

Late Quaternary benthonic foraminifera in a bathyal core from the Leeward Islands, Lesser Antilles, NE Caribbean Sea

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ABSTRACT – The 3.13 m long bathyal piston core En20-2 from the northern Leeward Islands (17°49.9'N, 63°02.4'W, water depth 680 m) was sampled every 20 cm. The Pleistocene–Holocene boundary occurred at 107 cm, and the base of the core lay above the Atlantic extinction of *Pulleniatina obliquiloculata* (34 ka BP). The core yielded throughout both (a) a deep-water association (DWA) of middle bathyal benthonic foraminifera and (b) a shallow-water association (SWA; up to 56% of total recovery) comprising back-reef, epiphytal species. The environmental trends suggested by the two groups are compared.

Although sea-levels during the Late Pleistocene and Early Holocene rose abruptly, there was no abrupt change in the DWA at the Pleistocene–Holocene boundary, but a gradual change from a higher-productivity fauna (*Bulimina* spp., *Uvigerina* spp.) at the base of the core to a lower-productivity fauna (*Cassidulina* spp., *Globocassidulina* spp.) at the top. Microhabitat preference changed from shallow-infaunal at the core base to primarily epifaunal at the top. Diversity and species dominance did not differ significantly between the Late Pleistocene and the Holocene.

Percentage abundances of species were calculated separately for the DWA and SWA. Seventy significant correlations were found between the percentage abundances of individual DWA and SWA species, the two strongest correlations – both positive – being between (a) *Neonorbina terquemi* and *Uvigerina laevis*, and (b) *Amphistegina gibbosa* and *Cassidulina curvata*. The percentage abundance of *U. laevis* decreased up-section, whereas the percentage abundance of *A. gibbosa* increased up-section, reflecting a change in the nutrient flux over time that impacted on both the DWA and the SWA. Positive correlations between the DWA low-productivity indicator *Globocassidulina subglobosa* and the SWA species *Asterigerina carinata*, *Elphidium discoidale*, *Peneroplis bradyi* and *P. proteus* suggests that these four SWA species comprise a guild. *J. Micropalaeontol.* 27(2): 177–188, November 2008.

KEYWORDS: *Uvigerina laevis*, *Amphistegina gibbosa*, Pleistocene, Holocene, deglaciation

INTRODUCTION

The Late Quaternary foraminiferal palaeoecology of the Leeward Islands (NE Caribbean Sea, Fig. 1) is little known. In comparison, the Recent Caribbean benthonic foraminifera have been the subject of over 136 papers, and about 1200 species have been recorded in the region, although most studies of these have been restricted to shallow-water, circum-island environments (Culver & Buzas, 1982).

Regarding Recent, deeper-water foraminifera, Norton (1930) examined a sample from Albatross Station 2715, west of Nevis (lat. 16°54'N, long. 63°12'W, depth approx. 1400 m) from which he recorded 83 species of benthonic foraminifera (Norton, 1930, table 1) and in which he found abundant *Rhabdammina discreta* Brady (see also Cushman, 1918–31). Hofker (1980) examined recent material in samples from 5–850 m depth from Saba Bank (lat. 17°12'N, long. 63°12'W) and listed a distinct group of species found between 100 m and 850 m. He did not record species' abundances, but noted that the deeper-water samples yielded approx. 2% displaced, shallow-water foraminifera. Elsewhere Hofker (1956, 1979) described the upper bathyal foraminifera near St Croix (lat. 17°5'N, long. 64°0'W, about 100 km west of the Leeward Islands) but, once again, did not give relative abundances. This and other bathyal material was discussed further in Hofker (1976). Further south, Galluzzo *et al.* (1990) examined the Holocene fauna between 1016 m and 3130 m in the Grenada Basin, which lies between the Windward

Islands and the Aves Ridge (i.e. southwest of Guadeloupe, between 12–15.5°N and 61–63°W). They suggested spreading of Sub-Antarctic Intermediate Water (SAIW) and Caribbean Bottom Water (CBW) to control the distribution of Holocene benthonic foraminifera in the Grenada Basin, and that a low-oxygen assemblage dominated by *Bulimina aculeata*, *B. alazanensis*, *Osangularia culter*, *Uvigerina auberiana* and *U. peregrina* is developed in the SAIW between 1000 m and 2100 m.

Regarding Late Pleistocene assemblages of the Leeward Islands and adjacent areas, coverage is similarly thin. Phleger *et al.* (1953) listed the percentage abundance of benthonic foraminifera in Piston Core 267 which, taken east of Puerto Rico (lat. 17°47'N, long. 65°14'W; water depth 2105 m) penetrated *Globigerina* ooze. However, finding that it yielded throughout its whole 11.8 m length not only autochthonous, deep-water foraminifera, but also allochthonous, shallow-water specimens, Phleger *et al.* (1953) declined to discuss its palaeoecology. Sen Gupta *et al.* (1982) examined the benthonic foraminifera of the past 127 ka in three bathyal cores (depths near 2000 m) from the western Grenada Basin, west of the Windward Island of the Lesser Antilles. They suggested that the benthonic fauna changed only subtly at planktonic biostratigraphical zonal boundaries, even though the latter, being based on fluctuations in populations of *Globorotalia menardii*, reflect fluctuations in palaeoclimate.

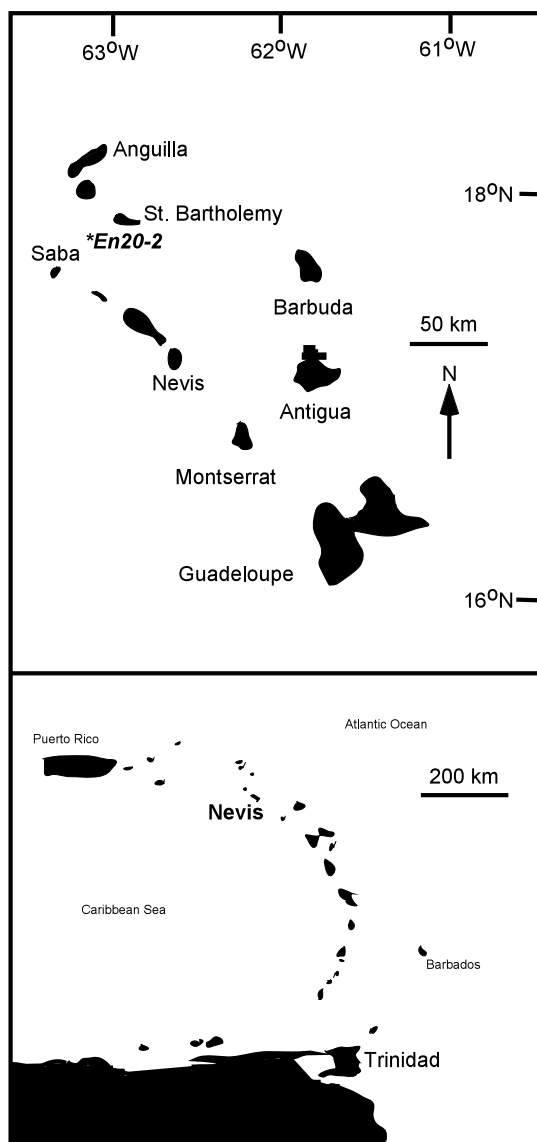


Fig. 1. Map of the Leeward Islands, NE Caribbean Sea, showing the location of Core En20-2. The older island arc (eastern Guadeloupe through Anguilla) lies to the east.

This paper addresses this shortage of published knowledge by examining the benthonic foraminiferal assemblages from the 3.13 m long Core En20-2 from the middle bathyal of the volcanic arc platform about 30 km NE of Saba (lat. $17^{\circ} 49.9' \text{N}$, long. $63^{\circ} 02.4' \text{W}$; water depth 680 m; Fig. 1). This is one of a series of piston cores recovered for sedimentological analysis throughout the Lesser Antilles island arc in the mid-1980s (Reid *et al.*, 1996). This core yielded both a middle bathyal, deep-water association (DWA) and a shallow-water association (SWA) throughout its length.

MATERIAL AND METHODS

The northern Lesser Antilles comprise two island arcs: an eastern, Oligocene arc now much eroded and capped by limestone, and a western, Pliocene and younger volcanic arc (Martin-Kaye, 1969). Core En20-2 was collected midway

between the two. Despite its proximity to the volcanic arc, Core En20-2 comprises primarily (a) yellow-grey, deep-water carbonate, (b) allochthonous shallow-water carbonate and (c) windblown quartz dust derived from the Sahara Desert. Within the core the Late Pleistocene–Holocene (Y–Z, 12 ka BP) boundary, drawn using a shift in the abundance of *Globorotalia menardii*, occurs at 107 cm (Reid *et al.*, 1996, table A2). The base of the core lies above the mid-Wisconsin (about 35 ka BP) disappearance of *Pulleniatina obliquiloculata*. Sedimentation rates were about 9 cm ka^{-1} during the Holocene, and $>9 \text{ cm ka}^{-1}$ during the Late Wisconsin.

Reid *et al.* (1996, fig. 2) found olive-grey, calcareous turbidites at 120–130 cm and 190–199 cm within the core, both marked by decreases in the amount of material $<63 \mu\text{m}$. These were derived from the direction of the limestone Caribbean arc. Although the volcanic islands of St Kitts, Saba and St Eustatius are nearer Core En20-2, Reid *et al.* (1996) did not find any volcanic turbidites in the core, confirming that sediment transport was predominantly from the east.

Samples 1 cm thick were taken every 20 cm (i.e. approximately every 2 ka). Most came from *in situ* *Globigerina* ooze, but sample 120–121 cm came from the younger turbidite. The material was washed over a $63 \mu\text{m}$ sieve, air dried, and dry sieved over a $125 \mu\text{m}$ mesh. More than 300 benthonic foraminifera were picked from the $>125 \mu\text{m}$ fraction. The author is aware that removal of the 63 – $125 \mu\text{m}$ fraction can result in the exclusion of environmentally sensitive species (Schröder *et al.*, 1987). As suggested by Sen Gupta *et al.* (1987), the 63 – $125 \mu\text{m}$ fraction was surveyed for species that would otherwise go unrecorded. The few species limited to this fraction comprised mostly *Brizalina lowmani* and *B. simplex*, which were not abundant.

The specimens $>125 \mu\text{m}$ were sorted into species and allocated to either the DWA or the SWA on the basis of known environmental preferences. DWA species were identified using publications by Cushman (1918, 1920, 1922b, 1923, 1924, 1929, 1930, 1931), Cushman & Parker (1931), Phleger & Parker (1951), Phleger *et al.* (1953), Parker (1954), Schnitker (1971), Sen Gupta & Schafer (1973) and Hofker (1956, 1976, 1980). SWA species primarily comprised epiphytal species that live in back-reef areas, and were documented in water shallower than 10 m by Cushman (1921, 1922a, 1929), Buzas *et al.* (1977), Wilson (2006a, b) and Wilson & Ramscook (2007). The reader is referred to these papers for species' biographical details. Although Hofker (1980, p. 23) suggested *Angulogerina occidentalis* lives between 100 m and 1000 m, here it is included in the SWA; Buzas *et al.* (1977) recorded it from the back-reef in Discovery Bay, Jamaica and Phleger *et al.* (1953) recorded it as *Angulogerina selseyensis* in shallow water along the north coast of Cuba. Phleger *et al.* (1953) found it in Core 267, off St Croix, but stated that these specimens had been displaced from shallow water.

For each sample the percentage of the total benthonic foraminiferal assemblage comprising the DWA and SWA was calculated. The diversity of the DWA was quantified using species richness S and the information function H' , where

$$H' = -\sum p_i \ln(p_i) \quad (1)$$

and p_i is the proportional abundance of the i th species. Dominance was quantified using the equitability index E , where

$$E = e^{H'/S} \quad (2)$$

The measure E is always <1 , maximum values occurring when species are equally abundant. For further details of these measures, see Hayek & Buzas (1997) and Magurran (2004). Statistical measures were compared using Pearson's product moment correlation coefficient and Student's t -test, both with a 95% significance level.

The 16 samples from Core En20-2 were considered too few for meaningful cluster analysis. Changes in abundance biozones were instead investigated using SHE Analysis for Biozone Identification (SHEBI; see Buzas & Hayek, 1998; Osterman *et al.*, 2002), in which values of E are calculated cumulatively and plotted as $\ln(E)$. Any major break in slope of the graph of $\ln(E)$ is considered to mark a biofacies boundary. Previous workers have plotted $\ln(E)$ against $\ln(n)$, the cumulative number of specimens. However, as this can produce a cluttered graph, $\ln(E)$ was plotted against sample depth instead.

RESULTS

The middle bathyal deep-water association (DWA, Table 1) comprised between 43.5% (sample 240–241 cm) and 88.0% (sample 120–121 cm, turbidite) of the benthonic foraminiferal recovery from each sample (mean 59%). The remaining foraminifera comprised a displaced, shallow-water association indicative of a back-reef, inner neritic environment. The high recovery of the DWA from sample 120–121 cm is presumed to be due to entrainment of deep-water specimens by the turbidite as it flowed over the seafloor. Linear regression did not reveal any significant trend in the percentage of the total fauna as deep-water benthonic foraminifera, and Student's t -test did not find any significant difference between the mean percentage recovery of the DWA from the Holocene (mean=61.9%) and the Late Pleistocene, no matter whether the turbidite sample 120–121 cm was included or excluded (mean=57.4% and 54.0%, respectively).

The DWA comprised 141 species or species groups. Per-sample species richness ranged between $S=37$ (60–61 cm) and 62 (120–121 cm, turbidite). However, mean S did not differ significantly between the Holocene (mean $S=46$) and the Late Pleistocene, no matter whether the sample from the turbidite was included or excluded (mean=52 and 50.9, respectively).

Only 20 species each comprised $>5\%$ of the DWA recovery from any one sample (Table 1). These 20 form the basis of this report. They were not distributed uniformly throughout the core. The percentage abundance of *Bulimina striata mexicana*, *Ehrenbergina undulata* and *Uvigerina laevis* decreased upwards through the core (Fig. 2). *Ehrenbergina undulata*, which formed up to 9.3% of the DWA during the Late Pleistocene, is virtually absent from the Holocene section (i.e. above 107 cm). In contrast, *Cassidulina laevigata*, rare during the Late Pleistocene, became more abundant during the Holocene (Fig. 3).

Values of the information function for the DWA ranged between $H'=3.08$ (sample 0–1 cm) and 3.62 (200–201 cm), with a mean of 3.35. Because H' and n , the number of specimens per sample, were significantly correlated ($r=0.519$, $p<0.05$), trends in H' are not discussed further.

The equitability index ranged between $E=0.508$ (0–1 cm) and 0.645 (60–61 cm), with a mean of 0.579. This measure was not significantly correlated with either n ($r=-0.02$, $p=0.94$) or H' ($r=0.424$, $p=0.10$). The mean E of 0.568 during the Holocene did not differ significantly from that during the Late Pleistocene, no matter whether the turbidite sample 120–121 cm was included or excluded (mean=0.586 and 0.591, respectively).

SHE Analysis indicates that there is no change in DWA abundance biozone coincident with the Late Pleistocene/Holocene boundary (Fig. 4). That the value of $\ln(E)$ was constant between 121 cm and 141 cm may be due to elevated numbers of DWA specimens and species in the turbidite at 120–121 cm, and so is concluded not to be coincident with a change in abundance biozone. Thus, when SHE Analysis of abundance biozones is conducted from the top of the core downwards, the only change in abundance biozone indicated lies between 261 cm and 281 cm.

DISCUSSION

It is not possible to make direct sample-by-sample comparisons between the 3.13 m long Core En20-2 and the 11.80 m long Core 267, collected east of Puerto Rico by Phleger *et al.* (1953). The occurrence of *Pulleniatina obliquiloculata* at 40 cm depth within Core 267 indicates that the latest Pleistocene and Holocene was much thinner here than in En20-2. In addition, the DWA benthonic fauna throughout Core 267 was quite different, being dominated by *Nummuloculina irregularis* ($\leq 21\%$), *Uvigerina auberiana* and variants ($\leq 21\%$, possibly including *U. laevis*) and *Robertina bradyi* ($\leq 22\%$).

It is unlikely that the two calcareous turbidites in En20-2 had any lasting ecological effect on the DWA; Hess *et al.* (2005) found that climax communities are re-established as quickly as nine months after the deposition of a turbidite.

Environmental implications of the deep-water assemblage (DWA)

The sea transgressed rapidly in the NE Caribbean during the Late Pleistocene and Early Holocene, stressing the shoal-water coral reefs in three metre-scale, rapid rises in sea-level (Blanchon & Shaw, 1995). This left the Lesser Antillean islands surrounded by broad wave-cut shelves (Le Friant *et al.*, 2004) and eroded alluvial fans that had developed around the volcanic islands during the Late Pleistocene, producing up to 15 m high cliffs (Wilson, 2005). However, there were no abrupt changes in Core En20-2 in the middle bathyal DWA coincident with the Pleistocene–Holocene boundary. Instead, as was the case along the western margin of the Grenada Basin (Sen Gupta *et al.*, 1982), the changes were gradual. This indicates that, although sea-level rose on the order of 120 m (Blanchon & Shaw, 1995, fig. 3), the factor(s) responsible for the change in foraminiferal associations was (were) neither depth nor some other variable directly correlated with it.

It is, instead, likely that at least one factor forcing the gradual change was itself related to a change in surface productivity and the associated nutrient flux to the seafloor. The En20-2 DWA contains a mixture of species indicative of high and low surface-productivity areas (cf. Loubere & Faraduddin, 2002, fig. 11.5), the changing proportions of which indicate that surface productivity at the sample site was not constant throughout the Late

| Species | Depth (cm) | | | | | | | | | | | | | | | |
|-----------------------------------|------------|-------|-------|-------|-------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | 0-2 | 20-21 | 40-41 | 60-61 | 80-81 | 100-101 | 120-121 | 140-141 | 160-161 | 180-181 | 200-201 | 220-221 | 240-241 | 260-261 | 280-281 | 300-301 |
| <i>Amphicoryna hirsuta</i> | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 0 |
| <i>Amphicoryna sublineata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 |
| <i>Anomalinoidea alazanensis</i> | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Anomalinoidea nucleatus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Anomalinoidea robustus</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Anomalinoidea semipunctata</i> | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>Astacolus cf. crepidulus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Astacolus crepidulus</i> | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Bifarina advena</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 5 | 3 | 0 | 1 | 1 | 0 | 3 |
| <i>Bolivina floridana</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bolivina subspinescens</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Brizalina catanensis</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Brizalina fragilis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Brizalina goesii</i> | 1 | 1 | 0 | 2 | 1 | 2 | 3 | 4 | 4 | 5 | 4 | 2 | 2 | 0 | 0 | 1 |
| <i>Brizalina sp. indet.</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Brizalina spinata</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Brizalina striata</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Brizalina translucens</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bulimina aculeata*</i> | 0 | 8 | 0 | 0 | 3 | 1 | 2 | 10 | 25 | 10 | 16 | 0 | 6 | 0 | 0 | 5 |
| <i>Bulimina alazanensis</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bulimina marginata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 7 | 3 | 4 | 7 | 0 | 2 | 1 |
| <i>Bulimina striata mexicana*</i> | 1 | 2 | 3 | 6 | 16 | 14 | 8 | 21 | 28 | 40 | 24 | 7 | 13 | 13 | 17 | 20 |
| <i>Buliminella milletii</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cassidulina carinata*</i> | 10 | 1 | 1 | 0 | 5 | 7 | 17 | 0 | 0 | 9 | 11 | 3 | 5 | 1 | 5 | 4 |
| <i>Cassidulina curvata*</i> | 30 | 10 | 20 | 16 | 0 | 0 | 1 | 0 | 3 | 30 | 0 | 1 | 0 | 1 | 9 | 0 |
| <i>Cassidulina laevigata*</i> | 1 | 4 | 14 | 7 | 17 | 11 | 10 | 28 | 29 | 22 | 13 | 17 | 17 | 27 | 24 | 7 |
| <i>Cibicides bradyi*</i> | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cibicides cicatricosus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Cibicides floridanus</i> | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cibicides kullenbergi*</i> | 0 | 0 | 7 | 5 | 8 | 5 | 12 | 0 | 1 | 9 | 1 | 0 | 3 | 5 | 3 | 0 |
| <i>Cibicides robertsonianus*</i> | 3 | 9 | 7 | 0 | 4 | 3 | 0 | 1 | 0 | 3 | 7 | 1 | 1 | 1 | 0 | 1 |
| <i>Cibicides sp. 1</i> | 7 | 4 | 7 | 0 | 0 | 0 | 7 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 8 | 0 |
| <i>Cibicides sp. indet.</i> | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 0 |
| <i>Cibicides umbonatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Clavulina novangliae</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cornuloculina inconstans</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 6 | 10 | 5 | 3 | 3 | 3 | 4 |
| <i>Cylindroclavulina bradyi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |

Table 1. Continued.

| Species | Depth (cm) | | | | | | | | | | | | | | | |
|--|------------|-------|-------|-------|-------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | 0-2 | 20-21 | 40-41 | 60-61 | 80-81 | 100-101 | 120-121 | 140-141 | 160-161 | 180-181 | 200-201 | 220-221 | 240-241 | 260-261 | 280-281 | 300-301 |
| <i>Dentalina communis</i> | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Dentalina consobrina emaciata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dentalina</i> sp. indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Dentalina subsoluta</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| <i>Dorothia scabra</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| <i>Eggerella bradyi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 0 |
| <i>Ehrenbergina spinea</i> | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 |
| <i>Ehrenbergina undulata</i> * | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 14 | 11 | 10 | 19 | 5 | 14 | 8 | 4 | 16 |
| <i>Entosolenia flintiana plicatura</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eponides</i> (?) sp.indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Fissurina laevigata</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Fissurina orbignyana antillea</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 |
| <i>Fissurina</i> sp. indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 2 | 3 | 6 | 8 | 3 | 1 |
| <i>Flintina lingulata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Fursenkoina compressa</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| <i>Gaudryina</i> (<i>Pseudogaudryina</i>) <i>atlantica</i> | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Gavelinopsis translucens</i> * | 1 | 4 | 8 | 6 | 3 | 0 | 0 | 1 | 26 | 22 | 15 | 6 | 10 | 13 | 9 | 1 |
| <i>Globocassidulina crassa</i> * | 3 | 0 | 2 | 10 | 23 | 4 | 17 | 3 | 13 | 0 | 2 | 2 | 5 | 4 | 3 | 7 |
| <i>Globocassidulina</i> s. <i>subcalifornica</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 4 | 3 | 0 | 0 | 2 |
| <i>Globocassidulina subglobosa</i> * | 11 | 32 | 6 | 14 | 3 | 5 | 2 | 3 | 34 | 39 | 11 | 8 | 4 | 14 | 18 | 6 |
| <i>Glomospira gordialis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gordiospira fragilis</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gyroidinoides altiformis</i> | 1 | 1 | 0 | 0 | 4 | 0 | 7 | 8 | 0 | 6 | 2 | 0 | 0 | 1 | 4 | 1 |
| <i>Gyroidinoides cf. neosoldanii</i> | 0 | 1 | 0 | 1 | 2 | 3 | 0 | 0 | 5 | 0 | 1 | 4 | 1 | 3 | 9 | 1 |
| <i>Gyroidinoides lamarkiana</i> | 0 | 2 | 5 | 0 | 3 | 3 | 1 | 3 | 1 | 0 | 6 | 0 | 3 | 1 | 0 | 0 |
| <i>Gyroidinoides neosoldanii</i> | 0 | 2 | 3 | 6 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Hanzawaia concentrica</i> | 1 | 5 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 4 | 2 | 4 | 1 | 0 | 2 | 2 |
| <i>Hoeglundina elegans</i> * | 17 | 14 | 18 | 0 | 2 | 1 | 12 | 4 | 14 | 24 | 8 | 3 | 3 | 2 | 4 | 2 |
| <i>Lagena costata</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lagena crenata capistrata</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Lagena hexagona</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Lagena hispidula</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lagena lagenoides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Lagena</i> sp. A | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lagena</i> sp. B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lagena</i> sp. indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lamarckina atlantica</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

Table 1. Continued.

| Species | Depth (cm) | | | | | | | | | | | | | | | |
|---|------------|-------|-------|-------|-------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | 0-2 | 20-21 | 40-41 | 60-61 | 80-81 | 100-101 | 120-121 | 140-141 | 160-161 | 180-181 | 200-201 | 220-221 | 240-241 | 260-261 | 280-281 | 300-301 |
| <i>Laticarinina pauperata</i> | 0 | 2 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 4 | 1 |
| <i>Lenticulina calcar</i> | 3 | 3 | 1 | 4 | 1 | 5 | 12 | 3 | 2 | 4 | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Lenticulina gibba</i> | 0 | 1 | 3 | 1 | 3 | 3 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| <i>Lenticulina iota</i> | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 |
| <i>Lenticulina melvilli</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lenticulina orbicularis</i> | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lenticulina peregrina</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lenticulina rotulata</i> | 4 | 0 | 1 | 1 | 6 | 7 | 3 | 1 | 0 | 7 | 2 | 3 | 1 | 2 | 2 | 0 |
| <i>Lenticulina</i> sp. A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Marginulina</i> cf. <i>perprocera</i> | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 |
| <i>Martinottiella communis</i> | 1 | 0 | 0 | 6 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 5 | 0 |
| <i>Melonis baarleanus</i> | 7 | 1 | 2 | 0 | 0 | 0 | 5 | 11 | 16 | 14 | 0 | 3 | 2 | 2 | 6 | 4 |
| <i>Nodosaria pyrula</i> | 0 | 0 | 2 | 0 | 4 | 3 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| <i>Nodosaria</i> sp. indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Nonion formosum</i> | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 3 | 7 | 2 | 0 | 1 | 2 | 3 | 0 |
| <i>Nummuloculina irregularis</i> | 1 | 2 | 6 | 3 | 5 | 3 | 8 | 4 | 6 | 6 | 3 | 3 | 1 | 3 | 1 | 1 |
| <i>Oridorsalis umbonatus</i> | 2 | 1 | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 7 | 0 | 0 | 2 | 5 | 1 |
| <i>Osangularia rugosa</i> * | 17 | 3 | 15 | 10 | 11 | 4 | 1 | 1 | 38 | 11 | 5 | 2 | 7 | 11 | 6 | 7 |
| <i>Percutazonaria subculeata glabrata</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Plancostoma luculentum</i> | 0 | 0 | 3 | 0 | 3 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Planulina ariminensis</i> * | 7 | 7 | 7 | 14 | 20 | 21 | 22 | 14 | 15 | 38 | 8 | 12 | 8 | 7 | 10 | 9 |
| <i>Planulina foveolata</i> | 0 | 1 | 3 | 0 | 0 | 2 | 3 | 1 | 10 | 17 | 9 | 4 | 1 | 1 | 0 | 4 |
| <i>Prolixoplecta exilis</i> | 0 | 0 | 1 | 2 | 1 | 7 | 1 | 2 | 2 | 0 | 5 | 1 | 1 | 5 | 7 | 2 |
| <i>Pseudoclavulina mexicana</i> | 1 | 0 | 0 | 0 | 3 | 2 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pseudoglandulina comatula</i> | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Pullenia bulloides</i> | 1 | 0 | 3 | 0 | 1 | 1 | 2 | 13 | 12 | 13 | 2 | 2 | 0 | 1 | 5 | 2 |
| <i>Pullenia quinqueloba</i> | 1 | 0 | 2 | 0 | 3 | 0 | 2 | 1 | 3 | 0 | 1 | 2 | 0 | 2 | 0 | 0 |
| <i>Pullenia subcarinata</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pycnamidulina albatrossi</i> | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pyrgo comata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pyrgo murrhina</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pyrgo phlegeri</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pyrgo subphaerica</i> | 0 | 0 | 1 | 2 | 4 | 0 | 6 | 6 | 0 | 4 | 0 | 1 | 0 | 0 | 4 | 0 |
| <i>Quinqueloculina cruziana</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Ramulina globulifera</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Rectobolivina dimorpha</i> | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 4 | 0 |
| <i>Reussella miocenica</i> | 1 | 4 | 1 | 0 | 1 | 1 | 0 | 3 | 3 | 0 | 0 | 1 | 0 | 4 | 1 | 0 |

Table 1. Continued.

| Species | Depth (cm) | | | | | | | | | | | | | | | | | | |
|---|------------|-------|-------|-------|-------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--|--|--|
| | 0-2 | 20-21 | 40-41 | 60-61 | 80-81 | 100-101 | 120-121 | 140-141 | 160-161 | 180-181 | 200-201 | 220-221 | 240-241 | 260-261 | 280-281 | 300-301 | | | |
| <i>Robertinoides bradyi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | | | |
| <i>Saracenaria italica</i> | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | | | |
| <i>Sigmoilina sigmoidea</i> | 1 | 0 | 2 | 3 | 0 | 0 | 9 | 1 | 0 | 5 | 1 | 1 | 0 | 0 | 6 | 0 | | | |
| <i>Sigmoilinita tenuis</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Sigmoilopsis schlumbergeri</i> | 1 | 1 | 0 | 0 | 0 | 2 | 14 | 4 | 0 | 3 | 1 | 2 | 1 | 3 | 8 | 2 | | | |
| <i>Siphonina bradyana*</i> | 14 | 11 | 8 | 23 | 32 | 42 | 48 | 31 | 23 | 38 | 17 | 6 | 6 | 26 | 39 | 9 | | | |
| <i>Siphotextularia concava</i> | 0 | 0 | 1 | 3 | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | | | |
| <i>Sphaeroidina bulloides</i> | 1 | 0 | 1 | 0 | 1 | 4 | 0 | 1 | 1 | 4 | 2 | 3 | 0 | 2 | 2 | 0 | | | |
| <i>Spirillina inaequalis</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Spirillina</i> sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Spiroplectammina floridana</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Stomatorbina concentrica</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | | | |
| <i>Textularia agglutinans</i> | 0 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Textularia albatrossi</i> | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Textularia lateralis*</i> | 0 | 0 | 0 | 4 | 5 | 12 | 17 | 14 | 14 | 12 | 0 | 14 | 4 | 2 | 5 | 1 | | | |
| <i>Textularia mayori</i> | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Textularia pseudotrochus</i> | 2 | 0 | 1 | 4 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Textularia</i> sp. A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Textularia</i> sp. aff. <i>T. conica</i> | 0 | 0 | 0 | 2 | 2 | 4 | 2 | 9 | 9 | 6 | 7 | 2 | 1 | 0 | 0 | 2 | | | |
| <i>Textularia</i> sp. indet. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | | | |
| <i>Trifarina bradyi*</i> | 2 | 2 | 7 | 6 | 7 | 28 | 26 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | | |
| <i>Uvigerina auberiana</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | | |
| <i>Uvigerina</i> ex. gr. <i>peregrina*</i> | 5 | 4 | 18 | 0 | 0 | 3 | 7 | 3 | 7 | 9 | 7 | 0 | 4 | 1 | 0 | 0 | | | |
| <i>Uvigerina flintii</i> | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Uvigerina hispidocostata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Uvigerina laevis*</i> | 0 | 1 | 0 | 2 | 4 | 8 | 4 | 10 | 16 | 16 | 20 | 23 | 19 | 18 | 9 | 30 | | | |
| <i>Valvulineria</i> cf. <i>humilis</i> | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | | | |
| <i>Valvulineria mexicana</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 0 | | | |
| <i>Valvulineria nuttalli</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| <i>Valvulina pennatula</i> | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | | | |
| <i>n</i> | 173 | 159 | 213 | 175 | 236 | 261 | 356 | 265 | 459 | 516 | 270 | 194 | 179 | 229 | 277 | 172 | | | |
| <i>S</i> | 43 | 42 | 48 | 37 | 51 | 55 | 62 | 49 | 51 | 58 | 47 | 59 | 48 | 53 | 50 | 43 | | | |
| <i>H</i> | 3.084 | 3.157 | 3.379 | 3.173 | 3.324 | 3.394 | 3.514 | 3.309 | 3.34 | 3.552 | 3.404 | 3.623 | 3.369 | 3.378 | 3.452 | 3.147 | | | |
| <i>E</i> | 0.508 | 0.559 | 0.611 | 0.645 | 0.544 | 0.541 | 0.542 | 0.558 | 0.553 | 0.601 | 0.64 | 0.635 | 0.605 | 0.553 | 0.631 | 0.541 | | | |
| DWA as percentage of total recovery | 56 | 50.6 | 70.3 | 58.3 | 67.9 | 68.5 | 88 | 63.8 | 49.5 | 64.6 | 54.4 | 50.5 | 43.5 | 55.3 | 60.1 | 44.6 | | | |

Species forming >5% of the deep water association in any one sample are indicated with an asterisk. *n*, number of specimens per sample; *S*, species richness; *H*, information function; *E*, equitability index; DWA, deep-water association.

Table 1. Middle bathyal benthonic foraminifera in Core En20-2.

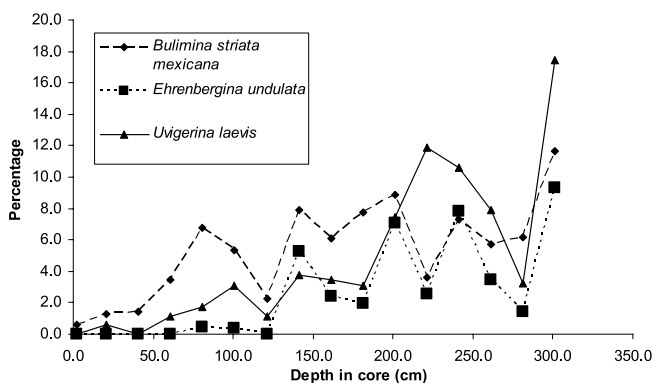


Fig. 2. Percentage abundances of *Bulimina striata mexicana*, *Ehrenbergina undulata* and *Uvigerina laevis*, showing decreasing abundance through Core En20-2.

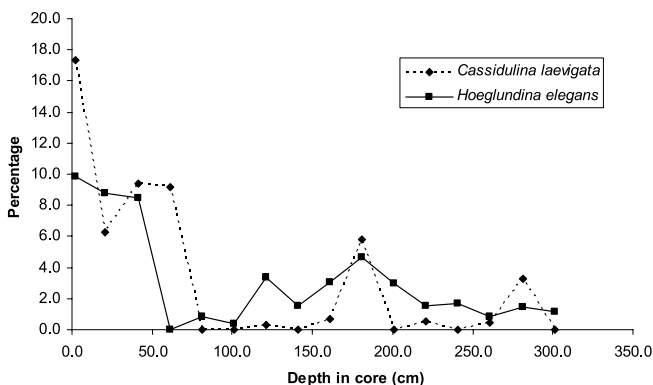


Fig. 3. Percentage abundances of *Cassidulina laevigata* and *Hoeglundina elegans* in Core En20-2, indicating increasing abundance in the Holocene (above 107 cm).

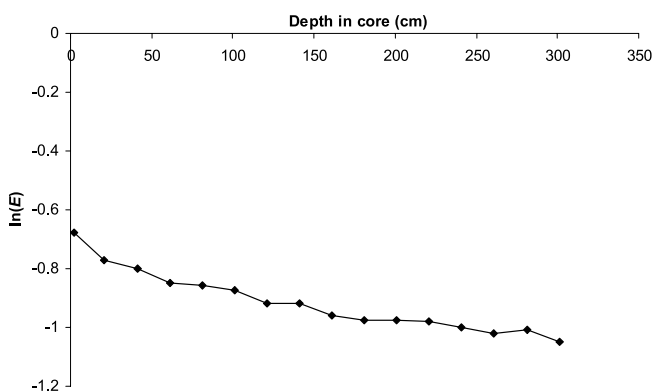


Fig. 4. Cumulative values of $\ln(E)$ in Core En20-2, showing lack of biofacies change coincident with the Late Pleistocene/Holocene boundary at 107 cm.

Quaternary. The percentage of the DWA's 20 most abundant species that comprise high productivity indicators (*Bulimina aculeata*, *B. striata mexicana*, *Uvigerina* ex gr. *peregrina* and *U. laevis* – see Loubere & Faraduddin, 2002) decreased from 32% of the recovery at the core base to 3.5% at the top (Fig. 5). However, this hypothesis needs further testing. In general, dominance tends to increase with increasing organic loading (Gooday, 2003; Smart & Gooday, 2006), but in En20-2 the

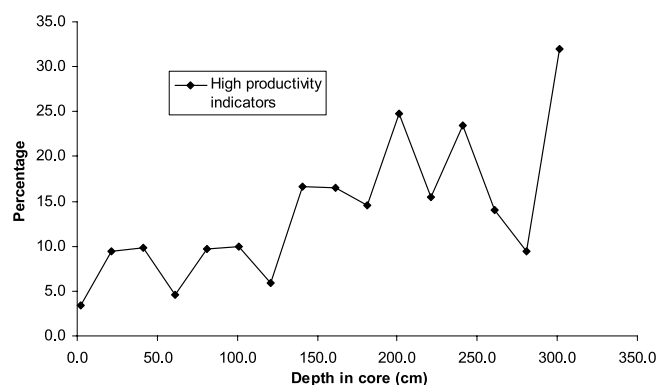


Fig. 5. Percentage of the deep-water association in Core En20-2 comprising species adapted to an input from high surface productivity (*Bulimina aculeata*, *B. striata mexicana*, *Uvigerina* ex gr. *peregrina* and *U. laevis*).

correlation between the percentage of the DWA comprising high productivity indicators and the DWA equitability index was insignificant ($r=0.126$).

Similar declines in certain *Uvigerina* spp. during the Holocene have been noted elsewhere: Schönfeld & Altenbach (2005) examined the distribution of costate *Uvigerina* in the Late Pleistocene and Holocene of the NE Atlantic Ocean, and found *U. pygmaea* to dominate Late Pleistocene assemblages, but *U. peregrina* and *U. peregrina parva* to be common in the Holocene. They concluded that the limiting factor for *U. pygmaea* was a balanced input of food comprising haptophyteae algae and diatoms, and suggested that the latest Pleistocene deglaciation triggered the decline of this factor and led to the early Holocene extirpation of *U. pygmaea* from the NE Atlantic. It is possible that disruption of some similar factor led to the decline of *U. laevis* in the NE Caribbean Sea. However, in contrast with the extirpation of *U. pygmaea*, the decline in *U. laevis* was gradual, rather than abrupt.

Licari *et al.* (2003, table 3) documented the microhabitat preferences of bathyal species off the tropical coast of West Africa. Comparison with their results indicates that, in concert with the change in surface productivity, a change occurred in the microhabitat preferences of the En20-2 DWA. The high-productivity indicators *Bulimina aculeata*, *B. striata mexicana*, *Uvigerina* ex gr. *peregrina* and *U. laevis*, which were more abundant lower in the core, at present occupy shallow infaunal microhabitats. In contrast, the low-productivity indicators *Cassidulina laevigata* and *Hoeglundina elegans*, which were more abundant in the En20-2 Holocene section, are epifaunal. Thus, as surface productivity decreased, there was a change from a shallow-infaunal to an epifaunal DWA.

Interactions between shallow- and deep-water environments

Core En20-2 yielded both *in situ* middle bathyal specimens and displaced, predominantly back-reef, species. It is not clear from which island or islands the SWA was derived, although, unless there was a major change of surface current direction during the Late Quaternary, it is probable that the source lay to the east. Culver & Buzas (1982) noted that species compositions of modern assemblages around the islands of the Lesser Antilles do not differ significantly, so it is unlikely that the change in the

composition of the SWA in Core En20-2 reflects a shift in the site of origin over time. Fourcade & Butterlin (1988) used displaced large foraminifera to infer palaeoenvironmental conditions at the site of origin, but most of the occurrences they discussed were entrained in turbidites. In contrast, the SWA in core En20-2 is not limited to turbidites, but occurs throughout, perhaps as a consequence of offshore transport of foraminifera during the frequent hurricanes that make landfall in the Leeward Islands (cf. Li *et al.*, 1997, 1998), or on floating marine-plant debris (cf. Bock, 1969; Wilson & Ramscook, 2007). The co-occurrence of both the DWA and SWA in En20-2 provides an opportunity to examine whether they responded in concert to environmental changes. This was tested by comparing the percentage abundances of species in the two associations, the percentages being computed independently for the two associations and contrasted using Pearson's product moment correlation coefficients. The SWA comprised 96 species, but only 19 formed >5% of the SWA in any one sample (see Appendix A). These 19, together with the 20 most abundant species in the DWA, form the basis for this comparison.

The predominantly back-reef species comprising the SWA were not distributed evenly throughout the core. *Amphistegina gibbosa* was more abundant above 121 cm and *Cibicidoides pseudoungerianus* above 201 cm. In contrast, the percentage abundance of *Neonorbina terquemi* and *Sigmavirgulina tortuosa* decreased from the bottom of the core to the top. Three shallow-water species showed successive spikes in percentage abundance: *S. tortuosa* (160–161 cm, 24.9% of SWA), *Tretomphalus bulloides* (140–141 cm, 36.9%) and *Cymbaloporetta squammosa* (120–121 cm, 14.8%), but the palaeoenvironmental significance of these is as yet unclear.

Although species' percentage abundances in the SWA and DWA were calculated independently, there are 70 statistically significant correlations between shallow- and deep-water species (Table 2). The two strongest were between *Neonorbina terquemi* and *Uvigerina laevis* ($r=0.761$, $p=0.001$) and *Amphistegina gibbosa* and *Cassidulina curvata* ($r=0.754$, $p=0.001$). The percentages of the SWA and DWA comprising *A. gibbosa* and *U. laevis* respectively were negatively and significantly correlated ($r=-0.576$, $p=0.019$, Fig. 6). *Amphistegina gibbosa* is intolerant of nutrient enrichment (Hallock, 2000) and its greater abundance in the upper part of Core En20-2, especially in the Holocene section, indicates that the nearshore environment was subject to a lower nutrient flux during the Holocene. In contrast, *U. laevis*, like other hispid *Uvigerina*, is indicative of high productivity areas (Loubere & Faraduddin, 2002) and its greater percentage abundance in the lower part of the core indicates higher productivity at that time. These data suggest that the seas around the northern Lesser Antilles were subject to a greater nutrient flux during the Late Pleistocene than during the Holocene, the change in flux affecting both the SWA and the DWA. One further correlation supports this hypothesis. Loubere & Faraduddin (2002) recorded *Bulimina striata mexicana* as indicative of high productivity seas, and the percentage abundance of this species in the DWA is negatively correlated with that of the SWA *A. gibbosa* ($r=-0.527$).

Globocassidulina subglobosa, which Loubere & Faraduddin (2002) characterized as being a deep-water benthonic typical of low productivity areas, had a particularly marked positive

correlation with *Asterigerina carinata* (Fig. 7), but is also positively correlated with *Elphidium discoidale*, *Peneroplis bradyi* and *P. proteus*. However, there is no significant correlation between *G. subglobosa* and *A. gibbosa*. This might reflect the presence of several species guilds in the SWA (Wilson, 2006b) – a guild being a functional cluster of species that interact among themselves more strongly than with other species in the assemblage (see Jaksic, 1981; Jaksic & Medel, 1990). Particular shallow-water species guilds suggested by these data comprise *A. gibbosa*+*C. pseudoungerianus* and *A. carinata*+*E. discoidale*+*P. bradyi*+*P. proteus*.

Other strong ($r>0.7$) shallow and deep-water correlations occur between *Angulogerina occidentalis* and *Siphonina bradyana*, *Cibicides* sp. A and *Cibicoides bradyi*, *Neonorbina terquemi* and *Ehrenbergina undulata*, *Peneroplis bradyi* and *Globocassidulina subglobosa*, and between *Peneroplis proteus* and *Hoeglundina elegans*. However, despite the manner in which fluctuations in the nutrient flux have apparently governed species abundances in both shallow and deep water, the values of the equitability index for the SWA and DWA were not significantly correlated ($r=0.267$).

CONCLUSIONS

In the Caribbean region, the end of the Pleistocene was marked by a rise in sea-level of about 120 m, which occurred in three pulses during Late Pleistocene and earliest Holocene times. This is not, however, marked by a sudden change in the middle bathyal foraminiferal community in Core En20-2 from the NE Caribbean Sea. Instead, through the Late Pleistocene (i.e. above the 34 ka BP Atlantic extinction of *Pulleniatina obliquiloculata*) and Holocene there was a decrease up-section in shallow infaunal foraminifera indicative of input from high surface productivity, which was compensated by an increase in the abundance of epifaunal species adapted to low surface productivity. This is presumed to reflect a decrease in the nutrient flux to the NE Caribbean Sea throughout the latest Pleistocene and Holocene. The indications are that the decrease was gradual, rather than abrupt.

Samples throughout Core En20-2 yielded not only an *in situ* middle bathyal association, but also approximately equal numbers of allochthonous inner neritic, epiphytal specimens. The latter might have been derived either from shallow-water sediment displaced during hurricanes, or from floating marine-plant debris. Comparison of the two associations reveals that the environmental conditions they indicate varied in unison. The decline in deep-water species adapted to a high surface productivity was matched by an increase in shallow-water species intolerant of a high nutrient flux. Thus, the decline in nutrient flux affected both the inner neritic (predominantly back-reefal) and middle bathyal environments. The data presented here provided an opportunity to compare environment variations in both deep and shallow water, as evidenced by benthonic foraminifera, and showed the power of incorporating an allochthonous fauna into an environmental interpretation. Whereas previous workers have tended to dismiss allochthonous foraminifera as being of little interest other than as indicators of provenance, it has been demonstrated here that comparison of allochthonous and autochthonous assemblages can reveal information of palaeoenvironmental significance.

| Shallow water species | | | | | | | | | | | | | | | | | | |
|--------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Deep-water species | | | | | | | | | | | | | | | | | | |
| <i>Amphistegina gibbosa</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Angulogerina occidentalis</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Asterigerina carinata</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Caribbeanella polystoma</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Cibicidoides pseudoungerianus</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Cibicides</i> sp. A | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Cymbaloporella squammosa</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Elphidium discoidale</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Miliolinella circularis</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Neonorbina terquemii</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Penereopsis bradyi</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Penereopsis proteus</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Quinqueloculina laevigata</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Quinqueloculina lamarkiana</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Rosalina bahamaensis</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Sagrina pulchella</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Sigmavirgulina tortuosa</i> | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |

Only species forming >5% of the assemblage in any one sample are included. Dashes indicates insignificant correlations. Correlations >0.7 in bold.

Table 2. Statistically significant Pearson's product moment correlations coefficients ($p < 0.05$) between species' percentage abundances in the deep- and shallow-water associations, Core En20-2

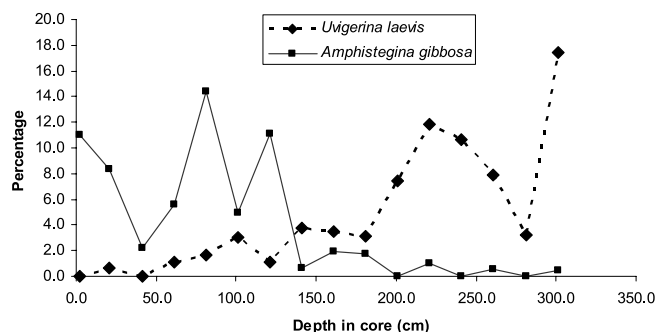


Fig. 6. Graph showing the percentage abundance of the deep-water association as *Uvigerina laevis* and the percentage abundance of the shallow-water association as *Amphistegina gibbosa*.

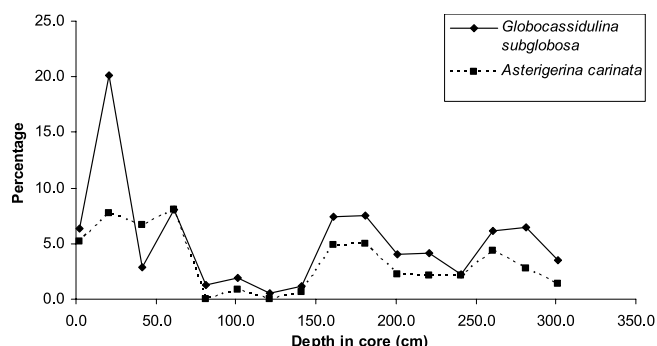


Fig. 7. Graph showing the percentage abundance of the deep-water association as *Globocassidulina subglobosa* and the percentage abundance of the shallow-water association as *Asterigerina carinata*.

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APPENDIX. SWA SPECIES FORMING >5% OF THE SWA RECOVERY FROM ANY ONE SAMPLE

Amphistegina gibbosa d'Orbigny, 1839
Angulogerina occidentalis (Cushman)=*Uvigerina occidentalis* Cushman, 1922
Asterigerina carinata d'Orbigny, 1839
Caribbeanella polystoma Bermúdez, 1952
Cibicides sp. A
Cibicides pseudoungerianus (Cushman)=*Truncatulina pseudoungeriana* Cushman, 1922
Cymbaloporetta squamosa (d'Orbigny)=*Rotalia squamosa* d'Orbigny, 1826

Elphidium discoidale (d'Orbigny)=*Polystomella discoidalis* d'Orbigny, 1839
Miliolinella circularis=*Triloculina circularis* Bornemann, 1855
Neonorbina terquemi (Rzehak)=*Discorbina terquemi* Rzehak, 1888
Peneroplis bradyi Cushman, 1930
Peneroplis proteus d'Orbigny, 1839
Quinqueloculina laevigata d'Orbigny, 1826
Quinqueloculina lamareckiana d'Orbigny, 1839
Quinqueloculina polygona d'Orbigny, 1839
Rosalina bahamaensis Todd & Low, 1971
Sagrina pulchella d'Orbigny, 1839
Sigmavirgulina tortuosa (Brady)=*Bolivina tortuosa* Brady, 1881
Tretomphalus bulloides (d'Orbigny)=*Rosalina bulloides* d'Orbigny, 1839

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