

Distribution of modern coccolithophore assemblages in the southwest Indian Ocean off southern Africa

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ABSTRACT—Living coccolithophore assemblages were investigated in 35 surface water samples taken from the Natal Valley (southwest Indian Ocean) in January and November, 1983 and February, 1984. Fifty-nine species were recognised using a scanning electron microscope (S.E.M.). Cluster analysis revealed four different species assemblages dominated by *Emiliania huxleyi*, *Umbilicosphaera hulburtiana*, *Umbellosphaera tenuis* and *Gephyrocapsa oceanica*. Significant differences in species composition between the sampling periods are attributed to seasonal fluctuations. The regional distribution of the assemblages reflects two different oceanographic regimes: 1) The Agulhas Current, which is a nearly stable feature and 2) the area of the Agulhas Return Current, characterised by rapidly changing hydrographic and ecological conditions.

INTRODUCTION

Coccolithophores are restricted to the mixed layer of the world's oceans, except in polar regions, but are most abundant in the uppermost 50 m of the water column (McIntyre & Bé 1967). Biogeographical floral zones have been established on the basis of their distribution, which is predominantly influenced by temperature, salinity and fertility of surface water (McIntyre & Bé, 1967; Honjo & Okada 1974). Thus, the distribution pattern of coccolithophore assemblages in the oceans reflects water-mass and current distributions. Coccoliths compose 30–60% of deep sea calcareous sediments since the Jurassic (Berger & Roth, 1975) and can therefore be used as proxy indicators for palaeoceanographic research (Honjo, 1976; Roth & Coulbourn, 1982; Winter, 1982).

This study is an attempt to relate the distribution of living coccolithophores in surface waters of the southwest Indian Ocean (southern part of the Natal Valley) to the oceanographic conditions of the Agulhas Current region and comprises part of a larger project now being undertaken to reconstruct the palaeoceanographic history of the southwest Indian Ocean off southern Africa.

OCEANOGRAPHY

The dominant oceanographic feature of the study area is the Agulhas Current (Fig. 1). It divides at 27° S into a coastal branch (route a), which follows the continental shelf edge and a cyclonic branch (route b) which has the Mozambique Ridge as its eastern boundary. At about 32° S, route b turns westward to merge with the coastal main current east of East London (Grundlingh, 1977; Pearce, 1977). This situa-

tion is thought to have been relatively stable since the Miocene/Pliocene boundary (5 my Bp, Martin, 1981). South of 34° S, the current diverges from the continental shelf edge and turns east at about 15° E to form the Agulhas Return Current (Grundlingh, 1977; Harris *et al.*, 1978). The interaction of the western boundary currents with the upwelling regime occurring around the south and southwest coast produces a region of complicated dynamic interaction and eddy formation (retroflexion regime) that is in a continuous state of flux (Lutjeharms, 1981). The northern boundary of the retroflexion region reaches the Mozambique Ridge (Grundlingh & Lutjeharms, 1979) and should therefore also influence the study area.

SAMPLES AND METHODS

For logistical reasons, it was only possible to collect surface water samples. Nevertheless, coccolithophore assemblages encountered in surface water samples appear to be representative of the upper photic layer down to 50 m (Okada & Honjo, 1973). Fifty-six samples were taken together with salinity and temperature measurements during three cruises to the Natal Valley. Nine of these were collected between January 3 to 27, 1983 and twenty between February 12 to 25, 1984 aboard R. V. "Thomas B. Davie" (cruises 434 and 446). Twenty-seven stations were also sampled between November 8 to 23, 1983 aboard R. V. "Meiring Naudé" (cruise 83/19) (Fig. 2, Table 1). All water samples were prefiltered on board with a 63 µm sieve and then passed through 47 mm millipore-filters with a nominal pore size of 0.8 µm. A small section of the filter paper was mounted on a glass slide, rendered

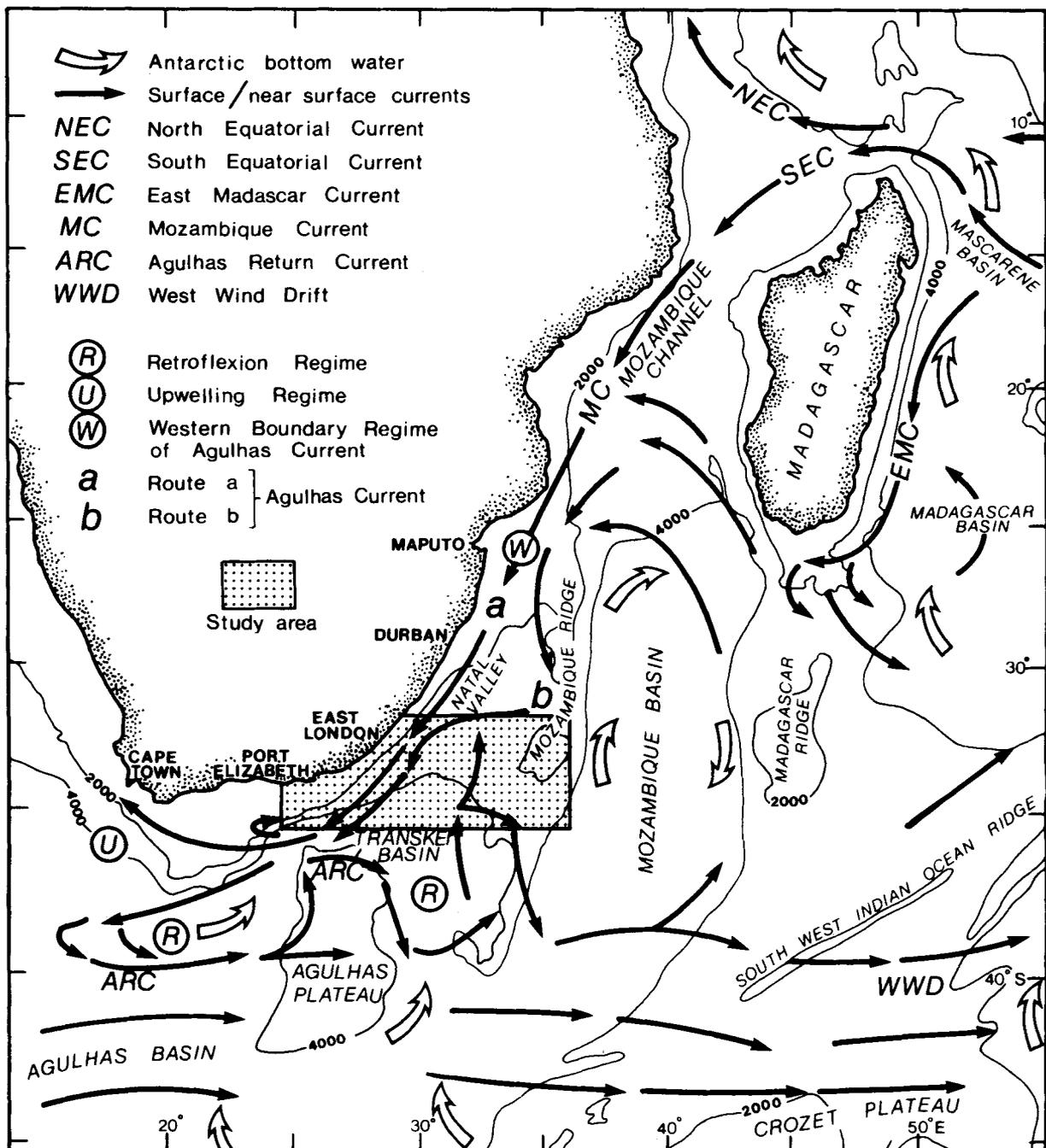


Fig. 1 Oceanography of the southwest Indian Ocean modified after Martin (1981) and Lutjeharms (1981).

transparent using immersion oil and observed under crossed nicols with a Leitz Laborlux 12-Pol microscope at $\times 1000$ magnification. Standing crop was then calculated by counting the number of cells corresponding to an area on the filter representing 10 ml of filtered sea water.

A filter section of about 25 mm² was placed on an aluminium stub and coated with an Au-Pd film in a

vacuum evaporator. A Cambridge S-200 S.E.M. was used to identify up to 425 coccolithophores per sample. Altogether, 59 taxa were identified (Table 1) following mainly the taxonomy of Okada & McIntyre (1977) and Winter *et al.* (1979).

Samples with < 100 specimens per stub as well as oil contaminated ones were considered statistically insignificant and were excluded leaving 35 samples for

statistical analysis (Table 1). The similarity between two cases (stations) or clusters in the variable space was calculated as the normalised chi-squared test of equality in the two relevant sets of frequencies using relative frequencies of the twenty most abundant species. This analysis was run on the Univac 1100/81 computer at the University of Cape Town using the BMDP-statistical package (Programme P2M, Dixon, 1981).

RESULTS

Standing Crop

Standing crop varied between zero and 34×10^3 cells/l in January, 1983; between 8×10^3 and 55×10^3 in November, 1983 and between 10×10^3 and 50×10^3 cells/l in February, 1984. The average abundance of 11×10^3 for February, 1984 and 15×10^3 cells/l for November, 1983 compares favourably with the most abundant samples taken world-wide from the open oceans (17×10^3 cells/l, Okada & Honjo, 1973). Stations 6744 (February, 1984) and 6 (November, 1983) show coccolithophore abundances of 38×10^3 and 46×10^3 cells/l, whereas adjacent stations 6670 and 6687, sampled in January, 1983, are barren. The highest standing crop values were recorded in an approximately 125 km wide strip parallel to the coast and in the vicinity of 33°S and 31°E .

Diversity

Species diversity (H' , Pielou, 1966) varied greatly during each sampling period (Table 1) ranging between 0.78 (station 6747) and 2.6 (6764) in February, 1984; between 0.73 (18) and 2.04 (7) in November, 1983 and between 0.44 (6671) and 2.49 (6681) in January, 1983.

Similar ranges were also observed by Honjo & Okada (1974) between 20°S to 45°N in the eastern Pacific and by Winter (1985) off the coast of California between 33° and 34°N . In general, we found that areas of relatively low species diversity have high coccolithophore abundances and are located close to shore.

Community structure

Cluster analysis was used to determine the degree of similarity in coccolithophore assemblages between stations. The matrix of the initial distances (before clustering) of the 35 relevant stations in the 20-dimensional species-space (Appendix 1) is the basis for the clustering process. In this way, four main assemblages A to D are recognised, characterised by the dominance of one species. According to the abundance of subordinate species, the assemblages can be divided into different cluster types as summarised in Table 2 (see also Fig. 3). The AE-cluster diverges from the A1-type in that *G. ericsoni* is more abundant and has a relatively high percentage of *D. tubifera*. The A-assemblage consists mostly of November, 1983 samples, whereas B, C and D assemblages were found at February, 1984 stations. Of note is that *E. huxleyi* contributes only between 7 and 14% of the February nanoflora except for stations 6761, 6752 (both AE) and 6754, 6772 (both D) which show abundant *E. huxleyi*. The high percentage of *U. hultburiana* (66% in B1 and 28% in B2) is also noteworthy. This species is common in the euphotic zone in the equatorial to transitional region of the Pacific and North Atlantic Oceans (Okada & McIntyre, 1977); its dominant presence in the Indian Ocean has so far been undocumented.

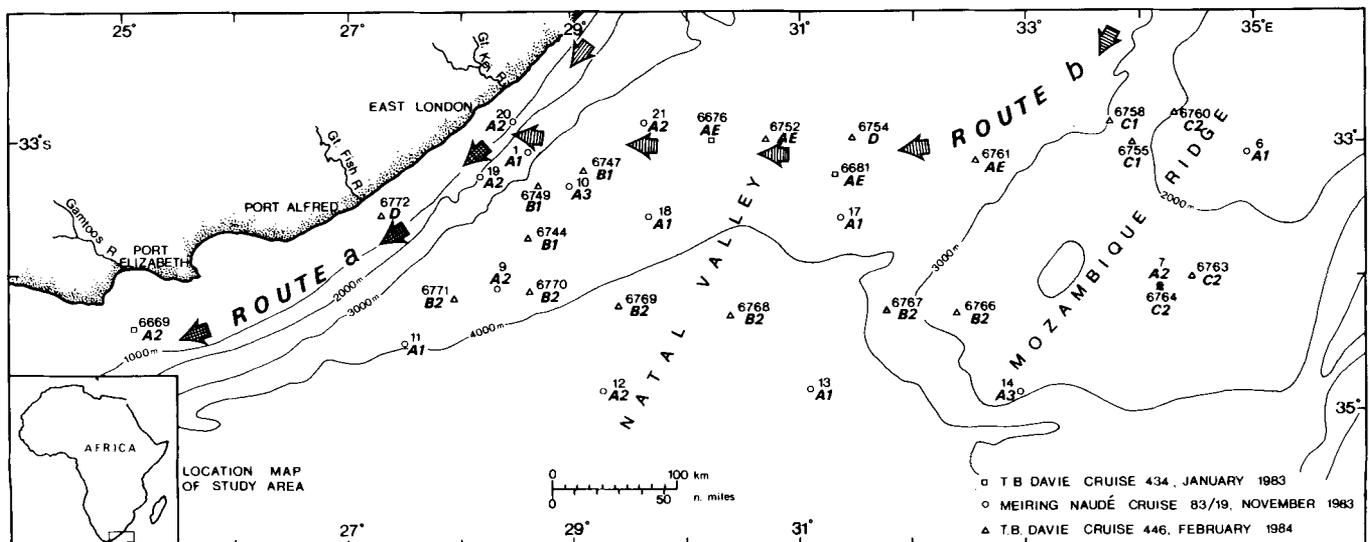


Fig. 2. Study area, sample locations and distribution of coccolithophore cluster types. Arrows mark the path of the Agulhas Current. The region south of route b and east of route a shows characteristics of the unstable "Retroflexion Regime".

Assemblage	Dominant species	Cluster type	2nd most abund. sp.	3rd most abund. sp.	Sampling period
A	<i>E. huxleyi</i>	A1	<i>G. ericsoni</i>	<i>U. hultburtiana</i>	N
		A2	<i>G. ericsoni</i>	<i>U. irregularis</i>	N, J
		A3	<i>U. tenuis</i>	<i>U. hultburtiana</i>	N
		AE	<i>G. ericsoni</i>	<i>U. hultburtiana</i>	F, J
B	<i>U. hultburtiana</i>	B1	<i>U. tenuis</i>	<i>E. huxleyi</i>	F
		B2	<i>U. irregularis</i>	<i>E. huxleyi</i>	F
C	<i>U. tenuis</i>	C1	<i>U. irregularis</i>	<i>U. hultburtiana</i>	F
		C2	<i>D. tubifera</i>	<i>U. irregularis</i>	F
D	<i>G. oceanica</i>	–	<i>E. huxleyi</i>	<i>U. hultburtiana</i>	F

Table 1. Sample parameters and absolute frequency counts of observed coccolithophore species. Asterisks mark oil contaminated samples.

DISCUSSION

The coccolithophore assemblages in the study area are dominated by placolith-bearing epipelagic species. Cluster analysis clearly separates stations of the two main sampling periods, November, 1983 and February, 1984 (Fig. 3). *E. huxleyi*, which was dominant in samples taken in November, 1983, is only a subordinate component in most of the February, 1984 samples. This striking difference in species composition cannot solely be explained by the fact that station positions were different for both periods because stations 7(A2) and 6764(C2), 9(A2) and 6770(B2), 10(A3) and 6747(B1) collected at almost the same locations are also characterised by different coccolithophore composition (Fig. 2).

Since most of our samples were taken during November and February, i.e. at beginning and end of summer time, the difference in the species composition is probably related to seasonal fluctuations. Seasonal changes in coccolithophore assemblages have also been observed in the western North Atlantic (Okada & McIntyre, 1979), the Bermudas (McIntyre & Bé, 1967) and the North Pacific (Reid, 1980). In these regions, the relative abundances of *U. hultburtiana*, *U. irregularis* and *U. tenuis* were found to be highest during the summer months and positively correlated with the surface water temperature, whereas *E. huxleyi* was dominant in colder water during winter due to the reduced presence of the former three species, which flourish in warmer water (Okada & McIntyre, 1979). The close relationship between these species and water temperature is also reflected by our results, if the dominant species of the assemblage or cluster types are considered. Clusters A1 to A3 occur in water of

relatively low temperature of less than 22.6°C. Assemblages and clusters C, D and AE were found in water of 23.7–24.6°C, whereas the B assemblage was associated with slightly higher temperatures of 24.6–24.9°C.

It seems that the main sampling periods of November, 1983 and February, 1984 are further distinguished by the regional distribution of individual cluster types. The February, 1984 samples (triangles, Fig. 2) are distributed in a distinctive pattern: stations characterised by C cluster types are located over the Mozambique Ridge; AE clusters occur in the area influenced by the cyclonic route b of the Agulhas Current; stations with B2 clusters are aligned horizontally over the Natal Valley and B1 clusters occur in the western part of the study area near the confluence of the two routes a and b of the Agulhas Current. On the other hand, individual cluster types (e.g. A1) of samples collected in November, 1983 (circles) appear to be more randomly distributed, even though the sampling grid was of similar width to that used in February, 1984.

We suspect that the differences in the regional distribution between stations of November, 1983 and February, 1984 are due mainly to the rapidly fluctuating currents and eddies in the retroflexion area of the Agulhas Current. The changing pattern of surface waters in this region influences ecological conditions and consequently the coccolithophore population. The continuous instability may generate a number of patterns in the distribution of coccolithophore assemblages, two of which have been recorded: 1) dispersed (e.g. November, 1983) and 2) coherent (e.g. February, 1984) distribution of cluster types.

Much more stable hydrographic features are the two main routes a and b of the Agulhas Current (Fig. 2). Along these the encountered assemblages are primarily represented by AE – (stations 6676, 6752, 6681, 6761) and A2 – (stations 19, 20, 21, 6669) cluster types. Both clusters contain samples taken about one year apart (Fig. 3) thus indicating more inherent stability in this region than in the area of retroflexion. A2 cluster types occurring in the area of retroflexion might be carried into this region by the Return Current (Fig. 1).

Analysis of the relevant stations reveals that both Agulhas Current routes can be characterised by high relative abundances of *E. huxleyi* and *G. ericsoni*. Stations 6754 and 6772 (Fig. 2, both D-assemblage) located within the two main routes, also show a high abundance of *E. huxleyi*. However, the D-assemblage is dominated by *G. oceanica* thus suggesting a different hydrographic environment. Station 6754 probably represents the semi-stable water mass encircled by the cyclonic b-route of the Agulhas Current, whereas the assemblage of station 6772 off the Great Fish River mouth could have been transported from the area of station 6754 by the currents.

Although sample collection over a large area was limited to the surface using a relatively coarse station grid, the information obtained suggests that coccolithophores reflect the general oceanographic environment, and can thus supplement other methods such as buoy drift experiments (Gründlingh, 1977; Gründlingh & Lutjeharms, 1979) or satellite image methods (Harris *et al.*, 1978), in determining hydrographic regimes.

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Fig. 3. Relative frequency distributions for the 20 most abundant species and the parameters salinity (S), temperature (T), standing crop (C) and diversity (D). Sample number prefixes J, N and F refer to

- | | |
|--------------------------|---------------------------|
| 1) <i>E. huxleyi</i> | 6) <i>H. carteri</i> |
| 2) <i>G. ericsoni</i> | 7) <i>D. tubifera</i> |
| 3) <i>G. oceanica</i> | 8) <i>R. clavigera</i> |
| 4) <i>U. hulburtiana</i> | 9) <i>R. longistylis</i> |
| 5) <i>U. sibogae</i> | 10) <i>U. irregularis</i> |

Averaged environmental parameters and frequency counts of cluster characterising species are

stations sampled in January and November, 1983 and February, 1984. All stations are clustered by closest distance in the 20-dimensional species space. Key for histogram bars:

- | | |
|--------------------------|----------------------------|
| 11) <i>U. tenuis</i> | 16) <i>S. pulchra</i> |
| 12) <i>S. molischii</i> | 17) <i>A. brasiliensis</i> |
| 13) <i>S. nodosa</i> | 18) <i>C. arethusae</i> |
| 14) <i>S. pirus</i> | 19) <i>P. mirabilis</i> |
| 15) <i>S. protrudens</i> | 20) <i>S. papillifera</i> |

displayed on the lower right side. Asterisks denote the percentage of all residual species.

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