



Late quaternary sea bottom conditions in the southern Panama basin, Eastern Equatorial Pacific



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ABSTRACT

A paleoceanographic reconstruction of the southern Panama Basin for the last 23,000 years, based on the benthic foraminiferal analysis from the deep sea core ME0005A-24JC (0.01°N, 86.28°W, water depth 2941) is presented. Cluster and SHEBI (SHE Analysis for Biozone Identification) analyses performed on the benthic foraminiferal assemblages, evidence a faunal turnover in the early Holocene at 14 ky BP. Between 23 and 14 ky BP, *Fursenkoina rotundata*, *Hoeglundina elegans*, *Globobulimina affinis*, *Globobulimina pacifica*, *Cibicidoides wuellerstorfi* and *Uvigerina hispidocostata* were common. Conversely, from 14 ky to the present, the assemblage is represented by *Chilostomella oolina*, *Laticarinina pauperata*, and *Uvigerina proboscidea*. This faunal turnover suggests significant fluctuations in oxygen content at the sea floor and the organic matter (OM) influx, which could reflect: (1) fluctuations in the surface productivity related to the equatorial divergence and, (2) OM advection caused by the dynamic of the deep sea currents.

Paleoproductivity estimates and benthic foraminiferal rates depict a general trend towards lower values since the Last Glacial Maximum (LGM) with a conspicuous change at 14 ky BP. Therefore, the paleoceanographic reconstructions of the ME0005A-24JC core suggest a transition from La Niña-like conditions during the LGM to El Niño-like conditions in the recent, as previously proposed for the Eastern Equatorial Pacific. Estimates of the paleo-intensity of deep sea currents based on the relative percentage abundance of the epifaunal foraminifera *Cibicidoides wuellerstorfi* suggest stronger deep sea currents on the Carnegie Ridge before 14 ky BP.

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1. Introduction

The Eastern Equatorial Pacific (EEP) is a key area for understanding of both, past climate fluctuations and future world climate scenarios. With this goal in mind, a number of investigations have focused on the paleoceanographic mechanisms in the EEP for the last 25 ky BP (e.g. Arrhenius, 1952; Pedersen et al., 1988; Herguera, 2000; Loubere, 2002; Lyle et al., 2005; Koutavas and Lynch-Stieglitz, 2003; Benway et al., 2006; Kienast et al., 2007; Bradtmiller et al., 2010; Kusch et al., 2010; Martínez and Robinson, 2010; Rincon-Martínez et al., 2010; Cabarcos, 2011; Dubois et al., 2011; Yu et al., 2012; De la Fuente et al., 2015). However, some phenomena challenge more accurate paleoclimatic modeling in the EEP: (1) the seasonal movements of the Intertropical Convergence Zone (ITCZ) that control rainfall patterns, (2) the heat and moisture

transference from the Caribbean Sea to the EEP, which affects physicochemical variables such as the sea surface salinity (SSS), (3) regional or seasonal upwelling phenomena which control biological productivity and, (4) meso-scale convective complexes, i.e. the Chocó Jet, which control rainfall patterns (e.g. Pak and Zaneveld, 1974; Benway and Mix, 2004; Poveda et al., 2006; Fiedler and Talley, 2006; Garreaud et al., 2009). Furthermore, over-imposed on all these processes there are quasi-periodic climatic events such as El Niño-Southern Oscillation or ENSO phenomenon (e.g. Clement et al., 1999; Carré et al., 2012).

The referred phenomena have hampered the study of the recurrence and variability of the ENSO and its relationship with the physicochemical changes at the EEP. For instance, paleoceanographic interpretations using the Last Glacial Maximum (LGM) as scenario have proven to be controversial (e.g. Lyle et al., 1992; Patrick and Thunell, 1997; Loubere et al., 2003; Bradtmiller et al., 2006; Dubois et al., 2009; Leduc et al., 2010; Kienast et al., 2012). The pioneering study of the CLIMAP project (1978) concluded that sea surface temperatures (SST) did not drop >2 °C for the EEP

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during the last glaciation. In contrast, several paleoclimatic reconstructions on continental records from South America suggest a decrease in the temperature of about 5 °C during the same period (e.g. Stute et al., 1995; van der Hammen and Hooghiemstra, 2000). Recently, new analytic methods (i.e. modern analogs, neuronal networks) and proxies (i.e. alkenones, Mg/Ca in calcareous tests) have improved SST estimates for the EEP for the late Quaternary and the Holocene (i.e. MARGO Project, 2009).

Furthermore, following the LGM there is a discrete interval of time (20–18 ky BP), when several aspects could affect the resolution of the proxies used: (1) the depth of the lysocline, (2) physiological features of the organisms used as proxies, (3) winnowing and focusing processes and, (4) seasonal controls. For instance, some studies suggest that SSTs between 3 and 5 °C were highly influenced by La Niña-like events while others propose an opposite scenario with dominant El Niño-like events (e.g. Pisias and Mix, 1997; Beaufort et al., 2001; Koutavas et al., 2002; Martínez et al., 2003; Leduc et al., 2009; Rincon-Martínez et al., 2010). In addition, the physicochemical parameters of the deep sea water masses in the EEP, which are influenced by surface productivity, also show a highly dynamic pattern for the LGM (e.g. Loubere, 1999, 2000; Martínez et al., 2006; Ovsepyan and Ivanova, 2009; Bradmitler et al., 2006, 2010).

Due to its proximity to the Galapagos Archipelago and the Equatorial Front, the deep sea ME0005A-24JC core (0.01°N, 86.28°W, water depth 2941 m) is one of the most studied sedimentary records in the EEP, having also a robust age control (Lyle et al., 2005; Kienast et al., 2006, 2007; Dubois et al., 2009, 2011). This study contributes with the knowledge of the EEP paleoceanography by: (1) a high resolution benthic foraminiferal analysis (samples each 400 years) and, (2) a bottom of deep sea benthic foraminiferal assemblages. Estimates of bottom paleoxygenation reconstruction, (3) a surface paleoproductivity and, (4) an estimate of the past intensity of deep sea currents based on the occurrence of the benthic foraminifera *Cibicidoides wuellerstorfi*.

2. Study area

Deep sea core ME0005A-24JC, which is a reference site for ODP 202 Leg 1240, was retrieved in the southern of the Panama Basin, almost 400 km northeast of the Galapagos Archipelago (Fig. 1). The ME0005A-24JC core was retrieved from a typical abyssal hill ~150 km south of the Carnegie Ridge (Mix et al., 2003), where sediments are mainly pelagic and composed of foraminifera tests, coccolithophores and diatoms (Heath et al., 1973; Swift, 1977; Lyle et al., 1992; Mix et al., 2003). Sedimentation rates range between 5 and 7 cm/ky with a focusing factor >2 based on ²³⁰Th records, and an upper oxygenated level which ranges between 7 and 10 cm (Fig. 1; Lyle et al., 1992; Kienast et al., 2007; Singh et al., 2011).

Surface water masses over the Carnegie Ridge are controlled by: (1) the upwelling system associated to the equatorial divergence, which is more intense in the boreal summer (700–800 mgC/cm²d) and, (2) the Equatorial Front (EF) which is the boundary between water masses with cool (<25 °C) and high salinity (>34 psu) south part of the Equator and, warm (25 °C) and less saline (<34 psu) in the Panama Basin (Fig. 1; Fiedler and Talley, 2006). The distribution of the surface water masses is controlled by the Equatorial Counter Current (ECC), the Subsurface Current (SC) and the Southern Equatorial Current (SEC; Strub et al., 1998; Fiedler and Talley, 2006; Kessler, 2006). Both, the bottom water masses of the Panama Basin and the Carnegie Ridge are analogous (34.6 psu; 2–3 °C; 27.5 kg/m³), compared to their of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic values, which vary depending on their residence times (Laird, 1971; Kroopnick, 1974; Fiedler and Talley, 2006). Sub-surface water masses include the Antarctic Intermediate Water (AAIW) and the Lower Circumpolar

Deep Water (LCDW) which circulate from south to north along the Ecuador–Colombia Trench (Fig. 1; Lonsdale, 1976; Emery and Meincke, 1986). A sill on the middle Carnegie Ridge allows the exchange of deep water inside and outside the Panama Basin, being also a region with high lateral transport of sediments and large sand dunes (Lonsdale and Malfait, 1974).

3. Materials and methods

A total of 89 samples of the first 3.5 m of the ME0005A-24JC core were analyzed (sampling each 3–4 cm). Each sample (5–8 g) was washed with distilled water using the 63 and 150 μm fractions sieves. The retained material was dried and all the benthic foraminifera per sample (100–200 specimens) were counted to obtain statistically relevant populations (Fatela and Taborda, 2002; Forcino, 2012).

The taxonomic identification of the benthic foraminiferal assemblages was based on: (1) taxonomic keys (e.g. Boltovskoy and Gualançay, 1975; van Morkhoven et al., 1986; Clark and Patterson, 1993; Revets, 1996; Loeblich and Tappan, 1964; Seiglie, 1969; Bornmalm, 1997; Holbourn and Henderson, 2002; Revets, 2005), (2) foraminiferal reports from the EEP (e.g. Lalicker and McCulloch, 1940; Cushman and McCulloch, 1942; Bandy and Arnal, 1957; Smith, 1963, 1964; Bandy and Rodolfo, 1964; Golik and Phleger, 1977; Gualançay, 1986; Betancur and Martínez, 2003), (3) foraminiferal reports from selected deep sea settings worldwide (e.g. Douglas, 1973; Matoba and Yamaguchi, 1982; Thomas, 1985; Kaiho, 1992; Akimoto, 1990; Resig, 1990; Kaiho and Nishimura, 1992; Nomura, 1992; Rathburn and Corliss, 1994; McDougall, 1985; Schönfeld and Spiegler, 1995; Ohkushi et al., 2000; Szarek et al., 2005; Sarkar et al., 2009; De and Gupta, 2010). Both, the list of genera and their counts (percentage and total) are in Appendixes 1 and 2.

The diversity estimates Shannon Wiener (S) and evenness (E), were conducted using the Past software (Hammer et al., 2001), in addition to an SHEBI (“SHE Analysis for Biozone Identification”) analysis:

$$\text{SHEBI} = \ln(E)$$

SHEBI analysis searched general trends in the $\ln(E)$ values in order to identify different assemblage intervals in the ME0005A-24JC core (Buzas and Hayek, 1996, 1998, 2005; Hayek and Buzas, 1997; Wilson, 2008, 2011). A cluster analysis (Ward minimum variance) was also conducted. Only species with percentage abundances with $\geq 1\%$ of the total assemblage and counted in more of two samples were selected for the cluster analysis.

Mass accumulation rates (MAR) were calculated using the values of the estimated sedimentation rate and the dried sediment densities on each sample (*sensu* Mitch Lyle, Texas A&M University and unpublished data of Nicklas Pisias, Oregon State University). The analyzed interval of the ME0005A-24JC core follows the age model of Kienast et al. (2007). Estimates of benthic foraminiferal accumulation rates (BFAR) for the analyzed samples used the Herguera and Berger (1991)' formula:

$$\text{BFAR} = A \cdot \text{MAR}$$

For the determination of the BFAR in each sample, the number of individuals per gram of material (A) and the MAR of all the samples were used. By using the water depth of the ME0005A-24JC core ($Z = 2941 \text{ km}$), it was possible to estimate paleoproductivity (PP) applying Herguera (2000)'s equation:

$$\text{PP} = 0.4Z \cdot \text{BFAR} \cdot 0.5$$

As a check, these paleoproductivity estimates were compared

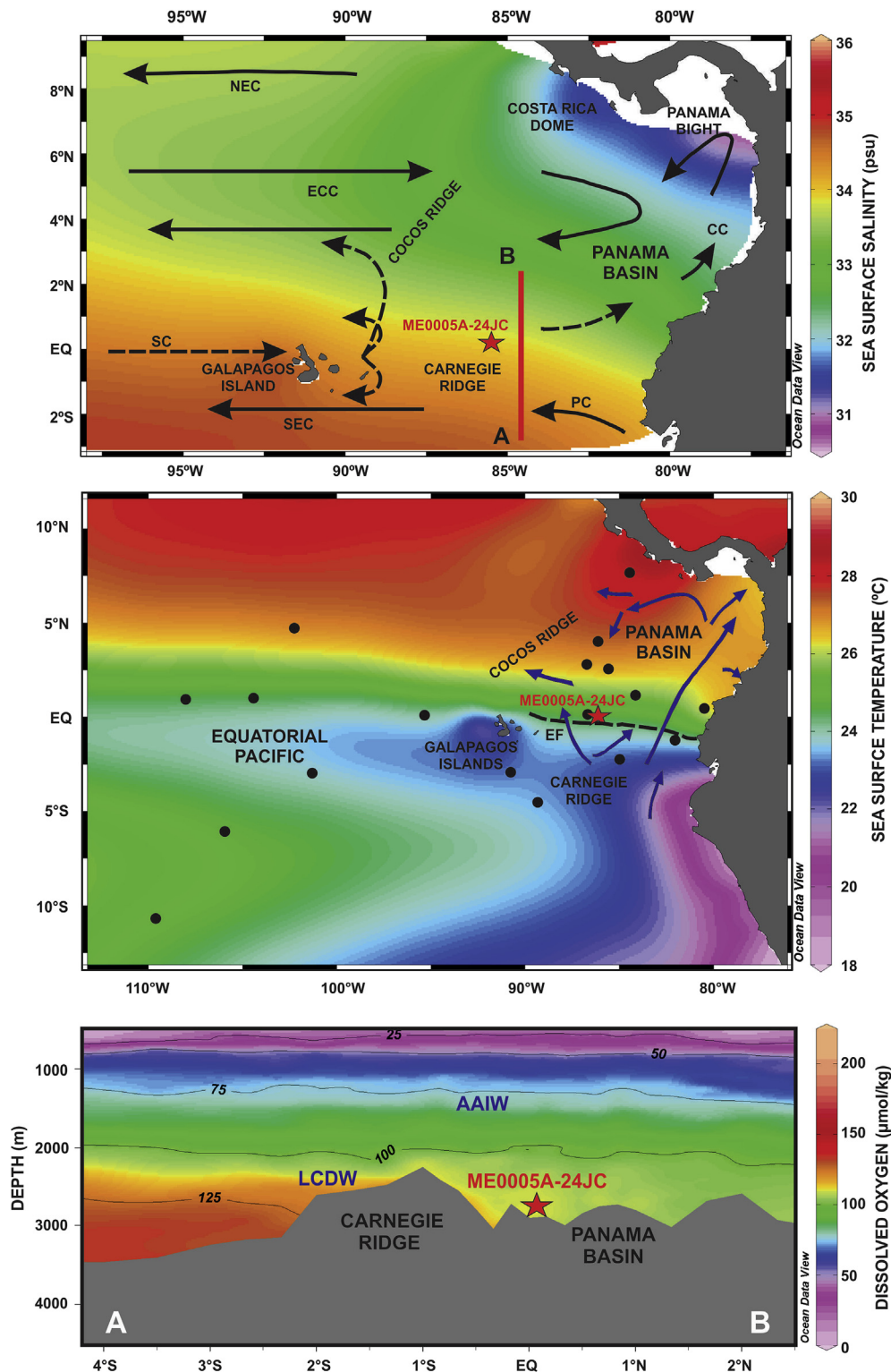


Fig. 1. Location and oceanographic setting of the ME0005A-24JC core. Top: Surface currents: North Equatorial Current (NEC), South Equatorial Current (SEC), Equatorial Counter Current (ECC), Subsurface (SC), Peru (PC) and Colombia (CC). Middle: Sites with studies of deep sea benthic foraminifera (black dots: Loubere, 1999, 2002; Herguera, 2000; Martínez et al., 2006; Ovsepyan and Ivanova, 2009; Arteaga, 2011). The line indicates the position of the Equatorial Front (EF) while the arrows indicate the direction of the bottom currents in the Panama Basin (Lonsdale and Malfait, 1974). Bottom: Average content of dissolved oxygen in the deep sea water masses of the central part of the Carnegie Ridge. Water masses: Antarctic Intermediate (AAIW) and Lower Circumpolar (LCDW). Oceanographic data of Antonov et al. (2010), Garcia et al. (2010) and Locarnini et al. (2010) using the program Ocean Data View (Schlitzer, 2010).

with foraminifera taxa who are particularly controlled by fluctuations in the paleoproductivity and paleoxygenation conditions (e.g. Kaminski et al., 1988; Murray, 1991, 2006; Rathburn and Corliss,

1994; Bernhard and Gupta, 1999; Schönfeld, 2002a; Sarkar et al., 2009; De and Gupta, 2010).

Finally, these paleoceanographic estimates obtained from the

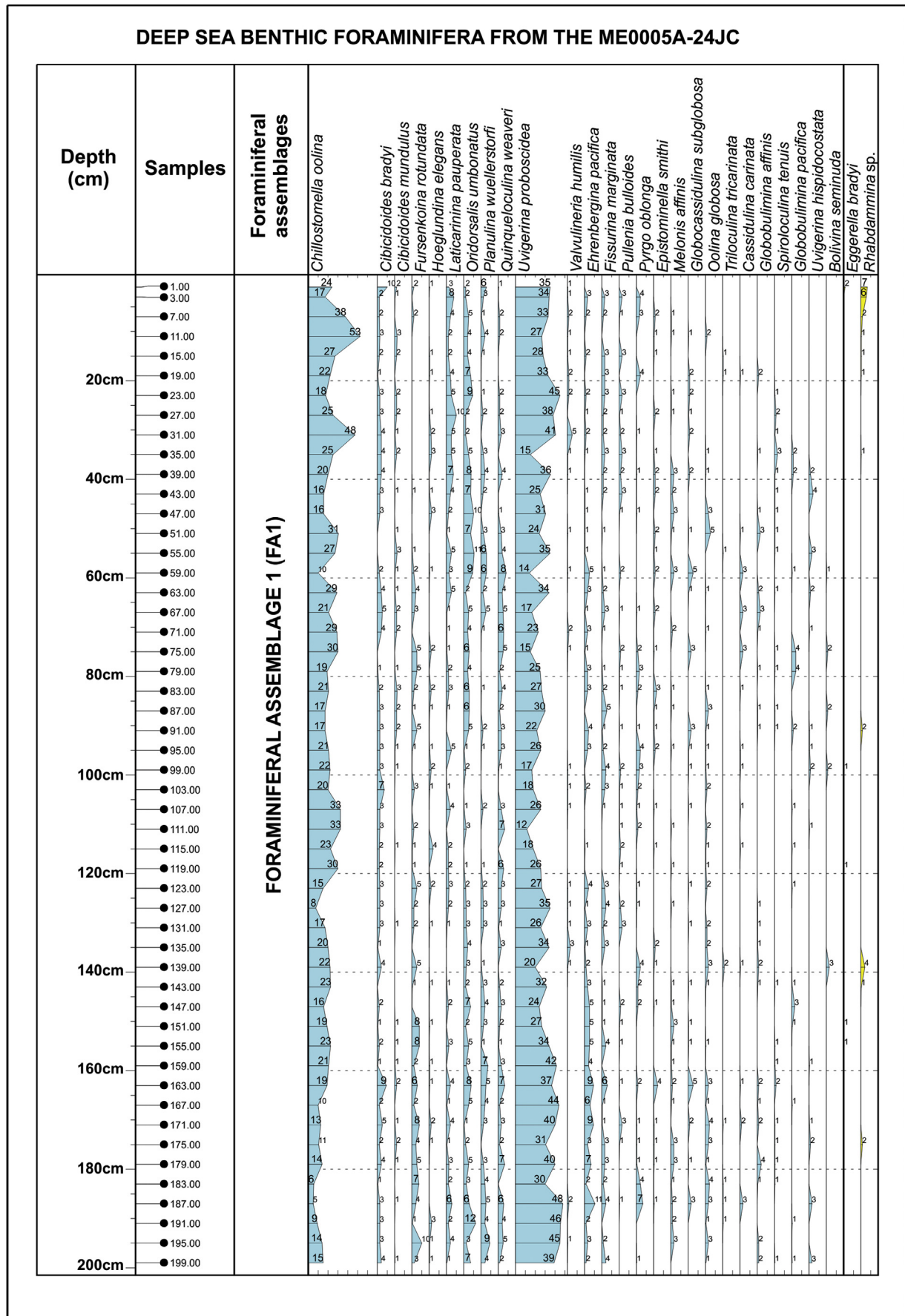


Fig. 2. Stratigraphic distribution of selected benthic foraminifera in the ME0005A-24JC core. Fig. 2a. Foraminifera of the interglacial interval. Fig. 2b. Foraminifera of the glacial interval. Plotted data using the program Stratabugs.

DEEP SEA BENTHIC FORAMINIFERA FROM THE ME0005A-24JC

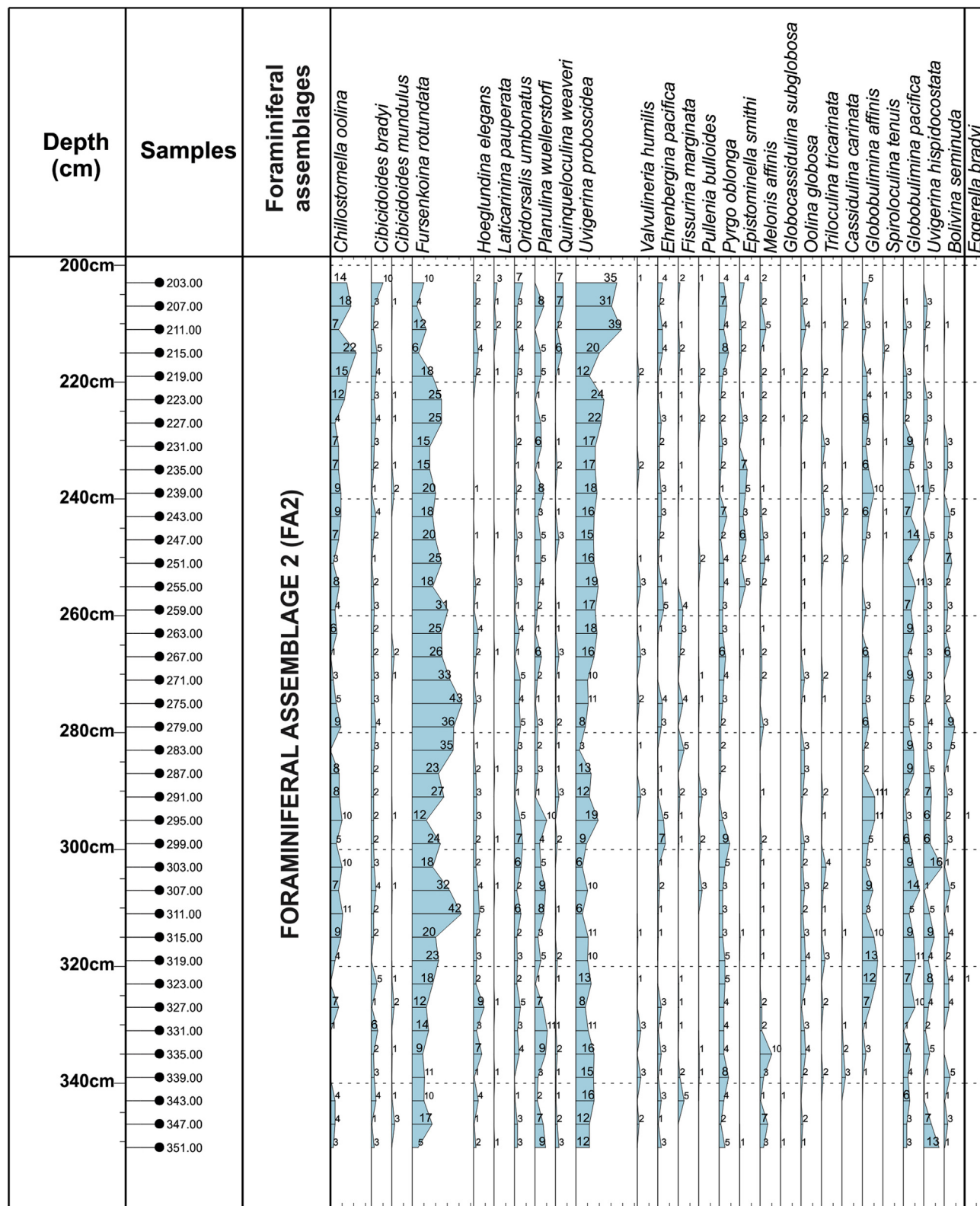


Fig. 2. (Continued).

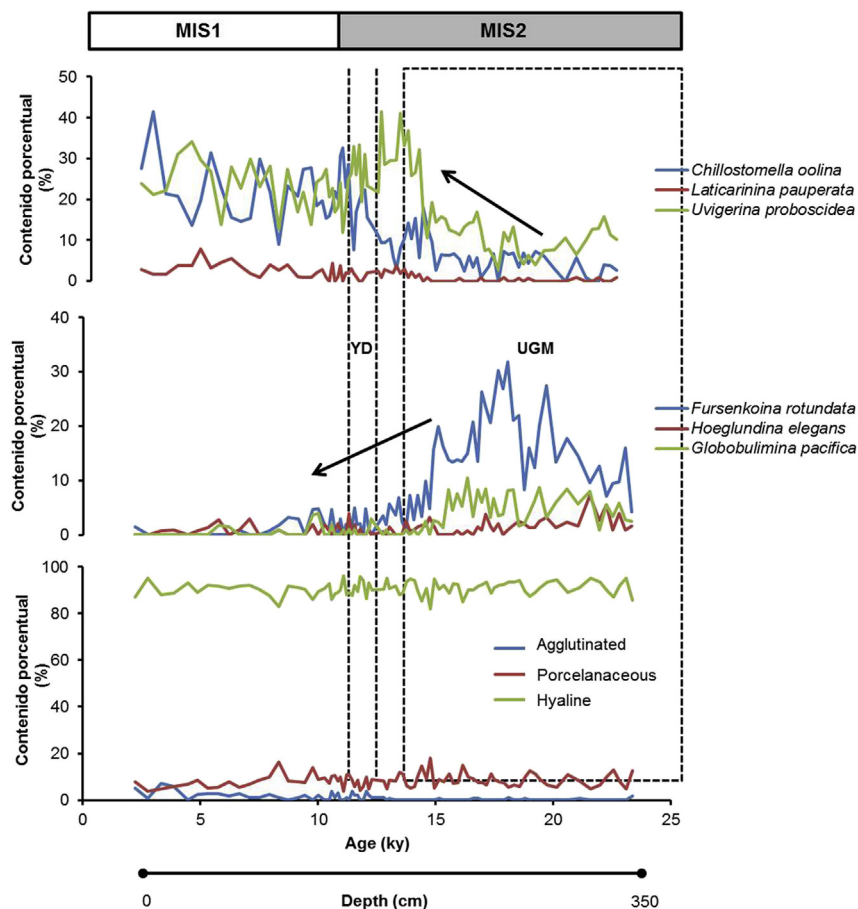


Fig. 3. Percentage abundances of the most representative taxa and the foraminiferal groups according to their type of test in the ME0005A-24JC core. Top: Percentage abundances of the species *Chillostomella oolina*, *Laticarinina pauperata* and *Uvigerina proboscidea*. Middle: Percentage abundances of the species *Fursenkoina rotundata*, *Hoeglundina elegans* and *Globobulimina pacifica*. Bottom: Percentage abundances of the hyaline, porcelanaceous and agglutinated forms. Note the fluctuations in the values in both the glacial (MS2) and interglacial (MS1) stages in the three figures.

ME0005A-24JC were compared with: (1) previous paleoceanographic inferences in the same core (Lyle et al., 2005; Kienast et al., 2006, 2007; Dubois et al., 2009, 2011), (2) paleoproductivity estimates based on benthic foraminiferal assemblages in the EEP (Loubere, 1999, 2002; Herguera, 2000; Martínez et al., 2006; Ovsepyan and Ivanova, 2009; Arteaga, 2011) and, (3) relevant paleoceanographic records in the EEP (e.g. Patrick and Thunell, 1997; Loubere et al., 2003; Bradtmiller et al., 2010; Leduc et al., 2010; Rincon-Martínez et al., 2010; Arellano et al., 2011; Kienast et al., 2012).

The BFAR estimates of the sites ME0005A-24JC, TR163-38 and ODP677B (Betancur and Martínez, 2003) are listed in the Appendix 3. The paleoproductivity estimates of the ME0005A-24JC (our study), and the sites TR163-38 and ODP677B (applying the Herguera's equation) are listed in the Appendix 4. The paleoproductivity estimates in the other cores were calculated using the BFAR data of Betancur and Martínez (2003).

4. Results

A total of 75 genera and 130 species of benthic foraminifera were identified along the core with a proportion of less than 200 specimens in each analyzed sample. Benthic foraminiferal assemblages from ME0005A-24JC core resemble those reported in sub-recent samples of the Carnegie ridge area (Gualancañay, 1986; Loubere and Fariduddin, 1999; Betancur and Martínez, 2003;

Patarroyo and Martínez, 2013a-b). The hyaline test is dominant in the benthic foraminiferal assemblages compared to the agglutinated and porcelanaceous tests, which are subordinated. Common hyaline forms are *Bolivina* spp., *Bulimina marginata*, *Chilostomella oolina*, *Cibicides* spp., *Fursenkoina* spp., *Globobulimina* spp., *Globocassidulina subglobosa*, *Hoeglundina elegans*, *Laticarinina pauperata*, *Oridorsalis umbonatus*, and *Uvigerina* spp. Less common hyaline forms are *Cassidulina carinata*, *Dentalina* spp., *Fissurina* spp., *Ehrenbergina pacifica*, *Epistominella* spp., *Gyroidina* spp., *Lagena* spp., *Oolina* spp., *Nonion* spp., *Melonis* spp., *Parafissurina* spp., *Pullenia quinqueloba*, *Siphonodosaria* spp., *Trifarina bradyi* and *Valvulineria* spp. Taxa such as *Pyrgo murhina*, *Quinqueloculina* spp., *Triloculina* spp. are present as porcelanaceous forms. Agglutinated forms along the core are *Cyclammina* spp., *Eggerella bradyi*, *Lagenammmina* spp., *Martinottiella communis*, *Paratrochammina challengerii*, *Rhabdammina* spp. and *Reophax* spp. (Figs. 2–3).

In addition, >70% of the total assemblage is represented by epifaunal foraminifera species in the 23 to 13 ky BP interval, whereas a steady decreasing trend in the percentage of infaunal foraminifera in the 13 ky BP to present is recognized (Fig. 4). The diversity (H') and evenness (E') indexes point to indicate poor diverse assemblages ($H' < 2$) lacking a clear predominance of one species ($E' < 0.2$) for the 13–23 ky BP interval. For the 13 ky BP to the present interval, an increasing trend in the diversity ($H' > 3$) and a decrease in the evenness values is observed ($E' < 0.2$; Fig. 4).

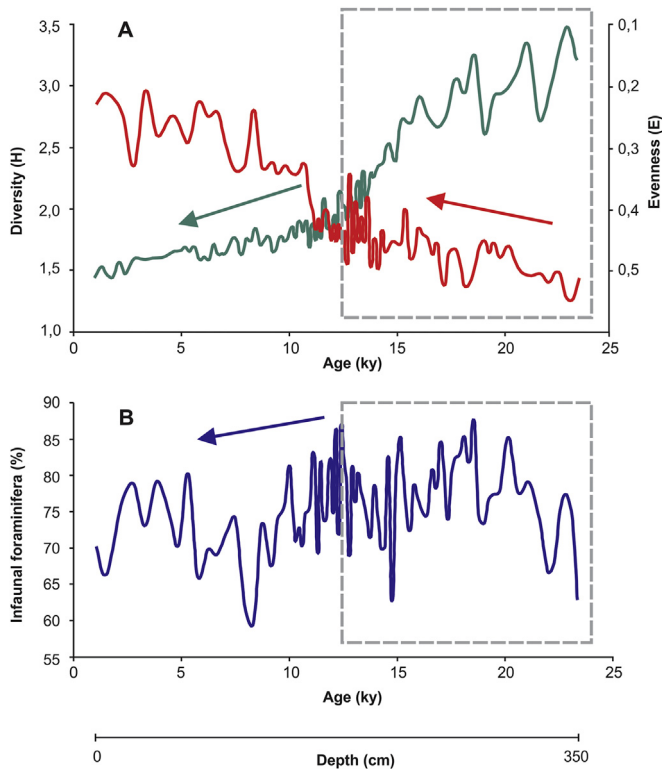


Fig. 4. (A) General trends of the diversity (red) and evenness (green) indexes of the benthic foraminiferal assemblages of the ME0005A-24JC core. The UGM is indicated as a gray dotted square. (B) Percentage distribution of the benthonic foraminifera with infaunal preferences. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Two abundance intervals were found at 170 cm using the general trends of $\text{Ln}(E)$ of the SHEBI analysis. Both intervals which are defined as FA1 and FA2, show $\text{Ln}(E)$ values ranging between -2.5 and -0.7 . Interval FA2 record values of $\text{Ln}(E)$ between -2.5 and -1.8 , whereas interval FA1 has values between -1.8 and -0.7 (Fig. 5). In addition, cluster analysis evidences two benthic foraminiferal assemblages, which are in concordance with the SHEBI analysis abundance intervals. These are:

Assemblage 1 (Biofacies Fur-Ciw-Gla) This biofacies Fur-Ciw-Gla is defined by a percentage abundance $>6\%$ in the total

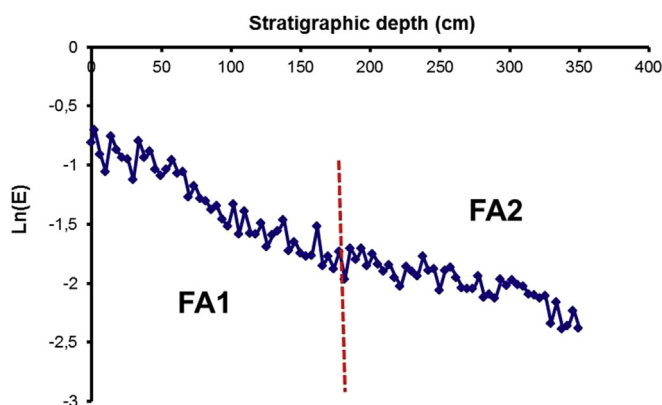


Fig. 5. Abundance biozones of benthic foraminiferal FA1 and FA2. These were defined using the values of $\text{Ln}(E)$ in the ME0005A-24JC core. The dotted line indicates the limit between the two abundance biozones at ~ 170 cm (13.04 ky according to the age model of Kienast et al., 2007).

assemblage of *Fursenkoina rotundata*, *Fursenkoina complanata*, *Cibicidoides wuellerstorfi* and *Globobulimina affinis*. Foraminifera such as *Hoeglundina elegans*, *Globobulimina pacifica*, *Uvigerina proboscidea*, *Uvigerina hispida*, *Uvigerina hispidocostata* and *Melonis* spp are also common. This biofacies, which is represented in 35 samples occurs in the 350–210 cm interval of the core and corresponds to the interval FA2 of the SHEBI analysis (Figs. 5–6). Based on the ME0005A-24JC core, the biofacies Fur-Ciw-Gla lived between 23.36 and 14.19 ky BP.

Assemblage 2 (Biofacies Cho-Lap-Uvp) This biofacies Cho-Lap-Uvp is defined by the common presence of *Chillostomella oolina*, *Laticarinina pauperata* and *Uvigerina proboscidea*. *Oridorsalis umbonatus*, *Pullenia bulloides* and *Epistominella smithi* are also present in this biofacies. The Cho-Lap-Uvp biofacies is represented in 54 samples in the upper 210 cm of the core and corresponds to the interval FA1 of the SHEBI analysis (Figs. 5–6). According to the ME0005A-24JC core age model, the biofacies Cho-Lap-Uvp has lived for the last 14 ky BP.

The estimated benthic foraminiferal accumulation rates (BFAR) suggest a major shift in bottom water conditions in ME0005A-24JC site at 12 ky BP. Between 23 and 12 ky BP, BFAR values were of ~ 200 specimens/cm²/ky, whereas these values ranged in ~ 100 specimens/cm²/ky for the last 12 ky BP (Fig. 7). Paleoproductivity estimates using the Herguera (2000) formula, show a similar pattern to the BFAR estimates, with values of >20 gC/cm²/ky between 23 and 12 ky BP and lower but constant values until the recent (<15 gC/cm²/ky). Finally, the estimation of the accumulation rate of the epifaunal foraminifera *Cibicidoides wuellerstorfi* shows a decreasing trend with low or null values for the last 10 ky BP (Fig. 7).

5. Discussion

Two contrasting paleoenvironmental scenarios are suggested, a glacial (between 23 and 12 ky BP) and an interglacial (12 ky BP and the present) in ME0005A-24JC site based on: (1) the general trends of the foraminiferal diversity and evenness (Figs. 3–4), (2) the benthic foraminiferal assemblages and abundance intervals identified with the cluster and SHEBI analyses (Figs. 5–6) and, (3) the benthic foraminiferal accumulation rates and paleoproductivity estimates (Fig. 7).

Glacial Scenario (23–12 ky BP): The higher proportion of infaunal foraminifera, such as *Fursenkoina rotundata*, *F. complanata*, and *Globobulimina affinis* and the epifaunal foraminifera *Cibicidoides wuellerstorfi* from the FA2 abundance interval, suggest low to moderate oxygenation of the bottom sediments (e.g. Gupta, 1997; Bornmalm et al., 1999; Murray, 2006). These conditions could be related to: (1) a higher input of organic matter (OM) coming from surface productivity and, (2) possible advection of OM as an effect of more intense bottom currents (~ 20 cm/s). Both the estimates of the BFAR and the paleoproductivity support the first condition, whereas the higher proportion of *C. wuellerstorfi*, an indicator of current intensity on the sea floor (Schönfeld, 2002a), supports the second condition. However, more dynamic bottom currents could supply more oxygen at the bottom floor and, therefore favor the degradation of the OM by bacterial activity (Bernhard and Gupta, 1999; Smart, 2002). For this reason, the use of *C. wuellerstorfi* as a bottom current indicator is still controversial as this species is also considered to be an indicator of higher surface productivity (e.g. Jorissen et al., 2007). Finally, the lower diversity of the foraminiferal assemblages can also be explained by lower oxygenation conditions at the bottom floor, based on using world analogs of foraminiferal assemblages in anoxic settings (e.g. Bernhard and Sen Gupta, 1999; Jorissen, 1999, 2007).

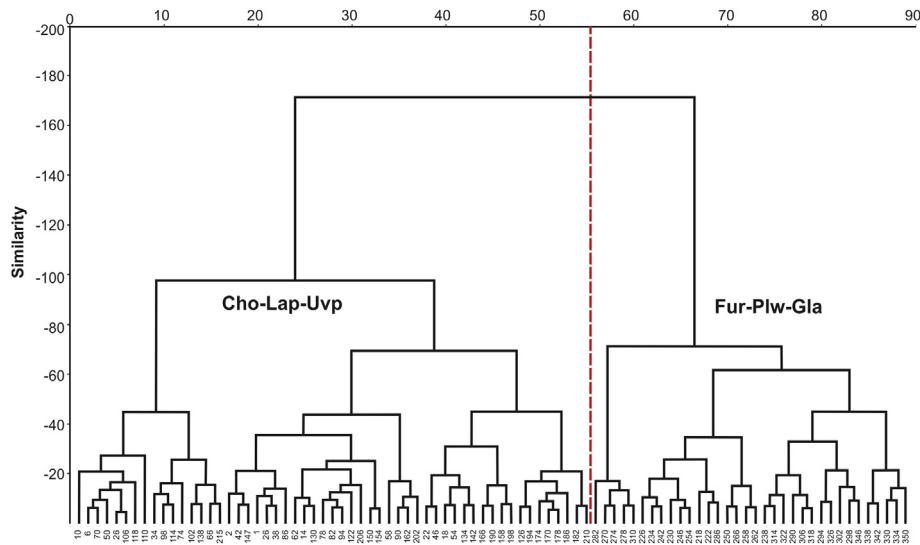


Fig. 6. Dendrogram of the analyzed samples in the ME0005A-24JC core. The cluster analysis followed the Ward minimum variance method. The dotted line indicates the limit between the two foraminiferal assemblages.

Interglacial Scenario (12 ky BP – recent): Around 12 ky BP there was an abrupt faunal turnover which define FA1 abundance interval. The common presence of *Chilostomella oolina*, *Laticarinina pauperata* and *Uvigerina proboscidea* suggest high to moderate oxygenation conditions in the sediments (Rathburn and Corliss, 1994; Loubere, 1999; Fontanier et al., 2002; Licari and Mackensen, 2005) and therefore a reduced supply of OM to the

area. Foraminiferal assemblages in this period were slightly more diverse, but with low values of evenness, probably related with more oxygenated settings according to previous studies (e.g. Bernhard and Reimers, 1991; Alve and Bernhard, 1995; Bernhard and Sen Gupta, 1999). However, an upward increase of taxa with low potential of preservation, i.e. the agglutinated forms, might control the low diversity values found in the most recent sediments. For instance, taxa such as *Cyclammina pusilla*, *Hyperammina*

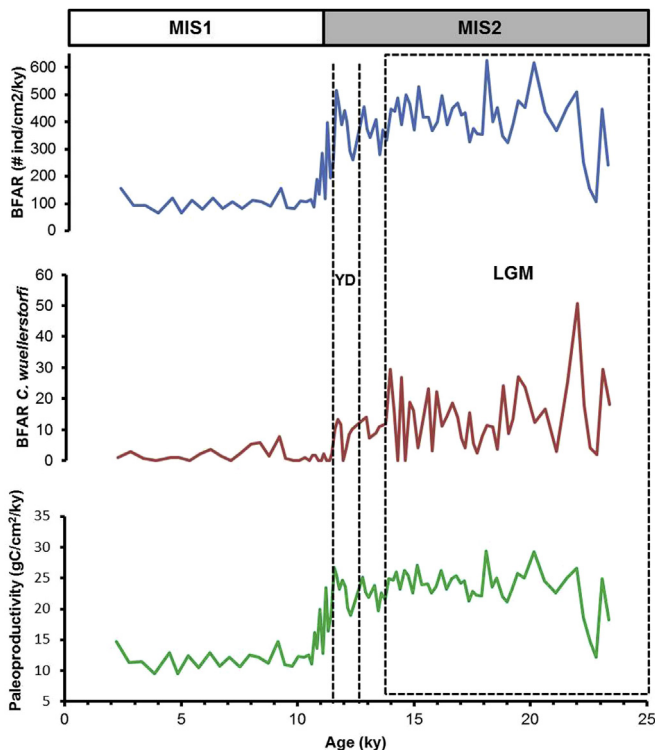


Fig. 7. Benthic foraminiferal accumulation rates (BFAR), *Cibicides wuellerstorfi* accumulation rate and paleoproductivity trends in the ME0005A-24JC core. Top: Benthic foraminiferal accumulation rate. Middle: Accumulation rate of *Cibicides wuellerstorfi* which is used as an indicator of higher bottom currents (Schönfeld, 2002a,b). Bottom: Paleoproductivity estimations applying the Herguera's (2000) equation.

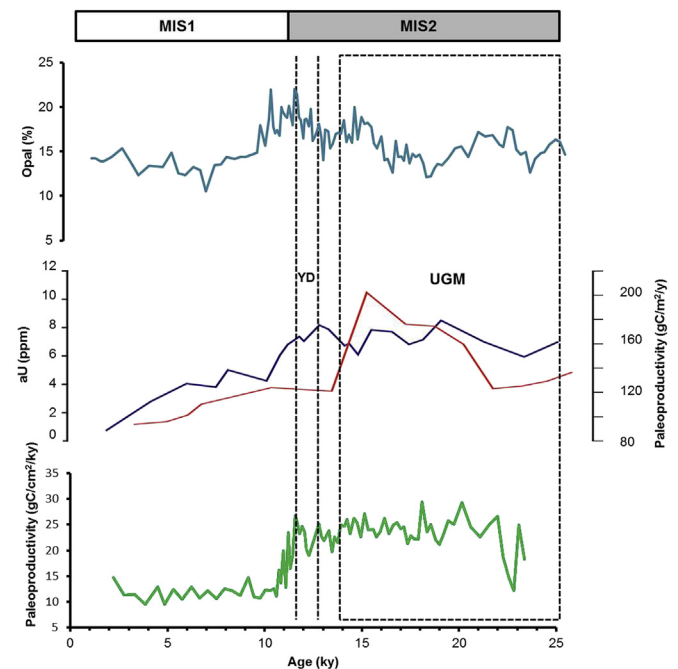


Fig. 8. Paleoceanographic studies in core ME0005A-24JC. Top: Percentage content of opal (pale blue; non-normalized with ^{230}Th), autogenic Uranium (aU, blue) and organic matter (red; Kienast et al., 2007; Bradtmiller et al., 2010; Dubois et al., 2011). Bottom: Paleoproductivity estimates based on benthic foraminiferal accumulation rates (BFAR; green) from this work. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

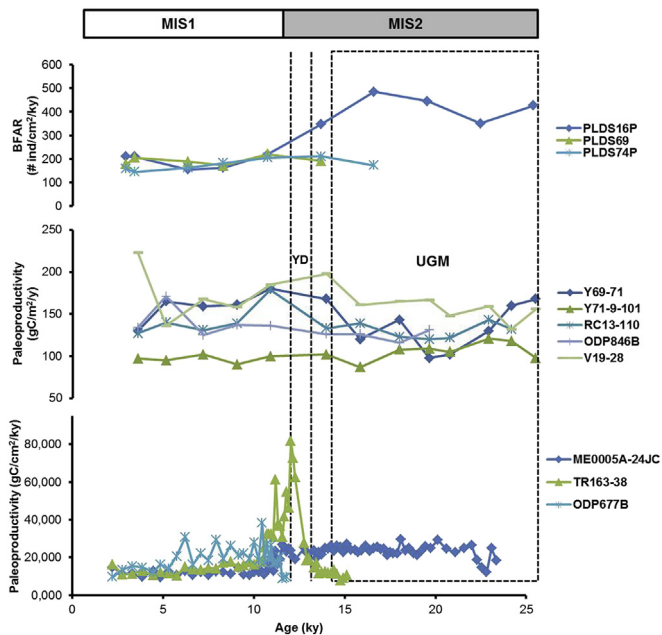


Fig. 9. Paleoproductivity estimates in the EEP based on BFAR (top; Herguera, 2000), transference functions (middle; Loubere, 1999) and applying the Herguera's (2000) equation (bottom; Betancur and Martínez, 2001; this work). Note the higher paleoproductivity values of the ME0005A-24JC core in the glacial time.

sp., *Opthalmidium* sp., and *Hormosinella* sp., only were present in the uppermost part of the core. Taphonomic features which indicated high reworking such as fragmented or altered tests were not detected along the core.

As indicated before, our paleoenvironmental interpretation was compared with: (1) paleoceanographic results from the same core and the Y69-71 site (nearby to the ME0005A-24JC; Figs. 8–9) and, (2) previous micropaleontological reports in the basin (Fig. 9).

The organic matter and opal content analyses (normalized with ^{230}Th) in the ME0005A-24JC core illustrate important fluctuations between the MIS2 (23–13 ky BP) and the middle and late Holocene values, which could be explained by a higher surface productivity during the last glaciation (Kienast et al., 2007; Dubois et al., 2011). In addition, estimates based on the coccolithophore record (N Index) in the ODP 202 Leg 1240 also suggest higher productivity conditions in the LGM (Cabarcos, 2011). These results agree with the higher BFAR and paleoproductivity values estimated in our study (Figs. 7–8). In addition, isotopic values of the ^{230}Th in the ME0005A-24JC core and the Y69-71 site, suggest higher lateral transport of bottom sediments (Ψ^4) in glacial times, reaching current values at 13 ky BP (Kienast et al., 2007, Fig. 8). A higher proportion of the epifaunal foraminifera *C. wuellerstorfi* might support this interpretation based on the ecological inferences of Schönfeld (2002a).

Reducing conditions have been suggested in the ME0005A-24JC core based on values of ~ 6 ppm of autigenic uranium (aU) and the higher proportion of the biomarker brassicasterol (Kienast et al., 2007; Bradtmiller et al., 2010; Dubois et al., 2009). The dominance, in our study, of taxa associated with low oxygenated conditions support these results for the last glaciation (Figs. 3–4). Additional data from the ME0005A-24JC core suggest low temperatures and more intense upwelling conditions based on the alkenone unsaturation index UK_{37} record (Kienast et al., 2006). Furthermore, based on the isotopic content of $\delta^{15}\text{N}$ record, it has been proposed there might have been alterations in the

nitrification processes in the EEP for the marine isotopic stages 2 and 1 (Martínez and Robinson, 2010; Dubois et al., 2011). In conclusion, geochemical data agree with the estimation of low oxygenation conditions in the bottom sediments, more dynamics bottom currents, and a higher surface productivity with lower temperatures for the glacial scenario. Therefore, assuming previous paleoproductivity models, the benthic foraminiferal data of the ME0005A-24JC core could be related to La Niña-like conditions in the LGM (e.g. Martínez et al., 2003; Rincon-Martínez et al., 2010). In contrast, since 11.7 ky BP the paleoceanographic conditions might have been similar to the present.

However, a direct comparison of the paleoproductivity estimates in the ME0005A-24JC core with similar studies in the EEP illustrates a higher complexity in the paleoenvironmental response of the foraminiferal assemblages. For the Y69-71 site, the paleoproductivity estimates, which were based on transference functions (e.g. Loubere, 1999; Loubere et al., 2003), suggest an opposite and contrasting scenario for the last glaciation, with a decrease of the paleoproductivity between 25 and 15 ky BP (Fig. 9). Several factors could influence these contrasting results: (1) the lower time resolution of the analyzed records (1–2.5 ky between each sample), (2) a higher proportion of benthic foraminifera in the samples (~ 200 individuals instead of ~ 150 in our study) and, (3) the use of some taxa, not assemblages, as paleoproductivity indicators. The first aspect is particularly relevant because previous paleoproductivity estimates were inferred with a resolution of 9–17 samples for the last 25 ky BP, whereas in the ME0005A-24JC the analysis reached a time resolution of 0.4 ky per sample. Therefore, it is likely that in previous analysis subtle, short term changes in the record were not detected at all. The second aspect is also relevant as differences between the collected total foraminiferal assemblages in Loubere (1999) and Loubere et al. (2003) studies, when compared with our data reinforce previous asseverations regarding the heterogeneous character of foraminiferal accumulation rates through the Panama basin (e.g. Herguera, 2000; Loubere et al., 2003). Therefore, the proposed paleoproductivity estimates from Y69-71 site not necessarily apply to an extent geographical area. In that sense, Loubere et al. (2003) have already proposed different paleoproductivity values in areas with high and low influence of the Equatorial Divergence and the Peru Upwelling system. Finally, the third case could be the most significant because in order to have a proper application of transference functions using the foraminiferal record we must have a complete idea of the environmental controls on those assemblages. Although the transference functions of Loubere and Fariduddin (1999) in the EEP have a complete quantitative framework, some paleoproductivity indicators such as *Uvigerina peregrina*, or *M. barleanum* which were used in the Y69-71 site had very low proportions or they were absent in the ME0005A-24JC core. Both sites have similar depths and they are close, probably illustrating that our knowledge of the environmental controls of deep sea benthic foraminifera in the Panama Basin still is incipient. Therefore, only after a complete survey of the living benthic foraminiferal assemblages, the use of transference functions for the recent past could be improved. Despite the contrasting results with studies, paleoproductivity estimates of the P6702-59 site (2.75°N, 85.33°W, water depth 3274 m; Loubere, 2002) seem to agree with our proposal of a decreasing trend in paleoproductivity since the LGM. Unfortunately, quantitative data of the P6702-59 site are unpublished and could not be compared with our data.

In order to have a regional idea of the signal in the ME0005A-24JC site, additional comparisons were effectuated with the paleoproductivity estimates of Herguera (2000) and Betancur and

Martínez (2001). From Herguera (2000) cores, only the site PLSD16P (3.19°S, 102.03°W, water depth 3251 m) suggests a decreasing pattern in the paleoproductivity for the last 20 ky BP. The other sites of that study, located westward the ME0005A-24JC, also suggest a slightly decreasing trend but they have moderate sample resolutions (Fig. 9). Furthermore, the paleoproductivity estimates of the TR163-38 and ODP677B sites (Betancur and Martínez, 2001) show an abrupt change in the paleoproductivity at 13 ky BP, having similar values to the recent conditions (10–20 gC/cm²/ky; Fig. 9). With a similar sample resolution of our study, the results are in concordance with the data of the ME0005A-24JC site. However, the proximity of the TR163-38 site to high productive zones such as the Equatorial Divergence and the Peru Upwelling system, could affect the signal of this record.

Additional comparisons were made with foraminiferal records of the basin, but without the previously discussed paleoproductivity estimates. In the KAMA-2 site (0.13°N 80.39°W, water depth 1315 m), the foraminiferal assemblages are analogous thus resembling the high productivity conditions of the ME0005A-24JC site in the LGM (Arteaga, 2011). Furthermore, the foraminiferal assemblages of the site MD02-2529 (8.12°N, 84.07°W, water depth 1619 m), retrieved from the northern Cocos Ridge suggest a decrease in productivity conditions at 15 ky BP. The minor proportion in the record, of high productivity taxa such as *U. peregrina*, *C. wuellerstorfi*, *B. mexicana* and *E. smithi* might support the inference of low ventilation conditions in the EEP during the late Holocene (Ovsepyan and Ivanova, 2009).

Compiling all the previous results of the ME0005A-24JC site it is clear that both the assemblage compositions and the paleoproductivity estimates (cf. Herguera, 2000), agree with the previous suggestions of a decrease in the productivity since the last glaciation (Pedersen, 1983; Pedersen et al., 1991, 1988; Emeis et al., 1995; Farrell et al., 1995; Yang et al., 1995; Betancur and Martínez, 2001; Kienast et al., 2007; Dubois et al., 2011; Yu et al., 2012; De la Fuente et al., 2015). However, some authors suggest that glacial productivity fluctuations were not constant along the EEP, being different south and north of the Equator (e.g. Herguera, 2000). In contrast, there are several works that propose an increase in productivity since the LGM (Loubere, 1999, 2000; Loubere et al., 2003; Pichat et al., 2004; Bradtmiller et al., 2006, 2010; Kienast et al., 2006). Some of these studies which were based on transference functions, therefore, they might be biased due to the absence of ecological data as previously mentioned. Regarding opal fluxes estimates, even though they were normalized with ²³⁰Th, several processes prevent them to be used as indicators of upwelling intensity. This is the case of variations in the supply of Fe from the continent could affect their imprint because paleoproductivity (e.g. Barber and Chavez, 1991; Pedersen et al., 1991; Farrell et al., 1995; Arellano et al., 2011). In addition, paleoproductivity estimates using the (²³¹Pa/²³⁰Th)_{xs,0} ratio has been used to identify a greater influence of the bottom currents in at least two cores from the EEP (Pichat et al., 2004). Therefore, the time resolution and accumulation rates in some parts of the EEP could lead to contradictory results because of sediment focusing and winnowing processes.

In conclusion, despite which paleoproductivity model is accepted for the EEP, foraminiferal assemblages of the ME0005A-24JC site strongly suggest a shift in paleoproductivity conditions since the LGM. Such changes have been proposed as heterogeneous through the EEP, being higher in areas with strong upwelling conditions or close to the continental margin such as

northern Peru or the Costa Rica Dome (e.g. Betancur and Martínez, 2001; Martínez et al., 2006; Ovsepyan and Ivanova, 2009). Furthermore, the benthic foraminiferal data of the ME0005A-24JC core support the previous model of low oxygenated bottom conditions for the southern Panama basin during the last glaciation (Bradtmiller et al., 2010). In addition, a higher proportion of *C. wuellerstorfi* in the glacial sediments of the ME0005A-24JC core could be related to more dynamic bottom currents. This aspect could be important, because the disturbance processes related to bottom currents might be the cause of decoupled results between the benthic foraminiferal data and other micropaleontological proxies (planktic foraminifera, coccolithophores; Martínez et al., 2006).

6. Conclusions

From the study of the quantitative study of the benthic foraminiferal assemblages of the ME0005A-24JC core it is concluded that:

1. There were two paleoceanographic bottom water scenarios in the southern part of Panama basin since the LGM.
2. Bottom currents were more dynamic and low oxygenated conditions, related to higher surface productivity are inferred for the 23 to 14 ky BP interval. In contrast, the foraminiferal content suggests bottom oxygen conditions and less dynamic bottom currents since the Younger Dryas, which could be similar to the present.
3. Two foraminiferal assemblages and intervals support the asseveration of a faunal turnover between 14 and 12 ky BP.
4. The glacial foraminiferal assemblage is characterized by *Fursenkoina rotundata*, *Hoeglundina elegans*, *Globobulimina affinis*, *G. pacifica*, *Cibicides wuellerstorfi* and *Uvigerina hispido-costata*, whereas the interglacial foraminiferal assemblage is dominated by *Chilostomella oolina*, *Laticarinina pauperata* and *Uvigerina proboscidea*.
5. Paleoproductivity estimates were higher in the LGM though in a magnitude that does not agree or refute previous interpretations for the EEP, though results agree with previous interpretations for glacial low-oxygenated bottom conditions.
6. Paleoproductivity estimates, based on benthic foraminiferal data, might support previous proposals of a higher recurrence of La Niña-like conditions between 23 and 12 ky BP.

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Appendix A

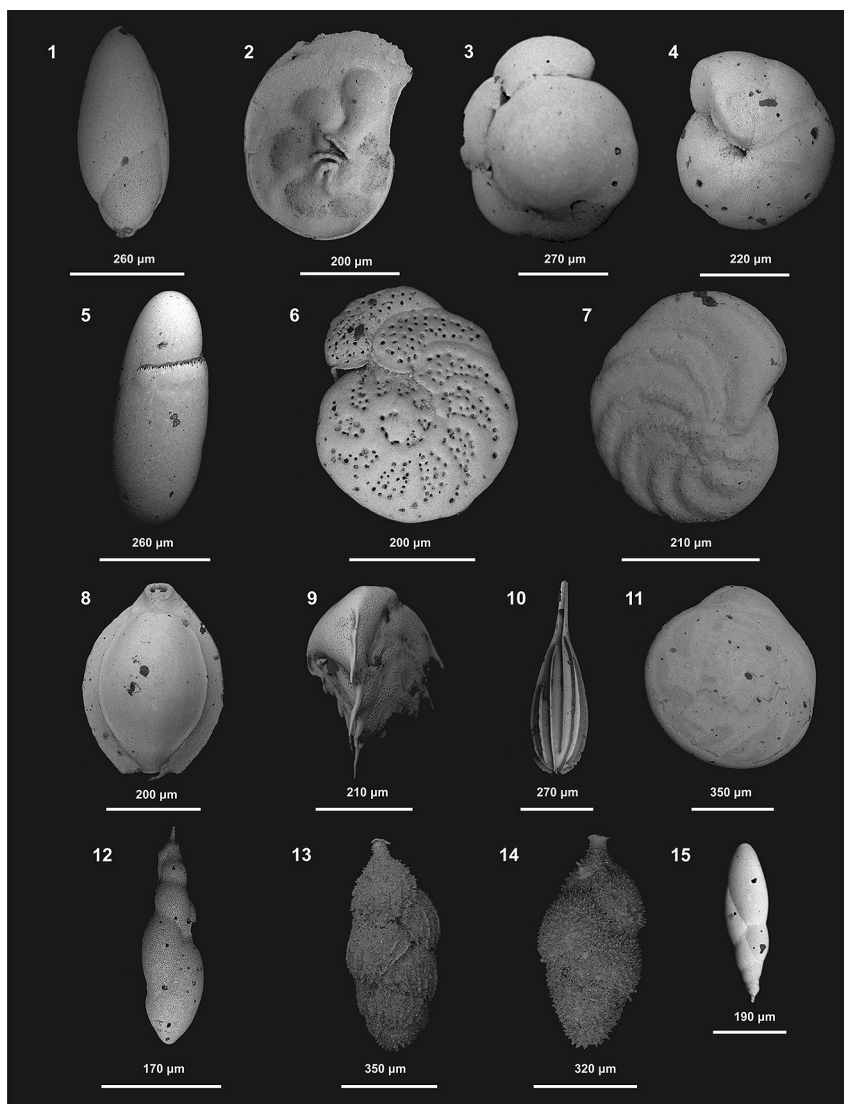


Plate 1. SEM photographs of the collected foraminifera from the ME0005A-24JC.

1. *Globobulimina affinis* (d'Orbigny); 303 cm, x510.
2. *Laticarinina pauperata* (Parker and Jones); 103 cm, x660.
3. *Oridorsalis umbonatus* (Reuss); 203 cm, x490.
4. *Melonis pompilioides* (Fichtel and Moll); 203 cm, x600.
5. *Chilostomella oolina* Schwager; 103 cm, x510.
6. *Cibicidoides wuellerstorfi* (Schwager); 203 cm, x500, dorsal view.
7. *Cibicidoides wuellerstorfi* (Schwager); 303 cm, x460, ventral view.
8. *Pyrgo murhina* (Schwager); 303 cm, x470.
9. *Ehrenbergina pacifica* Cushman; 203 cm, x630.
10. *Lagena striata* (d'Orbigny); 103 cm, x490.
11. *Hoeglundina elegans* (d'Orbigny); 303 cm, x380.
12. *Uvigerina proboscidea* Schwager; 103 cm, x780.
13. *Uvigerina hispidocostata* Cushman and Todd; 303 cm, x380.
14. *Uvigerina hispida* Schwager; 303 cm, x430.
15. *Fursenkoina rotundata* (Parr); 103 cm, x670.

Appendix B. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jsames.2015.07.010>.

References

Akimoto, K., 1990. Distribution of recent benthic foraminiferal faunas in the Pacific of Southwest Japan and around Hachijojima Island. Sci. Rep. Tohoku Univ.

- Sendai Geol. Second Ser. 60 (2), 288–291.
- Alve, E., Bernhard, J.M., 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. Mar. Ecol. Prog. Ser. 116, 137–151.
- Antonov, J.I., Seidov, D., Boyer, T.P., Locarnini, R.A., Mishonov, A.V., Garcia, H.E., Baranova, O.K., Zweng, M.M., Johnson, D.R., 2010. World Ocean Atlas 2009. In: Levitus, S. (Ed.), Salinity, vol. 2. NOAA Atlas NESDIS 69. ftp://ftp.nodc.noaa.gov/pub/WOA09/DOC/woa09_vol2_text_figures.pdf.
- Arellano, E., Pichevin, L.E., Ganeshram, R.S., 2011. High-resolution opal records from the Eastern tropical Pacific provide evidence for silicic acid leakage from HNLC regions during glacial periods. Quat. Sci. Rev. 30 (9–10), 1112–1121.

- Arrhenius, G., 1952. Sediment Cores from the East Pacific, p. 227. Reports of the Swedish Deep-Sea Expedition, 1947–1948, 5. Elander, Göteborg.
- Arteaga, R., 2011. Reconstrucción de las variaciones en el flujo de materia orgánica durante el Holoceno, registradas en el talud continental de la cuenca de Panamá, Pacífico Oriental Ecuatorial, con base en foraminíferos bentónicos. Proyecto de Grado Depto. Geología, Universidad EAFIT, Medellín.
- Bandy, O.L., Arnal, R.E., 1957. Distribution of recent foraminifera off west coast of Central America. AAPG Bull. 41, 2037–2053.
- Bandy, O.L., Rodolfo, K.S., 1964. Distribution of foraminifera and sediments, Peru-Chile trench area. Deep Sea Res. 11, 817–837.
- Barber, R.T., Chavez, F.P., 1991. Regulation of primary productivity rate in the equatorial Pacific. Limnol. Oceanogr. 36 (8), 1803–1815.
- Beaufort, L., de Garidel-Thoron, T., Mix, A.C., Pisias, N.G., 2001. ENSO-like forcing on oceanic primary production during the late Pleistocene. Nature 293, 2441–2444.
- Benway, H.M., Mix, A.C., 2004. Oxygen isotopes, upper-ocean salinity, and precipitation sources in the Eastern tropical Pacific. Earth Planet. Sci. Lett. 224, 493–507.
- Benway, H.M., Mix, A.C., Haley, B.A., Klinkhammer, G.P., 2006. Eastern Pacific warm pool paleosalinity and climate variability: 0–30 kyr. Paleoceanography 21, PA3008. <http://dx.doi.org/10.1029/2005PA001208>.
- Bernhard, J.M., Sen Gupta, B.K., 1999. Foraminifera of oxygen-depleted environments. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, Londres, pp. 201–216.
- Bernhard, J.M., Reimers, C.E., 1991. Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin. Biogeochemistry 15, 127–149.
- Betancur, M.A., Martínez, J.I., 2001. Productividad y oxigenación de la Cuenca de Panamá, Pacífico Colombiano, durante el Pleistoceno tardío-Holoceno: el registro de los Foraminíferos Bentónicos. Geol. Colomb. 26, 123–151.
- Betancur, M.A., Martínez, J.I., 2003. Foraminíferos bentónicos recientes en sedimentos de fondo de la cuenca de Panamá (Pacífico Colombiano), como indicadores de productividad y oxigenación. Bol. Investig. Mar. Costeras 32, 3–18.
- Boltovskoy, E., Gualançay, E., 1975. Foraminíferos Bentónicos Actuales de Ecuador. 1.- Provincia Esmeraldas, vol. 5. Instituto Oceanográfico Biológico, pp. 1–56.
- Bornmalm, L., 1997. Taxonomy and paleoecology of late Neogene benthic foraminifera from the Caribbean sea and Eastern Equatorial Pacific ocean. Fossils Strata 41, 1–96.
- Bornmalm, L., Widmark, J.G.V., Malmgren, B.A., 1999. Changes in circulation and trophic levels in the Pliocene Caribbean Sea: evidence from benthic foraminiferal accumulation rates. J. Foraminif. Res. 29 (3), 209–221.
- Bradt Miller, L.I., Anderson, R.F., Fleisher, M.Q., Burckle, L.H., 2006. Diatom productivity in the equatorial Pacific Ocean from the last glacial period to the present: a test of the silicic acid leakage hypothesis. Paleoceanography 21, PA4201. <http://dx.doi.org/10.1029/2006PA001282>.
- Bradt Miller, L.I., Anderson, R.F., Sachs, J.P., Fleisher, M.Q., 2010. A deeper respired carbon pool in the glacial equatorial Pacific Ocean. Earth Planet. Sci. Lett. 299, 417–425.
- Buzas, M.A., Hayek, L.A.C., 1996. Biodiversity resolution: an integrated approach. Biodivers. Res. 3, 40–43.
- Buzas, M.A., Hayek, L.A.C., 1998. SHE analysis for biofacies identification. J. Foraminif. Res. 28, 233–239.
- Buzas, M.A., Hayek, L.A.C., 2005. On richness and evenness within and between communities. Paleobiology 31, 199–220.
- Cabarcos, E., 2011. Análisis de alta resolución de las asociaciones de coccolitóforos en una región de surgencia del Pacífico Ecuatorial Oriental. MSc Project. Salamanca University, Spain, p. 121.
- Carré, M., Azzoug, M., Bentaleb, I., Chase, B.M., Fontugne, M., Jackson, D., Ledru, M.P., Maldonado, A., Sachs, J.P., Schauer, A.J., 2012. Mid-Holocene mean climate in the southeastern Pacific and its influence on South America. Quat. Int. 253, 55–66.
- Clark, F.E., Patterson, R.T., 1993. An illustrated key to the identification of unilocular genera of calcareous foraminifera. J. Paleontol. 67 (1), 20–28.
- Clement, A.C., Seager, R., Cane, M.A., 1999. Orbital controls on the El Niño/Southern oscillation and the tropical climate. Paleoceanography 14, 441–456.
- CLIMAP, 1978. The surface of the ice-age Earth. Science 191, 1131–1137.
- Cushman, J.A., McCulloch, I., 1942. Some Virguliniinae in the collections of the Allan Hancock Foundation. Allan Hancock Pac. Exped. 6 (2), 179–230.
- De la Fuente, M., Skinner, L., Calvo, E., Pelejero, C., Cacho, I., 2015. Increased reservoir ages and poorly ventilated deep waters inferred in the glacial Eastern Equatorial Pacific. Nat. Commun. 6. Article number: 7420. <http://dx.doi.org/10.1038/ncomms8420>.
- De, S., Gupta, A.K., 2010. Deep-sea faunal provinces and their inferred environments in the Indian Ocean based on distribution of recent benthic foraminifera. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 429–442.
- Douglas, R.G., 1973. Benthonic foraminiferal biostratigraphy in the Central North Pacific, leg 17. In: Winterer, E.L. (Ed.), Deep Sea Drilling Project, Initial Reports, vol. 17, pp. 607–672.
- Dubois, N., Kienast, M., Kienast, S., Normandeau, C., Calvert, S.E., Herbert, T.D., Mix, A., 2011. Millennial-scale variations in hydrography and biogeochemistry in the Eastern Equatorial Pacific over the last 100 kyr. Quat. Sci. Rev. 30, 210–223.
- Dubois, N., Kienast, M., Normandeau, C., Herbert, T.D., 2009. Eastern Equatorial Pacific cold tongue during the last glacial maximum as seen from alkenone paleothermometry. Paleoceanography 24, PA4207. <http://dx.doi.org/10.1029/2009PA001781>.
- Emeis, K.C., Dooze, H., Mix, A., Schulz-Bull, D., 1995. Alkenone sea-surface temperature and carbon burial at site 846 (Eastern Equatorial Pacific Ocean). The last 1.3 my. In: Pisias, N., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, vol. 138, pp. 605–613.
- Emery, W.J., Meincke, J., 1986. Global water masses: summary and review. Oceanol. Acta 9 (4), 383–391.
- Farrell, J.W., Raffi, I., Janecek, T.R., Murray, D.W., Levitan, M., Dadey, K.A., Emeis, K.C., Lyle, M., Flores, J.A., Hovan, S., 1995. Late Neogene sedimentation patterns in the eastern equatorial Pacific Ocean. In: Pisias, N., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, 138, pp. 717–756.
- Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil assemblages. Mar. Micropaleontol. 45, 169–174.
- Fiedler, P.C., Talley, L.D., 2006. Hydrography of the Eastern tropical Pacific: a review. Prog. Oceanogr. 69, 143–180.
- Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A.P., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. Deep Sea Res. 149, 751–785.
- Forcino, F.L., 2012. Multivariate assessment of the required sample size for community paleoecological research. Palaeogeogr. Palaeoclimatol. Palaeoecol. 315–316, 134–141.
- García, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., Baranova, O.K., Zweng, M.M., Johnson, D.R., 2010. World ocean Atlas 2009. In: Levitus, S. (Ed.), Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation, vol. 3. NOAA Atlas NESDIS 70. ftp://ftp.nodc.noaa.gov/pub/WOA09/DOC/wao09_vol3_text_figures.pdf.
- Garreaud, R.D., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day south American climate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 281, 180–195.
- Golik, A., Phleger, F.B., 1977. Benthonic foraminifera from the Gulf of Panama. J. Foraminif. Res. 7, 83–99.
- Gualançay, E., 1986. Foraminíferos del Rift de Galápagos. Acta Ocean. del Pacífico 3 (1), 149–155.
- Gupta, A.K., 1997. Paleogeographic and paleoclimatic history of the Somali Basin during the Pliocene–Pleistocene; multivariate analyses of benthic foraminifera site 241. J. Foraminif. Res. 27 (3), 196–208.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1). http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Hayek, L.A.C., Buzas, M.A., 1997. Surveying Natural Populations. Columbia University Press, Nueva York, p. 562.
- Heath, G.R., Moore, T.C., Roberts, G.L., 1973. Mineralogy of surface sediments from the Panama basin, Eastern Equatorial Pacific. J. Geol. 82, 145–160.
- Herguera, J.C., Berger, W.H., 1991. Paleoproductivity from benthic foraminifera abundance: glacial to postglacial change in the west-equatorial Pacific. Geology 19, 1173–1176.
- Herguera, J.C., 2000. Last glacial paleoproductivity patterns in the Eastern Equatorial Pacific: benthic foraminifera records. Mar. Micropaleontol. 40, 259–275.
- Holbourn, A.E., Henderson, A.S., 2002. Re-illustration and revised taxonomy for selected deep-sea Benthic Foraminifera. Palaeontol. Electron. 4 (2). http://palaeo-electronica.org/paleo/2001_2/foramin/issue2_01.htm.
- Jorissen, F.J., 1999. Benthic foraminiferal microhabitats below the sediment-water interface. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, Londres, pp. 161–179.
- Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Paleoceanographical indicators based on deep-sea benthic foraminiferal assemblage characteristics. Dev. Mar. Geol. 1, 263–325.
- Kaiho, K., 1992. Eocene to quaternary benthic foraminifera and paleobathymetry of the Izu-Bonin Arc, legs 125 and 126. In: Taylor, B., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, vol. 126, pp. 285–310.
- Kaiho, K., Nishimura, A., 1992. Distribution of Holocene benthic foraminifera in the Izu-Bonin Arc. In: Taylor, B., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, vol. 126, pp. 311–320.
- Kaminski, M., Grassle, J.F., Whitlatch, R.B., 1988. Life history and recolonization among agglutinated foraminifera in the Panama Basin. Abhandlungen der Geologischen Bundesanstalt 41, 229–243.
- Kessler, W.S., 2006. The circulation of the Eastern tropical Pacific: a review. Prog. Oceanogr. 69, 181–217. <http://dx.doi.org/10.1016/j.pcean.2006.03.009>.
- Kienast, M., MacIntyre, G., Dubois, N., Higginson, S., Normandeau, C., Chazen, C.R., Herbert, T.D., 2012. Alkenone unsaturation in surface sediments from the Eastern Equatorial Pacific: implications for SST reconstructions. Paleoceanography 27, PA1210. <http://dx.doi.org/10.1029/2011PA002254>.
- Kienast, S.S., Kienast, M., Jaccard, S., Calvert, S.E., Francois, R., 2006. Testing the silica leakage hypothesis with sedimentary opal records from the Eastern Equatorial Pacific over the last 150 kyr. Geophys. Res. Lett. 33, L15607. <http://dx.doi.org/10.1029/2006GL026651>.
- Kienast, S.S., Kienast, M., Mix, A.C., Calvert, S.E., Francois, R., 2007. Thorium-230 normalized particle flux and sediment focusing in the Panama Basin region during the last 30,000 years. Paleoceanography 22, PA2213. <http://dx.doi.org/10.1029/2006pa001357>.
- Koutavas, A., Lynch-Stieglitz, J., Marchitto Jr., T.M., Sachs, J.P., 2002. El Niño-like pattern in ice age tropical Pacific sea surface temperature. Science 297, 226–230.
- Koutavas, A., Lynch-Stieglitz, J., 2003. Glacial-interglacial dynamics of the Eastern Equatorial Pacific cold tongue-Intertropical convergence zone system reconstructed from oxygen isotope records. Paleoceanography 18 (4), 1089. <http://dx.doi.org/10.1029/2003PA000894>.
- Kroopnick, P., 1974. The dissolved O₂-CO₂-13C system in the Eastern Equatorial

- Pacific. Deep-Sea Res. 21, 211–227.
- Kusch, S., Eglinton, T.I., Mix, A.C., Mollenhauer, G., 2010. Timescales of lateral sediment transport in the Panama Basin as revealed by radiocarbon ages of alkenones, total organic carbon and foraminifera. *Earth Planet. Sci. Lett.* 290 (3–4), 340–350.
- Laird, N.P., 1971. Panama Basin deep water properties and circulation. *J. Mar. Res.* 29 (3), 226–234.
- Lalicker, C.G., McCulloch, I., 1940. Some *Textulariidae* of the Pacific ocean. *Allan Hancock Pac. Exped.* 6 (2), 115–143.
- Leduc, G., Schneider, R., Kim, J.H., Lohmann, G., 2010. Holocene and Eemian sea surface temperature trends as revealed by alkenone and Mg/Ca paleothermometry. *Quat. Sci. Rev.* 29, 989–1004. <http://dx.doi.org/10.1016/j.quascirev.2010.01.004>.
- Leduc, G., Vidal, L., Cartapanis, O., Bard, E., 2009. Modes of Eastern Equatorial Pacific thermocline variability: implications for ENSO dynamics over the last glacial period. *Paleoceanography* 24. <http://dx.doi.org/10.1029/2008PA001701>.
- Licari, L.N., Mackensen, A., 2005. Benthic foraminifera off west Africa (18N to 32S): do live assemblages from the Topmost sediment reliably record environmental variability? *Mar. Micropaleontol.* 55, 205–233.
- Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., Garcia, H.E., Baranova, O.K., Zweng, M.M., Johnson, D.R., 2010. World ocean Atlas 2009. In: Levitus, S. (Ed.), Temperature, vol. 1. NOAA Atlas NESDIS 68. ftp://ftp.nodc.noaa.gov/pub/WOA09/DOC/woa09_vol1_text_figures.pdf.
- Loeblich, A.R., Tappan, H., 1964. Sarcodina and foraminifera. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista, 2. Kansas University & Geological Society of America, Lawrence, p. 936.
- Lonsdale, P., 1976. Abyssal circulation of the southeastern Pacific and some geological implications. *J. Geophys. Res.* 81, 1163–1176.
- Lonsdale, P., Malfait, B.T., 1974. Abyssal dunes of foraminiferal sand on the Carnegie Ridge. *Geol. Soc. Am. Bull.* 85, 1697–1712.
- Loubere, P., 1999. A multiproxy reconstruction of biological productivity and oceanography in the Eastern Equatorial Pacific for the past 30,000 years. *Mar. Micropaleontol.* 37, 173–198.
- Loubere, P., 2000. Marine controls of biological production in the Eastern Equatorial Pacific Ocean. *Nature* 406, 497–500.
- Loubere, P., 2002. Remote vs. local control of changes in Eastern Equatorial Pacific bioproductivity from the last glacial maximum to the present. *Glob. Planet. Changes* 35, 113–126.
- Loubere, P., Fariduddin, M., 1999. Quantitative estimation of global patterns of surface ocean biological productivity and its seasonal variation on timescales from centuries to millennia. *Glob. Biogeochem. Cycles* 13, 115–133.
- Loubere, P., Fariduddin, M., Murray, R.W., 2003. Patterns of export production in the Eastern Equatorial Pacific over the past 130,000 years. *Paleoceanography* 18 (2), 1028. <http://dx.doi.org/10.1029/2001PA000658>.
- Lyle, M., 1992. Composition maps of surface sediments of the Eastern tropical Pacific Ocean. In: Mayer, L., et al. (Eds.), Proceedings of the Ocean Drilling Program, Initial Reports 138, pp. 101–115.
- Lyle, M., Mitchell, N., Pisias, N., Mix, A., Martínez, J.I., Paytan, A., 2005. Do geochemical estimates of sediment focusing pass the sediment test in the equatorial Pacific? *Paleoceanography* 20, PA1005. <http://dx.doi.org/10.1029/2004PA001019>.
- MARGO Project Members, 2009. Constraints on the magnitude and patterns of ocean cooling at the last glacial Maximum. *Nat. Geosci.* 2, 129–132.
- Martínez, J.I., Keigwin, L., Barrows, T.T., Yokoyama, Y., Southon, J., 2003. La Niña-like conditions in the Eastern Equatorial Pacific and a stronger Choco jet in the northern Andes during the last glaciation. *Paleoceanography* 18 (2), 1033. <http://dx.doi.org/10.1029/2002PA000877>.
- Martínez, J.I., Rincon, D., Yokoyama, Y., Barrows, T.T., 2006. Foraminifera and Coccolithophorid assemblage changes in the Panama Basin during the last deglaciation: response to sea-surface productivity induced by a transient climate change. *Paleogeogr. Palaeoclimatol. Paleoecol.* 234, 114–126.
- Martínez, P., Robinson, R.S., 2010. Increase in water column denitrification during the last deglaciation the influence of oxygen demand in the Eastern Equatorial Pacific. *Biogeosciences* 7, 1–9.
- Matoba, Y., Yamaguchi, A., 1982. Late pliocene to holocene benthic foraminifera of the Guaymas Basin, Gulf of California: sites 477 through 481. In: Curry, J.R., et al. (Eds.), Initial Reports of the Deep Sea Drilling Project 64(2), pp. 1027–1052.
- McDougall, K., 1985. Miocene to pleistocene benthic foraminifera and paleoceanography of the middle america slope, deep sea drilling project leg 84. In: von Huene, R., et al. (Eds.), Initial Reports of the Deep Sea Drilling Project, vol. 84, pp. 363–418.
- Mix, A., Tiedemann, R., Blum, P., the Shipboard Scientific Party, 2003. Proceedings of the Ocean Drilling Program. Initial Reports 202. http://www-odp.tamu.edu/publications/202_IR/202ir.htm.
- Murray, J.W., 1991. Ecology and Paleoecology of Benthic Foraminifera. Longman, Harlow, p. 397.
- Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge, p. 426.
- Nomura, R., 1992. Miocene benthic foraminifera at sites 794, 795 and 797 in the Sea of Japan with reference to the foram sharp line in the Honshu Arc. In: Suess, E., et al. (Eds.), Proceedings of the Ocean Drilling Program 127/128 Part 1, pp. 493–540.
- Ohkushi, K., Thomas, E., Kawagata, H., 2000. Abyssal benthic foraminifera from Northwestern Pacific (Shatsky Rise) during the last 298 kyr. *Mar. Micropaleontol.* 38, 119–147.
- Ovsepyan, E.A., Ivanova, E.V., 2009. Benthic foraminiferal assemblages as indicators of the paleoceanographic conditions in the Eastern Equatorial Pacific. *Oceanology* 49 (1), 121–129.
- Pak, H., Zaneveld, J.R.V., 1974. Equatorial front in the Eastern Pacific Ocean. *J. Phys. Oceanogr.* 4, 570–578. [http://dx.doi.org/10.1175/15200485\(1974\)004<0570:EFITEP>2.0.CO;2](http://dx.doi.org/10.1175/15200485(1974)004<0570:EFITEP>2.0.CO;2).
- Patarroyo, G., Martínez, J.I., 2013a. Foraminíferos bentónicos recientes en las aguas profundas de la cuenca de Panamá: Ecología y su posible relación con las corrientes de fondo. *Bol. Investig. Mar. Costeras* 42 (1), 33–58.
- Patarroyo, G., Martínez, J.I., 2013b. Distribution and environmental preferences of deep sea benthic foraminifera in the Panama Basin, Eastern Pacific Ocean. *Caldasia* 35 (2), 311–324.
- Patrick, A., Thunell, R.C., 1997. Tropical Pacific sea surface temperatures and upper water column thermal structure during the last glacial maximum. *Paleoceanography* 12, 649–657.
- Pedersen, T.F., 1983. Increased productivity in the Eastern Equatorial Pacific during the last glacial maximum (19,000 to 14,000 yr B.P.). *Geology* 11, 16–19.
- Pedersen, T.F., Nielsen, B., Pickering, M., 1991. Timing of late quaternary productivity pulses in the Panama Basin and implication for atmospheric CO₂. *Paleoceanography* 6, 657–677.
- Pedersen, T.F., Pickering, M., Vogel, J.S., Southon, J.N., Nelson, D.E., 1988. The response of benthic foraminifera to productivity cycles in the Eastern Equatorial Pacific: faunal and geochemical constraints on glacial bottom water oxygen levels. *Paleoceanography* 3, 157–168.
- Pichat, S., Sims, K.W.W., François, R., McManus, J.F., Brown Leger, S., Albarède, F., 2004. Lower export production during glacial periods in the equatorial Pacific derived from (²³¹Pa/²³⁰Th)_{xs,0} measurements in deep-sea sediments. *Paleoceanography* 19, PA4023. <http://dx.doi.org/10.1029/2003PA000994>.
- Pisias, N.G., Mix, A., 1997. Spatial and temporal oceanographic variability of the Eastern Equatorial Pacific during the late Pleistocene: evidence from radiolarian microfossils. *Paleoceanography* 12, 381–393.
- Poveda, G., Waylen, P.R., Pulwarty, R.S., 2006. Annual and interannual variability of the present climate in northern South America and southern Mesoamerica. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 234, 3–27.
- Rathburn, R., Corliss, B.H., 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. *Paleoceanography* 9, 87–150.
- Revels, S.A., 1996. The Generic Revision of Five Families of Rotaliine Foraminifera. In: Special Publication 34 Cushman Foundation for Foraminiferal Research, pp. 1–113.
- Revels, S.A., 2005. A key to the unilocular hyaline Foraminifera. *J. Micropaleontol.* 24, 145–158.
- Resig, J.M., 1990. Benthic foraminiferal stratigraphy and paleoenvironments off Perú, leg 112. In: Suess, E., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results 112, pp. 263–296.
- Rincon-Martínez, D., Steph, S., Lamy, F., Mix, A., Tiedemann, R., 2010b. Tracking the equatorial front in the Eastern Equatorial Pacific Ocean by the isotopic and faunal composition of planktonic foraminifera. *Mar. Micropaleontol.* 79, 24–40.
- Sarkar, S., De, S., Gupta, A.K., 2009. Late quaternary benthic foraminifera from ocean drilling program Hole 716A, Maldives Ridge, southeastern Arabian sea. *Micropaleontology* 55 (1), 23–48.
- Schlitzer, R., 2010. Ocean Data View, Software. Alfred Wegener Institute, Bremerhaven, Germany. Available at: <http://odv.awi.de>.
- Schönfeld, J., 2002a. Recent benthic foraminiferal assemblages in deep high energy environments from the Gulf of Cadiz (Spain). *Micropaleontology* 44, 141–162.
- Schönfeld, J., 2002b. A new benthic foraminiferal proxy for near-bottom current velocities in the Gulf of Cadiz, northeastern Atlantic Ocean. *Deep Sea Res.* 49, 1853–1875.
- Schönfeld, J., Spiegler, D., 1995. Benthic foraminiferal biostratigraphy site 861, Chile triple junction, Southeastern Pacific. In: Lewis, S.D., et al. (Eds.), Proceedings of the Ocean Drilling Program 141, pp. 213–221.
- Seiglie, G.A., 1969. Notes on species of the genera *Buliminella* and *Bulimina* (Foraminiferida). *Caribb. J. Sci.* 9 (3–4), 93–116.
- Singh, A.K., Marcantonio, F., Lyle, M., 2011. Sediment focusing in the Panama Basin, Eastern Equatorial Pacific ocean. *Earth Planet. Sci. Lett.* 309, 33–44.
- Smart, C.W., 2002. Environmental applications of deep-sea benthic foraminifera. In: Haslett, S.K. (Ed.), Quaternary Environmental Micropaleontology, pp. 14–58.
- Smith, P.B., 1963. Quantitative and Qualitative Analysis of the Family Bolivinidae. United States Geological Survey Professional Paper 429-A, pp. A1–A39.
- Smith, P.B., 1964. Ecology of Benthonic Species: Recent Foraminifera off Central America. United States Geological Survey Professional Paper 429-B, pp. B1–B55.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of tropical Brazil (5°C) during the last glacial maximum. *Science* 269, 379–383.
- Swift, S.A., 1977. Holocene rates of sediment accumulation in the Panama Basin, Eastern Equatorial Pacific: pelagic sedimentation and lateral transport. *J. Geol.* 85 (3), 301–319.
- Szarek, R., Kuhnt, W., Kawamura, H., Kitazato, H., 2005. Distribution of recent benthic foraminifera on the sunda shelf (South China Sea). *Mar. Micropaleontol.* 61, 171–195.
- Thomas, E., 1985. Late eocene to recent deep-sea benthic foraminifera from the central equatorial Pacific Ocean. In: Mayer, L., et al. (Eds.), Deep Sea Drilling Project, Initial Reports 85, pp. 650–694.
- Van der Hammen, T., Hooghiemstra, H., 2000. Neogene and quaternary history of

- vegetation, climate, and plant diversity in Amazonia. *Quat. Sci. Rev.* 19, 725–742.
- Van Morkhoven, F.P.C.M., Berggren, W.A., Edwards, A.S., 1986. Cenozoic cosmopolitan deep-water benthic foraminifera. *Bull. Centres Rech. Exploration-Production Elf Aquitaine* 11, 428. Pau.
- Wilson, B., 2008. Late quaternary benthonic foraminifera in a bathyal core from the leeward Islands, lesser Antilles, NE Caribbean Sea. *J. Micropalaeontol.* 27, 177–188.
- Wilson, B., 2011. Alpha and beta diversities of late quaternary bathyal benthonic foraminiferal communities in the NE Caribbean Sea. *J. Foraminif. Res.* 41 (1), 33–40.
- Yang, Y.L., Elderfield, H., Pedersen, T.F., Ivanovich, M., 1995. Geochemical record of the Panama Basin during the last glacial maximum. Carbon event shows that glacial ocean was not suboxic. *Geology* 23 (12), 1115–1118.
- Yu, P.-S., Kienast, M., Chen, M.-T., Cacho, I., Flores, J.A., Mohtadi, M., Mix, A.C., 2012. Influences of extratropical water masses on equatorial Pacific cold tongue variability during the past 160 ky as revealed by faunal evidence of planktic foraminifers. *J. Quat. Sci.* 27 (9), 921–931. <http://dx.doi.org/10.1002/jqs.2582>.