The distribution of deep-sea benthic foraminifera in core tops from the eastern Indian Ocean

Davide S. Murgese*, Patrick De Deckker

Department of Earth and Marine Sciences, The Australian National University, Canberra ACT 0200, Australia

Abstract

Relative abundances of benthic foraminifera in 57 core tops collected within a depth-range between 700 and 4335 m below sea level [b.s.l.] from the eastern Indian Ocean (mostly between Australia and Indonesia) were investigated quantitatively using Detrended Correspondence Analysis (DCA) to analyse species spatial-distribution. Canonical Correspondence Analysis (CCA) and correlation matrices were used to evaluate the relationships between the species distribution and environmental variables (temperature, salinity, dissolved oxygen, nitrate and phosphate concentrations, carbon-flux rate). Seven key-species proved useful for distinguishing environmental parameters.

Two groups of species are identified by means of the first DCA ordination axis. The first group increases in relative abundances with depth and includes three taxa: *Oridorsalis tener umbonatus*, *Epistominella exigua* and *Pyrgo murrhina*. These three taxa prefer a cold (< 3 °C) and well-oxygenated (> 3.5 ml/l) environment, with low carbon flux to the sea floor (< 3 g C m^{-2} $year^{-1}$). *O. tener umbonatus* and *P. murrhina* tend to indicate reduced food availability, whereas *E. exigua* may indicate periodic delivery (seasonal) of organic matter to the sea floor. The second group includes *Nummoloculina irregularis* and *Cibicidoides pseudoungerianus*, typical of upper-bathyal depths. *C. pseudoungerianus* is correlated with a warm (> 2.5 °C) environment characterised by high carbon-flux rate (> 2.5 g C m^{-2} $year^{-1}$). *N. irregularis* is associated with high dissolved-oxygen concentrations (> 3 ml/l) and its distribution is limited to south of 20 °S. In this area, the contemporary presence of the low salinity and well oxygenated Antarctic Intermediate Water and low primary productivity at the sea-surface (which causes low oxygen consumption at the sea floor) create the ideal conditions for this species.

The second ordination-axis scores identify another taxon, *Uvigerina proboscidea*. The distribution of this species is mainly limited to low latitudes (north of 25°S), where carbon flux rate is high (> 3.5 g C m^{-2} $year^{-1}$), due to higher primary productivity levels at the sea surface, and oxygen levels are low (< 3 ml/l) due to the organic matter oxidation and the presence of oxygen-depleted Indonesian Intermediate Water and North Indian Intermediate Water.
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Keywords: benthic foraminifera; carbon flux; Eastern Indian Ocean; Indonesian Throughflow; dissolved oxygen; nutrients; bathymetry; DCA; CCA; primary productivity; Western Australia; Indonesia

* Corresponding author.
  E-mail address: murgesedavide@libero.it (D.S. Murgese).

1. Introduction

Benthic foraminifera are common in marine sediments; they are cosmopolitan, have a good fossil preservation and represent a useful tool for oceanographic and palaeoceanographic studies. Nevertheless the study of modern assemblages is necessary to acquire a better understanding of the factors influencing the distribution of benthic foraminifera, especially from poorly investigated regions such as the eastern Indian Ocean.

Previous studies of benthic foraminifera from the southern Indian Ocean and eastern Indian Ocean have linked benthic foraminiferal distributions with deep-ocean hydrography. Corliss (1979a) studied the faunal content of core tops from the Southeast Indian Ridge and described two major deep-assemblages associated with Antarctic and Indian Bottom Waters. Peterson (1984) analysed deep-sea benthic foraminifera from the Ninetyeast Ridge and identified two major assemblages associated with deep-water masses and their physicochemical properties: *Globocassidulina sub-globosa–Pyrgo* spp.–*Uvigerina peregrina*, above 3800 m, associated with the Indian Deep Water, and *Epistominella exigua–Nuttallides umbonifera*, below 3800 m, associated with the more corrosive and oxygenated Indian Bottom Water.

Other research from the oceans around the Indonesian Archipelago considered samples collected also from shallower depths (above 2000 m). Van Marle (1988), in his study of benthic foraminifera from the Banda Sea, identified four major assemblages typical of four depth ranges. Miao and Thunell (1993) analysed recent benthic foraminifera from Sulu and South China Seas and found that sediment properties, such as organic carbon content, oxygen-penetration depth in sediment and water-masses undersaturation with respect to calcite, played a major role in determining the distribution of assemblages in both basins. Rathburn and Corliss (1994) observed a correlation between the abundance of deep dwelling/low-oxygen tolerant species and high-nutrient flux to the sea floor. Studying the benthic foraminifera composition of assemblages in the South China Sea and the Sulu Sea, Rathburn et al. (1996) found that the inter-basin differences in the faunal pattern were related to a large difference in bottom water temperature, whereas intra-basin varia-

tions were correlated with the organic-carbon content of the sediments.

The eastern Indian Ocean is characterised by a complex circulation system at the sea surface and at intermediate depth. This region is characterized by the end of the throughflow of waters from the Pacific Ocean that have travelled through the Indonesian Archipelago while changing to lower salinities at the sea surface. It is a complex region oceanographically, as many different currents interact between Indonesia and Australia, some of which change direction between seasons (Tomczak and Godfrey, 1994). As a consequence, environmental variables present strong latitudinal gradients in the water column. The monsoonal climate is responsible for the strong seasonality of the Java upwelling system and, together with the Indonesian Throughflow, for a significant difference in primary productivity between Indonesia and Australia. In this paper, core tops collected offshore Western Australia and offshore of the Java and Sumatra Islands have been analysed in order to investigate links that may relate benthic foraminifera to the oceanographic processes in these regions. Statistical analyses have been performed to define the relationships between the distribution of benthic foraminifera species and the environmental parameters measured for the studied area.

2. Materials and methods

A total of 57 core tops was utilised for this study with locations presented in Fig. 1.

Forty-four gravity cores were collected during two *RV Franklin* cruises offshore Western Australia: *Fr 10/95* in 1995 and *Fr 2/96* in 1996. The remaining 13 core tops were sampled from trigger cores collected during two cruises offshore Java and Sumatra: *Shiva* in 1990, *Barat* in 1994, using the *RV Baruna Jaya* (see Acknowledgements).

Short trigger cores (60 cm long) minimize the loss of surface material when collecting samples from the sea floor, but gravity cores may not return samples at the sediment–water interface. However, the set of core tops utilised for this study is the same as that used by Martinez et al. (1998), who sampled the cores on board of the *RV Franklin* soon after recovery, in order to avoid contamination and mixing. Other studies on the
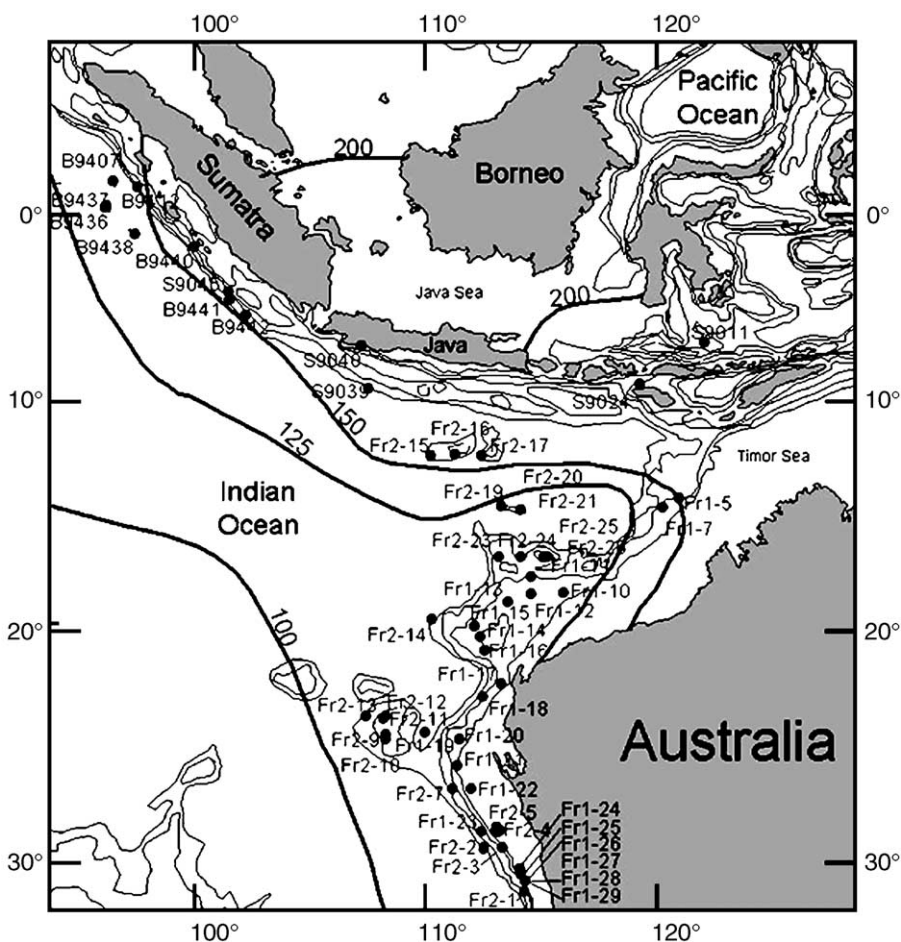
Fig. 1. Map showing the locations of the core tops studied here (for details refer to Appendix II) as well as the annual mean primary productivity (g C m^{-2} year^{-1}) at the sea-surface in the eastern Indian Ocean estimated from satellite data (after Antoine et al., 1996).

same core-tops were performed for analysis of clays (Gingele et al., 2001), pollens (van der Kaars and De Deckker, 2003), radiolarians (Rogers, 2004) and dino-flagellates (Young, oral communication, 2004).

Samples used for this study were obtained from the uppermost 1–2 cm of each core. About 3 cm^3 of material from each sample was soaked in a dilute (3%) hydrogen peroxide solution until clays had fully disaggregated, then washed with a gentle water jet through a 63 μm sieve and the coarse fraction was dried at 40 °C.

All the benthic foraminifera of the total assemblage from the fraction > 150 μm of each sample were counted. When the number of specimens in the sediment was less than 70 individuals, more material was washed and added for counting. The identification of benthic foraminifera was conducted on the basis of the descriptions in the Ellis and Messina catalogue (Ellis and Messina, 1940), Barker (1960), Phleger et al. (1953), Corliss (1979b), Van Marle (1988) and Hess (1998). Benthic foraminifera were mounted on a slide, identified, and the absolute number of specimens for each species recorded. Fragments of *Rhabdammina* sp., *Rhizammina* sp., and other tubular-shaped species were considered to indicate the presence of at least one specimen in the sample. An average of 241 specimens per sample was identified and counted. The fraction > 150 μm was selected in order to allow a comparison with previous works such as those of Corliss (1979a) and Peterson (1984).

An average of 53 taxa was isolated per sample and the absolute number of specimens for each species was converted to the percentage of total foraminifera present in each sample. Those species present with a percentage > 2% in at least 1 sample were used for statistical analyses. In order to acquire useful information for application to palaeoenvironmental and palaeoecological studies, agglutinated taxa, which presented poor preservation potential and were not found when analysing the fossil faunas from selected cores from the same area (Appendix I), were not considered for analyses. Note that the genera *Fissurina*, *Lagena*, *Lenticulina*, *Oolina* and *Parafissurina* were present in many samples with a high species diversity. The percentage of each species was generally low (< 2.5%). Therefore, all the species belonging to these genera and used for statistical analysis were grouped together as *Fissurina* spp., *Lagena* spp., *Lenticulina* spp., *Oolina* spp. and *Parafissurina* spp.

A total of 75 taxa was utilised in the Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (Appendix II). The DCA is a type of ordination particularly suitable in cases of databases with many zeros and for unimodal response models in which the abundance of any species follows a normal distribution (Jongman et al., 1987). DCA algorithm generates axes that maximise the dispersion of the species scores and that are constrained to be uncorrelated with each other (Jongman et al., 1987). DCA extracts the ordination axes from the species data by using the two-way weighted averaging algorithm (Jongman et al., 1987). This procedure allows the calculation of both species and samples scores as follows: (a) arbitrary and unequal values are taken as initial sample scores, (b) species scores are derived by calculating the weighted average of the sample scores for each species, (c) new samples scores are then derived by calculating for each sample the weighted average of the species scores, (d) sample scores are standardized to mean 0 and variance 1, and (e) standardized values are then used to obtain new species scores in step (b).

After a certain number of iterations, the species and samples scores stabilize and the algorithm ends (Jongman et al., 1987). In order to obtain uncorrelated ordination vectors, for the 2nd and higher axes values are orthogonalized with respect to the former axis between steps (c) and (d).

The axes are also calculated in such a way that at any point, on the ith axes, the mean value of the site scores on the subsequent axes is zero (Jongman et al., 1987). Canonical Correspondence Analysis (CCA) was then performed in order to explore the relationship between environmental variables and benthic foraminifera distribution. CCA is a direct gradient analysis, which generates axes that maximise the dispersion of the species scores and that are constrained to be a linear combination of the measured environmental variables (ter Braak, 1986). Also, in this case, for calculating samples and species scores, the two-way weighted averaging algorithm is used: in this case, sample scores used in step (b) are the fitted values of the multiple regression between sample scores calculated in step (c) and the environmental variables considered for the analysis. As for DCA, these axes have to be uncorrelated with each other. CCA ordination axes were assessed using the Monte Carlo Permutation test (190 unrestricted permutation: $p < 0.05$) (ter Braak and Smilauer, 1998). Statistical analyses were performed utilizing the software package CANOCO 4.0 (ter Braak and Smilauer, 1998).

The environmental variables for each core site were the annual means available from the World Ocean Atlas 94 (see Appendix III). These data were downloaded from the NOAA web site at http://www.nodc.noaa.gov/ocs/SELECT/dbsearch/dbsearch.html. The organic carbon fluxes were calculated using the annual productivity data derived from the Coastal Zone Colour Scanner (CZCS) archive by Antoine et al. (1996) (Fig. 1) for the years 1978–1986, applied to the formula by Suess (1980). The Berger and Wefer (1990) formula gave similar results, and therefore we will not use it.

Faunal characteristics were expressed using the Fisher's Alpha index α (Williams, 1964), Shannon-Weaver diversity index $H(S)$ (Murray, 1991), equitability E (Murray, 1991) and dominance D (den Dulk, 2000).

In order to investigate possible relations between faunal groups and environmental parameters, the percentages of the species belonging to agglutinated species, to presumed calcareous-infaunal species (Table 1) and to porcellaneous species were summed separately. The total percentage of each group (Table 2) was then correlated with the environmental parameters. We did not attempt to correlate environmental

Table 1
List of calcareous-infaunal species

Species	Mean %	References No.	References	No.
Amphicoryna spp.	0.04	2	Corliss (1985)	1
Astacolus spp.	0.07	2	Corliss and Chen (1988)	2
Astrononion spp.	1.20	16	Corliss (1991)	3
Bolivina robusta	0.32	1	Barmawidjaja et al. (1992)	4
Bolivina spp.	0.66	21	Bernhard (1992)	5
Bolivinita quadrilatera	0.40	22	Jorissen et al. (1992)	6
Brizalina dilatata	0.34	4, 14, 15	Buzas et al. (1993)	7
Brizalina semilineata	0.26	3	Miao and Thunell (1993)	8
Brizalina sp.	0.61	3	Gooday (1994)	9
Bulimina aculeata	2.26	3, 8, 19, 20	Jorissen et al. (1994)	10
Bulimina alazanensis	1.33	3, 8, 19	Rathburn and Corliss (1994)	11
Bulimina costata	0.58	3, 8, 19	Faridduddin and Loubere (1997)	12
Bulimina gibba	0.01	3, 8, 19	McCorkle et al. (1997)	13
Bulimina marginata	0.22	3, 8, 19	De Stigter et al. (1998)	14
Bulimina striata	0.22	3, 8, 19	Jannink et al. (1998)	15
Buliminella sp.	0.08	21	Jorissen et al. (1998)	16
Cassidulina laevigata	1.08	22	Bernhard and Sen Gupta (1999)	17
Cassidulina spp.	1.84	22[a]	Gooday and Rathburn (1999)	18
Ceratobulimina pacifica	1.16	2	Jorissen (1999)	19
Chilostomella oolina	0.39	3, 5, 11, 16, 22	Schmiedl et al. (2000)	20
Dentalina spp.	0.43	2	Ernst et al. (2002)	21
Eherenbergina trigona	1.18	2	Fontanier et al. (2002)	22
Fissurina spp.	3.61	2		
Fursenkoina spp.	0.38	3, 7		
Globobulimina affinis	0.01	3, 5, 7, 12, 15, 18, 22		
Globobulimina pacifica	0.16	3[a], 5, 7[a], 12[a], 15[a], 16, 18[a], 22[a]		
Globobulimina pupioides	0.03	3[a], 5, 7[a], 12[a], 15[a], 18[a], 22[a]		
Gyroidinoides altiformis	0.32	22		
Gyroidinoides orbicularis	0.47	22		
Gyroidinoides soldanii	0.88	22[a]		
Gyroidinoides spp.	4.45	22[a]		
Lagena spp.	1.70	2		
Lenticulina spp.	0.56	3, 11		
Marginulina spp.	0.31	2		
Melonis barleeanum	1.80	3, 7, 9, 22		
Melonis pompilioides	0.28	17		
Nodosaria spp.	0.14	2		
Nonion sp.	0.10	18		
Nonionella turgida	0.09	3, 6, 21		
Nonionella spp.	0.25	6[a]		
Oolina spp.	0.85	2		
Parafissurina spp.	0.56	2		
Pleurostomella sp.	0.10	13[a]		
Pullenia bulloides	3.11	3		
Pullenia spp.	4.81	3[a]		
Rectobolivina spp.	0.17	2		
Saracenaria italica	0.03	2		
Trifarina bradyi	0.02	3[a]		
Uvigerina peregrina	2.28	10, 22		
Uvigerina spp.	5.49	10[a], 22[a]		
Vaginulinopsis spp.	0.07	2		

The microhabitat classification of Corliss and Chen (1988) was applied only for those species for which a direct observation on living (rose-bengal stained) specimens was not available.

[a] References classifying comparable species, or species differently named.

Table 2
Faunal groups percentages calculated for each sample

Sample	Fr1–5	Fr1–7	Fr1–10	Fr1–11	Fr1–12	Fr1–13	Fr1–14	Fr1–15	Fr1–16	Fr1–17	Fr1–18	Fr1–19	Fr1–20	Fr1–21	Fr1–22	Fr1–23	Fr1–24	Fr1–25	Fr1–26
Agglutinated species %	5.66	5.37	12.09	4.90	5.36	13.91	7.79	7.95	14.07	10.93	11.27	5.28	10.23	12.36	8.89	16.84	9.59	10.37	5.99
Calcareous Infaunal species %	33.96	35.29	38.46	46.08	41.96	33.11	43.29	35.75	32.74	46.62	45.07	44.55	42.05	42.70	25.93	35.79	28.77	26.76	32.21
Porcellaneous species %	10.06	21.48	7.14	6.86	8.48	9.27	5.41	8.85	4.35	11.90	7.04	7.92	7.95	25.28	11.11	8.42	13.70	17.39	16.85

Table 2 (*continued*)

Sample	Fr1–27	Fr1–28	Fr1–29	Fr2–1	Fr2–2	Fr2–3	Fr2–4	Fr2–5	Fr2–7	Fr2–9	Fr2–10	Fr2–11	Fr2–12	Fr2–13	Fr2–14	Fr2–15	Fr2–16	Fr2–17	Fr2–19
Agglutinated species %	6.17	8.08	7.90	15.79	10.37	21.43	2.43	7.39	25.16	3.83	8.84	5.38	3.41	4.40	2.50	11.76	11.40	10.00	20.00
Calcareous Infaunal species %	32.10	45.45	29.12	28.20	34.15	27.68	32.02	33.66	27.67	37.16	29.25	37.69	32.20	31.87	16.79	21.18	27.19	40.00	22.86
Porcellaneous species %	15.43	25.25	14.90	14.29	7.93	10.71	19.73	21.98	5.66	8.20	12.93	5.38	3.96	16.48	8.21	11.76	8.77	15.00	11.43

Table 2 (*continued*)

Sample	Fr2–20	Fr2–21	Fr2–23	Fr2–24	Fr2–25	Fr2–26	B9407	B9412	B9436	B9437	B9438	B9440	B9441	B9442	S9011	S9024	S9039	S9040	S9045
Agglutinated species %	5.62	10.26	4.11	5.71	5.76	4.38	2.46	24.68	5.91	3.46	3.02	2.22	5.22	7.69	9.09	5.49	21.05	6.40	16.49
Calcareous Infaunal species %	30.90	26.50	42.47	45.45	27.75	39.42	5.41	22.08	23.15	26.30	18.46	25.56	46.09	68.27	56.97	68.63	23.68	71.20	37.11
Porcellaneous species %	13.48	10.26	4.11	5.92	5.76	8.76	1.97	6.49	11.33	11.42	19.80	3.33	7.83	3.85	1.82	3.53	5.26	0.00	14.43

parameters and the relative abundance of the calcareous-epifaunal group because the information available to identify members of this group is not as reliable as those for identification of infaunal groups.

3. Oceanography of the Eastern Indian Ocean

The oceanography of the eastern Indian Ocean is complex because of (1) the contemporary influence of the monsoonal climate, which causes periodical reversal of the flow direction of surface currents, and (2) the influence of the Indonesian Passageway, which connects Indian and Pacific Oceans (Rochford, 1961; Van Aken et al., 1988). During January–February (Boreal Winter), winds blow from SE Asia to NW Western Australia (Northwestern Monsoon). Conversely, during July–August (Boreal Summer) winds blow over SE Asia (Southeastern Monsoon) (Tchernia, 1980). The greater steric height in the Pacific Ocean, compared to that in the Indian Ocean, generates a flow that moves from the former to the latter ocean passing through the Indonesian Archipelago: this is the Indonesian Throughflow (ITF). The Indonesian seas act as a "dilution" basin: since the region is characterised by an excess of precipitation over evaporation, in these basins, water entering from the Pacific is progressively diluted and becomes fresher. Once Pacific waters enter the Indonesian Archipelago, tidal currents produce strong mixing which preserves the temperature stratification and causes complete homogenisation of the salinity field (Van Aken et al., 1988). After this process, the Pacific Ocean's characteristics tend to disappear, thus becoming the Indonesian Water (IW) at the sea surface and the Indonesian Intermediate Water (IIW) at intermediate depths (Fieux et al., 1996). In these deep basins, the renewal rate of water is low, thus enduring a long residence time. Under these conditions, the consequent prolonged biological oxygen-consumption is such that the water mass which flows out in the Indian Ocean, becomes strongly depleted in oxygen (< 2ml/l) (Postma and Mook, 1988).

3.1. Surface water oceanography

In the eastern Indian Ocean, the monsoonal climate influences mainly the northern hemisphere oceanic circulation, but its effects are also felt south of the equator. The oceanic surface circulation over this sector during the Northwestern Monsoon is illustrated in Fig. 2. West of Sumatra, the Indian Monsoon Current joins the Equatorial Counter Current and, together, they flow eastward as the South Java Current (SJC) (Wijffels et al., 1996). Once the SJC reaches 15°S, it flows westwards in the Southern Equatorial Current. From the Timor Sea, waters that originated in the Banda Sea move southwest as the warm and low salinity Leeuwin Current (LC). Parallel to the LC, there is the northward flow of the South Indian Ocean Gyre eastern component: the Western Australian Current (WAC) (Pearce, 1991). Close to the Australian coast, along the upper slope, the WAC flows below the less dense LC (Pearce and Creswell, 1985). During the Southeastern Monsoon, the SJC reverses its flow, this time moving westward (Tomczak and Godfrey, 1994).

3.2. Intermediate and deep water oceanography

The depth ranges and the characteristics of intermediate-, deep- and bottom-water masses present in this region are summarised in Fig. 3 (Warren, 1981). South of about 23°S, the Antarctic Intermediate Water (AAIW) is preponderant between 700 and 200 m; it is characterised by low salinity and temperature. It sits below the much evaporated South Indian Central Water (SICW).

Of interest here are the different dissolved-oxygen concentrations of each intermediate-water mass. A north–south gradient characterises the water column for this depth range: in the northern part of the region, the North Indian Intermediate Water (NIIW) and the IIW both present dissolved-oxygen levels < 2 ml/l, whereas south of 20°S, AAIW and the SICW are characterised by dissolved-oxygen concentrations > 4 ml/l (Fig. 3). The lateral mixing between these waters is marked by a variation of this parameter together with salinity changes (Wijffels et al., 2002).

3.3. Surface water productivity and organic-carbon fluxes

Although upwelling phenomena are present along the eastern boundaries of the Atlantic and Pacific
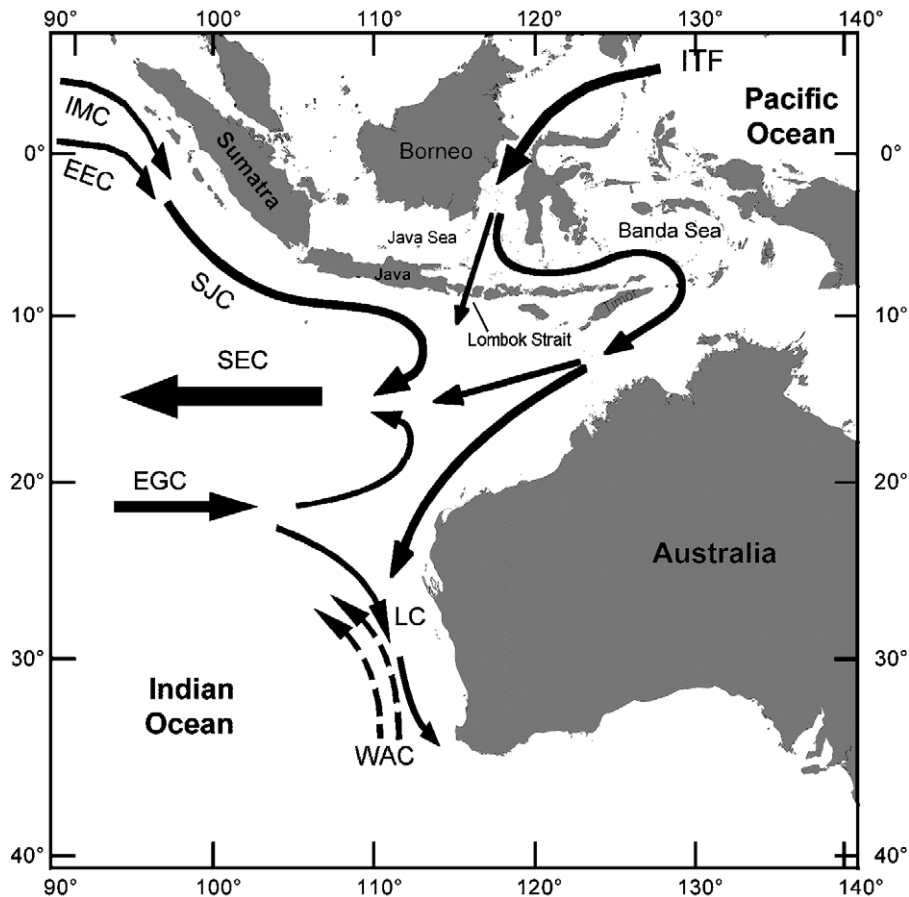
Fig. 2. Map of the eastern Indian Ocean showing the near-surface current systems of the Indonesian Throughflow (ITF) region. IMC=Indian Monsoon Current; ECC=Equatorial Counter Current; SJC=South Java Current; SEC=South Equatorial Current; EGC=Equatorial Gyral Current; LC=Leeuwin Current; WAC=Western Australian Current (after Wijffels et al., 1996).

Oceans, due to the Trade Winds action and Ekman transport, along the Indian Ocean's eastern boundary, the LC's poleward flow is strong enough to override the wind-driven equatorward flow. The result of this phenomenon is the absence of upwelling along the NW Western Australian coast (Smith, 1992; Tomczak and Godfrey, 1994). In the Indonesian region, during the Southeastern Monsoon (September–October), along the Java and Sumatra western coasts, the SJC westward flow determines an upward motion of the thermocline (Colborn, 1975) accompanied by a high concentration of dissolved inorganic phosphate at the bottom of the euphotic layer and by high plankton biomass: the South Java Upwelling System (SJS) (Wyrtki, 1962;

Fieux et al., 1994; Sprintall et al., 1999). The upwelling intensity is related to the monsoonal regime and, for this reason, is variable (Sprintall et al., 1999).

In the Indonesian Seas, productivity at the sea surface is conditioned by the monsoonal climate: during the Southeastern Monsoon, chlorophyll levels are high (> 1 mg/m^3), whereas during the Northwestern Monsoon they are generally low (0.1–0.2 mg/m^3). The concentration of chlorophyll at the sea surface is not the same for the entire region as a west–east phytoplankton biomass gradient is present (Wyrtki, 1958). In August and September, the eastern Banda Sea and the Arafura Sea are characterised by higher chlorophyll levels
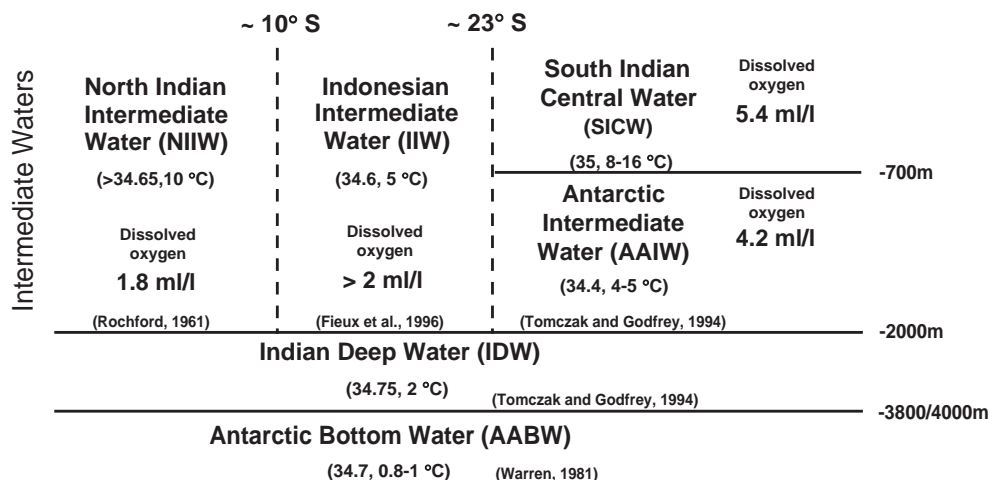
Fig. 3. Schematic distribution and characteristics of the important water masses distribution for the eastern Indian Ocean. Salinity and temperature for each water mass are given in brackets; the dissolved-oxygen concentration of intermediate waters is also indicated.

whereas more oligotrophic conditions are present in the Sulawesi Sea (Kinkade et al., 1997). This difference in productivity levels between the two regions is related to the "unbalance" between the water outflow to the Indian Ocean and the inflow of surficial water from the Pacific Ocean and the consequent vertical advection of intermediate waters of the Banda and Arafura Seas which compensates this deficit (Wyrtki, 1958). During January–February, a slight increase in chlorophyll in the Makasar Strait is related to river runoff (Kinkade et al., 1997).

Rainfall contributes to increase the amount of organic matter produced at the sea surface. Over Indonesia, rain occurs nearly throughout the year (Kripalani and Ashwini, 1997) and under these conditions rivers deliver a large amount of sediment to the ocean (Milliman and Meade, 1983; Milliman et al., 1999). Material delivered by the rivers represents an important source of nutrients, which favours phytoplankton growth at the sea surface (Parsons and Takahashi, 1973; Pettine et al., 1999). The opposite situation characterises the seas off northwestern and western Western Australia, where rainfall is less abundant and more concentrated in short periods of the year (Gingele et al., 2001). The amount of sediment discharged by the rivers in the ocean is significantly less than that from Indonesia (Milliman and Meade,

1983). These differences explain the productivity gradient at the sea surface existing between these two regions (Fig. 1).

4. Results

The study of benthic foraminifera from the 57 core tops identified a total of 210 species, whose mean abundance ranges between 8.96% (*Globocassidulina subglobosa*) and 0.002% (*Pseudogaudryina atlantica*).

4.1. Detrended correspondence analysis (DCA)

The algorithm calculated four ordination axes, which account for 33.2% of the species variance. The variance justified by each axis is listed in Table 3. The first two axes represent more than 50% of the variance explained with the DCA and for this reason only these two have been considered for further analysis. Species scores and weights are listed in Appendix IV. The scores indicate the degree of correlation of each species with

Table 3
Variance explained by each one of the four axes

Axis	Ax1	Ax2	Ax3	Ax4
Variance of species data	14.2%	8.4%	5.7%	4.6%

each axis; the species' weight indicates the influence of species on the analysis (ter Braak and Smilauer, 1998; Haslett, 2002).

The analysis of axis 1 allowed the identification of two groups of species. Species with negative score and high weight (in order of occurrences given in brackets): *Oridorsalis tener umbonatus* (55), *Pyrgo murrhina* (50) and *Epistominella exigua* (40) (for illustrations see Fig. 4). Species with positive score and high weight: *Cibicidoides pseudoungerianus* (27) and *Nummoloculina irregularis* (15) (for illustrations see Fig. 4).
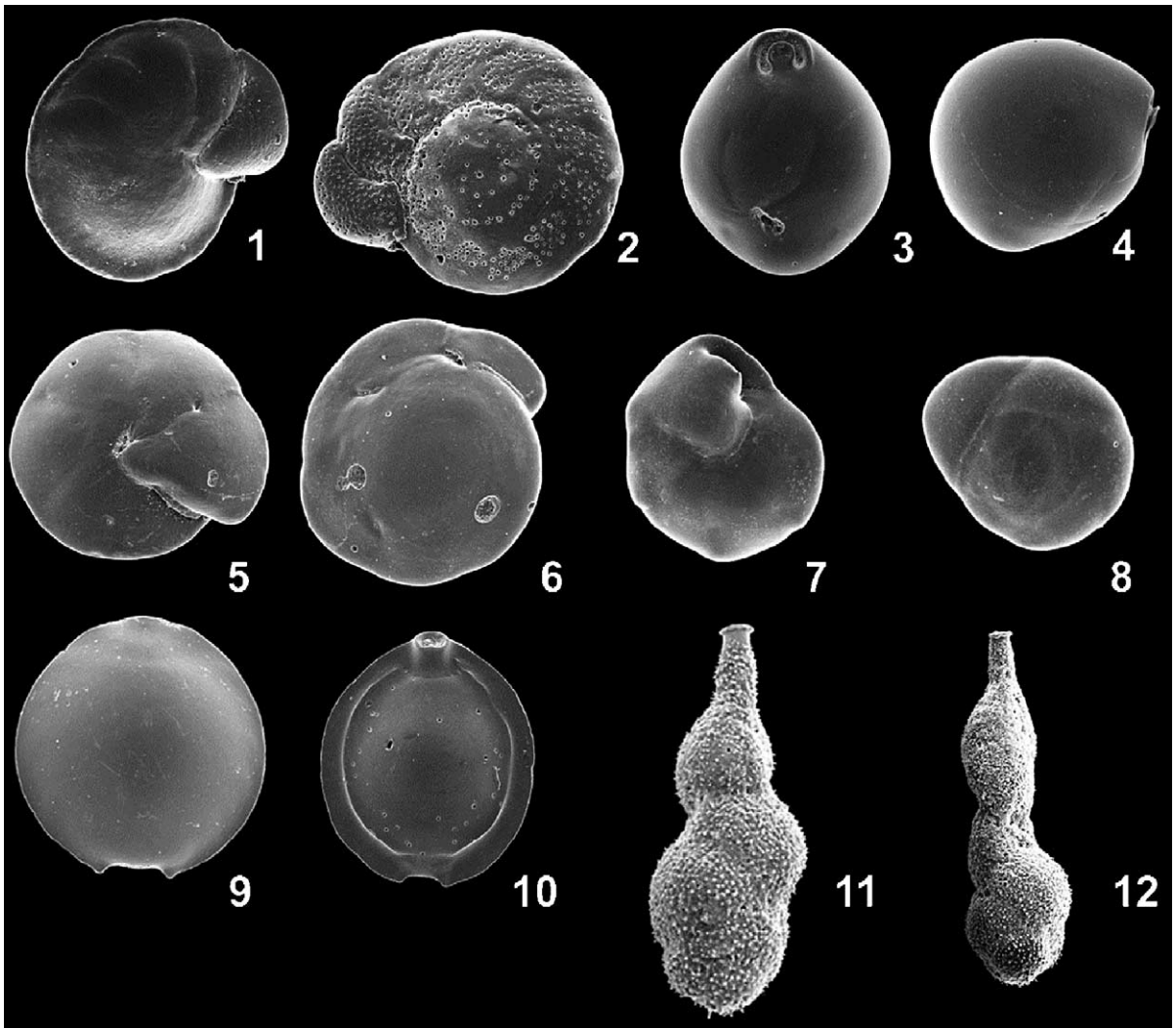
Fig. 4. Benthic foraminiferal species identified by means of DCA: (1) *C. pseudoungerianus* (Cushman), umbilical view; sample Fr 2–4, diameter 554 μm. (2) *C. pseudoungerianus* (Cushman), spiral view; sample Fr 2–4, diameter 750 μm. (3) *N. irregularis* (d'Orbigny), apertural view; sample Fr 2–4, length 365 μm. (4) *N. irregularis* (d'Orbigny), side view; sample Fr 2–4, length 250 μm. (5) *O. tener umbonatus* (Reuss), umbilical view; sample Fr 2–2, diameter 710 μm. (6) *O. tener umbonatus* (Reuss), umbilical view; sample Fr 2–21, diameter 730 μm. (7) *E. exigua* (Phleger and Parker), umbilical view; sample Fr 2–14, diameter 400 μm. (8) *E. exigua* (Phleger and Parker), spiral view; sample Fr 2–14, diameter 350 μm. (9) *P. murrhina* (Schwager), dorsal view; sample Fr 1–5, length 600 μm. (10) *P. murrhina* (Schwager), ventral view; sample Fr 1–5, length 750 μm. (11) *U. proboscidea* Schwager, side view; sample Fr 1–7, length 600 μm (12) *U. proboscidea* Schwager, side view; sample Fr 1–17, length 470 μm.

Based on the scores of axis 2, one species is characterised by high weight and positive score: *Uvigerina proboscidea* (43) (for illustrations see Fig. 4).

The samples' scores related to the first two axes of DCA were correlated to the environmental variables at each site (Table 4). The correlation matrix shows a significant correlation of axis 1 with most of the environmental variables taken into account, except for the phosphate- and nitrate-concentrations and for the primary productivity levels at the sea surface. This axis is negatively ($r < -0.60$) correlated with the following variables: depth, pressure and salinity; it shows a positive correlation ($r > 0.60$) with temperature and carbon flux. A weaker positive ($p < 0.05$) correlation exists between axis 1 and Fisher's Alpha Diversity Index, Shannon Index and Equitability, whereas an opposite correlation links this axis with dominance. Axis 1 is also weakly correlated ($p < 0.05$) with longitude, latitude and dissolved-oxygen concentration. Axis 2 shows a significant correlation with the following environmental variables: longitude, dissolved-oxygen concentration, salinity, phosphate, primary productivity at the sea surface, carbon flux (calculated applying the two formulae used in this study) and faunal characteristics (α, $H(S)$, E, D). The variable with the most significant correlation ($r = -0.52$; $p < 0.05$) with this axis is dissolved-oxygen concentration.

4.2. Correlation between environmental variables

The environmental variables (Fig. 5) utilised in this study appear to be related to depth (Table 4). Those that are positively correlated to this parameter are: pressure, salinity, dissolved-oxygen concentration, dominance, primary productivity and longitude. Those characterised by a negative correlation are: temperature, carbon flux, $H(S)$, E and D.

Two relevant relationships are not related to depth variation: (a) the dissolved-oxygen concentration is negatively correlated with phosphate and nitrate; (b) the primary productivity at the sea surface is strongly correlated with longitude.

4.3. Correlation between the percentages of the species and the environmental variables

The correlation coefficients between the percentages of the taxa considered in the DCA and the environmental variables were also calculated (Appendix V). The analysis of the coefficients was carried out assuming the mean percentage of each species as indication of the taxon's relevance. The five species identified by means of DCA appear to be related to the environmental variables considered in this study, in particular with those whose correlation with the DCA ordination axes is high.

Oridorsalis tener umbonatus, *Epistominella exigua* and *Pyrgo murrhina* show a significant positive correlation primarily with depth ($p < 0.05$) (Fig. 6a, b, and c), and a lesser degree with salinity and, with the exception of *O. tener umbonatus*, the dissolved-oxygen concentration. They have a negative correlation with temperature and carbon flux. *E. exigua* and *P. murrhina* also show a negative correlation with the faunal diversity, and a positive one to dominance.

On the other hand, *Cibicidoides pseudoungerianus* and *Nummoloculina irregularis* are negatively correlated with depth (Fig. 6d and e), thus pressure, and positively with temperature. *C. pseudoungerianus* is positively correlated with carbon flux (Fig. 6d), and *N. irregularis* is also positively correlated with salinity (Fig. 6e) and the faunal diversity.

Uvigerina proboscidea is positively correlated to the carbon flux and negatively with the dissolved-oxygen concentration (Fig. 6f).

4.4. Canonical Correspondence Analysis (CCA)

In order to evaluate how well the environmental variables explained the distribution of the identified species a Canonical Correspondence Analysis (CCA) was performed. The total variance explained by the algorithm is 30.7%, close to the percentage of variance explained by the mean of DCA. CCA produced axes that are mirror-like to those produced by DCA. The relationships species-axes are the same as those given by the indirect gradient analysis. In Table 5, the interset correlations between the environmental variables and the canonical axes are given. The relationship between species distribution and depth is indicated also by this ordination technique, as underlined by the strong correlation between the first axis and this variable. A similar observation can be made for temperature, salinity and carbon flux. There is also a significant correlation between the second axis of the CCA and two environmental variables: dissolved-oxygen concentra-

Table 4
Correlation matrix of the DCA ordination axes samples scores (on Ax1 and Ax2) and the environmental variables

	Ax1	Ax2	Lat.	Long.	Depth	Diss. oxygen	Salinity	Temp.	Press.	Phosp.	Nit.	PP	C flux(z)	$H(S)$	E	D	α
Ax1	1.00																
Ax2	0.06	1.00															
Lat.	**0.36**	− 0.09	1.00														
Long.	− **0.31**	**0.48**	**0.56**	1.00													
Depth	− **0.90**	− 0.09	**0.29**	− **0.36**	1.00												
Diss. oxygen	− **0.37**	− **0.52**	− **0.44**	− 0.01	**0.50**	1.00											
Salinity	− **0.69**	**0.28**	**0.49**	− **0.40**	**0.61**	− 0.15	1.00										
Temp.	**0.88**	0.15	− 0.19	0.22	− **0.91**	− **0.45**	− **0.60**	1.00									
Press.	− **0.90**	− 0.09	**0.29**	− **0.36**	**1.00**	**0.50**	**0.61**	− **0.91**	1.00								
Phosp.	− 0.08	**0.34**	**0.41**	− 0.15	− 0.08	− **0.63**	**0.40**	− 0.07	− 0.08	1.00							
Nit.	− 0.19	0.21	**0.37**	− 0.24	0.13	− **0.45**	**0.46**	− 0.24	0.13	**0.40**	1.00						
PP	− 0.22	**0.42**	**0.86**	− **0.45**	**0.31**	− 0.25	**0.37**	− 0.20	**0.31**	0.14	0.25	1.00					
C flux(z)	**0.82**	**0.37**	0.05	0.11	− **0.80**	− **0.51**	− **0.48**	**0.92**	− **0.80**	− 0.03	− 0.17	0.12	1.00				
$H(S)$	**0.52**	− **0.27**	− **0.53**	**0.56**	− **0.53**	− 0.09	− **0.37**	**0.41**	− **0.53**	− 0.05	− 0.17	− **0.44**	**0.27**	1.00			
E	**0.58**	− **0.35**	− **0.55**	**0.52**	− **0.55**	− 0.02	− **0.47**	**0.45**	− **0.55**	− 0.08	− **0.28**	− **0.47**	**0.30**	**0.91**	1.00		
D	− **0.41**	0.19	**0.42**	− **0.45**	**0.42**	0.09	0.24	− **0.33**	**0.42**	0.04	0.06	**0.34**	− 0.24	− **0.91**	− **0.74**	1.00	
α	**0.44**	− **0.37**	− **0.46**	**0.39**	− **0.42**	0.02	− **0.37**	**0.33**	− **0.42**	− 0.06	− 0.15	− **0.34**	0.20	**0.82**	**0.85**	− **0.68**	1.00

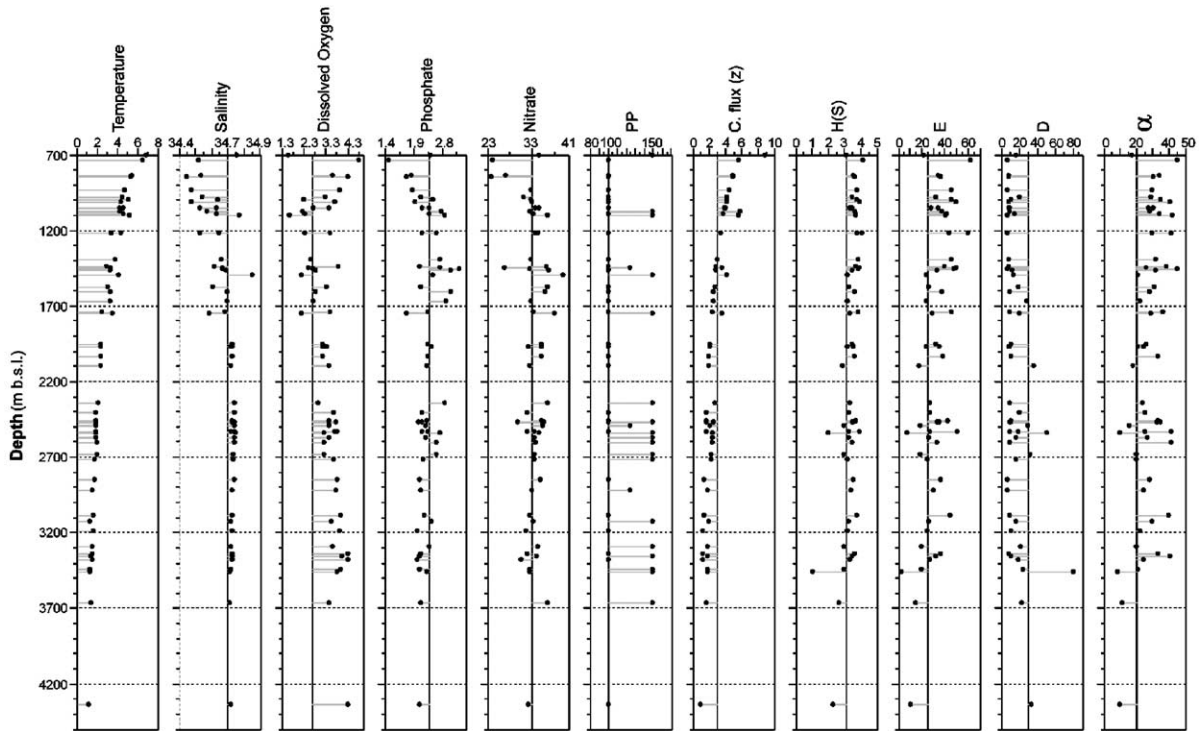In bold are indicated those correlations significant at $p < 0.05$.

Fig. 5. Values of the environmental variables considered in this study versus depth. PP=Primary Productivity at the sea surface; C flux (z)=carbon flux calculated using Suess' (1980) formula; $H(S)$=Shannon-Weaver index; E=Equitability; D=Dominance; α=Fisher's Alpha index. Note that and arbitrary line was placed for some parameters to clearly show departing values for different depth zonations.

tion and phosphate. The relationships between the environmental variables, the Canonical Correspondence axes, and the seven species identified by DCA are shown in Fig. 7. Oridorsalis tener umbonatus, Epistominella exigua and Pyrgo murrhina are on the right side of the diagram and show a close relationship with depth. Cibicidoides pseudoungerianus and Nummoloculina irregularis are on the left side, showing a negative correlation with these parameters. The second taxon shows a correlation with the three diversity indexes. U. proboscidea is negatively correlated with dissolved-oxygen concentration.

4.5. Correlation between the agglutinated, calcareous-infaunal and porcellaneous taxa and the environmental variables

In order to investigate the relationship between the three groups of benthic foraminifera (agglutinated,

calcareous-infaunal and porcellaneous) and the environmental variables the correlation matrix shown in Table 6 was calculated.

The distribution of the agglutinated group is positively correlated with α and $H(S)$, but shows a negative correlation with dominance. The calcareous-infaunal species distribution is negatively correlated with dissolved oxygen, depth, and pressure, but positively with C flux(z), temperature and longitude. The distribution of porcellaneous taxa is negatively correlated to salinity, latitude, phosphate and nitrate concentrations and dominance. This group of species shows a positive correlation with dissolved oxygen, equitability and α.

5. Discussion

The distribution of the 75 species analysed appears to be mainly controlled by depth. On the

basis of the score sign on axis 1 and the weight of each species two major groups of taxa were identified: one positively correlated with depth (species with negative score on axis 1) and one charac-

terised by the opposite (species with positive score on axis 1).

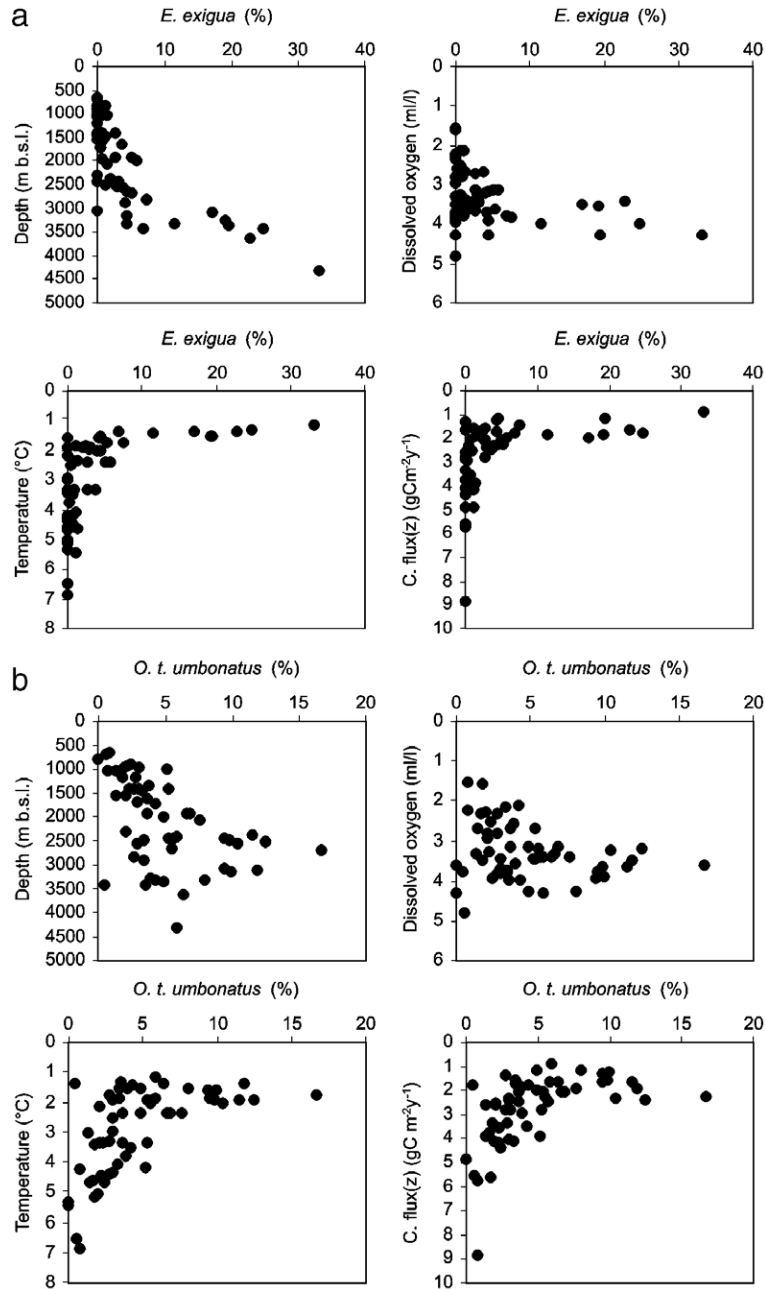The first group includes three species: *Oridorsalis tener umbonatus*, *Epistominella exigua* and *Pyrgo*

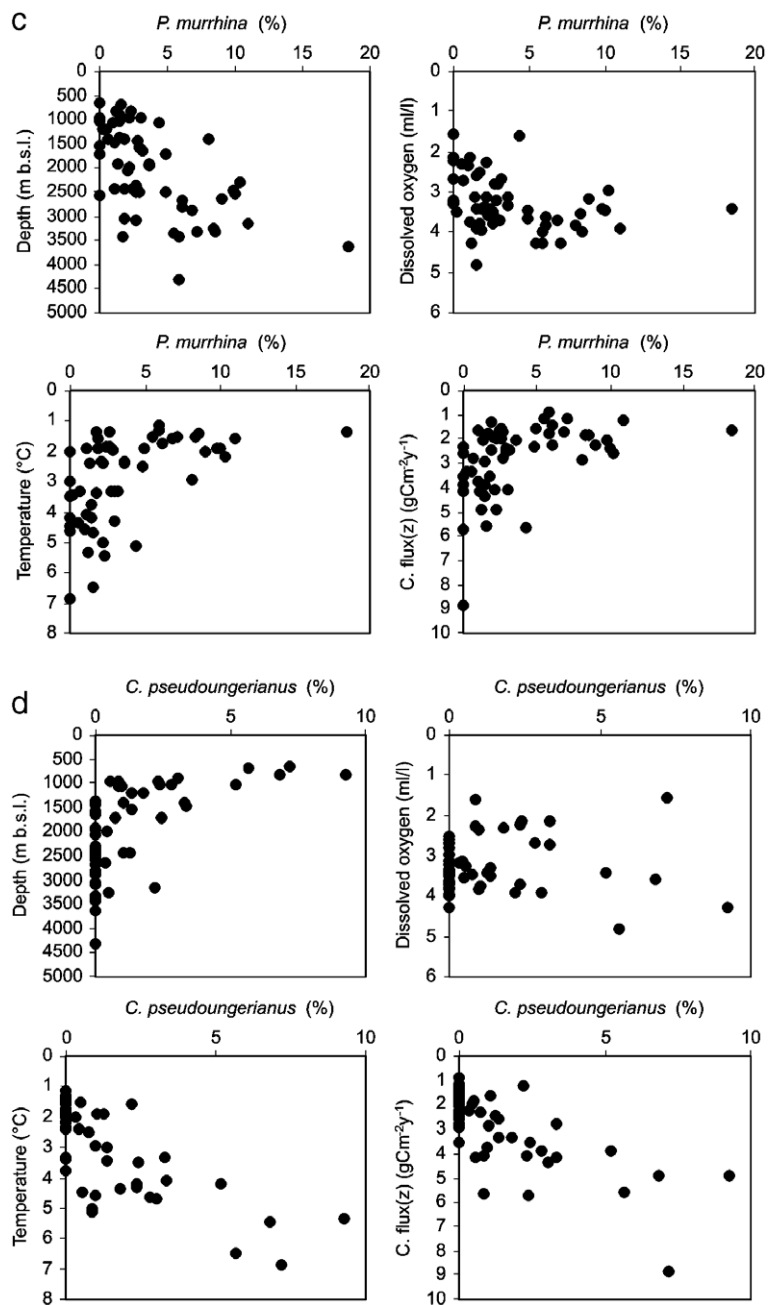Fig. 6. Main species percentages plotted versus environmental variables.

Fig. 6 (*continued*).

murrhina. The distribution of these three taxa is strongly controlled by depth (Fig. 6). In this region, the measured variables–with the exception of phosphate and nitrate–are all correlated to depth: any

variation of the latter determines a modification of the other parameters. According to the correlations between species percentages and the environmental variables, *O. tener umbonatus*, *E. exigua* and *P.*
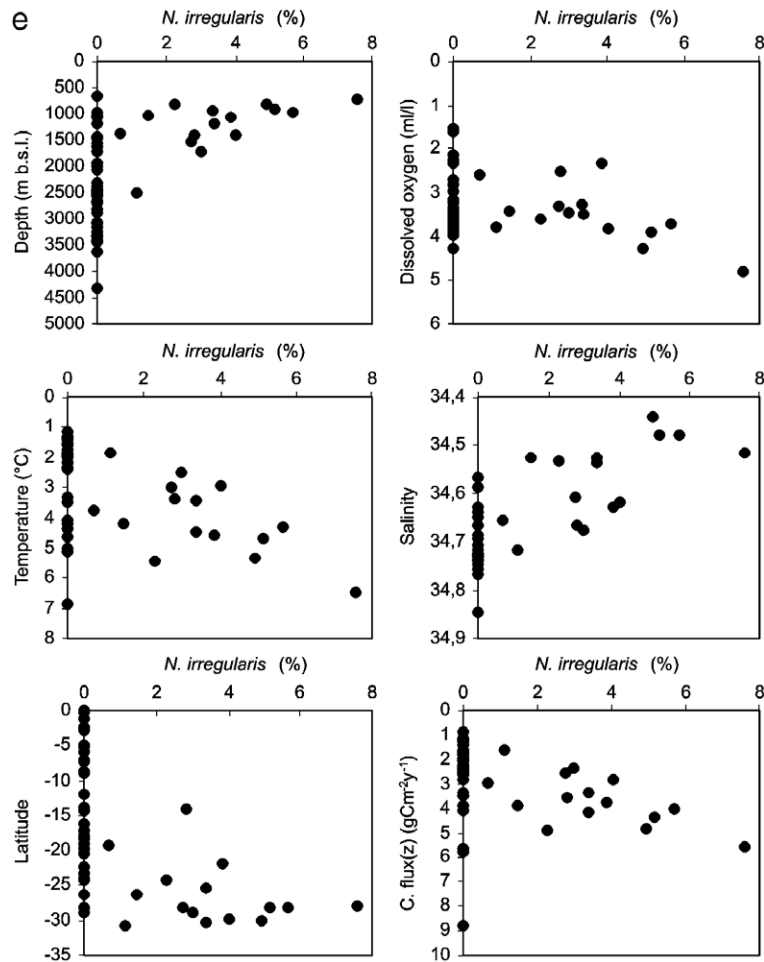
Fig. 6 (*continued*).

murrhina thrive in a deep environment charac-
terised by a temperature > 2.5 °C, good oxygena-
tion (> 3.5 ml/l) and oligotrophic conditions, where
the amount of organic matter reaching the sea floor
is reduced and/or concentrated in specific periods.
In the eastern Indian Ocean, *O. tener umbonatus*
was found to be abundant in deep water (> 2500
m) by Corliss (1979a) and Peterson (1984), who
associated this species to Antarctic Bottom Water
and Indian Deep Water respectively. In the Atlantic
Ocean, the Sulu Sea and the South China Sea, *O.
tener umbonatus* increases in relative abundance
with increasing depth and decreasing organic car-
bon values (Mackensen et al., 1985; Miao and
Thunell, 1993; Rathburn and Corliss, 1994). Rath-

burn and Corliss (1994) state that this species can
use limited amounts of food.

Epistominella exigua has been observed to inhabit
phytodetritus layers deposited on the sea-floor
(Gooday, 1988, 1993; Smart et al., 1994). This species
is known to behave as an *r*-strategist (Jannink et al.,
1998), being able to grow and reproduce rapidly in the
presence of phytodetritus (Kurbjeweit et al., 2000),
thus becoming the most abundant taxon and reaching
a high dominance, which is the case in samples in
which *E. exigua* is found.

This adaptative mechanism could favour its
appearance in the presence of pulsed fluxes of organic
matter in an environment prevalently characterised by
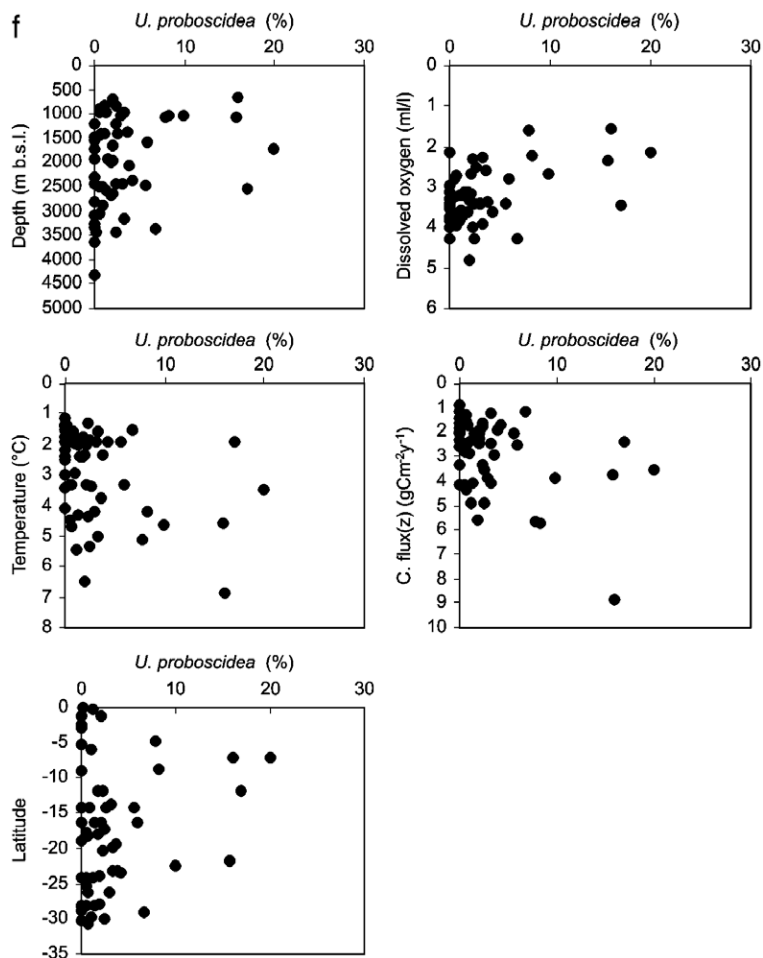oligotrophic conditions. These pulses could be related

Fig. 6 (*continued*).

to the monsoonal climate: the change of wind direction determines the presence/absence of the South Java Upwelling System, offshore Java and Sumatra, and, by affecting rainfall levels, the amount of riverine discharge offshore northwest Western Australia.

In the Indian Deep Water assemblage, as defined by Peterson (1984), one of the relevant taxa among *Pyrgo* spp., was *Pyrgo murrhina*. In the Sulu Sea, Miao and Thunell (1993) found that the abundance of their *P. murrhina* assemblage was negatively correlated with sediment organic carbon content and positively correlated with the thickness of the oxygenated layer in the sediment.

The second group is dominated by *Cibicidoides pseudoungerianus* and *Nummoloculina irregularis,* whose distribution is limited to the upper water col-

umn between 700 m and 2000 m water depth (Fig. 6), where water temperature is higher than 2.5–3 °C.

The distribution of *Cibicidoides pseudoungerianus* is strongly correlated to the carbon flux and this species becomes abundant when values of this parameter are $\geq$ 2.5 g C m^{-2} year^{-1} (Fig. 6d). A limited distribution of this species above 2000 m was observed by others, who said it is typical of neritic-bathyal (Barbieri, 1998) and bathyal settings (Spencer, 1996). In the Atlantic Ocean, *C. pseudoungerianus* is present in samples from the upper 1500 m with a carbon-flux > 2 g C m^{-2} year^{-1} (Altenbach et al., 1999).

Nummoloculina irregularis is a miliolid whose distribution is related to a salinity < 34.65 and to dissolved-oxygen concentrations of > 3 ml/l: in the eastern Indian Ocean these conditions occur mainly

Table 5
Inter-set correlation of environmental variables with Canonical Correspondence axes

	CCA1	CCA2	CCA3	CCA4
Latitude	0.31	− 0.52	0.31	− 0.04
Longitude	− 0.34	− 0.01	− 0.27	0.05
Depth	0.91	0.16	0.14	0.00
Diss. Oxygen	0.35	0.78	0.05	0.14
Salinity	0.71	− 0.41	− 0.13	0.08
Temperature	− 0.88	− 0.09	0.18	− 0.07
Pressure	0.91	0.16	0.14	0.00
Phosphate	0.10	− 0.61	− 0.25	− 0.08
Nitrate	0.22	− 0.42	−0.23	0.03
PP	0.22	− 0.29	0.38	0.10
C flux(z)	− 0.83	− 0.20	0.36	0.11
$H(S)$	− 0.54	0.22	− 0.46	0.00
E	− 0.59	0.34	− 0.40	0.05
D	0.41	− 0.13	0.32	0.04
α	− 0.45	0.31	− 0.38	− 0.08

south of 20°S. The low salinity level (34.4), which characterises the latitudinal and depth range where this species is found, is due to the presence of the Antarctic Intermediate Water (AAIW). High dissolved-oxygen concentrations are related to two major factors: the presence of the AAIW, whose oxygen concentration is > 4 ml/l, and low primary productivity at the sea surface (Fig. 1), which results in a low organic carbon flux to the sea floor. When little organic matter reaches the sea floor, there is no oxygen depletion related to its oxidation. Miliolid taxa have been associated with increased ventilation in the Arabian Sea (den Dulk et al., 2000). This taxon is not found at latitudes and depths where low salinity is due to the presence of the Indonesian Intermediate Water (IIW), which has low dissolved-oxygen concentrations (< 2 m/l). Salinity levels do not appear to play a role as important as dissolved-oxygen concentrations.

Based on DCA axis 2 results, *Uvigerina proboscidea* is positively correlated with the carbon flux and negatively with the dissolved-oxygen concentration. The percentage of this species is higher for values of the carbon flux of ≥ 3.5 g C m^{-2} year^{-1} and of dissolved-oxygen concentration below < 3 ml/l (Fig. 6f). The distribution of *U. proboscidea* is mainly limited to regions north of 25°S and between 700 and 2000 m depth. These spatial ranges are characterised by two factors: (a) the presence of oxygen-depleted water masses such as Indonesian Intermedi-

ate Water (IIW) and North Indian Intermediate Water (NIIW) and (b) high primary productivity at the sea surface, with consequent high carbon flux (Fig. 6f). In one sample (B9442) at a depth greater than 2000 m this species has a high relative abundance, but in this sample the carbon flux is above ≥ 3.5 g C m^{-2} year^{-1}. The distribution of *U. proboscidea* thus might be related to the co-variance of these two parameters: oxygen and carbon flux, which are commonly correlated because the dissolved-oxygen concentration is determined by its base-level value typical for each water mass combined with the oxygen depletion due to the oxidation of organic matter. Rathburn and Corliss (1994) observed that the abundance of *U. proboscidea* in the Sulu Sea was related to high organic carbon values irrespective of bottom-water oxygen levels. Miao and Thunell (1993) identified a the *Uvigerina* spp. assemblage in that same ocean, and in the South China Sea the *Globocassidulina subglobosa/Uvigerina* assemblage, both abundant above 1500 m, at the shallowest oxygen penetration in the sediment and the highest carbon content in the surface sediments. In the Indian Ocean, *U. proboscidea* has been utilised in palaeoenvironmental studies as an indicator species of past periods of enhanced productivity periods by, e.g. Gupta and Srinivasan (1992) and Wells et al. (1994).

5.1. Faunal trends

The percentages of the three benthic foraminiferal faunal groups were correlated with the environmental variables.

The calcareous-infaunal species group seems to be typical of a shallow and relatively warm environment characterised by a high carbon flux rate and low dissolved-oxygen concentrations. The positive correlation with longitude (Table 6) could reflect the fact that these conditions are found close to the margins of the continental shelves, in areas with a high primary productivity at the sea surface. In the eastern Indian Ocean, primary productivity at the sea surface shows a NW–SE gradient: values increase while moving from offshore the western Western Australia coast towards the Indonesian region and the Banda Sea (Fig. 1). At shallow depths along this gradient, the carbon flux increases while the concentration of dissolved oxygen concen-
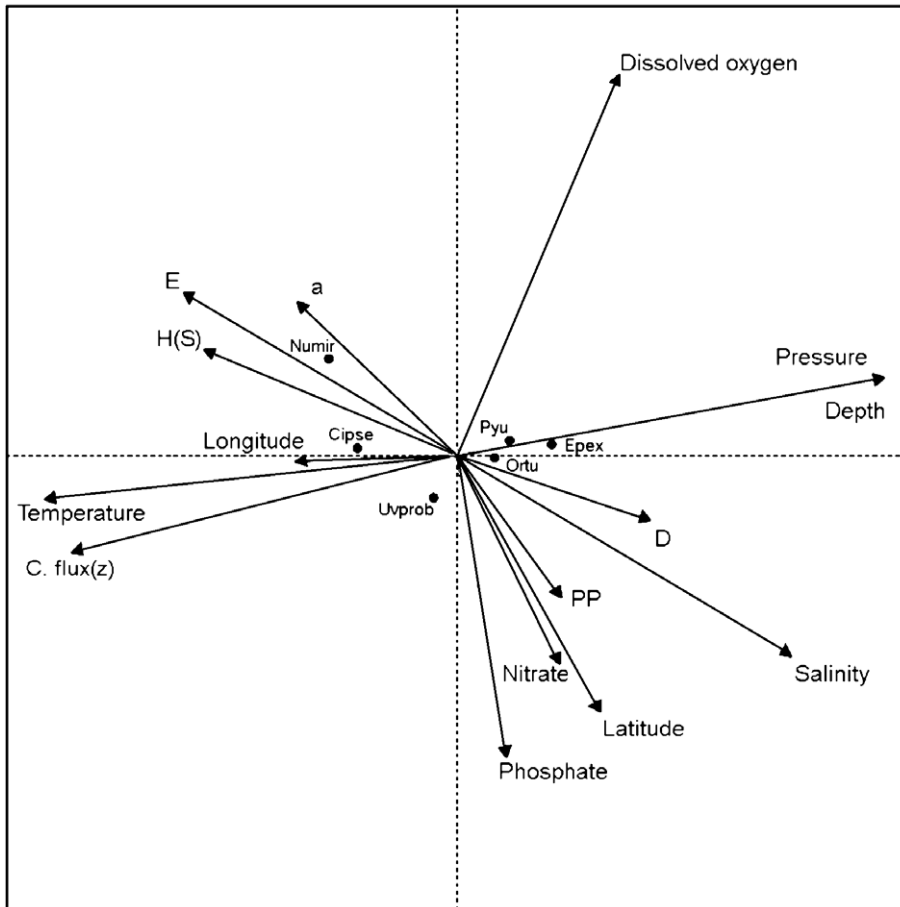
Fig. 7. Diagram showing the relationships between the environmental variables (arrows) and the first two CCA axes (see text for further explanation). The length of each arrow indicates the influence of each variable on the two axes and the angles between the arrows and the axes are inversely proportional to the correlation variable-axis. The six species individuated with DCA are also plotted on the diagram and their position outlines their relationships with the CCA axes and with the environmental variables. Species codes: Cipse=*Cibicidoides pseudoungerianus*; Numir=*Nummoloculina irregularis*; Ortu=*Oridorsalis tener umbonatus*; Epex=*Epistominella exigua*; Pyu=*Pyrgo murrhina*; Uvprob=*Uvigerina proboscidea*.

tration decreases, due to the presence of oxygen-depleted water masses (IIW and NNIW) and the oxidation of organic matter. Infaunal taxa thrive under an enhanced carbon supply as reported by Rathburn and Corliss (1994), Schmiedl et al. (1997) and Gooday and Rathburn (1999). The studied area is characterised by prevalently oligo-trophic/mesotrophic conditions. In such an environment, the living conditions for infaunal species become progressively more favourable (Jorissen et al., 1995): if more organic matter reaches the sea floor, more of it will be buried in the sediment,

representing an increased food source for the infau-nal taxa (e.g., Fontanier et al., 2002).

The porcellaneous species, on the other hand, seem to prefer environmental conditions charac-terised by low salinity, high dissolved-oxygen con-centrations, low concentrations of nutrients and high species-diversity. These conditions are present main-ly in the southern region, where the presence of AAIW causes the occurrence of low salinity levels and dissolved oxygen concentrations are high be-cause little organic matter reaches the sea floor due to the low primary productivity levels. This supports

Table 6
Correlation coefficient between the percentages of the agglutinated, calcareous-infaunal and porcellaneous taxa and the environmental variables considered in this study

	Agglutinated	Calcareous-infaunal	Porcellaneous
Latitude	− 0.11	0.01	− **0.38**
Longitude	0.05	**0.32**	0.09
Depth	0.17	− **0.51**	− 0.14
Dissolved oxygen	0.15	− **0.54**	**0.39**
Salinity	0.05	− 0.08	− **0.44**
Temperature	− 0.17	**0.46**	0.08
Pressure	0.17	− **0.51**	−0.14
Phosphate	0.05	0.19	− **0.31**
Nitrate	0.01	0.11	− **0.31**
PP	0.05	0.00	− 0.21
C flux(z)	− 0.17	**0.53**	0.02
$H(S)$	**0.28**	0.21	0.37
E	0.23	0.12	**0.40**
D	− **0.29**	− 0.20	− **0.32**
α	**0.49**	0.06	**0.33**

Those correlations significant at $p > 0.05$ are indicated in bold.

the observations from other regions, which indicate that this group of taxa is indicative of enhanced ventilation (den Dulk et al., 2000; Huang et al., 2002).

6. Conclusions

This study links benthic foraminifera from 57 coretops from the eastern Indian Ocean with environmental variables. The possible relations between foraminiferal distribution and oceanographic characteristics in this area have been investigated considering different variables identifying the water masses described for the region: temperature, salinity, oxygen concentration. Concentrations of nutrients (nitrate and phosphate) also have been included. In order to define possible links with processes occurring at the surface of the ocean, levels of primary productivity were used to estimate organic carbon flux at the sea floor, utilising Suess' (1980) formula.

The distribution of benthic foraminifera appears to be primarily controlled by depth and the first ordination axis produced by both the ordination techniques used is strongly correlated with this factor. Correlation coefficients and Canonical Corre-

spondence Analysis (CCA) outline how several of the measured environmental variables are significantly correlated to this parameter. Therefore, the observed faunal depth-related patterns appear to be the consequence of a co-variation of different factors: temperature, carbon flux, salinity, dissolved oxygen, phosphate.

Detrended Correspondence Analysis (DCA) was performed on a group of selected species (Section 2) in order to define the relationship between benthic foraminiferal faunas and environmental variables.

Two groups of species were identified by the first ordination axis:

(1) *Oridorsalis tener umbonatus*, *Epistominella exigua* and *Pyrgo murrhina* whose percentages increase with depth. These three taxa prefer a cold and well-oxygenated environment, where the carbon flux to the sea floor is low. In this group of species, two taxa are interpreted as indicators of reduced food availability: *O. tener umbonatus* and *P. murrhina*. *E. exigua* dominates the faunas in the samples in which it is found. This feature is interpreted as the expression of an opportunistic behaviour (*r*-strategist) triggered by pulsed fluxes of organic matter to the sea floor. *E. exigua* could be a seasonality indicator and its blooms could be associated with the presence of the South Java Upwelling System, offshore Java and Sumatra, or an increased riverine discharge offshore northwest Western Australia.

(2) *Cibicidoides pseudoungerianus* and *Nummoloculina irregularis*: these two species are typical of shallow depth. *C. pseudoungerianus* is typical of a warm environment and a high carbon flux. *N. irregularis* is associated with high dissolved oxygen concentrations. The presence of this species is mainly limited to a region south of 20°S, and depths between 700 m and 2000 m b.s.l., where AAIW present. The presence of AAIW (characterised by relatively low salinity and high dissolved-oxygen concentrations) and low primary productivity create the ideal conditions for this species.

Another species was identified by mean of axis 2 of DCA: *Uvigerina proboscidea*. This species thrives in areas characterised by carbon flux ≥ 3.5 g C m^{-2}

year^{-1} and low dissolved-oxygen concentrations (<3 ml/l). These conditions occur where high primary productivity at the sea surface leads to a high carbon flux with subsequent low oxygen levels, partially due to the presence of oxygen-depleted intermediate water masses (IIW and NIIW).

The three major groups of taxa (agglutinated, calcareous-infaunal and porcellaneous) were correlated with environmental variables considered in this study. Calcareous-infaunal taxa are indicative of high carbon-flux rates and low dissolved-oxygen concentrations, whereas porcellaneous taxa indicate high dissolved-oxygen.

Acknowledgements

Appendix A. Faunal references for the species used for statistical analyses

Anomalina globulosa—Barker, 1960, p. 117, pl. 94, Figs. 4, 5;

Astrononion echolsi—Anderson, 1975, p. 94, pl. 11, Fig. 4; Corliss, 1979b, p. 8, pl. 3, Figs. 16–17; Mead, 1985, p. 235, pl. 4, Figs. 3, 4;

Bolivina robusta—Cushman, 1942, p. 17, pl. 2 Fig. 2; Van Marle, 1988, p. 139, pl. 1, Fig. 26; Hess, 1998, p. 76, pl. 10, Fig. 3;

Bolivina seminuda—Cushman, 1942, p. 26, pl. 7 Fig. 6; Heremelin, 1989, p. 60, pl. 10, Figs. 17, 18;

Bolivinita quadrilatera—Cushman, 1942, p. 2, pl. 1, Figs. 1–4; Barker, 1960, p. 86, pl. 42, Figs. 8–12;

Brizalina dilatata = *Bolivina dilatata* Reuss, Mendes et al., 2004, pl. 2, Fig. 1;

Brizalina semilineata—Van Mar1e, 1988, p. 147, pl. 5, Figs. 7, 8;

Bulimina aculeata—Van Marle, 1988, p. 147, pl. 5, Fig. 17; Sven, 1992, p. 45, pl. 5, Fig. 9a, b; den Dulk, 2000, p. 167, pl. 2, Figs. 2, 3;

Bulimina alazanensis—den Dulk, p. 167, pl. 2, Fig. 5; Hess, 1998, p. 76, pl. 10, Fig. 10;

Bulimina costata—Barker, 1960, p. 104, pl. 51, Figs. 11, 13;

Bulimina marginata—Murray, 1971, p. 119, pl. 19;

Cassidulina crassa—Boltovsky, 1978, p. 154, pl. 2, Fig. 19; Van Marle, 1991, p. 9, Figs. 13–15;

Cassidulina laevigata—Hess, 1998, p. 77, pl. 13, Fig. 8;

Cassidulina reflexa—Phleger et al., 1953, p. 45–46, pl. 10, Figs. 6, 7;

Ceratobulimina pacifica—Cushman and Harris, 1937, p. 176, pl. 29, Fig. 9a–c; Van Marle, 1988, p. 143, pl. 3, Figs. 21–23;

Chilostomella oolina—Barker, 1960, p. 114, pl. 55, Figs. 12–14, 17, 18; Ingle and Kolpack, 1980, p. 132, pl. 6, Figs. 9, 10; Van Marle, 1991, p. 128, pl. 10, Figs. 12, 13;

Cibicidoides bradyi—Corliss, 1979b, p. 9, pl.3, Figs. 1–3; Heremelin, 1989, p. 85, pl. 17, Figs. 2–4;

Cibicidoides kullenbergi—Corliss, 1979b, p. 10, pl. 3, Figs. 4–6;

Cibicidoides pseudoungerianus—Hess, 1998, p. 78, pl. 16, Figs. 1, 2;

Cibicidoides robertsonianus—van Morkhoven et al., 1986, p. 41, pl. 11, Fig. 1a–c;

Cibicidoides wuellerstorfi—Hess, 1998, p. 78, pl. 16, Figs. 5–7;

Eggerella bradyi—Wells et al., 1994, p. 192, pl. 1, Figs. 11, 16;

Ehrenbergina trigona—Phleger et al. 1953, p. 46, pl. 10, Figs. 12, 13;

Epistominella exigua—Phleger et al., 1953, p. 43, pl. 9, Figs. 35, 36; den Dulk, 2000, p. 169, pl. 7, Fig. 4a–b;

Epistominella umbonifera—Corliss, 1979b, p. 7, pl. 2, Figs. 10–12;

Fursenkoina fusiformis—Violanti, 2000, p. 485, pl. 3, Fig. 7;

Gavelinopsis lobatulus—Barker, 1960, p. 182, pl. 88, Fig. 1; Van Marle, 1991, p. 151, pl. 14, Figs, 10–12;

Globobulimina pacifica—Ingle and Kolpack, 1980, p. 136, pl. 2, Figs. 7, 8; Van Marle, 1991, p. 90, pl. 5, Figs. 11, 12;

Globocassidulina subglobosa—Van Marle, 1988, p. 143, pl. 5, Fig. 22; Van Marle, 1991, p. 120, pl. 10, Figs. 10, 11; Hess, 1998, p. 81, pl. 13, Fig. 14;

Gyroidinoides altiformis—Jones, 1994, p. 106, pl. 107, Fig. 6a–c;

Gyroidinoides lamarckianus=*Gyroidina lamarckiana* (d'Orbigny), Phleger et al. 1953, p. 41, pl. 8, Figs. 33, 34; Hess, 1998, p. 82, pl. 15, Figs. 7–9;

Gyroidinoides orbicularis—Corliss 1979b, pl. 5, Figs. 1–3;

Gyroidinoides polius—Mead, 1985, p. 238, pl. 5, Figs. 4–7;

Gyroidinoides soldanii—Corliss, 1979b, pl. 5, Figs. 4–6;

Hauerinella inconstans—Barker, 1960, p. 24, pl. 12, Figs. 5, 7, 8;

Hoeglundina elegans—Barker, 1960, p. 215, pl. 105, Figs. 3, 4, 5, 6;

Hyalinea balthica—den Dulk, 2000, p. 170, pl. 4, Fig. 9a, b;

Karreriella bradyi (Cushman)—Van Marle, 1988, p. 147, pl. 5, Figs. 23, 24;

Laticarinina pauperata—Boltovskoy, 1978, p. 162, pl. 4, Fig. 32; Van Marle, 1991, p. 153, pl. 15, Figs. 13–15;

Martinottiella communis—Barker, 1960, p. 98, pl. 48, Figs. 1, 2, 5;

Melonis barleeanum—Corliss, 1979b, p. 10, pl. 5, Figs. 7, 8; Wells et al., 1994, p. 197, pl. 3, Figs. 11, 12; Hess, 1998, p. 84, pl. 13, Fig. 5;

Melonis pompilioides—Ingle and Kolpack, 1980, p. 142, pl. 9, Figs. 14, 15; Van Marle, 1991, p. 187, pl. 20, Figs. 4–6;

Miliolinella oblonga=*Miliolinella* (?) *oblonga* (Montagu), Barker, 1960, p. 10, pl. 5, Fig. 4a, b;

Nonionella turgida—*Noninella turgida* (Williamson), Violanti, 2000, p. 487, pl. 5;

Nummoloculina irregularis—Barker, 1960, p. 2, pl. 1, Figs. 17, 18; Van Marle, 1991, p. 68, pl. 4, Fig. 3; Sven, 1992, p. 77, pl. 4, Fig. 14;

Oridorsalis tener umbonatus—Pflum and Frerichs, 1976, p. 120, pl. 6, Figs. 5–7;

Osangularia cultur—Wells et al., 1994, p. 199, pl. 4, Fig. 3;

Pullenia bulloides—Hess, 1998, p. 87, pl. 13, Figs. 9, 10;

Pullenia quinqueloba—Van Marle, 1988, p. 148, pl. 3, Fig. 5; Hess, 1998, p. 87, pl. 13, Figs. 11, 12;

Pyrgo depressa—Wells et al., 1994, p. 195, pl. 2, Figs. 3, 6;

Pyrgo elongata—Barker, 1960, p. 4, pl. 2, Fig. 9a, b;

Pyrgo lucernula—Barker, 1960, p. 4, pl. 3, Figs. 5, 6;

Pyrgo murrhina—van Morkhoven et al., 1986, p. 50, pl. 15, Figs. 1, 2; Hess, 1998, p. 88, pl. 9, Fig. 1;

Quinqueloculina seminulum—Van Marle, 1991, p. 65, pl. 3, Figs. 11–13;

Quinqueloculina venusta—Boltovskoy, 1978, p. 167, pl. 6, Figs. 32–33;

Rectobolivina dimorpha—Van Marle, 1988, p. 148, Fig. 2;

Robertina tasmanica—Barker, 1960, p. 102, pl. 50, Fig. 17;

Sigmoilopsis schlumbergeri—Wells et al., 1994, p. 195, pl. 2, Fig. 7;

Siphotextularia catenata—Corliss, 1979b, p. 5, pl. 1, Fig. 7;

Siphotextularia curta—Heremelin, 1989, p. 31, pl. 1, Fig. 4;

Sphaeroidina bulloides—Hess, 1998, p. 90, pl. 9, Fig. 14;

Textularia agglutinans—Barker, 1960, p. 88, pl. 43, Figs. 1–3;

Textularia lythostrota—Heremelin, 1989, p. 30, pl. 1, Figs. 2–5;

Textularia pseudogramen—Barker, 1960, p. 88, pl. 43, Figs. 9–10; Van Marle, 1988, p. 139, pl. 1, Fig. 14;

Trioculina tricarinata—Van Marle, 1988, p. 149, pl. 4, Fig. 24; Hermelin, 1989, p. 38, pl. 3, Figs. 6, 7;

Triloculina trigonula—Barker, 1960, p. 6, pl. 3, Figs. 15, 16;

Uvigerina peregrina—Boltovskoy, 1978, p. 171, pl. 8, Fig. 4; Ingle and Kolpack, 1980, p. 146, pl. 3, Fig. 6; Wells et al., 1994, p. 199, pl. 4, Figs. 12, 13;

Uvigerina proboscidea—Boltovskoy, 1978, p. 171, pl. 8, Figs. 22, 23; Van Marle, 1991, p. 106, pl. 8, Figs. 12–14; Wells et al., 1994, p. 199, pl. 4, Figs. 9, 10, 14;

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2005.03.005.

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