

The ecology of three sandy beaches on the Skeleton Coast of South West Africa

by

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Received: 5 December 1984

Accepted: 18 March 1985

ABSTRACT

Three sandy beaches situated approximately 225 km apart along the Skeleton Coast of South West Africa, were surveyed and quantitatively sampled for macrofauna and meiofauna. The two more southerly beaches receive inputs of drift kelp and support a rich macrofauna concentrated about the drift-line and resembling that of similar beaches along the west coast of South Africa. The northernmost beach receives negligible macrophyte debris and has a relatively impoverished fauna, distributed lower down the beach. The fauna in this northern area includes species with tropical affinities indicating that it lies in a region beyond the influence of the Benguela upwelling system.

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1 INTRODUCTION

Some 42% of the southern African coast-line is fringed by pure sand beaches (Bally *et al.*, in press) but research in this habitat only commenced quite recently with Brown's (1964, 1971) studies on the ecology of beaches around the Cape Peninsula. Vigorous sandy beach research programmes have subsequently developed at the Universities of Port Elizabeth and Cape Town. These have resulted in the publication of quantitative surveys of the fauna of sandy beaches in the Eastern Cape (McLachlan, 1977), Natal (Dye *et al.*, 1981), Transkei (Wooldridge *et al.*, 1981) and the Southern Cape (McLachlan *et al.*, 1981) as well as further work on the Cape Peninsula (Koop and Griffiths, 1982; Griffiths *et al.*, 1983) and the South Western Cape (Bally, 1983). The extensive beaches that stretch along the North-western Cape and South West African coasts remain poorly explored. The only works published from this area to date are a fauna list for Sandvis lagoon (Kensley and Penrith, 1977) and a brief survey of beaches in the Walvis Bay area (McLachlan, 1985), although Bally *et al.* (in press) report that between Walvis Bay and the Kunene River, sandy beaches make up 44% of the coast and mixed shores of sand and rock another 40%.

In this study we aim to extend the above ecological survey coverage to include three sandy beaches in the Skeleton Coast Park, in the extreme north of South West Africa. Although this area lies well within the tropics, the southern section of the park continues to support kelp beds, which are normally associated with cool-temperate waters. These beds are less extensive than those found along the west coast of South Africa and are composed of a different species, *Laminaria schintzei*. The kelp beds are not noticeable more than 65 km north of Möwe Bay, although stranded plants continue to be cast ashore for a further 40 km.

2 METHODS

Three open ocean beaches situated approximately 225 km apart along the shore-line of the Skeleton Coast Park were selected as study sites (Fig. 1). From south to north these were at 20°51'S 13°25'E, near Toscanini (Beach A); at 19°04'S 12°32'E, south of the

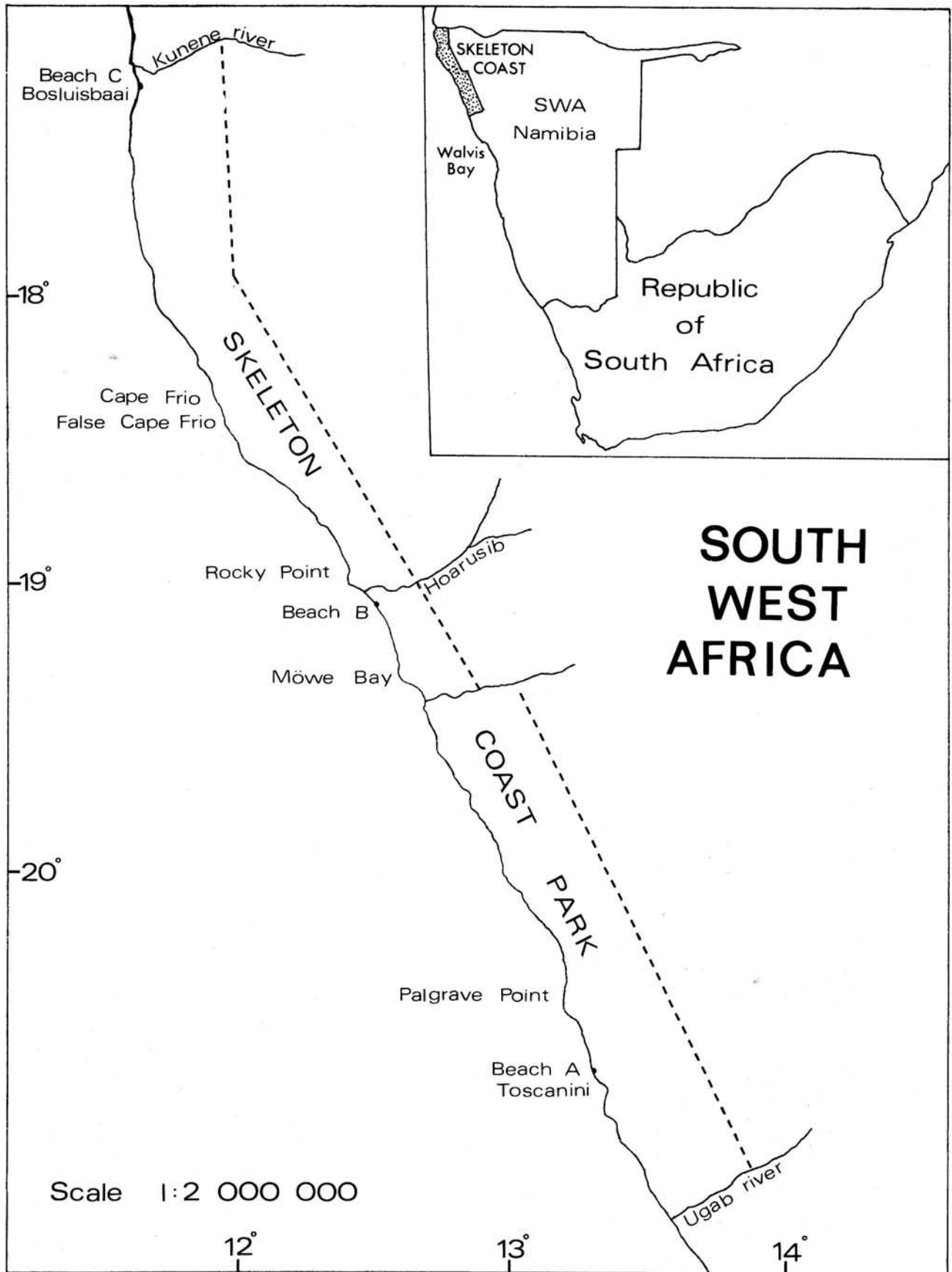


FIGURE 1: Map showing the position of the Skeleton Coast and location of sites mentioned in the text.

Hoarusib River mouth (Beach B); and at Bosluisbaai, 17°15'S 11°45'E (Beach C).

The sites were visited between August and November 1983 and at each site a transect was surveyed across the beach at low water of spring tides, using the procedure outlined by Day (1969). The depth of the water-table was estimated by digging holes at various points across the transect. Sea water temperatures were taken with a mercury thermometer and the width of the surf zone and size of swell estimated visually. Sediment samples were taken at the high-water mark, mid-tide level and at low water of springs and subsequently analysed for particle size distribution, using a series of graduated sieves.

For estimation of macrofauna each beach was divided into five zones, based on Salvat's physical system of beach zonation, as modified by Pollock and Hummon (1971). Within each zone five randomly distributed samples of 0,1 m² were excavated to a depth of 30 cm and passed through a 1 mm mesh. All organisms retained by the sieve were removed to glass vials and preserved in 10% formalin. The samples were subsequently sorted to species and each species identified as far as possible. The individuals were then counted and the dry biomass obtained after 4 days at 60°C. Mean biomass values and species counts from each zone were subsequently calculated up to 1 m² and, knowing the width of each zone, a total value was obtained per linear metre of beach. Quantitative samples were supplemented by wider searches aimed at detecting larger and more mobile organisms, such as flying insects, scorpions and crabs. A list was also compiled of the reptiles, birds and mammals seen on each beach during the survey period.

Meiofauna were sampled by extracting sand cores to a depth of 30 cm at high-, mid- and low-water marks. These were preserved in 10% formalin and returned to the laboratory, where the meiofauna were extracted using a modified Oostenbrink apparatus (Fricke, 1979). Meiofauna were lightly stained with rose-bengal and counted under a dissecting microscope. Counts were subsequently calculated up to 100 cm³ and increased by 10% to allow for animals lost during extraction (Fricke, 1979).

3 RESULTS

3.1 The study sites

Profile diagrams for beaches A, B and C are shown in Figures 2, 3 and 4 respectively.

Beach A was situated just north of a small kelp bed near Toscanini, an old mining camp deserted in 1975. The beach was backed by barren overburden hummocks, in front of which lay a storm drift-line consisting mostly of very old, dried kelp mixed with miscellaneous flotsam and jetsam. At the time of sampling the storm drift-line included quantities of

fairly fresh wrack, which had probably been introduced by very high seas some 12 days prior to our arrival. A second current drift-line of fresh wrack was scattered broadly in the area just below the high-water springs (HWS) level.

Beach B lay 3 km south of the Hoarusib River mouth, about 1 km north of the nearest kelp bed. The beach was backed by dune hummocks covered by *Salsola* sp., which began about 120 m beyond the HWS mark. The dry sand zone was scattered with old dried-out kelp debris. Small numbers of fresh kelp plants were deposited along the current drift-line, just below the HWS mark.

Beach C was situated in Bosluisbaai, a large bay approximately 17 km south of the Kunene River mouth. The upper beach was very wide and flat with a steep slope occurring at the seaward margin. There was no drift material deposited in the intertidal zone, but the storm drift-line was scattered with driftwood and numerous dried out Chondrichthyes egg cases. The first dune hummocks, which were covered by *Salsola* sp., lay 250 m landward of the HWS mark and were backed by large open sand-dunes.

The physical characteristics of the three beaches are summarised in Table 1. Using the exposure rating system of McLachlan (1980) Beach B would be rated as exposed and Beaches A and C as very exposed.

3.2 The invertebrate macrofauna

The abundance and biomass of each of the macrofaunal species recorded at the three study sites is given in Table 2. Species recorded during our general survey, but not collected in the quantitative samples, are arbitrarily given an abundance of one individual per running metre of beach. The distribution patterns of the more abundant species are depicted in Figs. 2, 3 and 4.

The upper reaches of Beaches A and B had a much richer and more diverse macrofauna than found on Beach C. This can be attributed to the presence of

TABLE 1: Principal physical features of three study beaches on the Skeleton Coast. Exposure rating is based on the scheme proposed by McLachlan (1980).

	Beach A Toscanini	Beach B Hoarusib	Beach C Bosluisbaai
Date of survey	Oct 1983	Aug 1983	Nov 1983
Width of intertidal zone (m)	39	35	49
Intertidal slope	1:13	1:16	1:13
Median grain size	580 µm	275 µm	350 µm
Estimated swell height	1,5—2,0m	1,0—1,5m	2,0—2,5m
Estimated width surf zone	100m	150m	100m
Water temperature	13°C	14,9°C	17,5°C
Exposure rating (0—20)	16 (very exposed)	15 (exposed)	17 (very exposed)

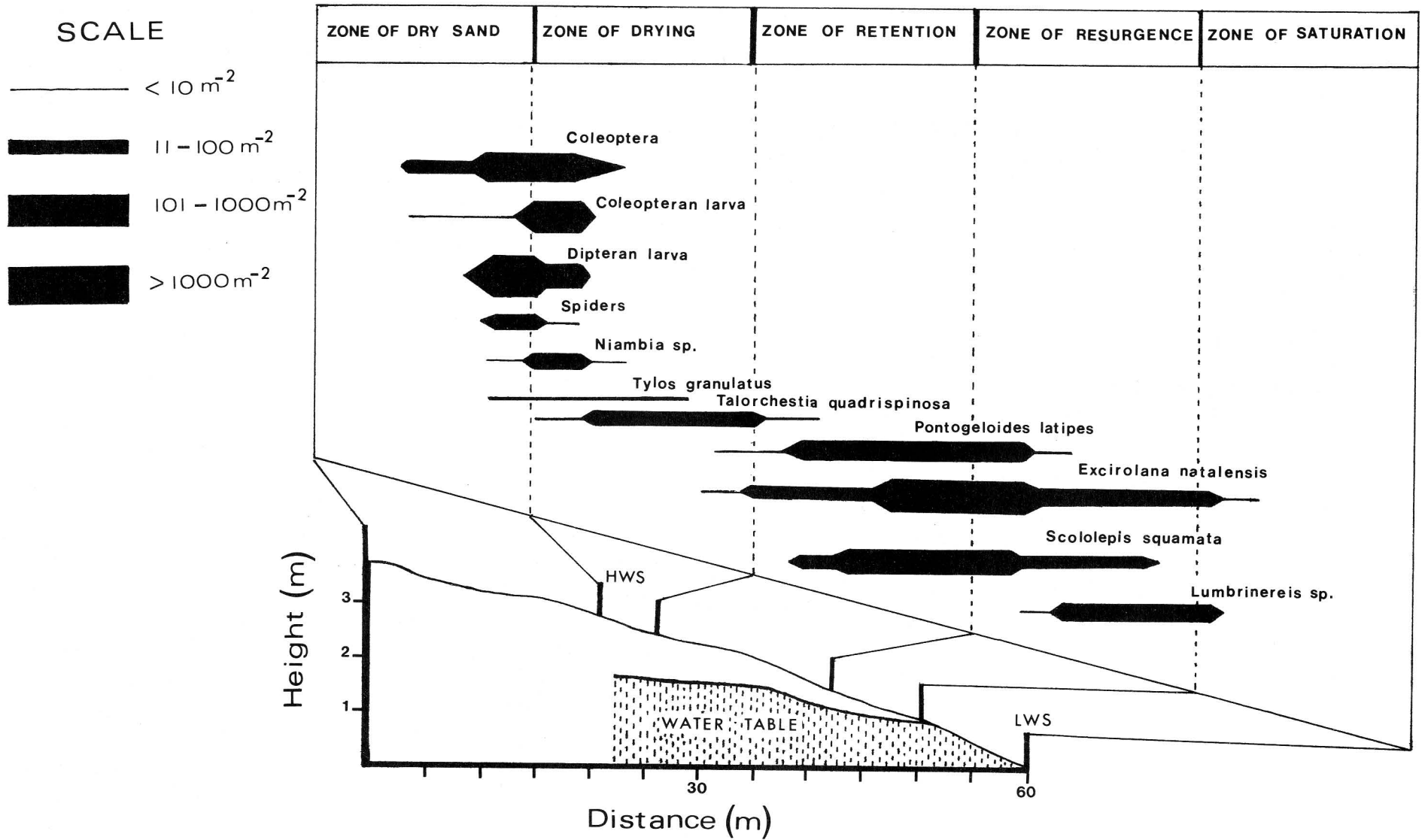


FIGURE 2: Beach A: Toscanini. Profile diagram showing beach zones and distribution patterns of abundant macrofaunal organisms.

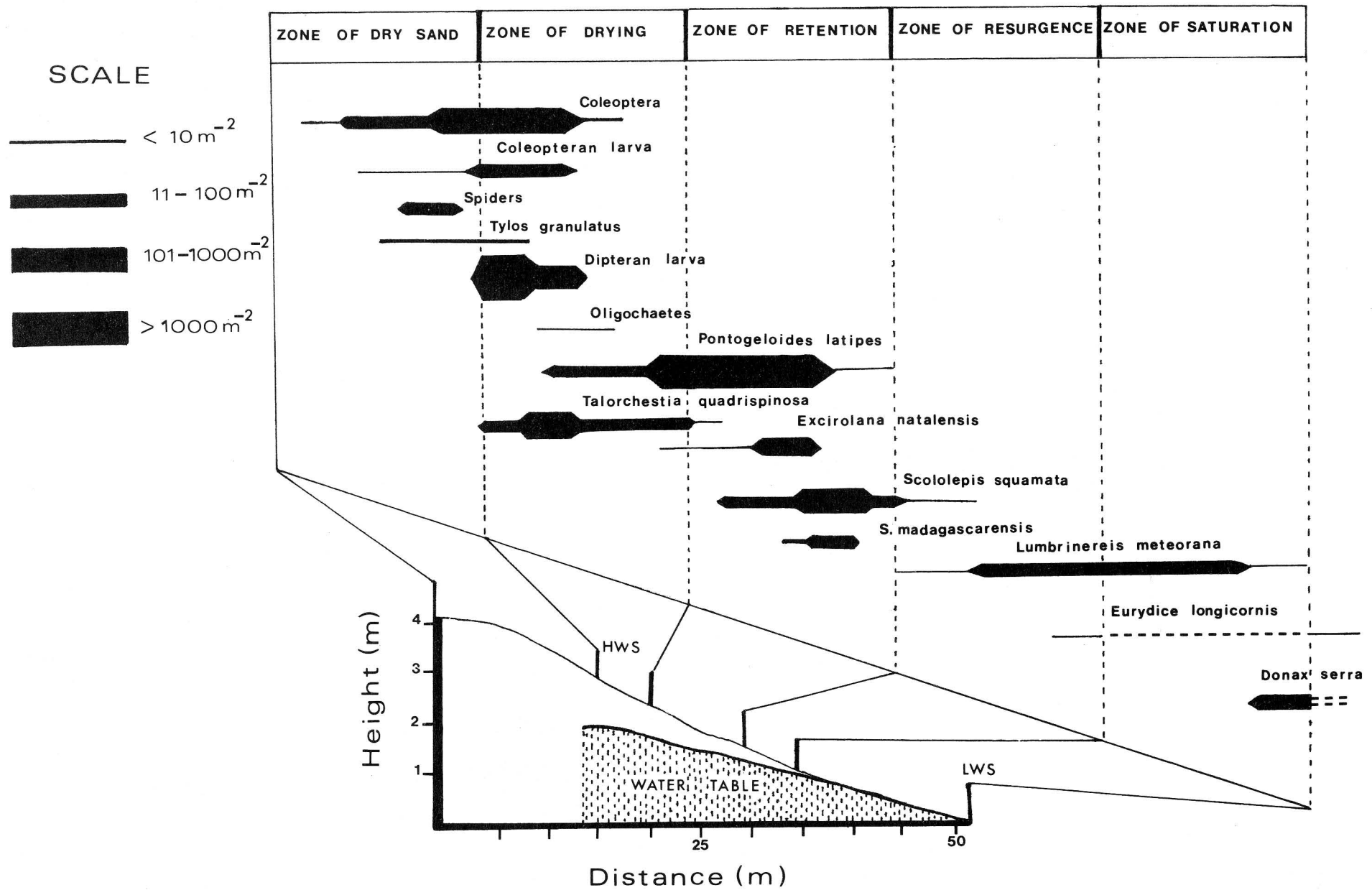


FIGURE 3: Beach B: Hoarusib. Profile diagram showing beach zones and distribution patterns of abundant macrofaunal organisms.

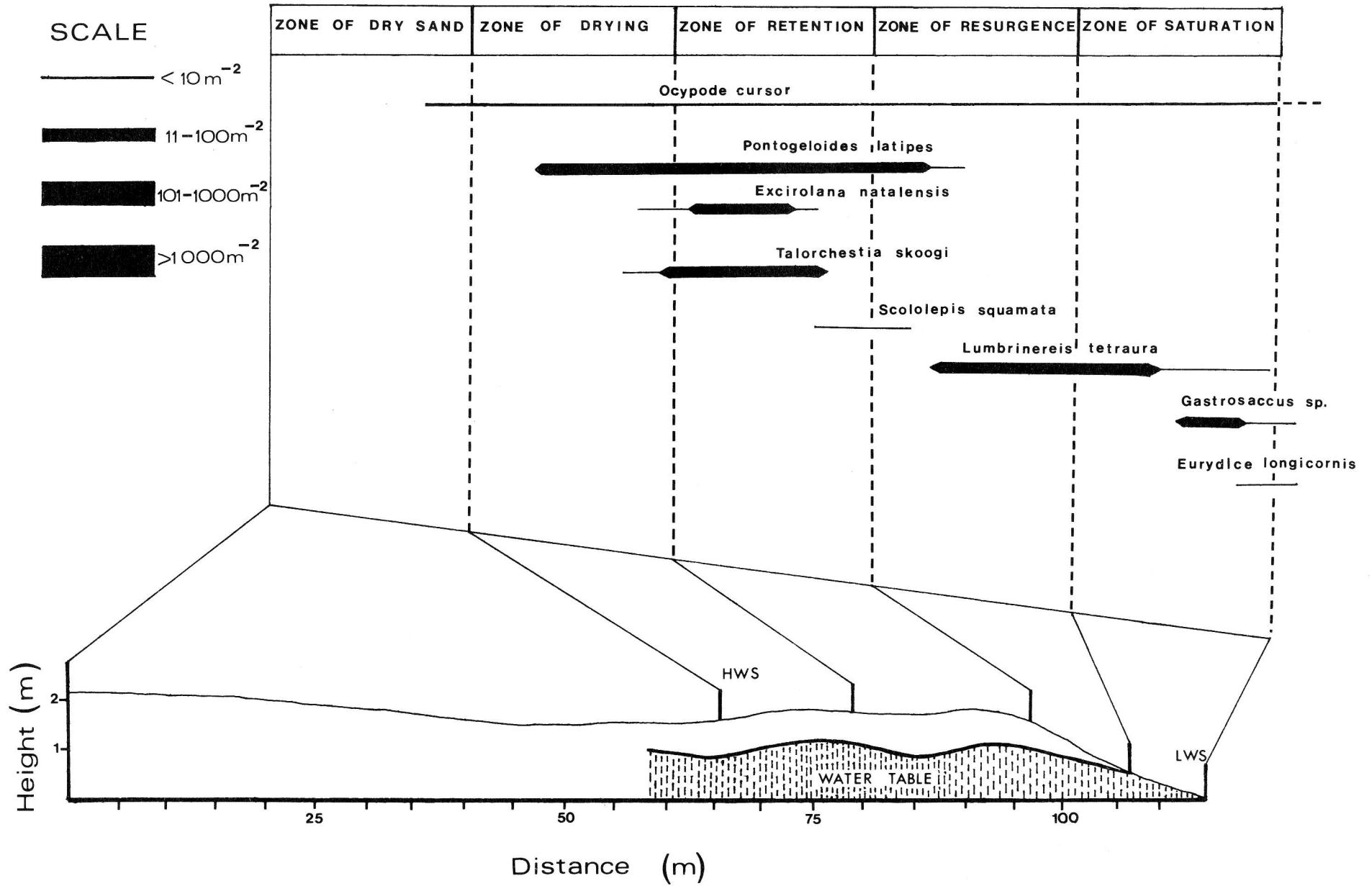


FIGURE 4: Beach C: Bosluisbaai. Profile diagram showing beach zones and distribution patterns of abundant macrofaunal organisms.

drift algae on Beaches A and B, since this attracts both air-breathing arthropods of marine origin, such as the amphipod *Talorchestia quadrispinosa* and the isopod *Tylos granulatus* (which feed on drift algae) and mari-

TABLE 2: The abundance and biomass of macrofaunal invertebrates recorded in three sandy beaches along the Skeleton Coast.

	Beach A Toscanini		Beach B Hoarusib		Beach C Bosluisbaai	
	Num- bers m ⁻¹	gm ⁻¹ dry mass	Num- bers m ⁻¹	gm ⁻¹ dry mass	Num- bers m ⁻¹	gm ⁻¹ dry mass
ANNELIDA						
<i>Lumbrinereis</i> sp.	200	1,7	—	—	—	—
<i>L. meteorana</i>	—	—	690	6,1	—	—
<i>L. tetraura</i>	—	—	—	—	392	3,6
Oligochaeta	—	—	20	0,1	—	—
<i>Scololepis</i>	—	—	—	—	—	—
<i>madagascarensis</i>	—	—	90	0,5	—	—
<i>S. squamata</i>	2160	13,8	398	2,1	56	0,3
MOLLUSCA						
<i>Donax serra</i>	—	—	128	9,8	—	—
ARACHNIDA						
Fam. Ceromidae (Solifugae)	—	—	1	0,1	—	—
Fam. Dysderidae	1	0,1	1	—	—	—
Fam. Lycosidae	24	0,3	34	0,5	—	—
<i>Opisththalmus</i>	—	—	—	—	—	—
<i>littoralis</i> (Scorpiones)	1	1,2	1	1,2	—	—
ISOPODA						
<i>Eurydice longicornis</i>	—	—	10	0,1	16	0,1
<i>Excirrolana natalensis</i>	2078	23,3	72	0,8	190	2,4
<i>Niambia</i> sp.	38	0,1	54	0,1	—	—
<i>Pontogeloides latipes</i>	457	5,7	1438	18,7	844	11,7
<i>Tylos granulatus</i>	32	10,9	12	3,1	—	—
AMPHIPODA						
Fam. Lyssianassidae	12	0,1	32	0,1	—	—
<i>Talorchestia</i>	—	—	—	—	—	—
<i>quadrispinosa</i>	182	0,5	358	1,5	—	—
<i>T. skoogi</i>	—	—	—	—	280	1,7
MYSIDACEA						
<i>Gastrosaccus</i> sp.	—	—	—	—	48	0,1
BRACHYURA						
<i>Ocypode cursor</i>	—	—	—	—	1	5,8
INSECTA						
<i>Acanthoscelis</i>	—	—	—	—	—	—
<i>ruficornis</i>	36	10,2	—	—	—	—
<i>Acritus lightfooti</i>	36	0,1	50	0,1	—	—
<i>Aleochara</i>	—	—	—	—	—	—
<i>salsipotens</i>	285	0,2	170	0,1	—	—
<i>Bembix carinata</i>	—	—	1	0,1	1	0,1
<i>Bledius allutellus</i>	—	—	130	0,1	—	—
<i>Cercyon maritimus</i>	35	0,1	170	0,6	—	—
<i>Euymorpha cyanipes</i>	—	—	1	0,1	1	0,1
Histeridean (larvae)	150	0,6	30	0,1	—	—
<i>Ophyra</i> sp. (larvae)	2625	10,2	3200	12,4	—	—
<i>Pachylopus dispar</i>	18	0,1	130	0,6	—	—
<i>Pachylopus</i> sp.	36	0,2	12	0,1	—	—
<i>Pachyphaleria</i>	—	—	—	—	—	—
<i>capensis</i>	231	4,4	382	7,6	—	—
<i>Phyllodrepa hessei</i>	—	—	90	0,1	—	—
Tenebrionidae (larvae)	36	0,1	122	0,5	—	—
<i>Zophosis gracilipes</i>	1	0,1	1	0,1	1	0,1
Total no. species	22	—	30	—	11	—
Total biomass m ⁻¹	—	84	—	67,4	—	26

time representatives of terrestrial groups, notably the Arachnida and Insecta. The Arachnida recorded are carnivorous on other arthropods, but the insect fauna of the upper beach incorporates both herbivores and predatory forms. The herbivores included the Coleoptera *Pachyphaleria capensis* and *Cercyon maritimus*, which feed on drier wrack and larvae of the fly *Ophyra* sp., which consumes more recently deposited material. Predatory forms included Coleoptera, such as *Acanthoscelis ruficornis*, *Aleochara salsipotens*, *Pachylopus* spp. and the tiger beetle *Euymorpha cyanipes*, as well as the fly-hunting sphecoid wasp *Bembix carinata*. This kelp associated drift-line fauna is similar to that described from Cape Peninsula beaches by Griffiths and Stenton-Dozey (1981) and Stenton-Dozey & Griffiths (1983).

The upper reaches of Beach C, in the north, supported far fewer species, the only insects recorded being the tenebrionid *Zophosis gracilipes*, the highly mobile predatory tiger beetles *Euymorpha cyanipes*, and wasps *Bembix carinata*. A few ghost crabs *Ocypode cursor*, which are typical of more tropical beaches, were recorded and the amphipod *Talorchestia quadrispinosa*, which is common southwards to the Cape Peninsula was replaced by *T. skoogi*. The latter species has not previously been recorded south of the Angolan border.

The midshore of all three beaches was dominated by the scavenging isopods *Excirrolana natalensis* and *Pontogeloides latipes*, as well as deposit-feeding polychaetes of the genus *Scololepis*.

Fairly dense populations of the polychaete genus *Lumbrinereis* were recorded on the lower beach at all three sites, but these were of a different species in each case. The carnivorous isopod *Eurydice longicornis* was present in low numbers on Beaches B and C, but was not recorded at Toscanini. Mysids of the genus *Gastrosaccus*, which are important on the lower shore on many South African beaches, were found only in small numbers at Beach C. Molluscs were poorly represented. The white mussel *Donax serra* was found only at Beach B and plough shells (*Bullia* spp.) were not recorded at any of the study sites. In total the fauna of Beaches A and B was unusually diverse, with 22 and 30 macrofaunal species respectively, while Beach C, to the north, had only 11 species. Similarly, total biomass values decreased from south to north with Beach C supporting less than half the standing stock of invertebrates found at either of the two other sites.

3.3 Vertebrates

The bird, mammal and reptile species recorded at our three study sites are listed in Table 3. The number of birds sighted at Beach C was significantly lower than at the two more southerly sites. While detailed bird counts were not made in the course of this study, unpublished data maintained by the Skeleton Coast Park

TABLE 3: Vertebrate species observed during the surveys of three sandy beaches on the Skeleton Coast.

Species	Beach A Toscanini	Beach B Hoarusib	Beach C Bosluisbaai
REPTILIA			
<i>Meroles reticulatus</i> (reticulated sand lizard)	+	+	—
AVES			
<i>Arenaria interpres</i> (Turnstone)	+	—	—
<i>Cercomela tractrac</i> (Tractrac Chat)	+	—	—
<i>Calidris alba</i> (Sanderling)	+	—	—
<i>Calidris ferruginea</i> (Curlew Sandpiper)	+	—	+
<i>Charadrius marginatus</i> (Whitefronted Plover)	+	+	+
<i>Corvus albus</i> (Pied Crow)	—	+	—
<i>Hirundo rustica</i> (European Swallow)	+	+	—
<i>Larus dominicanus</i> (Kelp Gull)	+	+	+
<i>Pluvialis squatarola</i> (Grey Plover)	+	+	—
MAMMALIA			
<i>Canis mesomelas</i> (Jackal)	+	+	+
Gerbillinae (Gerbils)	+	+	—
Number species	11	9	4

indicates that Beach B supports approximately 28 shore birds km⁻¹ in summer and 8 km⁻¹ in winter. By contrast the area incorporating Bosluisbaai (Beach C) supports only about 0.4 shore birds km⁻¹. Amongst the mammals, jackals *Canis mesomelas* were observed at all three localities. These are thought to feed on lizards and gerbils, both of which were recorded at Beaches A and B, as well as the arthropods present on the upper shore of all sites. More elusive visitors to this area include the brown hyaena *Hyaena brunnea*, whose spoor is sometimes seen on the beaches and the lion *Panthera leo*, which scavenges off seal carcasses in the vicinity of the Hoanib River mouth.

3.4 Meiofauna

The numbers of meiofauna organisms recovered from the surface 30 cm of sand on each of the three study

TABLE 4: Numbers of meiofaunal organisms (per 100cm³) in sand samples collected from the surface 30cm of three beaches along the Skeleton Coast.

HWS = High water of springs; ML = mean sea level; LWS = low water of springs.

Taxon	Beach A Toscanini			Beach B Hoarusib			Beach C Bosluisbaai		
	HWS	ML	LWS	HWS	ML	LWS	HWS	ML	LWS
Nematoda	22	33	74	17	65	35	44	19	20
Platyhelminthes	4	17	7	7	10	9	—	—	—
Harpacticoida	—	6	—	—	—	9	—	4	—
Acarina	—	—	—	—	—	—	—	4	—
Isopoda	—	—	—	—	—	—	—	—	3
Totals	26	56	81	24	75	53	44	27	23

beaches are shown in Table 4. Nematodes were the most abundant meiofaunal forms on all three beaches, with Platyhelminthes second in importance on Beaches A and B. Harpacticoid copepods were poorly represented at all sites. Overall meiofaunal densities were low, never exceeding 100 individuals per 100 cm³. Highest densities were recorded at the low-water mark on Beach A, at mid-tide level at Beach B and at the high-water mark on Beach C.

4 DISCUSSION

The composition and distribution of the macrofauna on Beaches A and B conforms closely with the pattern described from the South-western Cape (Bally, 1983) and Langstrand, near Walvis Bay (McLachlan, in press). The range of most temperate species found along the Cape west coast thus extends well into the tropics. This is facilitated by the cold upwelling water of the Benguela Current, which moves northwards along the west coast and which maintains water temperatures well below the levels found at equivalent latitudes on the east coast of Africa.

Another similarity linking Beaches A and B with those on the Cape west coast region is that both receive an energy subsidy in the form of kelp wrack stranded along the drift-line. This material drastically affects the energetics of the beach and hence the nature, distribution and biomass of the fauna (Griffiths *et al.*, 1983). In particular herbivorous air-breathing arthropods and their associated predators are attracted to the upper reaches of the beach, increasing the species diversity at higher tidal levels. This semi-terrestrial component contributes substantially to both the species diversity and biomass of the fauna at Beaches A and B.

Beach C has a somewhat different fauna, partly because it does not receive kelp wrack and thus has far fewer air breathing arthropods. In this respect it is similar to the beach at Paaltjies, near Walvis Bay (McLachlan, 1985) which also lacks a drift-line.

In terms of individual species, however, the fauna of Bosluisbaai (Beach C) also shows some important differences from sites further to the south. The amphipod *Talorchestia quadrispinosa*, for example, is replaced by the closely related *T. skoogi*, a tropical species not previously found south of the Angolan border. Similarly the giant oniscoid isopod *Tylos granulatus*, which is so typical of temperate west coast beaches, gives way to the ghost crab *Ocypode cursor*, a tropical form with similar scavenging habits. The appearance of these species at Bosluisbaai can be taken as indicative that this beach lies within a different zoogeographical province to Beaches A and B and that the temperate fauna extending south to Cape Point has given way to one with more tropical affinities. Such a contention is supported by surveys of rocky shores in the region (Penrith & Kensley, 1970 *a* and *b*;

Kensley and Penrith, 1973, 1980), which demonstrated a transition from a temperate to a tropical fauna over a stretch of coast roughly centred around Rocky Point. Similarly physical oceanographic evidence, reviewed by Shannon (in press) indicates that, although there is some uncertainty as to the precise limits of the Benguela upwelling system (which may indeed shift seasonally) Cape Frio is a frequently accepted northern boundary (Shannon *et al.*, 1981; Nelson & Hutchings, 1983).

An unusual feature of all three study sites was the paucity of molluscs recorded. White mussels (*Donax serra*) were found only at Beach B and plough shells (*Bullia* spp.) were completely absent. McLachlan (in press) records a similar phenomenon in the Walvis Bay region, particularly at Langstrand. This is in marked contrast to the situation on most South African beaches, where the Mollusca generally dominate the fauna, especially in terms of biomass. The reasons for these differences are unclear, although both *Donax serra* and the west coast *Bullia digitalis* are essentially cool water forms and the role of the latter is probably also taken over by *Ocypode cursor* in the northern part of our study areas.

Overall macrofaunal species diversity was high at Beach A and particularly at Beach B (22 and 30 species respectively), but was greatly reduced at Beach C (11 species). This is a direct reflection of the large numbers of insects and arachnids associated with drift kelp at the two southern sites.

Macrofaunal biomass values for the three beaches fall well within the wide range reported for exposed or high-energy beaches. These vary from as low as 7g m⁻¹ at Chilca, Peru (Pencaszadek, 1971). Bally (1981) reported mean annual biomass values of 92,324 and 683 g m⁻¹ for three beaches on the west coast of South Africa and McLachlan (in press) found macrofaunal standing stocks of 123 g m⁻¹ and 47g m⁻¹ on Paaltjies beach and Langstrand near Walvis Bay. The values obtained from the Skeleton Coast beaches, therefore, lie at the lower extreme of the range recorded for comparable beaches of the south-western coast of Africa. This can be attributed to the poor representation or absence of molluscs at our study sites, as these tend to comprise the vast bulk of the macrofauna on beaches for which higher biomass figures have been reported.

As might be expected the abundance and diversity of the avifauna decrease to the north in response to the decline in food availability. This conforms with the general trend of decreasing species diversity at lower latitudes discussed by Hockey *et al.* (1983). The presence of reptilian and large mammal predators is a somewhat unusual feature of these remote areas, but is not thought to exert any great ecological impact.

Although our examination of the meiofauna was superficial the results show the density of meiofaunal organisms to be unexpectedly low. The composition was

also unusual in that harpacticoids were relatively rare and platyhelminthes, usually a very minor constituent of the fauna, were second in abundance only to nematodes. This may, however, simply be a consequence of shallow depths sampled and the low densities encountered.

The beaches of the Skeleton Coast of South West Africa thus appear to lie in a biogeographical transition zone. The effects of this transition are apparent both in the composition of the fauna of the beaches and in their ecological energetics, since the southern beaches receive a large energy input in the form of stranded kelp, while the northernmost beach, lying outside the distribution of these algae, does not. The fauna to the south is thus rich in upper shore, kelp-consuming species and their associated predators, while that in the north is dominated by lower shore opportunistic scavengers.

In addition to the observation made above, this study also highlights two observations more universally pertinent to the study of sandy beaches. Firstly, comparisons that are made between beaches are most meaningful when they are made within a single biogeographical zone. And secondly, the structure and composition of offshore communities can have marked effects on beach ecology.

5 ACKNOWLEDGEMENTS

We are indebted to Dr Eugène Joubert of the Department of Agriculture and Nature Conservation for his support of this research programme. Assistance with the field-work was kindly provided by the following staff members of the Skeleton Coast Park — Rudi Loutit, John Patterson, Frans Hoëb, Elifas Ganuseb and, particularly, Peter Tarr. We are grateful to E. Winkler and the staff of the SAIMR in Swakopmund for allowing us to use their laboratories.

6 REFERENCES

- BALLY, R.
 1981: The ecology of three sandy beaches on the west coast of South Africa. Ph.D. Thesis, University of Cape Town.
 1983: Intertidal zonation on sandy beaches of the west coast of South Africa. *Cah. Biol. mar.* **24**: 84–103.
- BALLY, R., McQUAID, C.D. and BROWN, A.C.
 In press: Shores of mixed sand and rock: an unexplored marine ecosystem. *S. Afr. J. Sci.*
- BROWN, A.C.
 1964: Food relations on the intertidal sandy beaches of the Cape Peninsula. *S. Afr. J. Sci.* **60**: 35–41.
 1971: The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 1: Introduction. *Trans. roy. Soc. S. Afr.* **39**: 247–279.
- DAY, J.H.
 1969: A guide to marine life on South African shores. Cape Town: A.A. Balkema.

- DYE, A.H., McLACHLAN, A. and WOOLDRIDGE, T.
1981: The ecology of sandy beaches in Natal, South Africa. *S. Afr. J. Zool.* **16**: 200—209.
- FRICKE, A.H.
1979: Meiofauna extraction efficiency by a modified Oostenbrink apparatus. *Helgolander wiss. Meeresunters.* **32**: 436—443.
- GRIFFITHS, C.L. and STENTON-DOZEY, J.
1981: The fauna and rate of degradation of stranded kelp. *Estuar. Coastal Shelf Sci.* **12**: 645—653.
- GRIFFITHS, C.L., STENTON-DOZEY, J. and KOOP, K.
1983: Kelp wrack and the flow of energy through a sandy beach ecosystem. In: McLachlan A. & Erasmus T. (eds). *Sandy Beaches as Ecosystems*. The Hague: Dr. W. Junk.
- HOCKEY, P.A.R., SIEGFRIED, W.R., CROWE, A.A. and COOPER, J.
1983: Ecological structure and energy requirements of the sandy beach avifauna of southern Africa. In McLachlan A. & Erasmus T. (eds). *Sandy Beaches as Ecosystems*. The Hague: Dr. W. Junk.
- KENSLEY, B.F. and PENRITH, M-L.
1973: The constitution of the intertidal fauna of rocky shores of Moçamedes, southern Angola. *Cimbebasia* (A)2: 113—123.
1980: The constitution of the fauna of rocky intertidal shores of South West Africa. Part III. The north coast from False Cape Frio to the Kunene River. *Cimbebasia* (A) 5: 201—214.
- KENSLEY, B.J. and PENRITH, M.J.
1977: Biological survey of Sandvis I, introduction and fauna list. *Madoqua* **10**: 181—190.
- KOOP, K. and GRIFFITHS, C.L.
1982: The relative significance of bacteria, meio- and macrofauna on an exposed sandy beach. *Mar. Biol.* **66**: 295—300.
- McLACHLAN, A.
1977: Composition, distribution, abundance and biomass of the macrofauna and meiofauna of four sandy beaches. *Zool. Afr.* **12**: 279—306.
1980: The definition of sandy beaches in relation to exposure: a simple rating system. *S. Afr. J. Sci.* **76**: 137—138.
- 1985: The ecology of two sandy beaches near Walvis Bay. *Madoqua* **14**,2 155—163.
- McLACHLAN, A., WOOLDRIDGE, T. and DYE, A.H.
1981: The ecology of sandy beaches in southern Africa. *S. Afr. J. Zool.* **16**: 219—231.
- NELSON, G. and HUTCHINGS, L.
1983: The Benguela upwelling area. *Prog. Oceanogr.* **12**: 333—356.
- PENCHASZADEH, P.E.
1971: Observaciones cuantitativas preliminares en playas arenosas de la costa central del Peru, con especial referencia a las poblaciones de Muy-Muy (*Emerita analoga*) — (Crustacea, Anomura Hippidae). *Contr. Inst. biol. mar. Mar del Plata* **177**: 3—19.
- PENRITH, M-L. and KENSLEY, B.F.
1970a: The constitution of the intertidal fauna of rocky shores of South West Africa. Part I. Lüderitzbucht. *Cimbebasia* (A)1: 191—239.
1970b: The constitution of the fauna of rocky intertidal shores of South West Africa. Part II. Rocky Point. *Cimbebasia* (A)1: 243—268.
- POLLOCK, L.W. and HUMMON, W.D.
1971: Cyclic changes in interstitial water content, atmospheric exposure and temperature in a marine beach. *Limnol. Oceanogr.* **16**: 522—535.
- SHANNON, L.V.
(in press): Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev.*
- SHANNON, L.V., NELSON, G. and JURY, M.R.
1981: Hydrological and Meteorological aspects of upwelling in the southern Benguela current. In: *Coastal Upwelling* F.A. Richards (ed). American Geophysical Union, Washington D.C.
- STENTON-DOZEY, J. and GRIFFITHS, C.L.
1983: The fauna associated with kelp stranded on a sandy beach. In: McLachlan, A. & Erasmus, T. (eds) *Sandy Beaches as Ecosystems*. The Hague: Dr. W. Junk.
- WOOLDRIDGE, T., DYE, A.H. and McLACHLAN, A.
1981: The ecology of sandy beaches in Transkei. *S. Afr. J. Zool.* **16**: 210—218.