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Foraminifera and coccolithophorid assemblage changes in the Panama Basin during the last deglaciation: Response to sea-surface productivity induced by a transient climate change

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Abstract

The responses of community assemblages of planktonic and benthonic foraminifera and coccolithophorids to transient climate change are explored for the uppermost 2 m of cores ODP677B (1.2°N; 83.74°W, 3461 m) and TR163-38 (1.34°S; 81.58°W, 2200 m), for the last ~40 ka. Results suggest that the deglaciation interval was a time of increased productivity and a major reorganization of planktonic trophic webs. The succession in dominance between the planktonic foraminifera species *Globorotalia inflata*, *Globigerina bulloides*, and *Neogloboquadrina pachyderma* denote four periods of oceanographic change: (1) advection (24–20 ka), (2) strong upwelling (20–15 ka), (3) weak upwelling (14–8 ka) and (4) oligotrophy (8 ka to present). Strong upwelling for the deglaciation interval is supported by the low *Florisphaera profunda*/other coccolithophorids ratio and the high percentage abundance of *Gephyrocapsa oceanica*. Benthonic foraminifera assemblage changes are different in both cores and suggest significant regional variations in surface productivity and/or oxygen content at the seafloor, and a decoupling between surface productivity and export production to the seafloor. This decoupling is evidenced by the inverse relationship between the percentage abundance of infaunal benthonic foraminifera and the percentage abundance of *N. pachyderma*. The terrigenous input of the Colombian Pacific rivers, particularly the San Juan River, is suggested as a possible mechanism. Finally, the *Globorotalia cultrata*/*Neogloboquadrina dutertrei* ratio is used to reconstruct the past influence of the Costa Rica Dome-Panama Bight and cold tongue upwelling systems in the Panama Basin. A northern influence is suggested for the late Holocene (after 5 ka) and the last glacial (before 20 ka), whereas a southern influence is suggested for the 20–5 ka interval. There is a correspondence between our reconstructed northern and southern influences and previously proposed positions of the Intertropical Convergence Zone (ITCZ) after the Last Glacial Maximum (LGM).

Keywords: Paleoceanography; Quaternary; Panama Basin; Eastern Equatorial Pacific; Foraminifera; Coccolithophorids

1. Introduction

Transient climate changes force the structure and functioning of marine communities in ways that are still poorly understood (e.g. Cronin, 1999). However,

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the potential exists for untangling paleocommunity information as a proxy of climate change, i.e. by determining community assemblage changes and their disassembly and reassembly through time. This lack of understanding of how microplankton communities respond to rapid climate change has prompted paleoceanographers to suggest that paleoclimate reconstructions should be based more on individual species than on assemblages (e.g. Cronin, 1999).

The understanding of regional precipitation patterns, upwelling dynamics and the frequency and intensity of ENSO-like events in the Eastern Equatorial Pacific (EEP), largely depends on the reconstruction of the past mean position of the Intertropical Convergence Zone (ITCZ). Numerous attempts using, mostly, geochemical proxies, have provided contradictory results with regard to a northerly or southerly position of the ITCZ and the presence of La Niña- or El Niño-like conditions for the last glacial maximum (LGM; e.g. Beaufort et al., 2001; Koutavas et al., 2002; Stott et al., 2002; Martinez et al., 2003). None of these studies have explored neither the response of microplankton to transient climate changes nor the potential of microfossils as paleoceanographic proxies in this area. The EEP offers a unique opportunity to explore microfossil assemblage changes at the last deglaciation (19–10 ka) because of the presence of oligotrophic and eutrophic systems resulting from the interaction of Caribbean, Pacific and Andean climate states operating at millennial and sub-millennial frequencies.

So far the question of whether productivity increased or decreased in the EEP during the LGM has remained elusive and can be tracked back to the pioneering work of Arrhenius (1952; for a review see Loubere, 1999, 2001). Although the view that productivity was reduced (Loubere and Fariduddin, 2003), and that seafloor conditions were not suboxic (Yang et al., 1995) during the LGM have gained support, still the mechanisms of how the EEP reached its present productivity pattern are still poorly understood. Our contribution supports the view that productivity was reduced during the LGM, although we demonstrate, by means of a multiproxy approach, that it increased during the deglaciation. By comparing the relative abundance of planktonic and benthonic foraminifera, and coccolithophorids from two deep-sea records judi-

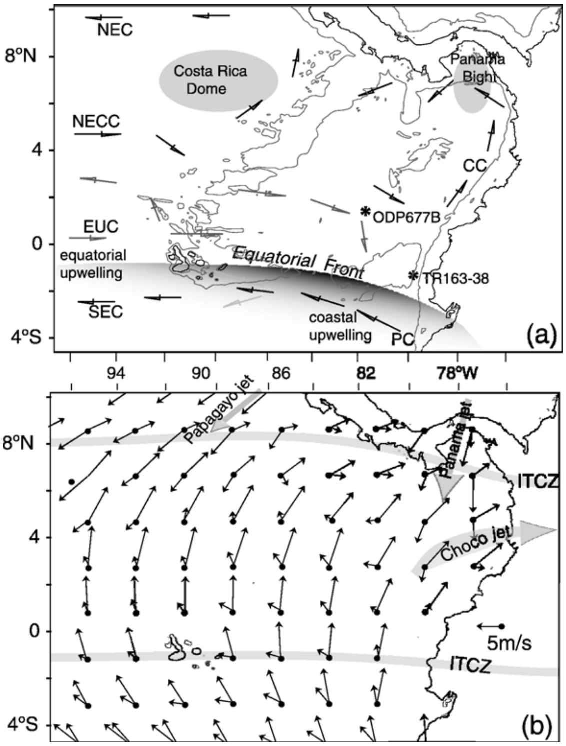

Fig. 1. The Panama Basin: (a) bathymetry, core locations, surface currents and upwelling systems, (b) annual extreme wind directions, the intertropical convergence zone (ITCZ) in September (~8°N) and March (~1°S) and the Papagayo, Panama and Choco jets. NEC = North Equatorial Current, NECC = North Equatorial Countercurrent, EUC = Equatorial Undercurrent, SEC = South Equatorial Current, CC = Colombia Current, PC = Peru Current.

ciously located at the center and the southern extreme of the Panama Basin, we will demonstrate that surface productivity in the Panama Basin is mainly controlled by the interplay of the Costa Rica Dome-Panama Bight and the cold tongue upwelling systems, and to a lesser extent by the terrigenous input. This interpretation contrasts with our previous contribution where we argued that a La Niña-like state was dominant for the ~19–35 ka interval and that this state triggered a stronger atmospheric Choco jet, which affected the northern Andes, and provoked intense precipitation and the descent of glaciers in the Central Cordillera of Colombia (Martinez et al., 2003).

1.1. Methods

The uppermost 2 m of cores ODP677B (1.2°N; 83.74°W, 3461 m water depth) and TR163-38 (1.34°S; 81.58°W, 2200 m water depth; Fig. 1a), collected in the center of the Panama Basin and under the Equatorial Front in the eastern extreme of the Carnegie Ridge, respectively, were selected for study. Each core was sampled at 2–3 cm intervals in order to cover the last ~40 ka. This resulted in a time resolution of ~0.5 to 1 ka. Samples were prepared for planktonic and benthonic foraminifera and coccolithophorids. For foraminiferal analyses, samples were soaked in water and diluted hydrogen peroxide until the reaction stopped. The samples were then wet sieved to acquire 63 and 150 μm size fractions, and dried at ~40 °C. Counting of specimens was done on a sub-sample of ~300 specimens in the >150 μm size fraction obtained with the aid of an Otto microsplitter. Coccolithophorid samples were prepared using the standard smear slide procedure (e.g. Perch-Nielsen, 1985). Details of foraminifera and coccolithophorid data were reported in previous papers (e.g. Betancur and Martinez, 2001; Ruiz, 2001; Martinez et al., 2003). Similarly, details of the chronostratigraphic control using stable oxygen isotopes and accelerator mass spectrometry radiocarbon dates (AMS^{14}C) on *Neogloboquadrina dutertrei* are given in Martinez et al. (2003).

2. The intertropical convergence zone (ITCZ), sea-surface circulation and productivity patterns

The ITCZ shifts meridionally, between 9°N in August and 1°S in February, following the relative strength of the southeast and northeast trade winds, respectively (Fig. 1b). This seasonal fluctuation of the ITCZ affects sea-surface temperature (SST), salinity (SSS) and upwelling intensity all over the EEP (e.g. Forsbergh, 1969; Donguy and Henin, 1980). In the Panama Basin two major atmospheric jets, the Panama and the Choco jets, are driven by the dynamics of the ITCZ and SST meridional patterns (Fig. 1b; e.g. Rodriguez-Rubio and Stuardo, 2002; Poveda and Mesa, 1997). Conversely they are responsible for upwelling dynamics, rain patterns and marine productivity. Similar to the Tehuantepec and Papagayo atmospheric jets, which cross the Central American isthmus through topographic gaps, the Panama jet crosses the isthmus and enhances upwelling by pushing sea-water away from the coast causing decreases in sea level and SST (e.g. Legeckis, 1988; Rodriguez-Rubio and Stuardo, 2002). The Panama jet and its associated upwelling system operate in February–March when the northeast trade winds intensify and the ITCZ is in its most southerly position. Sea level drops ~11 cm and SST decreases ~7 °C relative to their mean values, and upwelling reaches a speed of 45×10^{-4} cm s^{-1} which results in chlorophyll values in excess of 20 μg L^{-1} (e.g. Stevenson, 1970; Rodriguez-Rubio and Stuardo, 2002; Rodriguez-Rubio et al., 2003) and a primary production that ranges between 8.3 and 75 mmol C m^{-2} dy^{-1} (Bishop and Marra, 1984; Bishop et al., 1986), which is less than half that of the cold tongue.

The Choco jet, which enters the continent at ~5°N, results from the westerly deflection of the southeast Trade winds once they cross the equator (Fig. 1b). The strength of the Choco jet depends on the meridional SST gradient across the equator in the EEP. The Choco jet is strongest (6–8 ms^{-1} at 925 hPa) during October–November when the SST gradient, between NINO1+2 regions and the Panama Bight, is ~3–5 °C at 925–1000 hPa (Poveda and Mesa, 2000). Advection of moisture by the Choco jet into the continent is of the order of ~0.08 m s^{-1}. The Choco jet over western Colombia rises by orographic lifting, thus resulting in meso-scale convective cells. Intense precipitation in western Colombia, makes this one of the rainiest localities on Earth (Poveda and Mesa, 2000), and a region with the highest fresh water discharge (2550 m^3 s^{-1}) and sediment yield (16×10^6 t year^{-1}) of the Americas to the Pacific (Restrepo et al., 2002). This results in a fresh water (<28 psu) lid that extends across the Colombian margin to eventually mix with the saltier oceanic waters. The effects on productivity of this water discharge and sediment yield in the Panama Basin are still to be explored.

Because of the quasi-periodic disruption of the SST meridional pattern caused by El Niño in the EEP, the Choco jet generally weakens causing dryness in the northern Andes. Dryness in northern South America also shows a good correlation with the ‘cold tongue index’ (e.g. Dettinger et al., 2001), whereas precipitation shows a good correlation with the Southern Oscillation Index (SOI), SST at NINO-3 and -4, and wind velocity at NINO-4 (Poveda and Mesa, 1997).

Along with the stronger Choco jet in the latter part of the year, when the ITCZ is in its northerly position, the EEP is bathed by the cold, nutrient-rich cold tongue derived from the Peru Current and the warm and less nutrient-rich Equatorial Counter Current that meet along the Equatorial Front (Fig. 1a; e.g. Wooster, 1969; Pak and Zaneveld, 1974). Upwelling caused by divergence (Ekman transport) is an important component of the cold tongue and affects the uppermost 200 m of the water column transporting ~47 Sv (e.g. Wyrtki, 1981; Tomczak and Godfrey, 1994). The source of the cold tongue upwelled water is the equatorial undercurrent (EUC) which runs along the equator at 40 m water depth in the EEP, and originates in the southwest Pacific (Toggweiler et al., 1991; Tomczak and Godfrey, 1994). The EUC transports up to 35–40 Sv and is stronger during January–June and weaker during July–December (e.g. Tomczak and Godfrey, 1994).

The cold tongue upwelling system is considered as a high-nutrient, low-chlorophyll (HNLC) region due to the inefficient consumption of nutrients by plankton. Despite this deficient use of nutrients, chlorophyll content reaches $<1\ \mu g\ L^{-1}$ and primary production varies between 80 and 160 mmol C $m^{-2}day^{-1}$ during La Niña phase. Conversely, chlorophyll content is $>0.05\ \mu g\ L^{-1}$ and primary production is 35 mmol C m^{-2} day^{-1} during El Niño phase. Diatoms and picoplankton are dominant during La Niña and El Niño phases, respectively (Chavez et al., 1999).

The Costa Rica Dome upwelling system results from divergence at the eastern termination of the north equatorial countercurrent (NECC) which is derived from the north and south equatorial currents. At the Costa Rica Dome, the thermocline depth is at a minimum and ascending water moves at 10^{-6} m s^{-1} from 75 to 200 m depths, thus resulting in chlorophyll values in excess of 2 mg m^{-3} (e.g. Wyrkti, 1964; Fiedler, 2002; McClain et al., 2002). Even though the Costa Rica Dome starts to form in February–March, it intensifies between July and November, i.e. following the ITCZ (Fiedler, 2002), If the meridional position of the ITCZ varied in the past, the intensity of upwelling along the Costa Rica Dome may have varied too. Compared to the cold tongue, iron availability is high in the Costa Rica Dome, where it is brought in by the Papagayo wind jet from Central America (Fung et al., 2000; Fiedler, 2002). Mean zooplankton productivity at the Costa Rica Dome is comparable to the cold tongue and is significantly larger than at the Panama Bight (Fiedler, 2002).

These significant differences in chlorophyll content, primary productivity and plankton content result in different food webs between the cold tongue, Costa Rica Dome, and Panama upwelling systems (e.g. Owen and Zeitzschel, 1970; Honjo, 1982; McClain et al., 2002). Therefore, microfossils preserved on the seafloor should reflect the dynamics of their interaction in the past allowing inferences on the strength of the Papagayo, Panama and Choco jets and, conversely, on the past position of the ITCZ, and/or the relative intensity of the Trade winds.

3. Results

3.1. Planktonic and benthonic foraminifera and coccolithophorid assemblage changes

3.1.1. Planktonic foraminifera

Similar to planktonic foraminifera assemblages from core-top samples from the EEP (Martinez and Bedoya, 2001), donwcore assemblages in cores ODP677B and TR163-38 are dominated by *N. dutertrei* (Fig. 2). For the Holocene, the percentage abundance of *N. dutertrei* varies between ~60% in core ODP677B and >70% in core TR163-38. For the last glacial it fluctuates between ~40% and ~65% with minimum values close to the deglaciation. Under the hypothesis of a high productivity LGM scenario the expected percentage values of *Globigerina bulloides*, a cool and upwelling indicator (e.g. Bé et al., 1985; Hemleben et al., 1989), should be higher for the glacial interval and should show a positive correlation with other upwelling proxies like *Globorotalia inflata* and *Neogloboquadrina pachyderma*. However, this is not the case. What is observed is a conspicuous faunal dominance succession between *G. inflata*, *G. bulloides* and *N. pachyderma* in both cores (Fig. 2). The succession is more marked in core TR163-38, where *G. inflata* is dominant between 24 and 20 ka, and almost disappears at 14 ka. Contemporaneous with its abrupt fall at ~20 ka, *G. bulloides* increases to become dominant until ~15 ka when it is replaced by the steady increase of *N. pachyderma* which started at 20 ka. *N. pachyderma* dominated between 14 and 8 ka. Similarly, in core ODP677B, *G. inflata* drops in abundance between 18 and 14 ka at the same time that *G. bulloides* became dominant between 18 and 10 ka. *N. pachyderma* increases at ~16 ka and its percentage abundance, though with strong fluctuations, remains

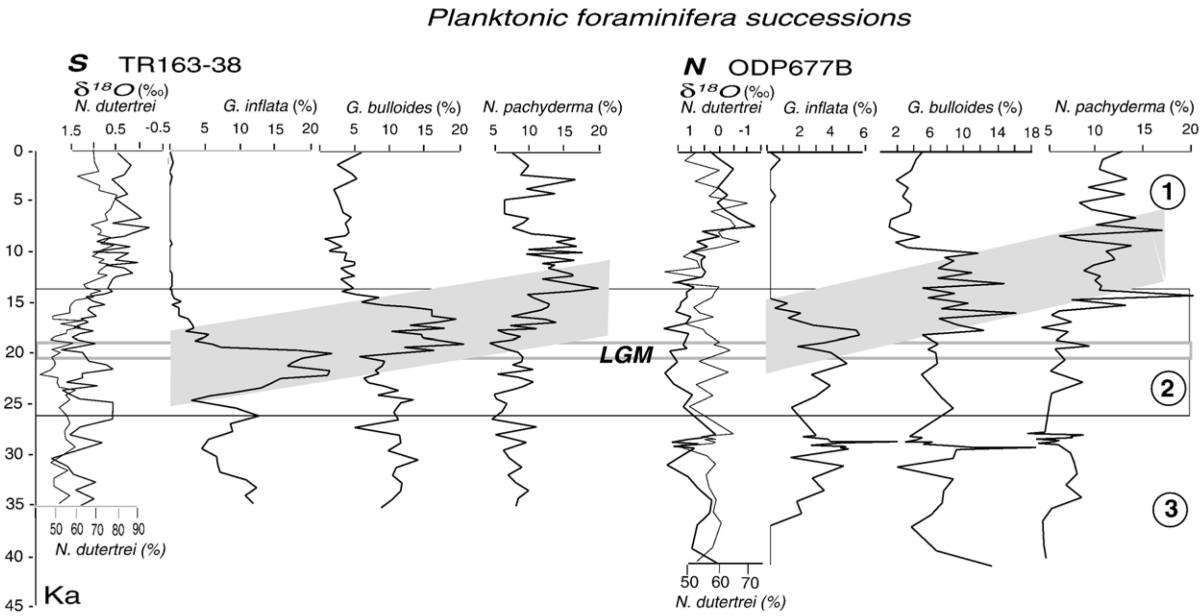

Fig. 2. Planktonic foraminiferal assemblage change (percentage abundance) against time (ka) for cores TR163-38 and ODP677B. The oxygen isotope curve of *N. dutertrei* (thick line) and its percentage abundance (thin line) are also included. LGM = last glacial maximum; 1, 2, and 3 = isotope stages.

around 10% throughout the Holocene. The dominance of *G. bulloides* in both cases corresponds to the deglaciation interval, when the percentage abundance of symbiont-barren species was high, and planktonic foraminiferal fragmentation was low (Martinez et al., 2003). Bearing in mind age model uncertainties and a preservational bias, the *G. bulloides* percentage abundance curves resemble the absolute abundance (#/g) of *Uvigerina* and fecal pellets (Pedersen et al., 1988) and the percentage of organic carbon (C_{org}) in core P7 (2°36.26′N; 83°59.18′W; Yang et al., 1995). The organic carbon mass accumulation rate (MAR) however does not match this pattern. It is highest between 21 and 17 ka, peaking at ~20 ka when it reaches 80 mg cm^2 ky^{-1} (Pedersen et al., 1991).

The present day distributions of *Globorotalia cultrata* (a synonym of *G. menardii*) and *N. dutertrei* respond to a strong meridional gradient (SST, nutrients and salinity) where the former species dominates in the north associated with the Costa Rica Dome and Panama Bight upwelling systems, and the latter species dominates in the south associated with the cold tongue upwelling system (Fig. 3a–b; Martinez and Bedoya, 2001). The Shannon diversity Index (*H*) and evenness (*E*) also show northward increasing patterns disrupted by an abrupt change at the Equatorial Front (Fig. 3b). *H* provides a measure of uncertainty of finding a species in an assemblage, by random sampling. *H* would be larger when each one of the species in a sample are represented in the same proportion. By contrast, *E* is a measure of the distribution of species abundances in an assemblage. Larger *E* values mean that all the species occur in the same proportion, whereas low *E* values mean that the assemblage is dominated by few species (e.g. Hayek and Buzas, 1997). The lowermost, *H* and *E*, values (<0.5) occur in association with the cold tongue, whereas higher and more spread values (0.4–0.9) occur across the Panama Basin. North of 5°N the influence of the Panama Bight–Costa Rica Dome upwelling systems is readily apparent by *H* values between 0.5 and 0.8 (Fig. 3b). Therefore, the *G. cultrata*/*N. dutertrei* ratio and the Shannon diversity index (*H*) and evenness (*E*) can be used as indicators of the influence of either, the Panama–Costa Rica Dome or the cold tongue upwelling systems in the EEP (Fig. 4). The *G. cultrata*/*N. dutertrei* ratio shows analogous patterns in cores ODP677B and TR163-38. It is high in the late Holocene, after 5 ka, and the last glacial, before 20 ka, and displays low intermediate to low values for the 20–5 ka interval (Fig. 4). The 20 and 5 ka boundaries also coincide with conspicuous changes in the percentage abundance of a number of species, e.g. *G. inflata*, *N. pachyderma* and *G. glutinata* in

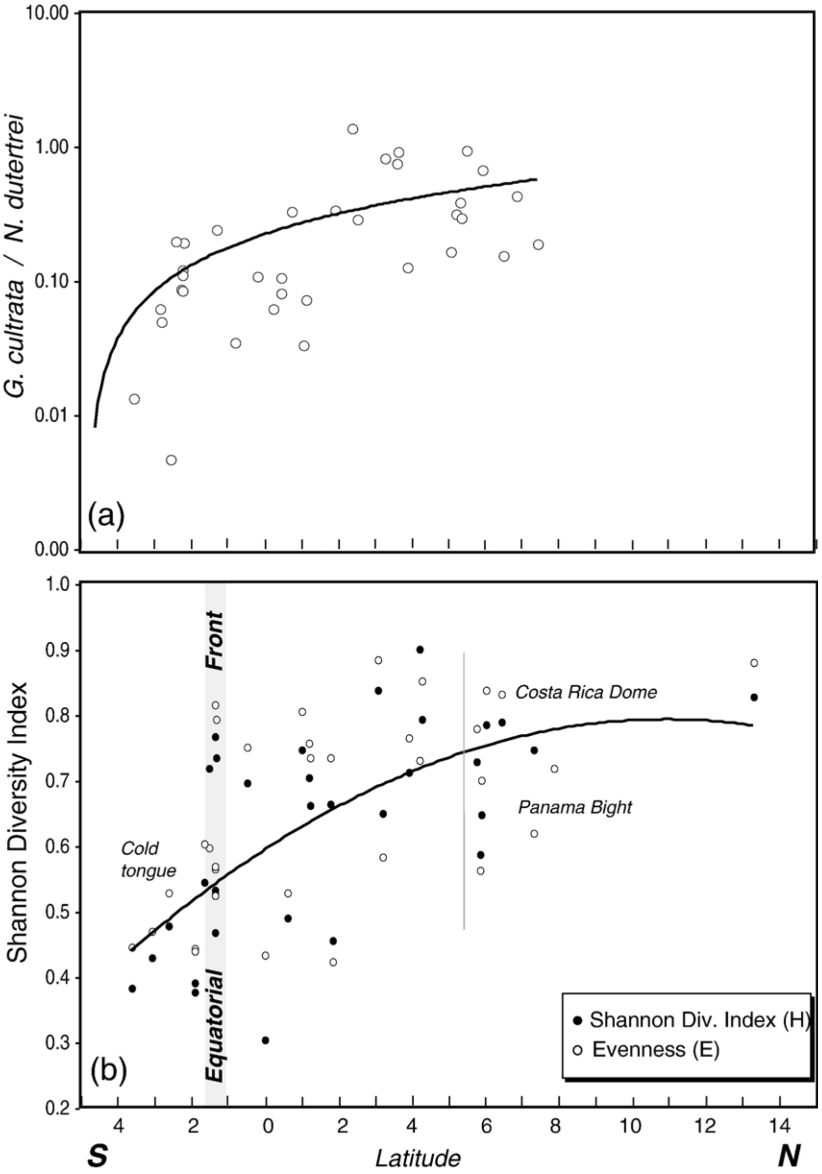

Fig. 3. (a) *G. cultrata*/*N. dutertrei* ratio against latitude in the eastern equatorial Pacific (EEP), and (b) Shannon diversity index (*H*) and evenness (*E*) on planktonic foraminifera against latitude from core-top EEP samples. Note the conspicuous increase of the *G. cultrata*/*N. dutertrei* ratio and the Shannon diversity index at the Equatorial Front (data in Martinez and Bedoya, 2001).

core TR163-38. There is some correspondence between our interpreted northern and southern influences and the Shannon diversity Indices in both cores, e.g., a southern influence between 14 and 5 ka in core TR163-38 corresponds to a Shannon diversity Index of <0.6. For other intervals the relationship does not hold, thus denoting a complex reorganization of planktonic foraminifera communities during transient climate change, e.g. between 10 and 20 ka when diversity was high contrary to an expected southern influence predicted by the *G. cultrata*/*N. dutertrei* ratio (Fig. 4). Shannon diversity shows a positive correlation with the percentage abundance of *G. bulloides* in both cores and a negative correlation with *N. pachyderma* in core TR163-38. It is worth noting is that there is some similarity between our *G. cultrata*/*N. dutertrei* ratio curve and the Si/Al ratio in core P7 (Yang et al., 1995). Taking into consideration age model uncertainties the similarity would mean a larger Al input from the south before 20 ka and after 4 ka.

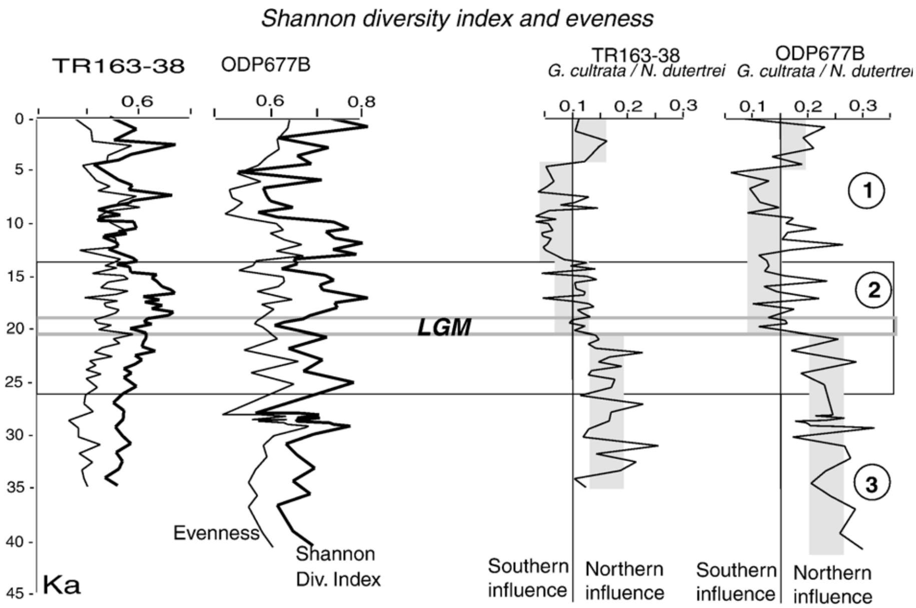

Fig. 4. *G. cultrata/N. dutertrei* ratio and Shannon diversity index and evenness on planktonic foraminifera against time (ka) for cores TR163-38 and ODP677B. LGM = last glacial maximum; 1, 2, and 3 = isotope stages.

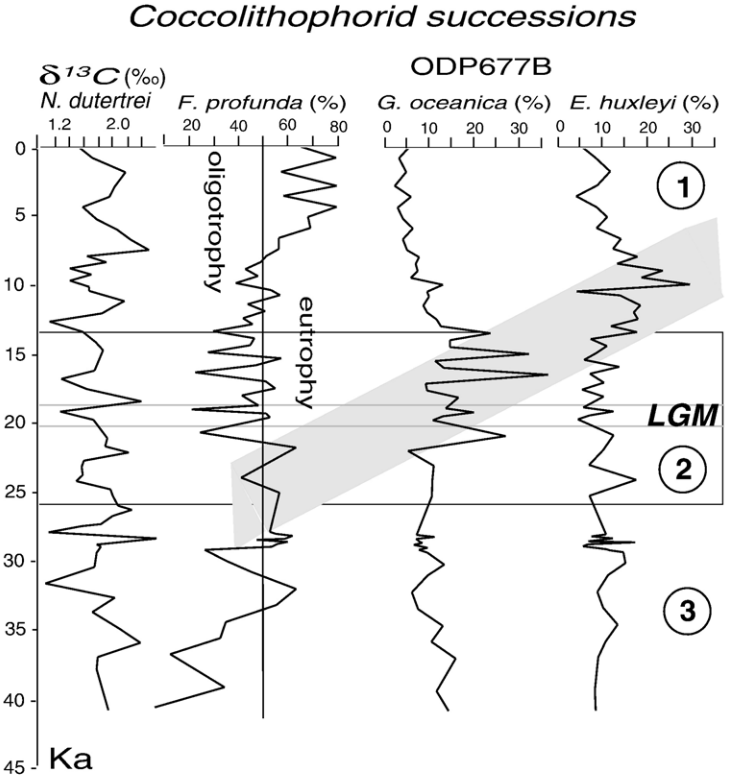

Fig. 5. Coccolithophorid assemblage changes (percentage abundance) of *F. profunda*, *G. oceanica* and *E. huxleyi* in core ODP677B. Note that the percentage abundance of *F. profunda*/other coccolithophorids ratio is used to indicate oligotrophy and eutrophy. LGM = last glacial maximum; 1, 2, and 3 = isotope stages.

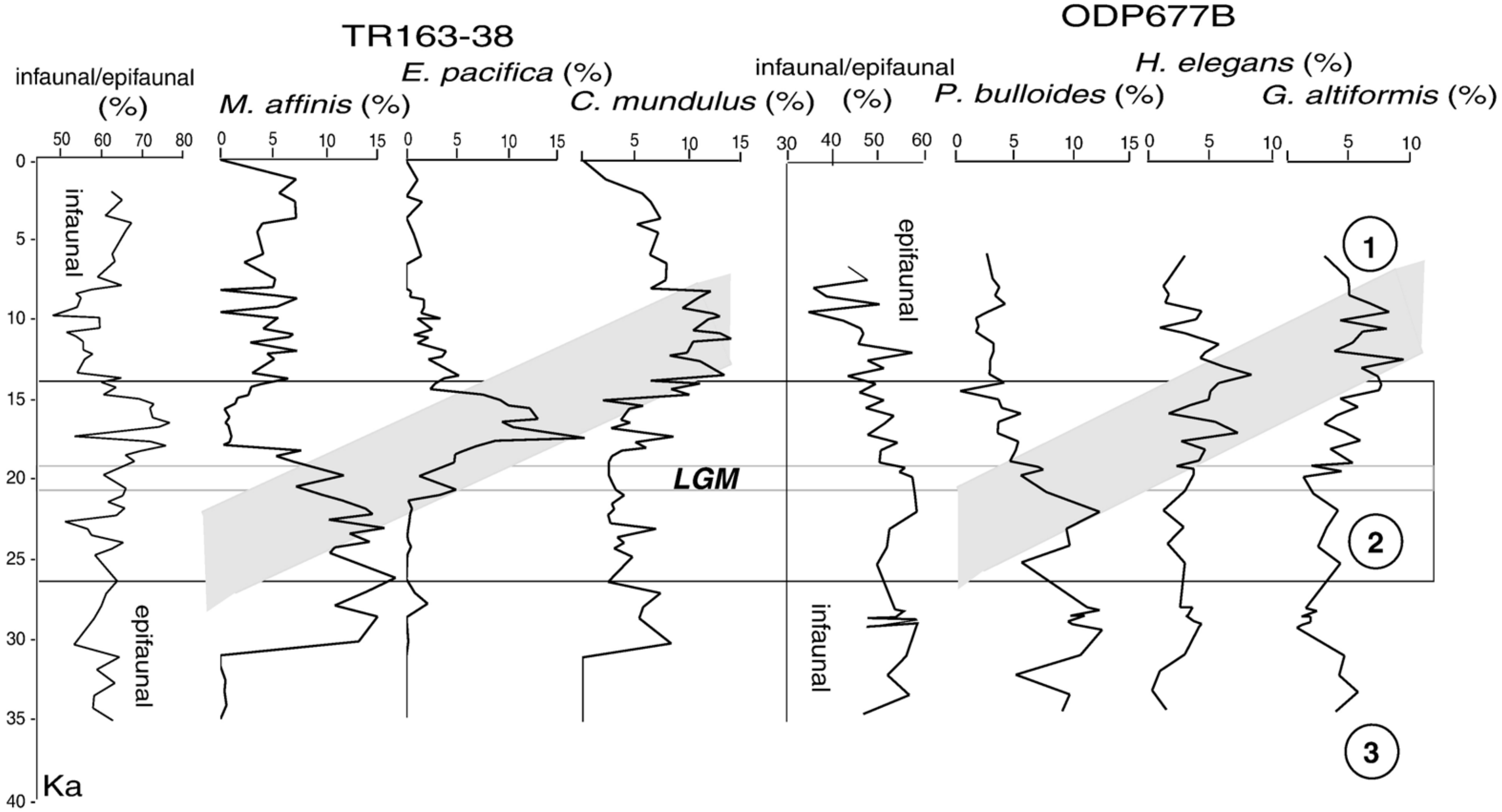

Fig. 6. Benthonic foraminiferal assemblage changes (percentage abundance) against time (ka) for cores TR163-38 and ODP677B. The percentage abundance of infaunal and epifaunal benthonic foraminifera are also included. LGM = last glacial maximum; 1, 2, and 3 = isotope stages.

3.1.2. Coccolithophorids

The uppermost 2 m of core ODP677B is dominated by *Florisphaera profunda*, *Gephyrocapsa* spp., *Gephyrocapsa oceanica*, *Emiliania huxleyi* and *Pseudoemiliana lacunosa*. Like the planktonic foraminifera, there is a conspicuous succession of taxa around the deglaciation interval. *F. profunda* dominates prior to 21 ka before being succeeded by *G. oceanica* that falls in abundance at 14 ka. *E. huxleyi* then dominates before finally falling in abundance at ~8 ka (Fig. 5; Ruiz, 2001). A similar succession is recorded in core TR163-11 located on the Cocos Ridge (Ruiz, 2001). The *F. profunda*/other coccolithophorids ratio has minima in early stage 1, late stage 2 and early stage 3, thus suggesting eutrophic conditions induced by upwelling. The *F. profunda*/other coccolithophorids ratio is inverse to the percentage abundance of *G. oceanica*, and *G. bulloides* thus reflecting a productivity increase at least for the deglaciation interval.

3.1.3. Benthonic foraminifera

There is a clear difference in benthonic foraminiferal composition between cores ODP677B and TR163-38. *Cibicidoides mundulus*, *Melonis affinis* and *Cassidulina carinata* exceed 4% in core TR163-38 compared to *Oridorsalis umbonatus* and *Uvigerina mantaensis* which are >10% in core ODP677B.

Infaunal benthonic foraminifera exceed 60% in core TR163-38, except for the 8–15 ka interval and short intervals at ~17.5, 23, and 31 ka when values are lower (Fig. 6). Maximum values are found at the deglaciation interval between 19 and 15 ka. For core ODP 677B infaunal benthonic foraminifera fluctuate around 50%, before 12 ka, and 40% between 6 and 12 ka (Fig. 6). In both cores, the percentage abundance of infaunal benthonic foraminifera shows an inverse relationship with the percentage abundance of *N. pachyderma*.

In core TR163-38, *M. affinis*, *E. pacifica* and *C. mundulus* form a succession series (Fig. 6). *M. affinis* is abundant between 31 and 18 ka, when it is followed by *E. pacifica* that peaks at ~17 ka and became reduced at 15 ka. This reduction coincides with the increased abundance of *C. mundulus* until ~8 ka. Similarly, in core ODP677B, *P. bulloides* is abundant until the LGM, when is replaced by *Hoeglundina elegans* that peaks at ~14 ka. *Gyroidina altiformis* seems to increase gradually from the LGM until 10 ka (Fig. 6).

4. Discussion

The documented micropaleontological patterns and assemblage changes appear to indicate that the deglaciation interval was a time of increased productivity and a major reorganization of planktonic trophic webs. Even though the succession of the planktonic foraminifera species *G. inflata*, *G. bulloides*, and *N. pachyderma* are analogous in both cores, there is a lead signal, on the order of 1 to 3 ka, in core TR163-38 compared to ODP677B. This suggests that the response of marine planktonic communities to climate change was first felt south of the equator. The increase in *G. inflata*, an intermediate-to deep-dwelling species, suggests that the seasonal advection of southern subtropical waters into the Panama Basin in the ~35–16 ka interval occurred when the oxygen minimum zone (OMZ) was apparently weaker (e.g. Luz, 1973; Martinez et al., 2003). A stronger OMZ after 16 ka would have favored the presence of organic and terrigenous particles, as is observed today off the Peruvian coast (Pak et al., 1980). This might have affected the life cycle of *G. inflata*.

Conversely, the increase of *G. bulloides* during deglaciation, suggests that the intensification of upwelling and the simultaneous development of the OMZ which would have prevented the invasion of the Panama Basin by *G. inflata*. The decrease in abundance of *G. inflata* at ~16 ka is close to the $\delta^{13}C$ minimum in *N. dutertrei* recorded in core TR163-19 (2°15.5′N; 90°57.1′W), which was radiocarbon dated to be ~15.9 ca. ka, and interpreted to be the result of a major warming and nutrient rearrangement of the Southern Ocean and transmission of the $\delta^{13}C$ signal to the EEP through the EUC (Spero and Lea, 2002). By contrast, planktonic foraminifera in core RC11-238 (1.52°S; 85.82°W; 2573 m), collected west of core TR163-38, depicts a succession of *G. inflata*, *N. pachyderma* and *G. bulloides* (Faul et al., 2000). In this core, *N. pachyderma* is more abundant before 14 ka, whereas *G. bulloides* peaks between 16 and 12 ka. Advection is interpreted as the most likely mechanism to explain the large percentage abundance of these species during the LGM and the deglaciation interval (Faul et al., 2000). The inverse succession of *N. pachyderma* and *G. bulloides* in core RC11-238, compared to core TR163-38, might be due to its site location just south of the Equatorial Front, where the nutrient-rich Equatorial Undercurrent (EUC) upwells, compared to the site location of core TR163-38 to the north of it, where the influence of the EUC is minor (e.g. Stevenson and Taft, 1971; Pak and Zaneveld, 1973; Palacios, 2004). Furthermore, the peak in planktonic foraminifera flux (100 to 300×10^3 shells.cm^{-2}.kyr^{-1}) occurs during the deglaciation, between 19 and 13 ka (Faul et al., 2000), thus strengthening our interpretation for a larger productivity event during deglaciation, and not during the

LGM. The seasonal decoupling of the thermocline depth and the surface position of the Equatorial Front (Wooster, 1969), and the dynamics of the EUC (Pak and Zaneveld, 1974; Loubere, 2000, 2001; Palacios, 2004) suggest that following the peak in abundance of *G. inflata*, differences in the thermocline depth, at longer time scales, were significant and would have favored *N. pachyderma* and *G. bulloides* blooms, south and north of the Equatorial Front, respectively.

The assemblage change pattern is also exhibited by coccolithophorids in core ODP677B with the distribution of *F. profunda*, for the interval preceding 21 ka, suggesting a deep nutricline, oligotrophic conditions and a reduced continental influence (cf. Okada and Honjo, 1973; Molfino and McIntyre, 1990; Ahagon et al., 1993). For the 21–14 ka interval, the increase of *G. oceanica*, an upper to middle photic-dwelling species, suggests a shallower nutricline, more eutrophic conditions and/or increased continental influence (cf. Okada and Honjo, 1973; Okada, 1992). Both, the *F. profunda*/other coccolithophorids ratio and the percentage abundance of *G. oceanica* are in agreement with the percentage abundance of *G. bulloides*, and thus support the view that eutrophic conditions were present in the deglaciation interval. Finally, for the 14–8 ka interval, *E. huxleyi*, an opportunistic coccolithophorid species that at present inhabits the upper photic zone (e.g. Okada and Honjo, 1973; Siesser, 1993), signals the end of the productivity pulse that started at the LGM in the center of the Panama Basin. Our observations, therefore, show that the deglaciation interval was a time of higher productivity, eutrophy and southern influence. However, the lack of correspondence between the low *G. cultrata/N. dutertrei* ratio, indicator of a southern influence, and high Shannon diversity values appear at odds with the present pattern. This suggests that trophic webs for the southern Panama Basin and the Equatorial Front experienced a major reorganization. At present, the base level of trophic webs in the Costa Rica Dome and Panama and the cold tongue upwelling systems are dominated by picoplankton and dinoflagellates, and diatoms, respectively. Similarly, primary consumers in the Costa Rica Dome and Panama and the cold tongue upwelling systems are dominated by copepods and euphausiids, and chaetognaths and clupeoid fish, respectively (e.g. Owen and Zeitzschel, 1970; Honjo, 1982; Dossier and Donguy, 1985; Bishop et al., 1986). In these trophic webs the role of planktonic foraminifera has not been appropriately documented, though it is clear that *G. cultrata* benefits from the seasonal character of the Panama upwelling system (e.g. Thunell et al., 1983; Thunell and Reynolds, 1984) and probably preys on picoplankton and dinoflagellates. Similarly, *N. dutertrei* benefits from the high seasonal productivity of the cold tongue upwelling system and probably preys abundantly on diatoms.

By contrast benthonic foraminifera assemblage changes are different in both cores and indicate significant regional variations in surface productivity and/or oxygen content at the seafloor (e.g. Jorissen et al., 1995). The larger mean infaunal percentage abundance in core TR163-38 compared to core ODP677B indicates that surface productivity and/or a lower oxygenation of the seafloor has been more important (cf. Corliss and Chen, 1988) at the former location due to the close influence of the cold tongue and the shallower water location of the site. A connection between the upper ocean and the seafloor is apparently represented by the inverse relationship between the percentage abundance of infaunal benthonic foraminifera and the percentage abundance of *N. pachyderma*. This odd relationship suggests that the source of particulate organic matter falling to the seafloor might be different to the one sustaining *N. pachyderma*. A possible candidate could be the terrigenous input of the Colombian Pacific rivers, particularly the San Juan River. This organic matter supply to the seafloor could occur through both surface and mid-water currents as is observed today in the Panama Basin (e.g. Asper et al., 1992) and off the Peruvian coast (Pak et al., 1980).

The epifaunal benthonic species *E. pacifica* and *H. elegans* increased during the deglaciation following the decline in abundance of *M. affinis* and *P. bulloides*. This might indicate a change in the source of organic matter, without an apparent change in oxygenation conditions at the seafloor, nor a significant change in productivity, for the deglaciation interval. Like *E. huxleyi*, *C. mundulus* that is an opportunistic species, and its abundance suggests an increase in seasonality (e.g. Okada, 1992).

If the reconstructed influence of the northern or the southern upwelling systems is correct, and if their nutrient content did not change much in the past, these influences should reflect the mean position of the ITCZ in the past. A northern or southern influence, therefore, should suggest that the ITCZ was in a southerly or northerly position, respectively. However, the mean position of the ITCZ, even today, is hard to sustain due to its wide seasonal variation, in the order of 10° of latitude. It might be that the reported fluctuations reflect the seasonal strength of the northeast and southeast trade winds rather than changes in the position of the ITCZ. With this view in mind, northeast trade winds would have been seasonally stronger before the LGM and after 5 ka. Conversely, the southeast trade winds would have been seasonally stronger from 14 ka to 5 ka, at least at the site location of core TR163-38. Between the LGM and 14 ka the strength of the trade winds seem to be similar to today. These results are in agreement with previous suggestions for a more northern location of the ITCZ between 10 and 5 ka, and an increasing southern location for the period between ~5 ka and the present, e.g. in the Cariaco Basin (core ODP 1002C, Haug et al., 2001; core CAR7-1, Tedesco and Thunell, 2003) and the Galapagos Islands (core V21-30, Koutavas et al., 2002). Drier conditions are suggested for Central and northern South America for the same period which have been related to a southerly position of the ITCZ and insulation forcing (e.g. Ruter et al., 2004).

During our previous SST reconstruction we showed that SST at core TR163-38 dropped by ~4 °C, between 23 ka and the LGM, whereas it did not change for core ODP677B. The significant change in SST in the former core is driven by the large percentage abundance of *G. inflata*, a species whose presence in the EEP is regarded as the result of advection rather than upwelling. If this is true, the apparent discrepancy surrounding the co-occurrence of *G. inflata* and the “northern influence”, i.e. the *G. cultrata*/*N. dutertrei* ratio, could be reconciled by considering their co-occurrence as a result of strong seasonal variations. Alternatively, it might be that *G. inflata* drives spurious SST results due to its deep-dwelling habitat, and the northern influence is real for the last glacial period. This would mean that El Niño-like rather than La Niña-like conditions dominated the region during the last glacial.

5. Summary and conclusions

Our study documents a set of micropaleontological assemblage changes that suggests that the Panama Basin for the deglaciation interval was a time of increased productivity and a major reorganization of planktonic trophic webs, at the same time that there was a decoupling between nutrient supply to the sea surface and the seafloor. The succession of planktonic foraminifera species *G. inflata*, *G. bulloides*, and *N. pachyderma* suggests advection for the 24–20 ka interval, strong upwelling for the 20–15 ka interval, weak upwelling for the 14–8 ka interval and oligotrophy for the 8 ka to Present interval. Stronger upwelling for the deglaciation interval is supported by the low *F. profunda*/other coccolitophorids ratio and the high percentage abundance of *G. oceanica*. Benthonic foraminifera assemblage changes were found to be different in both cores thus suggesting significant regional variations in surface productivity and/or oxygen content at the seafloor, and a decoupling between surface productivity and the supply of phytodetritus to the seafloor. This decoupling is evidenced by the inverse relationship between the percentage abundance of infaunal benthonic foraminifera and the percentage abundance of *N. pachyderma*. The terrigenous input of the Colombian Pacific rivers, particularly the San Juan River, is suggested as a possible mechanism. The *G. cultrata*/*N. dutertrei* ratio is used to reconstruct the past influence of the Costa Rica Dome–Panama Bight and cold tongue upwelling systems in the Panama Basin in the past. A northern influence is suggested for the late Holocene (after 5 ka), and the last glacial (before 20 ka), whereas a southern influence is suggested for the 20–5 ka interval. There is a correspondence between our reconstructed northern and southern influences and previously proposed positions of the Intertropical Convergence Zone (ITCZ) after the Last Glacial Maximum (LGM).

Over all, our main finding is that foraminifera and coccolithophorid assemblages response to deglacial climate change occurred in a sequence of distinct stages, each defined by characteristic species blooms. The transition from the LGM to the Holocene was not a smooth mono-dimensional shift between two end-member biotic states, but rather occurred in numerous successive steps involving community reorganizations. It further demonstrates that microfossil assemblages are unlikely to be controlled by a single oceanographic variable. It appears that there are multiple controls involving advection, upwelling, nutrient input from rivers and the competition between northern and southern upwelling systems linked to dominant wind patterns.

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