INTERTIDAL ZONATION ON SANDY BEACHES OF THE WEST COAST OF SOUTH AFRICA.

by

Rod Bally

Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7700, South Africa

Résumé

Deux systèmes ont été proposés pour expliquer la zonation de la macrofaune sur des plages à sédiments meubles. Dahl (1952) a suggéré l'existence de trois zones caractérisées par des espèces indicatrices alors que Salvat (1964) en a proposé quatre qui seraient déterminées par les conditions hydrodynamiques existant dans le sédiment. La zonation de la macrofaune de la côte Ouest de l'Afrique du Sud a été examinée sur trois plages non-abritées. Avec l'aide de plusieurs analyses statistiques, quatre zones de distributions intertidales ont été déterminées. Ces zones correspondent à celles de Salvat (zones de dessèchement, rétention, résurgence et saturation) et décrites en termes hydrodynamiques par Pollock et Hummon (1971). Les avantages du système de Salvat par rapport à celui de Dahl sont discutés, ainsi que la relation entre la zonation de la côte Ouest de l'Afrique du Sud et celles des autres plages du monde.

Introduction

Intertidal zonation has long been of interest to marine biologists since the intertidal zone is firstly the most accessible marine environment and, secondly, forms the interface between the marine and terrestrial environments into which organisms originating from both of these have migrated and adapted. Because of the gradient between marine and terrestrial conditions formed by tidal cycles, organisms have adapted differentially to these intermediate conditions which has resulted in the formation of intertidal distribution zones.

The existence of intertidal zonation has long been recognized, with a universal zonation scheme for rocky shores first proposed by Stephenson and Stephenson in 1949, and gaining general acceptance since then (Lewis, 1964 ; Stephenson and Stephenson, 1972).

Zonation on sandy shores was first noted by Stephen (1929, 1930) on Scottish shores and, subsequent to his studies, a number of workers observed this phenomenon on other beaches (eg. Newcombe, 1935; Watkin, 1942; Brady, 1943 and Southward, 1953). Owing to the difficulty of determining distributions of organisms in sandy beaches due to their burrowing habits, however, it was only in 1952 that a universal zonation scheme for beaches was proposed by Dahl, who suggested that there were three zones defined in terms of the fauna living in each zone.

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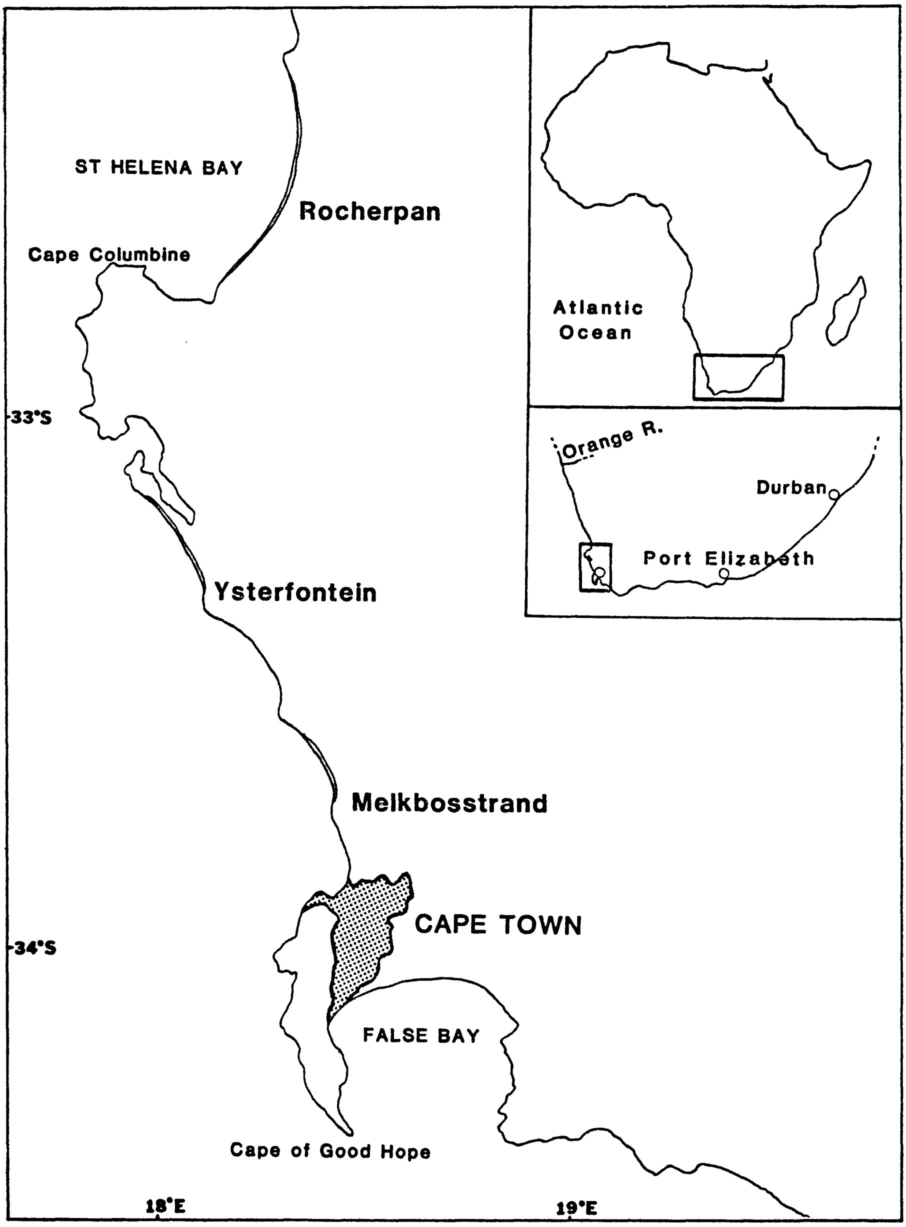

FIG. 1
The positions of the three beaches (Melkbosstrand, Ysterfontein and Rocherpan) studied on the west coast of South Africa.

On the other hand, Salvat (1964, 1966, 1967) proposed a zonation system based on the physical parameters responsible for zonation. This system is not subject to zoogeographical and distributional limitations since it is not dependent on the presence of characteristic taxonomic groups. Yet the zones can still be recognized by the species found in them and Dahl's zonation can be easily superimposed on Salvat's scheme. The latter, however, is more universally applicable than the former.

During the course of a study on the ecology of three sandy beaches on the west coast of South Africa, the intertidal distribution of the macrofauna was investigated. Both Dahl's and Salvat's zonation schemes were examined in the context of the results obtained and are discussed in the sections that follow.

Methods and materials

Three sandy beaches on the west coast of South Africa, at Melkbosstrand, Ysterfontein and Rocherpan (Fig. 1) were sampled seasonally over a period of 18 months. Some physical characteristics of these beaches are given in Table 1. Organisms were collected at low spring tides from sampling grids of four stations stretching across the beach by four stations stretching 150metres along the beach. At each of the 16 stations, sand was removed from quadrats measuring 50×50cm to a depth of 30cm. This sand was then washed through a 1mm mesh sieve and the organisms retained were preserved for identification and counting in the laboratory.

TABLE 1

Physical characteristics of the beaches studied

Beach	Mean grain size (phi)	Exposure	Mean width (m)	Number of species
Melkbosstrand	2.25	High Energy	90.0	23
Rocherpan	1.60	High Energy	48.9	18
Ysterfontein	2.31	High Energy	59.7	22

To test the association of species into zones, dendrograms were generated by a computer programme using a Bray-Curtis similarity matrix and log-transformed data of species numbers. From the similarity matrix, a further programme constructed two-dimensional ordination diagrams using multi-dimensional scaling and calculating the stress produced by reducing the multi-dimensional scaling to two dimensions. The acceptability of the stress values obtained were determined using Levine (1978).

An information statistic programme then compared the species' presence, absence and abundance for each grouping derived from the ordination diagrams. This showed at 90 and 95percent confidence levels which species were characteristic for each zone, and at what densities. The results obtained from the information statistic programme should be treated with a certain amount of caution, however. For example, the Isopod *Excirolana natalensis* is an indicator species of the zone of drying on fine-grained beaches, but is not always present in sufficiently large numbers to be significant at the 90 or

95percent confidence levels. Its presence in a sample is indicative of the zone of drying, but its absence is not indicative of the other zones.

Results

A list of commonly occurring species for the three beaches is shown in Table 2. Using the data obtained from the collections, similarity analysis using the abundance-weighted Bray-Curtis similarity measure was employed. The selected dendrograms and two-dimensional ordination diagrams shown in Fig. 2 to 4, clearly separate species numbers and distributions into four distinct zones corresponding to those proposed by Salvat (1964). Indicator species derived from the information statistic programme are listed in Table 3. Fig. 5 shows the zonation of species on the three beaches of the west coast of South Africa that were the subject of this study.

TABLE 2
Common macrofaunal species of the west coast beaches studied
(+ = species present)

Species	Rocherpan	Melkbosstrand	Ysterfontein
Oligochaetes		+	
Pachyphaleria capensis	+	+	+
Acanthoscelis ruficornis	+	+	+
Insect larvae	+	+	+
Niambia sp.	+	+	+
Talorchestia capensis	+	+	+
T. quadrispinosa	+	+	+
Tylos granulatus	+	+	+
Excirolana natalensis	+	+	+
Eurydice longicornis	+	+	+
Pontogeloides latipes	+	+	+
Scolelepis squamata		+	+
Donax serra	+	+	+
Sigalion capense		+	+
Pseudharpinia excavata	+	+	+
Nephtys capensis		+	+
Cerebratulus fuscus	+	+	+
Gastrosaccus psammodytes	+	+	+
Urothoe grimaldii	+	+	+
Cumopsis robusta	+	+	+
Austrocuma platyceps		+	+
Nematodes	+	+	+
Bullia digitalis	+	+	+
Total species	18	23	22

It could be argued that this is a tautological study, since four intertidal levels were sampled and four zones were found. If the results had corresponded to Dahl's zonation, however, the analysis would have only distinguished three zones, which is clearly not the case. The results obtained in this study therefore do not support Dahl's hypothesis.

TABLE 3

Indicator species for each zone derived from the Information Statistic programme (++=95percent significance, +=90percent significance)

Species	ROCHERPAN			MELKBOSSTRAND			YSTERFONTEIN		
	Significance	Frequency		Significance	Frequency		Significance	Frequency	
		Subset 1	Subset 2		Subset 1	Subset 2		Subset 1	Subset 2
		Zone of Drying	Retention		Drying	Retention		Drying	Retention
Tylos granulatus	++	14	0	++	28	0		2	0
Oligochaete	—	—	—	+	3	0	—	—	—
Talorchestia spp.	++	41	0	—	—	—		7	0
Niambia sp.	++	35	3	—	—	—		2	0
Excirolana natalensis	++	18	59		2	0	++	35	0
Pontogeloides latipes	++	0	5	++	0	12		9	6
Eurydice longicornis	++	0	19	++	0	132	++	0	1138
Donax serra		0	1	+	0	4	++	0	820
Scolelepis squamata	—	—	—	++	0	1491	++	0	5245
		Retention	Resurgence		Retention	Resurgence		Retention	Resurgence
Excirolana natalensis	++	59	15	—	—	—	—	—	—
Niambia sp.	+	3	0	—	—	—	—	—	—
Pontogeloides latipes		5	4	++	12	1	++	6	0
Eurydice longicornis	++	19	114	++	132	320	++	1138	1586
Donax serra	++	1	723	++	4	111	++	820	15
Scolelepis squamata	—	—	—	++	1491	0	++	5245	3
Gastrosaccus psammodytes	++	0	49	++	0	13	++	0	8
Cumopsis robusta	+	0	3	—	—	—	—	—	—
Pseudharpinia excavata	++	0	167	+	0	3	++	0	7
Sigalion capense	—	—	—	+	0	3		0	1
Cerebratulus fuscus	—	—	—	—	—	—		0	2
Bullia digitalis	—	—	—	—	—	—		0	2
		Resurgence	Saturation		Resurgence	Saturation		Resurgence	Saturation
Excirolana natalensis		15	8	—	—	—	—	—	—
Pontogeloides latipes		4	1		1	0	—	—	—
Eurydice longicornis	++	114	15	++	320	24	++	1586	296
Donax serra	++	723	53	++	111	33		15	12
Gastrosaccus psammodytes	++	49	12	++	13	298	++	8	444
Cumopsis robusta	+	3	0	—	—	—	++	0	48
Pseudharpinia excavata	++	167	42	++	3	15		7	8
Cerebratulus fuscus	++	0	6	—	—	—		2	2
Sigalion capense	—	—	—		3	4		1	4
Scolelepis squamata	—	—	—	—	—	—	+	3	0
Bullia digitalis	—	—	—	++	0	11	++	2	29
Urothoe grimaldii	—	—	—	++	0	18	++	0	14

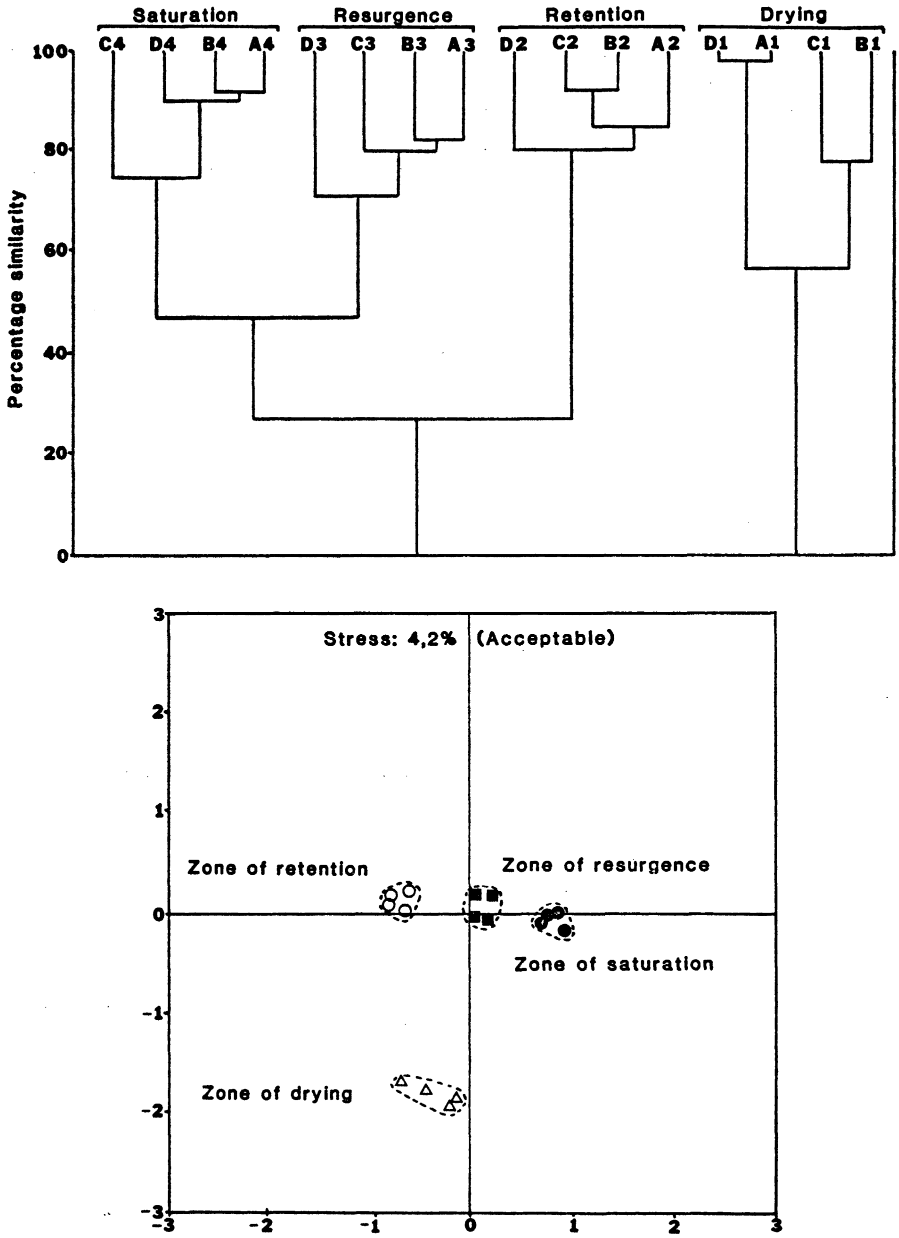

FIG. 2

Dendrogram and two-dimensional ordination diagram of log-transformed macrofaunal species numbers at Melkbosstrand.

Discussion

An overview of Dahl and Salvat's zonation schemes

Dahl (1952) suggested three intertidal zones defined in terms of the fauna living in each zone. The supralittoral is characterized

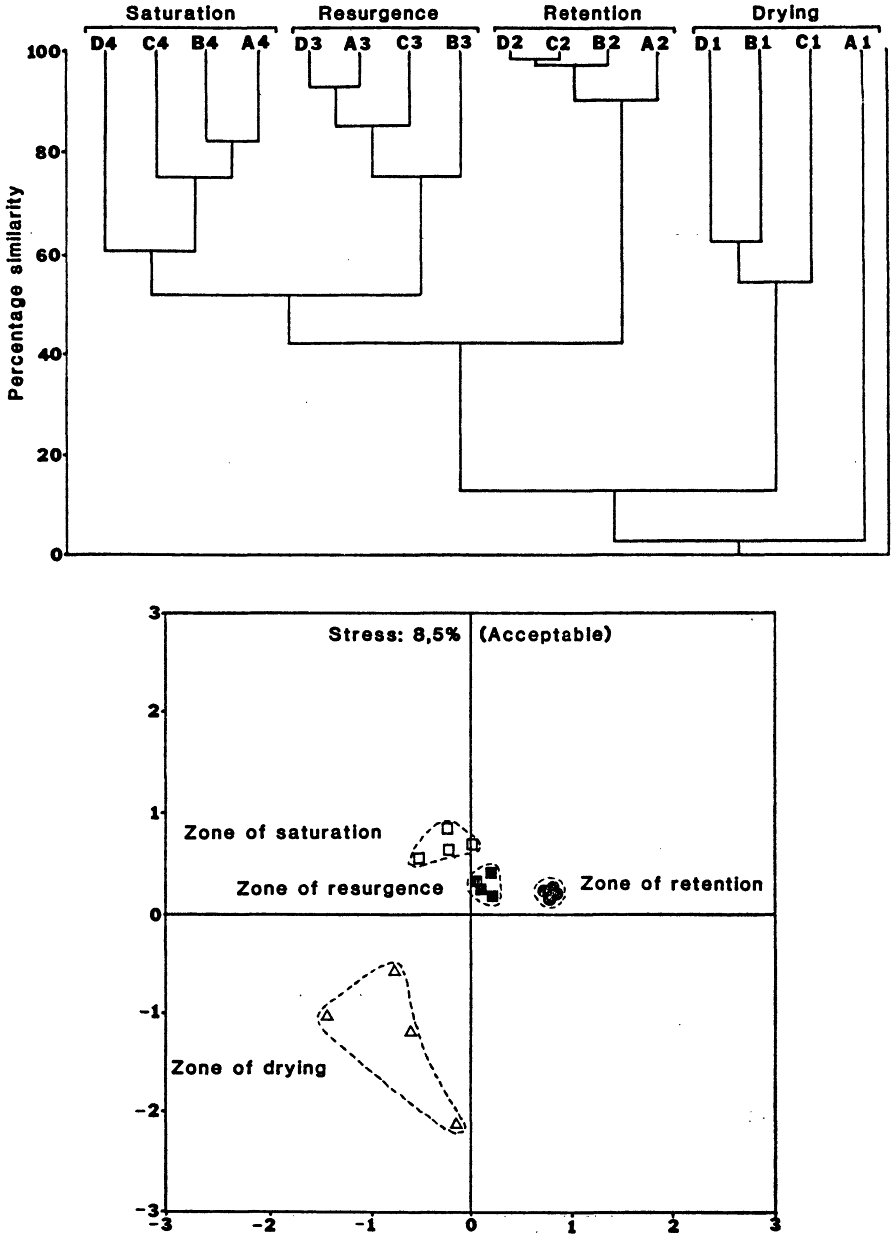

FIG. 3
Dendrogram and two-dimensional ordination diagram of log-transformed macrofaunal species numbers at Ysterfontein

by the presence of air-breathing crustaceans with either talitrid Amphipods (eg. *Talorchestia, Orchestia, Talitrus*) or ocypodid Decapods (*Ocypode*) being the dominant types. The midlittoral zone is characterized by cirolanid Isopods (eg. *Eurydice, Cirolana*), although haustoriid Amphipods may also be found.

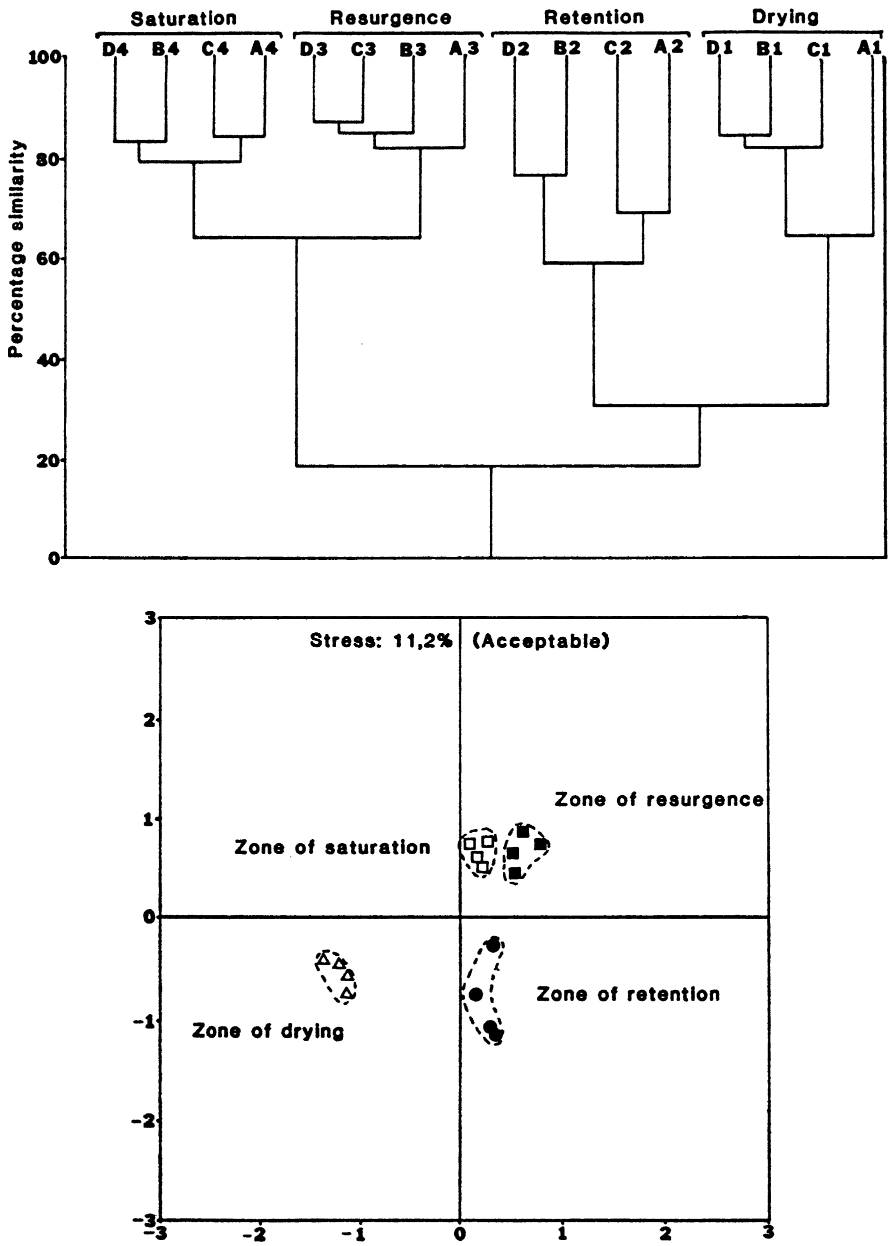

FIG. 4

Dendrogram and log-transformed ordination diagram of log-transformed macrofaunal species numbers at Rocherpan

The lowest zone is the sublittoral, characterized by the hippid crab *Emerita* in the tropics, oedicerotid and haustoriid Amphipods in the temperate northern regions, oedicerotid Amphipods in temperate southern regions, lysianassid Amphipods in the arctic and phoxocephalid Amphipods in the southern hemisphere. In addition, this zone supports a diversity of molluscs and Polychaetes on all beaches (Dahl, 1952).

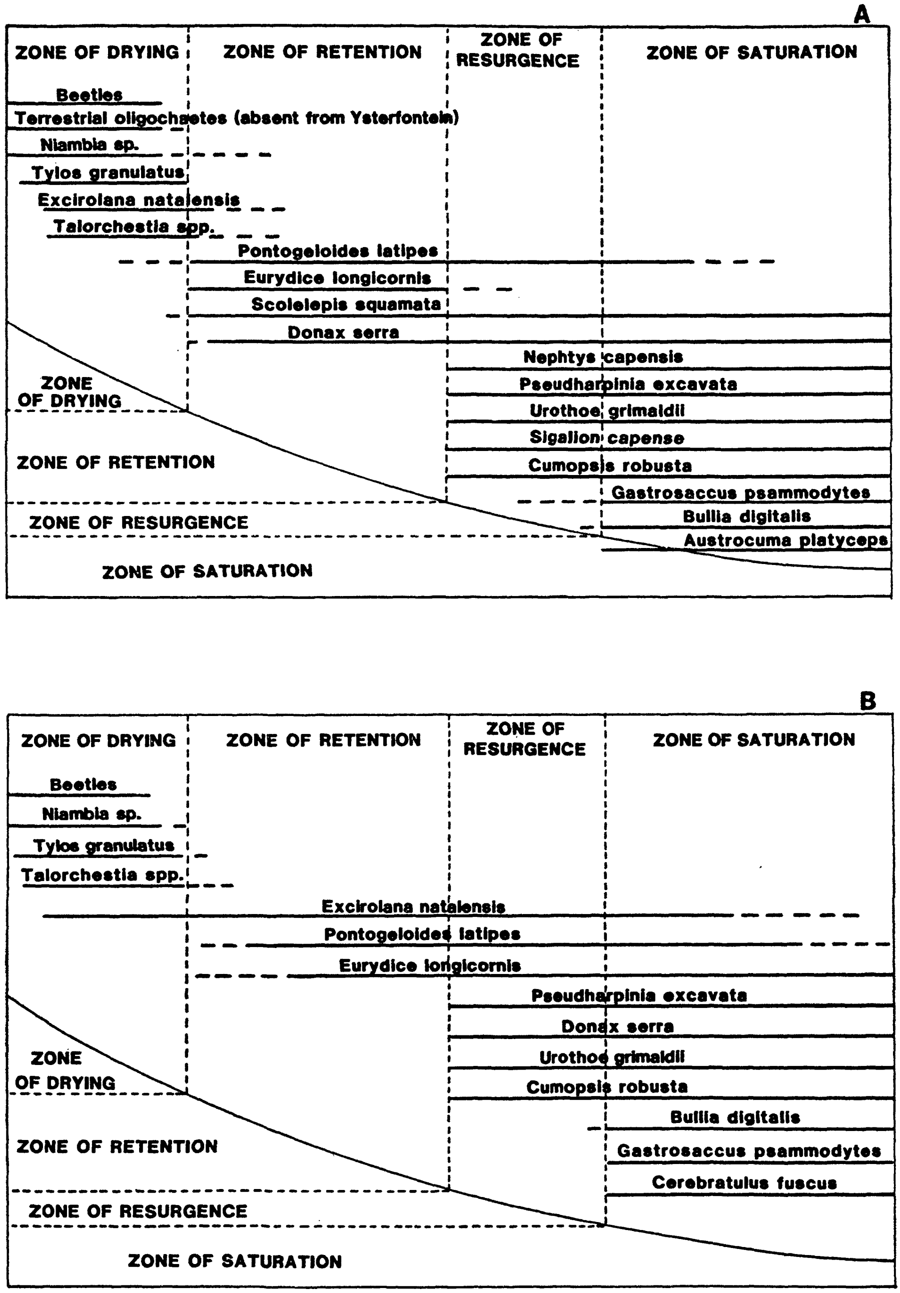

Fig. 5

The zonation of macrofaunal species on the west coast of South Africa. A: fine-grained beaches (eg. Melkbosstrand, Ysterfontein). B: coarse-grained beaches (eg. Rocherpan)

Dahl's intertidal zone classification for sandy beaches has been widely accepted, with certain reservations and modifications. Pichon (1967), MacNae and Kalk (1962) and Wade (1967), for example, found talitrids and ocypodids co-existing. Pichon (1967), Wade (1967), Gauld and Buchanan (1956) and Schuster-Dieterichs (1956) also found cirolanid Isopods mixed with these air-breathing crustaceans. Jones (1971, 1974) and Eleftheriou and Jones (1976) found that cirolanid Isopods (genus *Eurydice*) varied their zonation both according to species and according to locality within a single species. Thus cirolanid Isopods tend to occur not only within the zone classified by Dahl as midlittoral, but in parts of his supralittoral and sublittoral as well. On a slightly more sheltered beach than the type classified by Dahl, Wood (1968), in New Zealand, found cirolanid Isopods absent from the midlittoral, although they do occur in this zone on other New Zealand beaches (Morton and Miller, 1968; Fincham 1974, 1977).

Dahl's sublittoral zone is characterized by a diverse fauna, as well as by certain characteristic crustaceans. This would appear to be the case generally (eg. Pichon, 1967), but both Gauld and Buchanan (1956) and Philip (1974) found higher diversities in the midlittoral than the sublittoral. In addition, phoxocephalids occur not only in the southern hemisphere, but have also been reported from the sublittoral zones of many northern hemisphere beaches (eg. Gauld and Buchanan, 1956; Pearse *et al.*, 1942; Dexter, 1969, 1972, 1974, 1976, 1979). Finally, Dexter (1972) found a cirolanid Isopod in all three zones. Dahl's classificatory system therefore appears to hold good in the majority of exposed beaches, with regional exceptions to his rules.

His system is not always valid in more sheltered beaches, as was found by Epelde-Aguirre and Lopez (1975) in Coronel Bay, Chile, where cirolanid Isopods were confined to the sublittoral, occurring together with *Emerita* and some polychaetes. Brown (1973) found a sphaeromatid Isopod (genus *Exosphaeroma*) replacing a cirolanid species on sheltered, fine-grained beaches of the Cape Peninsula in South Africa.

Whereas Dahl had proposed a zonation scheme similar to the rocky shore plan of Stephenson and Stephenson (1949), i.e. based on the fauna colonizing the various zones, Salvat (1964) divided the beach into four levels based on the degree of moisture in the sediment. The uppermost zone is dry sand, only reached by large waves at high-water springs, or by spray. Below that is the zone of retention reached by all tides. Gravitational water on the beach is lost at emersion, but water of retention is conserved. The next zone, the zone of resurgence, is subject to considerable water movement, both from incoming and outgoing tides. As the tide ebbs, gravitational water lost from the zone of retention flows through the sand of this zone and appears at the surface of the beach as streams. Salvat defined this zone as extending shorewards to the point where the water table lies within 20cm of the surface. Finally, the zone of saturation is permanently saturated with water, but in this level interstitial water circulation is reduced considerably.

The work of Pollock and Hummon (1971) on cyclic changes in interstitial water content in a semi-protected beach has confirmed the existence of Salvat's four levels. Pollock and Hummon did, however, subdivide the uppermost zone into one of dry sand and a lower zone of drying sand. The zone of dry sand is almost completely terrestrial and only rarely receives seawater, whereas the zone of drying receives seawater more frequently and loses capillary water by evaporation. The former zone corresponds to the zone of salt-hardened sand reported by Bascom (1951).

Withers (1977) is the only study to date, other than those of Salvat (1966, 1967), to make use of Salvat's zonation scheme in describing the intertidal distribution of soft-shore macrobenthos. Although the zones of resurgence and saturation both fall into Dahl's sublittoral zone, Withers found a distinct separation of species between these two zones.

Zonation on beaches of the South African west coast

At the high-water mark (Dahl's supralittoral and Pollock and Hummon's zone of drying), a mixture of terrestrial and marine adapted animals occurs. Thus, on all three beaches, the tenebrionid beetle *Pachyphaleria capensis* and the carabid beetle *Acanthoscelis ruficornis* are found as well as coleopteran and dipteran larvae, often in association with washed-up kelp. The terrestrial Isopod *Niambia* sp. also wanders down to this level at low tide, and occasionally into the zone of retention below. At Melkbosstrand, lumbricid Oligochaetes are also found, especially after rain.

The marine-derived fauna in this zone consists of the giant oniscoid Isopod *Tylos granulatus*, the talitrid Amphipods *Talorchestia capensis* and *T. quadrispinosa*, *Excirolana natalensis*, a cirolanid Isopod, as well as the cirolanid *Pontogeloides latipes*. The first three species are air-breathing (the herbivorous and scavenging *Tylos* are often found in the vicinity of stranded kelp), but *Excirolana* and *Pontogeloides* are true marine Isopods that survive in this zone by migrating up and down the beach with the spring to neap tide cycle. The presence of the cirolanids indicates that this zone is Pollock and Hummon's zone of drying rather than the zone of dry sand.

The zone of retention (or Dahl's midlittoral) supports a lower diversity of species than the zone of drying, since the terrestrial species are not habitually found here, and in fact the diversity of marine species is greater in this zone than in the one above it (Fig. 6). This zone is characterized by great densities of the semi-sessile spionid Polychaete *Scolelepis squamata* on fine-grained beaches, the only sedentary species found on these beaches. Associated with this Polychaete are large numbers of juvenile *Donax serra*, a Bivalve that adopts intertidal zonation between various size-classes (De Villiers, 1975a). At Rocherpan, both *Donax* and *Scolelepis* are absent from this zone. All three beaches support *Eurydice longicornis* (another cirolanid Isopod) and *Pontogeloides* at this level, the former being found in great densities (up to 8000 per m²) associated with *Scolelepis*. At Rocherpan, *Eurydice* is largely supplanted by *Excirolana* *natalensis,* which becomes the dominant species. During low tide, some terrestrial species may extend down to the zone of retention and thus both *Talorchestia* and *Niambia* are occasionally found here.

The zone of resurgence (part of Dahl's sublittoral) supports a greater diversity of species than the previous zones, although numbers and biomass values per unit area may be lower than in the zone of

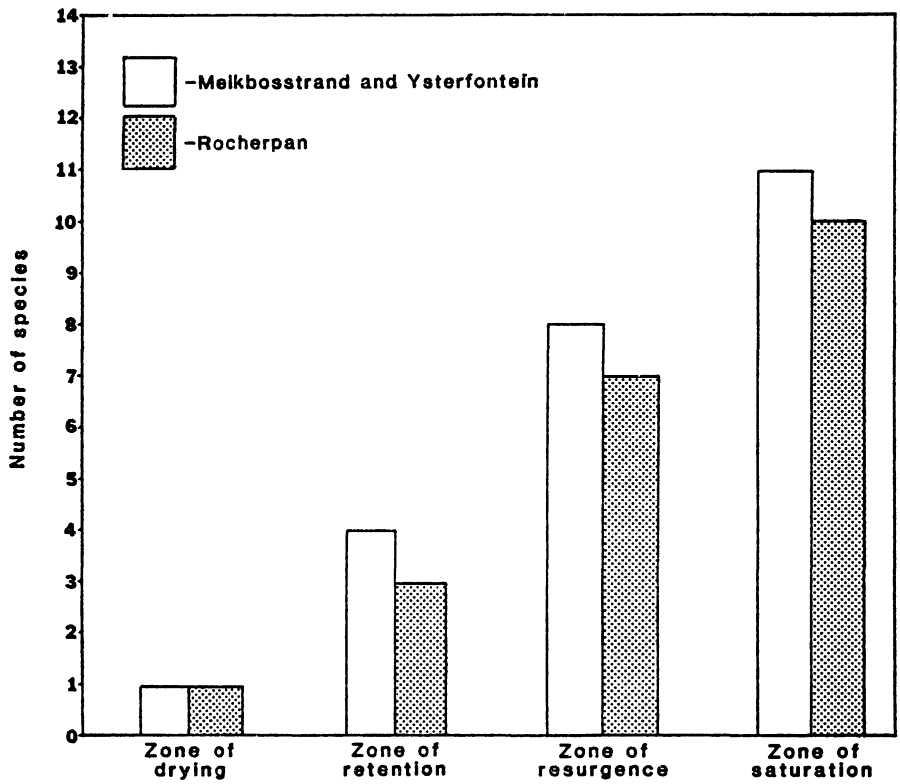

FIG. 6

The diversity of water-breathing macrofaunal species in each zone on South African west coast beaches

retention. Species also found in higher zones are *Donax, Eurydice, Pontogeloides* and, at Rocherpan, *Excirolana.* Other species found at this level are *Pseudharpinia excavata,* a phoxocephalid Amphipod, *Urothoe grimaldii,* an haustoriid Amphipod and the cumacean *Cumopsis robusta.* At Melkbosstrand and Ysterfontein the Polychaetes *Sigalion capense* and *Nephtys capensis* and, occasionnaly, the psammophilous mysid *Gastrosaccus psammodytes* are also found in this zone.

The zone of saturation (the lower portion of Dahl's sublittoral) supports large numbers of *Gastrosaccus* and *Pseudharpinia,* as well as *Eurydice, Urothoe, Cumopsis* and *Donax.* All three beaches also carry the scavenging prosobranch Gastropod *Bullia digitalis* and the Nemertean *Cerebratulus fuscus.* At Rocherpan, small Nematodes (unidentified) were also found while, at Melkbosstrand and Ysterfontein, *Sigalion* and *Nephtys* occur, as well as small numbers of *Austrocuma platyceps,* a cumacean.

Thus, each of the four zones has its own distinctive association of species, as was shown by Salvat (1964) at Arcachon. As might be expected from a mobile fauna, however, there is often some overlap into other zones by a few individuals of indicator species.

Zonation on other beaches

Only one specific account on the zonation of South African sandy beaches (that of McLachlan, 1980) has been published, although zonation is briefly discussed in a number of papers. Brown (1964, 1971) gives general descriptions of the zonation on beaches of the Cape Peninsula, while Brown and Jarman (1978) reproduce without comment a zonational diagram of Muizenberg beach in False Bay. These differ little from the zonation found on west coast beaches except for the presence of *Callianassa kraussi* and *Exosphaeroma truncatitelson* on sheltered beaches.

Along the south coast, there is a gradual displacement of west coast species by south coast species, although small numbers of more tropical species such as *Ocypode* spp. and *Emerita austroafricana* also begin to appear (McLachlan *et al.*, 1981). The beaches of the Transkei and Natal are briefly described by Wooldridge *et al.* (1981) and Dye *et al.* (1981) respectively. Major changes in faunal composition occur in the Transkei relative to the south and west coasts (Wooldridge *et al.*, 1981), the temperate species being replaced by tropical ones. Dye *et al.* (1981) found the zonation of the macrofauna to be in agreement with Dahl's (1952) zones for warm-water regions.

On beaches of the south and east coasts of South Africa, therefore, the general scheme of zonation is similar to that found on west coast beaches. The differences noted above are mainly due to biogeographical and distributional differences.

On a world-wide basis, the most notable features of South African west coast beaches are the absence of ocypodid and hippid crustaceans at the high and low water marks respectively. Both *Ocypode* and *Emerita* are restricted to warm temperate and tropical waters (Dahl, 1952; Efford, 1976), so the absence of these two genera from the west coast could be due to low ambient temperatures caused by the cold, northward-flowing Benguela current.

It is interesting to speculate on the ecological niches left empty by the absence of these two Decapods. *Emerita* is a filter-feeder and its niche is probably largely filled by *Donax,* a genus that occurs with *Emerita* elsewhere (eg. Trevallion *et al.*, 1970; MacNae and Kalk, 1962). Kensley (1974) notes that the northern-most distribution of *Tylos granulatus* on the west coast barely overlaps the southernmost spread of *Ocypode cursor* in northern Namibia, while Wolcott (1978) has shown that *O. quadrata* is mainly a predator, only 10percent of its dietary intake being from scavenged material. On the other hand, Kensley (1974) has shown that *Tylos* is primarily a scavenger.

Tylos granulatus and *Tylos capensis* are the largest intertidal Isopods in the world and one reason for their large size could be the absence of predatory *Ocypode* and the fact that they are able to scavenge without competition from that genus. It may be, therefore, that *Tylos granulatus* replaces *Ocypode cursor* on west coast beaches in a manner similar to the replacement of ocypodids by talitrids suggested by Dahl (1952).

The predatory role of *Ocypode* is probably filled by the sanderling *Crocethia alba,* preying on small invertebrates, the black oystercatcher *Haematopus moquini* and the southern black-backed gull *Larus dominicanus* which feed on *Donax* to a considerable extent. The sanderling has also been found to crop *Donax* siphons on eastern Cape beaches (McLachlan *et al.*, 1980), while in Jamaica and Texas this species has been observed feeding on small *Donax* spp. (Wade, 1967; Loesch, 1957). Other birds feeding on intertidal invertebrates include the curlew sandpiper *Calidris ferruginea* (Puttick, 1979), the white-fronted sand plover *Charadrius marginata* (A. Crowe, pers. comm.) and the silver gull *Larus novaehollandiae* which has been observed feeding on talitrids and kelp flies at the drift line (J. Cooper, pers. comm.). Many of these birds probably scavenge as well, but their activity is confined to the daytime, leaving a night-time scavenging niche to be filled by *Tylos.* J. Cooper (pers. comm.) has observed that there seems to be a reduction in the number of gulls in the intertidal zones of tropical areas in comparison to the beaches of the west coast of South Africa and this may be due to competition in both scavenging and predation from ocypodids.

The zonation shown by the three species of cirolanid Isopods with respect to one another is also of interest. Although cirolanid Isopods are found on the majority of exposed beaches (Dahl, 1952; Trevallion *et al.*, 1970; Penchaszadeh, 1971), only single species are usually found. Where geographical distributions overlap, there may be a succession of one species by another as is the case on the west coast of India (Eleftheriou and Jones, 1976) between *Eurydice indicis* and *E. peraticis.* In Britain, *Eurydice pulchra* and *E. affinis* occur together in mixed populations occupying the same zones (Jones and Naylor, 1967; Withers, 1977) although in France, Salvat (1966) reported that these species occupy different zones.

This is also the case in Madagascar where Pichon (1967) found *Excirolana natalensis* in the zone of drying and *E. orientalis* in the zone of retention. In Kenya, Jones (1971) found both a succession of species along an exposure gradient and a zonational succession.

A similar situation is found on west coast beaches. As reported by Brown (1973), the sphaeromatid Isopod *Exosphaeroma truncatitelson* replaces *Eurydice longicornis* on more sheltered beaches, while this study has shown that *Excirolana natalensis* replaces *Eurydice* on coarse-grained ones. Both Brown (1973) and this study have shown that *Pontogeloides latipes* occurs in small numbers on all beaches.

On west coast beaches, zonation also occurs between the three cirolanid Isopod species (Fig. 5). *Eurydice longicornis* is the most pelagic of the three species, often being found in large numbers at the surface up to 1km offshore above sandy bottoms (C. Brownell, pers. comm.). *Eurydice* occurs intertidally in all zones except the zone of drying, in densities of up to 8000 per square metre.

Pontogeloides latipes is found in low numbers in the zone of resurgence and in greater numbers in the zone of retention, while it is usually absent from the zones of saturation and drying. Finally, *Excirolana natalensis* only occurs in the zone of drying on fine-grained beaches, but occupies most of the intertidal zone in coarse-grained ones, where it is the dominant species. This suggests that

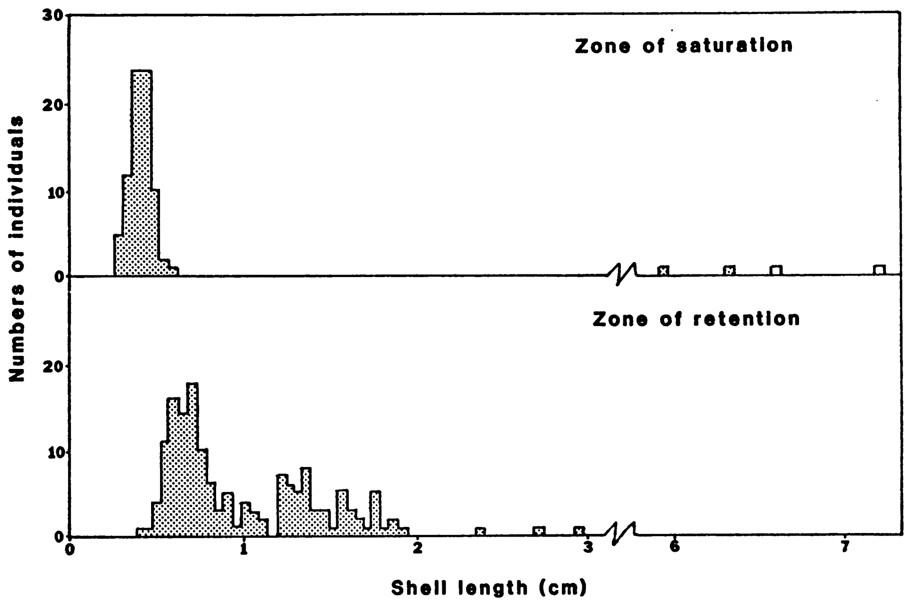

FIG. 7
The size-distribution of individuals of *Donax serra* at Melkbosstrand according to zones.

there is some competitive exclusion between these three carnivorous and scavenging species, especially on fine beaches between *Eurydice* and *Excirolana.*

Intertidal zonation between individuals of a particular species on the basis of size or age has been found in many sandy beach species. Stephen (1930) originally observed this phenomenon in *Cardium edule* and *Tellina tenuis.* Since then, zonation by size has been found mainly in molluscs, for example, in the filter-feeding Gastropod *Olivella biplicata* (Edwards, 1969) and in the Bivalves *Donax denticulatus* (Wade, 1967), *D. faba* (Alargaswami, 1966) and *D. serra* (De Villiers, 1975a; McLachlan and Hanekom, 1979). In addition, zonation by size has been noted in the Isopod *Excirolana braziliensis* (Glynn *et al.,* 1975; Dexter, 1977) and in the hippid Decapod *Emerita asiatica* (Philip, 1974).

Zonation by size on west coast beaches is most noticeable in *Donax serra.* De Villiers (1975a) notes that small individuals of this species are found near the top of the beach, with the size of individuals gradually increasing towards the low-water mark. Hanekom (1975) found little zonation by size in this species on east coast beaches. McLachlan and Hanekom (1979) note that the intertidal size-class distribution of *Donax serra* on east coast beaches is the reverse to that observed on the west coast.

On a few occasions, it was found that the lower beach had both large and very small individuals of *Donax* (1.9 to 5.0mm in length). Those higher up the shore measured from 4.5 to 29.0mm in length (Fig. 7). In these cases, therefore, the situations described by both De Villiers and Hanekom could be found.

From these results, the following zonational life-history of *Donax serra* on west coast beaches may be hypothesized. Very small mussels settle out from the veliger larval stage near the low-water mark (in the zone of saturation). At this stage, however, they are vulnerable to predation by fish. As they grow above a certain size, that may depend on the mussel's ability to gain a firm footing in the substratum (Wade, 1967), they migrate up to the zone of retention, where the time of vulnerability to fish predation is much reduced. Here the mussels grow until reaching a size that may be determined by prey selection by the gull *Larus dominicanus* or by being too large for successful predation by fish at lower intertidal levels or by an ability to compete effectively with larger individuals, after which they move down the beach to the zone of saturation or to the subtidal fringe. De Villiers (1975b) found that individuals of *Donax serra* reach maturity when they attain 37.0 to 54.0mm in length. This suggests either that individuals move into the zone of saturation and sublittoral fringe at the onset of sexual maturity, or that sexual maturity is delayed until the animals move into these zones, which would be more suitable for spawning, due to continuous immersion and increased food availability.

Edwards (1969) lists differences in osmotic, temperature and dessiccation tolerances as the reasons for segregation by size of individuals of the Gastropod *Olivella* across the intertidal zone. In the case of *Donax*, physiological differences in resistance to environmental extremes are unlikely to account entirely for the two-fold size sorting found in this species. The ability to maintain zonation mentioned by Wade (1967) must be added to Edward's list.

Some size-based zonation was also observed in *Eurydice longicornis* in that the larger individuals seem to occur mainly lower down the shore. Unlike *Donax*, however, mature individuals were found in the zone of retention. *Excirolana natalensis* did not show the clear-cut zonation described for *E. braziliensis* by Glynn *et al.* (1975) and Dexter (1977).

Conclusions

It is clear from this study that the zonation of the macrofauna on the sandy beaches of the west coast of South Africa falls into four distributional zones as proposed by Salvat. A comparison with the zonation encountered on sandy beaches discussed in the literature shows that those on the west coast of South Africa follow the pattern shown by exposed beaches elsewhere in the world. Zonation occurs not only between species, but also between size classes within some species across the intertidal zone.

Summary

Two schemes have been proposed to explain the zonation shown by the macrofauna on sandy beaches. Dahl (1952) suggested three zones characterized by indicator species, while Salvat (1964) proposed four zones determined by the hydrodynamic conditions occurring within the sediment. Zonation on the west coast of South Africa was studied on three exposed beaches. Four intertidal distribution zones were determined using several statistical analyses. These zones were found to correspond to those proposed by Salvat (zones of drying, retention, resurgence and saturation) and described in hydrodynamic terms by Pollock and Hummon (1971). The advantages of the system proposed by Salvat over that of Dahl are discussed, and the zonation found on west coast sandy beaches is compared with that found on other beaches of the world.

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