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Trends in Caribbean Paleoproductivity related to the Neogene closure of the Central American Seaway

Sreepat Jain*, Laurel S. Collins

Department of Earth Sciences, Florida International University, Miami, Florida, USA

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Abstract

This study tests the hypothesis that the late Miocene to early Pliocene constriction and closure of the Central American Seaway (CAS), connecting the tropical Atlantic and East equatorial Pacific (EEP), caused a decrease in productivity in the Caribbean, due to decreased coastal upwelling and an end to the connection with high-productivity tropical Pacific waters. The present study compared paleoceanographic proxies for the interval between 8.3 and 2.5 Ma in 47 samples from south Caribbean ODP Site 999 with published data on EEP DSDP Site 503. Proxies for Site 999 include the relative abundance of benthic foraminiferal species representing bottom current velocity and the flux of organic matter to the sea floor, the ratio of infaunal/epifaunal benthic foraminiferal species and benthic foraminifer accumulation rates (BFARs). In addition, we calculated % resistant planktic foraminiferal species and used the previously published % sand fraction and benthic carbon isotope values from Site 999.

During early shoaling of the Isthmus (8.3–7.9 Ma) the Caribbean was under mesotrophic conditions, with little ventilation of bottom waters and low current velocity. The pre-closure interval (7.6–4.2 Ma) saw enhanced seasonal input of phytodetritus with even more reduced ventilation, and enhanced dissolution between 6.8 and 4.8 Ma. During the post-closure interval (4.2–2.5 Ma) in the Caribbean, paleoproductivity decreased, current velocity was reduced, and ventilation improved, while the seasonality of phytodetrital input was reduced dramatically, coinciding with the establishment of the Atlantic–Pacific salinity contrast at 4.2 Ma. Our data support the hypothesis that late Miocene constriction of the CAS at 7.9 Ma and its closure at 4.2 Ma caused a gradual decrease in paleoproductivity in the Caribbean, consistent with decreased current velocity and seasonality of the phytodetrital input. © 2006 Elsevier B.V. All rights reserved.

Keywords: Benthic foraminifera; Paleoproductivity; Central American Seaway; Late Neogene; Caribbean

1. Introduction

The development of the southern Central American isthmus initiated a series of climatic, oceanographic and biotic changes (Keigwin, 1982; Collins, 1996; Collins et al., 1996a; Haug and Tiedemann, 1998; Haug et al., 2001; Lear et al., 2003; Coates et al., 2003, 2004; Steph,

2005) that started sometime in the middle Miocene (15–12 Ma; Duque-Caro, 1990; Coates et al., 2003). Land-based data indicate initial docking of the Central American arc with South America between 12.8 and 9.5 Ma (Coates et al., 2004). Thereafter, the tropical marine connection between the Atlantic and the Pacific oceans was progressively restricted, and complete closure of the Central American Seaway (CAS) occurred between 4.2 and 3.5 Ma (Keigwin, 1982; Haug and Tiedemann, 1998). Sea level rises subsequent to the complete CAS closure may have breached the isthmian barrier and thus, the final closure of

* Corresponding author. Tel.: +1 305 348 2365; fax: +1 305 348 3877.
E-mail address: sjain002@fiu.edu (S. Jain).

the CAS has been proposed to have occurred between 2.88 (Steph, 2005) and 2.76 Ma (Kameo, 2002). Closure of the CAS has been thought to be a primary or contributing factor in the abrupt intensification of Northern Hemisphere Glaciation beginning about 3.2 Ma (Keigwin, 1982; Driscoll and Haug, 1998; Haug and Tiedemann, 1998).

Progressive shoaling of the isthmian sill caused divergence of oceanographic conditions in the Caribbean and the Eastern Equatorial Pacific (EEP; Keigwin, 1982). Paleooceanographic models (Maier-Reimer et al., 1990; Mikolajewicz and Crowley, 1997) and data indicate that seaway constriction and closure affected the Atlantic environments more than the EEP (Keigwin, 1992; Tiedemann and Franz, 1997; Haug and Tiedemann, 1998; Haug et al., 2001). Changes argued to have occurred in that area include strengthening of the Gulf Stream, enhanced thermohaline overturn, development of the Caribbean warm pool, enhanced sea-surface salinity (Keigwin, 1982; Haug and Tiedemann, 1998; Haug et al., 2001), increased average sea-surface temperature (Gussone et al., 2004), and enhanced carbonate deposition (Keigwin,

1982; Farrell et al., 1995). In addition, biologic productivity in the western Atlantic (Allmon et al., 1996) and Caribbean (Collins, 1996; Collins et al., 1996) may have decreased due to decreased current velocity and coastal upwelling (Teranes et al., 1996). In the EEP, in contrast, seasonality and primary productivity may have increased (Keigwin, 1982; Jones and Hasson, 1985; Teranes et al., 1996), and coastal upwelling may have intensified and expanded along the EEP coast of South America (Ibaraki, 1997).

Evidence for Central American Seaway constriction around 8 Ma comes from benthic $\delta^{13}\text{C}$ values (Wright et al., 1991; Billups, 2002), with the Atlantic recording increasing higher values (improved ventilation) thereafter. A study of Nd isotopes from ferromanganese nodules at the Blake Plateau (Reynolds et al., 1999; Frank et al., 1999) indicated a Pacific deepwater signal (shown by high ϵ^{Nd} values) until 8 Ma; thereafter, with CAS restriction, low ϵ^{Nd} values reflected a younger, North Atlantic source. Stable isotopes of oxygen from this region (Spezzaferri et al., 2002; Fig. 1a) indicated a brief but distinct cooling phase after ~ 8 Ma, attributed to the onset of NADW

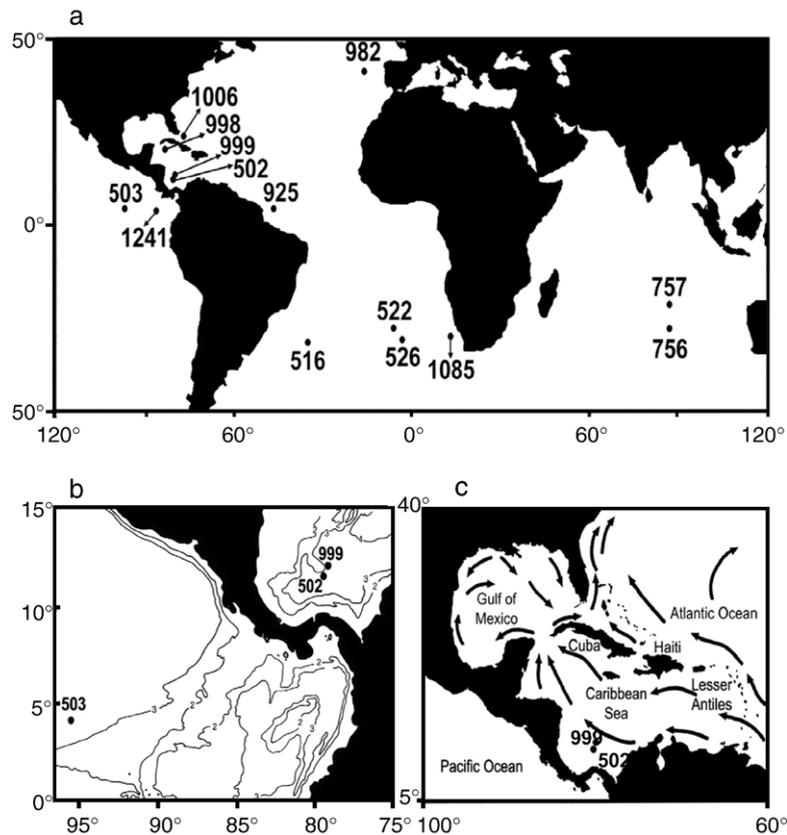


Fig. 1. a). Locality map of Ocean Drilling Program sites and Deep Sea Drilling Project (DSDP) sites mentioned in the text. b). Detailed bathymetric map (contour line values in kilometers) of the three sites (ODP Site 999 and DSDP Sites 502 and 503) mentioned in the text. c). Present surface water circulation with the Caribbean Current entering the Caribbean Sea between islands of the Lesser Antilles.

Table 1
Proxies and site data used in the present study

Oceanic conditions	Proxies	Data source
Paleoproductivity	1 Flux proxies: wide-, low- and high-flux species	ODP 999 ¹ ; DSDP 503 ²
	2 Relative abundance ratio of infaunal/epifaunal species	ODP 999 ¹
	3 Benthic foraminifer accumulation rates (BFAR)	ODP 999 ¹ ; DSDP 502 ^{3,4}
Current velocity	4 Relative abundance of <i>C. wuellerstorfi</i> + <i>G. subglobosa</i>	ODP 999 ¹
Oligotrophy	5 Relative abundance of <i>Nuttallides umbonifera</i>	ODP 999 ¹ ; DSDP 502 ³
Dissolution	6 Sand fraction percentage	ODP 999 ⁵
	7 Resistant species percentage (res%)	ODP 999 ⁶
Ventilation	8 Stable isotopes of carbon	ODP 999 ⁵

1. Jain and Collins (this study).
2. McDougall (1996).
3. Bormmalm (1997).
4. Bormmalm et al. (1999).
5. Haug and Tiedemann (1998), Bickert et al. (2004).
6. Chaisson and d'Hondt (2000).

caused by CAS restriction. Similarly, a cold and well-oxygenated (proto-NADW) watermass at the Ceara Rise between 8.5 and 7 Ma has also been proposed as a response to the closure of the CAS (Lear et al., 2003).

A global climate-ocean ecosystem model study (Schneider and Schmittner, 2006) showed that a reduced flow of nutrient-rich subsurface waters from the Pacific into the Atlantic led to decreased biological productivity in the North Atlantic. In the eastern tropical Pacific, the restriction of the nutrient-rich outflow led to nutrient accumulation that in turn resulted in a strong increase in productivity (Schneider and Schmittner, 2006).

The Caribbean late Neogene paleoproductivity has been estimated using benthic foraminifera accumulation rates (BFARs) and the composition of nannofossil assemblages (Kameo, 2002). Bormmalm et al. (1999) used BFAR data (>125 µm fraction) from Caribbean Deep Sea Drilling Project (DSDP) Site 502 and Pacific DSDP Site 503 (Fig. 1) to describe oligotrophic to mesotrophic conditions between 6.5 and 6.2 Ma, and decreased paleoproductivity until the end of the studied section at 1.8 Ma, punctuated by short-term mesotrophic conditions (4.1 to ~ 3.9 Ma and ~ 3.8 to 3.7 Ma) interpreted from increased relative abundances of *Epistominella exigua* (all ages are recalibrated to timescale of Shackleton and Crowhurst, 1997).

Quantitative analysis of nannofossil assemblages from ODP Sites 998 (northern Caribbean) and 999 (southern Caribbean; Fig. 1) documented that the thermocline/nutricline was shallow, with minor upwelling between 3.5 and 3.1 Ma at Site 999 (Kameo, 2002). From 3.1 to

2.7 Ma, the thermocline/nutricline deepened and the upper waters became oligotrophic as a result of the completion of the closure of the CAS at 2.77 Ma.

We test the hypothesis that the late Miocene to early Pliocene gradual constriction and final closure of the CAS caused a decrease in paleoproductivity in the Caribbean. Paleoproductivity proxies (Table 1) are compared over the time interval from 8.3 to 2.5 Ma at Caribbean Site 999 and EEP Site 503 (McDougall, 1996; Fig. 1).

2. Methods

2.1. Site locations

The study focused on two main sites, one from the western Caribbean, ODP Site 999, the other from the EEP DSDP Site 503 (Fig. 1a; Table 2). These sites were chosen for their proximity to the former Central American Seaway (Fig. 1a) and available high-resolution biochronology (Site 503: Keigwin, 1982; Zenker et al., 1987; Keller et al., 1989; Site 999: Kameo and Bralower, 2000; Chaisson and d'Hondt, 2000). Both sites have relatively stratigraphically complete sections (Keigwin, 1982; McDougall, 1996; Bormmalm, 1997; Bormmalm et al., 1999; Bickert et al., 2004). The EEP benthic foraminiferal dataset of McDougall (1996) has a chronologic resolution (51 samples) comparable to that of the present study of Site 999 (47 samples), and it used the same (>63 µm) size fraction, but benthic foraminifera were picked from twice the volume (20 cm³) of sediments as opposed to the standard 10 cm³ of sediments for ODP Site 999 (Table 3). Hence, Site 503 data were not combined with the present data but are compared as a separate dataset.

Table 2
Location of sites of Ocean Drilling Program (ODP) and Deep Sea Drilling Project (DSDP) mentioned in the text

Sites	Latitude	Longitude	Depth (m)	Region
ODP Site 925	04° 12' N	43° 29' W	3042	Tropical Atlantic
ODP Site 1241	05° 50' N	86° 26' W	2027	East Pacific
DSDP Site 503	04° 02' N	95° 38' W	3672	Caribbean Sea
DSDP Site 502	11° 46' N	79° 22' W	3051	Caribbean Sea
ODP Site 999	12° 44' N	78° 44' W	2828	Caribbean Sea
ODP Site 998	19° 29' N	82° 56' W	3180	Caribbean Sea
ODP Site 1006	24° 24' N	79° 27' W	658	Bahamas Margin
ODP Site 982	57° 31' N	15° 52' W	1145	North Atlantic
ODP Site 757	17° 01' S	88° 10' E	1652	Indian Ocean
DSDP Site 522	26° 06' S	05° 07' W	4451	Indian Ocean
ODP Site 756	27° 21' S	87° 35' E	1241	Indian Ocean
ODP Site 1085	29° 22' S	13° 59' E	1713	South Atlantic
DSDP Site 526	30° 07' S	03° 08' W	1066	Indian Ocean
DSDP Site 516	30° 16' S	35° 17' W	1313	Indian Ocean

Table 3

Rarefaction analysis and comparison of sample size and specimen numbers for the Caribbean ODP Site 999 and Pacific DSDP Site 503 (McDougall, 1996 dataset)

		MacDougall 1996	This study	
		DSDP Site 502	ODP Site 999	
		20 cm ³	10 cm ³	
Caribbean	Number of core samples	51	47	
	Minimum specimen number	15	43	
	Maximum specimen number	659	675	
	Average specimen number	270	210	
	Rarefaction	# of species at present specimen numbers	46	43
		Specimens needed for comparable 20 cm ³ samples	NA	~ 750
	Expected no. of species (if similar sediment volume)	46	46	
East Equatorial Pacific (DSDP Site 503)	Number of core samples	36		
	Minimum specimen number	15		
	Maximum specimen number	374		
	Average specimen number	153		

Note a minimum of ~ 750 specimens are needed to be picked from each Site 999 samples to compensate for 20 cm³ of sediment volume used by McDougall (1996).

The Colombian Basin in the Caribbean Sea, where both ODP Site 999 and DSDP Site 502 are located (Fig. 1b), exceeds a water depth of 4000 m, and is separated from the Atlantic Ocean by a shallow sill at a water depth of 1645 m at the Windward Passage, between Haiti and Cuba (Fig. 1c). The main ocean currents in the Caribbean Sea are an extension of the North and South Equatorial currents that enter the Caribbean Sea as the Caribbean Current from the southeast (Lesser Antilles; see Fig. 1c) to flow in a generally northwestern direction into the Gulf of Mexico (for details see Wüst, 1964). Sediments at Site 999 (study area;

Fig. 1) between 150 and 0 mbsf consist mainly of nannofossil clays with abundant foraminifers and foraminiferal clays, whereas between 230 and 150 mbsf they consist of fine-grained, homogenous, olive-gray nannofossil clays with fewer foraminifers (ODP Initial Reports, Leg 165, Sigurdsson et al., 1997).

2.2. Preparation of samples

Benthic foraminiferal analysis was carried out on 47 samples from ODP Site 999. Sediment samples of 10 cm³

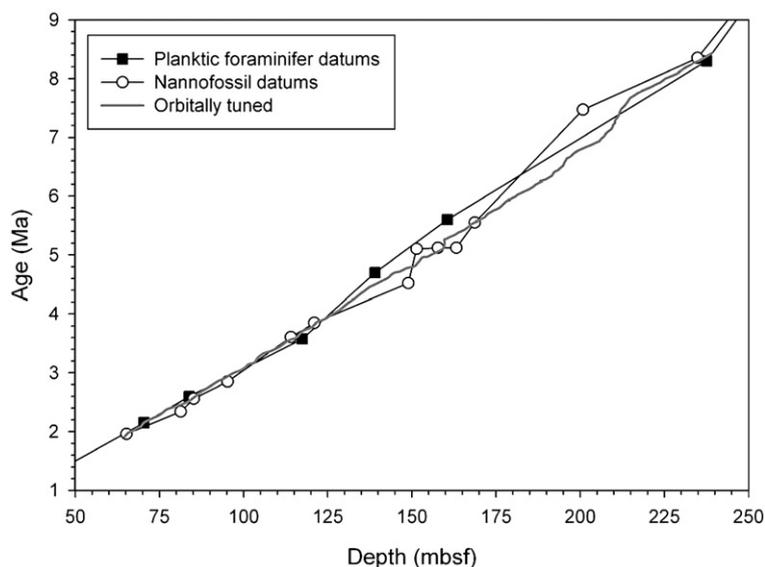


Fig. 2. ODP Site 999a age versus depth diagram. Orbitally tuned age (dotted line; after Bickert et al., 2004) is compared with the shipboard biostratigraphic datums based on nannofossil events (open circles; Kameo and Bralower, 2000) and orbitally tuned planktic foraminifer datum points (solid squares; after Chaisson and d'Hondt, 2000).

were treated with 1% hydrogen peroxide for 24 h and washed through a stainless steel sieve (63 μm mesh), then dried in an oven at 50 °C or less for 24 h. Benthic foraminifers >63 μm were picked from the whole sample, sorted by species, mounted on faunal slides and identified under a stereomicroscope. Table 3 lists a comparison of the specimen and species counts of all the datasets under study from the Caribbean (DSDP Sites 502 and 999) and Pacific DSDP Site 503.

2.3. Age models

The Site 999 age model (Kameo and Bralower, 2000) is based on nannofossil datums calibrated to the astronomically tuned timescale of Shackleton and Crowhurst (1997; Fig. 2). The planktic foraminiferal datum levels are also in close agreement (Chaisson and d'Hondt, 2000; Fig. 2). In this paper we use the age model after Bickert et al. (2004), who provided orbitally tuned ages that compare well with the shipboard biostratigraphic datums based on nannofossil events (Fig. 2). Kameo and Bralower (2000) estimated the ages of their biohorizons based on an orbitally tuned time scale of Backman and Raffi (1997) and the age of the nannofossil datums and bioevents were taken from Raffi and Flores (1995). Bickert et al. (2004) adjusted the latter calibration of bioevents to the astronomically dated timescale of Shackleton and Crowhurst (1997). No nannofossil data are available for DSDP Site 503, hence two datums are taken as tie points: the first appearance of *Globorotalia pleisotumida* (8.30 Ma at 234.7 mbsf) and the Matuyama/Gauss boundary (2.47 Ma at 47.95 mbsf; Zenker et al., 1987; Keller et al., 1989; Kent and Spariosu, 1982a,b; McDougall, 1996; Bornmalm, 1997; Bornmalm et al., 1999). All data used for comparison with Site 999 are also recalibrated to the Shackleton and Crowhurst (1997) timescale.

The present study compares the timing of changes in paleoproductivity with previously documented paleoceanographic events (Table 4; Keigwin, 1982; Haug and Tiedemann, 1998; Driscoll and Haug, 1998; Haug et al., 2001). These events, also recalibrated to the Shackleton and Crowhurst (1997) timescale, are used to divide the 8.3–2.5 Ma study period into the following three intervals: a) Early shoaling (8.3–7.9 Ma), b) Pre-closure (7.9–4.2 Ma), and c) Post-closure (4.2–2.5 Ma).

2.4. Proxies

All proxies used in the present study are given in Table 1 and the data in Appendix A. Dissolution was evaluated with two proxies: percent sand fraction and % resistant planktonic species (res%). Percent sand fraction is widely

Table 4

Timeline of the Central American Seaway constriction and closure based on previous deep sea core-based studies

Age (Ma)	Events	References
4.2	Atlantic–Pacific salinity contrast	Caribbean ODP Site 999: (Haug et al., 2001) DSDP Site 502: (Keigwin, 1982) Pacific ODP Site 846: (Haug et al., 2001) DSDP Site 503: (Keigwin, 1982)
7.9	Changes in benthic foraminifer $\delta^{13}\text{C}$ values	North Atlantic (Bahamas margin) ODP Site 1006: (Spezzaferri et al., 2002)
8–7		Pacific composite ODP Sites (Billups, 2002)
8	Changes in Pb and Nd isotopes	Atlantic composite ODP Sites: (Reynolds et al., 1999) Atlantic–Pacific composite ODP Sites : (Frank et al., 1999)

used as an indicator of relative dissolution intensity and the preservational state of deep-sea carbonates (Berger, 1970; Berger, 1982; Curry and Lohmann, 1985; Peterson and Prell, 1985; Cullen and Curry, 1997; Conan et al., 2002). The calculation of res% (Conan et al., 2002) was based on rare=3%, few=15% and common=30% of planktic foraminiferal species, categorized into two groups: (a) the resistant species *Globorotalia menardii*, *G. scitula*, *G. tumida*, *Neogloboquadrina dutertrei* and *N. pachyderma*; and (b) the susceptible species *Globigerina bulloides*, *G. falconensis*, *Globoturborotalita rubescens*, *Globigerinella aequilateralis*, *Globigerinoides ruber*, *G. sacculifer* and *Orbulina universa*. Single specimens and specimens of questionable identity were not included in the analysis (Chaisson and d'Hondt, 2000). The percent of resistant species was calculated as $\text{res}\% = 100 * (r / (r + s))$, where r is the cumulative relative abundance of resistant planktic species and s is susceptible species. The planktic foraminiferal dataset of Chaisson and d'Hondt (2000) are recalibrated to the Shackleton and Crowhurst (1997) timescale and those data points that were closely comparable in age (± 0.10 Ma) with Site 999 (this study) were used (Appendix B). In all, 39 planktic foraminiferal data points of Chaisson and d'Hondt (2000) were used (Appendix B). The Pearson's product moment correlation between the two dissolution proxies res% and % sand fraction is statistically significant ($p < .009$; $r = -0.418$); increased res% and decreased % sand fraction values indicate enhanced dissolution.

Basin ventilation is inferred from $\delta^{13}\text{C}$ values of epibenthic foraminifers (Site 999 data from Haug and Tiedemann, 1998; Bickert et al., 2004). The $\delta^{13}\text{C}$ values recorded in foraminiferal tests reflect the $\delta^{13}\text{C}$ values of the dissolved inorganic carbon of ambient water masses in the ocean (McCorkle and Keigwin, 1994). The oceanic $\delta^{13}\text{C}$ is inversely correlated to nutrient concentration. When organic matter settles to the seafloor, it decomposes, thus releasing ^{12}C thereby depleting ^{13}C in the water; the water then becomes enriched in nutrients, causing low $\delta^{13}\text{C}$ values in benthic foraminiferal tests. Hence, the $\delta^{13}\text{C}$ recorded by epibenthic foraminifers is extensively used as a nutrient proxy to reconstruct deep ocean paleocirculation (Duplessy et al., 1984; Sarnthein et al., 1994; Mackensen et al., 2001; Mackensen and Licari, 2004). Low benthic $\delta^{13}\text{C}$ values may indicate a higher supply of organic matter from the surface to the seafloor (increased productivity) or, as above, a watermass with higher nutrient content. Higher organic content or nutrients and their subsequent oxidation would deplete the available dissolved oxygen, and, over sufficient time, resulting in a poorly ventilated basin. In the Caribbean, low epibenthic $\delta^{13}\text{C}$ values have been interpreted to indicate a poorly ventilated basin (Haug and Tiedemann, 1998; Bickert et al., 2004), whereas higher $\delta^{13}\text{C}$ values suggest young, nutrient-depleted Upper North Atlantic Deep Water (Haug and Tiedemann, 1998; Haug et al., 2001; Bickert et al., 2004). A similar approach has been used in the Pacific to infer basin ventilation history (Kennett and Ingram, 1995; Behl and Kennett, 1996; Stott et al., 2000). Therefore, in the present study, epibenthic $\delta^{13}\text{C}$ values of *Cibicides wuellerstorfi* from Haug and Tiedemann (1998) and Bickert et al. (2004) are used as a proxy to infer basin ventilation.

The cumulative relative abundance of *C. wuellerstorfi*+*Globocassidulina subglobosa* is used here as a proxy for assessing current velocity (*C. wuellerstorfi*: Lutze and Thiel, 1989; Kaminski et al., 1988; Sarnthein and Altenbach, 1995; *G. subglobosa*: Murray, 1991; Mackensen

et al., 1995; Schmiedl, 1995; Schmiedl and Mackensen, 1997; Hayward et al., 2002, 2004). *C. wuellerstorfi* and *G. subglobosa* show similar trends and hence are considered a proxy for current velocity (Fig. 3).

The availability of food for benthic foraminifers is assessed with the relative abundance of *Nuttallides umbonifera*, higher values of which suggest increased oligotrophy and reduced food. Its increased relative abundance has been widely correlated with the occurrence of young, cold, carbonate-corrosive, oligotrophic and oxic bottom waters (Mackensen et al., 1995; Smart and Gooday, 1997; Hayward et al., 2002, 2004). Some authors correlate its increased relative abundance with corrosiveness of the watermass (Corliss, 1979; Bremer and Lohmann, 1982; Mackensen et al., 1995; McDougall, 1996), whereas others consider this species as an indicator of extreme oligotrophy (Gooday, 1993; Loubere, 1994). If increased relative abundance of *N. umbonifera* is indicative of corrosiveness, % sand fraction (a proxy for dissolution) should decrease with increasing *N. umbonifera*, but in the present study, they are positively and significantly correlated ($p < .001$, $N = 47$; $r = 0.498$). Others (McDougall, 1996; Bornmalm, 1997) linked *N. umbonifera* to corrosive AABW, but during the Neogene, the deep-water connection between the Caribbean and the Atlantic was over a relatively shallow sill (water depth of 1645 m) at the Windward Passage. Even if the upper depth limit of AABW extended up to as shallow as 2200 m during glacial stages (Franz and Tiedemann, 2002) the sill would have been too shallow for the >4000-m-deep AABW to enter the Caribbean.

Paleoproductivity was estimated with 1) the accumulation rates of benthic foraminifera (BFARs), 2) the relative abundance ratio of infaunal/epifaunal species (*I/E* ratio), and 3) the relative abundance of indicator species for organic carbon flux to the seafloor. These are explained below.

1) BFAR is the number of foraminifers/cm²/kyr, considered an indicator of change in surface productivity and

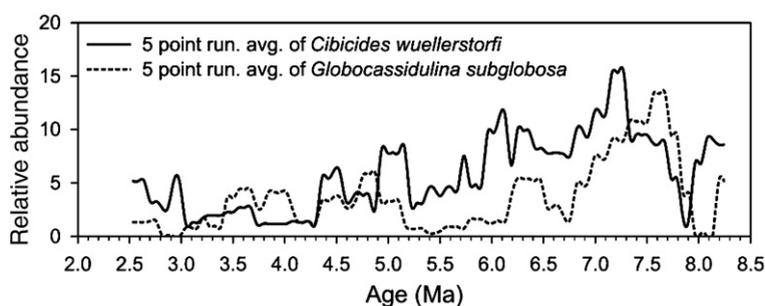


Fig. 3. Comparison of relative abundances of *C. wuellerstorfi*+*G. subglobosa* from Site 999. Bold (solid and dotted) lines are five-point smoothed running averages. The species are collectively considered a proxy for current velocity because of their similar trends.

Table 5

List of relative abundances of calcareous infaunal and epifaunal species used in constructing the *I/E* ratio for Site 999

Species	Reference Nos.
Infaunal species	
<i>Astacolus</i> spp.	2
<i>Astrononion</i> spp.	16
<i>Bolivina seminuda</i> Cushman	4
<i>Bolivina</i> spp.	1, 3, 8, 15, 19, 21
<i>Bolivina subaenariensis</i> Cushman	15
<i>Bulimina alazanensis</i> Cushman	3, 8, 19
<i>Bulimina rostrata</i> Brady	15
<i>Bulimina</i> spp.	15
<i>Chilostomella oolina</i> Schwager	3, 5, 11, 14, 16, 22
<i>Dentalina</i> spp.	2
<i>Ehrenbergina trigona</i> Goës=	2
<i>Textularia triquetra</i> Münster	
<i>Fissurina</i> spp.	2
<i>Globobulimina affinis</i> (D'Orbigny)=	3, 5, 7, 12, 15, 18, 22
<i>Bulimina affinis</i> D'Orbigny	
<i>Globobulimina pacifica</i> Cushman	3, 5, 7, 12, 15, 16, 18, 22
<i>Globobulimina</i> spp.	3, 5, 7, 12, 15, 16, 18, 22
<i>Globocassidulina subglobosa</i> (Brady)=	11, 13, 22
<i>Cassidulina subglobosa</i> Brady	
<i>Gyroidina altiformis</i> Stewart and Stewart=	22
<i>G. soldanii</i> D'Orbigny <i>altiformis</i> Stewart and Stewart	
<i>Gyroidina neosoldanii</i> Brotzen=	22
<i>Gyroidina soldanii</i> D'Orbigny	
<i>Gyroidina orbicularis</i> (D'Orbigny)=	22
<i>Gyroidina orbicularis</i> D'Orbigny	
<i>Gyroidina</i> spp.	22
<i>Lagena</i> spp.	2
<i>Lenticulina</i> spp.	3, 11
<i>Marginulina</i> spp.	2
<i>Melonis barleeanum</i> (Williamson)	3, 7, 9, 22
<i>Melonis</i> spp.	3, 7, 9, 22
<i>Nodosaria</i> spp.	2
<i>Nonion</i> sp.	18
<i>Nonionella</i> spp.	6
<i>Oolina</i> spp.	2
<i>Parafissurina</i> spp.	2
<i>Pleurostomella</i> sp.	13
<i>Pullenia bulloides</i> (D'Orbigny)=	3
<i>Nonionina bulloides</i> D'Orbigny	
<i>Pullenia</i> spp.	3
<i>Sphaeroidina bulloides</i> D'Orbigny	3, 5, 7, 12, 15, 16, 18, 22
<i>Uvigerina peregrina</i> Cushman	10, 22
<i>Uvigerina</i> spp.	10, 22
Epifaunal species	
<i>Anomalinoidea</i> spp.	19
<i>Cibicides</i> sp.	1, 2, 3, 14
<i>Cibicides wuellerstorfi</i> (Schwager)=	1, 2, 3, 14
<i>Anomalina wuellerstorfi</i> Schwager	
<i>Epistominella exigua</i> (Brady)=	13
<i>Pulvinulina exigua</i> Brady	
<i>Epistominella</i> sp.	8

Table 5 (continued)

Species	Reference Nos.
Epifaunal species	
Miliolids	3, 14
<i>Nuttallides umbonifera</i> (Cushman)=	5
<i>Pulvinulina umbonifera</i> Cushman	
<i>Oridorsalis umbonatus</i> (Reuss);	4
<i>Truncatulina tenera</i> Brady	
<i>Osangularia culter</i> (Parker and Jones)	1, 18
Ecological references	
Corliss (1985)	1
Corliss and Chen (1988)	2
Corliss (1991)	3
Barmawidjaja et al. (1992)	4
Bernhard (1992)	5
Jorissen et al. (1992)	6
Buzas et al. (1993)	7
Miao and Thunell (1993)	8
Gooday (1994)	9
Jorissen et al. (1994)	10
Rathburn and Corliss (1994)	11
Fariduddin and Loubere (1997)	12
McCorkle et al. (1997)	13
de Stigter et al. (1998)	14
Jannink et al. (1998)	15
Jorissen et al. (1998)	16
Bernhard and Sen Gupta (1999)	17
Gooday and Rathburn (1999)	18
Jorissen (1999)	19
Schmiedl et al. (2000)	20
Ernst et al. (2002)	21
Fontanier et al. (2002)	22

subsequent food supply (flux of organic carbon) to the seafloor (Gooday, 1988; Herguera and Berger, 1991; Herguera, 1992). BFARs are calculated from the product of the sedimentation rate (cm/ka; determined by linear interpolation between age control points; Fig. 2), dry bulk density (g/cm^3), and number of benthic foraminifers per gram of dry sediment (BF/g). Dry bulk density values were interpolated from shipboard physical properties data (ODP Site 999: Sigurdsson et al., 1997; DSDP Sites 502 and 503: Prell et al., 1982). Note, however, that Herguera (1992) used the $>125 \mu\text{m}$ size fraction; herein we used the $>63 \mu\text{m}$.

There are differences in calculations of BFAR between this study and that of Bornmalm (1997) and Bornmalm et al. (1999) as follows. Previous BFAR estimates (Bornmalm, 1997; Bornmalm et al., 1999) for DSDP Site 502 are calculated on the time scale of Berggren et al. (1985, 1995) but in the present contribution the Shackleton and Crowhurst (1997) timescale is used for comparisons across the datasets. Hence, all data for DSDP Sites 502 and 503 are recalculated to the Shackleton and Crowhurst (1997) timescale, and those data that are comparable in age ($\pm 0.10 \text{ Ma}$) with Site 999 BFARs (this study) were used. 34

Table 6

List of relative abundances of high- and low-flux benthic foraminiferal species used for ODP Site 999 and DSDP Site 503 (dataset of McDougall, 1996)

Species	Reference nos.
High-flux species	
<i>Bolivina</i> spp.	1, 3, 5, 8, 12, 14, 15, 18, 19
<i>Bulimina</i> spp.	1, 7, 8, 14, 15, 18
<i>Chilostomella oolina</i> Schwager	8, 12, 13
<i>Globobulimina</i> spp.	1, 2, 5, 7, 8, 11, 13, 14, 15, 17, 18
<i>Gyroidina</i> spp.	6
<i>Melonis barleeanum</i> (Williamson)	1, 2, 7, 8, 9, 11
<i>Melonis</i> spp.	1, 2, 7, 8, 9, 11
<i>Pullenia</i> spp.	4, 16
<i>Sphaeroidina bulloides</i> D'Orbigny	5, 1, 6
<i>Uvigerina peregrina</i> Cushman	8, 9, 11, 12, 13
<i>Uvigerina</i> spp.	8, 9, 11, 13, 17
Low-flux species	
<i>Cibicides</i> sp.	1, 2, 6, 8, 10, 16
Miliolids	1, 2, 6, 8, 10
<i>Nuttallides umbonifera</i> (Cushman)	1, 2, 6, 8, 10
<i>Oridorsalis umbonatus</i> (Reuss)	1, 2, 6, 8, 10
<i>Osangularia culter</i> (Parker and Jones)	1, 2, 6, 8, 10
<i>Hoeglundina elegans</i> (Cushman)	1, 2, 6, 8, 10
Ecological references	
(Altenbach, 1992)	1 (Loubere, 1991) 11
(Altenbach et al., 1999)	2 (Loubere, 1996) 12
(Bernhard et al., 1997)	3 (Lutz and Coulbourne, 1984) 13
(Corliss and Chen, 1988)	4 (Miller and Lohmann, 1982) 14
(Corliss et al., 1986)	5 (Rathburn and Corliss, 1994) 15
(Fontanier, et al., 2002)	6 (Sarnthein and Altenbach, 1995) 16
(Gooday et al., 2001)	7 (Schmiedl and Mackensen, 1997) 17
(Gooday, 2003)	8 (Schmiedl et al., 1997) 18
(Jorissen et al., 1998)	9 (Sen Gupta et al., 1981) 19
(Loubere and Fariduddin, 1999)	10

BFAR data points were used from the Bormmalm (1997) dataset (Appendix C).

Previous DSDP Site 502 BFAR estimates were calculated assuming a linear sedimentation rate of 3 cm/kyr (Bormmalm, 1997; Bormmalm et al., 1999), but recalculations for this study noted that the sedimentation rate varied between 2.4 and 2.8 cm/kyr for DSDP Site 502. (b) Site 502 benthic foraminifers were picked from a coarse size fraction (>125 µm) which excludes smaller species (Schröder et al., 1987), thereby reducing the benthic foraminiferal counts and BFAR estimates (Fig. 5a). Estimates of benthic foraminifers picked from the >63 µm fraction (this study; Site 999), reveal that as much as ~27% of smaller species such as *E. exigua* (an index of seasonal phytodetrital input; Fig. 5b) would be lost

in using the coarser sieve size fraction (>125 µm). Similarly, BFARs from the two Colombian Basin sites (DSDP Site 502: Bormmalm, 1997; Bormmalm et al., 1999 and Site 999; Fig. 5c) at closely comparable time intervals (±0.10 Ma difference; Appendix C), the BFAR values are lower at intervals when smaller species like *E. exigua* constitute a greater proportion of the total benthic foraminiferal assemblage (Fig. 5c), demonstrating the usefulness of picking benthic foraminifers from the >63 µm sieve size fraction.

For DSDP Sites 502 and 503 (McDougall, 1996 data), the weight of the sediments from which benthic foraminifers were picked was not measured, so BFAR estimates could not be calculated. Interestingly, a five-point running average comparison of BFAR estimates between Sites 999 (>63 µm fraction) and 502 (>125 µm; Bormmalm, 1997) reveals similar trends (Fig. 5a).

2. Taxa from Site 999 included in the construction of the *I/E* ratio are given in Table 5 and the values in Appendix A. For the *I/E* ratio calculations, the summed relative abundance of infaunal and epifaunal taxa make up more than one-third (average ~90%) of the total benthic foraminiferal population. None of the species were excluded in calculating the *I/E* ratio.

3. The third proxy for paleoproductivity are relative abundances of species that are associated with the a) high flux (eutrophy), b) low flux (oligotrophy), and c) variable flux (mesotrophy). Table 6 lists all the species included in the high and low-flux species category along with their relevant references. The variable flux (mesotrophy) species are represented by the relative abundance of *E. exigua* which was used to identify intervals where rates of organic flux to the seafloor ranged broadly (<0.9–100 g/m²/yr; Gooday, 2003), including areas with seasonally produced fluxes of phytodetritus (Gooday and Lamshead, 1989; Gooday, 1993; Smart et al., 1994; Thomas et al., 1995; Thomas and Gooday, 1996; Smart and Gooday, 1997).

3. Results

The results for indicators of dissolution (% sand fraction and res%) are given below for the entire studied interval between 8.3 and 2.5 Ma to eliminate dissolution as a potential cause for perceived changes in paleoproductivity (Fig. 4). Results for watermass ventilation (benthic δ¹³C), current velocity (cumulative relative abundance of *C. wuellerstorfi*+*G. subglobosa*), oligotrophy (relative abundance of *N. umbonifera*) and paleoproductivity proxies (BFAR, *I/E* ratio and flux indicator species) are given below for the three intervals of seaway closure (Early shoaling, Pre and Post-closure).

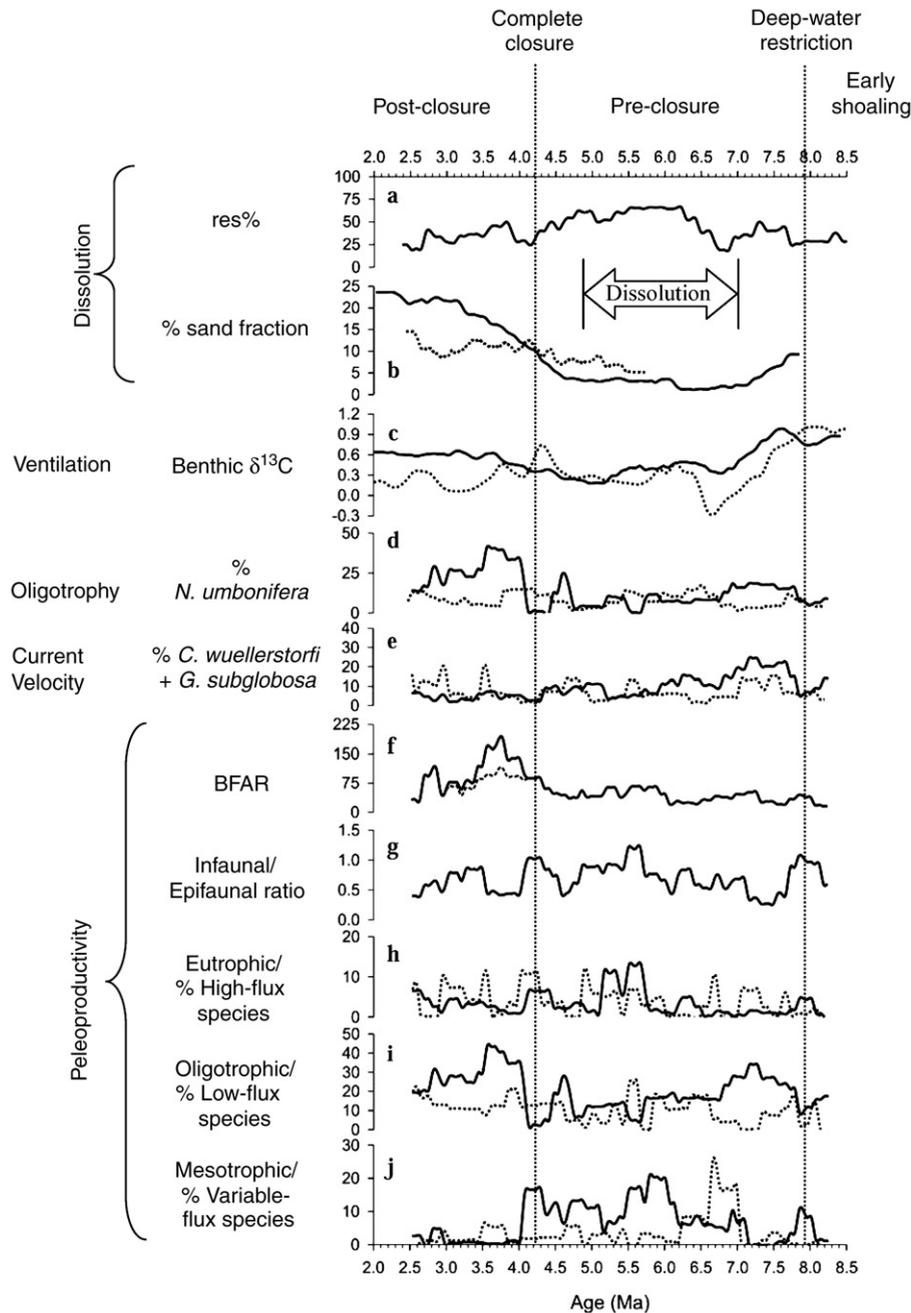


Fig. 4. Five-point smoothed running averages of proxies for the three intervals Early shoaling, Pre-closure and Post-closure. All bold lines (solid and dashed) are five-point smoothed running averages. For Caribbean ODP Site 999 (black solid lines of 4a–j), the res% (a) is calculated from the dataset of Chaisson and d’Hondt (2000) and % sand fraction (b) and benthic $\delta^{13}\text{C}$ (c) are from Haug and Tiedemann (1998) and Bickert et al. (2004). For Pacific sites (dotted lines of 4d–j), foraminiferal data are from McDougall (1996) for DSDP Site 503, the % sand fraction (4b) are from the dataset of Steph (2005), ODP Site 1241, and 4c is a benthic $\delta^{13}\text{C}$ composite curve after Billups (2002). Dashed lines in f are BFAR estimates calculated without *N. umbonifera* counts.

3.1. Dissolution (% sand fraction and res%)

Consistently lower % sand fraction (mean of 2.5% out of a total 100) and higher res% values (mean 52%) are

noted for the Caribbean between 6.8 and 4.8 Ma (Fig. 4). Thereafter, % sand fraction values increased (mean 22%) and res% (mean of 34%) decreased gradually until the end of the studied interval at 2.5 Ma. No sand fraction values

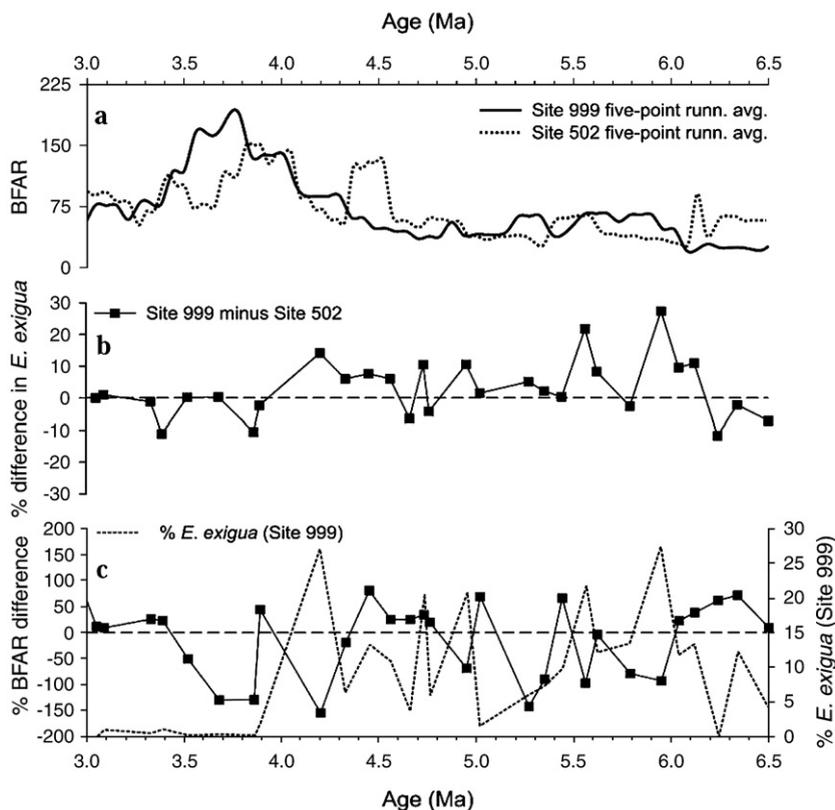


Fig. 5. Comparison of relative abundances of *E. exigua* picked from a coarser size fraction ($>125\ \mu\text{m}$; data from DSDP Site 502, [Bormmalm, 1997](#); [Bormmalm et al., 1999](#)) and finer fraction ($>63\ \mu\text{m}$; this study of ODP Site 999), and its relationship with BFAR estimates, Colombian Basin. a). BFAR: Dotted lines are for DSDP Site 502 (after [Bormmalm, 1997](#)) and dashed lines are for Site 999. Dashed lines with solid squares in b and c are Site 999 minus Site 502 values of BFAR and relative abundance of *E. exigua*, respectively.

(data of [Haug and Tiedemann, 1998](#); [Bickert et al., 2004](#)) for the pre-8 Ma interval are available for Site 999. The res % values ([Chaisson and d'Hondt, 2000](#); [Fig. 4a](#)) at Site 999, remained lower until 6.8 Ma (mean 30%), increased between 6.8 and 4.8 Ma (mean 60%) and then decreased (mean 35%; [Fig. 4](#)). The % sand fraction values in the Caribbean remained similar to the Pacific until 4.2 Ma, but then, diverged with progressively higher values (mean 22%) in the Caribbean than at the Pacific site (mean 7%; [Fig. 4b](#)).

3.2. Paleoproductivity and other patterns

3.2.1. Early shoaling (8.3–7.9 Ma)

Values of the paleoproductivity proxies BFAR, *I/E* ratio and high- and variable-flux species increased in the Caribbean, while values of low-flux species and benthic $\delta^{13}\text{C}$ decreased. The cumulative relative abundance of *C. wuellerstorfi*+*G. subglobosa* show low values at both the Caribbean and Pacific sites ([Fig. 4e](#)). The relative abundance of *N. umbonifera* displays low values at both Caribbean and Pacific sites ([Fig. 4d](#)). The Pacific site shows almost no

change in these proxies, except for benthic $\delta^{13}\text{C}$ values which peaked and were higher than in the Caribbean (0.98‰ $\delta^{13}\text{C}$ as compared to the Caribbean 0.80‰; [Fig. 4c](#)).

3.2.2. Pre-closure (7.9–4.2 Ma)

This interval in the Caribbean is marked by increasing values of BFAR, *I/E* ratio and high- and variable-flux species, decreasing values of low-flux species, lower relative abundances of *C. wuellerstorfi*+*G. subglobosa* and *N. umbonifera*, and gradually decreasing benthic $\delta^{13}\text{C}$ values ([Fig. 4](#)). Both *C. wuellerstorfi*+*G. subglobosa* and *N. umbonifera* show an initial increase between 7.6 and 7.1 Ma, followed by decreasing values in the Caribbean ([Fig. 4d](#) and [e](#)). Increased relative abundance of *E. exigua* is noted between 6.2 and 5.5 Ma and it is three times higher ($\sim 25\%$) than to the Pacific values ($\sim 8\%$) ([Fig. 5](#)). In the Caribbean, between 6.8 and 4.8 Ma, the res% values are high ($\sim 75\%$) and % sand fraction values are low ($<5\%$) ([Fig. 4](#)).

The Pacific site experienced slightly increasing values of *N. umbonifera*, lower values of *C. wuellerstorfi*+

G. subglobosa than the Caribbean and very low values of variable-flux species except between 7 and 6.3 Ma, when they were similar to those in the Caribbean. The benthic $\delta^{13}\text{C}$ values at the Pacific site sharply decreased between 7.9 and 6.6 Ma and then generally followed the same trend as in the Caribbean (Fig. 4c). Preservation is moderate for both benthic and planktic foraminifers (Chaisson and d'Hondt, 2000; Appendix B).

3.2.3. Post-closure (4.2–2.5 Ma)

This interval in the Caribbean is marked by a steep increase in the relative abundance of *N. umbonifera* and that of low-flux species with minimum relative abundance values of *C. wuellerstorfi*+*G. subglobosa* (Fig. 4d and e). Lower values are also noted in the Caribbean for the *I/E* ratio and variable- and high-flux species. BFAR values in the Caribbean increased dramatically between 4.2 and 3.6 Ma, as opposed to lower values of *I/E* ratio and variable- and high-flux species (Fig. 4). BFAR values gradually declined after 3.6 Ma until the end of the studied

interval at 2.5 Ma. An increase in values of the latter coincide with an increase in relative abundance of *N. umbonifera* (Fig. 4d, f). The BFAR values excluding *N. umbonifera* (Fig. 4f) follow the same gradually decreasing trends of the *I/E* ratio and variable- and high-flux species noted for the Caribbean.

Trends between the Caribbean and the Pacific sites diverge for low-flux species, the relative abundance of *N. umbonifera*, % sand fraction and benthic $\delta^{13}\text{C}$ values. Values for the latter two remained lower at the Pacific site throughout the rest of the investigated interval (until 2.5 Ma), whereas the former two remained higher in the Caribbean. High-flux species fluctuated in relative abundance at the Pacific site, but remained higher than at the Caribbean site (Fig. 4).

4. Discussion

In the Caribbean, a striking pattern documented by Bornmalm (1997, > 125 μm sieve fraction) is that of a large

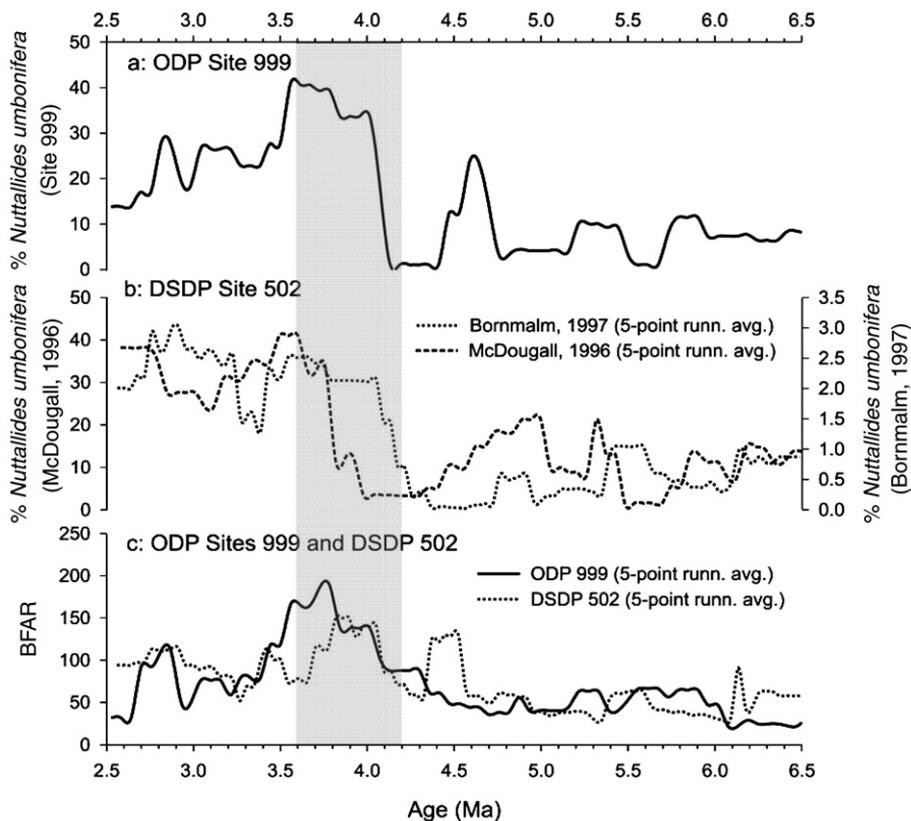


Fig. 6. Comparison of five-point smoothed running averages of relative abundances of *N. umbonifera* and BFAR from Colombian Basin ODP Site 999 (this study) and DSDP Site 502 (data from McDougall, 1996; Bornmalm, 1997; Bornmalm et al., 1999). Solid black lines (a and c) are for ODP Site 999 dataset (this study), dashed lines (b) are for the McDougall (1996) dataset from DSDP Site 502 and dotted lines (b and c) are for the Bornmalm (1997) DSDP Site 502 dataset. Note the common interval of increase in the oligotrophy-indicator taxon *N. umbonifera* between 4.2 and 3.5 Ma (shaded bar) in all datasets (a–b) and increased BFAR values (c) during its peak relative abundance 4.2–3.6 Ma.

Table 7

Pearson's product moment correlation (r) analysis between the relative abundance of oligotrophy-indicator taxa *Nuttalides umbonifera*, % sand fraction (dissolution) and paleoproductivity proxies benthic foraminifera accumulation rates (BFAR) and infaunal/epifaunal benthic species ratio (*I/E* ratio)

	<i>N. umbonifera</i>	% Sand fraction	% res	BFAR	<i>I/E</i> ratio
<i>N. umbonifera</i>	1				
% Sand fraction	.498** 0.001	1			
% res	-0.137 0.411	-.418** 0.009	1		
BFAR	.639** .0001	0.306 0.062	-0.02 0.92	1	
<i>I/E</i>	-.363* 0.025	-0.299 0.069	0.065 0.696	0.087 0.602	1

Sigma is 2-tailed.

**Correlation is significant at the 0.01 level (2-tailed).

*Correlation is significant at the 0.05 level (2-tailed).

$N=47$.

increase in BFAR values between 4.2 and 3.6 Ma (Fig. 6a), which the present data confirm (Fig. 6). Although these authors interpreted the rise as a result of decreased velocity of bottom-water currents and sustained organic input, the other paleoproductivity proxies contradict increased organic input (Fig. 4). Also during this time, *N. umbonifera*, dominated the assemblage (McDougall, 1996; Bormmalm, 1997; Bormmalm et al., 1999). Correlation (Table 7) between the relative abundance of *N. umbonifera* and BFAR is significant and positive, whereas with the *I/E* ratio, it is negative and significant (Table 7). If BFAR estimates exclude the *N. umbonifera* (Fig. 4f: dotted line), they follow the same trend as that of the *I/E* ratio. This suggests that BFAR calculated from the >125 μm sieve fraction might not be a reliable estimator of surface

productivity in oligotrophic areas, just as it is not reliable in areas of high-productivity (Hess and Kuhnt, 2005).

4.1. Early shoaling (8.3–7.9 Ma)

The Early shoaling (8.3–7.9 Ma) within the Caribbean was marked by mesotrophic conditions (increase in variable-flux species and higher values of the *I/E* ratio) with reduced ventilation (decreased benthic $\delta^{13}\text{C}$ values) (Fig. 4). At 7.9 Ma, reduced current velocity of bottom waters is indicated by the lowest values ($\sim 3\%$) of the relative abundance of *C. wuellerstorfi*+*G. subglobosa* recorded for the entire 8.3–2.5 Ma. This would be expected with increased restriction of watermass exchange between the Caribbean and the Pacific as also predicted by changes in benthic $\delta^{13}\text{C}$ values (Wright et al., 1991; Spezzaferri et al., 2002; Billups, 2002), low ϵ^{Nd} values (Reynolds et al., 1999; Frank et al., 1999), and low bottom-water temperatures (Lear et al., 2003) at around ~ 8 Ma. Restriction of nutrient-rich Pacific deep-waters would have initiated increased oligotrophy in the Caribbean. This is evident by the rapid increase in abundance of low-flux species and in the increased relative abundance of *N. umbonifera* after 7.9 Ma (as much as 27% of the total benthic foraminiferal assemblage). A brief period (7.9–7.6 Ma) just after the Early shoaling interval was characterized by higher current velocity with better ventilated bottom waters. During this interval, an increased relative abundance of the low-flux species and *N. umbonifera*, along with a steep decline in the relative abundance of the *I/E* ratio and low BFAR values, also indicate increased oligotrophic conditions. This suggests that just after the constriction of the CAS, between 7.9 and 7.6 Ma, oligotrophic conditions prevailed in the Caribbean. This inferred brief interval of oligotrophic conditions in the Caribbean, between 7.9 and 7.6 Ma, can

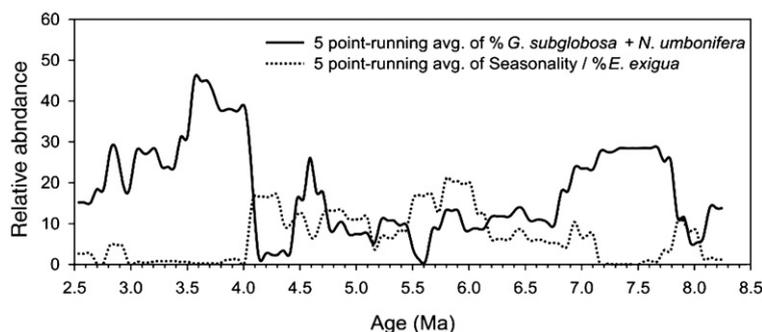


Fig. 7. Seasonality of phytodetrital input in the Caribbean as represented by the relative abundance of *E. exigua* (dotted lines), compared with species that show strong negative correlation with seasonality of phytodetrital input as represented by the cumulative relative abundances of *N. umbonifera*+*G. subglobosa* (black solid lines). Note their negative correlation (Pearson product moment correlation $r=-0.47$; $p<.0001$), which is consistent with recent North Atlantic data (Sun et al., 2006), and the greatly reduced seasonality of phytodetrital input after 4.2 Ma (Post-closure interval).

be attributed to the introduction of a well-oxygenated (well ventilated) and nutrient-depleted watermass, similar to the present day North Atlantic Deep Water (NADW) into the Caribbean after the CAS constriction at ~ 8 Ma (Wright et al., 1991; Lear et al., 2003). No changes are observed for the Pacific site, where all proxy values remained low (Fig. 4). If the seaway were open, proxy trends at both the Caribbean and Pacific sites should display similar trends (Fig. 4). But the diverging trends between these two sites, beginning at 7.9 Ma, of a) high-flux and low-flux species, b) the oligotrophy-indicator taxon *N. umbonifera*, and c) benthic $\delta^{13}\text{C}$ values, strongly support a change in regime at both sites, previously attributed to the CAS constriction at 8 Ma and resulting restriction of deepwaters into the Caribbean.

4.2. Pre-closure (7.9–4.2 Ma)

The Caribbean between 7.6 and 4.2 Ma was marked by a period of enhanced seasonality of phytodetrital input leading to mesotrophic conditions and poor ventilation (Fig. 4). The seasonality of phytodetrital input (the relative abundance of *Epistominella exigua*) was three times higher in the Caribbean than in the Pacific. Additionally, between 7.6 and 4.2 Ma, the Pacific, as compared to the Caribbean, experienced moderately reduced paleoproductivity and lower seasonality of phytodetrital input (Fig. 7).

Present data indicate that in the Caribbean, paleoproductivity not only increased during the Pre-closure interval (7.9–4.2 Ma), but had two peaks, between 7.6 and 6.7 Ma and 6.1–5.5 Ma (Fig. 4). Similar to Caribbean Site 999 (this study), Atlantic Sites 982 and 926 (Bickert et al., 2004; Table 2) and Pacific Sites 289, 588, 846 and 849 (Billups, 2002; Fig. 4c; Table 2) record decreased benthic $\delta^{13}\text{C}$ values between 7.6 and 6.7 Ma (see also Wright et al., 1991; Hodell et al., 1994; Wright and Miller, 1996; Shackleton and Hall, 1997; Hodell et al., 2001). This “carbon isotope shift” (between 7.6 and 6.7 Ma) is interpreted to reflect a global decrease in $\delta^{13}\text{C}$ of the ocean’s dissolved inorganic carbon pool, variously and tentatively attributed to: a) increased global erosion of organic carbon from terrigenous soils and shelf sediments during a drop in sea level as a result of Antarctic glaciation (Shackleton and Kennett, 1975; Berger and Vincent, 1986; Hodell et al., 1994; Bickert et al., 2004); b) a global shift from C_3 - to C_4 -dominated ecosystems (the expansion of grasslands and C_4 plants), accompanied by an overall decrease in the global biomass, thereby resulting in the decrease in marine $\delta^{13}\text{C}$ values (Cerling et al., 1997; Bickert et al., 2004); and c) globally (Diester-Haass et al., 2005) and locally for the Caribbean (Bickert et al., 2004), an observed increase in dissolution resulting from increased terrigenous input that

enhanced the dissolution of nutrients and led to higher paleoproductivity.

The present data (Site 999) also indicate much higher values of wide-flux species (phytodetrital input) as compared to those of the *I/E* ratio and BFAR’s between 7.6 and 6.7 Ma (Fig. 4) suggesting that increased paleoproductivity in the Caribbean is likely to be linked to enhanced input of phytodetritus. High magnetic susceptibility records (Bickert et al., 2004) during this interval also affirm the enhanced introduction of terrigenous material into the Caribbean, resulting in the higher input of organic matter. Benthic foraminiferal biomass is known to increase due to the introduction of terrigenous organic matter (Wefer et al., 1998). Accompanied higher dissolution (but not enough to alter the benthic and planktic foraminiferal biomass; Appendix B), due to increased terrigenous flux, is also noted for this interval (Bickert et al., 2004). Thus, it is most plausible, that the enhanced paleoproductivity in the Caribbean between 7.6 and 6.7 Ma is likely a result of enhanced terrigenous flux caused by sea level changes (Haq et al., 1987) during the progressive shoaling of the Panamanian isthmus (Duque-Caro, 1990; Collins et al., 1996).

Another interval of enhanced paleoproductivity in the Caribbean, between 6.1 and 5.5 Ma, coincides with the abundance of the cool water, sinistral-coiled planktic foraminiferal species *Neogloboquadrina pachyderma*, whose enhanced relative abundance has been well correlated with areas associated with seasonal upwelling and increased surface productivity (Keigwin, 1982; Chaisson and d’Hondt, 2000). This presence of unusually cold surface waters, probably on a seasonal basis between 6.3 and 5.3 Ma has previously been interpreted as late Miocene upwelling in the western Caribbean (Keigwin, 1982; Chaisson and d’Hondt, 2000; all data calibrated to the Shackleton and Crowhurst, 1997 timescale). The interval of colder surface waters in the Caribbean could have been caused by a jet of Pacific North Equatorial Countercurrent-Equatorial Undercurrent that passed through the 200–500 m deep Panama isthmian strait during severe CAS constriction ~ 6 Ma (Collins et al., 1996), which explained the occurrence of Pacific endemic benthic foraminifers such as *Cassidulina corbyi* and *Planulina charapotoensa*, and the unusual co-occurrence of the planktonic foraminiferal groups *Globorotalia conomiozea/G. miotumida* (cool water) and *G. menardii* (warm water) in the Caribbean deposits of Panama.

4.3. Post-closure (4.2–2.5 Ma)

N. umbonifera, a proxy for oligotrophy in the Caribbean, exclusively dominated the benthic foraminiferal

	Intervals of closure	Carib.-Pacific sill depth (m)	Dominant species	Oceanographic events	Dissolution	Watermass ventilation	Current velocity	Paleo-productivity	Seasonality of Phytodetritus	
2.5	POST-CLOSURE		<i>Nuttallides umbonifera</i>			Very High	Low	Low	Low	
3.0										
3.5										
4.0	PRE-CLOSURE	<100	<i>Epistominella exigua</i>	Salinity contrast	Increased	Poor-to Moderate	Reduced	High	High	
4.5										Low
5.0		<150								High
5.5		<500								Low
6.0			<i>Melonis barleeaanum</i>	MAXIMUM PALEOPRODUCTIVITY						High
6.5			<i>Cibicides wuellerstorfi</i>							Low
7.0										High
7.5					Low					
8.0	EARLY SHOALING	<1000				High	Low	High	Low	

Fig. 8. A summary of major events in the Caribbean as discussed in the text.

assemblages from 4.2 to 2.5 Ma (Fig. 5b). Decreased current velocity with little change in organic content (Bormmalm et al., 1999) has been suggested as a possible cause; however, present data show both reduced current velocity and paleoproductivity. The increasing divergence of Atlantic–Pacific benthic $\delta^{13}\text{C}$ and % sand fraction values (Haug and Tiedemann, 1998; Haug et al., 2001; Steph et al., 2005) also indicate a better ventilated Caribbean. Thus, the above data indicates that the Caribbean became increasingly oligotrophic between 4.2 and 2.5 Ma (Fig. 4), whereas, the Pacific witnessed increased paleoproductivity, higher seasonality and lower ventilation (Fig. 4).

5. Conclusions

The hypothesis that late Miocene and early Pliocene constriction and closure of the Central American Seaway (CAS) caused primary paleoproductivity in the Caribbean to decrease is supported by the present data. Increased oligotrophy and decreased Caribbean current velocity are resulted from to the restriction of

nutrient-rich tropical Pacific deep waters at 7.9 Ma and, again, after the complete CAS closure at 4.2 Ma. Complete seaway closure at 4.2 Ma favored enhanced paleoproductivity and increased current velocity at the Eastern Equatorial Pacific site. A summary of these major events in the Caribbean are shown in Fig. 8.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.marmicro.2006.11.003](https://doi.org/10.1016/j.marmicro.2006.11.003).

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