$ values have been re-ported as being due to high seasonal variation in primary productivity from surface waters to the bottom waters (Mackensen et al., 1993). The $\delta^{13}C$ values of *C. kullenbergi* in this study were 0.26 ± 0.10‰ lower compared to SACW $\delta^{13}C_{DIC}$ (Table 1), so *C. kullenbergi* could have cal-cified their tests in a layer of low $\delta^{13}C$ at the sediment-water interface influenced by labile carbon deposition (Mackensen et al., 1993).

The $\delta^{13}C$ values of infaunal *U. peregrina* reflect the $\delta^{13}C_{DIC}$ profile of sediment pore waters and can vary according to phytodetritus input and decomposition rates of organic material (McCorkle et al., 1990; Schmiedl et al., 2004; Fontanier et al., 2006). We observed a cross-shelf gradient of $\delta^{13}C$ values in the CFUS as a function of different patterns of phytodetritus input (Fig. 4). At the outer shelf, $\delta^{13}C$ of *U. peregrina* presented positive values, indicating low phytodetritus input and re-mineralization at the sediment surface. In the middle shelf, the more negative values of $\delta^{13}C$ reflect increased flux of labile carbon, with the oceanographic conditions prevailing in this region establishing this site as a sediment depocenter with intermittent phytodetritus inputs (Cruz et al., 2013; Mendoza et al., 2014; Venancio et al., 2016). The $\delta^{13}C$ values of the inner shelf also suggest decomposition of seasonal labile carbon, but at a lower rate than observed for the mid shelf region, which is in agreement with the different phytodetritus depositional patterns in each area (Fig. 4) (Sanders et al., 2014).

4.2. Oceanographic features driving benthic foraminiferal disturbances

Observations on the species assemblages in the three cores revealed the dominance of the opportunistic *G. subglobosa*, low relative abun-dances of highly productive infaunal genera such as *Bolivina*, *Bulimina*, *Cassisulina* and *Uvigerina* (Smart, 2008; Smart et al., 2010), and the absence of deep infaunal species characterizing low oxygen conditions (such as *Globobulimina* spp. and *Chilostomella* spp.) (Grunert et al.,

Table 1
Site depth, mean annual temperature, equilibrium calcite $\delta^{18}O$, bottom water stable isotopes, and mean $\delta^{18}O$ and $\delta^{13}C$ of benthic foraminiferal species from the three studied cores.

Core	Depth	Temp.[a]	$\delta^{18}O_{EQ}$[b]	$\delta^{18}O_w$[c]	$\delta^{13}C_{DIC}$[c]	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$
	(mbsl)	(°C)	(VPDB)	(VSMOW)	(VPDB)	(VPDB) *C. kullenbergi*		(VPDB) *U. peregrina*	
BCCF10-01	128	17.72	− 0.37	0.46 ± 0.10	1.30 ± 0.22	0.65 ± 0.24	1.04 ± 0.10	1.02 ± 0.17	0.25 ± 0.09
BCCF10-09	120	17.72	− 0.37	0.46 ± 0.10	1.30 ± 0.22	–	–	1.22 ± 0.26	0.15 ± 0.17
BCCF10-15	79	18.85	− 0.61	0.46 ± 0.10	1.30 ± 0.22	–	–	1.10 ± 0.06	0.16 ± 0.11

[a] Annual temperature data extracted from World Ocean Atlas 2013 from latitude 23°S, longitude 41°W and depths 80 and 125 m.
[b] Values based on Kim and O'Neil (1997) equation. SMOW values converted to VPDB scale using Friedman and O'Neil (1977) equation.
[c] Isotopic data from SACW according Venancio et al. (2014).

2015) (Figs. 2 and 3). We only found epifaunal species (such as *Cibicides* spp. and *D. berthelotti*) at the outer shelf (Fig. 3). Considering the TROX model proposed by Jorissen et al. (1995), which is a concept of benthic foraminiferal microhabitats linking food availability and environmental oxygenation, the CFUS can be designated as a well-oxygenated zone with low to moderate productivity, but one that is also disturbed by phytodetritus inputs to the seafloor via episodic biological pump events. Oxic conditions dominate the bottom water and sediment of this zone, except during the brief periods of high phytodetritus input when short-term suboxic conditions are observed (Diaz et al., 2012). The labile carbon is quickly consumed by the benthic communities and degraded in the first centimeters of sediment, preventing accumulation of large amounts of organic carbon in the sediments and limiting the abundance of highly productive infaunal species.

High abundances of *G. subglobosa* are commonly linked to the ability of this species to reproduce rapidly under the stressful condition of intense phytodetritus delivery from subsurface waters to the sediment (e.g., Heinz, 2001; Gooday et al., 2010). In the Brazilian margin, this species has also been highlighted as an indicator of oligotrophic, well-oxygenated bottom water, and strong transport of BC (Eichler et al., 2008; Nagai et al., 2009; Paquette et al., 2016; Eichler et al., 2016). The other opportunistic species we found was *A. weddellensis*, a taxon that exhibits a similar ecology to *G. subglobosa*, but that may also be associated with high diatom flux and productivity (Stefanoudis et al., 2017). *Globocassidulina subglobosa* and species from the *A. weddellensis* subgroup are indicative of intermittent and/or pulsed phytodetritus inputs (Ohkushi et al., 1999; Hayward et al., 2002). The low abundances of species of the *B. marginata* subgroup and the rarity/absence of species commonly found in marine continental shelf environments suggests a disturbance caused by phytodetritus (Figs. 2 and 3). We explain further in the next section how *B. marginata* appears to compete for phytodetritus with other opportunists. In spite of the similar high hydrodynamics of the bottom waters of the inner and outer shelves, as revealed by grain size distribution (Cruz et al., 2018) (Fig. 4), the benthic assemblage of the inner shelf is differentiated from those of the mid and outer shelves by a bathymetric effect, as evidenced by the *R. auberii* assemblage (Figs. 3 and 6). Association of *T. angulosa* with *C.*

carinata is linked to shallow depths, high sand content, and cold water temperatures, whereas an *A. weddellensis* and *C. carinata* association is typically related to pulses of organic matter (Hayward et al., 2002). As the same, *Buccella frigida* (and other species from the same genus) are related to cold shelf water and high seasonal productivity (Polyak and Mikhailov, 1996; Cann and Cronin, 2004; Slubowska et al., 2005), which is in accordance with the oceanographic conditions of the inner shelf area.

4.3. Temporal disturbances of the benthic community

Disturbances in marine environments are key processes determining community structure and may affect species diversity, as reported in many studies (e.g., Norkko et al., 2006; Corliss et al., 2009; Gooday et al., 2010). Species diversity and organic carbon supply have been reported as dependent variables in some studies performed in oligotrophic regions (e.g., Gooday and Rathburn, 1999; Kurbjeweit et al., 2000). However, when benthic communities are subjected to intense phytodetritus inputs, the resulting increase in the metabolic activity of benthic organisms may result in changes to oxygen consumption and species diversity of the benthic community (Gooday, 2002; Corliss et al., 2009). Consequently, a negative correlation between species diversity and organic carbon content might be expected. However, the dissimilarity observed in the three cores studied here represent an instance of organic material decomposition by other reactions that not only involve oxic remineralization (Soetaert et al., 1996; Diaz et al., 2012).

The opportunists *G. subglobosa* and *A. weddellensis* react very quickly to phytodetritus exported to the sediment surface. These r-strategist species colonize phytodetritus aggregates in the sediment surface, obtaining an advantage over other species that react more slowly to the phytodetritus (Heinz, 2001). Colonization and dominance by opportunists results in a reduction of the diversity of benthic foraminifera (Corliss et al., 2009), as observed here for the three CFUS cores. Differences in intensity/frequency of phytodetritus inputs result in varying impacts on benthic diversity. Despite the minimum and maximum values of species diversity in the CFUS agreeing with other continental

Table 2
Shannon diversity index of benthic foraminifera from this study and other continental shelf areas.

Location	Depth (mbsl)	Size fraction (μm)	H′	Age	Reference
Mediterranean Sea	40–108	> 50	1.8–3.5	Recent	Bousi et al. (2012)
Marmara Sea	13–482	> 63	2.5–3.7	Recent	Avşar (2010)
Portugal Margin	90–96	> 125	2.4–3.2	Last 2000 yr	Bartels-Jónsdóttir et al. (2006)
Spain NW Margin	115	> 63	2.2–3.3	Last 4500 yr	Nagai et al. (2016)
Portugal N Margin	10–700	> 63	1.7–3.4	Recent	Martins et al. (2012)
Brazil S Margin	27–209	> 63	1.0–2.6	Recent	Eichler et al. (2008)
Brazil S Margin	5–60	> 63	1.8–3.0	Recent	Paquette et al. (2016)
Brazil SE Margin	26–103	> 63	0.6–3.3	Recent	Vieira et al. (2015)
Brazil SE Margin	40–1000	> 63	1.2–3.7	Recent	Yamashita et al. (2016)
Brazil SE Margin	44	> 63	1.1–2.7	Last 9000 yr	Nagai et al. (2016)
Brazil SE Margin	79–128	> 63	2.0–3.1	Last 200 yr	(this study)

shelf areas (Table 2), we did find evidence of a cross-shelf gradient. Lower species diversity was observed in CFUS areas under the influence of seasonal and intermittent phytodetritus input, whereas higher species diversity was observed in less disturbed areas, where upwelling events are only dependent on variations in the internal front of the BC (Venancio et al., 2016) (Fig. 5). Highly diverse communities present a range of functional traits that promote resilience and reduce the impacts of disturbances (Randall et al., 2013). Our results confirm that distinct levels of disturbance can influence community-level species diversity in different ways.

The upwelling events in the mid and inner shelf domains are extremely sensitive to winds, which can initially favor primary production by rapid turnover of water masses. However, reduced wind stress curl can suddenly disrupt the upwelling process (Venancio et al., 2016), thereby reducing primary productivity and creating abrupt shifts in the benthic community, as we observed between 1910 and 1960 CE. The increased diversity in 1910 CE reflects enhanced community resilience arising from disturbances of high phytodetritus inputs. However, we identified a new phase of disturbance in the community after 1960 CE when resumption of environmental disruption again decreased species diversity (Fig. 5). We identified a proportional shift of about 0.4 in diversity values over the cores with greater temporal coverage (BCCF10-01 and BCCF10-09), suggesting that timing of phytodetritus export is similar for the different cores we sampled, even under the influence of different oceanographic processes. Therefore, the frequency (seasonal and intermittent pulses) of phytodetritus inputs seems to greatly impact benthic communities in terms of their species diversity. Corliss et al. (2009) reported a similar response in a North Atlantic benthic community, demonstrating a strong influence of pelagic-benthic linkage created by episodic pulses of organic matter in reducing diversity indexes.

Our MDS also reflects our diversity analysis on the multidecadal scale, corroborating that phytodetritus disturbances are linked to changes in the intensity of upwelling events. MDS1, comprising species typical of shallow continental shelves, presented a strong positive correlation with the species diversity index, which contrasted with MDS2 ($p < 0.0001$; $p < 0.05$, respectively) that was constituted by the opportunistic *G. subglobosa* (Figs. 5 and 6). These relationships lead us to presume that MDS1 represents species that can compensate the negative effects of opportunistic species dominance to disturbances, supporting the spatial insurance hypothesis (Loreau et al., 2003). Species typical of shallow continental shelves in this region, such as *B. frigida*, *E. bradyi*, *R. auberii* and others, may also act as a functional complement to the community across space and time, insuring the community against stressful conditions (Shanafelt et al., 2015). The negative correlation between MDS1 and MDS2 shows that MDS-linked species abundances tend to fluctuate relative to each other as variation through time diminishes, supporting the portfolio effect for an ideal diverse community (Randall et al., 2013; Schindler et al., 2015). The contrasting trend of MDS2 compared to MDS1 highlights a negative interaction (competition) between *G. subglobosa* and other species from the continental shelf over the past two centuries. The opportunistic *G. subglobosa* is well adapted to phytodetrital disturbances and can induce decreased diversity by promoting the loss of k-selective taxa, as observed up to 1910 CE and after 1960 CE (Fig. 5). In this sense, biodiversity of the benthic foraminiferal community of the CFUS seems to be far from stable.

During the most pronounced phytodetritus input events (around 1840, 1880, and 1990 CE) both opportunist and generalist species benefited, with both showing increased abundance and fluxes (dark gray bars in Fig. 2). The only exception was *B. marginata*, a species that showed a negative correlation with *G. subglobosa* abundance ($p < 0.01$). Some studies have reported *B. marginata* as an opportunistic infaunal species that inhabits low oxygen environments and is indicative of high seasonal pulses of phytodetritus and unstable conditions (Eichler et al., 2014; Drinia et al., 2016; Duros et al., 2017).

Considering the opportunistic behavior of *B. marginata* and *G. subglobosa*, the reproductive potential of these species could drive population growth and competition for phytodetritus (Van der Zwaan et al., 1999). R-selective species, such as *G. subglobosa* and *A. weddellensis*, could limit the growth of *B. marginata*, especially during periods of high food availability (dark gray bars in Fig. 2). Despite losing out to rapidly colonizing species, *B. marginata* presents greater resilience to periods of lower flux and/or food quality changes than most other species (light gray bars in Fig. 2).

The most recent highly productive phase in the CFUS is marked by strong biological and isotopic changes in the bottom water. After 1970 CE, higher BFAR and BFAR$_{phfree}$ indexes coincided with accumulated organic carbon, decreased diversity, and depletion of ^{13}C in *U. peregrina* tests (Fig. 4). These results confirm increased phytodetritus and carbon accumulation in sediments, promoting changes in pore water composition by remineralization. Venancio et al. (2016) reported an intensification of upwelling signal by δ^{13}C values of *G. ruber* (pink) and the abundance of cold-water *T. quinqueloba* in the same period (Fig. 4). According to these authors, SACW intrusions into the photic zone lower sea surface temperatures and draw nutrients and depleted δ^{13}C$_{DIC}$ to the surface, thereby improving primary productivity in the water column. Souto et al. (2011) also verified an intensification of upwelling events by planktonic foraminifera from the same region, and linked the prolonged presence of SACW upwellings to atmospheric factors. Southward displacement of the Intertropical Convergence Zone (ITCZ) may intensify northeastern winds off the Southeastern Brazilian coast and, consequently, the upwelling events and pulses in primary productivity. However, data derived from the NCEP 20th Century Reanalysis V2 calculated by Venancio et al. (2016) do not show a clear trend for increased values of wind stress at 40°S over the last century and, according to these authors, this may reflect an issue with spatial coverage and resolution. In also reanalyzing century-long ocean and atmospheric data for the entire length of southwestern boundary currents, Wu et al. (2012) observed a general trend for enhanced wind stress curl, sea surface temperature and BC strength after 1950 CE compared to the period 1900–1950 CE, with results that are consistent with the observed trends in upwelling events in the CFUS.

Higher export of phytodetritus, as indicated by species assemblages and stable isotopes of planktonic and benthic foraminifera, supports the existence of an efficient biological pump due to upwellings induced by intensified northeastern winds. While an efficient biological pump plays an important role in the climatic system through uptake, storage and transfer of atmospheric CO$_2$ to the ocean bottom (Fariduddin and Loubere, 1997; Lutz et al., 2007), it may also disturb biological interactions and perturb benthic biodiversity, thereby affecting community stability and successional processes following disturbances.

5. Conclusion

The distribution of the benthic foraminiferal community in the CFUS was greatly disturbed by the frequency and timing of phytodetrital inputs produced by different oceanographic processes in the region. The shift between *C. kullenbergi* δ^{13}C and δ^{13}C$_{DIC}$, the dominance of *G. subglobosa*, the rarity/absence of species in the *B. marginata* subgroup, and the variability in species diversity confirmed the instability of the benthic community due to phytodetritus. In 1910 CE, benthic community diversity recovered following a change from high to low phytodetrital input, exhibiting resilience to disturbing conditions. The negative correlation between MDS1 (explained by *R. auberii* assemblage) and MDS2 (explained by *G. subglobosa*) demonstrates an ability for MDS1 species to compensate for the negative interactions of opportunistic species (MDS2) arising from disturbances across the community structure. Despite this compensatory effect, the CFUS benthic community seems to be far from a stable diversity, due to the reproductive potential of r-selective

species inhibiting *B. marginata* growth during episodes of high phytodetritus input.

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Appendix A. Species reference list

Alabaminella weddellensisi (Earland) = *Eponides weddellensis* Earland, 1936.

Bolivina ordinaria Phleger & Parker, 1952.

Bolivina striatula Cushman, 1922.

Buccella frigida (Cushman) = *Pulvinulina frigida* Cushman, 1922.

Bulimina aculeata d'Orbigny, 1826.

Bulimina marginata d'Orbigny, 1826.

Cassidulina carinata (Silvestri) = *Cassidulina laevigata* var. *carinata* Silvestri, 1896.

Cibicides Montfort, 1808.

Discorbinella bertheloti (d'Orbigny) = *Rosalina bertheloti* d'Orbigny, 1839.

Eponides Montfort, 1808.

Evolvocassidulina bradyi (Norman) = *Cassidulina bradyi* Norman, 1881.

Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady, 1881.

Gyroidina umbonata (Silvestri) = *Rotalia soldanii* var. *umbonata* Silvestri, 1898.

Islandiella australis (Phleger &Parker) = *Cassidulina australis* Phleger & Parker, 1951.

Islandiella curvata (Phleger &Parker) = *Cassidulina curvata* Phleger & Parker, 1951.

Pseudononion japonicum Asano, 1936.

Rosalina bradyi (Cushman) = *Discorbis bradyi* Cushman, 1915.

Rotorbis auberii (d'Orbigny) = *Rosalina auberii* d'Orbigny, 1839.

Trifarina angulosa (Williamson) = *Uvigerina angulosa* (Williamson, 1858).

Uvigerina peregrina Cushman, 1923.

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