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Planktonic foraminiferal assemblages in surface sediments from the southwest African continental margin

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ABSTRACT

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The relative abundance and distribution of planktonic foraminifera species on the southwest African continental margin have been determined from 152 surface sediment samples. Of the 23 recorded taxa, only 8 make a significant contribution to the foraminiferal assemblages. Individual species proportions are closely related to the surface water hydrography of the Benguela System and the associated upwelling phenomena. Three foraminiferal assemblages can be distinguished by correlation analysis on the abundances of the major taxa. Species composition of these assemblages range from polar taxa in the upwelling area (left-coiling *Neogloboquadrina pachyderma* and *Globigerina quinqueloba*) to transitional taxa in the offshore oligotrophic environment (*Globorotalia inflata* and *Globorotalia truncatulinoides*). *Globigerina bulloides* and right-coiling *Neogloboquadrina pachyderma* are preferentially distributed in the highly productive intermediate zone of the Benguela System, where upwelled and oligotrophic offshore waters mix. Variability of the hydrological processes (upwelling intensity, strength of the frontal features) may be inferred from frequency variations of individual species, and diversity patterns.

Introduction

Living species of planktonic foraminifera are globally distributed in distinct latitudinal belts, and have been grouped into five major provinces, which show a close relationship to the hydrographic features of oceanic water masses (Bé and Tolderlund, 1971; Bé and Hutson, 1977). Surface currents control to a great extent the shape of these faunal provinces (Parker, 1971). This is especially noticeable in the area of the southwest African continental margin, where the Benguela Current, one of the major eastern-boundary currents, carries the transitional faunal zone equatorward of its usual latitudinal limits (Bé and Tolderlund, 1971).

Continental-shelf circulation off the western coast of southern Africa is quite complex, as it involves the interaction of different water masses on a small geographical scale. A combination of the Benguela Current, forming the eastern branch of the South Atlantic anticyclonic gyre, and the prevailing southerly winds, results in major coastal upwellings of cold, nutrient-rich waters along the west coast of South Africa and Namibia. Studies on the distribution of inshore marine fauna, mainly crustaceans and molluscs, suggest that the Benguela System, which extends to within 20° of the equator, forms an effective cold-water barrier to the poleward movement of warm-water Atlantic-Ocean species and to the equatorward movement of warm-water Indian-Ocean species (Morgan and Wells, 1991). Recent observations of Lutjeharms and Stockton (1987), Meeuwis and Lutjeharms (1990) and Shannon et al. (1990), among others, however, provide evidence of intra-annual instabilities at the southern and northern boundaries of the Benguela System, as well as of relaxation of the oceanic thermal front during quiescent upwelling conditions. These phenomena may allow the

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transfer of fauna from the northern and southern warm areas to the Benguela region.

Previous micropalaeontological studies of planktonic foraminifera off South West Africa (see review by Rogers and Bremner, 1991) have been based on a small number of surface-sediment samples and dealt with only localised areas and hydrographic features of the Benguela System (e.g. Herbert, 1987; Rogers, 1977; Siesser, 1973). The only extensive regional study by Lowry (1987) listed the planktonic foraminiferal species encountered in several traverses across the continental margin, and recognised a single Benguela assemblage dominated by the polar species *Neogloboquadrina pachyderma* and the transitional species *Globorotalia inflata*.

The present study relies on an extensive collection of surface sediments and documents the distribution of planktonic foraminiferal species on the southwest African continental margin, and their relationships with the complex surface-water hydrography of the Benguela System. The approach, geographic area, and material in this study are similar to those used in a previous paper dealing with Recent calcareous nannofossils (Giraudeau, in press). These studies are part of a larger project on the reconstruction of the palaeoceanography of the Benguela System, based on the community structure of planktonic microfossils.

Hydrography

The ocean circulation off the west coast of southern Africa has been summarized by Nelson and Hutchings (1983), Shannon (1985), and Pearce (1991) amongst others. The Benguela Current is the broad equatorward drift of cool surface waters flowing from 34°S (Cape Town) along the southwest African coast (Fig. 1). At 23°S (Walvis Bay), a divergence separates the main western stream of the current from its coastal branch flowing further north off Angola (Moroshkin et al., 1970).

The northern boundary of the System is the convergence zone between the poleward-flowing Angola Current and the coastal branch of the Benguela (A in Fig. 1). The position of this front varies seasonally between 14° and 16°S, although poleward intrusion of warm Angola water can be traced occasionally as far south as 23°S (Meeuwis and Lutjeharms, 1990). The southern boundary of the Benguela System, the Agulhas Front (B in Fig. 1), is defined as the retroflection area of the Agulhas Current. Equatorward advection of rings of Agulhas water beyond Cape Town are a permanent feature of the southern Benguela (Lutjeharms and Valentine, 1981).

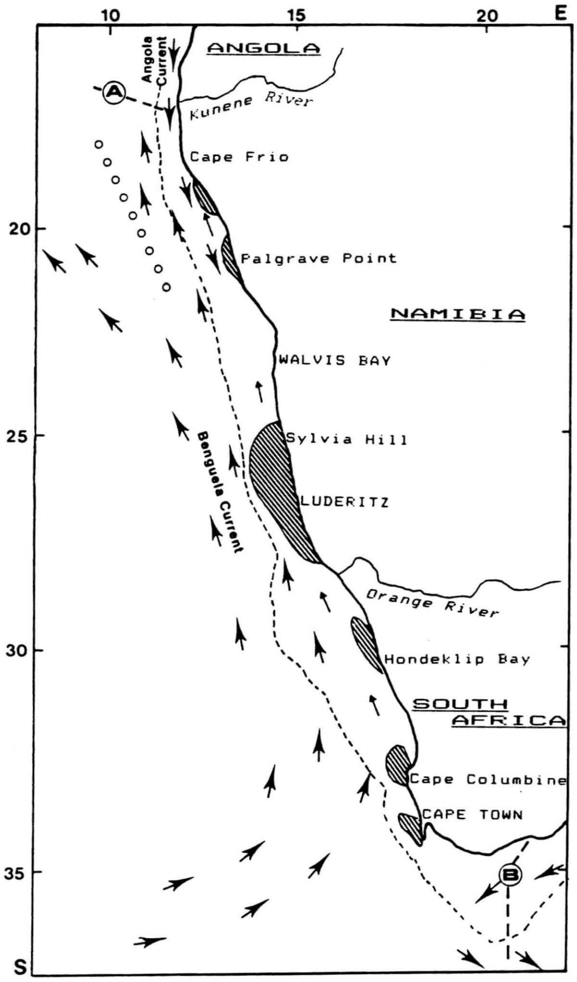

Fig. 1. Circulation patterns of the Benguela System (after Bremner, 1983; Shannon, 1985). *A* = Angola front; *B* = Agulhas Front; circles = Benguela Divergence; dashed line = shelfbreak; shaded areas = main upwelling cells.

The combined effect of the Benguela drift and the prevailing southerly winds results in coastal upwelling of cold, low-salinity, nutrient-rich waters along the 1700 km of coastline between 35° and 20°S. The location of the thermal front, separating the coastal upwelled water from the offshore, oligotrophic water, roughly coincides with the position of the shelfbreak. Maximum mean annual sea-surface salinity and temperature differences between coastal and offshore environment are 0.7%. and 6°C, respectively (Fig. 2b and c). Variabilities in the velocity and frequency of the windstress result in regional modulations of the upwelling process. Regions south of 31°S (Hondeklip Bay) and north of 25°S (Sylvia Hill) experience a distinct seasonal upwelling pattern (upwelling strongest in spring–summer and winter, respectively), whereas from Hondeklip Bay (31°S) to Sylvia Hill (25°S), upwelling is perennial, this region experiencing the most intense and persistent upwelling along the west coast. Farther north, the surface waters become progressively warmer and more saline, due to reduced upwelling and the admixture of Angola-derived water (Fig. 2b and c).

Data and Methods

Samples used in this study are part of the collection of surficial sediments off South Africa and Namibia collected during numerous cruises of the R.V. *Thomas B. Davie* by personnel of the Joint Geological Survey/University of Cape Town Marine Geoscience Unit.

Initially, 164 grabs and short gravity cores were selected and processed for micropalaeontological analysis. For each sample, a small quantity of sediment was retained for the nannofossil examination, while the remainder was washed through a set of 63 and 125 µm sieves. On average, 300 tests of planktonic foraminifera per sample were picked from each > 125 µm fraction, giving a 95% chance of finding species at the 0.5% abundance level (McIntyre and Bé, 1967). Several coastal samples had only 100 to 300 specimens, but they represent low-diversity assemblages for which a reliable description can be obtained from smaller counts.

Examination of smear-slides for nannofossil assemblages showed that all but seven samples range into the *Emiliania huxleyi* Acme Zone of Gartner (1977), i.e. they are younger than 80,000 yrs B.P. (Thierstein et al., 1977). These seven samples were removed from the database, together with five samples located on the Kunene Shelf, which show either evidence of carbonate dissolution (high amount of foraminiferal fragments) or extreme dilution by terrigenous components. The remaining 152 surface samples (Table A1, see Appendix) are evenly distributed on the continental margin from 35° to 17°S (Fig. 2a).

Planktonic foraminifera were identified following the classical taxonomic concepts of Bé (1967) and Parker (1962). In addition, *Globorotalia menardii* s.s. and *Globorotalia tumida* were combined into the taxonomic category *G. menardii*, as these two closely related species cannot be readily differentiated and have similar geographic distributions in the World Ocean (Dowsett and Poore, 1990). *Neogloboquadrina pachyderma* was split into left- and right-coiling individuals, and the abundance of each expressed in terms of the total abundance of the planktonic-foraminiferal assemblages, because sinistral and dextral individuals of this species have different geographical distributions (Bé and Tolderlund, 1971; Kennett, 1976). The transitional forms [P–D intergrade of Kipp (1976)] between *N. pachyderma* and *Neogloboquadrina dutertrei* were combined with right-coiling *N. pachyderma*. In this context, the species name *N. dutertrei* is allocated to specimens of *Neogloboquadrina* which have at least 5 chambers and a wide umbilicus, whereas right-coiling *N. pachyderma* includes the tightly coiled forms with 4 or 4.5 chambers and a small umbilicus, usually bordered by a lip.

Hydrographic data, provided by the South African Data Centre for Oceanography (SADCO), in the form of winter and summer sea-surface temperatures and salinities, were used for plotting mean annual conditions (Fig. 2b and c). The geographic resolution of the temperature and salinity data are 0.25° and 1°, respectively.

To associate, statistically, foraminiferal taxa with similar distributional patterns, a standard correlation analysis (Pearson product-moments correlation) was used to generate a matrix of correlations coefficients from the original matrices of relative species frequencies. Correlation coefficients between hydrological data (mean annual sea-surface temperature and salinity) and the abundance of invidual taxa at the sample locations were also calculated.

The Shannon–Weaver diversity index and

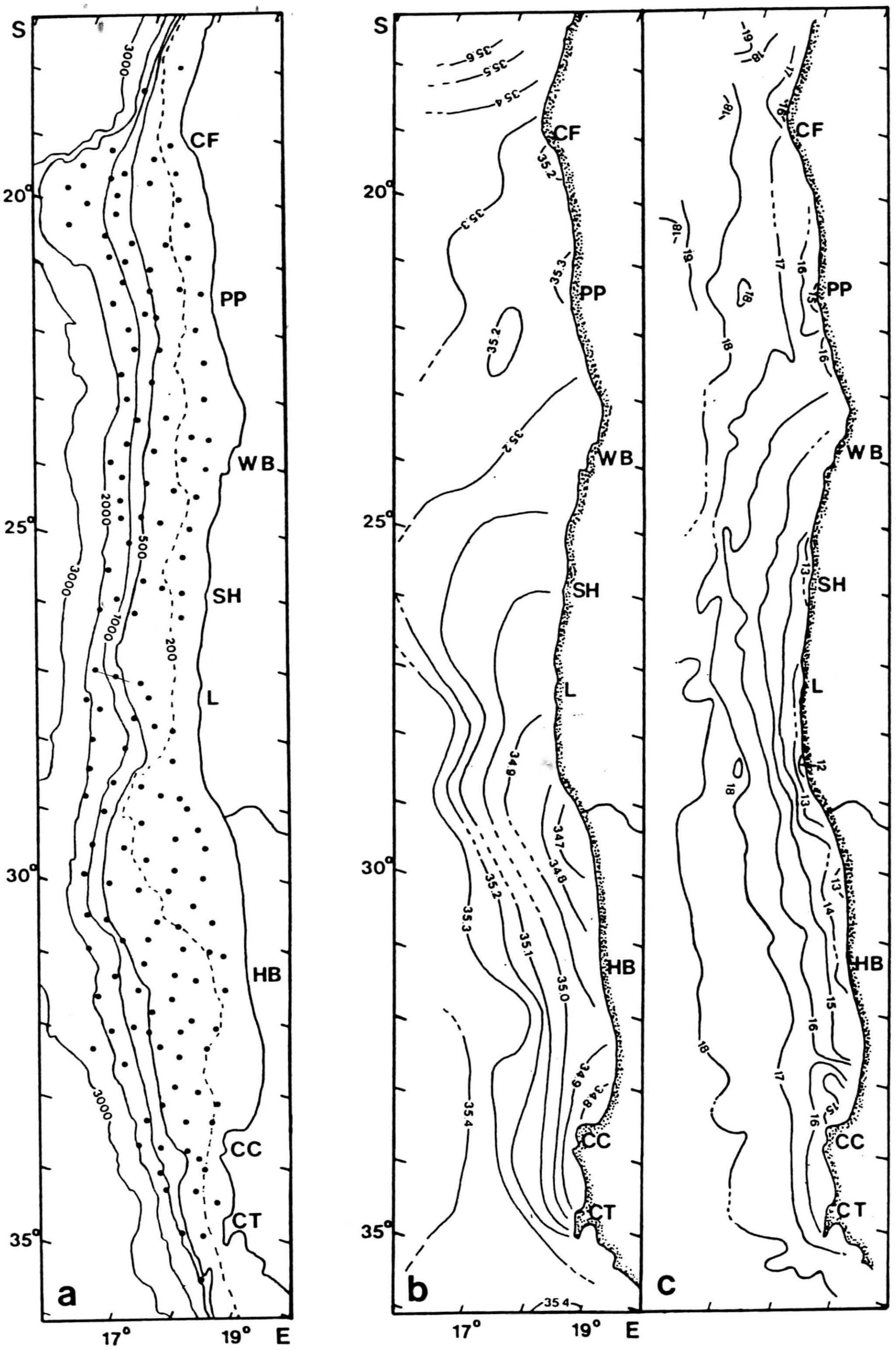

Fig. 2. (a) Bathymetric chart of the study area showing sample locations (dots). Depths in meters. (b) Mean annual sea-surface salinity (‰). (c) Mean annual sea-surface temperature (°C). Compiled from data provided by the South African Data Centre for Oceanography (SADCO).

Buzas–Gibson equitability index were computed from the species-count data. These supplement water-mass characteristics defined by foraminiferal assemblages and environmental properties (Ottens, 1991).

Results

Distributional patterns of individual species

Twenty four taxa were identified within the study area (Table 1). Of these, 8 occur with a maximum frequency >10%. The other 16 species comprise less than 10% in all of the 152 surface samples. Distributional patterns of the 8 major taxa are described in order of decreasing average abundance.

With an average abundance of 24.7%, *Globorotalia inflata* is the most common taxon preserved in the surface sediment of the study area. This correlates with the distribution of living specimens in Atlantic surface waters, where *G.inflata* is the only indigenous species of the Transitional faunal zone which extends in an equatorward direction along the Benguela region (Bé and Tolderlund, 1971; Kipp, 1976). *G. inflata* reaches a peak abundance of 70% south of 27°S (Lüderitz; Fig. 3a), where it is associated with the main flow of the Benguela Current. Although poorly represented in coastal samples, this species can dominate the foraminiferal assemblages in middle-shelf environments with reduced upwelling conditions, as between 27° and 28°S and south of 32°S (Hondeklip Bay). Average values are lower north of 27°S, but abundances still increase in an offshoreward direction, despite thermohaline gradients between upwelled and oligotrophic offshore waters weaker than those in the southern area.

TABLE 1

Taxonomic categories and summary statistics of their relative percent abundance

Taxa	Occurrence (%)	
	Average	Maximum
Candeina nitida	0.04	1
Globigerina bulloides	18.12	45.3
Globigerina digitata	0.00	0.4
Globigerina falconensis	0.87	8.4
Globigerina quinqueloba	3.61	25.1
Globigerina tenellus	0.01	0.9
Globigerinella aequilateralis	0.55	5.2
Globigerinita glutinata	0.30	1.9
Globigerinoides conglobatus	0.14	1.9
Globigerinoides ruber	1.11	6.6
Globigerinoides sacculifer	0.81	6.9
Globorotalia crassaformis	0.09	1.7
Globorotalia hirsuta	0.39	3.2
Globorotalia inflata	24.74	73.6
Globorotalia menardii	0.05	0.9
Globorotalia scitula	0.06	1.1
Globorotalia truncatulinoides	1.51	10.3
Hastigerina pelagica	0.07	1.1
Neogloboquadrina dutertrei	3.41	20.0
Neogloboquadrina pachyderma (R)	24.12	60.7
Neogloboquadrina pachyderma (L)	15.29	78.2
Orbulina universa	4.02	28.6
Pulleniatina obliquilocuta	0.04	2.1
Sphaerodinella dehiscens	0.00	0.4

G. inflata reaches >30% off Cape Frio in the northern part of the study area, which corresponds with the high frequencies reported for this species (between 20 and 30%) by Van Leeuwen (1989) in Recent samples on the eastern part of the Walvis Ridge. These observations raise problems, however, since the area lies east of the Moroshkin divergence and is far removed from the main oceanic branch of the Benguela (see Fig. 1). It is assumed that the interaction of the two major hydrological features in this area (the northern boundary of active coastal upwelling and the Angola front), generates an environment favorable for *G. inflata*.

Right-coiling *Neogloboquadrina pachyderma* is the second most abundant taxon and, together with *G. inflata*, accounts for an average of 50% of the total planktonic foraminifera population in the study area. Dextral *N. pachyderma* occurs mostly in Subantarctic and Transitional waters (Bé, 1969), with a preferred temperature range of 10° to 18°C (Bé and Tolderlund, 1971). As with most Subantarctic species, this taxon is eurythermal, ranging northward into subtropical, and in some cases tropical areas (Bé and Hutson, 1977; Kennett, 1979). Relative frequencies of more than 20% have been reported by Van Leeuwen (1989) in the surface sediments of the Angola Basin north of 15°S.

Distributional maps of living species by Bé and

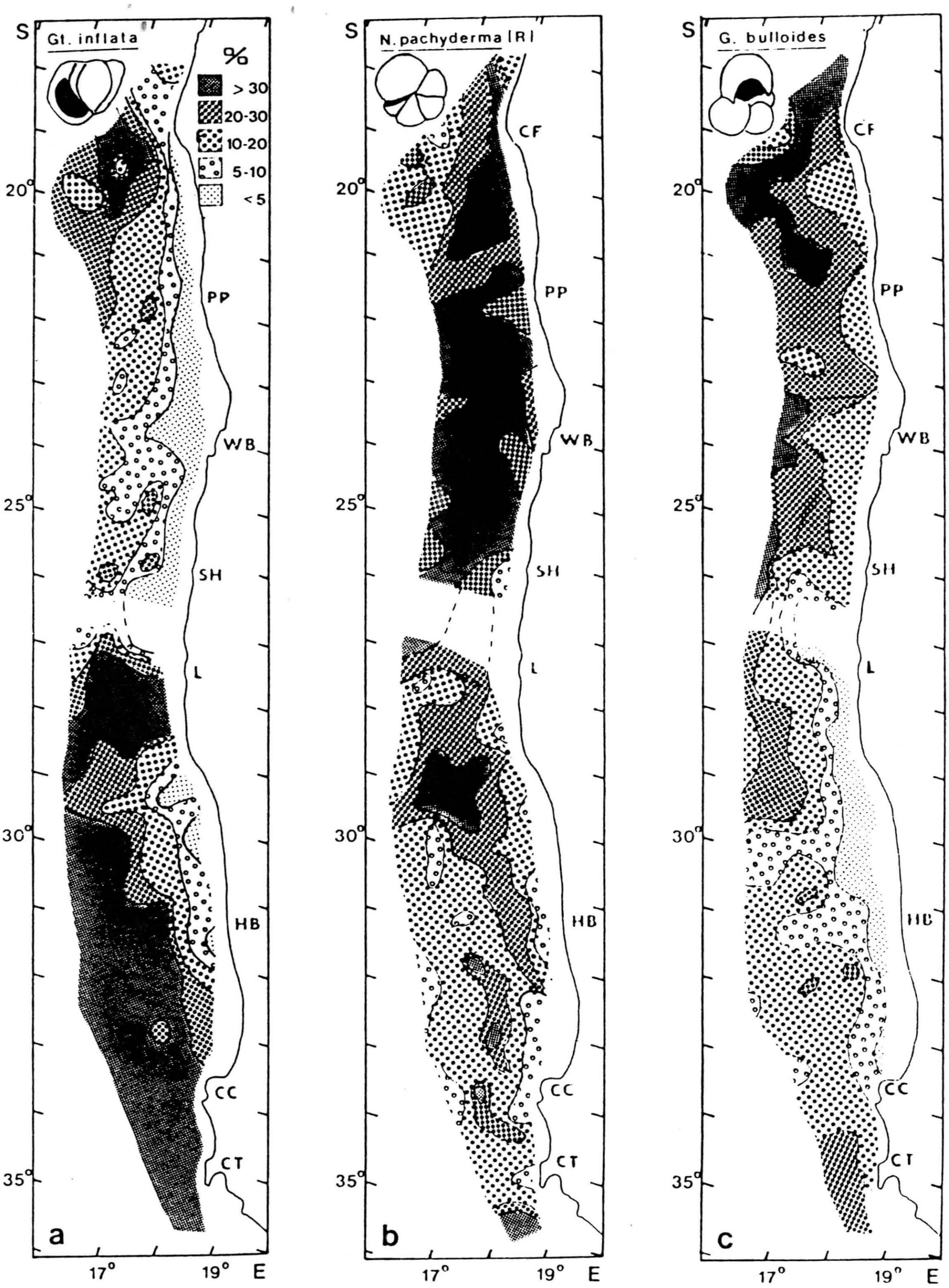

Fig. 3. Relative percent distribution of *Globorotalia inflata* (a), right-coiling *Neogloboquadrina pachyderma* (b), *Globigerina bulloides* (c).

Tolderlund (1971) indicate an isolated patch of right-coiling *N. pachyderma* along the Namibian continental margin, with higher frequencies (up to 10%) in a small area in the northern part of the Benguela System. This pattern correlates with the distribution of dextral *N. pachyderma* in the surface sediment beneath the Benguela System, although frequencies are three times higher than in the living assemblages (Fig. 3b; Table 1). This taxon is most abundant north of 26°S (Lüderitz–Sylvia Hill), where it accounts for 20 to 60% of the total planktonic foraminiferal assemblages in both shelf and slope sediments. North of 21°S (Palgrave Point), right-coiling *N. pachyderma* is concentrated more in the coastal samples, under areas influenced by the coastal branch of the Benguela Current. South of 27°S (Lüderitz), maximum abundances are restricted to a narrow band of sediments beneath the frontal region marking the transition between the coastal-upwelling cell and offshore oligotrophic water.

Globigerina bulloides is typically a subpolar species. In the southern Atlantic, maximum frequencies (>20%) occur in the region of central and northern subantarctic waters between 55° and 40°S (Kennett, 1979). From this latitudinal belt, *G. bulloides* is carried equatorward within the Benguela Current, where it dominates the living planktonic foraminiferal assemblages with frequencies locally reaching >50% (Bé and Tolderlund, 1971). This species is also found in high abundances in isolated tropical regions of upwelling such as the Cariaco Basin (Peterson et al., 1991), the western Arabian Sea (Prell and Curry, 1981; Kleijne et al., 1989), and the continental margin off northwest Africa (Thiede, 1975). As a consequence, it has been postulated that its distribution and abundance are directly related to food availability, rather than to a specific temperature-range (Reynolds and Thunnell, 1985).

Although making up locally more than 40% of the foraminiferal association (Table 1), *G. bulloides* (average occurence 18%) is not the dominant species in surface sediments beneath the Benguela System, as might be expected from the distributional maps of Bé and Tolderlund (1971, figs. 6–8, p. 120). The distribution pattern of *G. bulloides* (Fig. 3c) is similar to that of the dextral variety of *N. pachyderma*. Highest abundances occur north of 25°S (Sylvia Hill), where it is evenly distributed along the entire continental margin, with a discernible seaward gradient of increasing abundance. South of 25°S, zones of high abundance (20%) occur in the vicinity of the shelfbreak, coinciding with the seaward limit of the upwelled water. In the areas of strong coastal upwelling, between Lüderitz and Cape Columbine, *G. bulloides* is a minor component (<5%; Fig. 3c).

Left-coiling *Neogloboquadrina pachyderma* and *Globigerina quinqueloba* constitute the cold-end members of the modern planktonic foraminiferal spectrum. In the South Atlantic, their distributional maxima occur in Antarctic and Subantarctic waters (Bé and Tolderlund, 1971), although these two varieties are adapted to somewhat different optimum conditions. Left-coiling *N. pachyderma* forms up to 100% of the planktonic-foraminiferal assemblages south of the Antarctic Convergence, in surface waters with temperatures below 4°C. High abundances of *G. quinqueloba* have been recorded on both sides of the Antarctic Convergence, with a maximum up to 70% found south of Africa at 50°S for a temperature of 10°C (Bé and Hutson, 1977; Kennett, 1979). The similarity in ecological preferences of these two taxa explains their comparable distribution patterns in the surface sediments of the Benguela System.

The abundance maxima of *G. quinqueloba* and sinistral *N. pachyderma* underlie the areas of coastal upwelling. Left-coiling *N. pachyderma* (Fig. 4a) dominates the foraminiferal assemblages beneath the most intense and frequent upwelling cells, which occur in the central and southern parts of the Benguela System (Lutjeharms and Meeuwis, 1987). Locally, this taxon occurs in the highest abundances (up to 78%) found in the present study for a single species, but decreases sharply in the vicinity of the shelfbreak. In deep sediment samples (below 1000 m water-depth on the slope), left-coiling *N. pachyderma* is a minor component (<5%) of the foraminiferal assemblages.

The preference of *G. quinqueloba* for slightly warmer sea-surface temperatures than sinistral *N. pachyderma* is evident in the Benguela System (Fig. 4b). Although common in the vicinity of the Cape Columbine and Hondeklip Bay upwelling

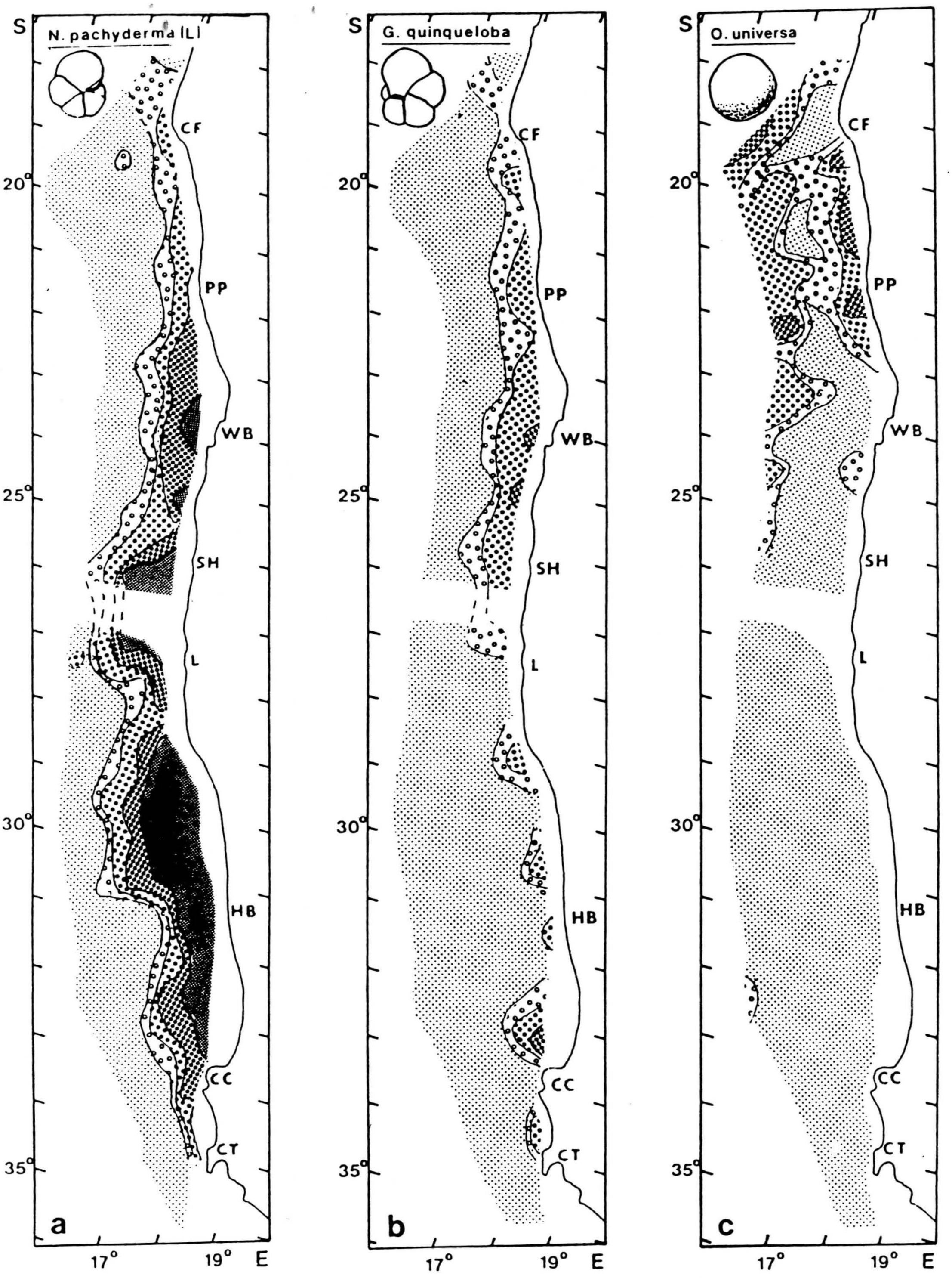

Fig. 4. Relative percent distribution of left-coiling *Neogloboquadrina pachyderma* (a), *Globigerina quinqueloba* (b), *Orbulina universa* (c). (Legend: see Fig. 3a.)

cells, *G. quinqueloba* prefers the coastal part of the northern upwelling regime, where it comprises up to 25% of the foraminiferal assemblages in diatomaceous ooze there. Thiede (1975) recorded a similar distribution on the continental margin off West Africa, where *G. quinqueloba* is the dominant species in the upwelling assemblages of the coastal diatom-rich sediments between Cape Blanc and Cape Vert.

Orbulina universa is an ubiquitous species in tropical, subtropical, and transitional waters (Bé and Tolderlund, 1971) and highest frequencies occur in the surface layer of strong current systems and upwelling regions near continental margins (Smith, 1963; Berger, 1970). Studies on both living (Bé and Tolderlund, 1971) and fossil (Bremner, 1983; Herbert, 1987) assemblages showed that *O. universa* is a common species in the northern Benguela region, with abundances typically higher than 20%. The findings of this study confirm these previous observations, although the distribution of this species is more restricted than anticipated (Fig. 4c). Highest abundances (up to 28%) occur in two distinct belts: a narrow coastal area from 22°S to 19°S which is clearly associated with the northern Namibian upwelling regime, and a more extensive zone on the upper slope from 25°S to the northern limit of the study area. South of 25°S, *O. universa* is virtually absent from the planktonic foraminiferal assemblages in both upwelling and offshore environments. *O. universa* is the only major foraminiferal species in the present study, to show such a well-developed latitudinal distribution. High abundances are probably related to the combination of warm (> 18°C) and nutrient-rich conditions, which characterize the surface waters of the northern Benguela region.

Neogloboquadrina dutertrei is a tropical–subtropical species which is particularly abundant in major current systems near continental margins. *N. dutertrei* has commonly been found in upwelling regions (Thiede, 1975; Fairbanks et al., 1982; Kroon and Ganssen, 1989; Sautter and Thunell, 1991), and is thus often referred to as a fertility index (Berger and Killingley, 1977; Peterson et al., 1991). The Benguela System appears to constitute a cold-water barrier to the development of *N. dutertrei*. Although abundant in the waters off Angola (Van Leeuwen, 1991), and off the southern tip of Africa (Bé and Hutson, 1977), this species makes up less than 5% of the living foraminiferal assemblages in the Benguela surface waters (Bé and Tolderlund, 1971).

The average relative abundance of *N. dutertrei* on the Benguela seafloor is about 3% (Table 1), agreeing with the frequency pattern in the surface waters. It is preferentially distributed south of 24°S in the deeper sediment samples (Fig. 5a). Highest abundances (up to 20%) occur seaward of the Sylvia Hill upwelling cell (25°S), while the species is common (5–10%) in plumes seaward of the Lüderitz and Hondeklip Bay upwelling cells, providing evidence of its preference for nutrient-rich waters.

Globorotalia truncatulinoides is predominantly a subtropical species, although it shows biogeographic differences between the northern and southern Atlantic surface waters. In the northern hemisphere it never ranges north of the subtropical waters, whereas in the southern hemisphere it occurs in surface waters with temperatures as low as 4°C (Kennett, 1979). In the South Atlantic, *G. truncatulinoides* is preferentially distributed in transitional waters, together with *Globorotalia inflata*, but seems to be virtually absent from the Benguela surface waters (Bé and Tolderlund, 1971). As with *N. pachyderma*, *G. truncatulinoides* shows distinct coiling provinces (Bé, 1969; Thiede, 1971), the sinistral variety dominating in transitional and subantarctic waters of the South Atlantic.

The distribution of *G. truncatulinoides* in the surface sediment of the Benguela System (Fig. 5b) is very similar to the patterns displayed by *G. inflata* (see Fig. 3a) although on average the former makes up less than 2% of the foraminiferal assemblages, i.e. 25 times less than *G. inflata*. Abundances higher than 2% are found along the main path of the Benguela Current, south of 25°S, and seaward of the area of coastal upwelling. In this area, the coiling direction is predominantly sinistral. The transition from left- to right-coiling occurs off Walvis Bay (23°S), although the northernmost nearshore samples still contain almost exclusively the sinistral variety.

The remaining 16 taxa together make up less than 5% of the total foraminiferal assemblages (Table 1). These minor species are typically sub-

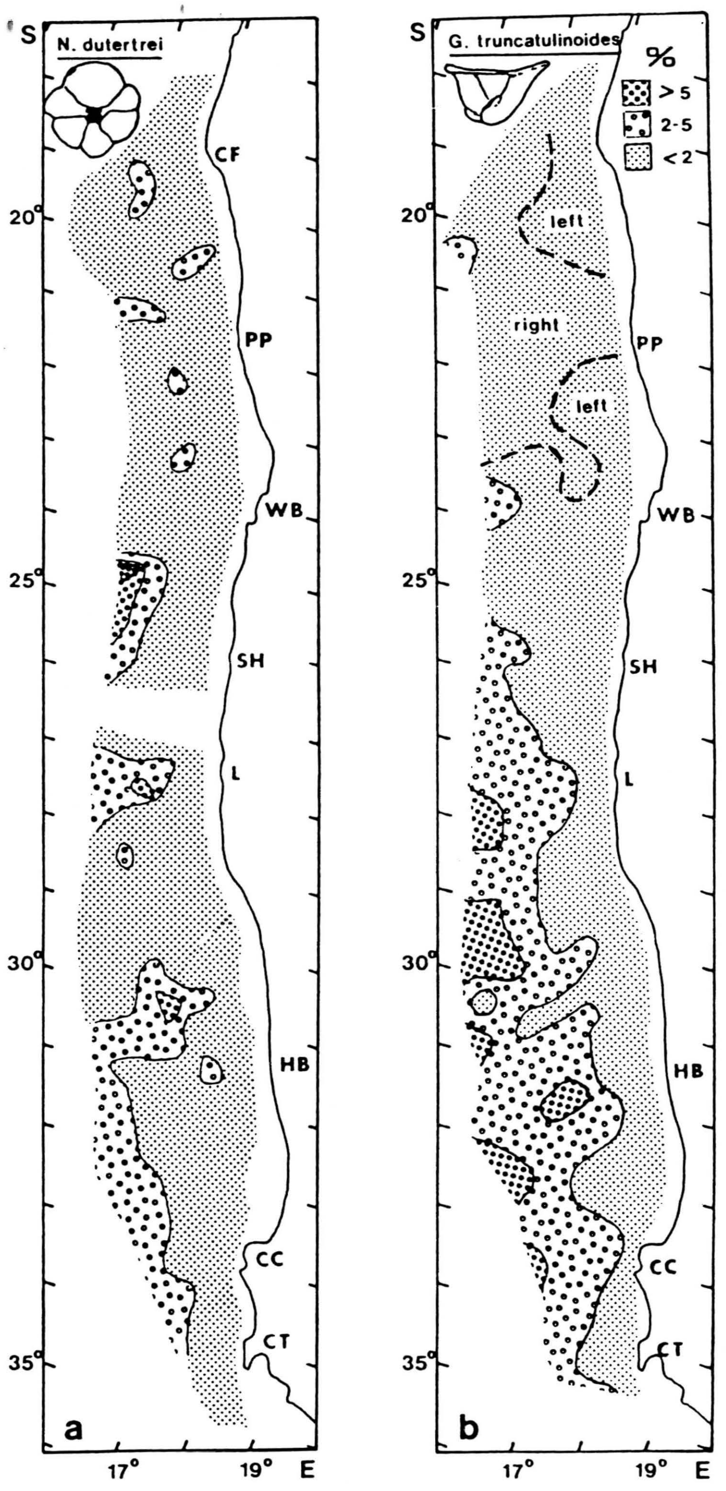

Fig. 5. (a) Relative percent distribution of *Neogloboquadrina dutertrei* (Legend: see Fig. 3a). (b) Relative percent distribution of *Globorotalia truncatulinoides*; the dashed line shows the dominance reversal between left- and right-coiling specimens.

tropical–tropical forms except *Globigerinita glutinata* (cosmopolitan), *Globorotalia hirsuta* (transitional–subtropical), and *Globorotalia scitula* (subpolar–transitional; Bé and Tolderlund, 1971; Bé and Hutson, 1977).

Correlation analysis

Results of correlation analyses applied to both foraminiferal counts and sea-surface parameters are shown in Table 2, and suggest three positively correlated pairs of taxa.

A first pair consists of species of *Globorotalia* (*G. inflata* and *G. truncatulinoides*). These are negatively correlated with two other taxa, left-coiling *N. pachyderma* and *G. quinqueloba*, which form a second pair of mutually positively correlated elements. Both *G. inflata* and *G. truncatulinoides* reach high frequencies in sediments beneath the main path of the Benguela Current, south of 25°S. It is assumed that these species are carried in a northwesterly direction along the oceanic branch of the Benguela Current, west of the Moroshkin divergence, into a region not included in the study area. This pair is therefore termed the oceanic association, and can be used in the Benguela System as an index of oligotrophic waters. As indigenous species of the South Atlantic transitional waters, *G. inflata* and *G. truncatulinoides* constitute the warm-end members among the eight major foraminiferal taxa of the Benguela, and their abundance variations positively correlate with the sea-surface temperature data (Table 2).

The second pair of positively correlated taxa, left-coiling *N. pachyderma* and *G. quinqueloba*, can be referred to as the upwelling association. These taxa dominate the foraminiferal assemblages in coastal samples, and display a sharp gradient of decreasing abundance in the vicinity of the shelf-break at the seaward boundary of the upwelling cells. Left-coiling *N. pachyderma* and *G. quinqueloba* are thus strongly negatively correlated with sea-surface temperature. The low correlation coefficient between *G. quinqueloba* and sea-surface salinity (Table 2) results from the preferential distribution of this species in the northern upwelling regime, which exhibits a very weak offshore salinity gradient (see Fig. 2b).

Right-coiling *N. pachyderma* and *G. bulloides* form the third pair of positively correlated taxa (Table 2). Their distribution on the seafloor approximates to the position of the frontal area, which separates the upwelling cells from the offshore, oligotrophic waters. This transition zone is poorly defined in the northern Benguela, where right-coiling *N. pachyderma* and *G. bulloides* are evenly distributed in both shelf and slope environments under the coastal branch of the Benguela Current. This third group is therefore termed the intermediate association.

TABLE 2

Correlation coefficients between all pairs of major taxonomic categories and sea-surface parameters. Abbreviations: *infl.* = *G. inflata*; *trunc.* = *G. truncatulinoides*; *bull.* = *G. bulloides*; *pach.*R = right-coiling *N. pachyderma*; *pach.*L = left-coiling *N. pachyderma*; *quin* = *G. quinqueloba*; *univ.* = *O. universa*; *dut.* = *N. dutertrei*; Temp. = mean annual sea-surface temperature; Salin. = mean annual sea-surface salinity

Taxa	*infl.*	*trunc.*	*bull.*	*pach.*R	*pach.*L	*quin.*	*univ.*	*dut.*
infl.								
trunc.	+**.57**							
bull.	−.23	−.13						
*pach.*R	−**.58**	−.28	+**.34**					
*pach.*L	−**.44**	−**.34**	−**.59**	−.19				
quin.	−**.51**	−**.39**	−.17	+.12	+**.43**			
univ.	−.25	−.23	.00	+.13	−**.30**	.00		
dut.	+.17	+.18	+.15	−.08	−**.30**	−**.31**	.00	
Temp.	+**.46**	+**.42**	+**.46**	−.06	−**.74**	−**.65**	+.27	+.29
Salin.	+.29	+**.38**	+**.50**	+.04	−**.75**	−.26	+**.35**	+.21

O. universa and *N. dutertrei* do not show positive correlation with any of the other major foraminiferal species (Table 2) and their distributional patterns do not coincide with one of the three hydrological regimes previously described.

Diversity indices

Of the different ways to approach a measure of diversity, the most commonly used is the Shannon–Weaver information function, given by the equation:

$$H(S) = -\sum p_i \ln p_i$$

where pi is the proportion of the ith species (Pielou, 1966). $H(S)$ being mainly determined by the proportion of the common species, it increases very little with the addition of rare species (Gibson and Buzas, 1973), and thus is useful in comparing diversity in different size samples. The use of $H(S)$ is particularly suited to the present study, as sample sizes vary from 100 (coastal samples) to more than 300 specimens. Discussing the Shannon–Weaver index, Williams and Johnson (1975) clearly showed that at high latitudes in the southern hemisphere, diversities of planktonic foraminifera in surface sediments decrease with increasing latitude, and that there is a strong correlation between decreasing diversity and decreasing sea-surface temperature.

Contoured Shannon–Weaver indices (Fig. 6) show that diversity in the Benguela System decreases toward the coast, mirroring the general pattern of sea-surface temperatures. This trend is particularly evident in the area of strongest upwelling activity from 32°S to 26°S (north of Cape Columbine to north of Lüderitz) due to the dominance of left-coiling *N. pachyderma*. Although low-diversity patches coincide with the Walvis Bay and Sylvia Hill upwelling cells, the pattern of decreasing values of $H(S)$ toward the coast is less evident in the upwelling regime of the northern Benguela, where the species dominance is equally shared between polar (left-coiling *N. pachyderma* and *G. quinqueloba*) and subpolar (right-coiling *N. pachyderma* and *G. bulloides*) taxa.

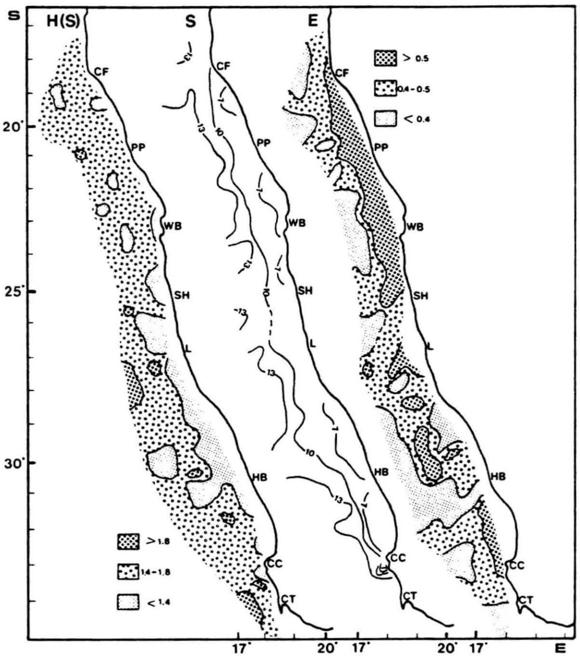

Fig. 6. Contoured maps of planktonic foraminiferal diversity indices: $H(S)$ = Shannon–Weaver index; S = species diversity (number of species); E = Buzas–Gibson index (equitability).

Figure 6 shows the contoured maps of two other diversity indices: the species diversity (S), which is simply the number of species found in a sample, and the Buzas–Gibson index for equitability (E), which measures the deviation of an assemblage from a sample of equally distributed species. Both these indices are highly dependent on sample size: S is likely to increase with sample size because of the addition of rare species. Therefore, the equitability, defined by Buzas and Gibson (1969) as the ratio:

$$E = e^{H(S)}/S$$

decreases when sample size increases because of the addition of rare species which increase S but have little effect on the value of $H(S)$. Athough the trends inferred from S and E may be biased in the present study by the difference in sample sizes, they display evident relationships with the hydrography of the Benguela system.

Species diversity (S) (Fig. 6) indicates a general decrease in the number of taxa toward the coast. This pattern cannot be directly linked to the preferred depth-habitats of the planktonic foraminifera in the surface waters, since all the sediment samples were collected below 100 m water-depth, and thus may contain tests of the deeper-living taxa (see Bé, 1977). Variations in the value of *S* may be better explained by hydrological factors. Increases in the number of foraminiferal species are due to the introduction of rare, mainly subtropical–tropical taxa, which occur in the warm, stable environment of the offshore areas. In contrast, the coastal region, with cool, upwelled water, is colonized by a few opportunistic polar and subpolar species, which successfully cope with this stressed environment.

Equitability contours (*E*) in the Benguela System have a more complex pattern. High equitability is encountered along the entire northern upwelling regime, and in the vicinity of the southernmost upwelling center, south of Hondeklip Bay (Fig. 6). In central areas, from 31° to 26°S, maximum values approximatively correspond with the seaward position of the upwelling front. In this frontal area, as in the northern and southernmost coastal regions, the foraminiferal assemblages have a subpolar character, a low species diversity (absence of the rare subtropical–tropical species), and are not dominated by a single taxon. Low values of the equitability index define two hydrologically different areas: (1) The upwelling regime off the Orange River Bight, where the foraminiferal assemblages have a marked polar aspect, being characterized by a low species diversity and an overwhelming dominance of the sinistral variety of *N. pachyderma.* (2) The offshore regime of the Benguela, which is characterized by high species diversity, and the dominance of transitional (*G. inflata*—southern offshore regime) or subpolar (*G. bulloides* and right-coiling *N. pachyderma*—northern offshore regime) taxa.

Discussion and conclusion

Variations in the process and intensity of the main oceanographic regimes within the Benguela region can be inferred from the faunal abundance patterns. Although a unique association characterizes the entire coastal-upwelling area, spatial variations in the distribution of the major species (*G. quinqueloba* and left-coiling *N. pachyderma*) clearly indicate variability in upwelling processes. Waters which well up along the coast originate from the South Atlantic Central Water (SACW; Schell, 1970) and are generally brought up from a depth of 100–300 m, while intensification of upwelling results in waters from a greater depth being involved. The coastal area from 31° to 26°S experiences the most intense upwelling (Shannon, 1985; Lutjeharms and Meeuwis, 1987), and here the waters may locally originate from a depth of more than 300 m (Shannon, 1985). North of 25°S, less intense wind stress results in a decreasing intensity of the upwelling process. Upwelled waters thus originate from a shallower depth than in the southern upwelling region. This difference in source area of the upwelled waters, together with the seasonal admixture of Angola-derived waters in the northern Benguela region, is responsible for the preferential colonization of the northern coastal area by *G. quinqueloba*, the warm-end member of the foraminiferal upwelling association, whereas left-coiling *N. pachyderma* is overwhelmingly dominant in the more intense upwelling cells of the southern Benguela. The presence of the latter taxon (locally >70%), may also suggest contributions from Antarctic Intermediate Water (AAIW) in the upwelling of the southern regions. The AAIW/SACW boundary lies at approximately 600 m depth off the southwest African margin (Shannon, 1985), and theoretically would prevent pure AAIW reaching the surface, even under strong upwelling activity. As pointed out by Hart and Currie (1960), however, it is possible that SACW contains a small proportion of AAIW, which would explain the relatively high abundance of left-coiling *N. pachyderma* in the southern Benguela coastal area.

G. bulloides and right-coiling *N. pachyderma* are the main components of the intermediate association, which characterized the mixed environment between the coastal upwelling and offshore oligotrophic regimes. Studies on zooplankton communities of the Benguela System (Kruger and Boyd, 1984; Shannon and Pillar, 1986) indicate that peaks of zooplankton abundance occur in the vicinity of the upwelling front, immediately seaward of the main upwelled water. Similarly, phytoplankton concentrations on the shelf are uneven, with observations by Shannon et al. (1984) suggesting that during active upwelling, both the newly upwelled water and the oceanic water are depleted in chlorophyll *a*. As a result, the maximum concentration of phytoplankton occurs as a narrow band offshore of the upwelling centres. The location and strength of the frontal features are thus of prime importance in estimating the potential phyto- and zooplankton production of an upwelling environment.

The distribution of the intermediate foraminiferal association in the surface sediments of the Benguela region correlates strongly with the location and strength of the upwelling front. In the southern Benguela, the restriction of this association to the vicinity of the shelfbreak reflects the position of a sharp frontal feature caused by enhanced upwelling. In the northern Benguela a diffuse front gives rise to a broad zone of productivity, which in turn is reflected by the extensive distribution of *G. bulloides* and right-coiling *N. pachyderma* in the surface sediments across the continental margin. The intermediate foraminiferal association can therefore be used as a productivity index for the Benguela surface waters.

Results presented in this paper indicate that both the individual species and diversity patterns of planktonic foraminifera show a consistent relationship to the surface-water hydrography of the Benguela System, with the three main oceanographic regimes (upwelling, intermediate, and oceanic) supporting different foraminiferal associations. The species composition of these associations is consistent with the general latitudinal distribution of foraminifera in South Atlantic surface waters, which, in turn, emphasizes sea-surface temperatures as the most important environmental parameter controlling their occurrence within the Benguela system. Regional modulations of the upwelling process (origin of the upwelled water, strength of the frontal features) are clearly reflected by the distribution and frequency of individual taxa.

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Appendix: TABLE A1

Locations of surface samples. No. = sample number

No.	Lat. (S)	Long. (E)	Depth (m)	No.	Lat. (S)	Long. (E)	Depth (m)
110	34.16	17.47	331	3340	32.54	16.32	1335
136	33.40	17.44	249	3343	32.13	15.57	1368
295	34.53	18.21	380	3344	31.48	15.37	1430
1710	34.14	18.09	235	3348	30.42	14.49	1575
1721	33.47	18.08	125	3354	28.38	13.54	1780
2233	33.10	16.56	655	3355	27.50	13.42	2070
2260	32.45	17.13	303	3376	25.52	13.44	408
2279	32.24	17.42	178	3381	25.36	13.23	970
2288	32.20	16.51	300	3388	25.36	14.31	158
2290	32.17	17.14	210	3399	25.16	14.27	142
2360	31.39	17.11	210	3401	25.16	14.03	200
2361	31.18	16.57	241	3403	25.15	13.41	332
2363	31.18	17.15	192	3406	25.20	13.06	1530
2377	30.50	17.09	165	3408	24.46	13.14	932
2441	32.40	17.35	232	3433	24.26	12.59	1446
2444	32.39	16.47	381	3436	24.17	13.19	635
2445	31.56	16.51	272	3438	24.16	13.40	308
2447	31.55	16.28	350	3441	24.16	14.10	135
2456	31.31	16.44	285	3459	24.06	12.57	1403
2463	31.08	16.22	292	3478	23.46	14.09	147
2466	31.01	15.22	285	3480	23.46	13.48	202
2471	30.46	15.44	193	3483	23.46	13.14	326
2474	30.47	16.18	268	3485	23.46	12.48	1170
2476	30.49	16.42	240	3487	23.36	12.33	1570
2676	32.07	15.23	2685	3518	22.56	14.04	125
2677	31.25	15.15	1662	3520	22.55	13.42	142
2693	30.31	15.13	305	3525	22.56	12.48	850
2698	30.15	14.30	650	3546	23.16	14.07	127
2705	30.05	15.46	200	3548	23.15	13.46	160
2707	30.05	16.09	175	3551	23.15	13.13	386
2714	30.20	17.01	150	3553	23.16	12.47	1003
2715	30.21	16.49	173	3566	24.46	14.13	149
2718	30.25	16.15	230	3576	31.08	15.52	437
2721	30.24	15.41	256	3577	31.22	16.05	453
2724	30.14	14.53	475	3578	31.42	16.09	420
2748	29.55	16.39	160	3663	17.15	11.33	110
2751	29.47	16.13	180	3668	17.56	11.17	828
2754	29.46	15.39	195	3687	18.36	11.53	175
2764	33.11	17.37	260	3696	18.48	11.42	280
2772	33.09	17.24	380	3701	19.19	10.31	1292
2789	33.19	17.44	184	3704	19.22	11.03	941
2819	33.46	17.13	1108	3708	19.22	11.46	305
2845	29.46	14.44	439	3711	19.22	12.17	128
2847	29.45	14.18	956	3725	19.33	11.13	802
2858	29.38	15.49	190	3763	22.35	12.31	1509

2881	29.16	14.16	1000	3764	22.15	12.20	1462
2890	29.17	15.18	180	3767	22.16	12.51	370
2893	29.17	15.48	178	3772	22.15	13.48	115
2896	29.17	16.18	155	3791	21.54	12.26	880
2914	29.11	14.49	205	3794	21.35	12.13	1252
2926	28.53	15.34	182	3812	21.15	13.17	129
2929	28.52	16.10	125	3816	21.15	12.34	390
2942	28.49	15.11	164	3817	21.15	12.24	683
2946	28.47	14.18	594	3820	21.16	11.48	1502
2957	28.37	15.56	122	3822	20.55	11.47	1260
2970	28.30	15.36	135	3825	20.56	12.20	541
2980	28.13	13.50	1622	3828	20.55	12.53	252
2982	28.17	14.17	850	3844	20.35	12.13	339
2987	28.17	15.07	182	3846	20.35	11.52	810
2989	28.16	15.27	139	3848	20.35	11.30	1222
2998	28.10	14.45	198	3850	20.15	10.34	1433
3014	27.46	15.09	153	3852	20.15	11.16	1072
3019	27.48	14.20	1000	3855	20.15	11.48	601
3110	31.43	15.57	628	3861	20.14	12.50	117
3151	27.17	13.39	1730	3869	19.55	11.22	825
3154	27.18	14.18	423	3872	19.55	10.51	1244
3156	27.18	14.39	315	3874	19.44	10.26	1353
3158	27.16	15.00	175	3914	18.59	12.07	135
3175	27.12	13.24	2060	3919	18.54	10.58	1100
3181	26.57	14.22	364	3922	19.09	11.18	528
3199	26.47	14.10	375	3938	19.44	12.42	100
3201	26.47	13.47	458	3947	20.07	12.22	218
3203	26.47	13.22	1530	3981	20.48	13.11	110
3252	25.48	13.11	1500	4010	21.45	13.34	118
3308	31.05	17.28	132	4014	21.45	12.51	311
3337	33.37	17.03	1209	4040	22.45	13.13	320
3339	33.13	16.33	1472				

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