

# Relationship of benthic foraminiferal diversity to paleoproductivity in the Neogene Caribbean

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## Abstract

Diversity trends 8.3–2.5 Ma in Caribbean deep-sea foraminifera, as interpreted from the indices Fisher's  $\alpha$  and the Information Index [ $H(S)$ ] parallel paleoproductivity proxies (benthic foraminiferal infaunal/epifaunal species ratio, benthic foraminifer accumulation rates and flux of organic carbon to the seafloor). Paleoproductivity never reached a eutrophic threshold value above which we would predict opposite trends of high paleoproductivity and low diversity, consistent with stressful conditions. Instead, results are similar to those from other studies of oligotrophic settings that show a positive and statistically significant correlation between paleoproductivity and diversity. The correlations between current intensity and watermass oxygenation with diversity are negative and statistically significant. These results are also borne out by Principal Component Analysis (PCA). Intervals of increased relative abundance of *Epistominella exigua*, a proxy for seasonality of phytodetrital input to the seafloor, coincide with increased diversity, suggesting that pulsed paleoproductivity enhanced the diversity signal in the Caribbean.

Diversity and paleoproductivity peaked in the Caribbean at 7.9 Ma, and declined thereafter due to the cut off of the nutrient-rich Pacific deep waters (<1000 m) into the Caribbean. From 7.6 to 4.2 Ma, both diversity and paleoproductivity increased. With the complete closure of the Caribbean–Pacific seaway at 4.2 Ma, both diversity and paleoproductivity gradually decreased from a high at 4.2 Ma to moderate values until the end of the study interval at 2.5 Ma. Major intervals of significant shifts in Caribbean diversity and paleoproductivity were also confirmed with SHEBI analysis that displays a diverging trend between the Pacific and Caribbean sites since 7.9 Ma, with the Caribbean displaying decreasing values. In summary, in the Caribbean, decreased paleoproductivity due to the gradual constriction and the final closure of the Central American Seaway (CAS) led to decreased deep-sea benthic foraminiferal diversity and that both benthic foraminiferal diversity and paleoproductivity maintained a positive relationship.

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## 1. Introduction

The rise of the Panamanian isthmus and the environmental changes linked with the closure of the Central

American Seaway (CAS) provides an opportunity that allows for better understanding of the relationship between tectonic, climatic and oceanographic changes on one hand (Keigwin, 1982; Duque-Caro, 1990; Collins et al., 1996; Haug and Tiedemann, 1998; Haug et al., 2001; Bickert et al., 2004) and patterns of speciation, extinction and morphological evolution of organisms on

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the other (Vermeij and Petuch, 1986; Roopnarine, 1996; Collins et al., 1996; Jackson et al., 1999; Jackson and Johnson, 2000). Previous studies from the western Atlantic (Allmon et al., 1996) and Caribbean (Vermeij and Petuch, 1986; Collins, 1996; Collins et al., 1996) predicted that seaway constriction and closure led to decreased biologic productivity caused by decreased current velocity and coastal upwelling and conversely, increased seasonality and primary productivity in the Eastern Equatorial Pacific (Keigwin, 1982; Jones and Hasson, 1985; Teranes et al., 1996; Ibaraki, 1997). The late Miocene–early Pliocene gradual constriction to complete closure of the CAS also ended the input of high-productivity Pacific waters, leading to decreased paleo-productivity in the Caribbean (Jain and Collins, 2007).

Deep-sea benthic foraminiferal diversity is largely controlled by changes in trophic conditions (the availability of food), oxygen concentration and current velocity (Mackensen et al., 1990, 1995; Schmiedl et al., 1997; Levin et al., 2001; Gooday, 2003). All are known to induce varied changes in surface-water productivity (Thomas and Gooday, 1996). A positive relationship between benthic foraminiferal diversity and productivity is commonly reported from oligotrophic ocean areas (Arctic: Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Eastern Central Atlantic: Heinz et al., 2004; South China Sea: Hess and Kuhnt, 2005), whereas a negative one is observed in generally eutrophic environments such as the Arabian Sea (Den Dulk et al., 1988; Gooday et al., 1998). For example, in the oligotrophic, ice-covered Arctic Ocean (the least productive area of the world; Wollenburg and Mackensen, 1998), benthic foraminiferal associations are mainly controlled by the availability and competition for food, whereas watermass characteristics, bottom current velocity, substrate composition and water depth are of minor importance (Wollenburg and Mackensen, 1998). In those areas, when they are (seasonally) ice-free, high standing stocks and high benthic foraminiferal diversities reflect increased primary production rates; both increase with increasing food supply (Wollenburg and Mackensen, 1998).

Given these previous findings, this study examines the hypothesis that reduced paleoproductivity caused by the complete closure of the CAS resulted in decreased diversity in the Caribbean. To examine this, paleoproductivity and diversity between 8.3–2.5 Ma at the Caribbean Ocean Drilling Program (ODP) Site 999 (Fig. 1) were compared with those of Pacific Deep Sea Drilling Project (DSDP) Site 503 (McDougall, 1996) dataset. Two diversity indices Fisher's  $\alpha$  and the Information Index  $H(S)$ , along with the related measure

of assemblage Equitability, were compared with proxies (variables) of paleoproductivity — the relative abundance ratio of benthic foraminiferal infaunal/epifaunal species ( $I/E$  ratio), benthic foraminifer accumulation rates (BFAR), flux of organic carbon to the seafloor ( $J_{sf}$ ), benthic foraminifer dissolved-oxygen index (BFOI) and current velocity (Jain and Collins, 2007). Ventilation of the basin was inferred from the stable isotopes of carbon (benthic  $\delta^{13}C$ ; dataset of Haug and Tiedemann, 1998; Bickert et al., 2004 from ODP Site 999). For comparison with the Pacific, the benthic  $\delta^{13}C$  dataset of Billups (2002) was used. The seasonality of phytodetrital input to the seafloor was estimated by the relative abundance of *Epistominella exigua* (Thomas and Gooday, 1996; Smart and Gooday, 1997; Jain and Collins, 2007).

## 2. Previous Caribbean diversity studies

There are two previous studies of the Neogene Caribbean and tropical Eastern Equatorial Pacific diversity. A comparison of benthic foraminifera  $>63 \mu m$  from DSDP sites 503 (Pacific) and 502 (Caribbean; Fig. 1) from 0.2–8.5 Ma noted that “diversity [based on species abundance ( $S$ ) and the Information Index  $H(S)$ ] remained fairly constant in each site, averaging 43 species in the Caribbean and 38 species in the Pacific” (McDougall, 1996). Both McDougall's (1996) and the present study uses  $>63 \mu m$  sieve size fraction. Another study of the same two sites (Bornmalm, 1997; 1.8–6.4 Ma) based on  $>125 \mu m$  sieve size fraction, that excludes smaller individuals and species (Schröder et al., 1987), noted “no major difference in diversity between the holes” (DSDP Sites 502 and 503; Fig. 1). The present study differs from these previous ones in using the  $>63 \mu m$  size fraction data of benthic foraminifera picked from  $10 \text{ cm}^3$  sediment samples from ODP Site 999 (Fig. 1), and compares assemblage diversities between the Caribbean and Pacific sites with paleoproductivity trends associated with the gradual constriction to closure of the Central American Seaway for the interval 8.3–2.5 Ma.

## 3. Methods

Taxonomic standardization is strictly maintained when comparing with previous benthic foraminiferal studies (McDougall, 1996; Bornmalm, 1997; Bornmalm et al., 1999). All the above studies (including this one) have also compared their specimens with the type specimens kept at the Smithsonian Museum of Natural History, Washington DC. Additionally, the same sets of reference materials have been used for taxonomic identification of benthic foraminifera to maintain strict

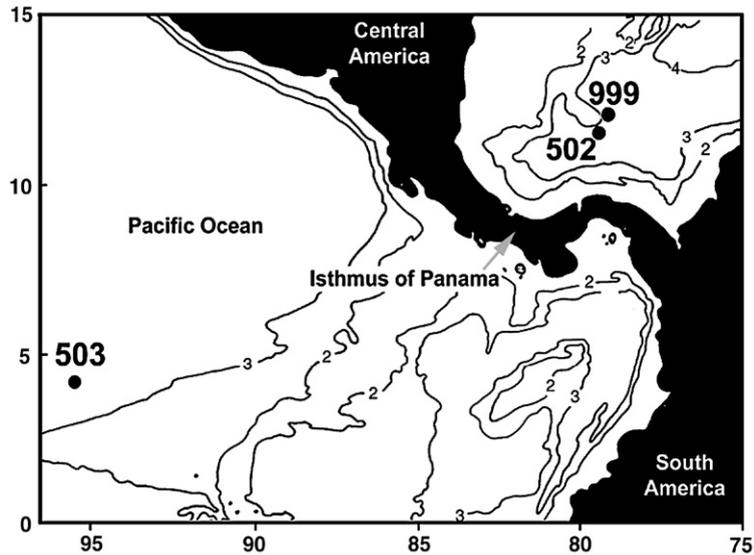


Fig. 1. Locality map of Ocean Drilling Program (ODP) Site 999 (this study) and the Deep Sea Drilling Project (DSDP) Sites 502 and 503 mentioned in the text. The bathymetry of sites are shown by contour line (values are in kilometers).

taxonomic standardization. We have also recalculated all the diversity measures from the published dataset (McDougall, 1996; Bornmalm, 1997).

### 3.1. Site locations

Western Caribbean ODP Site 999 and East Equatorial Pacific DSDP Site 503 (Fig. 1; Table 1) were studied because of their 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). Their relatively complete stratigraphy enabled precise Atlantic–Pacific diversity comparisons (Keigwin, 1982; McDougall, 1996; Bornmalm, 1997; Bornmalm et al., 1999; Chaisson and D'Hondt, 2000; Bickert et al., 2004). We also compared paleobathymetries for all the sites under study, to rule out paleodepth as a potential cause for changes observed in benthic foraminiferal diversity analyses.

### 3.2. Preparation of samples

Benthic foraminiferal analysis was carried out on 47 samples chosen at 1-cm interval from ODP Site 999. Sediment samples of 10 cm<sup>3</sup> were treated with 1% hydrogen peroxide for 24 h and washed through a stainless steel sieve with 63 μm mesh and dried in an oven at 50 °C for up to 24 h. All benthic foraminifers were picked from the samples, mounted on faunal slides and identified to the species level wherever possible.

### 3.3. Age models

In this paper, all data are calibrated to the astronomically tuned timescale of Shackleton and Crowhurst (1997). This age model is after Bickert et al. (2004), and compares well with the shipboard biostratigraphic datums based on nannofossil events. The planktic foraminiferal datum levels are also in close agreement (Chaisson and D'Hondt, 2000; for details see Jain and Collins, 2007).

### 3.4. Calculation for diversity measures

All proxies and diversity measures used in the present study are listed in Table 2 and the corresponding data are given in Table 3. The paleoproductivity proxies (benthic foraminiferal infaunal/epifaunal species ratio, benthic foraminifer accumulation rates and flux of organic matter to the seafloor), and proxies for current velocity and oligotrophy were recently analyzed by Jain and Collins (2007). Hence, they are only explained briefly, as follows.

Table 1

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

	Latitude	Longitude	Depth (m)	Region
DSDP Site 502	11° 29' N	79° 22' W	3051	Caribbean Sea
ODP Site 999	12° 44' N	78° 44' W	2828	Caribbean Sea
DSDP Site 503	04° 03' N	95° 38' W	3672	East Equatorial Pacific

Table 2  
Proxies and diversity measures used in the present study

Proxies		Sources
Oligotrophy	1 Relative abundance of <i>Nuttallides umbonifera</i>	ODP 999 <sup>a</sup> ; DSDP 502 <sup>b</sup>
Pulsed phytodetrital input	2 Relative abundance of <i>Epistominella exigua</i>	
Paleoproductivity	3 Flux of organic carbon	ODP 999 <sup>a</sup>
	4 Benthic foraminifer accumulation rates (BFAR)	
	5 Relative abundance of infaunal/epifaunal species	
Watermass ventilation	6 Stable carbon isotopes of benthic foraminifers	ODP 999 <sup>c, d</sup>
Oxygenation	7 Benthic Foraminifer Oxygen Index (BFOI)	ODP 999 <sup>c</sup>
Current velocity	8 Relative abundances of <i>Cibicides wuellerstorfi</i> + <i>Globocassidulina subglobosa</i>	ODP 999 <sup>a</sup>
Diversity	9 Fisher's $\alpha$	DSDP 502 <sup>b</sup> ; ODP 999 <sup>c</sup>
	10 Information Index $H(S)$	
	11 Equitability	

<sup>a</sup> Jain and Collins (2007).

<sup>b</sup> McDougall (1996).

<sup>c</sup> Haug and Tiedemann (1998), Bickert et al. (2004).

<sup>d</sup> Billups (2002).

<sup>e</sup> This study.

The species/genera from Site 999 included in the construction of the  $I/E$  ratio are given in Table 4. For the  $I/E$  ratio calculations, the summed relative abundance of infaunal and epifaunal taxa make up ~95% of the total benthic foraminiferal population. The remaining 5% are unidentifiable specimens. The BFAR's are the number of foraminifers per  $\text{cm}^2/\text{kyr}$ , considered an indicator of change in surface productivity and subsequent food supply to the seafloor (Gooday, 1988; Herguera and Berger, 1991; Herguera, 1992; Gooday, 2003). BFAR is calculated from the product of the sedimentation rate ( $\text{cm/ka}$ ), dry bulk density ( $\text{g/cm}^3$ ), and number of benthic foraminifers per gram of dry sediment (BF/g). Dry bulk density values are from the shipboard physical properties data (ODP Site 999: Leckie et al., 2000; DSDP Sites 502 and 503: Prell et al., 1982). The flux of organic matter to the seafloor ( $J_{\text{sf}}$ ; Herguera, 1992, 2000) is calculated as:  $J_{\text{sf}}=6.5 * \text{BFAR}^{0.64}$  (Herguera, 1992, 2000).

The higher relative abundances of *Nuttallides umbonifera* (= *Pulvinulinella umbonifera* Cushman, 1933) have previously been documented to suggest increased oligotrophy and reduced food in the Caribbean (Jain and Collins, 2007). Its increased relative abundance has also 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 workers correlate its increased relative abundance with corrosiveness of the watermass (Corliss, 1979; Bremer and Lohmann, 1982; Mackensen et al., 1995; McDougall, 1996), whereas still others consider this species as an indicator of extreme oligotrophy (Gooday, 1993, 2003; Loubere, 1994). However, its increased abundance is suggested to indicate increased oligotrophy and reduced food. Current velocity is accessed by the combined relative abundances of *Cibicides wuellerstorfi*+*Globocassidulina subglobosa* (Jain and Collins, 2007).

The diversity indices Fisher's  $\alpha$  and the Information Index  $H(S)$  are used as measures of species richness (Hayek and Buzas, 1997). The computer program Paleontological Statistics (Ryan et al., 1995; Harper, 1999) and tables of Hayek and Buzas (1997; App. 4) are used for calculations. Diversity analyses are enhanced with the analysis of Equitability (Hurlbert, 1971; Gibson and Buzas, 1973), a measure of the relative abundance of each species. Equitability values range from 0, indicating low Equitability or high single-species dominance, to 1, indicating equal abundance of all species or maximum Equitability (Routledge, 1980; Alatalo, 1981).

The inability to clearly differentiate the role played by evenness ( $E$ ) and the number of species ( $S$ ) in influencing  $H(S)$  was solved by using SHE analysis, first described by Hayek and Buzas (1997, 1998). One community may have a higher  $H(S)$  than another community either because it has a larger number of species or because the individuals are distributed more evenly among those species. SHE analysis decomposes  $H$  into  $S$  and  $E$  ( $H=\ln S+\ln E$ ), which indicate the species distribution (Hayek and Buzas, 1997). In a dataset, the stability of  $H$  is determined by examining the values of  $\ln S$  and  $\ln E$  (Hayek and Buzas, 1997; Osterman et al., 2002). By graphing  $\ln S$  and  $\ln E$ , into which SHE decomposes  $H$ , it enables one to determine whether the data fit the log series, broken stick or log normal species abundance distribution. This is important to identify the accuracy of the datasets, as most natural populations follow the log series distribution of species (Hayek and Buzas, 1997).

SHE analysis for biofacies identification (SHEBI; Buzas and Hayek, 1998) was also performed. The rationale is that if all the data are from a single statistical population, then the plot of  $\ln E$  vs.  $\ln N$  should be a straight line. Any significant linear shift would indicate a different biofacies and hence the presence of a faunal boundary. Thus, SHEBI is used in the present study to verify whether boundaries inferred are the same as those inferred from paleoceanographic proxies under study

Table 3  
Paleoproductivity and diversity dataset for the interval 8.3–2.5 Ma

Age	Fisher's $\alpha$	$E$	BFAR	$I/E$ ratio	Flux ( $J_{sf}$ )	BFOI	Current velocity	Benthic $\delta^{13}C$	Depth (mbsf)
2.53	18.00	0.85	17.26	0.26	40.24	87.50	9.38	0.637	2912.92
2.65	14.96	0.89	46.00	0.79	75.35	90.91	5.96	0.548	2915.92
2.77	16.62	0.74	138.03	0.61	152.23	94.19	3.41	0.672	2918.92
2.88	19.26	0.78	83.74	0.66	110.56	96.30	2.15	0.342	2922.42
2.98	12.78	0.91	18.22	0.29	41.65	98.00	8.24	0.886	2925.42
3.05	18.56	0.78	81.23	0.83	108.43	87.97	1.86	0.468	2928.42
3.09	23.35	0.74	70.77	0.73	99.27	92.20	2.25	0.778	2929.40
3.33	19.93	0.82	46.68	0.58	76.06	93.81	4.78	0.586	2934.92
3.39	23.54	0.76	111.57	1.12	132.84	95.00	1.04	0.586	2937.92
3.52	16.72	0.70	124.99	0.58	142.86	95.71	8.36	0.71	2941.42
3.68	24.03	0.62	205.42	0.36	196.34	95.45	3.53	0.618	2944.42
3.86	14.49	0.71	168.84	0.48	173.18	98.91	4.31	0.18	2947.42
3.89	22.20	0.70	107.03	0.40	129.36	97.42	6.31	0.716	2950.92
4.20	26.56	0.78	96.34	1.21	120.93	89.89	1.76	0.358	2960.42
4.33	22.13	0.86	78.98	0.85	106.49	76.15	3.54	0.396	2963.42
4.45	20.30	0.86	44.04	0.85	73.28	94.00	13.86	0.307	2966.45
4.56	19.53	0.83	52.99	0.61	82.49	93.83	5.73	0.075	2969.92
4.66	14.48	0.82	35.31	0.26	63.62	95.24	6.57	0.177	2972.92
4.73	14.36	0.86	35.11	0.72	63.39	98.08	9.28	-0.017	2975.92
4.76	16.73	0.86	41.73	0.53	70.79	93.14	9.86	0.141	2976.95
4.95	14.89	0.80	70.04	1.28	98.61	96.40	7.12	0.265	2982.42
5.02	19.75	0.88	10.75	0.50	29.72	93.75	15.16	0.193	2985.41
5.27	18.77	0.81	78.70	1.07	106.25	91.09	3.68	0.354	2988.92
5.35	14.71	0.83	47.31	0.78	76.72	98.36	3.89	0.315	2991.92
5.44	10.41	0.84	34.10	0.97	62.21	92.31	5.59	0.268	2994.95
5.56	15.45	0.78	72.74	1.43	101.03	84.31	2.92	0.15	2998.42
5.62	15.33	0.82	59.86	0.98	89.18	91.55	7.88	0.539	2999.92
5.79	16.47	0.83	52.76	0.56	82.26	94.20	8.72	0.258	3004.47
5.95	17.32	0.77	76.65	0.97	104.47	95.58	4.19	0.344	3007.92
6.04	10.36	0.87	16.92	0.35	39.73	97.92	17.65	0.325	3010.92
6.12	10.57	0.90	26.95	0.60	53.51	96.15	7.62	0.803	3013.92
6.24	14.33	0.85	30.57	0.86	58.01	90.63	13.18	0.326	3017.42
6.34	11.72	0.88	18.30	0.82	41.77	90.74	17.34	0.474	3020.42
6.50	14.83	0.85	25.92	0.38	52.20	98.20	9.68	0.652	3023.42
6.69	14.19	0.88	37.12	0.69	65.68	96.67	28.13	0.22	3026.92
6.82	20.56	0.86	44.26	0.76	73.51	92.75	7.14	-0.05	3029.92
6.88	7.52	0.84	33.40	0.33	61.39	97.80	22.43	0.454	3032.70
6.98	17.45	0.84	36.90	0.95	65.44	95.74	6.6	0.523	3033.17
7.01	10.73	0.82	55.11	0.43	84.59	99.22	31.34	0.373	3035.78
7.31	13.10	0.81	47.94	0.29	77.37	98.57	17.34	0.718	3039.70
7.60	8.86	0.96	6.22	0.25	20.94	97.90	23.07	0.855	3043.03
7.74	6.29	0.87	34.13	0.62	62.25	97.14	20.97	1.163	3045.73
7.84	12.07	0.90	33.53	1.13	61.54	95.00	8.61	0.353	3049.20
7.92	35.17	0.84	53.77	0.99	83.26	80.49	2.8	0.845	3052.27
8.02	25.03	0.90	23.63	0.96	49.20	90.48	3.83	0.813	3055.22
8.16	24.96	0.94	13.78	0.91	34.84	90.48	6.82	0.851	3058.76
8.25	13.92	0.95	17.11	0.30	40.01	98.00	20.4	0.84	3061.66

ODP Site 999a benthic  $\delta^{13}C$  dataset is after Haug and Tiedemann (1998) and Bickert et al. (2004).  $J_{sf}$ =Flux of organic carbon to the seafloor.

(Table 2). Both the general SHE methodology and SHEBI analyses have previously been applied to the study of benthic foraminiferal abundance distributions from the Atlantic Ocean with satisfactory results (Buzas and Hayek, 1998; Osterman et al., 2002; Small and McCarthy, 2002).

The Benthic Foraminifer Oxygen Index (BFOI; Fig. 2) estimates dissolved-oxygen levels in the ocean water based on a set of indicator benthic foraminiferal species that are morphologically categorized and oxygen sensitive into Dysoxic (*D*), Suboxic (*S*), and Oxidic (*O*) groups (Kaiho, 1994). The BFOI is calculated as  $\{[O/(O+D)] \times 100\}$  and

Table 4

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

Species	Reference no.
<i>Infaunal species</i>	
<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= <i>Textularia triquetra</i> Münster	2
<i>Fissurina</i> spp.	2
<i>Globobulimina affinis</i> (D'Orbigny)= <i>Bulimina affinis</i> D'Orbigny	3, 5, 7, 12, 15, 17, 18, 22
<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)= <i>Cassidulina subglobosa</i> Brady	11, 13, 20, 22
<i>Gyroidina altiformis</i> Stewart and Stewart= <i>G. soldanii</i> D'Orbigny <i>altiformis</i> Stewart and Stewart	22
<i>Gyroidina neosoldanii</i> Brotzen= <i>Gyroidina soldanii</i> D'Orbigny	22
<i>Gyroidina orbicularis</i> (D'Orbigny)= <i>Gyroidina orbicularis</i> D'Orbigny	22
<i>Gyroidina</i> spp.	22
<i>Lagena</i> spp.	2
<i>Lenticulina</i> spp.	3, 11
<i>Marginulina</i> spp.	2
<i>Melonis barleeianum</i> (Williamson)	3, 7, 9, 22
<i>Melonis</i> spp.	3, 7, 9, 22
<i>Nodosaria</i> spp.	2
<i>Nonion</i> spp.	18
<i>Nonionella</i> spp.	6
<i>Oolina</i> spp.	2
<i>Parafissurina</i> spp.	2
<i>Pleurostomella</i> spp.	13
<i>Pullenia bulloides</i> (D'Orbigny)= <i>Nonionina bulloides</i> D'Orbigny	3
<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
<i>Epifaunal species</i>	
<i>Anomalinoidea</i> spp.	19
<i>Cibicides</i> spp.	1, 2, 3, 14
<i>Cibicides wuellerstorfi</i> (Schwager)= <i>Anomalina wuellerstorfi</i> Schwager	1, 2, 3, 14
<i>Epistominella exigua</i> (Brady)= <i>Pulvinulina exigua</i> Brady	13
<i>Epistominella</i> spp.	8
Miliolids	3, 14
<i>Nuttallides umbonifera</i> (Cushman)= <i>Pulvinulinella umbonifera</i> Cushman	5

Table 4 (continued)

Species	Reference no.
<i>Oridorsalis umbonatus</i> (Reuss); <i>Truncatulina tenera</i> Brady	4
<i>Osangularia culter</i> (Parker and Jones)	1, 18
<i>Ecological references</i>	
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

the species used are outlined in several papers by Kaiho and others (Kaiho, 1994, 1999a,b, Kaiho et al., 2006). The BFOI values between -40-0 represent suboxic conditions with estimated dissolved-oxygen levels ranging from 0.3–1.5 mL/L, Low oxia between 0–50 indicating 1.5–3 mL/L and High oxia with BFOI values ranging from 50–100 with dissolved-oxygen levels between 3.0–>6.0 mL/L (Kaiho, 1994).

### 3.5. Correlation and Principal Component analyses

Pearson product moment correlation analysis (commonly expressed as *r*) is used to describe the strength of an association between variables (of diversity and paleoproductivity). Significant correlations between variables suggest that the value of one variable can be predicted, to some extent, by the value of the other. We have also used Principal Component Analysis (PCA), a mathematical technique for simplifying a multidimensional dataset (here 8 proxies: Fisher's  $\alpha$ , Equitability, *I/E* ratio, BFAR, Flux, BFOI, Watermass ventilation and Current velocity), by reducing it to lower dimensions for interpretive analysis. The PCA is an orthogonal linear transformation that transforms the data to a new coordinate system such that the greatest variance by any projection of

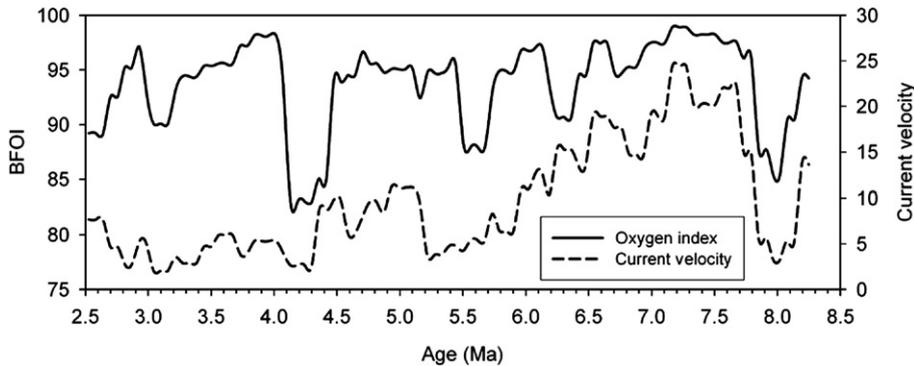


Fig. 2. Comparison of relative abundances of *Cibicides wuellerstorfi*+*Globocassidulina subglobosa* from Site 999. Bold (solid and dashed) lines are five point smoothed running averages. The species are collectively considered a proxy for current velocity because of their similar trends (see Jain and Collins, 2007 for details).

the data comes to lie on the first coordinate (called the first principal component; here as Component 1), the second greatest variance on the second coordinate (here as Component 2), and so on. Our first 3 components explain 82% of the total variance.

#### 4. Results

Defining paleobathymetries that are comparable between the Caribbean and Eastern Pacific is difficult because their biofacies have remained different through the study interval. Another complication is that although ODP Site 999 was drilled at 2829 m water depth, it has seen only the deepest North Atlantic water entering across raised sills in the Greater Antilles; at present, the deepest Atlantic water received by the Colombian Basin is about 1815–2300 m deep (Sturges, 1965), although it may have been deeper in the past. The Caribbean faunas at Site 999, dominated by *Nuttallides umbonifera* and *Oridorsalis umbonatus* with common *Cibicides wuellerstorfi*, *Epistominella exigua* and *Melonis barleeanum*, are similar to lower bathyal–abyssal, Late Quaternary faunas of the Colombian Basin (Bertrand, 1986) and Venezuela Basin (Gaby and Sen Gupta, 1985). The Pacific faunas at Site 503, drilled at 3572 m water depth, are also lower bathyal–abyssal, containing diagnostic elements such as *E. exigua*, *Gyroidina planulata*, *Laticarinina pauperata*, *N. umbonifera* (as *Epistominella umbonifera*), *Pullenia quinqueloba*, *Quinqueloculina venusta* and *Uvigerina hispida* (McDougall, 1985, 1996). Although these taxa are also found at Site 999, other common Caribbean taxa (e.g., *C. wuellerstorfi*) do not occur at the Pacific site. Shallower tropical Eastern Pacific biofacies as described by Smith (1964) and McDougall (1985) seem no more comparable to the Caribbean Site 999 biofacies, so we have compared

the general lower bathyal–abyssal biofacies from each side of the Panamanian isthmus (Fig. 1).

Additionally, in the present study, the number of species ( $S$ ) and specimens ( $N$ ) are not directly compared for diversity analysis between the DSDP Sites 502 and 503 (McDougall, 1996) and the ODP Site 999 (this study). Though benthic foraminifers were picked from the same sieve size fraction ( $>63 \mu\text{m}$ ) in these studies, the datasets of DSDP Sites 502 and 503 are from  $20 \text{ cm}^3$  of sediments (McDougall, 1996) as opposed to  $10 \text{ cm}^3$  in this study. Rarefaction analysis indicates that in order to directly compare  $S$  and  $N$  values from the Caribbean Site 999 with the Pacific Site 503 (McDougall, 1996 dataset), a minimum of  $\sim 750$  specimens need to be picked from each Site 999 sample. Thus,  $S$  and  $N$  values are not directly compared.

A positive and statistically significant correlation is noted between Fisher's  $\alpha$  and  $H(S)$  for the Caribbean

Table 5  
Relationship of Fisher's  $\alpha$  and  $H(S)$  based on Pearson's product moment correlation ( $r$ ) analysis

	Fisher's $\alpha$	$H(S)$
a) $N=47$		
Fisher's $\alpha$	1	
$H(S)$	0.708 <sup>a</sup>	1
	0.0001	
Equitability	-0.304 <sup>b</sup>	-0.070
	0.038	0.655
b) $N=49$		
Fisher's $\alpha$	1	
$H(S)$	0.682 <sup>b</sup>	1
	0.0001	
Equitability	-0.191	-0.060
	0.272	0.720

(a) Caribbean ODP Site 999 and (b) Pacific DSDP Site 503.

<sup>a</sup> Correlation is significant at the 0.01 level (2-tailed).

<sup>b</sup> Correlation is significant at the 0.05 level (2-tailed).

( $r=0.708$ ;  $p<.0001$ ;  $n=47$ ; Table 5a) and Pacific sites ( $r=0.682$ ;  $p<.0001$ ;  $n=51$ ; Table 5b). These significant correlations suggest that both Fisher's  $\alpha$  and  $H(S)$  are equally good measures for assessing benthic foraminiferal diversity. Thus, hereafter, Fisher's  $\alpha$ , the more commonly used diversity measure is referred as Diversity and is used

for all quantitative analyses. However, changes in the Information Index [ $H(S)$ ] are briefly mentioned in the Results section and shown in Fig. 3.

Potential changes in diversity are described against previously documented paleoceanographic events that affected seaway closure during this interval (Keigwin,

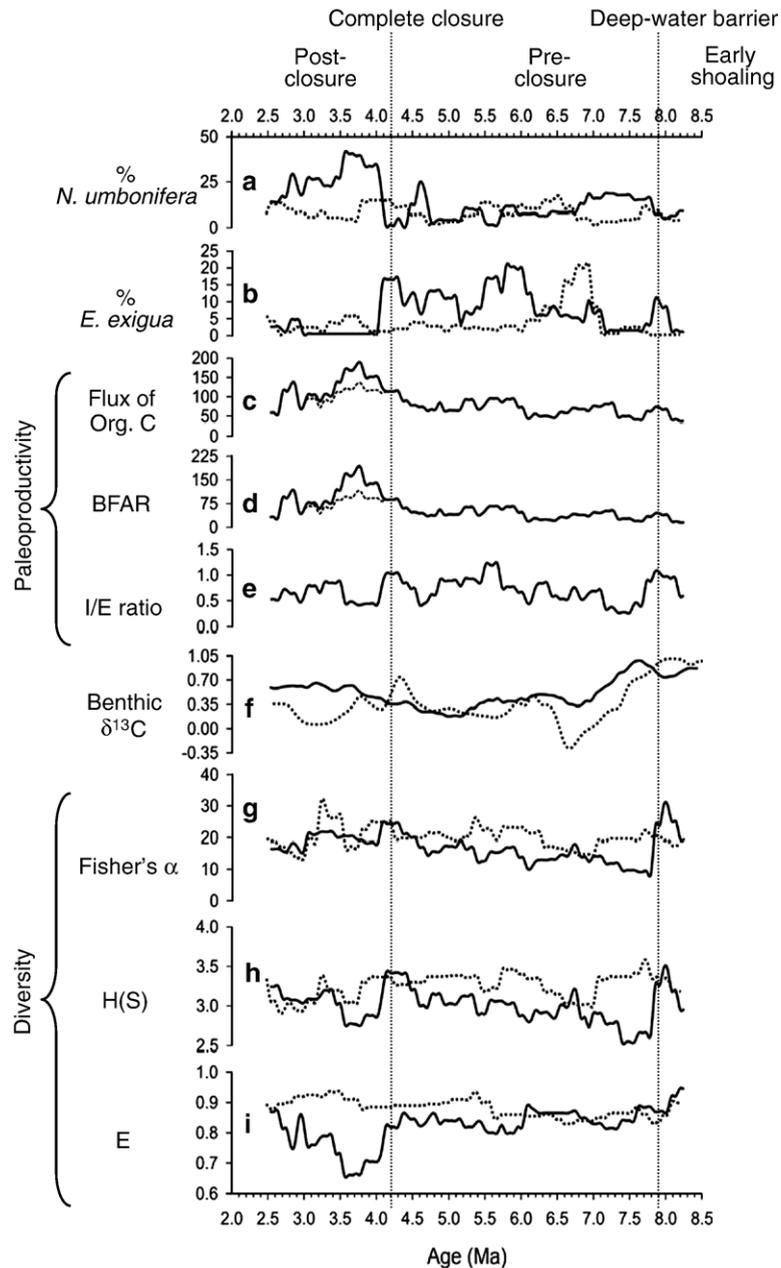


Fig. 3. Five point smooth running average of paleoproductivity proxies and diversity indices between 8.3–2.5 Ma. Dotted lines (a–b and f–i) are from the Pacific DSDP Site 503 (McDougall, 1996 dataset). Black lines (a–i) are from western Caribbean ODP Site 999a (present work). Bold line (dotted and solid) are five point smooth running averages. Benthic  $\delta^{13}C$  dataset (f, black line) is also from ODP Site 999a (data from Haug and Tiedemann, 1998; Bickert et al., 2004) and the dotted line is from a composite Pacific benthic  $\delta^{13}C$  dataset of Billups (2002). Dashed lines in c–d are flux of organic carbon to the seafloor ( $J_{sf}$ ) and BFAR estimates calculated without the anomalously high relative abundance of *Nuttallides umbonifera* from ODP Site 999a (present work).

Table 6

Timeline of Central American Seaway constriction and closure from previous deep sea core-based studies used to mark intervals in the present study

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 foraminiferal $\delta^{13}\text{C}$ 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)

1982; Haug and Tiedemann, 1998; Driscoll and Haug, 1998; Haug et al., 2001). The main events listed in Table 6 are used to divide the 8.3–2.5 Ma study period into 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) (see Jain and Collins for details). Effects of the CAS closure on

Caribbean diversity are further tested for the Pre- and Post-closure interval against proxies for paleoproductivity (benthic foraminifer accumulation rates, benthic foraminiferal infaunal/epifaunal species ratio, and flux of organic carbon to the seafloor), benthic foraminifer oxygenation index, current velocity, watermass ventilation, and depth.

#### 4.1. Early shoaling (8.3–7.9 Ma)

The early shoaling of the Central American isthmus was marked in the Caribbean by the highest values in this study of the diversity measures Fisher's  $\alpha$  and  $H(S)$  (35, 3.6 respectively), and by decreasing Equitability from 0.95 to 0.84 (Fig. 3). The  $I/E$  ratio, BFAR and  $J_{\text{sf}}$  values increased in the Caribbean. Relatively high but decreasing benthic  $\delta^{13}\text{C}$  values ( $\sim 0.85\text{‰}$ ), low abundances of *Nuttallides umbonifera* ( $\sim 5\%$  of the total benthic foraminiferal assemblage) and relatively increased abundance of *Epistominella exigua* (as much as 15%) are also noted at the Caribbean site (Fig. 3). Both oxygenation index (hereafter BFOI; the dissolved-oxygen index; Fig. 2) and current velocity also decreased sharply at the Caribbean site (Fig. 2).

At the Pacific site, the diversity measures have a similar pattern to that of the Caribbean site, but display slightly lower values (Fig. 3). The relative abundance of *Epistominella exigua* is also much lower at the

Table 7

Pearson's product moment correlations ( $r$ ) of all the Caribbean proxies (mentioned in Table 2 and used here) with diversity (Fisher's  $\alpha$ ) for the study interval 7.6–4.2 Ma

		Fisher's $\alpha$	$E$	BFAR	$I/E$ ratio	$J_{\text{sf}}$ (flux)	BFOI	Current velocity	Benthic $\delta^{13}\text{C}$	Depth
Diversity	Fisher's $\alpha$	1								
Equitability		–0.361	1							
		0.059								
Paleoproductivity	BFAR	0.597**	–0.786**	1						
		0.001	0.0000							
	$I/E$ ratio	0.458*	–0.522**	0.656**	1					
		0.014	0.004	0.0000						
	$J_{\text{sf}}$ (flux)	0.574**	–0.810**	0.992**	0.644**	1				
		0.001	0.0000	0.0000	0.0000					
Oxygenation	BFOI	–0.542**	0.197	–0.495**	–0.561**	–0.472*	1			
		0.003	0.315	0.007	0.002	0.011				
Current velocity		–0.600**	0.433*	–0.538**	–0.626**	–.545**	0.496**	1		
		0.001	0.021	0.003	0.0000	0.003	0.007			
Watermass ventilation	Benthic $\delta^{13}\text{C}$	–0.398*	0.299	–0.220	–0.269	–0.256	0.235	0.319	1	
		0.036	0.123	0.262	0.166	0.189	0.229	0.098		
Depth		–0.618**	0.294	–0.445*	–0.376*	–.435*	0.484**	0.581**	0.500**	1
		0.0000	0.128	0.018	0.048	0.021	0.009	0.001	0.007	

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

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

$N=28$ .

Pacific site ( $< \sim 2\%$ ), but that of *Nuttallides umbonifera* is similar to that noted at the Caribbean site. Peak benthic  $\delta^{13}\text{C}$  values for the entire study interval at the Pacific site are noted during this brief interval ( $\sim 0.87\text{‰}$ ) (Fig. 3).

#### 4.2. Pre-closure (7.9–4.2 Ma)

The Pearson product moment correlations ( $r$ ) for this Pre-closure interval (7.9–4.2 Ma) between Caribbean

diversity (Fisher's  $\alpha$ ) and paleoproductivity proxies ( $I/E$  ratio, BFAR and  $J_{st}$ ) are positive and statistically significant (Table 7). Negative and significant correlations are noted between diversity and BFOI, current velocity, watermass ventilation, and depth (Table 7).

The beginning (7.9–7.6 Ma) of the Pre-closure interval in the Caribbean is marked by a steep decrease in values of Fisher's  $\alpha$  and  $H(S)$  (7.5, 2.5 respectively), and a smaller increase in  $E$ , from 0.84 to 0.90 (Fig. 3). In the Caribbean, during this brief interval,  $I/E$  ratio, BFAR

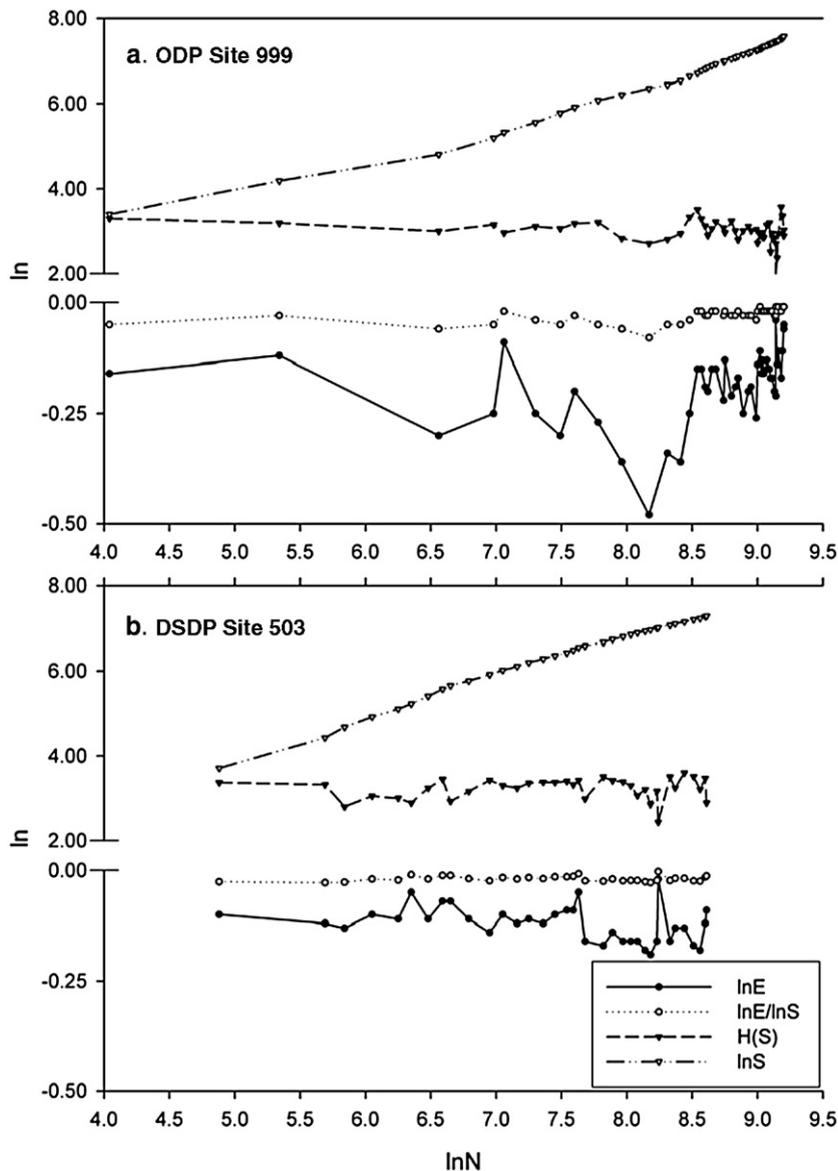


Fig. 4. Plots of  $\ln S$ ,  $H(S)$  and  $\ln E$  (SHE) against  $\ln N$  for the Caribbean ODP Site 999 (a) and Pacific DSDP Site 503 (b).  $S$  is the number of species,  $H(S)$  is Information Index,  $E$  is Equitability, and  $N$  the number of individuals. For a log series distribution, the slopes for  $\ln S$  and  $\ln E$  should be equal but opposite and  $H$  should be constant, whereas for a log normal distribution  $\ln E / \ln S$  should remain constant. Both the Caribbean (a) and the Pacific (b) datasets thus best fits a log normal distribution. Note the sensitivity of  $\ln E$  (for details see text).

and  $J_{sf}$  recorded a decrease, benthic  $\delta^{13}C$  values remained high, and the relative abundance of *Epistominella exigua* decreased sharply (to <1%) and *Nuttallides umbonifera* correspondingly increased (to ~25%). Both current velocity (3 to ~23%) and oxygenation (85 to >95) increased steeply (Fig. 2). As compared to the Caribbean, the Pacific site between 7.9–7.6 Ma recorded higher values of Fisher's  $\alpha$  and  $H(S)$  (~22, ~3.6 respectively), slightly lower but increasing  $E$ , and lower relative abundances of both *E. exigua* and *N. umbonifera* (both <~2%; Fig. 3). Benthic  $\delta^{13}C$  values began a large decrease that continued until 6.7 Ma from ~0.95‰ to ~-0.25‰ (Fig. 3).

The time period between 7.6 to 4.2 Ma in the Caribbean is marked by steadily increasing values of Fisher's  $\alpha$  (from 7 to 27) and  $H(S)$  (from 2.5–3.35) with a corresponding decrease in  $E$  from 0.90 to 0.78 (Fig. 3). The  $I/E$  ratio, BFAR and  $J_{sf}$  gradually increased until the end of the interval and benthic  $\delta^{13}C$  values steadily declined from ~1.2‰ to ~0.35‰. Additionally, in the Caribbean, the relative abundance of *Epistominella exigua* increased to its peak values (27% of the total benthic foraminiferal assemblage) at ~6 Ma and then continued to remain moderately high (~15%) until the end of the Post-closure interval at 4.2 Ma, whereas *Nuttallides umbonifera* gradually decreased to almost 0% (Fig. 3). Both current velocity (~25 to ~3%) and oxygenation (>95 to <85) decreased to lowest values for the entire studied interval (Fig. 2).

At the Pacific site, Fisher's  $\alpha$  (~22) dramatically increases between 7.9–7.25 Ma, with the latter having its highest values at ~7.6 Ma for the entire interval. Fisher's  $\alpha$  and  $H(S)$ , except between 7.8–6.7 Ma show similar trends. Thereafter, Fisher's  $\alpha$  increased with peak values at ~5.4 (Fig. 3).  $E$  at the Pacific site remains low between 7.6–5.7 Ma and then abruptly increases between 5.7–5.4 Ma. Between ~5.4–4.2 Ma, Fisher's  $\alpha$  decreased slightly and  $E$  gradually increased. The benthic  $\delta^{13}C$  values at the Pacific site remained similar to the Caribbean but varied more. The relative abundance of *Epistominella exigua* at the Pacific site dramatically decreased to <5% of the total benthic foraminiferal assemblage, except for a large peak (~20%) between 7.1–6.6 Ma, whereas *Nuttallides umbonifera* gradually increased (~15%) until 6.5 Ma and then decreased to <3% (Fig. 4).

In summary, diversity trends between the Caribbean and Pacific sites diverge at 7.9 Ma and again at ~6.7 Ma, being always higher at the Pacific site. Equitability on the other hand shows divergent trends slightly later at ~6 Ma. At the Caribbean site, peak values of Fisher's  $\alpha$  and  $E$  are noted at ~5.4 Ma.

#### 4.3. Post-closure 4.2–2.5 Ma

In the Caribbean, during the Post-closure interval 4.2–2.5 Ma, diversity [(Fisher's  $\alpha$  and  $H(S)$ ] values peaked at 4.2 Ma (27 and 3.5 respectively) and then decreased to moderate values (~20 and 3 respectively; Fig. 3). However,  $H(S)$  differs somewhat from Fisher's  $\alpha$ , it drops until 3.5 Ma and then increases to moderate values.  $E$  also decreases from ~0.84 to ~0.61 until 3.5 Ma and then gradually increases until the end of the study interval at 2.5 Ma (from ~0.6 to 0.9; Fig. 3). The  $I/E$  ratio in the Caribbean also decreased between 4.2 and 3.5 Ma as opposed to an increase noted in the other two paleoproductivity proxies, BFAR and  $J_{sf}$ . However, after 3.5 Ma, all three paleoproductivity proxies show a gradually decreasing trend in the Caribbean. A dramatic decrease to extremely low values (<3% of the total benthic foraminiferal assemblage) is also noted for the relative abundance of *Epistominella exigua*. An increase in the relative abundance of *Nuttallides umbonifera* to its highest values (making up as much as ~50% of the total benthic foraminiferal assemblage) at the beginning of the interval was followed by a gradual decline thereafter (to <10%). Benthic  $\delta^{13}C$  values in the Caribbean increased steadily throughout the Post-closure interval (0.36 to 0.70‰; Fig. 3). Oxygenation dramatically increased between 4.2–3.7 Ma from ~83 to ~97 and then reduced to moderate values of ~90 (Fig. 2). Current velocity greatly reduced after 4.2 Ma to moderately low values of ~5% (Fig. 2).

At the Pacific site, both Fisher's  $\alpha$  increase (~25) until ~4.2 Ma and decrease until 3.6 Ma (~15).  $E$  shows opposing trends and gradually increases from 0.90 to a plateau of ~0.95. Between 3.6–3.2 Ma all values increase again, with maximum values of Fisher's  $\alpha$  (~33), so far recorded (Fig. 3). After 3.6 Ma,  $E$  gradually decreases until the end of the studied section at 2.5 Ma, whereas a steep decrease is noted for Fisher's  $\alpha$  between 3.3–3 Ma (Fisher's  $\alpha$ : ~30 to ~15), and followed by increasing values until 2.5 Ma (~20). The relative abundance of *Epistominella exigua* at the Pacific site remained low (<5%) whereas that of *Nuttallides umbonifera*, correspondingly, decreased between 4.2–3.5 Ma (~20% to <1%) and then increased until the end of the studied section at 2.5 Ma to almost ~12% (Fig. 3). The benthic  $\delta^{13}C$  values at the Pacific site progressively decreased (mean 0.35‰) as compared to those at the Caribbean site (mean 0.70‰).

In contrast to the Caribbean,  $E$  at the Pacific site progressively increased between 4.2–3.6 Ma, thereafter it gradually declined, whereas at the Caribbean site it increased until the end of the studied interval at 2.5 Ma

Table 8

Pearson's product moment correlations ( $r$ ) of all the Caribbean proxies (mentioned in Table 2 and used here) with diversity (Fisher's  $\alpha$ ) for the study interval 4.2–2.5 Ma

		Fisher's $\alpha$	Equitability	BFAR	I/E ratio	$J_{sf}$ (flux)	BFOI	Current velocity	Benthic $\delta^{13}C$	Depth
Diversity	Fisher's $\alpha$	1								
Equitability		-0.468	1							
		0.092								
Paleoproductivity	BFAR	0.271	-0.900**	1						
		0.348	0.0000							
	I/E ratio	0.491	0.032	0.034	1					
		0.075	0.913	0.908						
	$J_{sf}$ (flux)	0.312	-0.907**	0.992**	0.126	1				
		0.278	0.0000	0.0000	0.668					
Oxygenation	BFOI	-0.282	-0.247	0.347	-0.374	0.322	1			
		0.330	0.395	0.225	0.187	0.261				
Current velocity		-0.612*	0.286	-0.309	-0.696**	0.369	0.276	1		
		.020	0.322	0.282	0.006	0.194	0.339			
Watermass ventilation	Benthic $\delta^{13}C$	-0.070	0.150	-0.326	-0.366	-0.353	0.112	0.483	1	
		0.813	0.608	0.256	0.198	0.216	0.704	0.080		
Depth		0.546*	-0.581*	0.548*	0.273	0.570*	0.284	-0.182	-0.281	1
		0.043	0.029	0.043	0.344	0.033	0.325	0.534	0.331	

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

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

$N=14$ .

(Fig. 3).  $H(S)$  at both the sites follow similar trends, with a decrease between 4.2–3.6 Ma, increase until 3.2 Ma, a brief interval of decrease until 3 Ma and then an increase until the end of the study interval. However, Fisher's  $\alpha$  does not follow similar trends for the 2 sites between 4.2–3.9 Ma. The Caribbean site records a sharp decrease between 4.2–4 Ma, followed by a gradual increase in

values until 3 Ma, where as at the Pacific site, Fisher's  $\alpha$  increased between 4.2–3.9 Ma, decreased until 3.6 Ma and then dramatically increased to maximum values at 3.2 Ma. Thereafter, Fisher's  $\alpha$  values decreased rapidly until 3 Ma and then gradually increased (Fig. 3).

The Pearson product moment correlations ( $r$ ) for the Caribbean Post-closure interval (4.2–2.5 Ma) between

Table 9

Pearson's product moment correlations ( $r$ ) of all the Caribbean proxies (mentioned in Table 2 and used here) with diversity (Fisher's  $\alpha$ ) for the entire study interval 8.3–2.5 Ma

		Fisher's $\alpha$	Equitability	BFAR	I/E ratio	$J_{sf}$ (flux)	BFOI	Current velocity	Benthic $\delta^{13}C$	Depth
Diversity	Fisher's $\alpha$	1								
Equitability		-0.304*	1							
		0.038								
Paleoproductivity	BFAR	0.336*	-0.898**	1						
		0.021	0.0000							
	I/E ratio	0.334*	-0.061	0.105	1					
		0.022	0.682	0.481						
	$J_{sf}$ (flux)	0.352*	-0.910**	0.989**	0.176	1				
		0.015	0.0000	0.0000	0.235					
Oxygenation	BFOI	-0.566**	0.009	-0.055	-0.517**	-0.095	1			
		0.0000	0.950	0.713	.0000	0.524				
Current velocity		-0.591**	0.465**	-0.481**	-0.463**	-0.518**	0.449**	1		
		-0.0000	0.001	0.001	0.001	0.0000	0.002			
Watermass ventilation	Benthic $\delta^{13}C$	0.053	0.113	-0.058	-0.231	-0.100	0.063	0.165	1	
		0.724	0.450	0.699	0.118	0.504	0.676	0.268		
Depth		-0.218	0.551**	-0.519**	0.077	-0.527**	0.119	0.564**	0.120	1
		0.142	0.0000	0.0000	0.605	0.0000	0.425	0.0000	0.422	

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

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

$N=47$ .

diversity and paleoproductivity proxies (BFAR,  $I/E$  ratio and Flux) are positive but not statistically significant (Table 8). However, the relationship between diversity and current velocity is negative and statistically significant, and with depth positive and statistically significant (Table 8).

Additionally, the Pearson product moment correlations ( $r$ ) for the entire studied interval between 8.3–2.5 Ma in the Caribbean (Table 9) also yields a positive and statistically significant correlation between diversity and proxies of paleoproductivity (BFAR,  $I/E$  ratio and  $J_{sf}$ ), negative and statistically significant correlations with Equitability, Oxygenation (Benthic Foraminiferal Oxygen Index; BFOI) and Current velocity (Table 9). Watermass ventilation (benthic  $\delta^{13}C$ ) and Depth did not yield significant correlations (Table 9). A brief summary of correlations for all the intervals is given in Table 10.

#### 4.4. SHE and SHEBI analyses

SHE analysis for both Pacific and Caribbean datasets indicate decreasing values of  $\ln E$ ,  $H(S)$  and  $\ln S/\ln E$  through time (Fig. 4). However,  $\ln S/\ln E$  shows the least deviation and the slope of  $\ln S$  vs.  $\ln E$  is near 4, indicating a log normal distribution of species for both datasets (Fig. 4; Hayek and Buzas, 1997; Buzas and Hayek, 1998). At both Caribbean and Pacific sites,  $\ln E$  is the most variable when plotted against  $\ln N$  as compared to  $\ln S$  and  $H(S)$  (Fig. 4). Thus, abrupt slope changes in  $\ln E$  are used by SHEBI to mark faunal boundaries (Fig. 5). These compositional boundaries, which show departure from the linear trend

(Buzas and Hayek, 1998), reveal that at Site 999 (Fig. 5a–e) changes occur at 7.92 Ma, 7.6 Ma, 6.11 Ma, 6.69 Ma, 5.95 Ma (Fig. 5e), 5.01 Ma, 4.32 Ma, 3.68 Ma (Fig. 5d), 2.98 (Fig. 5c) and 2.77 Ma (Fig. 5b) and for the Pacific DSDP Site 503 (Fig. 5f–j) the boundaries are at 7.92 Ma, 7.25 Ma, 6.69 Ma (Fig. 5j), 5.44 Ma (Fig. 5i), 3.95 Ma, 2.96 Ma (Fig. 5h) and 2.58 Ma (Fig. 5g).

Thus, only three boundaries, at 7.92 Ma, 6.69 Ma and between 2.96–2.98 Ma, are similar between the two sites across the isthmus (Fig. 5). Additionally, a diverging trend (slope of  $\ln E$ ) is also noted between Pacific and Caribbean sites beginning at 7.9 Ma, with the Pacific (Fig. 5f) displaying gradually increasing trend until 2.96 Ma and the Caribbean decreasing trend until 3.68 Ma (Fig. 5a).

#### 4.5. Principal Component Analysis

The 3-dimensional principal component plot of eight Caribbean proxies (variables) from Site 999 ( $N=47$ ) for the 8.3–2.5 Ma interval is given in Fig. 6a and a 2-dimensional representation in Fig. 6b. The first 3 components/axes explain 82% of the observed variability in the Caribbean. Diversity, as measured by Fisher's  $\alpha$ , and proxies for paleoproductivity ( $I/E$  ratio, BFAR and Flux), have a positive relationship (positive loading) whereas current velocity, watermass ventilation and equitability have a negative relationship (negative loading) on the first axis, which alone explains 45% of the variability. Oxygenation as such does not play a role. It is only when we consider the third dimension,

Table 10

Summary of Pearson's product moment correlations ( $r$ ) of all the Caribbean proxies (mentioned in Table 2 and used here) with diversity (Fisher's  $\alpha$ ) for all the study intervals

a		b	c	d	e
Intervals		Total	Pre-closure	Post-closure	Phytodetritus
Proxies/indices		8.3–2.5 Ma	7.6–4.2 Ma	4.2–2.5 Ma	7.6–4.2 Ma
Diversity		Fisher's $\alpha$			+**
Equitability		–*	–	–	–**
Paleoproductivity	BFAR	+*	+**	+	+**
	$I/E$ ratio	+*	+*	+	+**
	$J_{sf}$ (flux)	+*	+**	+	+**
	Oxygenation	BFOI	–**	–**	–
Current velocity		–**	–**	–*	–**
Watermass ventilation	Benthic $\delta^{13}C$	+	–*	+	–
Depth		–	–**	+*	–*
Number of samples		47	28	14	28

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

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

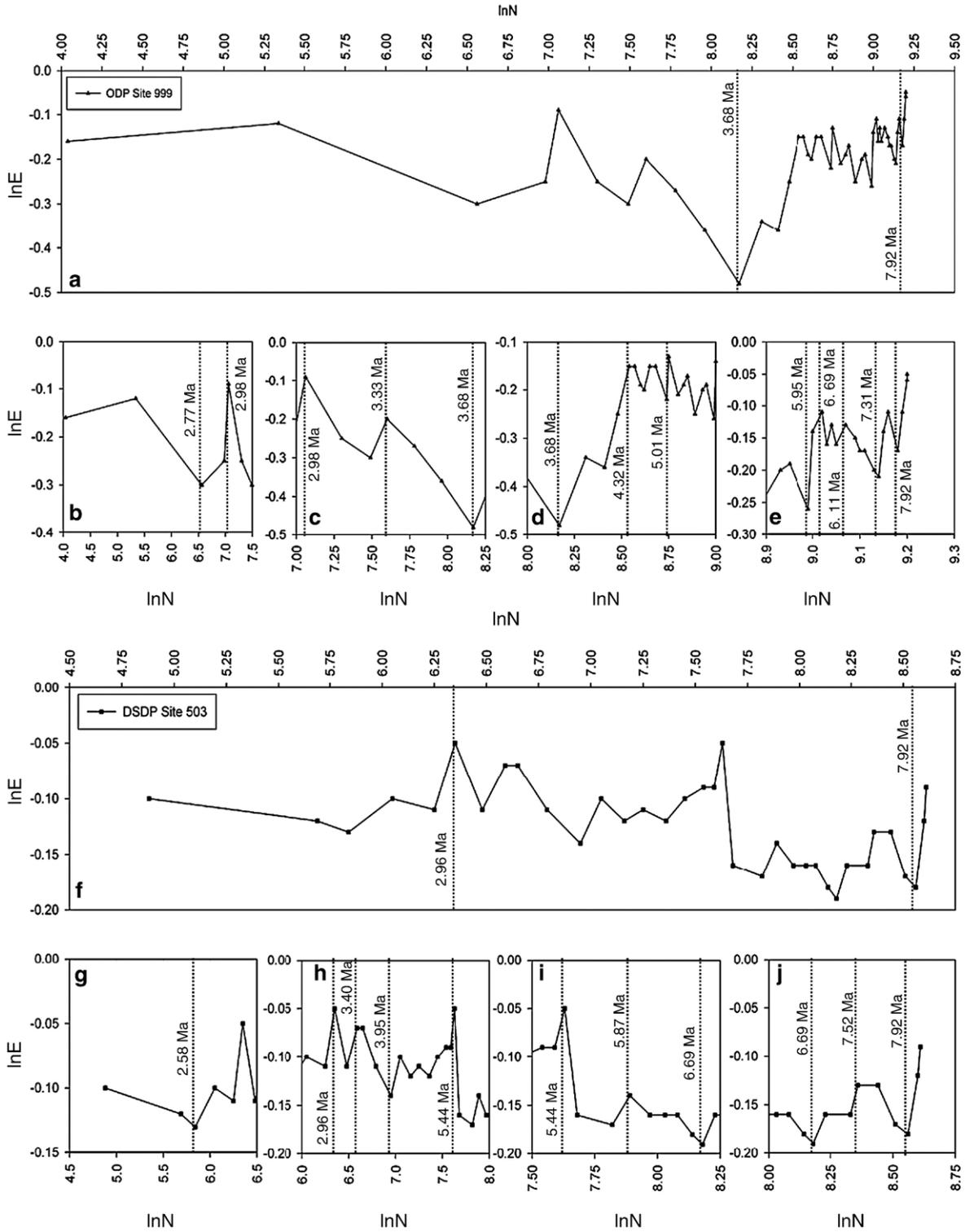


Fig. 5. Plots of  $\ln E$  against  $\ln N$  for the Caribbean ODP Site 999 (a–e) and Pacific DSDP Site 503 (f–j). Dashed lines indicate ages at which biofacies are identified (SHEBI: SHE Biofacies Identification). Note the common 7.92 Ma and  $\sim 2.98$  Ma boundaries at both Caribbean and Pacific sites and the divergence in trends of  $\ln E$  between Pacific and Caribbean sites after 7.9 Ma (e and j). The Caribbean displays decreasing values until a low at 3.68 Ma (a) whereas the Pacific displays increasing values until 2.96 Ma (f).

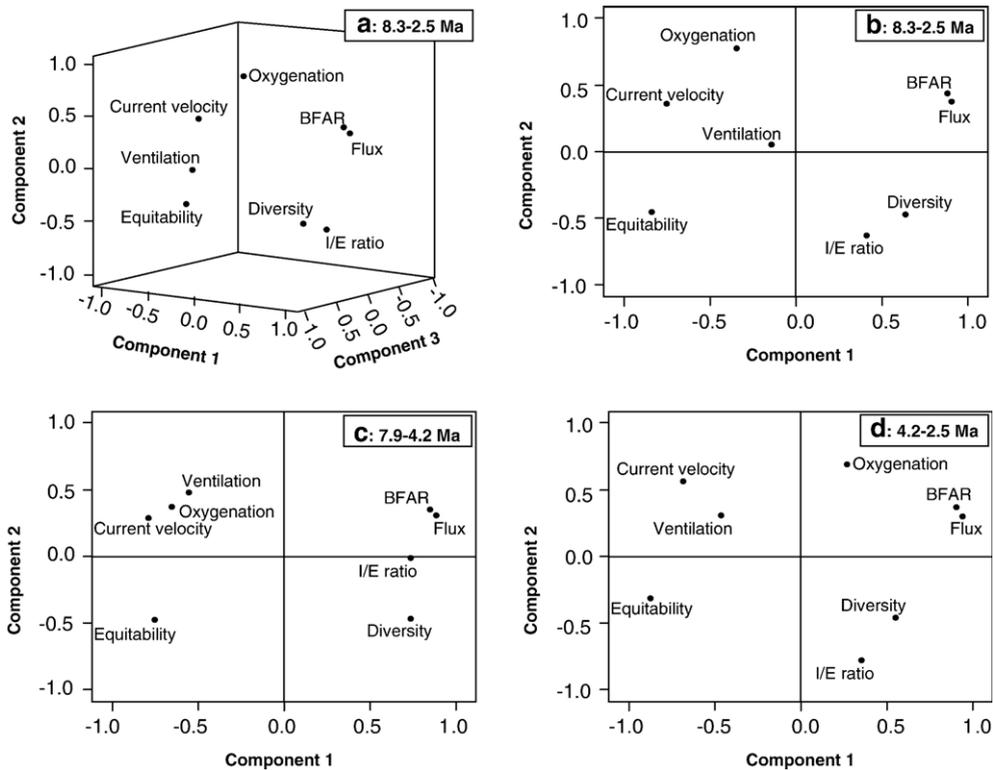


Fig. 6. Principal Component Analysis between diversity and eight variables (Paleoproductivity: BFAR,  $I/E$  ratio and  $J_{sd}$ ), Oxygenation (Benthic Foraminiferal Oxygen Index; BFOI), Current velocity (abundances of *Cibicides wuellerstorfi*+*Globocassidulina subglobosa*), Watermass ventilation (benthic  $\delta^{13}C$ ), Equitability, and Depth (in m). (a): A 3-dimensional principal component plot of eight Caribbean proxies (variables) from Site 999 ( $N=47$ ) for the 8.3–2.5 Ma interval, (b): a 2-D representation of (a), (c): for the Pre-closure interval (7.9–4.2 Ma) and (d): for the Post-closure interval (4.2–2.5 Ma).

explaining approximately 12%, that ventilation becomes important. This observed proxy is the sole contributor to the separation afforded by the third axis.

The 8.3–2.5 Ma interval is shown in Fig. 6b. This figure shows the 8 proxies (variables) plotted on the derived 2-dimensional space of the first two PC's. Here, watermass ventilation is not an influence in the separation of points. We chose to include this figure to make the observed situation clearer without the added dimension of ventilation. Both diversity and proxies for paleoproductivity ( $I/E$  ratio, BFAR and Flux) continue to have a positive relationship (positive loading), whereas watermass ventilation, oxygenation, current velocity, and equitability have a negative relationship (negative loading) on the first axis, which alone explains 45% of the variability in the dataset. The first two axes altogether explain about 69% of the total variance in the dataset. While the loadings on current velocity and oxygenation (BFOI) are similar to each other, large and negative, the loadings for BFAR and flux are likewise similar, large, but positive. This indicates that each set of proxies (variables) provides equivalent measurement

and can contribute to the variability in this system. However, both sets of proxies are necessary factors to provide a complete picture for this time interval in the Caribbean. The first axis alone can explain 45% of the total variability and if only this axis is considered, then diversity and the  $I/E$  ratio are positive and quite close while current velocity and oxygenation, just as  $E$ , provide the other side of the picture. Additionally,  $E$  has a negative loading, as expected by the explanation of the decomposition equation and the relationship of  $H$ ,  $\alpha$  and  $E$  (Buzas and Hayek, 2005).

The Pre-closure interval (7.9–4.2 Ma) is shown by Fig. 6c. The first two components together explained 68% of the variability. The first component explained 54% of the variability. Each of the variables has high loading on the first axis, with a contrast between diversity and current velocity, oxygenation and ventilation (negative loading). Here also, both diversity and proxies for paleoproductivity ( $I/E$  ratio, BFAR and Flux) continue to have a positive relationship (positive, loading). Here, current velocity is of only minor importance.

The loading for the Post-closure interval (4.2–2.5 Ma) is shown in Fig. 6d. The first 2 components explained 73% of the variability while the third added an additional 13% for a total of 86%. The first component alone explained 46% and the second 27%. Both diversity and proxies for paleoproductivity (*I/E* ratio, BFAR and Flux) continue to have a positive relationship (positive loading), whereas watermass ventilation, current velocity, and equitability have a negative relationship (negative loading). However, oxygenation now has a positive loading with diversity (Fig. 6d).

In summary, for the entire interval (8.3–2.5 Ma) in the Caribbean, Diversity (Fisher's  $\alpha$ ), and proxies for paleoproductivity (*I/E* ratio, BFAR and Flux) have a positive relationship (positive loading) whereas current velocity, watermass ventilation and equitability have a negative relationship (negative loading). For the Pre-closure interval (7.9–4.2 Ma), this holds true, but in addition, for the Post-closure interval (4.2–2.5 Ma), oxygenation also has a positive loading with diversity and paleoproductivity (Fig. 6).

Thus, for the Caribbean, both the analyses of correlation (Tables 7–10) and PCA (Fig. 6) indicate that a) diversity and paleoproductivity have a positive relationship (Fig. 6a–b), that for the Pre-closure interval (7.9–4.2 Ma; Fig. 6c), besides the continued positive relationship between diversity and paleoproductivity, watermass ventilation, and current velocity have a negative relationship with diversity and the latter plays only a minor role. and c) that for the Post-closure interval (4.2–2.5 Ma; Fig. 6d), the same holds true but here oxygenation has a positive loading with diversity (Fig. 6d).

## 5. Discussion

In the Caribbean, similar to other well-oxygenated oligotrophic settings (Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000), a positive and significant correlation is noted between benthic foraminiferal diversity and paleoproductivity. Additionally, the oxygen levels at both Pacific and Caribbean sites were well above the stress threshold throughout the study interval (8.3–2.5 Ma) as shown by low abundances of species characteristic of such stressed environments (e.g. *Bulimina*, *Bolivina*, *Globobulimina* and *Uvigerina*). These species combined do not exceed more than 7% of the total benthic foraminiferal assemblage.

The Early shoaling interval (8.3–7.9 Ma) is marked by parallel increasing trends of diversity and paleoproductivity proxies at both Caribbean and Pacific sites, suggesting that there was relatively free exchange of watermass between the two sites through an open

Central American Seaway (Fig. 3). Any restriction of watermass between the two sites should have initiated differing patterns of diversity and paleoproductivity.

During the Pre-closure interval (7.9–4.2 Ma) in the Caribbean, both diversity and paleoproductivity declined sharply between 7.9 to 7.6 Ma whereas at the Pacific site, they continued to increase (Fig. 3). This abrupt decrease in the Caribbean also coincides with better ventilation (higher benthic  $\delta^{13}\text{C}$  values), increased oxygenation (high BFOI values), current velocity and reduced seasonality of phytodetrital input (Figs. 2–3). Reduction in the input of phytodetritus (lower relative abundance of *Epistominella exigua*) would result in reduced availability of food to benthic foraminifers. Furthermore, the restriction of nutrient-rich Pacific waters into the well-oxygenated Caribbean would facilitate improved ventilation in the Caribbean, resulting in enhanced oxidation of the already reduced organic flux settling down to the seafloor. The fact that diversity also decreased rapidly indicates that it is closely linked to the availability of food (paleoproductivity) in the Caribbean. This decrease in both diversity and paleoproductivity in the Caribbean also coincides with an increased relative abundance of the oligotrophy indicator taxon *Nuttallides umbonifera* (Jain and Collins, 2007).

Thus, after the cut-off of the nutrient-rich Pacific waters into the Caribbean at around 7.9 Ma, the subsequent filling of the Caribbean with colder and more oxygen-rich watermass, would have facilitated increased oxidation of the available food resulting in reduced paleoproductivity (*I/E* ratio, BFAR and  $J_{\text{ST}}$ ), thereby also lowering Caribbean diversity (Fig. 3). This is also borne out by PCA analysis for this interval (Fig. 6c) where both diversity and paleoproductivity have a positive relationship and negative loadings for watermass ventilation, current velocity and oxygenation.

Therefore, increased oligotrophy (or decreased paleoproductivity) between 7.9–7.6 Ma is inferred in the Caribbean, as would be expected with increased restriction of watermass exchange with nutrient-rich Pacific waters and predicted by earlier studies also (Wright et al., 1991; Reynolds et al., 1999; Frank et al., 1999; Spezzaferrri et al., 2002; Billups, 2002; Bickert et al., 2004).

From 7.6–4.2 Ma, both diversity and paleoproductivity in the Caribbean and Pacific gradually increased to around the values seen at the beginning of the interval (Fig. 3). Pearson's product moment correlations between Caribbean diversity and paleoproductivity values for this duration are also statistically significant (Tables 7 and 10). This indicates that even during this interval of heightened paleoproductivity, paleoproductivity was

below the threshold that in a eutrophic setting would have resulted in stressed taxa and decreased diversity, but under oligotrophic conditions prevailing at this site promoted more niche partitioning and increased diversity (Jian et al., 2003; Hess and Kuhnt, 2005). This is further corroborated by increased values of diversity measures and paleoproductivity proxies between 7.6–6.7 Ma in the Caribbean (Fig. 3). This brief interval is also known as the Late Miocene Carbon Isotope Shift (Bickert et al., 2004), a global interval of decreased  $\delta^{13}\text{C}$  of ocean's dissolved inorganic carbon pool (Berger and Vincent, 1986; Bickert et al., 2004). Interestingly, diversity values during this critical interval steadily increased in the Caribbean as opposed to the Pacific site, which showed a corresponding decrease (Fig. 3). A higher resolution study is needed to underline the precise link between increased regional Caribbean diversity and enhanced global paleoproductivity.

From 7.2 to 4.2 Ma, the dominance of opportunistic benthic foraminiferal species such as *Epistominella exigua* resulted in decreased Equitability in the Caribbean. Correlation analysis between the relative abundance of *Epistominella exigua* and diversity indices in the Caribbean during the 7.6–4.2 Ma interval also show a positive and statistically significant relationship, suggesting that phytodetrital input enhanced the diversity signal (Table 11). Enhanced reproduction (increased metabolic

activity) and rapid colonization of the freshly deposited phytodetrital aggregates are known to facilitate increased benthic diversity (Gooday, 2003). Studies have also documented (Corliss and Silva, 1993; Gooday, 1996; Ohga and Kitazato, 1997) that taxa from areas receiving increased phytodetritus predominantly consist of opportunistic species that take advantage of the seasonal fluctuations of phytodetritus for their rapid growth and reproduction (Gooday, 1994, 1996; Gooday et al., 1998; Gooday, 2003). In such an environment of enhanced phytodetrital input, the faunal succession is largely a function of the carbon flux (Bernhard et al., 1997; Jannink et al., 1998). The PCA analysis for this interval (Fig. 6c) also indicates that diversity is strongly influenced by paleoproductivity.

The Post-closure interval (4.2–2.5 Ma) in the Caribbean is marked by an abrupt dip in diversity and Equitability that also coincides with the timing of establishment of the Atlantic–Pacific salinity contrast and the complete CAS closure (Keigwin, 1982; Haug et al., 2001; Fig. 3). Correspondingly, increased oligotrophy (peak abundance of *Nuttallides umbonifera*) and a rapid reduction in the seasonality of the phytodetrital input (*Epistominella exigua* fell to near 0%) has previously been predicted as a possible consequence of the CAS closure by Keigwin (1982). The presence of a nutrient-depleted environment

Table 11

Correlation (Pearson's product moment,  $r$ ) between the relative abundance of phytodetritus species *Epistominella exigua*, diversity and equitability in the Caribbean for the interval 7.9–4.2 Ma

		<i>E. exigua</i>	Fisher's $\alpha$	<i>E</i>	BFAR	<i>I/E</i> ratio	$J_{sf}$ (flux)	BFOI	Current velocity	Benthic $\delta^{13}\text{C}$	Depth
Phytodetritus	<i>E. exigua</i>	1									
Diversity	Fisher's $\alpha$	0.300**	1								
		0.049									
Equitability		-0.489**	-0.361	1							
		0.008	0.059								
Paleoproductivity	BFAR	0.514**	0.597**	-0.786**	1						
		0.005	0.001	0.0000							
	<i>I/E</i> ratio	0.656**	0.458*	-0.522**	0.656**	1					
		0.0000	0.014	0.004	0.0000						
	$J_{sf}$ (flux)	0.498**	0.574**	-0.810**	0.992**	0.644**	1				
		0.007	0.001	0.0000	0.0000	0.0000					
Oxygenation	BFOI	-0.177	-0.542**	0.197	-0.495**	-0.561**	-0.472*	1			
		0.369	0.003	0.315	0.007	0.002	0.011				
Current velocity		-0.518**	-0.600**	0.433*	-0.538**	-0.626**	-0.545**	0.496**	1		
		0.005	0.001	0.021	0.003	0.0000	0.003	0.007			
Ventilation	Benthic	-0.197	-0.398*	0.299	-0.220	-0.269	-0.256	0.235	0.319	1	
	$\delta^{13}\text{C}$	0.315	0.036	0.123	0.262	0.166	0.189	0.229	0.098		
Depth		-0.397*	-0.618**	0.294	-0.445*	-0.376*	-0.435*	0.484**	0.581**	0.500**	1
		0.036	0.0000	0.128	0.018	0.048	0.021	0.009	0.001	0.007	

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

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

$N=28$ .

(increased oligotrophy) is further corroborated by the divergent Atlantic–Pacific benthic  $\delta^{13}\text{C}$  trends beginning at 4.2 Ma, with the Caribbean becoming increasingly well ventilated (Haug and Tiedemann, 1998; Haug et al., 2001; Steph, 2005). This is also noted in PCA results where now oxygenation has a positive loading with diversity (Fig. 6d).

In summary, for the Post-closure interval (4.2–2.5 Ma), the present data indicate that the CAS closure at 4.2 Ma resulted in filling the Caribbean with nutrient-depleted and oxygen-rich waters (better ventilation and increased oxygenation). This fuelled increased oxidation of the available food for benthic foraminifers trickling down to the seafloor, leading to reduced paleoproductivity, which in turn, lowered benthic foraminiferal diversity (Fig. 3). This favored the dominance of few specialized species like *Nuttallides umbonifera* that were able to thrive in this changed environment, resulting in decreased Equitability during their dominance between 4.2–3.7 Ma (Fig. 3).

Thus, in an increasingly food-limited environment such as the Caribbean, subtle changes in food availability should greatly affect benthic foraminiferal diversity trends (Fig. 6). A brief summary of the events discussed so far are given in Fig. 7.

A present day analogue for describing the relationship of diversity and paleoproductivity noted in the Caribbean can be explained by combining the TROX model (trophic condition and oxygen concentration of Jorissen et al., 1995; Jorissen, 1999) and the parabolic curve of Levin et al. (2001), which explains the relationship of local species diversity and productivity (Gooday, 2003; Fig. 8). This composite model suggests that diversity is low in highly oligotrophic areas such as the Arctic Ocean (the left hand side of the parabolic curve) where food supply is very low and thus incapable of sustaining large number of species. Diversity is at a maximum in well-oxygenated bathyal and abyssal settings (central part of the parabolic curve) such as the Porcupine Abyssal Plain (Gooday, 1988; Gooday and Turley, 1990; Gooday, 2003). Diversity again reaches lower values in highly eutrophic areas (right side of the parabolic curve) such as the Arabian Sea Oxygen Minimum Zone (OMZ) or the Santa Barbara Basin (see Levin, 2003; Gooday, 2003), where stress caused by the abundance of species leads to reduced diversity. Thus, based on the present Caribbean data and the discussion above, the diversity trend through time extends from the mesotrophic to the oligotrophic regions of the TROX model and moves from the center

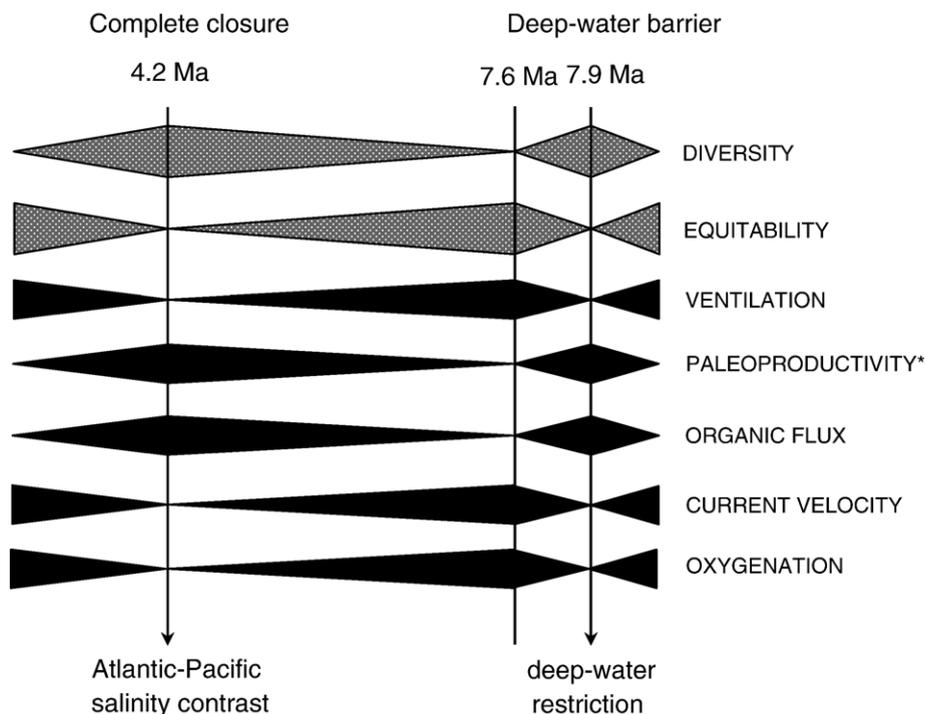


Fig. 7. Summary of major diversity and paleoproductivity changes observed in the Caribbean. Paleoproductivity\* = composite trends of flux of organic carbon to the seafloor ( $J_{st}$ ), BFAR and  $I/E$  ratio.

to the left hand side of the parabolic curve. The Pacific, on the other hand, moves from the mesotrophic to the eutrophic region and from the center to the right side of the curve (Fig. 8).

Finally, the present data are tested against SHEBI (SHE Biofacies Identification; Hayek and Buzas, 1997), whose boundaries are identified based on the departure from the linear trend of  $\ln E$  on a  $\ln N$  plot (Fig. 4; see Buzas and Hayek, 1998). The hypothesis is that major boundaries demarcated by SHEBI analysis should correspond to major intervals of significant change in

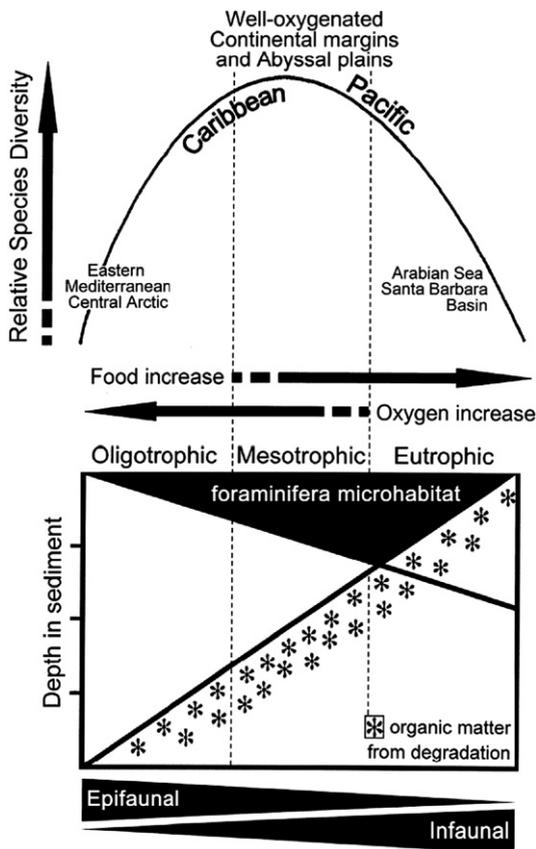


Fig. 8. Combination of the TROX model (trophic condition and oxygen concentration of Jorissen et al., 1995; Jorissen, 1999) and the parabolic curve of Levin et al. (2001) explaining the relationship of local species diversity and productivity (modified after Gooday, 2003). Diversity is low in highly oligotrophic areas such as the Arctic Ocean where food supply (flux of organic carbon to the seafloor=productivity) is very low and thus incapable of sustaining large number of species. Diversity is maximized in well-oxygenated bathyal and abyssal settings such as the Porcupine Abyssal Plain (Gooday et al., 1998). Diversity again reaches lower values in highly eutrophic areas such as the Arabian Sea Oxygen Minimum Zone (OMZ) or the Santa Barbara Basin (Gooday et al., 2000) where stress cause by the abundance of species leads to reduced diversity. The abundance of food and reduced predation facilitates increased diversities. However, when oxygen becomes limiting, diversities fall.

diversity and paleoproductivity proxies (Fig. 5). SHEBI analysis for both datasets reveal three similar boundaries, one at 7.92 Ma (corresponding to the predicted restricted flow of nutrient-rich Pacific deep waters into the Caribbean) and another between 2.96–2.98 Ma, which also corresponds with another major change in benthic foraminiferal assemblages recognized by earlier workers (Bornmalm, 1997; Bornmalm et al., 1999). The third boundary at 6.69 Ma, does not correspond to any known local or regional events (paleoceanographic or tectonic). However, beginning at 6.69 Ma, diversity and Equitability at both the sites show divergent trends, with increased Pacific values (Fig. 3) suggesting increased restriction of watermass across the seaway that appears to have influenced diversity measures more than paleoproductivity proxies. Lastly, the 2.77 Ma SHEBI boundary noted in the Caribbean, but not in the Pacific, also corresponds with a major change in the nannofossil abundance patterns reflecting the final closure of the Central American Seaway (Kameo, 2002).

## 6. Conclusions

Late Miocene to early Pliocene constriction and complete closure of the Central American Seaway led benthic foraminiferal diversity in the Caribbean to decrease abruptly at 7.9 Ma coincident with deep-water restriction. Thereafter, it increased slowly until seaway closure at 4.2 Ma, and dipped abruptly until 3.5 Ma, followed by values similar to the beginning of the Post-closure interval. Paleoproductivity in the Caribbean never reached a eutrophic threshold above which we would predict opposite trends of high paleoproductivity and low diversity. This is true even during the heightened interval of enhanced paleoproductivity in the Caribbean (7.6–6.7 Ma, the Late Miocene Carbon Isotope Shift), during which Caribbean diversity increased and Pacific diversity decreased.

Major intervals of significant shifts in Caribbean diversity and paleoproductivity are also confirmed with SHEBI analysis, displaying divergent trends between Pacific and Caribbean sites since 7.9 Ma, with the Caribbean displaying decreasing values. The second common SHEBI boundary, between 2.96–2.98 Ma, also corresponds to a major change in the Caribbean benthic foraminiferal assemblage. However, the 6.69 Ma boundary does not correspond to any known local or regional events (paleoceanographic or tectonic) at both the sites but marks another divergent trend in diversity measures. Generally, most SHEBI boundaries correspond closely to shifts noted in either diversity measures or paleoproductivity proxies at either of the sites. But, as compared to the Pacific, those at the Caribbean site correspond

more closely to known paleoceanographic and faunal events or with changes in diversity measures and paleo-productivity proxies recorded here. In summary, in the Caribbean, decreased paleoproductivity due to the gradual constriction and complete closure of the Central American Seaway (CAS) led to decreased deep-sea benthic foraminiferal diversity while benthic foraminiferal diversity and paleoproductivity maintained a positive relationship.

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