QUATERNARY OSTRACODS FROM THE CONTINENTAL MARGIN OFF SOUTH-WESTERN AFRICA. PART III. OCEANOGRAPHICAL AND SEDIMENTARY ENVIRONMENTS

By

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(With 34 figures and 7 tables)

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ABSTRACT

The distribution of benthic Ostracoda on the continental shelf and upper slope between Cape Agulhas and the Kunene River is shown to be related to various time-averaged oceanographical and sedimentary parameters. The microfossils represent mixed modern and relict assemblages, probably dating from Recent to late Holocene time (c. 7000 yr B.P.). For each of the 36 most abundant species (> 95% of the total ostracod assemblage, with 123 species) mean values for a range of environmental sea-floor parameters have been calculated. These relate to water properties (temperature, salinity, dissolved oxygen) and substrate characteristics (sand, mud, calcium carbonate, total organic matter, elemental Fe and authigenic mineral contents). Correlation coefficients between these parameters and individual species indicate which parameters are the most important in determining distributions.

On a regional scale, the various areas of the continental shelf are dominated by a particular species. North of about 24°S, upwelling-induced low dissolved oxygen and high total organic matter (MORG) values favour *Cytherella namibensis* (outer shelf) and *Palmoconcha walvisbaiensis* (inner to mid-shelf), respectively. Farther south, the influence of advected, well-oxygenated Antarctic Intermediate Water on to the uppermost slope and outer shelf controls the distribution of *Ruggieria cytheropteroides*, whereas on the mid- and inner shelf, variations in mud and terrigenous components are the main controls for *Pseudo-keijella lepralioides* and *Bensonia knysnaensis knysnaensis*, respectively. In water deeper than about 500 m, the dominant species along the whole margin is *Henryhowella melobesioides*, whose distribution is primarily controlled by temperature/salinity variations. (Closer inshore, mud content of bottom sediments is more important.) For the other most abundant species, the main environmental controls are substrate-dominated, with sand and calcium carbonate (mainly negative) the most important. Elemental Fe (which is used as a gauge of the terrigenous component) is also important (both positively and negatively), with total organic matter more frequently important than any of the bottom-water properties.

Barren areas (sparse or no ostracod faunas) occur in both shallow and deep water, and are associated with the effects of upwelling (north of 27°S), fluvial terrigenous input (Namaqualand inshore area), and isolation from sources of terrigenous and organic matter (either side of the Cape Canyon).

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INTRODUCTION

The taxonomy of the benthic Ostracoda from the continental shelf and upper slope off south-western Africa has been documented in parts I and II of this study (Dingle 1992, 1993). These supplemented earlier localized accounts by Brady (1880), Müller (1908), Klie (1940), Benson & Maddocks (1964) and Hartmann (1974). In the present paper, aspects of the distribution of the whole fauna will be assessed in relation to various environmental parameters of the bottom waters and sediments.

Ostracoda were isolated from 270 sea-floor sediment samples collected between Cape Agulhas and the Kunene River in water depths between 15 m and 950 m (Fig. 1). A total of 123 species, belonging to 54 genera, was recorded (Table 1). The sediment samples were collected during the period 1967–1985 from the University of Cape Town's R.V. '*Thomas B. Davie*' by personnel of the joint Geological Survey/University Marine Geoscience Unit.

The regional oceanography off south-western Africa has been summarized by Hart & Currie (1960), Stander (1964), Shannon (1966, 1985), Chapman & Shannon (1985), Lutjeharms & Meeuwis (1987), Shannon & Hunter (1988) and Shannon *et al.* (1990), amongst others.

Briefly, the essential elements consist of a three-layer deep-water configuration that abuts the continental margin (Antarctic Bottom Water (AABW), North Atlantic Deep Water (NADW) and Antarctic Intermediate Water (AAIW)) and a mixed layer on the continental shelf (Fig. 2). The latter has several complexly related components, and is subject to considerable variability. Surface waters for the most part emanate from the South Atlantic gyre and move in a northerly direction, more or less parallel to the coast. This is the main component of the Benguela Current, and strong wind stress over it results in quasi-permanent regions of subsurface upwelling of varying intensity (e.g. Lutjeharms & Meeuwis 1987). Other major features are the intrusion of sub-tropical Angola Current water adjacent to the north coast, typically as far south as 18°S, and periodic intrusions of vortices and filaments of warm Agulhas Current water around the southern tip of the Agulhas Bank from the western part of the Agulhas Retroflexion (e.g. Shannon et al. 1990). The latter typically extend no farther north than about 33°S, although there has been considerable debate on their role in large-scale transfer of warm South-Western Indian Ocean water into the central Atlantic (e.g. Gordon & Haxby 1990). Southward subsurface movement of shelf water has been documented by De Decker (1970) and Nelson (1989) along most of the west coast, whereas north of 25°S several authors have postulated a southward moving current just below the shelf break that transfers oxygen-deficient water from the Angola Basin (Hart & Currie 1960; Stander 1964; Chapman & Shannon 1985).

Sediment samples used in this study were collected using a Van Veen grab, which typically penetrates 10 cm beneath the sediment-water interface. Ostracod valves were separated using standard washing and picking techniques, and faunas were examined from > 125μ size fractions.

No physical oceanographical measurements were collected from the sample sites but, because of the mixed Recent-subrecent nature of the ostracod assemblages, this omission is not critical to the study. Long-term mean values of parameters at each site were obtained in two ways: by averaging bottom-water data in quarter-degree squares around



Fig. 1. Bathymetry of the continental margin off south-western Africa with sediment sample sites indicated. ● = ostracod-bearing, □ = barren samples,
WR = Walvis Ridge, OB = Orange Banks, CB = Childs Bank, CC = Cape Canyon.

TABLE 1

Species of Ostracoda recorded from the west-coast continental shelf. Species are listed alphabetically.

	Species	No. of specimens
*	Ambostracon (A.) flabellicostata (Brady, 1880)	490
*	Ambostracon (A.) keeleri Dingle, 1992	1 022
	Ambostracon (A.) levetzovi (Klei, 1940)	19
	Ambostracon sp. 3553	1
	Ambostracon sp. 3571	2
	Ambostracon (Patagonacythere) sp. 3556	14
	Argilloecia sp. 3483	14
	Aurila kliei Hartmann, 1974	44
*	Australoecia fulleri Dingle, 1993	96
	Australoecia sp. 3550	1
*	Austroaurila rugosa Dingle, 1993	91
*	Bairdoppilata simplex (Brady, 1880)	435
	?Basslerites (Loculiconcha) sp. 3444	2
	Bathycythere vanstraateni Sissingh, 1971	1
*	Bensonia k. knysnaensis Benson & Maddocks, 1964	1 311
*	Bensonia k. robusta Dingle, 1992	43
	Bradleya cf. B. dictyon (Brady, 1880)	1
	Bradleya (?Quasibradleya) sp. 3568	8
*	Buntonia bremneri Dingle, 1993	79
*	Buntonia deweti Dingle, 1993	8
*	Buntonia gibbera Dingle, 1993	- 39
*	Buntonia namaauaensis Dingle, 1993	37
*	Buntonia rogersi Dingle, 1993	46
*	Buntonia rosenfeldi Dingle, Lord & Boomer, 1990	47
	Buntonia sp. 3486	2
	Bythocythere sp. 3349	7
	Caudites sp. 3329	2
*	Chrysocythere craticula (Brady, 1880)	358
*	Coquimba birchi Dingle, 1993	86
*	Cytherella dromedaria Brady, 1880	702
*	Cytherella namibensis Dingle, 1992	422
	Cytherelloidea compuncta Dingle, 1993	1
	?Cytherois sp. 3538	7
	Cytheropteron cuneatum Dingle, 1993	4
	Cytheropteron frewinae Dingle, 1993	5
	Cytheropteron aff. C. frewinge Dingle, 1993	1
*	Cytheropteron trinodosum Dingle, 1993	75
*	Cytheropteron whatleyi Dingle, 1993	108
	Cytheropteron sp. 2878	7
	Cytheropteron sp. 2881	1
	Cytheropteron sp. 2882	1
	Cytheropteron sp. 2902	1
	Cytheropteron sp. 3406	1
	Cytherura siesseri Dingle, 1993	7
*	Doratocythere exilis (Brady, 1880)	637
	Doratocythere sp. 3584	1
	?Falklandia sp. 3546	2
	Hemicytherura petheri Dingle, 1993	3
	Hemicytherura sp. 3393	1
	?Hemicytherura sp. 3404	1
*	Henryhowella melobesioides (Brady, 1869)	429
*	Incongruellina venusta Dingle, 1993	92
	Kangarina hendeyi Dingle, 1993	1
	Kangarina mucronata (Brady, 1880)	36
	Kangarina sola Dingle, 1993	1
	Kangarina? sp. 3439	2
*	Krithe capensis Dingle, Lord & Boomer, 1990	143
*	Krithe spatularis Dingle, Lord & Boomer, 1990	12
	Krithe sp. 8 Dingle, Lord & Boomer, 1990	11
	Krithe sp. 9 Dingle, Lord & Boomer, 1990	12
	Kuiperiana angulata Dingle, 1992	62
	?Kuiperiana sp. 3320	2

TABLE 1 (cont.)

	Species	No. of specimens
	Macrocypria sp. 3471	5
*	Macrocypris cf. M. metuenda Maddocks, 1990	102
	<i>Meridionalicythere petricola</i> (Hartmann, 1974)	13
	Munsevella eggerti Dingle 1993	36
	Mutilus bensonmaddocksorum Hartmann, 1974	2
	Mutilus malloryi Dingle, 1993	17
*	Neocaudites lordi Dingle, 1993	25
*	Neocaudites osseus Dingle, 1993	142
*	Neocaudites punctatus Dingle, 1993	7
÷	Neocytherideis boomeri Dingle, 1992	511
*	Palmoconcha subriombolaea (Brady, 1880) Palmoconcha walvishajansis (Hartmann, 1974)	39
	² Palmoconcha walvisridaensis Dingle 1992	475
*	Paracypris lacrimata Dingle, 1992	533
	Paracytheridea sp. 3339	1
	Paradoxostoma griseum Klie, 1940	4
	Paradoxostoma aff. P. auritum Klie, 1940	23
	Paradoxostoma aff. P. luederitzensis Hartmann, 1974	16
	Parakrithella simpsoni Dingle, 1993	68
*	Parakriinella sp. 3408 Poseidonamicus panopsus Whatley & Dingle 1080	117
	Propontocypris of P (P) subreniformis (Brady 1880)	66
	Propontocypris ci. 1. (1.) subrenijornus (Blady, 1880) Propontocypris (?P.) sp. 3345	2
	Propontocypris (?Ekpontocypris) sp. 3434	ī
	Propontocypris (?Schedopontocypris) sp. 3535	1
*	Pseudokeijella lepralioides (Brady, 1880)	8 181
	?Quadracythere sp. 3333	12
*	Ruggieria cytheropteroides (Brady, 1880)	5 298
	Semicytherura clausi (Brady, 1880)	1
	Semicytherura sp. 3382	1
	Semicytherura sp. 3385	5
	Semicytherura sp. 3414	4
	Stigmatocythere sp. 3479	7
	Trachyleberis sp. 3586	1
*	Urocythereis arcana Dingle, 1993	166
	?Urocythereis sp. 3310	2
	2Urocythereis sp. 3472	1
	2Urocythereis sp. 3570	1
*	Xestoleberis africana Brady, 1880	500
	Xestoleberis capensis Müller, 1908	22
*	Xestoleberis hartmanni Dingle, 1992	20
	Xestoleberis ramosa Müller, 1908	3
	Xestoleberis sp. 3398	13
	Xestoleberis sp. 3524	1
	Indet sp. 3306	1
	Indet sp. 3343	1
	Indet. sp. 3412	î
	Indet. sp. 3426	8
	Indet. sp. 3429	1
	Indet. sp. 3447	1
	Indet. sp. 3481	1
	Indet sp. 3539	1
	Indet sp. 3543	2
	Indet. sp. 3574	1
	Indet. sp. 3576	1
	Indet. sp. 3578	1

*—thirty-six most-abundant species; these account for more than 95 per cent of total population, and have been used for most of the statistical analyses.



Fig. 2. Main oceanographical elements in relation to the position of the continental shelf edge off south-western Africa. Based on Shannon (1985), Lutjeharms & Meeuwis (1987) and Lutjeharms (1989). AAIW = Antarctic Intermediate Water, NADW = North Atlantic Deep Water, AABW = Antarctic Bottom Water, SMZ = salinity minimum zone, CCD = carbonate compensation depth, \oplus = southward motion, \oplus = northward motion.

sample sites, and by reading values at sites from regional maps constructed specifically for the purpose.

Physical oceanographical data were obtained from the South African Data Centre for Oceanography (SADCO), for temperature and salinity, and Sea Fisheries Research Institute, for dissolved oxygen. Dingle & Nelson (1993) provided a preliminary account of the bottom temperature, salinity and dissolved oxygen distributions, as well as details of the data processing and reliability. Briefly, this consisted of screening the 30 000 SADCO records to obtain 2 869 temperature and salinity readings. To construct regional maps, these measurements were averaged in 391 quarter-degree rectangles over the west-coast continental margin. A similar technique was used to produce 1 314 bottom-water dissolved-oxygen values, which were combined with results from the survey of De Decker (1970).

The texture and geochemistry of sea-floor sediments on the margin between the Kunene River and Cape Agulhas have been analysed in three doctoral theses by Birch (1975), Rogers (1977) and Bremner (1981). These workers used the same set of samples as in the present study. Their results have been summarized and refined in Birch *et al.* (1986), Bremner *et al.* (1986) and Rogers & Bremner (1991). Additional analytical details of the sedimentary geochemistry off Namibia have been presented by Bremner (1980, 1983) and Bremner & Willis (1993).

Geochemical and textural data for each site utilized in the present study were extracted from these publications, either as analyses of specific sediment samples or extractions from regional contoured maps. Reference should be made to Birch (1975), Rogers (1977) and Bremner (1981) for details of analytical techniques. Elemental analyses were performed on the $< 63 \mu$ fractions of sediments, which Bremner & Willis (1993) have shown provide a good estimation of overall sediment geochemistry.

RESULTS

Descriptive statistics (means, standard deviations and ranges) and Pearson productmoment correlation coefficient analyses have been performed on the 36 most abundant species of ostracods for a variety of environmentally relevant parameters (Table 2). The latter relate to the physical oceanography (bottom-water temperature, salinity and dissolved oxygen, water depth and geographic latitude) and nature of the bottom sediments (organic matter, texture and elemental geochemistry). The most abundant species account for 95.47 per cent of the total available ostracod fauna, and are illustrated in Figures 3-5.

These results allow me to supplement the distributional data presented in Parts I and II (Dingle 1992, 1993). The numerical data presented in the Appendix comprise what I believe to be a unique published compilation of environmental information for a modern ostracod fauna from such a large area of continental shelf (approximately 420 000 km²).

The correlation coefficients are used to supplement and highlight relationships between and within elements of the fauna. It should be remembered that strong correlation coefficients indicate which species are most strongly influenced (positively or negatively) by changes in the parameters and will not necessarily be those that have the highest (or lowest) mean values. In this sense, the correlation coefficient is a measure of

ABLE 2	Ily correlations >95 per cent significance (>0.1500) are listed.
T	Correlation coefficients between species and variables. Or

pnW	0.4365 0.3170 0.2004 0.2004 0.2504 0.6204 0.6204 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6221 0.6400 0.6228 0.6228 0.6204 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.6400 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.66000 0.660000 0.660000000000
Sand	$\begin{array}{c} -0.451(\\ -0.3245(\\ -0.3245(\\ -0.4807(\\ -0.48$
Apatite	$\begin{array}{c} 0.4242\\ -0.5610\\ 0.5165\\ -0.3400\\ 0.5165\\ -0.5610\\ -0.4875\\ -0.4875\\ -0.5610\\ 0.9330\\ 0.9330\\ 0.9330\\ -0.4141\\ -0.4141\\ -0.4037\\ 0.2368\\ 0.2368\\ 0.2826\\ 0.2826\\ 0.2826\\ 0.2826\\ 0.2700\\ -0.6268\\ 0.2826\\ 0.2700\\ -0.7378\\ 0.7378\\ \end{array}$
Glauc.	0.3126 0.4197 0.4364 0.4364 0.21697 0.9940 0.9940 0.9940 0.20713 0.2074 0.2074 0.2074 0.2850 0.1751 0.2850 0.4878 0.2614 0.2715 0.2725 0.2725 0.2725 0.2725 0.2725 0.2725 0.2725 0.2725 0.2725 0.2725 0.27555 0.27555 0.275555 0.27555 0.27555 0.27555 0.27555 0.27555 0.2
CaCO ₃	$\begin{array}{c} -0.2323\\ 0.1794\\ 0.9292\\ 0.9292\\ 0.5286\\ -0.4789\\ 0.5587\\ -0.6179\\ 0.5877\\ -0.6179\\ -0.6179\\ -0.6179\\ 0.5877\\ -0.6179\\ 0.2167\\ -0.5081\\ 0.9197\\ 0.1864\\ -0.4191\\ 0.1864\\ -0.4191\\ 0.1864\\ -0.2800\\ -0.2800\\ 0.1584\\ 0.1584\end{array}$
Fe	-0.3756 -0.37565 -0.4380 0.5765 0.5765 0.5199 -0.2269 -0.7089 -0.2269 -0.1815 -0.2254 -0.1815 -0.2254 -0.1815 -0.2254 0.3193 -0.2553 -0.4005 0.5926 0.5926 -0.4546 -0.4546 -0.4546 -0.4546 -0.2553 -0.4546 -0.4546 -0.4546 -0.4546 -0.4546 -0.4556 -0.4556 -0.4556 -0.4556 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.4566 -0.2555 -0.2555 -0.4566 -0.4566 -0.25555 -0.25555 -0.25555 -0.25555 -0.25555 -0.25555 -0.25555 -0.255555 -0.25555555 -0.255555555 -0.2555555555555555555555
MORG	$\begin{array}{c} 0.4070\\\\ 0.7747\\ 0.77100\\ 0.6889\\ 0.6889\\ 0.6889\\ 0.6889\\ -0.3013\\ 0.6889\\ 0.5324\\ 0.5324\\ 0.5324\\ 0.5324\\ 0.5363\\ 0.536\\ 0.5363\\$
Oxygen	0.1593
Salinity	0.5736 -0.2759 -0.2509 0.6954 -0.2946 -0.2946 -0.2946 -0.2758 -0.3715 0.2758 -0.3715 -0.3715 -0.3715 -0.3767 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2064 -0.2075 -0.2064 -0.2759 -0.2759 -0.2759 -0.2759 -0.2759 -0.2759 -0.2759 -0.2759 -0.2509 -0.2758 -
Temp.	$\begin{array}{c} 0.5298 \\ -0.1905 \\ 0.2796 \\ 0.2796 \\ 0.2626 \\ 0.2626 \\ 0.2064 \\ -0.6748 \\ -0.6748 \\ -0.5467 \\ -0.5467 \\ -0.1576 \\ 0.2134 \\ -0.2134 \\ 0.2134 \\ -0.2134 \\ 0.2134 \\ -0.4266 \\ 0.1732 \\ 0.3024 \\ -0.4569 \\ 0.1732 \\ 0.3024 \\ -0.4569 \\ 0.1732 \\ 0.3024 \\ -0.4569 \\ 0.1732 \\ 0.5493 \end{array}$
	Ambostracon flabellicostata Ambostracon keeleri Australoecia fulleri Austroaurila rugosa Buntonia bremneri Buntonia gibbera Buntonia gibbera Buntonia namibensis Buntonia rogersi Bairdoppilata simplex Chrysocythere craticula Cytherella dromedaria Cytheropteron whatleyi Doratocythere exilis Henryhowella melobesioides Incongruellina venusta Macrocypris for M. metuenda Neocytherideis boomeri Neocytherideis lordi Neocytherideis lo

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Fig. 3. Most abundant ostracod species on the continental shelf off south-western Africa arranged in order of latitudinal centre of distribution (mean of all observed sites, see Figure 6). Vertical bars are degrees of latitude (S); horizontal scales = 100 µ. A = Palmoconcha walvisbaiensis, B = Bensonia k. robusta, C = Cytherella namibensis, D = Neocaudites lordi, E = Incongruellina venusta, F = Buntonia rogersi, G = Krithe spatularis, H = Cytheropteron whatleyi, I = Bensonia k. knysnaensis, J = Buntonia rosenfeldi, K = Cytheropteron trinodosum, L = Ambostracon flabellicostata, M = Ruggieria cytheropteron oides, N = Buntonia gibbera, O = Buntonia namaquaensis.

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Fig. 4. The most abundant ostracod species on the continental shelf off south-western Africa arranged in order of latitudinal centre of distribution (mean of all observed sites, see Figure 6). Vertical bars are degrees of latitude (S); horizontal scales = 100 μ. A = Pseudokeijella lepralioides, B = Urocythereis arcana, C = Ambostracon keeleri, D = Krithe capensis, E = Poseidonamicus panopsus, F = Buntonia bremneri, G = Henryhowella melobesioides, H = Doratocythere exilis, I = Paracypris lacrimata, J = Chrysocythere craticula, K = Xestoleberis africana, L = Bairdoppilata simplex, M = Macrocypris cf. M. metuenda, N = Neocytherideis boomeri, O = Austroaurila rugosa.



Fig. 5. The most abundant ostracod species on the continental shelf off south-western Africa arranged in order of latitudinal centre of distribution (mean of all observed sites, see Figure 6). Vertical bars are degrees of latitude (S); horizontal scales = 100μ . A = Australoecia fulleri, B = Cytherella dromedaria, C = Neocaudites osseus, D = Xestoleberis hartmanni, E = Buntonia deweti, F = Coquimba birchi.

the sensitivity of the species to change in the parameter. In addition, correlation coefficients based on simple regression analyses are presented to show the relationships between the environmental variables (Table 3).

To aid reliability, descriptive statistics and correlation coefficients were performed only on samples containing > 100 valves (n = 45). Exceptions to this standard were regional latitudinal and depth distributions, and averages for environmental parameters for the following species, whose ranges into deeper water precluded its use: *Krithe capensis*, *K. spatularis*, *Buntonia rosenfeldi* and *Henryhowella melobesioides*.

PHYSICAL OCEANOGRAPHY

Latitudinal and depth distribution

Figure 6 shows the total and averaged north-south distribution of the most abundant species. Most species (19; 53%) have their northern limits straddling the Walvis Ridge, whereas others occur in the vicinity of Walvis Bay (7), Orange River (7) and the Cape Peninsula (3). In contrast, 33 species (92%) have their southern limits south of the Cape Peninsula.

The averaged position for each species is an indication of its centre of distribution (based on the number of observed sites). With the exception of three species, these all lie south of 27°S (Lüderitz), and only *Bensonia knysnaensis robusta* and *Palmoconcha walvisbaiensis* have their centres of distribution north of 23°S (Walvis Bay). Figures 3–5 illustrate each of the most abundant species, arranged in order of their southward latitudinal distribution.

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Correlation coefficients based on simple regression analyses between variables (sites with more than 100 specimens).

	Temp.	Salinity	Oxygen	MORG	Fe	CaCO ₃	Glauc.	Apatite	Sand	Mud
Temperature Salinity Oxygen MORG Fe CaCO ₃ Glauconite Apatite Sand	$\begin{array}{c} 1.0000\\ 0.9092\\ -0.7332\\ 0.3750\\ -0.1591\\ -0.4826\\ 0.1427\\ 0.1427\\ 0.0383\end{array}$	$\begin{array}{c} 0.9092\\ -0.8130\\ 0.4500\\ 0.4500\\ -0.2775\\ -0.2776\\ 0.0899\\ -0.1951\\ 0.1951\end{array}$	-0.7332 -0.8130 1.0000 -0.5795 0.3017 -0.3471 0.4525 -0.0150 0.3949	$\begin{array}{c} 0.3750\\ 0.4500\\ -0.5795\\ 1.0000\\ -0.3206\\ -0.1790\\ 0.0263\\ 0.0263\\ 0.0263\end{array}$	-0.1591 -0.2775 0.3017 -0.3206 1.0000 -0.2005 0.1950 0.0456 0.0456	-0.4826 -0.4902 -0.3471 -0.1790 -0.2005 1.0000 -0.2115 -0.0661 0.1104	-0.2182 -0.2756 0.4525 -0.3308 0.1950 0.1950 0.2568 0.2568 0.2788	$\begin{array}{c} 0.1427\\ 0.0899\\ -0.0150\\ 0.0263\\ -0.1108\\ 0.2568\\ 1.0000\\ 0.2922\\ 0.2922\\ \end{array}$	-0.0383 -0.1951 0.3949 0.0456 0.1104 0.1104 0.2728 0.2922 1.0000	-0.0506 0.1122 -0.3086 0.4906 -0.0185 -0.1653 -0.3094 -0.9306
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Fig. 6. Mean and ranges of the maximum latitudinal distribution of the most abundant species. Vertical scale is degrees of latitude (S). WR = Walvis Ridge, WB = Walvis Bay, LUD = Lüderitz, OR = Orange River, CC = Cape Columbine, CP = Cape Peninsula. The mean values are calculated on the number of sample sites; thus they represent weighted centres of distribution and not average positions between northern and southern limits.

Figure 7 shows the total and averaged across-shelf distribution of the most abundant species. With the exception of two species (*Krithe spatularis* and *K. capensis*), all the most abundant species have their upper depth limits (UDL) shallower than 200 m (i.e. in the inner-mid-shelf area), whereas, with the exception of three species (the least abundant of this category), they all have their LDL deeper than 200 m. The curve of averaged depth distributions has gradient changes separating two shelf faunas (at 250 m, I and II), and upper and mid-slope faunas (350 m, III, and 450 m, IV).

Figures 6 and 7 indicate that, with few exceptions (*Coquimba birchi, Buntonia deweti, B. gibbera, Bensonia k. robusta* and *Xestoleberis africana*), the most abundant species are relatively cosmopolitan in their distribution along and across the shelf (unlike many of the rarer taxa).

Regional variations in the abundances of several of the most abundant species were briefly considered by Dingle (1992), who presented along-shelf variations of the dominant



Fig. 7. Mean and ranges of maximum and minimum depth distribution of the most abundant species and barren sites. UDL = upper depth limit, LDL = lower depth limit. The mean values are calculated on the number of sample sites; thus they represent weighted centres of distribution and not average positions between upper and lower limits. I-IV on the upper border demarcate species grouped between gradient changes in the curve of mean values.

taxa within various latitudinal sectors. A more comprehensive analysis has been carried out, and is summarized in Figures 8 and 9. These represent projections of abundance values (as smoothed percentages of the total fauna) on to across-shelf (depth), and alongshelf (latitudinal) axes, respectively. A plan of the distribution of dominant taxa (> 20% total fauna) on the shelf and slope (Fig. 10) was constructed using Figures 8 and 9, and additional depth/abundance profiles computed at intervals of 5° latitude. A simple calculation of regional dominance gives the following abundances in order of rank: areas north of $24^{\circ}S$ — *Palmoconcha walvisbaiensis* = 32 per cent, *Cytherella namibensis* = 21 per cent; south of $24^{\circ}S$ — *Pseudokeijella lepralioides* = 36 per cent, *Ruggieria cytheropteroides* = 22 per cent, *Bensonia knysnaensis knysnaensis* = 6 per cent; in water > 500 m — *Henryhowella melobesioides* = 43 per cent.

The inner-outer-shelf region (0-300 m) is dominated by three species (Fig. 10). North of 23°S, *Palmoconcha walvisbaiensis* occurs on its own but, south of 25°S, is replaced, respectively, by *Bensonia k. knysnaensis* on the inner shelf and *Pseudokeijella*



Fig. 8. Variation of species dominance with depth across the continental margin. Constructed by projecting all data points on to a single axis, and smoothing each curve with a five-point running mean.

lepralioides on the mid-outer shelf. Immediately south of Walvis Bay, there is a mixed assemblage containing *Palmoconcha walvisbaiensis* and *Bensonia k. knysnaensis*. A further mixed zone occurs between c. 31.5° and 34°S, where the two dominant taxa are 'diluted' by the relatively diverse and abundant faunas off the south-western Cape (which contain many of the rarer taxa described by Dingle 1993).

Outer-shelf and uppermost-slope areas are dominated by two species: Cytherella namibensis in the north and Ruggieria cytheropteroides in the south. Upper and mid-slope areas are dominated by Henryhowella melobesioides, with a narrow mixed zone containing abundant Krithe (mainly K. capensis) and the deeper-water species of Buntonia (B. rosenfeldi, B. bremneri and B. namaquaensis) intervening between the Cytherella namibensis-Ruggieria cytheropteroides upper-slope assemblage and the Henryhowella melobesioides upper-mid-slope assemblage.

All three inner-outer-shelf dominant species typically constitute 40-50 per cent of the local populations; projecting their abundances on to a cross-shelf axis (Fig. 8) emphasizes that each taxon reaches its individual maximum at different depths: *Bensonia k. knysnaensis*, 50 m; *Palmoconcha walvisbaiensis*, 80-110 m; and *Pseudokeijella lepralioides*,



Fig. 9. Variation of species dominance, expressed as a percentage of total ostracod population, with latitude. Constructed by projecting all data points on to a single axis, and smoothing each curve with a five-point running mean. WR = Walvis Ridge, WB = Walvis Bay, LUD = Lüderitz, OR = Orange River, CC = Cape Columbine, CP = Cape Peninsula.

130-180 m. In contrast, a similar degree of dominance on the outer-shelf and uppermost slope is only reached south of 25°S (*Ruggieria cytheropteroides*), whereas north of Walvis Bay, *Cytherella namibensis* constitutes only 20–30 per cent, with other taxa being relatively more important. Below a transitional zone (450–550 m), *Henryhowella melobesioides* progressively increases its dominance, reaching > 70 per cent in water deeper than 900 m. Its eventual maximum (> 80%) occurs at 1 200 m on the middle slope, before rapidly declining below 1 500 m (Dingle *et al.* 1989, 1990; Dingle & Lord 1990).

Finally, summaries of regional simple population diversity (expressed as number of species/sample) show a preponderance of inner-mid-shelf species south of the Orange River (Figs 11, 12). Latitudinally, there is a progressive increase in population diversity from < 10 species north of the Walvis Ridge to > 50 species off the south-western Cape (Fig. 11). The increase in numbers is particularly high across the Walvis Ridge and in the vicinity of Walvis Bay, whereas between the latter and the Orange River, there is a plateau (33 species). A maximum is reached off the southern Namaqualand coast (45 species), south of which the diversity decreases slightly, reaching a low at 33°S (Cape





Columbine: 40 species), before rising very rapidly in the vicinity of the Cape Peninsula (55 species).

Across the shelf, maximum diversity (40 species) occurs between 160 m and 200 m (Fig. 12). There is a rapid increase from the inner shelf, with a subsidiary maximum (33 species) at 100 m, and an equally rapid decline into water between 200 m and 300 m. A diversity plateau (24 species) extends to 500 m, below which there are two further declines in species numbers (530 m and 710 m) to 10 species between 800 m and 900 m.

Temperature and salinity

The correlation coefficient between temperature and salinity is high (R = 0.8960; Fig. 13A) at all 270 continental-shelf sites, so that these two parameters vary sympathetically. The correlation between temperature and dissolved oxygen in the bottom waters is lower (R = -0.7432; Fig. 13B), whereas with other parameters (e.g. CaCO₃ and organic matter MORG) it is < 0.5000 (see Table 3).

The distribution of temperature and salinity preferences has three well-defined categories (Figs 14, 15). Two species prefer high temperature and high salinity (> 11°C, > 34.90‰) — *Palmoconcha walvisbaiensis* and *Bensonia k. robusta* — and, in both cases, their means are markedly different from those of other species.







Fig. 12. Variation of simple species diversity of total fauna with depth. The complete depth range of each species has been used and the assumption is that the species occurs at all sample sites between these limits. The curve is a five-point running mean through the sample sites plotted on to a single E-W axis.



Fig. 13. Best-fit regression curves for sea-floor parameters (using all sample sites, n = 270). A. Temperature against salinity (linear, R = 0.89603). B. Temperature against dissolved oxygen (exponential, R = -0.74323). Inner dashed lines = one standard deviation, outer dashed lines = two standard deviations.



Fig. 14. Mean and standard deviation (SD) of sea-floor temperature for species at each site containing > 100 specimens.

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Fig. 15. Mean and standard deviation (SD) of sea-floor salinity for species at each site containing > 100 specimens.

At low temperatures/salinities, three species have means below 7°C and 34.6‰: *Krithe spatularis, K. capensis* and *Buntonia rosenfeldi*, with *Henryhowella melobesioides* closely associated with this group.

The remainder of the most abundant species fall within the following ranges of mean temperatures and salinities: 10.17–8.73°C, and 34.89–34.70‰, respectively.

Correlation coefficients between the various species, and temperature and salinity are shown in Table 2. *Palmoconcha walvisbaiensis* correlates most positively with temperature and *Buntonia gibbera* with salinity, whereas *Ambostracon flabellicostata* correlates strongly with both. Four species correlate negatively, with *Buntonia namaquaensis* returning the largest values for both parameters.

Abundance and species diversity trends of the whole ostracod population (i.e. most abundant species plus rarer species in all samples) with temperature and salinity are shown in Figure 16.



Fig. 16. Relationship of diversity (top panel, light curve: number of species) and abundance (bottom panel, dark curve: number of valves/100 g sediment) for whole ostracod assemblage. A. Sea-floor temperature. B. Sea-floor salinity.

Maxima in both abundance and diversity lie within the temperature range $7^{\circ}-10^{\circ}$ C and salinity range 34.6%-34.9%. There are further minor peaks in the high temperature/ high salinity areas of the graphs, although these are not in phase, implying that at the higher values, one or other of the factors is dominant in determining the distribution patterns.

Dissolved oxygen

The distribution of species' means for sea-bottom dissolved oxygen is skewed towards a preference for high values (Fig. 17), although it must be remembered that,



Fig. 17. Mean and standard deviation (SD) of sea-floor dissolved oxygen for species at each site containing > 100 specimens.

according to the terminology of Chapman & Shannon (1985), the whole of the west-coast continental shelf falls within the category 'oxygen-depleted' (< 5 ml/l). Correlation coefficients between dissolved oxygen and other water parameters are greatest between salinity (-0.8130) and temperature (-0.7332), whereas between oxygen and sediment parameters, the closest links are with organic matter (-0.5795), glauconite (0.4525) and CaCO₃ (-0.3471) (Table 3).

There are four gradient changes in the mean oxygen curve (Fig. 17), isolating five unequally-sized groups of species. These occur at 3.4, 3.1, 2.8 and < 2.5 ml/l, with the bulk (21; 58%) plotting above > 3.4 ml/l, where *Krithe spatularis*, *Henryhowella melobes-ioides* and *Macrocypris* cf. *M. metuenda* occupy the top three rankings. Only two species have a preference for oxygen-deficient water (< 2 ml/l): *Palmoconcha walvisbaiensis* and *Bensonia k. robusta*. Their mean values (< 1 ml/l) are markedly lower than the next lowest groups, in which only two fall below 3.0 ml/l (*Buntonia namaquaensis* and



Fig. 18. Relationship of diversity (top panel, light curve: number of species) and abundance (bottom panel, dark curve: number of valves/100 g sediment) for whole ostracod assemblage. A. Sea-floor dissolved oxygen. B. Organic matter in sea-floor sediments.

Neocaudites lordi). Cytherella namibensis, Bensonia k. knysnaensis and Buntonia rogersi constitute a further group clearly able to tolerate a degree of oxygen depletion.

Correlation coefficients between species and dissolved oxygen are listed in Table 2. Two taxa strongly correlate with fluctuations in this parameter: *Cytherella namibensis* (negatively) and *Buntonia namaquaensis* (positively). A further three species (*Palmoconcha walvisbaiensis*, *Bensonia k. knysnaensis* and *Neocaudites lordi*) also correlate negatively with dissolved oxygen values.

Abundance and species diversity trends of the whole ostracod fauna (in all samples), with dissolved oxygen values, are shown in Figure 18A. These are similar to those displayed for the most abundant species data, and have a distinctly trimodal distribution, with maxima at 0.6 ml/l, 2.2-2.5 ml/l and the main maximum between 3.0-4.2 ml/l.

BOTTOM SEDIMENTS AND GEOCHEMISTRY

Correlations between the physical oceanographical and sedimentary parameters are shown in Table 3 (based on samples with > 100 specimens). The only relatively strong correlations are the negative relationships between temperature/salinity and calcium carbonate, and between oxygen and organic matter. Within the sediments, the only relatively high correlations are between mud and sand, and organic matter.

I have investigated the correlations between the overall ostracod abundance (number of valves/100 g sample), simple diversity (number of species/sample), and various parameters using both the whole data set (including and excluding barren sites), and only those samples with > 100 specimens (Table 4). In both cases, only the dissolved oxygen values showed relatively strong positive correlations, with the diversity having greater dependence than the abundance (to a maximum of 0.5575). Mud content showed the second-strongest correlation (to a maximum correlation of 0.3839). Correlations with both temperature and MORG are weak.

				and the second second second
	Temp.	Oxygen	Mud	MORG
WHOLE DATA SET. INCLUD	ING BARREN SITES			
Abundance	-0.056	0.239	-0.129	-0.105
Simple diversity	-0.197	0.489	-0.283	-0.268
WHOLE DATA SET, EXCLUE	DING BARREN SITES			
Abundance	-0.011	0.187	-0.080	-0.074
Simple diversity	-0.165 ^e	0.458 ^e	-0.281 ^e	-0.306 ^e
SITES WITH >100 SPECIMEN	NS			
Abundance	-0.1642	0.2167	0.3839	0.1075
Simple diversity	-0.2189	0.5575	0.2945	-0.0493

TABLE 4

Correlation coefficients (based on simple regression analyses) between environmental parameters and ostracod populations.

e = exponential model
 CaCO₃ reflects the biogenic component
 Fe reflects the terrigenous component
 MORG = organic matter
 Abundance = number valves/100 g sample
 Simple diversity = number species/100 g sample

Organic matter (MORG)

The distribution of mean values of organic matter in the bottom sediments plotted against species distribution is shown in Figure 19. Most species (23; 64%) have a preference for organic matter values within the range 2.7-3.9 per cent. Only one species



Fig. 19. Mean and standard deviation (SD) of organic matter (MORG) in sea-floor sediments for species at each site containing > 100 specimens.

(Austroaurila rugosa) has a low tolerance of organic matter (< 2.0%), whereas five others have mean values < 3 per cent (Neocytherideis boomeri, Bairdoppilata simplex, Poseidonamicus panopsus, Palmoconcha walvisbaiensis and Buntonia gibbera). The inclusion of Palmoconcha walvisbaiensis in this group may be anomalous, as the mean for this species — based on all sample sites — is 5.78 per cent. The species most tolerant of MORG (> 5.0%) are Coquimba birchi, Buntonia deweti and Xestoleberis hartmanni. Although, in general, the correlation between oxygen and organic matter in the sediments of the west coast is only moderately strong (R = -0.5795; Tables 3 and 4), the relationship is borne out by the mean preferences of Austroaurila rugosa and Neocytherideis boomeri (low MORG), and Bensonia knysnaensis robusta, Neocaudites lordi and Buntonia rogersi (high MORG).

Correlation coefficients between species and organic matter in bottom sediments are listed in Table 2. Two species correlate negatively with organic matter: *Macrocypris* cf.

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M. metuenda and *Henryhowella melobesioides*, whereas 12 species correlate positively, with *Cytheropteron trinodosum* showing the highest value (0.8102).

Abundance and species diversity trends of the whole ostracod fauna with organic matter are shown in Figure 18B. Although the curves are relatively complex, they are essentially bimodal: maximum abundances and diversity occur between one and 4.5 per cent organic matter in the sediments. These values are similar to those for the majority of the most abundant species (Fig. 19). In terms of species diversity, the maximum MORG values lie at the lower end of this range (c. 1.5%), whereas maximum population abundance occurs at somewhat higher values (3.0-3.5%). The effective cut-off maximum values for significant population abundance and species diversity are 7.0 and 7.5 per cent, respectively.

Terrigenous sediments

Variations in the elemental Fe content can be used to characterize the terrigenous component in marine sediments on the continental shelf off south-western Africa (e.g.



Fig. 20. Mean and standard deviation (SD) of Fe (= terrigenous component) in sea-floor sediments for species at each site containing > 100 specimens.

Bremner & Willis 1993). Figure 20 shows the mean values associated with the most abundant ostracod species. Three species lie at the upper end of the Fe (> 5%) curve: *Coquimba birchi, Xestoleberis hartmanni* and *Neocaudites osseus*. At the opposite end of the graph, the species associated with values of Fe < 2 per cent (i.e. terrigenous-poor environments) are *Buntonia gibbera, Krithe spatularis* and *Buntonia rosenfeldi*.

Correlation coefficients for Fe (Table 2) are strong only for *Buntonia namaquaensis* and *Buntonia rogersi* (negative), and *Xestoleberis africana* and *Australoecia fulleri* (positive).

Biogenic sediments

Variations in average values of $CaCO_3$ are used to express the biogenic component in bottom sediments (Fig. 21).



Fig. 21. Mean and standard deviation (SD) of $CaCO_3$ in sea-floor sediments for species at each site containing > 100 specimens. This factor is a good indicator of the biogenic component of bottom sediments. To illustrate the antipathetic relationship between biogenic and terrigenous components, the mean per cent of Fe is also plotted.

Twenty-six (72%) of the most abundant species occur in sediments with average calcium carbonate values > 50 per cent. Seven species occur in sediments with average values > 70 per cent, with *Buntonia gibbera* having a mean value > 85 per cent. *Palmoconcha walvisbaiensis* is the only species to occur in opal-rich sediments (mean value of 28% for all sample sites). The three species having the lowest affinity for carbonate-rich sediments (< 45%: *Xestoleberis hartmanni, Buntonia deweti* and *Coquimba birchi*) all have a high affinity for terrigenous material. This expresses the general relationship between CaCO₃ and terrigenous means (Fig. 21), which shows that, as the former decreases, the mean for Fe increases. A simple regression analysis between the values on this curve gives a correlation coefficient of -0.6264.

Correlation coefficients for $CaCO_3$ and various species are listed in Table 2, where the strongest relationships are between *Austroaurila rugosa* (positive) and *Cytheropteron trinodosum* (negative).



Fig. 22. Mean of authigenic minerals (phosphorite and glauconite) in sea-floor sediments for species at each site containing > 100 specimens.

Authigenic sediments

Authigenic minerals are relatively abundant on the continental margin off southwestern Africa (e.g. Birch *et al.* 1986; Bremner *et al.* 1986). To express the relationship between species distribution and authigenic bottom sediments, the combined average values of apatite (in the form of phosphorite) and glauconite have been plotted (Fig. 22). Note that data for *Krithe spatularis*, *K. capensis* and *Henryhowella melobesioides* have been omitted (too few samples contained authigenic minerals for reliable means).

The distribution falls into two clear groups: species with means > 4 per cent and those with < 3 per cent. In the higher category, *Australoecia fulleri* (9%) occurs apart from the other means, which lie approximately linearly between 7 and 4.5 per cent. Other species favouring authigenic-rich sediments are: *Macrocypris* cf. *M. metuenda*, *Cytherella dromedaria* and *Bairdoppilata simplex*. At the lower end of the curve, 11 species lie within a narrow preference band of 2.2-1.8 per cent.

Plotting phosphorite values separately (lower curve in Fig. 22) shows them to lie along an approximately sympathetic curve, with glauconite forming a somewhat greater proportion of the total at the higher value end of the curve.

Coefficient analyses for apatite and glauconite show that several species have strong correlations with both minerals: *Buntonia namaquaensis*, *Urocythereis arcana* and *Australoecia fulleri* (positive), and *Bensonia knysnaensis knysnaensis* and *Neocaudites lordi* (negative). Of these, only *Australoecia fulleri* and *Neocaudites lordi* prefer sediments with high and low mean values of authigenic minerals, respectively.

Sediment texture

Affinities for bottom-sediment types have been expressed in average values of sand $(> 63 \mu)$ and mud $(< 63 \mu$: silt + clay) (Fig. 23). In the mud-rich sediments (> 30% mud), there is strong representation by deeper-water taxa, with four of the first six species in ranking having average depth occurrences > 400 m (*Krithe spatularis, K. capensis, Buntonia rosenfeldi* and *Henryhowella melobesioides*: Fig. 7). The remaining two, *Coquimba birchi* and *Buntonia deweti*, are mid-inner-shelf taxa. Most species (92%) occur in sediments with average mud values > 20 per cent, and only three are strongly displaced off the curve at the mud-poor end of the graph: *Austroaurila rugosa* and *Bensonia k. robusta*.

The plot of average sand values is almost complimentary (the differences representing relatively small gravel components) and all species lie between approximately 60 and 90 per cent sand. The two main exceptions are *Palmoconcha walvisbaiensis* and *Buntonia namaquaensis*. Both values have high standard deviations and probably result from variance in the data set.

Correlation coefficients for sand and mud (Table 2) indicate that *Austroaurila rugosa* is the most sensitive indicator of changes in the ratio of the textural parameters (positive for mud, negative for sand).

POPULATION STRUCTURE

Brouwers (1988) and Whatley (1988) have both recently discussed the question of the structure of ostracod populations in assessing environments. Most podocopid ostracods moult eight times to reach maturity (Brouwers 1988), so that complete preservation of an



Fig. 23. Mean mud and sand content of sea-floor sediments for species at each site containing > 100 specimens.

ostracod population would give a juvenile : adult valve ratio of 8:1. Theoretically, any post-mortem partitioning by bottom currents will disturb this ratio, so that values < 8:1will indicate populations from which early instars have been winnowed, and values > 8:1 environments into which currents have carried fine suspensate, including early instars. Brouwers (1988) considers that the ideal 8:1 ratio is unlikely to be achieved in most natural environments, where the smallest instars are destroyed through predation, dissolution and crushing, and in her work she concluded that the 'ideal' ratio is likely to be 6:1 or 5:1.

Figure 24 is a histogram of the juvenile: adult ratio of the samples with > 100 ostracod valves and was constructed following the same technique employed by Brouwers (1988). Fifteen per cent of the sites have a ratio 7:1, and one site has the theoretically 'ideal' ratio 8:1. In addition, 44 per cent of the sites have a ratio between 6 and 5:1. Consequently, at 59 per cent of the sample sites, sedimentation has occurred under relatively low energy conditions (according to criteria used by Whatley 1983 and



Fig. 24. Histogram of juvenile : adult ratios in samples containing > 100 specimens.

Brouwers 1988). In contrast, 39 per cent of the sites have juvenile : adult ratios that indicate some post-mortem disturbance, and the majority of these (29% of the total) suggest removal of instars, presumably by currents.

The problem with this type of approach is that the instars of larger species are larger than adults of some smaller taxa, and that methods relying on the juvenile : adult ratio or a detailed population age structure, using all the various instar stages (e.g. Whatley 1988), take no account of size differences between species. Nevertheless, the results have been presented for comparative purposes, and possible implications for sea-floor conditions will be mentioned further in the discussion section.

BARREN SAMPLES

In understanding the distribution of the ostracod assemblages, a knowledge of the environments in which they are not found is almost as important as knowing the circumstances under which they do occur.

Of the 270 samples examined for ostracods, a surprisingly large number (81; 30.0%) were barren. These sites extend from west of the Cape Peninsula to just south of the Kunene River (Fig. 25) but are concentrated in two main inner-mid-shelf areas: north and south of the Orange River, and in deep water. In detail (Fig. 26), both shelf areas are further subdivided: a small cluster of sites occurs west of the Cape Peninsula between 200 m and 300 m, separated from the Namaqualand inner-shelf zone, whereas the extensive northern zone, which becomes progressively deeper south of Walvis Bay, is



Fig. 25. Distribution of sites barren of ostracods (black squares) in relation to ostracodbearing sediments (crosses). Areas numbered 1-5 are also shown in Figure 26, and described in the text.

separated from a small number of barren sites in deeper water on the Walvis Ridge Abutment shelf. I have numbered these areas 1-5 on Figures 25 and 26. The extensive barren zone on the upper slope lies in progressively deeper water from north to south $(550-1\ 000\ m)$. Within the barren areas, the ratio of barren to ostracod-bearing sites is high, reaching 2.8 : 1 off Namaqualand (mean of 1.8 : 1; Table 5).

In relation to the regional distribution of ostracod valves, there are frequent rapid transitions from barren areas to regions of relatively high abundance (> 20 valves/ sample - Fig. 26). In particular, this occurs along the western edge of the Walvis Bay-

Area*	Barren sites (B)	Ostracod-bearing sites (O)	Ratio B : O
1	7	9	0.7
2	7	3	2.3
3	49	20	2.5
4	11	4	2.8
5	7	8	0.9
Fotal	81	44	1.8

TABLE 5 Statistics of barren and ostracod-bearing samples.

*-areas indicated on Figure 25

Walvis Ridge sector (area 3), immediately west of the Orange River (area 4), and immediately south and inshore of the Cape Peninsula (area 5).

Environmental parameters of the barren sites

Mean values of various parameters within the areas 1-5, into which the barren samples are concentrated (Fig. 26), as well as overall means for all barren sites, are shown in Table 6.

In comparison with the mean values for the various ostracod species, the means for all barren samples show the following features:

1. High temperature (10.8°C) and high salinity (35.0‰). Only *Palmoconcha walvis*baiensis and Bensonia knysnaensis robusta are higher (Figs 14, 15).

2. Low dissolved oxygen (1.5 ml/l). Only *Palmoconcha walvisbaiensis* and *Bensonia k*. *robusta* are lower (Fig. 17).

3. High organic matter (6.6%). This value is higher than the average for any individual ostracod species (Fig. 19).

4. High mud content (47.3%). This value is 5 per cent higher than for any individual ostracod species (Fig. 23).

5. Low carbonate content (15.7%). This value is 10 per cent less than the lowest for any individual ostracod species, and less than half the mean for the rest of the most abundant species (Fig. 21).

6. Moderate average Fe values (nominally representing the terrigenous component of the sediments) (Fig. 20).

7. Moderate to high average authigenic mineral content (Fig. 22).

When the mean values of parameters in barren areas 1-5 are considered, however, it is clear that no single factor is responsible for the absence of ostracods from regions of the west-coast margin. Nevertheless, there are several factors in common between some of the areas.

Area 1. Upper-mid-slope (mean water depth 763 m). Characterized by low temperature, low salinity, relatively high organic matter and carbonate contents.



Fig. 26. Latitude-depth plan showing barren sites (black squares: areas 1-5 with thick outlines) and ostracod abundance (crosses: specimens/100 g sample). Vertical scale is degrees of latitude.
WR = Walvis Ridge, WB = Walvis Bay, LUD = Lüderitz, OR = Orange River, CC = Cape Columbine, CP = Cape Peninsula.

Parameter		B	arren areas	s*		All
Tarameter	1	2	3	4	5	samples
Depth (m)	763	287	94	107	218	182
Temperature (°C)	4.9	11.1	12.2	9.7	8.9	10.8
Salinity (%)	34.47	35	35.2	34.8	34.6	35
Dissolved oxygen (ml/l)	2.8	1	0.8	2.2	3.8	1.5
Organic matter (%)	6.5	6.9	7.6	4.2	0.98	6.6
Mud (%)	64	24.6	52.6	57.8	6.8	47.3
CaCO ₃ (biogenic) (%)	64.1	52.5	6.3	7.3	10.1	15.7
Fe (terrigenous) (%)	3.3	4.4	2.7	8.6	5.3	3.9
Opal (%)	0	0	32.1	0	0	19.2
Authigenic (%)	0.6	5.5	3.5	4	51.5	7.5

TABLE 6

Mean environmental parameters for barren areas.

*-areas indicated on Figure 25

Area 2. Mid-outer shelf on the Walvis Ridge Abutment (mean water depth 287 m). Characterized by warm, oxygen-depleted water and mixed carbonate/terrigenous, muddy sands with a high organic matter content.

Area 3. This is the most extensive of the barren areas. It lies on the inner-mid-shelf (mean water depth 93 m) and is characterized by warm, saline, oxygen-deficient waters over sediments that have high organic matter and high opaline silica contents. The sediments are depleted in carbonate, Fe (= terrigenous component) and authigenic minerals. This area can be subdivided into a smaller coastal zone between 19 and 20°S (area 3A) and the main zone centred on Walvis Bay, which extends from 21°S to the vicinity of Lüderitz (area 3B).

Area 4. A long, narrow, inner-shelf zone off the Namaqualand coast (mean water depth 107 m) that is characterized by high-terrigenous and low-carbonate muds. In contrast to area 3, the muds contain no opal and relatively little organic matter. The mean oxygen value of the bottom water is depleted (2.2 ml/l).

Area 5. On the mid-outer shelf (mean water depth 218 m) either side of the Cape Canyon. Characterized by water with high dissolved oxygen values over authigenic-rich, low-carbonate sands with a very low organic content. These sediments have particularly low mean mud values.

Sea bottom sediments in three of the areas (1, 3 and 4) have in common particularly high mean mud contents, but each differs in its mineralogical and/or oceanographical characteristics: the slope area 1 is a carbonate mud; the Walvis shelf area 3 is an organicrich, low-oxygen mud; and the Namaqua area 4 is terrigenous mud. The other two areas (2 and 5) have low mud contents. In the case of the Walvis Ridge Abutment (area 2), it shares in common with area 3 low oxygen and high organic matter contents, whereas on the outer shelf off the Cape Peninsula (area 5) the very low organic matter-high authigenic (especially glauconite) contents are probably limiting.

In summary, barren areas coincide with *one or more* of the following limiting factors: 1. High mud content of bottom sediments (> 57.8%).

2. Low dissolved oxygen in bottom waters (< 1.0 ml/l).

3. High (> 6.9%) or low (< 1.0%) organic matter in bottom sediments.

4. Low salinity bottom waters (< 34.47%).

5. High authigenic content (51.5%) of bottom sediments (which may equate with particularly low terrigenous supply).

DISCUSSION

'Modern' and 'relict' faunas

The ostracod assemblages used in the study were mixtures of living and dead specimens. The latter category presumably consisted of recently dead material, which are essentially the same age as the living specimens, and older dead specimens that represent a relict, sub-fossil fauna. In earlier accounts (Dingle 1992, 1993), a distinction was made between these 'modern' (living and recently dead) and 'relict' specimens, primarily on the basis of valve preservation. Opaque, corroded, stained and abraded valves were considered 'relict' in contrast to transparent, pristine specimens, some containing fragments of internal organs, which were considered only recently dead (i.e. 'modern').

The logic applied to the analysis of these two categories was that the sea-floor sediments off south-western Africa represent a quasi-equilibrium deposit developed since sea-level reached its present position, approximately 7000 years ago (Miller 1990). Consequently, the 'relict' ostracod fauna is a mixed assemblage of specimens ranging in age from 0 to 7000 years — the so-called post-glacial category, in contrast to the 'modern', extant category. I am sure that essentially this logic is sound, but recent examination of material from a box core west of Walvis Bay (at 132 m water depth, personal data) has cast doubts on the use of this technique to differentiate the two categories of differing ages.

Consequently, in this report I have adopted a conservative approach by considering the fauna as a whole, so that the species and assemblage distribution data relate to 'average' oceanographical and other environmental parameters, typified by present conditions, but in reality representing means over the period 7 000 years to the present. The available time series for assessing such parameters is, naturally, very short.

Oceanographical data

Modern mean annual sea-floor temperature, salinity and dissolved oxygen values for the west-coast continental shelf were compiled for the present study from a 60-year data base by Dingle & Nelson (1993). Their maps are summarized in Figure 27, on to which have been superimposed the mean annual positions of the upwelling cells of the Benguela system (from Lutjeharms & Meeuwis 1987). The salient points from Figure 27 will be briefly mentioned.

The high correlation coefficient between temperature and salinity values ($\mathbf{R} = 0.896$ for all stations) means that the structure of the two maps is very similar, although there are some differences in detail. Four main features are evident:



Fig. 27. Bottom water parameters and upwelling cells. A. Temperature. B. Salinity. C. Dissolved oxygen. After Dingle & Nelson (1993) and Lutjeharms & Meeuwis (1987).

1. The steep gradient along the shelf edge, where the temperature gradient in the Benguela region is typically $1^{\circ}C/100$ m between 400 and 1 000 m. This is related simply to the bathymetry at the shelf edge.

2. The large intrusion of $9^{\circ}C/34.7\%$ water on to the shelf off Namaqualand. This is attributed to a combination of bathymetry and wind stress. The main topographic features are the generally wide, deep shelf south of 30°S, and a superimposed transverse depression that crosses the shelf at 31.5°S (Fig. 1). The latter probably funnels all the cold water that wells up on to the shelf in this southern region (Peninsula and Columbine cells; Fig. 27), driven by the pumping action of the large cross-shelf wind divergences that are common in this area.

3. Sudden meridional shoaling of isotherms/isohalines. This effect is attributed to a flow of $6-8^{\circ}C/34.48-34.68\%$ water across the shelf as compensation for surface Ekman drift caused by the perennial equatorward winds. This colder water becomes entrained in the poleward undercurrent, resulting in a progressive decrease in the meridional temperature and salinity as far south as $30^{\circ}S$.

4. Localized 'hot spots' of warm, saline water in the form of south-westerly tongues stretching from nearshore across the shelf. In the extreme south ($c. 35^{\circ}$ S) this is caused by the intrusion of Agulhas Bank water, but elsewhere they correlate with upwelling cells to the extent that they indicate downwelling events following periods of intense upwelling. Nelson (1989) has suggested that this occurs via wind-generated continental-shelf waves that enhance or suppress upwelling. The upwelled surface waters are carried northward by wind action, whereas the bottom waters are deflected southward by the poleward undercurrent. Differences in temperature and salinity patterns can be partly accounted for by their respective diffusion rates (10:1).

The distribution of dissolved oxygen in the bottom waters is most closely identified with upwelling in the northern areas. There are two sources of oxygen-depleted (< 5 ml/l) water in the Benguela region. There is an offshelf (300 m) water mass that originates off Angola and is carried southward by the poleward undercurrent (Bubnov 1972; Chapman & Shannon 1985); this extends to about 25°S (occasionally 29°S) and wells up on to the shelf in the manner described above for the 6-8°C water (item 3). The Angolan lowoxygen water is further depleted by sea-floor biochemical action under the influence of the major Walvis Bay-Lüderitz upwelling cell, resulting in a large, shelf-wide oxygendeficient (< 2.0 ml/l) zone, north of 25°S (e.g. Basov 1976; Bailey et al. 1985; Shannon 1985; Dingle & Nelson 1993). The southern limit of this area is sharply outlined by the southern 1.5 ml/l contour, which corresponds with the edge of the upwelling cell (Fig. 27C). A stream of this oxygen-deficient water leaks southward under the influence of the poleward undercurrent, and forms a nearshore zone as far south as St Helena Bay. Further small zones of depletion occur by biochemical action off southern Namaqualand. In this connection, De Decker's (1970) observation of seasonality in oxygen depletion correlates with the seasonality of the poleward undercurrent (Dingle & Nelson 1993).

Relationships between ostracods and environmental parameters

Having looked at the mean values of the various parameters for each species, what can be said about their overall correlations? Bearing in mind that a wide range of environmental parameters influences the distribution of Ostracoda (see, for example, Neale 1965; Whatley 1983; Brouwers 1988; Athersuch *et al.* 1989), it is possible that

variations in any one parameter will be insufficient to control the geographical range of a taxon completely. Nevertheless, several authors have concluded that certain parameters are likely to be more important than others. In this category, temperature has been singled out as a major factor, so much so that it was the only parameter considered by Cronin & Dowsett (1990) along the continental shelf off eastern North America, whereas Valentine (1976) concluded that faunal distribution along the Pacific coast of North America was primarily controlled by water temperature related to upwelling. Athersuch *et al.* (1989) considered temperature to be the main ecological control (along with salinity) in distribution around the British Isles, and commented that variations in dissolved oxygen were of little significance. Brouwers (1988), on the other hand, believed that temperature, salinity and dissolved oxygen are the main physico-chemical controls for ostracod distribution off Alaska. For comparison, Brouwers (1988) recorded the following ranges in parameters on the Alaskan shelf (south-western African values in parenthesis): temperature, $5-5.5^{\circ}$ C ((3.0-14.0); salinity, (33.00-34.00%) ((34.39-35.5); and dissolved oxygen, (3-7 ml/1)(0.29-4.8).

The question of dissolved oxygen and the distribution of particular marine taxa has been raised by several authors and this is a factor that is especially relevant off southwestern Africa, where the whole of the continental shelf is oxygen depleted (< 5.0 ml/l), and large areas are deficient (< 2.0 ml/l) (e.g. Shannon 1985). Briefly, the structure of the vestibula of the genus *Krithe* has been linked to variations in dissolved oxygen levels (e.g. Peypouquet 1977; McKenzie *et al.* 1989; Riha 1989; Zhou & Ikeya 1992; but for an alternative viewpoint see Whatley & Quanhong 1993), whereas the physiological adaptations of certain taxa (particularly the genus *Cytherella*) have given them advantages in colonizing low-oxygenated environments (e.g. Whatley 1991).

Other factors have generally received less attention but, nevertheless, some authors have strongly asserted their importance (e.g. Whatley & Wall 1969; Whatley 1976). In this category fall factors such as substrate types (animal, plant and mineral, as well as textural variations), pH, food supply, light levels, turbulence (i.e. energy of the boundary layer), and so on. Athersuch *et al.* (1989) have reviewed the distribution of all the major taxa around the British Isles and concluded that certain taxa have preference for different substrates: *Xestoleberis* is primarily a phytal genus, whereas *Urocythereis, Palmoconcha, Cytheropteron, Cytherura* and all Trachyleberididae and Cytherideidae live on sand. However, many taxa appear to have no preference (e.g. *Aurila, Loxoconcha* and *Semi-cytherura*).

Clearly, it would be an unrealistically complex operation to acquire from the whole margin off south-western Africa time-averaged data on all the factors mentioned above, even if it were certain that there were no others of significance. Spot measurements during sample collection would have served little purpose and, unfortunately, data bases on most parameters are not available. Also, the circumstances in specific geographical areas will strongly bias the likelihood of particular factors playing crucial roles. In the present case, the large range in dissolved oxygen values, the overall lack of terrigenous input, the locally high contents of authigenic minerals, and the overall intensity of oceanic upwelling, make the continental margin off south-western Africa, if not unique, at least one of only five localities world-wide with similar conditions (the others being California, Peru, north-west Africa and the Gulf of Arabia). Adaptation to these conditions can be expected to have played an important role in the composition of the local faunas, and significant variations from the 'norm' of what has been described from, say north-western Europe or north-eastern North America, can be anticipated. In this connection, the large number of barren sites must be viewed as a response to the unusual environments, and not merely an aberration of the sampling and laboratory techniques.

Considering, firstly, the relationships between the environmental parameters themselves, Table 3 shows the correlation coefficients based on simple regression analyses between the parameters in those samples from which > 100 specimens were extracted. Here there will be a bias against deeper-water sites and areas unfavourable for ostracod colonization, where, in both cases, valve numbers are low. Some strong relationships are obvious (sand-mud, and temperature-salinity-oxygen), but the positions of MORG and CaCO₃ are less so.

To draw out the more subtle relationships, these values have been plotted (Fig. 28) on a similarity dendrogram, using an unweighted arithmetic average clustering technique



Fig. 28. Similarity dendrogram (unweighted arithmetic average) of environmental parameters.

(e.g. Legendre & Legendre 1983). This shows two main groupings at the 35-45 per cent similarity level. The strong antipathetic relationship between sand and mud (-0.9306) is linked to MORG through a positive correlation (0.4906) with mud, and to glauconite through a positive correlation with sand (0.3788).

The second grouping is based on the strong positive correlation between temperature and salinity (0.9092) and their negative correlation with dissolved oxygen (-0.8130 with salinity). These relationships are representative of the regional trends discussed by Dingle & Nelson (1993) and reflect properties of the major water masses and upwelling cells along the west coast (e.g. Fig. 27). They are negatively correlated with the calcium carbonate content of the bottom sediments (-0.4902 with salinity), implying that carbonate-rich sediments are less likely to occur in the warmer, more saline, sea-floor environments, as well as in outer-shelf areas where more oxygenated waters occur. Similar conclusions were reached by Rogers & Bremner (1991), who showed that the areas of most intense upwelling (between about 28° and 24°S, where bottom temperatures and salinities are particularly high) are underlain by sediments with low carbonate contents. Similarly, south of 29°S, where dissolved oxygen levels on the shelf are at their highest, low carbonate values characterize the whole shelf south and west of the Cape Peninsula. No comprehensive explanation for the latter situation has yet been advanced.

Elemental Fe (= terrigenous component) and apatite values have no close links with the other two groupings (< 20% similarity). The terrigenous input to the west coast is controlled by four major factors: Kunene River input north of the Walvis Ridge; the combined input of the Orange River and of the Olifants and Berg rivers on to the Orange–Namaqua shelf; and aeolian input between the Orange River and Walvis Bay. Whereas the latter phenomenon is to some extent linked to upwelling through regions of strong wind stress, there are no direct relationships between the terrigenous sources and the environmental factors investigated.

Tables 2 and 7 show which parameters are most strongly correlated with particular ostracod species. A simple gauge of which parameters are most effective in determining the distribution of species can be made by totalling the number of species most strongly correlated with each parameter. Fe and calcium carbonate rank joint first (5 species each), followed by sand (4 species). Amongst these, there is a preponderance of negative correlations, particularly with sand and, to a lesser extent, $CaCO_3$ (this conclusion is reinforced if a tally is made of the strongest positive and negative correlations for each species: sand = 13, calcium carbonate = 8, Fe = 8, and MORG = 8). The implication is that the abundance of the majority of ostracod species in the study has an antipathetic relationship to sandy and/or carbonate-rich substrates. In addition, neither temperature, salinity, nor oxygen is as important as MORG.

Considering the importance of environmental parameters in terms of the regionally dominant species (Figs 10, 29), however, presents a somewhat different picture. South of 24°S, the two dominant inner-shelf species *Pseudokeijella lepralioides* and *Bensonia knysnaensis knysnaensis* correlate with the mud (positively) and carbonate (negatively) content of bottom sediments, respectively. In the case of the latter, the strongest positive correlative is Fe, indicating that increases in abundance of *Bensonia k. knysnaensis* are dependent on decreasing carbonate, coupled with increasing terrigenous components. Farther offshore, *Ruggieria cytheropteroides* is positively correlated with dissolved oxygen. North of 24°S, the two dominant species are *Palmoconcha walvisbaiensis* (mid-

TABLE 7

Summary of strongest correlations between species and environmental parameters. These parameters are those that most negatively or positively influence the abundance of a particular species.

Species	Positive	Negative
Cytherella namibensis	MORG	oxygen
Bensonia k. knysnaensis	Fe	CaCO
Ruggieria cytheropteroides	oxygen	_
Henryhowella melobesioides	sand	mud (temperature
Pseudokeijella lepralioides	mud	sand
Palmoconcha walvisbaiensis	MORG	oxygen/Fe
Urocythereis arcana	apatite	
Macrocypris cf. M. metuenda	CaCO ₃	mud
Australoecia fulleri	Fe	
Bairdoppilata simplex	sand	apatite
Paracypris lacrimata	Fe	CaCO ₃
Cytheropteron whatleyi	salinity	sand
Cytheropteron trinodosum	MORG	CaCO ₃
Cytherella dromedaria	MORG	sand
Neocytherideis boomeri	sand	mud
Poseidonamicus panopsus	glauconite	CaCO ₃
Neocytherideis lordi	MORG	apatite
Incongruellina venusta	_	CaCO ₃
Buntonia rogersi	MORG	Fe
Ambostracon flabellicostata	salinity	sand
Buntonia bremneri	mud	sand
Xestoleberis africana	Fe	sand
Chrysocythere craticula	CaCO ₃	Fe
Austroaurila rugosa	CaCO ₃	sand
Doratocythere exilis	apatite	temperature
Neocytherideis osseus	mud	sand
Ambostracon keeleri	MORG	sand
Buntonia gibbera	MORG	sand
Buntonia namaquaensis	glauconite	Fe

Note: items in bold are the overall strongest correlatives.

For *H. melobesioides*, temperature is probably a better indicator for the deep-water assemblages.

inner shelf) and *Cytherella namibensis* (outer shelf-upper slope), and here the strongest correlations are with MORG (positive) and dissolved oxygen (negative), respectively. The latter species' strongest positive correlative is also with MORG, whereas the strongest negative correlative of *Palmoconcha walvisbaiensis* is dissolved oxygen. Consequently, both dominant taxa on the shelf off northern Namibia respond positively to increases in the quantity of organic matter in bottom sediments and negatively to increases in dissolved oxygen. *Henryhowella melobesioides* is the dominant species over the length of the margin in water deeper than 500 m (to about 1 500 m) and this species correlates most strongly with mud (-0.5360), with sand its strongest positive correlative. However, because of the relatively small sample sizes in deep water, these correlations are biased



Fig. 29. Distribution of dominant ostracod assemblages (shaded, from Figure 10) and barren areas (thick outline, 1-5 from Figure 26). Dashed line is the shelf break. Parameters in parentheses are strongest environmental correlatives for dominant species (positive or negative) from Table 7.





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towards the shallower water sites at which *H. melobesioides* occurs and in which it is a less-important component of the assemblage. Correlation coefficients based on the whole sample suite suggest that this species, on a regional basis, most strongly correlates with temperature (-0.5143) which, together with salinity, generally decreases with increasing latitude and depth (Fig. 27).

It is convenient to consider the distribution of ostracod assemblages in relation to regional environmental parameters in terms of the dominant taxa. Figure 29 shows the geographical distribution of the dominant taxa, together with the environmental parameters with which they are most strongly correlated, whereas Figures 30–32 show regional latitude–depth plans of variations in all the parameters investigated. To make a more sophisticated assessment of the relationships between individual species requires a multivariate approach, and this has been presented in a separate publication (Dingle & Giraudeau 1993).



Fig. 32. Latitude-depth plans of dominant ostracod assemblages and bottom-water and sea-floor sediment parameters. A. Sand. B. Mud.

The general conclusions from the discussion above are that the distributions of dominant taxa in the deeper-water areas are most strongly correlated with parameters related to the water-mass properties, whereas the mid- and inner-shelf taxa most strongly correlate with sedimentary characteristics (in particular Fe (= terrigenous component), calcium carbonate and sand). These correlations do not imply that such factors are the *only* controls but that they are, statistically, the most important for individual species.

To understand these correlations, it is important to remember that the oceanography and climate off south-western Africa are influenced by phenomena that, on a global scale, are not widely developed: intense oceanic upwelling, large-scale development of oxygen-depleted bottom water (< 5 ml/l), and low terrigenous input.

SUMMARY

Figure 33 shows the conceptual relationships between the distribution of the regionally dominant ostracods and the main oceanographical components of the west coast. In deep water, small-scale phenomena are subordinate to the regional water-column structure (see Fig. 2), so that the upper limit of the mid-lower-slope assemblage (dominated by *Henryhowella melobesioides*) is controlled by the position of the base of the salinity minimum zone in the AAIW (500-600 m) (see also Dingle *et al.* 1990).

Higher up the slope, the effects of shelf upwelling and the intrusion of shelf currents are felt. South of 28°S, the cold, low-salinity, oxygen-rich upper section of the AAIW sustains the upper slope-outermost shelf *Ruggieria cytheropteroides*-dominated assemblage, but northwards this gives way to the less abundant and diverse *Cytherella namibensis*-dominated assemblage that is influenced by warmer, more saline, oxygendepleted water just beyond the shelf edge moving into the region across the Walvis Ridge from the Angola Basin. Deflection of uppermost AAIW around the major bathymetric re-entrant along the northern side of the Orange Banks (27–28°S: Fig. 1) is probably a critical control in the location of this oceanic/faunal boundary. As Whatley (1991) has discussed, platycopid ostracods are particularly adapted to competing in lower-oxygen environments and, clearly, *C. namibensis* (in marked contrast to its more southern relation *C. dromedaria*), has taken advantage of this in areas that are unfavourable to most other species.

Moving farther on to the shelf, the influences of water mixing and upwelling are more pronounced. In the north, the off-shelf Angolan water mass advects oxygendepleted waters on to the Walvis–Lüderitz shelf, where intense upwelling, followed by further, biologically-induced oxygen extraction on the sea-floor, creates a reservoir of strongly oxygen-depleted shelf waters and organic enrichment in bottom sediments, which is the preferred environment of *Palmoconcha walvisbaiensis*. Under the influence of the poleward undercurrent, strong southward temperature, salinity and oxygen depletion gradients are created (Fig. 27), which progressively support different ostracod associations as the properties of the southward-moving water change, and it interacts with other, colder shelf waters in the vicinity of the Orange River. Hence, the *Palmoconcha walvisbaiensis*-dominated assemblage passes via a mixed zone (Central Namib association) into the coast-parallel assemblages dominated by *Pseudokeijella lepralioides* (positively correlated with mud) and *Bensonia k. knysnaensis* (negatively correlated with mud and positively correlated with Fe).



Fig. 33. Conceptual relationships between ostracod associations and the main oceanographic regimes and features plotted on a latitude-depth plan. Vertical scale is degrees of latitude, horizontal scale is water depth (km). Abbreviations: BKK = Bensonia k. knysnaensis, CN = Cytherella namibensis, CNA = Central Namib association, HM = Henryhowella melobesioides, PL = Pseudokeijella lepralioides, PW = Palmoconcha walvisbaiensis, RC = Ruggieria cytheropteroides, SWCA = South West Cape association, CB = Childs Bank.

The southern limit of oxygen-deficient water, together with intense upwelling of upper-level AAIW off the Cape Peninsula and intrusions of warm, Agulhas water filaments (Lutjeharms 1989), combine to produce the particularly diverse and abundant, but geographically small, South West Cape association.

Other aspects of interest are the high degree of strongest negative correlation with the sand content of the bottom sediments (13 (negative) : 3 (positive)), and the high degree of strongest positive correlation with the MORG values (8 : 0) (Table 7). These contrast with more equitable correlations with the terrigenous (Fe) and biogenic (CaCO₃) components (4 : 4 and 3 : 5, respectively).

The implications from these relationships are that the abundances of a large minority of species (34% in Table 7) are affected adversely by increases in the ambient sand content of their favoured substrates, the exceptions being Henryhowella melobesioides, Bairdoppilata simplex and Neocytherideis boomeri. Although few details have been published on bottom currents on the west-coast margin, indications are that they are generally low and poleward. Nelson (1989) suggested that, between Cape Point and the Orange River, a vector-averaged poleward velocity of 3.8 cm/sec exists, but noted that at 66 m off Chamais Bay (28°S) a current meter has recorded a long-term average of 1.7 cm/ sec north-west. Only along the outer Namaqua shelf, between 31°S and the vicinity of Cape Columbine (33°S), is there possible evidence for relatively high-velocity currents in the Benguela system (the Shelf Edge and Columbine jets), with surface velocities up to 40 cm/sec north-west (e.g. Shannon 1985; Nelson 1989). However, although Shannon (1985) suggested that these may have subsurface effects, Nelson (1989) indicated that they are merely high-velocity streams (40-50 cm/sec) in the general northward Benguela surface flow pattern (which itself varies from 5 cm/sec over the shelf to 30 cm/sec beyond the shelf edge). Strong and turbulent bottom currents are not, therefore, anticipated over any large part of the west-coast shelf, and few species can be expected to have adapted to such conditions. Perhaps this explains the susceptibility to increases in sand content (if it denotes somewhat higher bottom-water energy).

A further assessment of areas with high-velocity sea-floor currents can be related to possible post-mortem valve transportation. Figure 34 shows the latitudinal distribution of sample sites plotted against their juvenile : adult ratios. Sites with the lowest ratios are intuitively taken as those most subjected to higher sea-floor winnowing, and these all occur south of 30°S. The most-affected sites lie in water depths between 205 and 271 m in the vicinity of Childs Bank (see Figs 1, 33), where Nelson (1991 pers. comm.) has suggested that an extension of the Shelf Edge Jet could operate, although it should be emphasized that other sites on the mid–outer shelf in this area have ratios between 6 and 8:1. Winnowing is further suspected at two sites on the inner shelf, immediately west of the Cape Peninsula (120–140 m at 34°S, Figs 33, 34) and at an inshore site (42 m) near Cape Columbine (32.5°S, Fig. 34). In contrast, all sites north of Childs Bank as far as the Walvis Ridge, suggest quiet sea-floor conditions, as do the bulk of the sites off the Cape Peninsula.

No species has the organic content of bottom sediment as the parameter most adversely affecting its distribution, whereas an increase in the MORG value favourably affects 28 per cent of the taxa in Table 7, with *Palmoconcha walvisbaiensis*, *Ambostracon keeleri* and *Buntonia gibbera* particularly sensitive in this regard. On a continental shelf where the organic content of sediments is generally high and, overall, the most organic



Fig. 34. Latitudinal distribution of juvenile : adult ratios in samples containing > 100 specimens. Sediment partitioning by bottom currents is progressively indicated by ratios < 5 (see Brouwers 1988). This phenomenon is suggested at the sites with water depth > 200 m in the vicinity of Childs Bank.

rich in the Atlantic Ocean (Yemel'yanov 1975, quoted in Rogers & Bremner 1991), the ability not to be affected adversely by increases in MORG is clearly an ecological advantage.

Finally, in the distribution of barren samples (see Fig. 27), the direct and indirect effects of upwelling are probably the dominant influence north of 27°S (dissolved-oxygen values < 1.0 ml/l, MORG values > 6.9%), whereas fluvial input (area 4: terrigenous mud values > 58%) and topography (area 5 either side of the Cape Canyon, which shelters areas from organic-matter sources, and perhaps creates locally unfavourably strong seafloor currents) are important in the south.

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Statistical parameters for 95 per cent of ostracod population (36 species). ALL = full data set; 100 = sites with > 100 specimens.

Ranking: 2	Range 1.1-12.49 4.6-35.28 0.7-4.5 94-300 94-300 94-300 0.2-34.58 94-300 0.2-34.58 0.1-15 0.10 0.10 0.10 0.10 0.10 0.10 0.10 0.	Ranking: 4 Range 0.74.1 0.74.1 0.74.8 15-271 143-34.58 15-271 143-34.58 15-271 143-34.58 0.76.8 8.8.7 0-10 0.10 0.1	Ranking: 6 Range 7.1-12.9 7.1-12.9 7.1-12.9 2.5-4.1 1.4-6.8 40-271 8.4-34.9 3.7 0.20 0.10 0.10 0.10 8.7-52.6 0.00
centage: 22.1	100 S.D. S.D. S.D. 1.02 0.13 3.26 1.61 47.9 2.82 3.01 2.93 2.93 2.93 1.2.34 0 1.2.34 0	centage: 4.27 100 5.D. 1.02 8.D. 1.02 0.78 0.78 62.18 62.18 5.35 20 2.1.35 21.35 21.35 21.35 21.35 21.35 14.82 0 0	centage: 2.66 100 5.D. 1.09 0.1 0.43 0.43 1.61 55.1 2.43 20.47 1.27 2.48 20.47 1.276 12.26 13.06 4 12.76
Overall per	Average 9,14 34,73 34,73 3.36 30,32 30,32 30,32 31,55 65 33,55 2,18 23,56 2,18 23,56 0 0	Overall per Average 9,47 9,47 3,25 3,25 154.67 154.60 4,39 60.4 60.4 5,38 2,38 5,32 0 0	Overall per Average 3.57 3.57 3.57 3.57 3.72 3.72 3.72 3.73 71.78 1.76 3.78 71.78 73.62 26.18 0
()	Range 5, 12-12, 49 34, 39-35, 28 0, 7, 4, 5 0, 9-10, 44 94-590 19, 92-35, 35 1, -7 6, 92, 9 0, 345, 9 6, 7-63, 9 6, 7-63, 9	Range 7.29-12.85 34.54-35.13 0.74-4 15-303 0.5-7.4 15-303 0.5-7.4 15-303 20.43-34.77 7.9-91.1 0.3-11.1 34.9-95.9 2.1-52.6 00.01	Range 7-12.9 34.55-35.04 1-4.1 0.2-6.8 22.25-35.24 11-92 0-10 0-10 0-10 0-10 0-10 0-10 0-10 0-1
rady, 1880	ALL S.D. S.D. S.D. S.D. 1.39 0.15 0.15 0.15 0.15 0.97 1.23 1.22 1.22 26.32 26.32 1.4.07 1.4.07 1.4.07 1.4.07 1.4.07 1.4.01 1.4.0	gle, 1992 ALL S.D. 1.33 0.13 1.33 0.13 1.33 1.33 1.33 1.79 70.85 1.79 1.79 1.79 1.79 1.76 1.48 1.26 1.48 1.26 1.48 0.002	1880) ALL S.D. 1.11 0.01 0.01 0.01 0.02 2.78 2.78 2.78 1.112 5.99 3.299 3.299 3.299 0.110 0.110 0.110 0.110 0.110 0.110 0.110 0.110 0.11000 0.1100000000
teroides (B	Average 8.58 34.69 3.24 3.24 270 29.79 29.79 29.79 29.79 10.6 10.6 10.6 26.56 0	keeleri Din Average 9.61 34.76 3.4.76 3.045 3.045 3.045 4.68 6.2.91 4.68 6.2.91 4.68 73.2 0.0002	is (Brady, Average 9,14 9,14 34,73 34,743 34,743 34,743 34,743 34,743 34,743 34,743 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,744 34,7444 34,7444 34,74444 34,74444444444
Ruggieria cytherop	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Sand Mud Opal	Ambostracon (A.) Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaZO3 Glauconite Phosphorite Sand Opal	Doratocythere exil Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Opal
Ranking: 1	Range 7.1-12.9 34.6-35.28 0.7-4.1 1.3-6.8 40-271 19.91-34.58 3-7 16.5-92.9 0-10 0.3-45.9 38.9-91.6 7.9-52.6	Ranking: 3 Range 7.1-12.9 34.6-35.04 1.1.4 0.7-7.4 0.7-7.4 1.1.34.58 1.25.11-34.58 1.2.1.34.58 1.2.3.37 0.2 0.2 2.1.46.1 0-1	Ranking: 5 Range 7.5-12.9 34.6-35.04 2.5-4.1 1.3-6.8 40-300 29.63-34.58 40-300 29.63-34.58 16.5-71.2 0-10 0-10 0-0
itage: 34.2	$\begin{array}{c} 100\\ 8.D.\\ 1.45\\ 0.14\\ 0.14\\ 0.14\\ 0.14\\ 0.14\\ 0.14\\ 0.14\\ 0.14\\ 0.23\\ 0.09\\ 1.21\\ $	Itage: 5.48 100 S.D. 1.4 0.13 0.13 0.13 0.13 0.13 0.13 0.13 0.13	ltage: 2.93 100 8.D. 1.29 1.29 1.78 1.78 1.78 1.78 1.78 1.78 1.78 1.78
Overall percer	Average 9.33 9.34 9.33 34.74 33.35 30.98 3.38 65.57 2 3.33 5.33 23.33 23.37 0	Overall percer Average 9.73 34.75 3.05 4.75 3.05 4.75 50.66 1 1 8.06 50.66 1 1 0.03	Overall percer Average 9.27 34.7 3.38 3.38 3.321 3.3223 3.3223 3.3223 3.3223 3.3223 3.3223 3.3223 3.3223 3.32233 3.3223 3.3223 3.3223 3.32233 3.32233 3.32233 3.322333 3.322333 3.3223333 3.32233333333
	Range 6.55-12.9 34.6-35.28 0.9-9.1 40-500 19.19-35.24 2-9.5 2-9.5 0-55 0.3-45.9 36.1-96.1 7.9-63.9	docks, 1964) Range 7,1-13,28 34,6-35,18 0,09-4,3 0,18-8,8 15-283 19,19-34,77 2-11 12,9-89,3 0-2 0,6-45,9 47,3-95,9 2,11-46,1 0-1	Range 7.5-12.9 32.6-35.04 32.6-35.04 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.3 1.3-6.8 1.3-6.8 1.3-6.10 0.10 0.110 0.110 0.110 0.2-11.9 0.7-5-2.9 0.00
ady, 1880)	ALL S.D. S.D. S.D. 1.29 0.14 1.01 1.01 1.01 1.03 3.88 2.65 9.9 9.9 9.9 9.9 1.437 13.22 0	on & Mad ALL S.D. 1.5 0.16 1.13 0.16 1.13 71.05 2.18 71.05 13.92 0.59 112.52 13.87 0.18 0.18	ALL ALL S.D. 1.41 0.11 0.41 1.33 17.25 1.33 1.725 1.254 1.33 1.725 1.725 1.73 1.725 1.725 1.725 1.725 1.7755 1.7755 1.7755 1.7755 1.7755 1.7755 1.7755 1.7755 1.77
ilioides (Br	Average 9.55 34.78 3.06 3.06 3.05 3.05 4.12 4.68 4.28 4.28 4.28 4.28 4.28 25.34	wisis (Bens Average 10.31 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 34.82 353 34.82 35.83 34.82 35.83 34.82 35.53 34.82 34.82 35.53 35.83 35.93 35.83 35.93 35.83 35.93 35.73 35.93 35.73 35	ria (Brady, Average 9.41 3.77 3.13 3.13 3.13 3.13 3.57 3.13 3.57 3.13 3.57 3.57 3.55 3.55 3.55 3.55 3.55 3.5
Pseudokeijella lepra	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud	Bensonia k. knysnau Temperature Salinity Dissioved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Mud Opal	Cytherella dromeda Temperature Salinity Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud Opal

QUATERNARY OSTRACODS FROM SOUTH-WESTERN AFRICA

3 Ranking: 8	Range 7.1-12.9 34.6-35.04 3-4.1 1.3-4.1 40.227 28.42-34.52 28.42-34.52 28.42-34.52 16.5-92.9 0-1 0.8-6.8 8.7-52.6 0-0	Ranking: 10 Range 7.1-12.9 34.6-35.04 0.7-4 0.7-4 0.7-4 0.7-4 0.7-4 0.7-4 3.3-89 3.3-89 3.3-89 3.3-89 3.3-89 3.3-89 3.3-89 3.3-89 3.3-89 3.3-5-89 0.01-10 0.8-5.7 20.43-55 9 20.43-55 20.43-55 20.43-55 20.25 20.25 20.25 20.25 20.25 20.25 20.43 20.43-55 20.43-55 20.25 20.43-55 20.25 20.43-55 20.55 20.43-55 20.5	Ranking: 12 Range 7.1-11.5 34.6-34.92 1.55-4.1 1.3-5.9 1.5-300 15-300 15-300 15-300 22.93-34.57 7.13-92.9 0.010 0.3-11.6 533-891.6 7.9-46.1 7.9-46.1
entage: 2.1	100 S.D. 1.23 0.12 0.12 0.12 0.12 0.12 0.12 0.12 0.3 2.43 0.49 0.45 0.45 0.45 0.45 0.45 0.45 0.45 0.45	ntage: 2.04 100 8.D. 1.4 0.14 0.14 0.14 0.14 0.86 1.53 3.91 3.91 3.25 1.53 3.25 1.644 17.51 0 0	ntage: 1.82 100 8.D. 8.D. 110 80.5 3.14 1.67 3.14 1.67 3.14 1.65 3.14 1.63 3.74 10.64 11.12
Overall perce	Average 9.09 34.7 3.71 3.71 3.71 3.71 3.71 3.71 5.46 0.8 0.8 0.8 0.8 0.2 2.25 0.2 2.42 0.8	Overall percet Average 9.63 34.75 34.75 34.75 31.27 31.27 31.27 31.27 31.27 31.27 56.09 51.09 51.09 51.00 51	Overall percer Average 9.01 34.69 3.5 3.5 3.5 3.5 3.5 3.5 3.5 3.5
	Range 7.1-12.9 34.6-35.04 1.9-4.3 0.18-6.8 40-227 3-11 16.5-92.9 0.5-6.8 8.7-52.6 0-0	, 1880) Range 7.1-13.37 34.6-35.13 0.7-44.3 0.7-46.2 15-72.6 15-72.6 15-72.6 18.3-89.3 0-10 0.5-50.8 20.5-50.8 21-55.6 0-65.2 0-65.2 0-65.0 20.5-52.6	Range 5-12.16 5-12.16 34.5-35 1-4.8 0.5-5:9 15-545 22.25-34.97 7.13-92.9 0.3-17.2 34.9-96.1 5.49.7 0.049.7
le, 1992	ALL S.D. S.D. 1.27 0.11 0.11 0.11 0.54 2.65 2.64 2.73 0.73 0.73 0.73 0.73 0.73 0.73 0.73 0	ata (Brady ALL S.D. 1.64 0.18 0.18 1.22 59.84 4.8 1.22 59.84 1.22 59.32 59.32 59.32 59.32 59.32 1.09 11.09 11.09 11.09 11.09 11.09 11.09 11.09 11.09 11.09 11.00 10.00 10.00 10.00 10.00 10.00 10.00 10.00 10.00 1	, 1880) ALL S.D. 1.59 0.91 0.91 0.91 0.91 0.91 0.91 0.91 0.9
meri Dingl	Average 9.34 9.34 34.72 3.64 2.59 144 1.11 1.11 1.11 1.11 1.11 1.11 1.11	Average Average 10.17 34.81 2.73 4.34 1.28 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 29.73 20.75 20.75	<i>olex</i> (Brady Average 8.8 3.52 3.52 3.52 199 31.99 31.99 4.51 4.51 4.51 19.1 0.1
Neocytherideis boo	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaO Glauconite Phosphorite Phosphorite Mud Opal	Ambostracon (A.).) Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO Glauconite Phosphorite Sand Mud Opal	Bairdoppilata simp Bairdoppilata simp Salinity Dissolved oxygen Drganic matter Depth Latitude Fe Calauconite Phosphorite Sand Mud Mud
Ranking: 7	Range 7.5-12.9 34.6-35.04 2.4-4.1 1.6-6.8 15-300 28.43-34.58 3-7 33.5-92.9 1-8 0.8-11.9 47.5-86.4 13.6-52.6	Ranking: 9 Range 7.1-12.9 34.6-35.04 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 1.3-6.8 3.3-89.3 3.3-89.3 1-10 0.3-8.7 0.3-8.7 0.3-8.7 0.3-8.7 0.0-0	Ranking: 11 Range 10.5-12.76 34.92-35.28 0.7-1.55 1.44.4.2 31.200 19.91-26.05 4-7 74.6-75.7 0.91-19 33.9-90 33.9-90 7.3-7.9 0-0-0
itage: 2.22	$\begin{array}{c} 100\\ \text{S.D.}\\ 1.19\\ 0.12\\ 0.1$	ntage: 2.09 100 8.D. 115 0.115 0.45 1.77 2.67 2.67 2.92 1.33 2.92 1.4.86 0	age: 1.98 100 5.D. 1.23 0.49 0.49 1.4 86.82 3.4 1.7 1.7 0.78 0.71 0.71 0.42
Overall percer	Average 9.22 9.22 3.64 3.64 4.07 131 33.06 63.34 5.17 2.17 2.17 3.61 3.61 3.61 3.61 3.61 3.61 3.61 3.61	Overall percet Average 3.51 3.51 3.51 3.51 154 3.71 154 15 3.71 154 15 3.71 154 15 59,01 2.5 3.81 2.5 2.5 2.844 0 0	Overall percent Average 11.92 35.06 0.98 0.98 0.98 0.98 0.98 0.98 0.98 0.98
	Range 4.69-13.46 34.39-35.1 0.8-4.3 0.9-7 0.9-7 15-945 0.9-7 4.9-22.9 0.9-7 4.1.2-93.2 6.7-53.3 6.7-53.3	Range 5.7-12.9 34.6-35.04 1-4.7 1.4.7 1.3-6.8 40.545 10.545 22.25-34.77 22.25-34.77 22.25-34.77 22.25-34.77 22.25-34.77 0.01-32 0.03-45.9 47.5-91.6 7.0-0	1974) Range 8.5-14 34.9-35.32 0.4-1.6 1.56-17.5 1.5-17.5 1.5-280 1.5-280 1.7-53-26 1.5-280 1.5-280 1.7-83.5 0-19.7 0-50.8 3.6-90.1 6.506
1992	ALL S.D. S.D. 1.78 0.15 0.15 0.15 0.8 3.83 3.83 3.83 3.83 3.83 2.465 4.38 24.65 24.65 15.54 15.59 15.59	880 ALL S.D. ALL S.D. 0.79 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.779 0.776 0.7	Hartmann, ALL S.D. S.D. 1.26 0.37 0.37 0.37 2.35 30 5.1 2.35 30 5.1 10.71 10.71 10.71 21.34 21.38
ta Dingle,	Average 8.6 34.66 3.46 4.05 31.27 31.27 31.27 4.44 45.74 14.43 68.27 68.27 68.27 30.18	 a Brady, 11 Average Average 34.72 3.48 3.55 3.5	Average Average 12.5 35.14 0.814 0.87 3.59 3.59 1.62 7.97 24.55 25.55 25
Paracypris lacrima	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud Opal	Xestolebris african Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Phosphorite Mud Opal	Palmoconcha walw Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Phosphorite Mud Opal

ANNALS OF THE SOUTH AFRICAN MUSEUM

gle, 1992 Overall percentage: 1.76 Ranking: 14
ALL Average S.D. Range 9.35 2.34 5.5-13.46 34.79 0.23 34.42-35.28
ge Average
1001

Ranking: 20	Range 7.1-12.49 0.7-4 1.4-5.8 1.31-252 19.92-34.55 3.5-90.4 0-10 0.8-6.8 38.9-87 7.9-52.6 0-0	Ranking: 22	Range 7.5-10 44.61-34.69 2.5-4.1 1.3-6.3 1.3-6.3 1.3-6.3 2.5-4.1 1.3-6.3 2.5-4.1 37.9-99.3 1-10 0.3-11.9 58,9-96.1 7.9-41 0-0	Ranking: 24 Range 7,1-12,49 34,6-35,28 0,07-4,1 1,4-6,8 131-295 9,92-34,58 2-5 7,13-92,9 0,01-10 0,8-6,8 33,9-87 7,9-52,6 0-0
ntage: 0.45	100 S.D. 0.87 0.18 0.87 0.87 0.88 3.9 1.49 1.49 3.9 2.183 3.9 1.757 1.757 1.757 1.757 0.88	entage: 0.4	5.00 0.75 0.75 0.75 0.75 0.07 0.75 0.75	ntage: 0.38 100 5.D. 1.1 0.15 0.9 38.33 1.62 38.33 1.62 38.33 1.62 38.33 1.62 2.56 2.56 2.56 2.55 115.55 115.55 0 0
Overall percer	Average 9.25 34.75 3.35 3.35 3.63 3.63 3.63 3.63 3.63 3.6	Overall perce	Average 9.1 34.69 34.69 34.69 34.69 32.58 4.13 4.13 4.13 4.13 4.13 4.13 275.96 21.09 21.09	Overall percer Average 9.16 3.27 3.27 3.27 3.27 3.27 196 3.25 196 3.19 29.19 3.25 196 3.15 29.19 3.25 29.19 3.15 29.19 3.15 29.19 3.15 29.19 29.19 196 29.19 29.19 29.19 196 29.19 29.19 29.19 29.19 29.19 20.19 2
	Range 5.12-12.49 34.42-35.28 0.7-4.1 0.7-4.1 13.5-94 19.92-35.13 3.5-90.4 0.92-35.13 3.5-90.4 0.4-11.1 31.6-87 7.9-68.4 0-0		Range 3.9-13.5 3.9-13.5 3.42.35.26 2.5.4.7 1.3.6.3 1.3.6.3 1.3.6.3 1.3.6.3 1.3.9.9 1.7.9 0.0 1.7.741 7.741	Range 5.12-12.49 0.74.1 1.4-7 1.31-725 19.16-35.13 1.4-7 1.325 19.16-35.13 0.510.7 31.6-87 7.31.6-87 7.9-68.4 0-0
le, 1993	ALL S.D. S.D. S.D. 1.49 0.16 0.16 0.16 1.46 1.36 1.06 1.76 1.76 1.76 1.76 1.76 1.68 1.686 0.686	6993	ALL S.D. 2.99 0.28 0.26 0.46 1.92 1.92 1.92 3.56 3.56 0 0.67	e, 1993 ALL S.D. 1.51 0.17 1.51 0.17 1.83 143.9 143.9 143.9 19.67 19.67 19.67 19.67 19.67 15.73 15.73
atleyi Ding	Average 8.63 34.71 3.11 4.09 271 28.85 3.4 64.94 1.98 1.98 1.98 1.98 1.98 1.98 1.98 1.98	ri Dingle, 1	Average 34.81 34.81 34.81 34.81 32.89 32.89 44.31 45.3 185.3 55.53 79.25 20.89 0	uusta Ding Average 8.6 34.71 34.71 34.71 34.71 34.71 34.71 53.77 68.9 1.22 1.22 65.79 65.79 65.79 65.79 00
Cytheropteron wh	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CacO3 Glauconite Phosphorite Sand Mud Opal	Australoecia fulle)	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe Glauconite Phosphorite Sand Mud	Incongruellina ver Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Sand Mud Opal
Ranking: 19	Range 7.1-10 34.6-34.85 2.84.1 1.3-5 120-300 1.3-5 1.3-5 1.3-5 1.3-5 1.3-5 1.3-5 1.3-5 1.3-5 1.5-91.2 0-10 0.3-11.9 0-0	Ranking: 21	Range 7.1-9.9 34.6-34.72 3.4-4.1 1.4-6.3 1.5-300 28.42-34.58 3.5-91.2 1.5-300 3.5-91.2 1.1-11.9 58.9-84.88 1.5-2-41 0-0	Ranking: 23 Range 7.1–12.9 3.4.5.04 3.4.1 0.7–2.16 15.205 28.42–34.2 16.5–92.9 0–1 1.1–1.9 86.4–95.9 86.4–95.9 86.4–95.9 20.0
tage: 0.5	100 S.D. 0.73 0.73 0.07 45.4 2.05 2.05 2.28 3.3 8.6 8.6 8.6	tage: 0.4	8.100 0.79 0.79 0.79 0.05 0.05 0.05 0.05 0.05 0.05 0.05 0.0	(tage: 0.4 100 5.0.14 1.64 1.64 0.14 0.14 0.57 0.57 0.57 0.57 0.57 0.57 0.57 0.58 0.57 0.57 0.57 0.57 0.57 0.57 0.58 0.58 0.57 0.57 0.57 0.57 0.57 0.57 0.57 0.57
Overall percen	Average 8.76 34.7 3.68 3.68 3.44 30.81 30.81 30.81 204 28.42 2.86 2.86 2.86 2.86 2.86 2.86 2.86 2.8	Overall percen	Average 8.77 34.66 3.76 3.76 3.76 3.2.6 4.69 3.2.49 3.2.49 5.2.74 5.2.44 5.2.74 5.2.49 5.2.74 5.2.49 0 2.4.9 0	Overall percen Average 9.17 34.69 3.4.69 3.4.69 3.4.69 3.4.69 3.73 1.15 3.78 3.2.797 3.2.78 3.2.787 3.2.797 3.2.787 3.2.787 3.2.797 3.2.7977 3.2.797777777777777777777777777777777777
ngle, 1989	Range 3.9-13.64 34.41-35.32 0.45-4.1 1.08-14.6 42-850 22.25-34.77 1-5 15.2-91.2 0.3-11.9 0.3-11.9 7.9-42.5 0-0	1990	Range 3.9-13.5 3.9-13.5 0.45-4.8 0.45-4.8 0.18-13.1 42-850 21.9-34.97 21.9-34.97 21.9-34.97 234.9-96.1 5.6-49.7 5.6-49.7	Range 6-13.5 34.51-35.24 0.45-4.1 0.45-4.1 0.45-4.1 0.5-8 42-730 28.42-34.77 16.5-92.9 0-1 16.5-92.9 0-1 0-1 26.1-9 0-0
atley & Dir	ALL S.D. S.D. 2.34 1.14 1.14 1.14 1.04 1.04 1.04 1.04 1.0	Maddocks,	ALL S.D. S.D. 2.27 1.59 2.7 2.7 2.7 2.7 2.7 2.7 2.7 2.7 2.7 2.7	993 ALL S.D. 1.76 0.19 1.16 2.18 1.96 3.1.81 0.45 0.54 0.54 0.54
nopsus Wh	Average 8.97 34.75 2.76 2.76 3.33 30.87 30.87 30.87 30.87 5.67 65.67 65.67 65.67 65.67 65.67 21.82 21.82 21.82	metuenda	Average 34.81 2.63 2.63 4.48 4.48 60.23 3.05 3.95 3.95 3.95 3.95 3.95 3.95 3.95 3.9	a Dingle, 1 Average 34.79 34.79 34.79 3.99 3.99 3.28 32.83 32.83 32.83 32.83 32.83 32.83 32.83 32.83 32.83 32.83 1.3 1.3 1.3 1.3 1.3 1.3 1.3 1.3 1.3 1.
Poseidonamicus pa	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud	Macrocypris cf. M.	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud Opal	Austroaurila rugos Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Opal

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Overall percentage: 0.32 Ranking: 26	100	Average S.D. Range 9.27 0.52 8.5-10 3.65 0.19 3.3-3.9 3.65 0.19 3.3-3.9 3.76 3.2.8 1.20-220 32.53 2.55 28.42-34.58 4.19 0.98 3-5 2.13 3.18 1-10 2.13 1.99 0.3-5.7 74.6 15.85 47.5-91.6 24.94 16.27 7.9-52.6 0 0-0	Overall percentage: 0.19 Ranking: 28	100 Average S.D. Range INSUFFICIENT DATA Overall percentage: 0.17 Ranking: 30 Average S.D. Range INSUFFICIENT DATA	
Buntonia bremneri Dingle, 1993	ALL	Average S.D. Range Temperature 7.4 1.95 38.10 Salinity 34.59 0.13 34.4-34.8 Dissolved oxygen 3.8 0.5 2.5-4.8 Dissolved oxygen 3.8 0.5 2.5-4.8 Dissolved oxygen 3.5 1.86 1.3-7.3 Depth 3.57 1.86 1.3-7.3 Depth 30.98 4.09 17.57-34.78 Fe 3.78 1.72 1.99.3 CaCO3 5.32 13.799.3 3.789.3 Fe 3.78 1.72 1.99.3 Glauconite 2.27 0.41 0.3-6.4 Sand 63.9 2.033 13.799.3 Mud 35.99 20.23 7.975.9 Opal 0 0 0.0 0.0	Buntonia rosenfeldi Dingle, Lord & Boomer, 1990	ALL Average S.D. Range ALL Temperature 6.52 1.68 3.9 Salinity 3.66 0.78 2.4.5 Dissolved oxygen 3.66 0.78 2.4.5 Dissolved oxygen 3.26 0.11 34.39-34.75 Depth 3.25 1.47 1.26.6.7 Depth 3.29 5 1.46 1.5 CaCO ₃ 6.609 13.46 1.5 Fea 2.47 1.82 0.38 Phosphorite 2.47 1.82 0.55.5 Robal 0.0 Mud 0.5.5 1.92 1.5 Phosphorite 2.47 1.82 0.55.5 Mud 0.5.5 1.9 Bensonia knysnaensis robusta Dingle, 1992 Bensonia knysnaensis robusta Dingle, 1992 Temperature 12.47 0.52 11.71-13.02 Dissolved oxygen 0.78 0.12 0.609 Dissolved oxygen 0.78 0.12 0.609 Dissolved oxygen 2.198 11.5 20.43-33,43 Fea 2.10 0.82 1.5 2.44,51 Dissolved oxygen 0.78 0.12 0.609 Distolved oxygen 0.78 0.12 0.609 Distolved oxygen 0.78 0.12 0.609 Distolved 0.73 0.82 1.17,1-13.02 Distolved 0.73 0.82 1.15 2.043-33,43 Fea 2.198 1.15 2.043-33,43 Fea 2.198 1.15 2.043-33,43 Fea 2.109 1.15 2.043-33,43 Fea 2.11.71-13.02	CatCO3 01.36 26.32 11.77-53.33 Guaconite 0.008 0.004 0.001 Phosphorite 10.12 19.08 0.550 Sand 82.77 6.55 76.1-90 Mud 82.25 1.85 6.5-10.5 Opal 0.002 0.004 0-0.01
36 Ranking: 25		Range 8.5-9.5 3.61-34.75 3.55-3.7 3.55-3.7 3.55-3.7 3.55-3.7 80-140 33.96-34.51 33.5-46.5 1-1 0.8-1.1 47.5-74 25.7-52.6 0-0	31 Ranking: 27	Range 8.5-12.49 0.7-4.1 0.7-4.1 1.7-4.1 19.16-34.52 80-227 33.5-27 33.5-29 0.01-1 0.8-1.9 33.9-86.4 7.9-52.6 0.0 19.8-1.9 33.9-86.4 7.9-52.6 0.0 19.8-1.9 34.61-35.28 0.7-3.9 19.7-3.9 19.72-34.58 19.92-34.58 19.92-34.58	0.1-10.0 0.3-1.9 0.3-1.9 3.19-91.6 7.9-52.6 0-0
Overall percentage: 0.2	100	Average S.D. 9.24 0.42 9.24 0.42 3.66 0.27 3.66 0.27 3.61 1.27 113 25.07 1.1 4.1 0.23 5.8 1.1 1.0 0.95 0.21 60.75 18.74 9.12 1.0 0 0 0 0	Overall percentage: 0.3	Average 100 9.41 1.11 9.41 1.11 34.74 0.2 3.35 0.99 3.35 0.99 3.35 0.99 3.1.71 4.38 31.71 4.38 31.71 4.38 31.71 4.38 68.26 0.44 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.8 0.42 0.9 0 0.44 0.2 23.9 0.73 34.75 0.23 34.75 0.23 34.75 0.23 34.75 0.23 31.08 6.02 4.75 0.13 4.75 0.13 4.75 0.13 4.75 <td>0.72 0.72 1.03 0.52 63.35 19.05 63.35 19.05 0.7.84 0.0</td>	0.72 0.72 1.03 0.52 63.35 19.05 63.35 19.05 0.7.84 0.0
puimba birchi Dingle, 1993	ALL	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	heropteron trinodosum Dingle, 1993	ALL Average S.D. Range mity 34.71 0.19 34.42-35.28 solved oxygen 3.19 1.04 0.74.1 anic matter 2.4.12 1.07 0.74.1 anic matter 3.19 1.04 0.74.1 anic matter 2.4.12 1.97 0.74.1 2.03 66.72 20.68 5.27 19.16-34.52 4.78 80.453 0.74 0.74 0.47 0.01-1.2 sphorite 2.01 1.97 0.01-1.2 sphorite 2.01 1.97 0.01-1.2 anic rogersi Dingle, 1993 <i>uconia rogersi</i> Dingle, 1993 <i>utonia rogersi</i> Dingle, 1993 <i>tutonia rogersi</i> Dingle, 1993	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$

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5 Ranking: 32	Range 8.91-12.49 34.68.35.28 0.7-4 3.1-5 3.1-5 1.9.5271 19.92.2051 9.4-75.7 0.01-5.99 1.4-5.8 38.9-77.1 7.9-33 0-0	8 Ranking: 34 Range 8.5-9.4 3.6-3.465 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-3.75 3.6-2.7 3.6-2.7 3.7-25.7 2.7-25.7 0.00	 B. Ranking: 36 Range 8.5-9.4 8.5-9.4 3.65-3.7 5.6.8 120-140 34.54.5 33.546.5 33.546.5 1.1 0.8-1.1 47.5-74 25.752.6
ntage: 0.1	100 5.D. 2.01 0.33 0.33 60.63 6.08 6.08 6.08 6.08 5.2.88 2.28 2.28 2.28 2.28 10.36 10.36 0.58 0.58 0.58 0.58 0.58 0.58 0.58 0.58	ntage: 0.0 100 S.D. S.D. 0.03 0.03 0.05 1.15 1.15 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	ntage: 0.0 100 5.D 5.D, 0.03 1.28 1.28 0.03 1.28 0.21 0.28 0.19 0.21 0.21 0.21 0.21 0.21 0.02 0.02 0.02
Overall percer	Average 10.17 3.77 2.189 3.77 2.13 3.3 3.3 2.13 2.13 2.13 2.13 2.13 2	Overall perce Average 8.9 3.67 3.67 3.57 3.57 1.1 1.1 74 1.1 25.7 0	Overall perce Average 9.1 3.68 3.68 3.68 3.4.67 3.4.67 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 3.4.2 0.15 0.05 0.05 0.05 0.05 0.05 0.0000000000
	Range 5,12-12,49 34,39-55,28 0,74,5 0,9-6,5 19,92-34,75 1,55 4,9-88,2 0,56 0,8-6,4 38,9-96,1 6,7-58,3 0-56	Range 5.7-9.4 3.6-34.65 3.6-34.65 3.6-4.7 1.4-5 1.4-5 1.5-545 3.6-4.7 1.5-545 3.6-4.7 1.5-2-33.5 1.1-778 7.4-78.7 1.8-9-25.7 0-0	Range 8.5-9.4 34.61-34.76 3.65-3.7 3.65-3.7 3.65-3.7 3.65-3.7 3.65-8 120-140 34-34.52 3.5-6 3.5-5 3.5-6 3.5-7 4.5 1-1 0.8-1.1 4.7.5-74 0.08-1.1 4.7.5-74
le, 1993	ALL S.D. S.D. 0.26 0.268 1.16 1.16 1.16 1.16 1.16 1.91 1.95 1.93 1.95 0 0	s, 1992 ALL S.D. S.D. 0.64 0.64 0.32 1.12 1.1 1.12 1.12 1.12 1.12 1.12 1.	ALL S.D. S.D. S.D. S.D. S.D. S.D. S.D. S.
ensis Dingl	Average 7.63 34.62 34.62 34.62 3.16 336.12 30.12 30.12 58.6 58.6 58.6 53.49 65.8 30.87 0 0	<i>mni</i> Dinglu Average 8.18 3.463 3.463 3.463 3.463 3.42 34.2 34.2 34.2 34.2 34.2 34.2 34.	ngle, 1993 Average 9.1 3.68 3.68 3.68 3.68 3.467 5.9 130 34.2 60.75 60.75 0.95 0.75
Buntonia namaqua	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Sand Mud Opal	Xestoleberis hartme Temperature Salinity Dissolved oxygen Organic matter Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud Opal	Buntonia deweti Di Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCo Glauconite Phosphorite Sand Mud
Ranking: 31	Range 7.1-9.5 34.6-34.85 2.84 2.84 2.84 2.4.3 170-271 2.842-30.52 3-3 71.1-90.4 0-6 65.7-87 65.7-87 12.7-34.1 0-0	Ranking: 33 Range 8-12.76 8-12.76 34.534.99 0.7-3.45.99 0.7-3.45.99 120-295 3.24.534.09 120-295 20.43-34.09 7.13-78.7 0.01-1 0.94.2 69.2-90 7.3-30.4	Ranking: 35 Range ATA
age: 0.16	100 8.D. 0.84 0.09 0.45 0.45 0.45 0.45 0.45 0.45 0.73 0.73 0.73 0.73 0.73 0.73 0.73 0.73	tage: 0.1 100 2.10 1.16 1.16 1.04 2.556 5.556 5.559 5.559 5.59 1.04 1.18 1.04 1.04 0.5 0.5 0.5 0.1	age: 0.04 100 S.D.
Overall percent	Average 8.73 3.4.71 3.4.71 3.4.71 3.4.71 2.07 2.9.42 2.9.42 2.9.42 2.9.42 2.9.42 2.42 2	Overall percer Average 9.4 3.4.71 2.4.71 2.4.71 2.4.71 2.4.3 183 3.86 3.86 3.86 3.86 0.58 0.58 0.58 0.58 0.58 0.58 0.58 0.58	Overall percent Average INSUFI
	Range 7.1-9.5 3.7.1-9.5 3.4.6-34.85 2.8.4 2.4.3 2.4.3 170-272 2.2-3 71.1-90.4 0.6 1.4-6.8 65.7-87 12.7-34.1 0-0	Range 6.5-12.76 6.5-12.76 0.7-35.03 0.7-35.03 0.7-35.03 0.7-35.03 0.7-375 3.24-8.8 100-379 0.1 0.1 0.5-22.5 55.4-90 7.3-45.5 00.01	r, 1990 Range 3.8-7.1 2.1-4.7 1.3-6.5 392-905 392-905 1.5-78 1.5-285.1 0.46 0.6-7.8 0.46 0.6-7.8 0.46 0.6-7.8 0.00
	ALL S.D. 0.84 0.84 0.84 0.84 1.04 0.25 0.25 0.25 2.03 7.1 7.1 0.652	3 ALL S.D. 1.78 0.177 1.25 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.95 7.1.00 7.49 0.003	& Boome ALL S.D. 1.05 0.09 0.09 0.09 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65
ingle, 199.	Average 8.6 34.7 34.7 34.7 34.7 217 292 81.09 2.92 81.09 2.13 4.48 4.48 75.73 23.18 0	ingle, 199. Average 9.62 9.62 3.3.75 5.88 5.33 5.88 5.33 3.37 5.88 5.0.63 0.42 4.4 4.4 4.4 2.4.36 0.0008	ngle, Lord 5.83 3.449 3.94 3.94 3.063 3.063 3.05 63.09 63.09 63.09 63.09 63.09 63.09 63.09 63.09 63.09 63.09 63.09 63.03 63.36 3.82 10 83.21 83.
Buntonia gibbera L	Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO3 Glauconite Phosphorite Sand Mud	Neocaudites lordi I Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Sand Opal	Krithe spatularis Di Temperature Salinity Dissolved oxygen Organic matter Depth Latitude Fe CaCO ₃ Glauconite Phosphorite Phosphorite Mud Opal

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Range	3-14	34.39-35.5	0.29-4.1	0.2-20.7	18-990	17.57-34.09	0.61-11.8	0.1-70.8	69-0	0.3-18.1	0.7-98.1	0.7-99.1	0-88
S.D.	2.45	0.31	1.14	4.9	203	4.43	2.92	21.77	13.45	4.07	27.59	28.39	31.21
Average	10.82	35	1.46	6.58	182	24.8	3.93	15.7	4.21	3.31	50.35	47.34	19.29
	Temperature	Salinity	Dissolved oxygen	Organic matter	Depth	Latitude	Fe	CaCO ₃	Glauconite	Phosphorite	Sand	Mud	Opal

Note—the parameters given above are expressed as follows: temperature = $^{\circ}$ C; salinity = parts per thousand; dissolved oxygen = ml/l; organic matter = $^{\circ}$; depth = m; latitude = $^{\circ}$ S; Fe, CaCO₃, glauconite, phosphorite, sand, mud, opal = $^{\circ}$ C.



Dingle, R V. 1994. "Quarternary ostracods from the continental margin off south-western Africa. Part 3. Oceanographical and sedimentary environments." *Annals of the South African Museum. Annale van die Suid-Afrikaanse Museum* 103, 383–441.

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